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Diet Partitioning in a Diverse Centrarchid Assemblage in the Atchafalaya River Basin, Louisiana

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Abstract

We examined trophic and habitat resource partitioning among seven centrarchid species inhabiting four macrohabitat types in the Atchafalaya River basin (ARB), a 900-km² bottomland hardwood swamp in south-central Louisiana. Fish ($n = 2,036$) were collected at 24 sites by boat electrofishing, and trophic position was determined from stomach contents and tissue analysis of ¹⁵N and ¹³C stable isotope signatures ($n = 140$). Stomach content analysis (index of relative importance), Morisita's index of dietary overlap, and canonical correspondence analysis revealed little effect of ARB macrohabitat type on centrarchid trophic relationships despite significant habitat alterations in dredged canals. Analyses revealed substantial diet overlap among three predominately insectivorous species (Bluegill *Lepomis macrochirus*, Redspotted Sunfish *L. miniatus*, and Longear Sunfish *L. megalotis*), whereas much more distinctive trophic positions were occupied by Largemouth Bass *Micropterus salmoides* (dominant prey = fish), Black Crappies *Pomoxis nigromaculatus* (palaemonid shrimp), Redear Sunfish *L. microlophus* (mollusks), and Warmouths *L. gulosus* (crayfish). Stable isotope signatures reflected dietary differences among species and complemented stomach content analyses in assessing the feeding ecology of these centrarchids, although isotopic similarities were sometimes higher than actual similarities in diet composition. Results suggest that centrarchid functional morphology and prey selection, combined with the diversity and productivity of ARB littoral habitats, effectively reduce the potential for competition among the seven cohabiting centrarchids.

Partitioning along a resource axis promotes coexistence among species by reducing interspecific interactions among taxa and allowing high numbers of species to coexist in a relatively close spatial proximity (Ross 1986; Matthews 1998; Wheeler and Allen 2003). Previous studies examining niche segregation have demonstrated resource partitioning across several fish groups, including centrarchids (Laughlin and Werner 1980; Mittelbach 1984; Wheeler and Allen 2003), darters (Hlohowskyj and White 1983; Van Sink Gray et al. 1997), salmonids (Nakano et al. 1999), and cohabiting piscivores (Hartman and Brandt 1995; Amundsen et al. 2003). These studies suggest greater habitat, temporal, and diet

resource partitioning among fish species within genera as opposed to more distantly related taxa, often as a result of differential foraging behavior, seasonal behavioral changes, or interspecific competition (Laughlin and Werner 1980; Hlohowskyj and White 1983; Mittelbach 1984; Van Sink Gray et al. 1997; Nakano et al. 1999). However, reduced diet partitioning among congeners relative to confamilials has also been noted and attributed to greater similarities in body morphology, sensory acuity, foraging tactics, and digestive ability among closely related taxa (Ross 1986). Given that fishes exhibit differential levels of resource overlap with sympatric congeners and confamilials, it is of particular interest to

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understand how these sympatric species coexist, particularly in light of continuing aquatic habitat alterations that can impact foraging habitat heterogeneity, water quality, and forage production.

Given their abundance, diversity, and ecological specialization, freshwater sunfishes (family Centrarchidae) provide a unique opportunity to investigate population-, assemblage-, and ecosystem-level processes (Ross 1986; Helmus et al. 2007; Aday et al. 2009). Centrarchids are prevalent throughout the southeastern United States (Douglas 1974; Desselle et al. 1978; Ross 2001), where they often dominate the abundance and biomass of littoral fish assemblages (e.g., Werner et al. 1978; Bachmann et al. 1996; Winemiller et al. 2000). Depending on competitive interactions, trophic functional morphology (Wainwright 1996), and resource availability (Werner et al. 1977; Mittelbach 1984; Bootsma et al. 1996), sympatric centrarchids can exhibit strong partitioning of prey resources (George and Hadley 1979; Laughlin and Werner 1980).

Several centrarchid species have been the subject of trophic partitioning studies, including the Largemouth Bass *Micropterus salmoides* and Alabama Bass *Micropterus henshalli* (Wheeler and Allen 2003); the Rock Bass *Ambloplites rupestris* and Bluegill *Lepomis macrochirus* (Paterson et al. 2006); and the Bluegill, Pumpkinseed *Lepomis gibbosus*, and Green Sunfish *Lepomis cyanellus* (Werner and Hall 1976, 1979; Werner et al. 1977). The role of functional morphology in understanding and predicting trophic ecology has been examined (e.g., Lauder 1983; Wainwright and Richard 1995; Wainwright 1996), but no studies have examined the trophic relationships of more diverse assemblages of co-occurring centrarchids. Previous studies of fish-habitat relationships in the Atchafalaya River basin (ARB), Louisiana, have yielded 15 centrarchid species, with littoral fish assemblages dominated by Largemouth Bass, Black Crappies *Pomoxis nigromaculatus*, Bluegills, Warmouths *Lepomis gulosus*, Longear Sunfish *Lepomis megalotis*, Redear Sunfish *Lepomis microlophus*, and Redspotted Sunfish *Lepomis miniatus* (Rutherford et al. 2001; Troutman et al. 2007). The ubiquity of *Lepomis* species in ARB littoral fish assemblages would suggest the potential for (1) substantial trophic overlap given these species' similarity in gape, sensory acuity, and other morphological characteristics (Ross 1986); and (2) reduced growth and survival of these popular recreational fishes if trophic resources become limiting.

