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Effects of physicochemical properties and macrohabitat on the foraging ecology and condition of the centrarchid assemblage of the Atchafalaya River Basin, Louisiana

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EFFECTS OF PHYSICOCHEMICAL PROPERTIES AND MACROHABITAT ON THE
FORAGING ECOLOGY AND CONDITION OF THE CENTRARCHID ASSEMBLAGE OF
THE ATCHAFALAYA RIVER BASIN, LOUISIANA

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
In partial fulfillment of the
Requirements for the degree of
Master of Science

in

The School of Renewable Natural Resources

by
Brett Andrew Miller
B.S., Rhodes College, 2009
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DEDICATION

It is my hope that the passion exhibited within these pages will serve as a testament to my father, friend and expert fly fisherman, Dr. Jeff Miller, who taught me that although a multitude of essential life lessons can be discerned on a riverbank, it's the unyielding and obsessive desire instilled within the memories of landing the "biggest fish I've ever seen" that will last forever. Whether casting for trout in the Rockies, scanning the flats for bonefish or hooking bass behind the house, our experiences have forged an unbreakable bond amidst a respect for nature, and I will always be grateful for his continuous love, support, friendship and guidance.

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ABSTRACT

The Atchafalaya River Basin (ARB), Louisiana supports a diverse centrarchid assemblage, characterized by abundant populations of largemouth bass *Micropterus salmoides*, black crappie *Pomoxis nigromaculatus*, warmouth *Lepomis gulosus*, bluegill *Lepomis macrochirus*, redspotted sunfish *Lepomis miniatus*, longear sunfish *Lepomis megalotis* and redear sunfish *Lepomis microlophus*. This dynamic floodplain ecosystem is comprised of a mosaic of macrohabitats, including natural bayous, shallow lakes, dead-end and open pipeline canals. I conducted an extensive feeding ecology study to determine the influence of these macrohabitats on foraging activity through stomach content and stable isotope analyses. I collected 2,036 centrarchids with electrofishing efforts in the summers of 2011 and 2012. Canonical correspondence analysis of prey items revealed evidence of resource partitioning within the assemblage, as suggested by limited dietary overlap and significant separation of diets among the seven species ($F = 8.6516$, $P = 0.01$). Multivariate analysis of stable nitrogen ($\delta^{15}\text{N}$) isotopes revealed evidence of trophic specialization ($F = 24.29$, $P = 0.0001$) within the assemblage, despite moderate overlap in foraging habitat suggested by carbon ($\delta^{13}\text{C}$) signatures ($F = 2.76$, $P = 0.0147$). Results of the generalized linear mixed model ($F = 1.06$, $P = 0.3907$) and multivariate analyses of stable isotopes ($P = 0.86$) indicated that macrohabitat did not have an overall effect on diets or isotope values. Traditional dietary indices, such as index of relative importance values, indicated specialization in prey preference for each species, suggesting a limited degree of competition between centrarchids. In summary, despite physicochemical differences among macrohabitats, these results suggest that prey selection was species specific and independent of macrohabitat type.

Condition (relative weight) was also investigated to discern the potential influence of macrohabitat and physicochemical properties. Associations were species specific, indicating disparate manners of habitat utilization that may influence niche separation, although parameters such as dissolved oxygen differential were positively associated with multiple species. Although water quality and physical habitat characteristics differed among macrohabitats, trends in centrarchid condition suggest that while habitats within the ecosystem differ regarding their overall suitability as sunfish foraging habitat, all of the centrarchid species are generally able to flourish within the permanent waterbodies of the ARB floodplain.

CHAPTER 1: INTRODUCTION

1.1 ECOLOGICAL SEGREGATION IN FRESHWATER FISH ASSEMBLAGES

Resource partitioning facilitates coexistence within fish assemblages through segregation of food resources along prey type, foraging habitat, and foraging time axes (Schoener 1974; Matthews 1998). This segregation reduces interspecific interactions among taxonomic groups, trophic guilds or co-occurring species (Ross 1986), ameliorating competition and allowing high numbers of species to coexist (Matthews 1998; Wheeler and Allen 2003). Understanding the niche of a species can offer insight into its trophic role within an aquatic community (Leibold 1995; Layman et al. 2007), with niche differences among sympatric species based on trade-offs in morphology, physiology or behavior that permit differential use of available resources (Tilman 1987; Nakano et al. 1999).

