

## Quantifying resource partitioning in centrarchids with stable isotope analysis

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### Abstract

Stable isotope and gut content analyses were completed on multiple age classes of Detroit River rock bass (*Ambloplites rupestris*) and bluegill sunfish (*Lepomis macrochirus*) to determine the importance of resource partitioning in littoral centrarchids.  $\delta^{15}\text{N}$  signatures ranged from 10.9‰ to 12.8‰ in young of the year (YOY) to 7-yr-old rock bass and from 10.3‰ to 12.1‰ for YOY to 4-yr-old bluegills. YOY diets for both species had similar proportions of benthic and epiphytic prey, with YOY rock bass also having a planktonic dietary component. YOY rock bass consequently had a lighter  $\delta^{13}\text{C}$  signature than similarly aged bluegills, suggesting that these individuals are able to exploit prey from more energetically efficient open water habitats. Rock bass became piscivorous during the first full year of growth, with concomitant depletion of the  $\delta^{13}\text{C}$  signature with increasing age, typical of an isotopically depleted phytoplankton  $\delta^{13}\text{C}$  signal. By 7 yr of age, rock bass diets were dominated by crayfish and cyprinids, with no further significant depletion of the  $\delta^{13}\text{C}$  signature. For bluegills, diets were dominated by small benthic invertebrates, regardless of age.  $\delta^{13}\text{C}$  signatures in YOY and 1-yr-old bluegills remained enriched relative to rock bass of the same age, suggesting that bluegill sunfish remain in nearshore shallower littoral habitats for a greater proportion of their life history because of increased predation pressure. This pairing of stable isotope and gut content analyses provides a quantitative resolution of foraging history and habitat selection of species coexisting in a littoral community.

Understanding habitat selection and use in fish species is a time- and resource-intensive venture, often requiring the collection of high numbers of individuals and various collection methods to distinguish interspecific habitat preferences (Weaver et al. 1993). For littoral centrarchids such as sunfish (*Lepomis* sp.), crappie (*Pomoxis* sp.), rock bass (*Ambloplites rupestris*), and large- and smallmouth bass (*Micropterus* sp.), spawning periods often overlap (Scott and Crossman 1973), and the resulting young of the year (YOY) populations are likely to seek refuge under macrophyte cover (Werner et al. 1977; Weaver et al. 1997) with predator avoidance reinforcing such selection (Mittelbach 1981; Weaver et al. 1997). Additionally, prey selection, especially in small, gape-limited individuals, is restricted to small invertebrates, and prey selection can overlap among YOY of such species (Mittelbach and Persson 1998). With growth in size, these individuals pass through a series of ontogenetic niches (Werner and Gilliam 1984) whereby successively larger prey become potential forage, and habitat selection can change to reflect such preferences (Weaver et al. 1997). Yearling and older rock bass and smallmouth bass are observed to typically select the habitat complexity provided by structures

such as boulders and rocky outcrops (Weaver et al. 1997), whereas sunfish species tend to remain associated with littoral areas of macrophyte cover as they age (Hinch and Collins 1993). Although gut content analyses provide insight into foraging activities and potential habitat selection, consumed prey only represent a short time frame and potentially only a limited area of actual habitat selection (Bootsma et al. 1996). Furthermore, the degree of food assimilation will differ by the proportion of indigestible material in each of the diet items; thus, the composition of the diet might not reflect the materials assimilated into tissue growth (Bootsma et al. 1996). The stable isotope of carbon ( $\delta^{13}\text{C}$ ), however, is advantageous over such traditional methods by not only representing the assimilated fraction of the diet over an extended time frame but also identifying carbon sources not observed in the dietary snapshot provided by gut content analysis (Grey et al. 2001).