Of potential importance to these trophic interactions is the pervasive habitat alteration that has occurred in the ARB due to sediment accretion and the construction of flood control levees and canals for oil and gas exploration and extraction (Sabo et al. 1999a, 1999b; Hupp et al. 2008; Kaller et al. 2011; Kroes and Kramer 2013). These activities have substantially altered the areal extent, hydrology, channel structure, and function of this historically expansive floodplain, concentrating fishes into an ever-diminishing amount of permanently

wetted habitat (Tye and Coleman 1989; Kroes and Kramer 2013). Excavated canals have become a dominant aquatic feature of the ARB floodplain relative to natural bayous and lakes; the canals exhibit greater homogeneity of depth and less woody debris as a result of active management for navigation and resource extraction (Kroes and Kramer 2013). The entire ARB system experiences annual flooding, which influences water quality (Sabo et al. 1999a, 1999b) and fisheries productivity (Alford and Walker 2013). However, local conditions within canal, lake, and bayou macrohabitats and the position of these macrohabitats within the floodplain greatly modify the impact of the flood pulse (Kaller et al. 2011), particularly where aquatic invasive macrophytes are present (Colon-Gaud et al. 2004; Kaller et al., in press), thus creating a temporally and spatially dynamic and disparate set of physicochemical conditions for fishes. Concentration of ARB centrarchid assemblages in natural and man-made macrohabitats may have reduced or exacerbated trophic partitioning among these species; therefore, an assessment of the consequences of these habitat alterations may provide insight into fish trophic responses to anthropogenic disturbance in other floodplain systems. However, little research to date has addressed the trophic relationships and feeding ecology of centrarchid species within the ARB habitat mosaic (Fisher et al. 2012).

Fisheries biologists have traditionally used stomach content analyses to investigate predator-prey interactions, habitat selection, and foraging activities (Hyslop 1980; Rennó Braga et al. 2012), but these types of data may be biased due to inconsistent rates of digestion (Bootsma et al. 1996). In contrast, stable isotope composition reflects the composition of an individual fish's diet over an extended period of time because of the slow turnover rates of nitrogen and carbon (^{15}N and ^{13}C) isotopes within fish muscle (Fry et al. 1999; Clarke et al. 2005), which may provide information on the number of trophic levels (Minagawa and Wada 1984; Peterson and Fry 1987; Post 2002; Vander Zanden and Rasmussen 2002) and foraging habitat selection (France 1995; Hecky and Hesslein 1995; Vander Zanden and Rasmussen 1999). Consequently, ^{13}C and ^{15}N isotope signatures can be used to complement stomach content analyses in order to provide a more comprehensive examination of fish foraging ecology.

Given the consistently high diversity and abundance of centrarchids found in the ARB over the last two decades, we hypothesized that at least some of these species must be effectively partitioning the littoral forage base, although such relationships might vary among different macrohabitat types. Specifically, we wanted to evaluate whether centrarchid species were taking advantage of morphological (e.g., gape width and body size) and foraging habitat differences to partition available food within a habitat. We tested the hypotheses that (1) diets were more similar among congeneric species (*Lepomis* spp.) than among non-congeneric confamilials (Ross 1986); and (2) interspecific diet similarity was higher in more

altered canal macrohabitats than in lakes and bayous. To assess these hypotheses, we collected centrarchids from lakes, dead-end canals, natural bayous, and open canals in the ARB during 2011 and 2012, and we used stomach content analysis and stable isotope signatures to assess trophic partitioning and macrohabitat effects on centrarchid diet composition.

METHODS

Study site.—As the largest contiguous bottomland hardwood swamp in North America, the physicochemically dynamic ARB floodplain (Bryan and Sabins 1979; Kaller et al. 2011) provides a mosaic of interconnected aquatic habitats to resident aquatic species, with littoral areas supporting dense accumulations of woody debris and extensive beds of native and invasive macrophytes (Ruess 2004; Walley 2007). The ARB supports substantial fisheries production associated with the annual Atchafalaya River flood pulse (Bryan and Sabins 1979; Rutherford et al. 2001; Alford and Walker 2013), characterized by water levels that peak in spring and decline throughout the summer (Lambou 1990; Fontenot et al. 2001). We limited our study to a 900-km² area in the southeastern portion of the lower ARB; this area was bounded on the east by the Intracoastal Waterway and its adjacent guide levee and on the west by the main stem of the Atchafalaya River.

Field collections.—Collection sites were selected from three regions of the ARB (Flat, East Grand, and Murphy lakes; Figure 1) and included four principal macrohabitats: lakes, natural bayous, dead-end canals, and open canals. Dead-end canals were included as a separate macrohabitat because they are characteristically low-energy channels that are prone to stagnation and hypoxia (Sabo et al. 1999a). We sampled 24 fish collection sites (4 macrohabitats × 3 regions × 2 years; Figure 1) from August 1 to September 16, 2011, and from May 28 to July 11, 2012, when water levels were low enough to permit effective electrofishing—that is, when flood waters declined below natural bank levels (river stage < 3 m at U.S. Geological Survey gauge 07381515 [Butte La Rose]; Perret et al. 2010). We collected fish via standardized electrofishing techniques by using a boat-mounted DC electrofishing unit. Fish were collected for a total of 1,500 s (power-on time) between 0800 and 1200 hours along 200 m of shoreline at each site. All adult and subadult centrarchids were netted, placed in an ice slurry, and transported to the laboratory for dissection (Institutional Animal Care and Use Protocol A2011-16, Louisiana State University Agricultural Center). Minimum sizes of retained individuals were 150 mm for *Micropterus* spp., 125 mm for *Pomoxis* spp., and 100 mm for *Lepomis* spp. Because local conditions could affect sampling and dietary composition, we estimated macrophyte cover within a 1-m-wide strip surrounding the boat at the center of each sample reach; current velocity, dissolved oxygen, and turbidity were recorded with an in situ probe (Yellow Springs Instrument Co., Inc., Yellow Springs, Ohio).

Laboratory methods.—All stomach contents were removed from each fish and were stored in labeled vials containing a 10% solution of buffered formalin. After fixation for 7 d, samples were transferred to a 70% ethanol solution (Bowen 1996; Garvey and Chipps 2012) and then were identified to the order or family level (depending on the degree of digestion), counted, and weighed (wet weight). Diets were described in terms of the frequency of occurrence (% O_i), percent composition by number (% N_i), percent composition by weight (% W_i), and the index of relative importance (IRI_{*i*}) of consumed prey items:

$$\begin{aligned} \%O_i &= \frac{J_i}{P}, \\ \%N_i &= \frac{N_i}{\sum_{i=1}^Q N_i}, \\ \%W_i &= \frac{W_i}{\sum_{i=1}^Q W_i}, \end{aligned}$$

and

$$\text{IRI}_i = (\%N_i + \%W_i)(\%O_i),$$

where J_i is the number of fish that consumed prey type i ; P is the number of fish with food in their stomachs; N_i is the number of consumed prey in food category i ; Q is the number of prey types; and W_i is the weight of consumed prey in food category i (Chipps and Garvey 2007). We expressed IRI_{*i*} values as a percentage (referred to as IRI%) for between-species comparisons. A simplified version of Morisita's dietary overlap index based on % W_i was used to quantify the degree of resource overlap between potential competitors (Horn 1966; Garvey and Chipps 2012),

$$C_{ik} = \frac{2 \sum p_{ij} p_{ik}}{\sum_i p_{ij}^2 + \sum_i p_{ik}^2},$$

where p_{ij} and p_{ik} are the proportions of the resource i used by species j and k ; and n is the total number of prey categories.