Among fishes, trophic partitioning is often more apparent than habitat segregation (Schoener 1974; Ross 1986), although both may contribute to reduce niche overlap (Werner and Hall 1977). Fish trophic ecology is influenced by predator-prey interactions (Dewey and Jennings 1992; Weaver 1997), seasonal resource availability (Angermeier 1982), dietary specialization (Bootsma et al. 1996), habitat selection (Keast 1978), and ontogeny (Werner and Hall 1988), and plays an important role in the organization of species assemblages (Ross 1986). Previous studies examining niche segregation in freshwater and marine systems (Ross 1977) have demonstrated resource partitioning for a diversity of fish assemblages, including centrarchids (George and Hadley 1979; Mittelbach 1984; Wheeler and Allen 2003), darters (Hlohowskyj and White 1983; Gray et al. 1997), salmonids (Nakano et al. 1999), and cohabiting piscivores (Hartman and Brandt 1995; Amundsen et al. 2003).

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; Aday et al. 2009). Previous studies suggest a greater degree of resource partitioning among fish species within genera, as opposed to more distantly related taxa (Ross 1986; Matthews 1998), with sympatric centrarchids typically exhibiting strong trophic partitioning (George and Hadley 1979; Laughlin and Werner 1980; Wheeler and Allen 2003) based on competitive interactions, trophic specialization and resource availability (Werner et al. 1977; Mittelbach 1984; Bootsma et al. 1996). Spatial partitioning may also function to limit competitive interactions among littoral sunfishes (Mittelbach 1984; Warren 2009), with species coexistence aided by the high number of microhabitats available in structurally complex habitats (Weaver 1977).

The Atchafalaya River Basin (ARB) floodplain is a physicochemically dynamic aquatic system, with water levels, habitat availability, and water quality significantly influenced by the annual flood pulse of the Atchafalaya River. Within the floodplain, aquatic species have access to a mosaic of interconnected lakes, natural bayous, open pipeline canals, and dead end canals, with littoral habitat structure strongly influenced by dense accumulations of woody debris and extensive beds of native and alien macrophytes (Walley 2007). These macrohabitats support a diversity of invertebrates and fishes (Rutherford et al. 2001; Colon-Gaud et al. 2004; Troutman et al. 2007), including abundant populations of largemouth bass (*Micropterus salmoides*), crappies (*Pomoxis* spp.), and sunfishes (*Lepomis* spp.). Previous studies have examined habitat relationships of ARB centrarchids (Rutherford et al. 2001; Troutman et al. 2007), but little research has addressed the trophic relationships within this diverse assemblage. My study was designed to assess the trophic relationships among littoral ARB centrarchids, including the

potential influence of macrohabitat type on centrarchid trophic ecology. Although several previous studies have focused on trophic interactions between closely related taxa, such as largemouth bass and Alabama spotted bass (*Micropterus henshalli*) or bluegill (*Lepomis macrochirus*), pumpkinseed sunfish (*L. gibbosus*) and green sunfish (*L. cyanellus*) (Werner and Hall 1979; Wheeler and Allen 2003), few studies have addressed the trophic ecology of such a diverse assemblage of closely related fishes in such a spatially and temporally dynamic ecosystem. Specifically, my objectives were to use stomach content analyses and stable isotopes to determine the food habits of cohabiting sunfishes in different macrohabitats within the ARB (Chapter 2), and assess the potential macrohabitat and physicochemical effects on centrarchid condition (Chapter 3).

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CHAPTER 2: RESOURCE PARTITIONING WITHIN THE CENTRARCHID ASSEMBLAGE OF THE ATCHAFALAYA RIVER BASIN, LOUISIANA AS EVIDENCED BY STOMACH CONTENT AND STABLE ISOTOPE ANALYSES

2.1 INTRODUCTION

The Atchafalaya River Basin (ARB) is a 5,000 km² floodplain ecosystem of the Atchafalaya River, the major distributary of the lower Mississippi River in south-central Louisiana that flows approximately 275 km from its source near Simmesport to its mouth near Morgan City on the Gulf of Mexico (Ruess 1988; Lambou 1990; Ford and Nyman 2011). This floodway system is characterized by an interconnected network of aquatic macrohabitats, including lakes, natural bayous, open pipeline canals and dead end canals, each of which is characterized by differences in aquatic macrophyte coverage, physicochemistry, flow velocity, channel width, and depth. This diversity of aquatic habitat types is reflected in the ARB fish assemblage, with approximately 100 species of lotic and lentic fishes reported from the Atchafalaya River and its floodplain (personal communication, W.E. Kelso, Louisiana State University). Of the numerous fishes that inhabit the ARB littoral zone, sunfishes (Centrarchidae) often dominate fish collections in both numbers and biomass.