In freshwater systems,  $\delta^{13}\text{C}$  has proven beneficial for discriminating between two major pathways of carbon production (France 1995). Nearshore littoral zone production tends to be  $\delta^{13}\text{C}$  enriched relative to open water pelagic areas because of carbon cycling from detritus and benthic algae that exhibit less  $\delta^{13}\text{C}$  discrimination during carbon fixation than phytoplankton (France 1995; Hecky and Hesslein 1995). The  $\delta^{13}\text{C}$  signatures of pelagic organisms, however, are typically more depleted because of the isotopically lighter carbon signature of the open water phytoplankton base of the food web (France 1995). Additionally, deep profundal areas of lakes tend to be even more  $\delta^{13}\text{C}$  depleted presumably because of the fixation of respired carbon dioxide (Rau 1980). Contradictory to the stable isotope of nitrogen ( $\delta^{15}\text{N}$ ), which becomes enriched by approximately 3.4‰ per trophic level

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### Acknowledgments

The authors thank Harold Hagen for assistance with sample collection. This research was supported by a Natural Sciences and Engineering Research Council (NSERC) Discovery grant awarded to K. G. Drouillard and by a Canada Research Chair awarded to G. D. Haffner. Additional funding was also received from NSERC Postgraduate and University of Windsor tuition scholarships awarded to G. Paterson.

Table 1. Summarized biological and stable isotope data for rock bass and bluegill age classes.

Species	Age class (years)	<i>n</i>	Avg. total length (cm)	Avg. mass (g)	Avg. lipid content (% wet wt.)	Avg. $\delta^{13}\text{C}$ (‰)	Avg. $\delta^{15}\text{N}$ (‰)
Rock bass	YOY	145	4.7	1.6	1.5	-14.2	10.9
	1	36	8.4	9.1	1.5	-16.2	11.3
	2	20	11.4	28.8	2.4	-16.8	11.5
	4	5	16.4	97.9	2.0	-16.7	11.8
	6	3	23.2	211.1	2.1	-14.9	12.9
	7	2	23.9	248.2	1.6	-17.7	12.8
Bluegill	YOY	23	6.2	4.5	2.8	-13.2	10.3
	1	5	10.8	25.2	2.2	-12.3	10.6
	3	2	14.5	71.5	3.0	-15.2	10.6
	4	3	17.2	133.9	3.0	-16.4	12.1

(Minagawa and Wada 1984),  $\delta^{13}\text{C}$  signatures tend to be conserved as assimilated energy is passed along successive trophic levels and to exhibit an average enrichment of <1‰ between prey and predator (Vander Zanden and Rasmussen 2001). Thus, consumer  $\delta^{13}\text{C}$  signatures should provide insight to both feeding history and the primary habitat occupied during assimilation of the consumed prey material. For overlapping species such as littoral centrarchids, this natural marker should therefore be suitable for interpretation of prey and habitat selection behaviors. In this study, gut content and stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) analyses were completed with multiple age classes of rock bass and bluegill sunfish (*Lepomis macrochirus*) collected from the Detroit River. The purpose of this study was to quantify temporal and spatial overlap in resource partitioning between multiple age classes of these littoral centrarchid species with stable isotope and gut content analyses.

## Materials and methods

Rock bass and bluegill sunfish were collected in a benthic trawl net towed behind a research vessel near the confluence of Lake St. Clair and the Detroit River in October 2001. Specimens were wrapped in solvent (hexane)-rinsed aluminum foil, stored at 4°C, and transported to the laboratory for collection of biological data, including total and fork length and individual weight. A duplicate sample of rock bass for gut content analysis was preserved in a 10% formalin solution. For bluegills, gut content was identified from the frozen specimens before preparation for stable isotope analysis. Entire gut tracts were dissected from formalin-preserved specimens, and gut content, where present, was removed. Diet items were identified to a family or genus and species level if possible following identification keys outlined in Balcer et al. (1984) and Peckarsky et al. (1990).

Age determination was completed with sagittal otoliths removed from frozen individuals and following procedures outlined by the Otolith Research Laboratory (Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada). Difficulty in reading otolith annuli for rock bass >4 yr old resulted in the estimation of ages for these fish with life history tables (Scott and Crossman 1973) and from litera-

ture-based length-at-age ranges for this species (Putnam et al. 1995).