Although our hypotheses focused on among-species and among-macrohabitat differences, we used within-species generalized linear models to assess whether other potential factors should be considered, including fish total length, local water quality characteristics (e.g., dissolved oxygen, current velocity, and temperature), and macrophyte abundance (percent cover). In these preliminary analyses, we used a multinomial probability distribution and a generalized logit link function in R version 2.15.1 (Faraway 2006) to model prey IRI% as a response to macrohabitat; we included region, fish total length, local water quality, and macrophyte cover as covariables of potential importance in subsequent analyses. Statistically

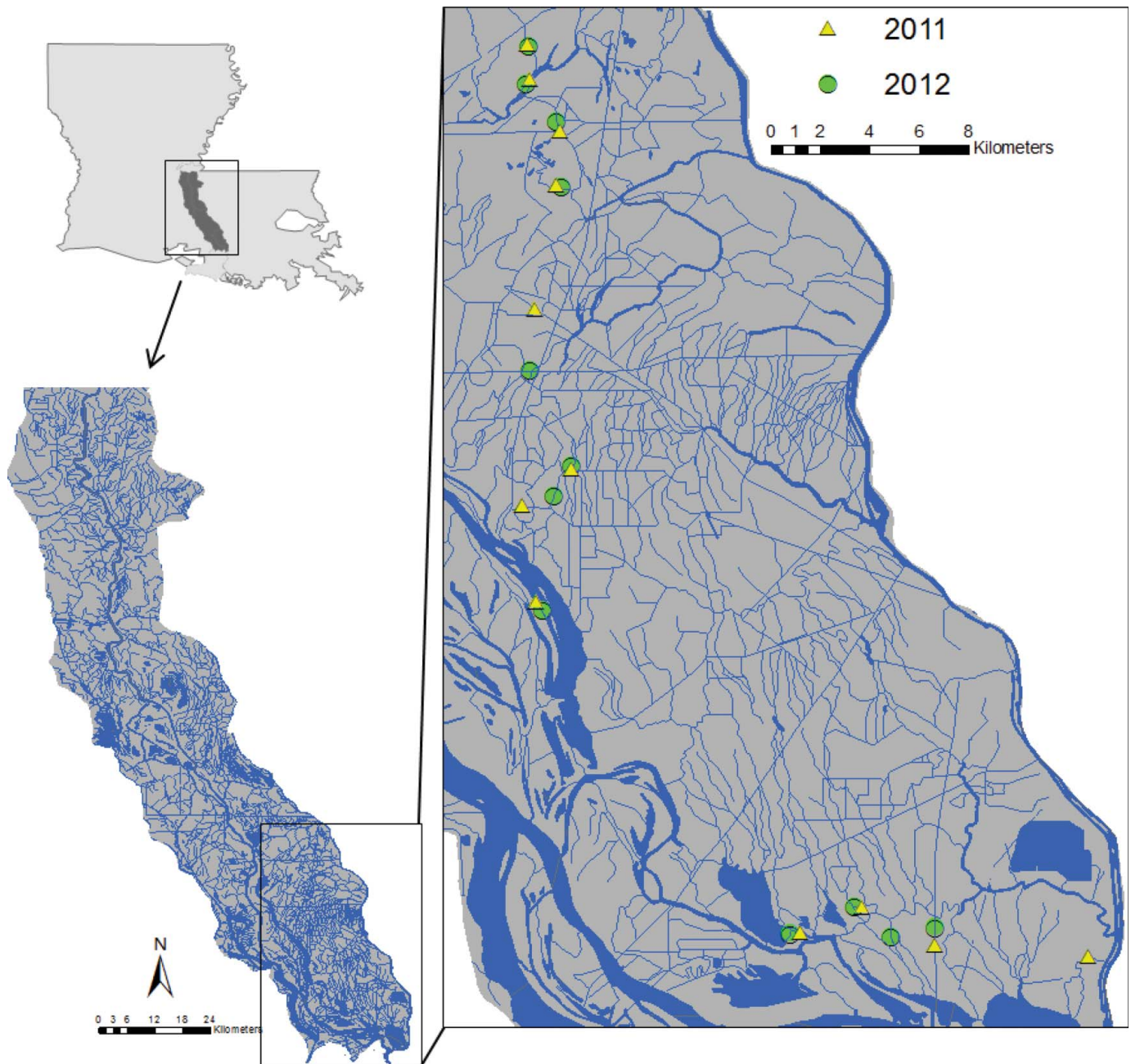


FIGURE 1. Locations of fish collection sites sampled during 2011 (triangles; $N = 12$) and 2012 (circles; $N = 12$) in the Flat Lake, Murphy Lake, and East Grand Lake regions of the lower Atchafalaya River basin, Louisiana (insets: location of the basin within the state, and location of the study area within the basin). [Figure available online in color.]

significant covariables were included in subsequent ordinations. Based on criteria provided by ter Braak (1987) and Lepš and Šmilauer (2003), we compared ordinations and chose canonical correspondence analysis (CCA; R version 2.15.1) to compare prey IRI% values among species; region, macrohabitat, and number of sampled fish were used as covariates. Statistical significance of diet-based fish species–macrohabitat

associations was tested with a permutation-based ANOVA (500 permutations) in R software.