The Centrarchidae includes 34 species of primarily freshwater fishes indigenous to North America (Near and Koppelman 2009). Several centrarchid species are prevalent throughout the southeastern United States (Douglas 1974; Desselle et al. 1978; Ross 2000), with 14 species reported from the Atchafalaya River Basin, including largemouth bass (*Micropterus salmoides*), crappies *Pomoxis* spp., and sunfishes *Lepomis* spp. (Gelwicks 1996; Rutherford et al. 2001). In addition to their central role as littoral invertivores and piscivores in the aquatic trophic structure of the ARB, several populations are economically important, with largemouth bass and crappie consistently reported as some of the most popular warmwater sportfishes in North America

(Chen et al. 2003; Cooke and Philipp 2009) and Louisiana (Kelso et al. 2001). As a dominant top-level predator, largemouth bass have the capability to significantly influence the structure of aquatic communities (Aday et al. 2009). In contrast, sunfishes typically occupy secondary consumer trophic levels, preying on zooplankton and macroinvertebrates and providing forage for a diversity of piscivorous vertebrates (Aday et al. 2009). Crappies are ecologically intermediate between sunfish and largemouth bass, with younger age classes ingesting invertebrates and older individuals becoming increasingly piscivorous (Aday et al. 2009).

Previous studies have indicated abundant populations of several centrarchids throughout the southeastern portion of the lower ARB, including largemouth bass, black crappie (*Pomoxis nigromaculatus*), and warmouth (*Lepomis gulosus*), bluegill (*L. macrochirus*), longear (*L. megalotis*), redear (*L. microlophus*) and redspotted (*L. miniatus*) sunfishes (Gelwicks 1996; Rutherford et al. 2001), with occasional collections of spotted bass (*Micropterus punctulatus*), white crappie (*P. annularis*), orangespotted (*L. humilis*) and green (*L. cyanellus*) sunfishes, and flier (*Centrarchus macropterus*). Although the habitat relationships of these species have been studied (e.g., Rutherford et al. 2001; Troutman et al. 2007), little research to date has addressed the trophic relationships and feeding ecologies of these abundant sunfishes, or the potential influence of macrohabitat characteristics on fish trophic relationships.

Understanding the feeding ecology of a fish assemblage can provide insights into the population dynamics of the species involved, as well as how they partition resources and select habitats and prey. In addition, studies of trophic ecology provide information on predator-prey interactions, energy transfer through the aquatic food web, and potential competitive interactions (Swanson et al. 2003), which is particularly important given the continued invasion of alien macrophytes, invertebrates, and fishes in U.S. waters (Ross 1986; Helfman 2007; Rennó Braga

et al. 2012). Ultimately, foraging success plays an integral role in an individual's reproductive success and fitness (Fry et al. 1999), and trophic web interactions are important considerations for management and conservation activities that alter the habitat structure and species composition of freshwater fish assemblages. Importantly, understanding predator-prey relationships within a fish assemblage can detect limitations to fish growth and assist in the development of population assessment models (Liao et al. 2002).

Fisheries biologists have traditionally used stomach content analyses to investigate predator-prey interactions (Hyslop 1980). These analyses provide detailed insight into habitat selection and foraging activities within an assemblage (Paterson et al. 2006). However, due to inconsistent rates of digestion, consumed prey may only characterize a narrow time frame of feeding activities and habitat selection (Bootsma et al. 1996), and may not adequately describe overall feeding ecologies and prey preferences. Isotopes can also be used to provide additional data on feeding relationships among trophic levels and fish foraging histories (Fry et al. 1999; Vander Zanden and Rasmussen 2002) by determining the stable isotope composition of individual fish, which reflects diet composition over an extended period of time. Stable isotope accumulations of nitrogen and carbon within fish muscle tissue have slow turnover rates, and consequently can provide information regarding longer-term measures of diet and feeding behavior (Fry et al. 1999; Clarke et al. 2005). Stable isotope analysis can thus be used to complement stomach content analyses, with each method providing valuable ecological information concerning the foraging ecology of a species.

Isotope analysis of carbon and nitrogen present distinctly different measures of an individual's feeding ecology. Carbon isotope ($\delta^{13}\text{C}$) signatures are passed along successive trophic levels and exhibit an average enrichment of <1‰ between predator and prey (Vander

Zanden and Rasmussen 2001). Carbon isotopes originate in aquatic food webs from either autochthonous plant production or allochthonous inputs of terrestrial based plant production (Grey et al. 2000). Consequently, the $\delta^{13}\text{C}$ signatures of littoral ARB centrarchids will provide data on feeding history and principal foraging habitats (Paterson et al. 2006), e.g., pelagic-dwelling fish and invertebrate prey have carbon values that are more depleted in relation to individuals inhabiting the littoral zone (Clarke et al. 2005). Conversely, stable nitrogen isotope concentrations within fish tissue provide insight regarding an individual's trophic feeding level, as $\delta^{15}\text{N}$ isotopic signatures increase at the approximate rate of 3.4‰ per each successive trophic level, a process known as trophic fractionation (Post 2002).