*Stable isotope analysis*—With the exception of YOY and 1-yr-old age classes, whole-body homogenates were dried at 75°C for 48 h and ground to a fine powder with a glass mortar and pestle (Vander Zanden et al. 2000). Between 0.8 and 1.1 mg of the dried powder was added to a tin capsule (3 × 5.5 mm) and subsequently folded closed and placed in an individually labeled sample tray. For YOY and 1-yr-old fish, pooled samples consisting of at least three individuals per sample were prepared as above for stable isotope analysis. All sample analyses were completed by the Environmental Isotope Laboratory (University of Waterloo, Waterloo, Ontario, Canada) with the use of a Micromass VG Isochrom continuous-flow stable isotope ratio mass spectrometer coupled to a Carlo Erba elemental analyzer. Stable isotope results are calculated relative to a reference standard and expressed as delta ( $\delta$ ) notation, as in Eq. 1,

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000 \quad (1)$$

where  $R = {}^{15}\text{N}/{}^{14}\text{N}$ . Nitrogen results were standardized against atmospheric  $\text{N}_2$  and carbon against  $\text{CO}_2$  in PeeDee limestone. International Atomic Energy Agency N1 and N2 (ammonium sulfates) and CH6 (sugar) standards were analyzed every five samples during evaluation of biological samples. Precision ( $\pm 2$  SD) of these internal standards are  $\pm 0.3\text{‰}$  and  $\pm 0.2\text{‰}$  for nitrogen and carbon, respectively, over several years of use. Duplicate analyses were also completed on 15% of the samples with variability estimates, reported as the standard error of the estimate, of 0.2‰ and 0.1‰ reported for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  results, respectively.

All statistical analyses were completed with SYSTAT version 8.0 for windows (Wilkinson 1998). The criterion for significance in all analyses was  $p < 0.05$ .

## Results

A total of 211 rock bass and 33 bluegills ranging in mass from ~1 to 246 g (4–24 cm) and 2 to 142 g (5–18 cm), respectively, were collected (Table 1). Including YOY, a total of six rock bass and four bluegill age classes were identified.

Table 2. Mean dietary data for rock bass and bluegill age classes. Values represent the average percent of total prey items enumerated in individual fish gut tracts ( $\pm 1$  standard error).

Prey category	Total prey items (%)					
	YOY	1	2	4	6	7
<b>Rock bass</b>						
Hydrachnidia	36.8( $\pm 1.0$ )	8.4( $\pm 3.0$ )	—	—	—	—
Cladocera	4.5( $\pm 3.2$ )	—	—	—	—	—
Copepoda	2.7( $\pm 4.9$ )	—	—	—	—	—
Amphipoda	5.9( $\pm 2.7$ )	13.2( $\pm 1.9$ )	3.0( $\pm 3.3$ )	—	—	—
Trichoptera	44.0( $\pm 0.9$ )	11.9( $\pm 2.4$ )	9.1( $\pm 3.3$ )	—	—	—
Diptera	0.6( $\pm 8.7$ )	19.7( $\pm 1.8$ )	3.0( $\pm 3.3$ )	—	—	—
Cyprinidae	—	23.5( $\pm 1.7$ )	75.8( $\pm 0.6$ )	100.0	66.7( $\pm 0.3$ )	66.7( $\pm 0.5$ )
Decapoda	—	0.8( $\pm 4.1$ )	—	—	33.3( $\pm 0.6$ )	33.3( $\pm 1.0$ )
Detritus/Other	5.6( $\pm 2.9$ )	22.5( $\pm 1.6$ )	22.4( $\pm 3.3$ )	—	—	—
		YOY	1	3	4	
<b>Bluegill</b>						
Amphipoda		28.4( $\pm 1.4$ )	37.6( $\pm 1.4$ )	—	—	
Trichoptera		45.0( $\pm 0.9$ )	22.3( $\pm 2.3$ )	—	31.0( $\pm 1.7$ )	
Gastropoda		16.1( $\pm 2.4$ )	6.7( $\pm 7.8$ )	100.0	69.0( $\pm 0.8$ )	
Pelecypoda		—	6.7( $\pm 7.8$ )	—	—	
Detritus/Other		10.5( $\pm 3.7$ )	26.7( $\pm 1.9$ )	—	—	

YOY rock bass were generally omnivorous, with prey items consisting of small invertebrates including water mites, trichopterans, cyclopoid as well as cladoceran zooplankton, amphipods, and chironomids (Table 2). Roughly 6% of the gut contents consisted of unidentifiable organic and detrital matter in these small fish. By the first full year of growth, small cyprinids constituted ~24% of the rock bass diet and became the dominant forage in all fish  $\geq 2$  yr of age. Crayfish (Decapoda) appendages were first observed in gut tracts of 1-yr-old fish, with large (~75 mm) individuals constituting ~33% of prey items for 6- and 7-yr-old rock bass.