Stable isotopes.—Tissue samples for ^{13}C and ^{15}N isotope analyses were obtained from randomly chosen fish collected between May 28 and July 11, 2012. For each of the seven centrarchid species, we prepared 20 total samples, including five individuals from each of the four

macrohabitats (total $N = 140$ samples across species). For each fish, we removed a sample ($1 \times 2 \times 2$ cm) of muscle tissue from the dorsal region posterior to the dorsal fin and above the lateral line. Samples were dried for 48 h at 50°C and then were homogenized with a mortar and pestle (Clarke et al. 2005). A 1-mg quantity (± 0.2 mg) of each tissue sample was analyzed for nitrogen and carbon composition by using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Seron Ltd., Cheshire, UK) at the Stable Isotope Facility, University of California, Davis. Isotope ratios of the tissue samples were compared with a reference material of known isotopic composition, and results were reported in delta (δ) notation expressed relative to the international standards of Vienna Pee Dee belemnite for carbon and air for nitrogen,

$$\delta^{15}\text{N or } \delta^{13}\text{C} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{reference}}} \right) - 1 \right] \times 1,000,$$

where R is the $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ ratio.

We plotted mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the seven centrarchid species to examine trophic relationships and foraging habitat use within the assemblage (Peterson and Fry 1987; Post 2002; Layman et al. 2007). We then performed a multivariate ANOVA (GLM procedure in SAS version 9.3; assumptions were evaluated prior to analysis) with Tukey-adjusted post hoc comparisons to test for differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among species.

RESULTS

Of the 2,036 individual centrarchids that we examined for stomach contents, 783 (38.5%) had empty stomachs or had ingested only unidentifiable plant material and were excluded from statistical analyses. Identifiable prey in the stomachs of the remaining 1,253 individuals indicated substantial differences in prey selection among several species within the centrarchid assemblage.

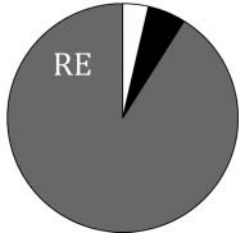
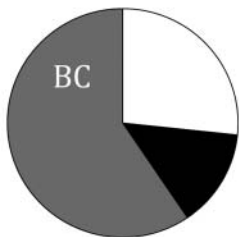
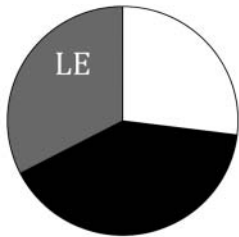
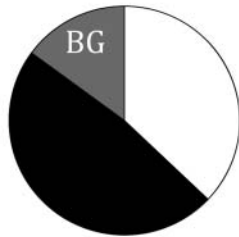
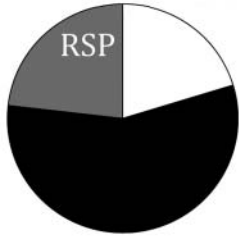
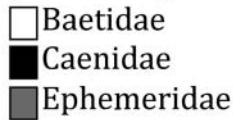
Largemouth Bass were primarily piscivorous, although cambarid crayfishes were also ingested (Table 1). Identifiable prey fishes in Largemouth Bass diets included sunfishes *Lepomis* spp., shads *Dorosoma* spp., Pirate Perch *Aphredoderus sayanus*, and shiners *Notropis* spp.; however, most fish were heavily digested and could not be identified to species (identified and unidentified fish were grouped as “fish” for statistical analyses). Black Crappies fed predominantly on freshwater shrimp (Palaemonidae), with amphipods, fish, ephemeropterans, and hemipterans comprising smaller dietary proportions (Table 1). Warmouths also consumed fish and hemipterans, but their diets were dominated by cambarids; identifiable individuals were almost exclusively red swamp crayfish *Procambarus clarkii*. Molluscivorous Redear Sunfish consumed mostly Asiatic clams *Corbicula fluminea* as well as physid snails, and their stomach contents typically included numerous unidentified shell fragments. The remaining three *Lepomis* species exhibited considerable overlap of prey items.

Bluegills, Longear Sunfish, and Redspotted Sunfish had diets that were dominated by aquatic insects, and partitioning of the insect forage base was evident among several of the cohabiting centrarchids (Figure 2). Bluegills fed

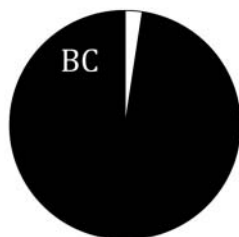
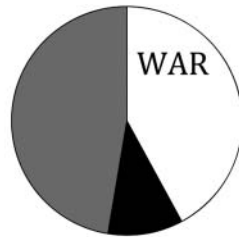
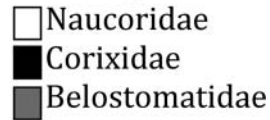
TABLE 1. Percent composition by weight (W%) and index of relative importance percentage (IRI%) for Largemouth Bass (LMB; $N = 220$; mean total length \pm SD = 278.5 ± 60.2 mm), Warmouths (WAR; $N = 156$; 159.9 ± 27.4 mm), Black Crappies (BC; $N = 229$; 203.8 ± 32.3 mm), Bluegills (BG; $N = 380$; 151.8 ± 24.6 mm), Redspotted Sunfish (RSP; $N = 106$; 126.2 ± 60.2 mm), Longear Sunfish (LES; $N = 94$; 119.1 ± 11.9 mm), and Redear Sunfish (RES; $N = 68$; 187.7 ± 25.0 mm) in the Atchafalaya River basin, Louisiana. Each species' highest IRI% value is highlighted in bold italics.