The goal of my study is to provide information concerning the resource utilization of the littoral centrarchid assemblage within the ARB ecosystem. With respect to their abundance and diversity, centrarchids serve as a model pathway to investigate population-, assemblage-, and ecosystem-level processes (Aday et al. 2009). This study was designed from an ecosystem perspective to provide a basis for understanding the interactions within the centrarchid assemblage (i.e., competition and niche overlap), as well as the collective impact of these abundant predators on other components of the littoral zone trophic web in the ARB. Additionally, although the feeding ecology of centrarchids has been a well-documented throughout their range, there is little information available regarding the complexities of sunfish foraging ecology within a spatially and temporally dynamic floodplain ecosystem.

2.2 METHODS

2.2.1 Site Description

The ARB is the largest contiguous bottomland hardwood swamp in North America, and the floodplain is comprised by a complex network of natural bayous, dredged oil and gas canals, and shallow lakes (Ruess 1988, 2004; Perret et al. 2010). The hydrology of the ARB is controlled primarily by the Atchafalaya River (avg. discharge 5,179 m³/s; Iseri and Langbein 1974), the largest tributary of the Mississippi River that conveys 30% of the combined flows of the Mississippi and Red rivers to the Gulf of Mexico (Rutherford et al. 2001). The ARB system is approximately 275 km in length from north to south and averages 25-35 km in width (Figure 2.1; Ford and Nyman 2011). The ARB supports substantial fisheries production associated with annual overbank flooding of the Atchafalaya River (Bryan and Sabins 1979; Rutherford et al. 2001; Alford and Walker 2011). The flooding results in substantial seasonal fluctuations in water levels, which peak in the spring and decline throughout late summer (Lambou 1990; Fontenot et al. 1997). Inundation of the southern ARB from the annual water level rise (4-5 meters) results in considerable areas of floodplain habitat becoming submerged for weeks to months (Snedden et al. 1999). Conversely, during low water, permanent excavated canals, natural bayous, and floodplain lakes represent distinct habitat types differing in habitat structure and physicochemistry (Sabo et al. 1999a,b). Many of these habitats sustain dense littoral beds of hydrilla (*Hydrilla verticillata*), coontail (*Ceratophyllum demersum*), fanwort (*Cabomba caroliniana*), water hyacinth (*Eichhornia crassipes*) and common salvinia (*Salvinia minima*). In addition to macrophytes, littoral zone habitat complexity is enhanced by submerged roots and stumps of baldcypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*) and black willow (*Salix nigra*; Walley 2007).