Young-of-year and 1-yr-old bluegill diets were dominated by gastropod, amphipod, and trichopteran prey, with the latter two categories combining to total at least half of the diet items identified in these age classes (Table 2). Gastropods were consistently observed in the diets of all bluegill age

classes and were the only prey item identified in the gut tracts of 3-yr-old fish. Zebra mussels (Pelecypoda) were observed in the gut tracts of 1-yr-old fish only; however, approximately one quarter of the diet for this age class could not be classified into a specific prey category. No evidence of prey size selectivity was observed with increasing bluegill body size or age.

$\delta^{13}\text{C}$  results can be influenced by sample lipid content from fractionation that occurs during synthesis and results in  $^{13}\text{C}$  depletion of lipid tissues (DeNiro and Epstein 1978). Lipid content averaged 1.9% of wet weight in rock bass and 2.7% in bluegills (Table 1). A one-way analysis of variance did not demonstrate any significant differences in lipid content between rock bass ( $p = 0.575$ ) or bluegill age classes ( $p = 0.131$ ). Additionally, linear regression did not demonstrate any significant relationships between lipid content and age, mass, or total length in either rock bass ( $r^2 < 0.037$ ;  $p > 0.345$ ) or bluegills ( $r^2 < 0.077$ ;  $p > 0.295$ ). On the basis of these and published data, lipid concentrations of  $\leq 3\%$  by weight are not expected to result in stable carbon isotope shifts of  $>0.2\text{‰}$  (Kling et al. 1992). A Student's  $t$ -test demonstrated average lipid content in bluegills to be significantly higher than was measured in rock bass ( $p < 0.001$ ).

Carbon stable isotope signatures ( $\delta^{13}\text{C}$ ) ranged from  $-12.6\text{‰}$  to  $-18.5\text{‰}$  in rock bass and from  $-10.8\text{‰}$  to  $-17.8\text{‰}$  in bluegills (Fig. 1; Table 1). Rock bass were on average  $-2\text{‰}$  more  $\delta^{13}\text{C}$  depleted than bluegills, with a mean carbon signal of  $-15.8\text{‰}$  compared with a bluegill average of  $-13.8\text{‰}$ . A Student's  $t$ -test demonstrated rock bass  $\delta^{13}\text{C}$  to be significantly more depleted than bluegill signatures ( $p = 0.001$ ). A one-way analysis of variance and Tukey's multiple comparisons test demonstrated YOY rock bass to be significantly  $\delta^{13}\text{C}$  enriched relative to all other age classes with the exception of 6-yr-old individuals ( $p =$

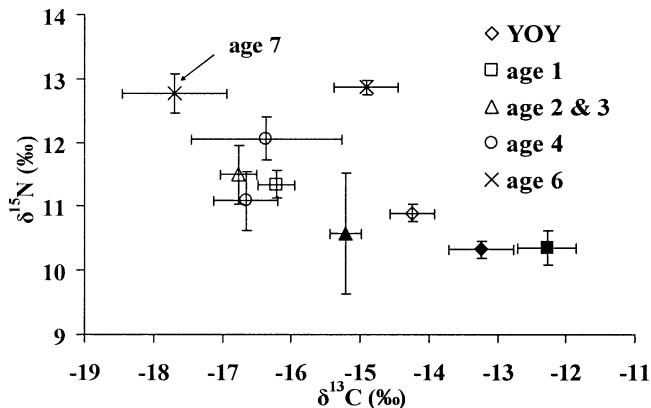


Fig. 1. Average carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope signatures in rock bass and bluegill age classes. Rock bass age classes are denoted by open symbols, with bluegills indicated by solid symbols. Error bars for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  indicate  $\pm 1$  SE.