Prey category	LMB		WAR		BC		BG		RSP		LES		RES	
	W%	IRI%	W%	IRI%	W%	IRI%	W%	IRI%	W%	IRI%	W%	IRI%	W%	IRI%
Fish	0.58	75.1	0.13	10.2	0.25	5.07	0.08	0.35	0.15	2.68	0.15	1.36	0.00	0.00
Cambaridae	0.41	22.1	0.78	75.5	0.05	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Palaemonidae	0.01	2.60	0.01	3.68	0.56	75.9	0.11	1.44	0.15	5.42	0.17	2.94	<0.01	0.01
Amphipoda	0.00	0.00	0.00	0.05	0.05	14.1	0.02	2.98	0.01	7.25	0.02	12.1	<0.01	0.01
Diptera	0.00	0.00	0.00	0.09	0.00	0.56	0.14	69.9	0.02	15.5	0.03	17.6	<0.01	0.69
Ephemeroptera	0.00	0.05	0.00	0.85	0.06	3.01	0.12	14.4	0.06	23.4	0.28	50.4	0.06	2.88
Hemiptera	0.00	0.07	0.04	4.72	0.01	1.10	0.10	1.67	0.18	14.9	0.03	0.33	0.00	0.00
Coleoptera	0.00	0.01	0.00	0.25	0.00	0.00	0.15	3.83	0.13	10.6	0.04	1.47	<0.01	<0.01
Hymenoptera	0.00	0.00	0.00	0.03	0.00	0.00	0.01	0.18	0.08	3.99	0.00	0.00	<0.01	<0.01
Corbiculidae	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.80	0.03	3.75	0.15	8.55	0.47	59.5
Physidae	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.12	0.06	3.03	0.02	0.54	0.23	20.5
Shell fragments	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	15.3
Fish eggs	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.71	0.01	5.33	0.01	0.81	0.00	0.00
Other prey	0.00	0.03	0.02	0.46	0.00	0.02	0.03	1.62	0.10	2.90	0.04	3.11	0.04	1.13

Ephemeroptera



Hemiptera



predominantly on dipterans (mostly chironomid and ceratopogonid larvae), although ephemeropterans, coleopterans, and hemipterans were also ingested. Longear Sunfish preyed heavily on ephemeropterans but also consumed dipterans, amphipods, and Asiatic clams. Ephemeropterans were also the most important prey type for Redspotted Sunfish, with additional diet contributions by dipterans, hemipterans, and coleopterans. Of the hemipterans that were consumed, naucorids comprised a greater portion of the diets of Bluegills and Redspotted Sunfish, whereas Warmouths fed extensively on belostomatids, and Black Crappies preyed almost exclusively on corixids (Figure 2). Within the Ephemeroptera, Black Crappies and Redear Sunfish consumed primarily ephemerids, whereas Bluegills, Redspotted Sunfish, and Longear Sunfish also preyed on baetids and caenids (Figure 2).

Morisita's diet overlap values were 0.75 for Bluegills and Redspotted Sunfish; 0.75 for Bluegills and Longear Sunfish; and 0.63 for Longear Sunfish and Redspotted Sunfish. Warmouths and Largemouth Bass exhibited a similar overlap index of 0.69, although Warmouth diets were distinct from the diets of other centrarchids (<0.26), as were the Redear Sunfish diets (<0.38 ; Table 2). The CCA reflected low to moderate diet overlap among species and highlighted the unique composition of diets consumed by Redear Sunfish, Black Crappies, and Largemouth Bass/Warmouths relative to the three more generalist centrarchid species ($F_{6, 112} = 8.65$, $P = 0.01$; Figure 3). The CCA included the covariables region, number of fishes, and macrohabitat, although interspecific diet differences attributable to macrohabitat were not significant ($F_{8, 112} = 1.13$, $P = 0.09$).

Analysis of mean isotope levels revealed significant differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures for the seven ARB centrarchid species (Wilks' $\lambda_{12, 40} = 0.07$, $P < 0.01$; Figure 4). For $\delta^{15}\text{N}$ ($F_{6, 27} = 23.07$, $P < 0.01$), piscivorous Largemouth Bass exhibited the highest value, followed by Black Crappies, Longear Sunfish, Redspotted Sunfish, Bluegills, Warmouths, and Redear Sunfish (Table 3). Overall variation in $\delta^{13}\text{C}$ among the species was minimal; significant

FIGURE 2. Families of Ephemeroptera (at least 50 individuals consumed) and Hemiptera (at least 25 individuals consumed) found in the stomach contents of Redspotted Sunfish (RSP), Bluegills (BG), Longear Sunfish (LES), Warmouths (WAR), Black Crappies (BC), and Redear Sunfish (RES) collected in the Atchafalaya River basin. Data represent the percentage numeric contribution of each family.

TABLE 2. Modified Morisita's diet overlap index values for percent composition by prey weight in the stomach contents of seven centrarchid species collected in the Atchafalaya River basin. Species codes are defined in Table 1.

Species	LMB	BC	WAR	BG	RSP	LES
LMB						
BC	0.38					
WAR	0.69	0.16				
BG	0.16	0.38	0.05			
RSP	0.40	0.53	0.26	0.75		
LES	0.28	0.56	0.09	0.75	0.63	
RES	0.01	0.01	0.00	0.24	0.14	0.38