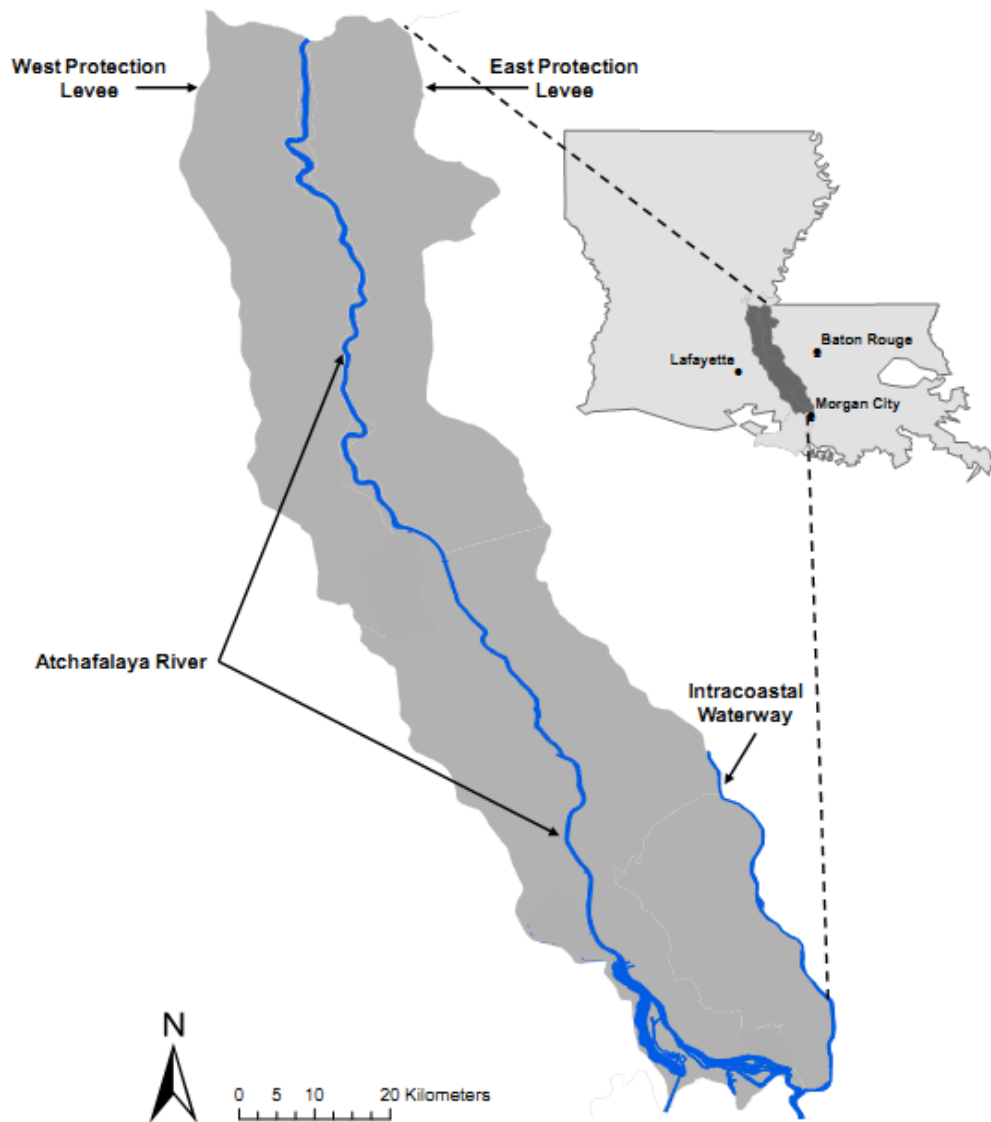


Figure 2.1: The Atchafalaya River Basin in south-central Louisiana.

Current water allocation practices and poor internal water movement have resulted in high rates of sediment deposition and poor water quality (Sabo et al. 1999a,b; Podey et al. 2006; Hupp et al. 2008; Kaller et al. 2001). Likewise, seasonal hypoxia may detrimentally affect fishes and zooplankton (Davidson et al. 1998; Rutherford et al. 2000), and can be exacerbated in dense beds of submerged and floating invasive aquatic plants (Colon-Gaud et al. 2004). Water quality in the floodway system is dependent on river stage and season, ranging from hypoxic dissolved

oxygen concentrations in backwater areas to oxygen-rich normoxic distributaries and lakes (Bryan and Sabins 1979; Hern et al. 1980; Rutherford et al. 2001; Kaller et al. 2011).

2.2.2 Sample Site Selection

Sampling was limited to a 900 km² area in the southeastern portion of the lower ARB bounded on the east by the Gulf Intracoastal Waterway (and accompanying guide levee) and on the west by the main stem of the Atchafalaya River. I randomly selected sites to represent the four defined macrohabitats: lakes, natural bayous, dead end excavated canals and open excavated canals. Sampling sites in these four macrohabitat sites were chosen in each of three regions in the southern ARB, including the Flat Lake, Murphy Lake and East Grand Lake regions (Figure 2.2). Sites representing each macrohabitat had similar characteristics, e.g., lakes had the largest channel widths, whereas pipeline canals exhibited an unimpeded flow in a straight direction for more than five kilometers. I sampled 12 sites in both 2011 and 2012, with 10 of the original 2011 sites resampled in 2012. Two additional sites were added in 2012 as the original sites were unreachable due to low water levels throughout the ARB.

2.2.3 Fish Collections

I sampled 24 fish collection sites from 1 August to 16 September 2011, and 28 May to 11 July 2012. These collection dates reflected water level conditions suitable for electrofishing, as catch per unit effort (CPUE) in the southeastern ARB declines when the river stage at the Butte La Rose gauge (USGS 07381515) exceeds 3 m (fishes move out of confined channels and onto the floodplain; Perret et al. 2010). Sampling was delayed in 2011 following an extensive flood event that kept the water stage between 3.34-7.03 m for the duration of the summer. Sampling was conducted between river stages 1.34-2.36 m in 2011 and 0.91-1.77 m in 2012 (Butte La Rose, USGS 07381515).