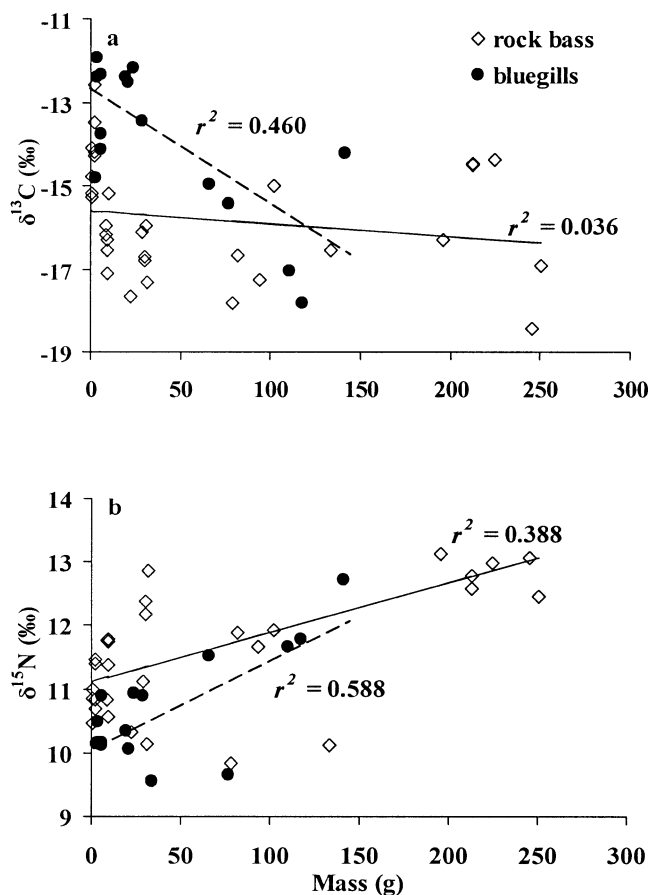


Fig. 2. Relationships between (a) carbon ( $\delta^{13}\text{C}$ ) and (b) nitrogen ( $\delta^{15}\text{N}$ ) stable isotope signatures and centrarchid mass. In both panels, the solid and dotted lines represent the best fit, least squares regression lines for rock bass and bluegills, respectively.

0.782). The only other significant difference in rock bass  $\delta^{13}\text{C}$  signatures was determined between the 2- and 6-yr-old individuals ( $p = 0.037$ ). For bluegills, YOY and 1-yr-old fish were found to be significantly enriched relative to 3- and 4-yr-olds (ANOVA;  $p = 0.003$ ); no other significant differences were observed between bluegill age class  $\delta^{13}\text{C}$  values. Depletion of  $\delta^{13}\text{C}$  was negatively correlated with body mass in both species; however, this relationship was significant for bluegills only ( $r^2 = 0.460$ ;  $p = 0.004$ ; Fig. 2).  $\delta^{13}\text{C}$  signatures were also negatively associated with age in both species; however, no significant relationships were observed between average  $\delta^{13}\text{C}$  signatures and centrarchid age (Fig. 3).

A frequency distribution histogram described two distinct distribution modes for rock bass and bluegill  $\delta^{13}\text{C}$  signatures (Fig. 4). For rock bass, 32% of the individuals sampled had  $\delta^{13}\text{C}$  signatures of roughly  $-16\text{‰}$ , but for bluegills, this mode was observed at  $-12\text{‰}$  with 31% of samples falling in this range. Additionally, a median  $\delta^{13}\text{C}$  value of  $-16.1\text{‰}$  was calculated for rock bass, whereas bluegill  $\delta^{13}\text{C}$  signatures were centered at  $-13.6\text{‰}$  with a 75th percentile value of  $-14.9\text{‰}$ . In rock bass, however, this upper percentile was determined at  $-16.8\text{‰}$ .