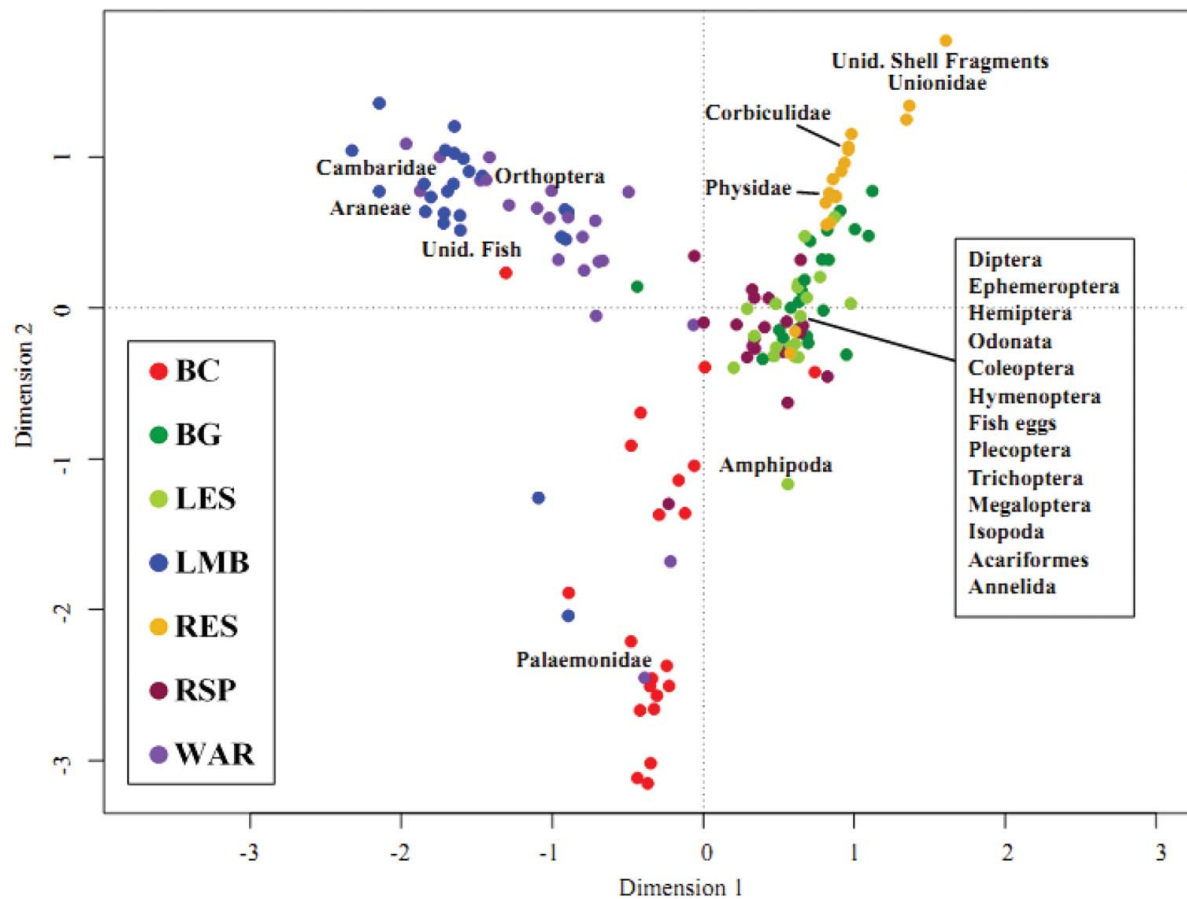


FIGURE 3. Results of canonical correspondence analysis, depicting percent index of relative importance (IRI%) values for prey categories in the diets of Black Crappies (BC), Bluegills (BG), Longear Sunfish (LES), Largemouth Bass (LMB), Redear Sunfish (RES), Redspotted Sunfish (RSP), and Warmouths (WAR) in the Atchafalaya River basin. [Figure available online in color.]

differences in $\delta^{13}\text{C}$ ($F_{6, 27} = 2.76$, $P = 0.01$) were primarily due to the high and low mean values for Longear Sunfish and Redear Sunfish, respectively (Table 3).

DISCUSSION

Analyses based on a priori macrohabitat designations did not reveal differences in the diets of centrarchids from excavated canals relative to natural lakes and bayous, although $\delta^{13}\text{C}$ values and the habitat affinities of invertebrate prey taxa did suggest the potential for partitioning on a more microhabitat scale between open water and the littoral zone and between vegetation beds and soft-bottomed benthic areas. The lack of apparent dietary differences between centrarchids collected from natural habitats and those sampled from excavated channels may be attributable to the 80 years of floodplain manipulations in the ARB. Anthropogenic alterations in floodplain habitat may have already selected for (1) fish species (e.g., Warmouth and Redear Sunfish) that can exploit unique prey resources (e.g., crayfish and mollusks) common in all ARB habitats or (2) more generalist fish species (e.g., Bluegill and

Longear Sunfish) that can effectively partition trophic resources in any macrohabitat based on differences in prey taxa, spatial distribution, or feeding times (e.g., Piet and Guruge 1997; Sibbing and Nagelkerke 2001).

Regarding our hypothesis of greater dietary overlap among *Lepomis* species relative to confamilial Black Crappies and Largemouth Bass, results depended on the particular species being considered. As expected, diet similarity between some of the *Lepomis* species and the larger-gaped Largemouth Bass and Black Crappies was relatively low (e.g., Redear Sunfish versus Black Crappies, Warmouths versus Black Crappies, and Longear Sunfish versus Largemouth Bass). However, the extent of overlap among the species of *Lepomis* ranged from considerable (e.g., Bluegills, Longear Sunfish, and Redspotted Sunfish) to minimal (e.g., Redear Sunfish and Warmouths versus the other *Lepomis* spp.). Bluegills, Redspotted Sunfish, and Longear Sunfish exhibit similarly small gape widths and similar overall body sizes—two morphological characteristics that are important in determining trophic position (Wainwright and Richard 1995). Elevated levels of dietary overlap can be indicative of competition if resources are limiting but can also

TABLE 3. Mean (\pm SD) nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotope ratios (range in parentheses) for seven centrarchid species collected in the Atchafalaya River basin ($n = 20$ fish/species). Species codes are defined in Table 1. For a given column, means with a lowercase letter in common are not significantly different.

Species	$\delta^{15}\text{N}$ (‰)	Species	$\delta^{13}\text{C}$ (‰)
LMB	16.06 ± 0.16 z (15.40, 16.87)	RES	-29.32 ± 0.18 z (-30.94, -28.03)
BC	15.44 ± 0.15 y (14.08, 16.42)	BC	-29.07 ± 0.15 zy (-30.23, -27.54)
LES	14.94 ± 0.13 yx (13.65, 15.95)	BG	-28.98 ± 0.27 zy (-31.47, -27.41)
RSP	14.83 ± 0.14 xw (13.96, 16.52)	WAR	-28.67 ± 0.20 zy (-30.13, -27.13)
BG	14.64 ± 0.13 xwv (13.57, 15.97)	LMB	-28.56 ± 0.16 zy (-29.58, -27.19)
WAR	14.38 ± 0.13 wv (13.49, 15.78)	RSP	-28.54 ± 0.24 zy (-30.62, -26.82)
RES	14.17 ± 0.12 v (12.83, 15.13)	LES	-28.38 ± 0.18 y (-29.47, -26.38)

reflect multispecies exploitation of abundant forage species (Hlohowskyj and White 1983; Matthews 1998). All three *Lepomis* species preyed heavily on chironomids and ephemeropterans but were likely exploiting abundant taxa that often dominate invertebrate assemblages in wetland ecosystems (e.g., Brooks 2000; Kashian and Burton 2000; Battle and Goladay 2001), including the ARB (Colon-Gaud et al. 2004; Fisher et al. 2012). Overall, the strength of dietary overlap among the cohabiting centrarchids appeared to be associated less with taxonomic relatedness than with interspecific differences in buccal morphology, foraging habitats, and prey characteristics.