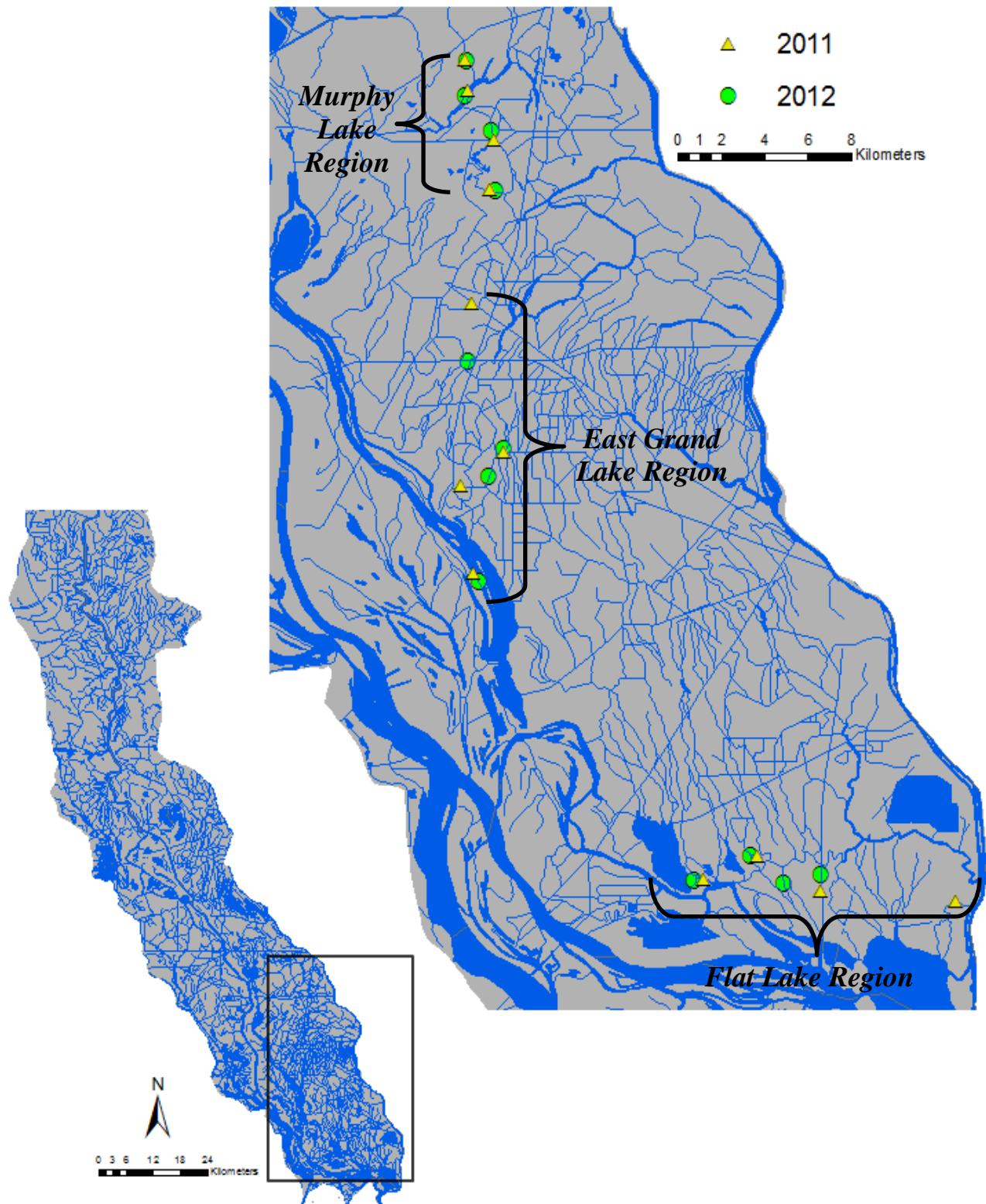


Figure 2.2: Fish collection sites sampled during 2011 (triangles, N=12) and 2012 (circles, N=12) in the lower Atchafalaya River Basin, Louisiana with sampled regions (text).

I collected fishes with standardized electrofishing techniques using a boat-mounted direct current (DC) electrofishing unit with a driver and two netters. Fishes were collected for a total of 1500 sec (on-time) between 0800 and 1200 hours from all microhabitats along 200 m of shoreline at each site. Common microhabitats within each transect included aquatic vegetation mats, live trees, deadfalls and stumps. All fish sampling was confined to mid-morning to reduce the potential for diel variability in diets within species. All adult centrarchids were netted, placed in an ice slurry, and transported to the School of Renewable Natural Resources, LSU AgCenter, Baton Rouge, Louisiana (LSU AgCenter IACUC A2011-16). Minimum sizes of retained individuals were >150 mm (*Micropterus* spp.), >125 mm (*Pomoxis* spp.), and >100 mm (*Lepomis* spp.).