The highest average  $\delta^{15}\text{N}$  value of  $12.9\text{‰}$  was measured

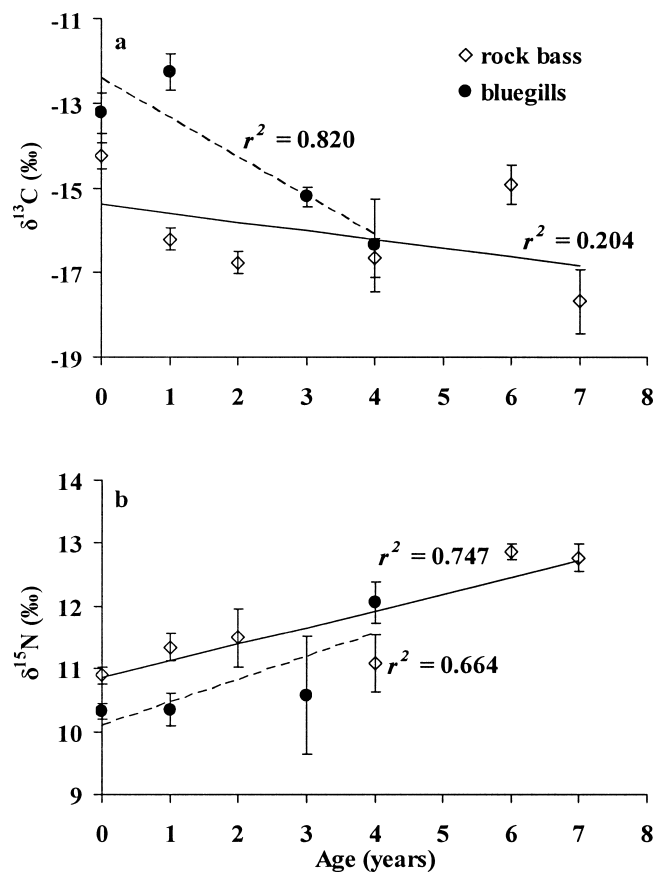


Fig. 3. Relationships between (a) carbon ( $\delta^{13}\text{C}$ ) and (b) nitrogen ( $\delta^{15}\text{N}$ ) stable isotope signatures and centrarchid age. In both panels, the solid and dotted lines represent the best fit, least squares regression lines for rock bass and bluegills, respectively. Error bars indicate  $\pm 1$  SE.

in 6-yr-old rock bass, with YOY averaging  $10.9\text{‰}$  and 7-yr-old fish similar to the prior year class at an average  $\delta^{15}\text{N}$  of  $12.8\text{‰}$  (Fig. 1; Table 1). Significant differences were observed (ANOVA;  $p = 0.003$ ) in rock bass  $\delta^{15}\text{N}$  values between YOY and the 6- and 7-yr-old age classes and also

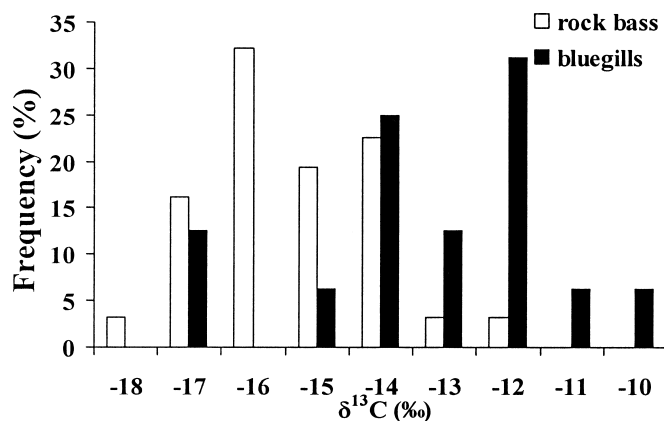


Fig. 4. Frequency distribution percentages of stable carbon isotope ratios in rock bass and bluegills collected from the Detroit River.



between 6-yr-old fish and 1- and 4-yr-old age classes. For bluegills,  $\delta^{15}\text{N}$  results ranged from 10.3‰ to 12.1‰ between YOY and 4-yr-old fish, respectively.  $\delta^{15}\text{N}$  values for 4-yr-old bluegills were also significantly different (ANOVA;  $p = 0.007$ ) between YOY and 1-yr-old age classes. A Student's  $t$ -test indicated that rock bass  $\delta^{15}\text{N}$  were significantly enriched relative to bluegill results ( $p = 0.003$ ).  $\delta^{15}\text{N}$  values were also positively correlated with age for both species; however, these relationships were found to be significant for rock bass only (Fig. 3;  $r^2 = 0.747$ ;  $p = 0.026$ ).