The ARB centrarchids exhibited a range of trophic specialization, with Redspotted Sunfish being the most generalized species; it was the only centrarchid that lacked a specific prey item with an IRI% value greater than 50%. Conversely, Redear Sunfish, Black Crappies, Warmouths, and Largemouth Bass exhibited dominance of particular prey items, likely related to differences in gape width (Wainwright and Richard 1995) and the diversity of prey available in the ARB littoral zone, which limited diet similarity among these fishes. Although Redear Sunfish, Warmouths, and Black Crappies all preyed extensively on invertebrates, Redear Sunfish were

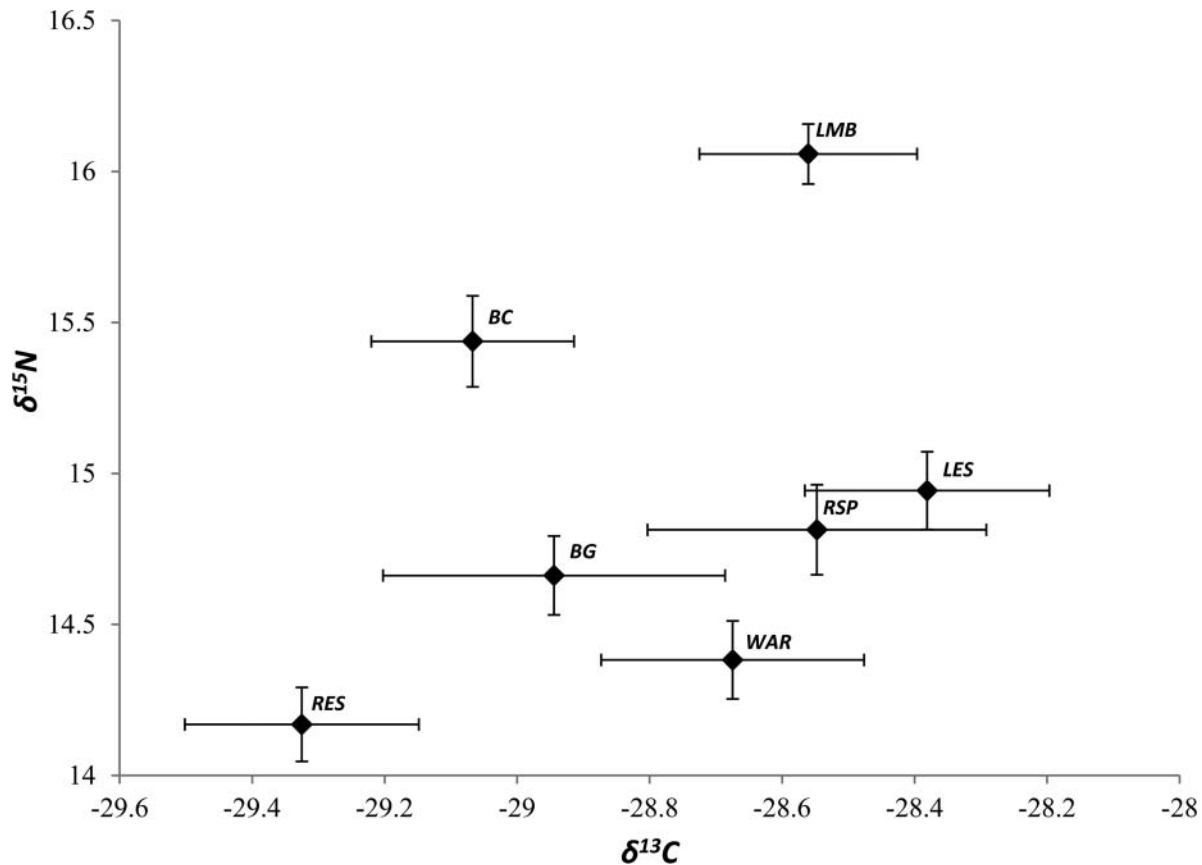


FIGURE 4. Mean carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope signatures (‰) for seven centrarchid species collected in the Atchafalaya River basin ($n = 20$ fish/species). Species codes are defined in Figure 3.

consistently molluscivorous (Huckins 1997; Wong et al. 2013), which accords with their unique pharyngeal morphology and capabilities for handling shelled prey (Lauder 1983). The consumption of mollusks therefore resulted in minimal overlap between Redear Sunfish and any of the other centrarchids. Warmouths exhibited greater diet diversity but consistently preyed on the abundant crayfish forage base (Bonvillain 2012; Alford and Walker 2013), similar to the results of previous diet studies (Germann et al. 1975; Guillory 1979).

Interestingly, despite a relatively large gape and an abundance of prey fishes in the ARB, the Black Crappies' diet was dominated by grass shrimp *Palaemonetes* spp., which resulted in moderate to low diet overlap with either Largemouth Bass or the cohabiting *Lepomis* species. These amphidromous river shrimp may have been particularly vulnerable to Black Crappie predation due to (1) their abundance in the ARB (Truesdale and Mermilliod 1979; Fisher et al. 2012); (2) their peaks in migration, which coincided with our summer sampling period; and (3) the nighttime movement of juvenile shrimp (Bauer and Delahoussaye 2008), which makes them highly vulnerable to nocturnal- and crepuscular-feeding crappies (Guy et al. 1992; Shoup et al. 2004; Tuten et al. 2008). The lack of fishes in the diet of this reportedly piscivorous centrarchid (Maceina et al. 1991; Muoneke et al. 1992; Mittelbach and Persson 1998) may have been related to increased foraging in open water beyond the vegetation as a response to competitive and/or predatory interactions (e.g., Mittelbach 1986) with larger piscivores, such as Largemouth Bass, Bowfins *Amia calva*, and Spotted Gars *Lepisosteus oculatus*, all of which are commonly found in the ARB littoral zone.