2.2.4 Stomach Content Analysis

I recorded the total length (mm) and weight (g) for each individual, and then dissected the stomach and stored all prey items in vials filled with 10% buffered formalin solution (3.9% formaldehyde aqueous solution buffered with sodium phosphate). After fixation of stomach contents for five to seven days, samples were transferred to a 70% ethanol solution and placed in labeled 20 mL scintillation vials (Bowen 1996; Garvey and Chipps 2012). After identifying prey items to the lowest practical taxonomic level, I enumerated each prey item and determined wet weights (mg) with a Mettler-Toledo scale (model AB01 228050). Macroinvertebrates were identified to order or family (depending on the degree of prey degradation) with the aid of a dissecting microscope and keys contained in Merritt et al. (2008). Because of severe degradation, I categorized all consumed fish prey as unidentified fish. Plant material encountered in stomachs was not included in the diet analyses.

Centrarchid diets were quantitatively described by the frequency of occurrence (O_i), percent composition by number (N_i), percent composition by weight (W_i) and index of relative importance (IRI_i) of consumed prey items (Chipps and Garvey 2007). Frequency of occurrence yields a measure of how often a prey item occurs within species' diets. Percent composition by number represents the ratio of the number of individuals of a specific prey to the total number of prey that were consumed by each species. Percent composition by weight describes the ratio of prey weight for a specific resource to the total weight of all consumed prey. The index of relative importance is a multi-metric index based on the frequency of occurrence and percent composition by number and weight dietary indices. I used the following equations to calculate each of the diet indices (Chipps and Garvey 2007):

$$O_i = \frac{J_i}{P}$$

$$N_i = \frac{N_i}{\sum_{i=1}^Q N_i}$$

$$W_i = \frac{W_i}{\sum_{i=1}^Q W_i}$$

$$IRI_i = (\%N_i + \%W_i)(\%O_i)$$

where symbols represent prey items (subscript i); fish (subscript j); number of fish (J); number of fish with food in their stomachs (P); number of fish containing prey i (J_i); number in food category i (N_i); number of food types (Q) and weight of prey type i (W_i). IRI prey values for each species were weighted to represent a percentage out of 100 (referred to as IRI%) for between-species comparisons. Levin's standardized index based on percent composition by weight was used to quantify the diet breadth for each species (Hurlbert 1978; Krebs 1989):

$$B_i = \frac{1}{n-1} \left(\frac{1}{\sum_j p_{ij}^2} - 1 \right)$$

where p_{ij} is the proportion of diet of species i that is comprised of prey j , and n is the number of prey categories. A simplified version of Morisita's dietary overlap index based on percent composition by weight and number was used to quantify the degree of resource overlap by 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_{ki} are the proportions of the resource i used by species j and k , respectively, and n is the total number of prey categories.

To examine potential macrohabitat effects on centrarchid diets, I conducted three analyses. First, I used a detrended correspondence analysis on the IRI% values (Program R, vers. 2.15.1) to determine whether the multivariate food item data were better described with a linear or unimodal ordination, and to produce standardized linear combination based scores for later analyses. Next, based on these results, I used canonical correspondence analysis (CCA; ter Braak 1986, 1987) to compare IRI% values of fish species and macrohabitats, using both the number of fishes sampled and regions as covariates (Program R, vers. 2.15.1). I tested the statistical significance of diet-based fish species-macrohabitat associations with a permutation-based analysis of variance (500 permutations, Program R, vers. 2.15.1). Last, a generalized linear mixed model was used to compare dietary differences among species for region and macrohabitat within region based on the species scores of the linear combinations produced by the detrended correspondence analysis (PROC GLIMMIX, SAS vers. 9.3, SAS Institute, Inc., Cary, N.C.).

2.2.5 Stable Isotope Analysis

Tissue samples for ^{13}C and ^{15}N isotopic analyses were collected from randomly chosen fishes collected at the sample sites from 28 May to 11 July 2012. I prepared 20 total samples (N=140) for each of the seven centrarchid species, with five individuals each from lake, natural bayou, dead end canal, and open canal macrohabitats. For each fish, I obtained a 1x2x2 cm (depth, width, length) sample of muscle tissue (skin removed) from the dorsal region posterior to the dorsal fin and above the lateral line. All samples were dried for 48 h at 50°C in a gravity flow drying oven (Fisher Scientific Isotemp 750G). Samples were then ground into a fine homogenate with a mortar and pestle (Clarke et al. 2005). I placed 1 mg (+/- 0.2 mg) of each sample into labeled tin capsules (Costech 041061), placed the capsules in 96-well trays (Electron Microscopy Sciences/ 70437-1), and shipped the tissue to the University of California-Davis Stable Isotope Facility for analysis.