## Discussion

Predation and competition are considered important mechanisms regulating resource partitioning in ecological systems (Schoener 1974). Which of these mechanisms dominates is a function of animal size and trophic position with smaller, primary consumers likely more restrained by predation than larger, more predatory individuals (Schoener 1974). Cyprinid forage were first observed in rock bass gut tracts during the first full year of growth, with coincident increases in trophic position, as indicated by  $\delta^{15}\text{N}$  signatures, occurring up to 6 yr of age. As fish become piscivorous, a series of ontogenetic niches (Werner and Gilliam 1984) must be passed through whereby successively larger invertebrate prey are consumed until sufficient body size is reached to consume other fish (Mittelbach and Persson 1998). The occurrence of cyprinid prey in the diet of 1-yr-old individuals indicate rock bass grew through such an ontogenetic niche at a smaller body size than bluegills and begin to forage on this type of energetically rich prey. This proposes that small rock bass must achieve an energetic advantage with the use of a more valuable food resource than bluegills to grow through the ontogenetic niche.

Young-of-year centrarchids often tend to school together in dense macrophyte patches (Weaver et al. 1997).  $\delta^{13}\text{C}$  signatures for macrophytes collected from the Detroit River/Lake Erie corridor average approximately  $-10\text{‰}$  (Mazak et al. 1997; Limén et al. 2005), with prey items such as gastropods and zebra mussels from this system representing the benthic and pelagic  $\delta^{13}\text{C}$  ranges at  $-13\text{‰}$  and  $-22\text{‰}$ , respectively (Mazak et al. 1997). The enriched  $\delta^{13}\text{C}$  signatures for these YOY relative to other age classes suggest a strong association of foraging within macrophyte beds and on food sources with a heavier benthic algal signal. Despite very similar diet compositions and trophic positions, as indicated by  $\delta^{15}\text{N}$ , however, the average YOY rock bass  $\delta^{13}\text{C}$  signature was 1‰ more depleted than similarly aged bluegills. The notable difference between diets for the YOY age class of these fish was the presence of a similar proportion of planktonic forage in the YOY rock bass diet, and these prey commonly have a lighter  $\delta^{13}\text{C}$  signal typified by phytoplankton production (France 1995; Hecky and Hesslein 1995; del Giorgio and France 1996). The more depleted  $\delta^{13}\text{C}$  signal of YOY rock bass suggests planktivory is more common than evidenced by gut content analysis and that these individuals might be integrating a range of heavier and lighter  $\delta^{13}\text{C}$  food sources (Hecky and Hesslein 1995; Bootsma et al. 1996). Such planktivorous foraging has been observed in bluegills

when the risk of predation is minimal and open waters can be exploited (Mittelbach 1981). Centrarchid predators, including largemouth bass (Werner et al. 1983), northern pike (Paukert and Willis 2003), and muskellunge species (Gillen et al. 1981), will reinforce habitat selection of YOY into macrophyte weed beds (Savino and Stein 1982; Gotceitas and Golgan 1987), and these piscivores have been collected from the study sampling area (Great Lakes Institute for Environmental Research, unpubl. data). The trichopteran prey identified in both YOY rock bass and bluegill gut tracts are indicative of feeding within macrophyte beds (Schramm and Jirka 1989; Keast and Fox 1992). However, the occurrence of planktonic prey and a more depleted  $\delta^{13}\text{C}$  signature for YOY rock bass contend that these individuals are less restrained by predation and are able to utilize more energetically efficient open water habitats for foraging (Mittelbach 1981).