Among the invertivorous species of *Lepomis*, the ingested ephemeropterans and hemipterans provided evidence of taxonomically based and habitat-based trophic partitioning. Bluegills, Redspotted Sunfish, and Longear Sunfish all preyed extensively on baetid and caenid mayflies, which are structurally associated taxa that are abundant in ARB plant beds (Colon-Gaud et al. 2004; Fisher et al. 2012). In contrast, burrowing ephemerids comprised the majority of mayflies that were consumed by Black Crappies and Redear Sunfish but probably for different reasons. Redear Sunfish likely encountered burrowing mayflies during benthic foraging for mollusks, whereas Black Crappies are water column feeders and probably captured mayflies that were moving to the surface to emerge. Movement of mayflies into the drift in the lower Mississippi River is distinctly nocturnal (Koetsier and Bryan 1989), and similar to the nocturnal movements of riverine shrimp, these movements may have made ephemerid mayflies particularly vulnerable to foraging Black Crappies.

In the ARB centrarchid assemblage, the Largemouth Bass was the only species with a high degree of piscivory, which minimized its trophic similarity with most of the other centrarchids. Fish typically predominate in diets of non-juvenile Largemouth Bass (e.g., Sammons and Maceina 2006), but

invertebrates can also comprise a significant portion of ingested prey, depending on habitat characteristics (e.g., Ahrenstorff et al. 2009). It is interesting that these large-gaped fish did not mimic Warmouths and prey heavily on crayfish, even though large crayfish were abundant and reportedly are important prey for basses in other systems (Schramm and Maceina 1986; Sammons and Maceina 2006; Warren 2009; Sammons 2012).

Stomach content analyses were mostly corroborated by the stable isotope data, which have been used to assess resource partitioning among centrarchids in other systems (Paterson et al. 2006). Differences in $\delta^{15}\text{N}$ signature among centrarchids suggested that trophic specializations were contributing to species coexistence within this floodplain ecosystem, although differences in isotope signatures were not as pronounced as the dietary differences indicated by stomach content analyses. Analyses of Largemouth Bass and Black Crappie samples yielded $\delta^{15}\text{N}$ values that were more enriched than those of the five *Lepomis* species, indicating that Largemouth Bass and Black Crappies represent the uppermost trophic position within the assemblage. Such a finding is consistent with their larger overall size, larger gape dimensions, and stomach contents and is similar to the isotope relationships observed for Largemouth Bass relative to Bluegills in the Everglades (Wang et al. 2014). Redear Sunfish exhibited the lowest $\delta^{15}\text{N}$ values, which reflected a more direct link to algal production via the grazing and filtering mollusks that comprised this species' diet.

The preponderance of aquatic insects in the diets of Bluegills, Redspotted Sunfish, and Longear Sunfish was evident in the similar $\delta^{15}\text{N}$ values for these species. Interestingly, the $\delta^{15}\text{N}$ analysis also suggested a high degree of trophic similarity between these small *Lepomis* species and the Warmouth, although a larger gape size permitted Warmouths to feed on the abundant crayfish forage base that was not exploited by the other three species. Differences in gape size likely contribute significantly to the persistence of Warmouths in the presence of other centrarchids, as this species can exploit larger invertebrates and small fishes (Ross 2001) that are probably less available morphologically to smaller-gaped fishes in the centrarchid assemblage.

Interspecific differences in mean $\delta^{13}\text{C}$ signatures of the seven centrarchids ($<1\text{‰}$) were less than those exhibited by Bluegills and Rock Bass in the Detroit River (Paterson et al. 2006); the difference between studies may be attributable to the legacy of industrial activity reducing benthic invertebrate prey (particularly ephemeropterans) in the Detroit River as compared with the ARB (Manny et al. 1988; Paterson et al. 2006). Although statistically similar, the trends in mean $\delta^{13}\text{C}$ signature among species supported the stomach content data in our study. Redear Sunfish and Black Crappies exhibited the most depleted $\delta^{13}\text{C}$ signatures, which is consistent with the importance of algal-feeding primary consumers, such as clams *Corbicula* spp., physid snails, and grass shrimp *Palaemonetes*

spp. (Beck and Cowell 1976; Barnese and Lowe 1990; Boltovskoy et al. 1995), in the diets of these two fishes. In a similar manner, the depleted $\delta^{13}\text{C}$ signatures of chironomids relative to ephemeropterans (Vander Zanden and Rasmussen 1999) were correlated with the greater importance of dipterans in the diets of Bluegills relative to Longear Sunfish and Redspotted Sunfish. However, there was no evidence of substantial differences in planktonic versus detrital carbon sources for the ARB centrarchids, as has been found for other fishes (e.g., Rodelli et al. 1984), and the overall similarity of the $\delta^{13}\text{C}$ signatures further emphasizes the importance of morphological and taxonomic trophic partitioning mechanisms in reducing the potential for interspecific competition.

Taken as a whole, the results of this study suggest that trophic competition is likely unimportant among the abundant members of the centrarchid assemblage in the ARB. Although we expected that the substantial anthropogenic modification of canal macrohabitats might alter food habits and niche relationships among the cohabiting centrarchids, diets differed little among the a priori macrohabitat designations. These results indicate the resilience of centrarchids to the historic and continuing changes in flow, depth, substrate composition, water quality, and macrophyte abundance associated with management of the ARB floodway (Kaller et al. 2011). As we expected, the levels of diet overlap between *Lepomis* species and confamilial Largemouth Bass and Black Crappies were predictably low, but interestingly the highest and lowest diet similarity values were exhibited among the congeneric species. Stable isotope analyses generally supported the results of stomach content analysis, but isotope signatures did not reflect differences in prey types that substantially reduced centrarchid diet overlap. Overall, morphological and behavioral differences among these centrarchid species, the diversity of available habitats and prey taxa in the ARB, and the seasonally dynamic water levels in this flood pulse ecosystem probably all play a role in facilitating resource partitioning and minimizing competition among these abundant littoral fishes.

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