Trophic-level effects have been demonstrated to influence the degree and variability of carbon enrichment between predator and prey (Vander Zanden and Rasmussen 2001; Post 2002). By 4 yr of age, rock bass had  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of  $-16.7\text{‰}$  and  $11.8\text{‰}$ , respectively, and a diet consisting solely of cyprinids. However, this  $\delta^{15}\text{N}$  signature had increased only 0.9‰ over that reported for YOY individuals compared with a depletion of 2.5‰ for  $\delta^{13}\text{C}$  between these rock bass age classes. Such a small change in  $\delta^{15}\text{N}$  implies only a minor increase in trophic status, even though a major diet shift has occurred. Furthermore, bluegill  $\delta^{13}\text{C}$  became 2.0‰ more depleted between YOY and 3-yr-olds, whereas essentially no change in  $\delta^{15}\text{N}$  trophic position occurred. Vander Zanden and Rasmussen (2001) estimated that trophic-level enrichment of carbon between predator and prey for freshwater fish averages  $\sim 1\text{‰}$ . With little or no change in  $\delta^{15}\text{N}$  trophic positions for these age classes of fish, these results indicate that trophic enrichment only weakly contributes to the pattern observed in  $\delta^{13}\text{C}$  values in this study.

As crayfish and cyprinid forage dominated the diets of older rock bass,  $\delta^{13}\text{C}$  signatures exhibited further depletion with age. Crayfish have been described as opportunistic omnivores grazing on aquatic macrophytes and consuming a wide variety of benthic items, including algae, detritus, and invertebrates (Whitledge and Rabeni 1997). This type of foraging by crayfish combined with the benthic  $\delta^{13}\text{C}$  signals reported for gastropods ( $-13\text{‰}$ ), macrophytes ( $-10\text{‰}$ ), algae ( $-7\text{‰}$ ), and detritus ( $-9\text{‰}$ ) from this system will result in crayfish assimilating the isotopic signature of their diet (Whitledge and Rabeni 1997). If rock bass exhibited high prey fidelity by feeding solely on crayfish, their carbon signatures would also be expected to emulate the heavier benthic signal expected of the crayfish diet (Hecky and Hesslein 1995). A  $\delta^{13}\text{C}$  signal of  $-22\text{‰}$  has been reported for Detroit River zebra mussels, providing an estimate of the phytoplankton  $\delta^{13}\text{C}$  signal in this system, and waterfowl feeding exclusively on this food item assimilate the zebra mussel  $\delta^{13}\text{C}$  signal (Mazak et al. 1997). The oldest rock bass, however, had a diet split between cyprinid forage and crayfish and a  $\delta^{13}\text{C}$  signature of  $-17.7\text{‰}$ . Such an intermediate carbon signature continues to support the integration of benthic (crayfish) and lighter (pelagic cyprinids)  $^{13}\text{C}$  food sources in the rock bass diet. Bluegill  $\delta^{13}\text{C}$  signatures, however, did not

exhibit any depletion until 3 yr of age and did not reach values similar to rock bass until their fourth year. This reveals that younger bluegill age classes feed primarily within macrophyte beds for a greater proportion of their life history than do rock bass of similar size. Small bluegills (<100 mm standard length) have been observed to avoid pelagic waters because of increased predation risk and are less restrained by predation once growth passes this body size (Mittelbach 1981). Furthermore, a potentially lower risk of predation and an ability to exploit planktonic prey might be an opportunity YOY rock bass require to pass through the ontogenetic niche leading to piscivory. More important, younger rock bass became piscivorous and achieved higher trophic positions than similarly aged bluegills, suggesting that temporal overlap in resource utilization between these species is minimal because of the influence of predation pressure on small individuals.

The distribution of  $\delta^{13}\text{C}$  signatures in these samples indicates population modes separated by  $-4\text{‰}$  between rock bass and bluegills, demonstrating that substantially different food resources are being utilized by these species. For co-existing populations such as these littoral centrarchids, this tendency to consume different prey is among the most common example of complementarity described for ecological systems (Schoener 1974). Ecological variables, including competition and specialization, are considered to be primary factors influencing such differences in feeding behavior (Bootsma et al. 1996). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures for these species help describe patterns in habitat selection, prey composition, and predator-prey relationships and indicate the latter has an important role in resource partitioning between these similar species. In this manner, the use of stable isotopes to describe habitat selection and temporal changes in foraging activity provides important insight into the relative importance of resource partitioning in species cohabiting compartments of aquatic ecosystems.

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*Received: 5 May 2005*

*Accepted: 21 October 2005*

*Amended: 31 October 2005*