Tissue samples were analyzed with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Seron Ltd., Cheshire, UK) for nitrogen and carbon compositions. Results were reported as δ values and were expressed relative to the international standards of V-PDB (Vienna PeeDee Belemnite) and air for carbon and nitrogen. These standards have a precision of $\pm 0.3\text{‰}$ and $\pm 0.2\text{‰}$ for nitrogen and carbon values, respectively. The isotope ratio of sample tissue was compared with the isotope ratio of a reference material with known isotopic composition. Results are reported with delta notation:

$$\delta^{15}\text{N} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{reference}}} \right) - 1 \right] \times 1000$$

$$\delta^{13}\text{C} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{reference}}} \right) - 1 \right] \times 1000$$

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

In order to examine trophic relationships, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean isotopic signatures were plotted according to species and macrohabitat (Layman et al. 2007). Although this analysis did not calculate the exact trophic position of individual fish, trophic relationships were still evident for each species (Peterson and Fry 1987; Post 2002), and I analyzed the relative position of each species in the bi-plot to infer characteristics of food web structure and habitat use within the assemblage. I used multivariate analysis of variance (MANOVA; PROC GLM, SAS vers. 9.3), with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as dependent variables, to test for differences between the nitrogen and carbon signatures of the centrarchid assemblage, as well as within the designated macrohabitats. Statistically significant differences in nitrogen and carbon signatures among species are depicted with alphabetical designations.

2.3 RESULTS

2.3.1 Stomach Content Analysis

Of the 2,036 fish that I examined for stomach contents, 783 (38.5%) had empty stomachs or had ingested only plant material and were excluded from further analyses. Identifiable prey in stomachs of the remaining 1,253 individuals (61.5%) indicated substantial differences in prey selection among species within the centrarchid assemblage. Largemouth bass were primarily piscivorous, with fish comprising 75.1% (IRI%) of their diet (Table 2.1). Prey species that could be identified included sunfish (*Lepomis* spp.), shad (*Dorosoma* spp.), pirate perch (*Aphredoderus sayanus*) and shiners (*Notropis* spp.), although most ingested fish were heavily digested and unidentifiable to species (grouped as unidentified fish for subsequent analyses). Of the invertebrates ingested by largemouth bass, cambarid crayfishes (likely red swamp crayfish *Procambarus clarkii*; Bonvillain 2012) comprised 22.1% of the diet (Table 2.1), with smaller

percentages of freshwater shrimp (Palaemonidae, likely river shrimp *Macrobrachium ohione* and grass shrimp *Palaemonetes* spp.; Bauer and Delahoussaye 2008; Walls 2009) and belostomatid hemipterans (Table 2.4).

Table 2.1: Mean dietary data presented as frequency of occurrence (O%), percent composition by number and weight (N%; W%), index of relative importance (IRI) and index of relative importance percentage (IRI%; bolded) for largemouth bass, warmouth and black crappie in the ARB.

	<i>Largemouth Bass (N=220)</i>					<i>Warmouth (N=156)</i>					<i>Black Crappie (N=229)</i>				
	O%	N%	W%	IRI	IRI%	O%	N%	W%	IRI	IRI%	O%	N%	W%	IRI	IRI%
<i>Unid. Fish</i>	0.61	0.47	0.58	0.64	75.1	0.21	0.14	0.13	0.05	10.2	0.2	0.01	0.25	0.05	5.07
<i>Cambaridae</i>	0.3	0.22	0.41	0.19	22.1	0.4	0.22	0.78	0.4	75.5	0.03	0	0.05	0	0.18
<i>Palaemonidae</i>	0.1	0.23	0.01	0.02	2.6	0.11	0.16	0.01	0.02	3.68	0.73	0.5	0.56	0.78	75.9
<i>Amphipoda</i>	0	0	0	0	0	0.01	0.02	0	0	0.05	0.32	0.41	0.05	0.15	14.1
<i>Ephemeroptera</i>	0.02	0.02	0	0	0.05	0.08	0.06	0	0	0.85	0.38	0.03	0.06	0.03	3.01
<i>Hemiptera</i>	0.03	0.02	0	0	0.07	0.15	0.13	0.04	0.02	4.72	0.26	0.03	0.01	0.01	1.1
<i>Araneae</i>	0.02	0.01	0	0	0.03	0.03	0.02	0.02	0	0.25	0	0	0	0	0
<i>Odonata</i>	0.02	0.01	0	0	0.02	0.13	0.16	0.01	0.02	4.14	0.02	0	0.01	0	0.01
<i>Coleoptera</i>	0.01	0.01	0	0	0.01	0.04	0.03	0	0	0.25	0.01	0	0	0	0
<i>Hymenoptera</i>	0	0	0	0	0	0.01	0.01	0	0	0.03	0.01	0	0	0	0
<i>Plecoptera</i>	0	0.01	0	0	0	0.04	0.03	0	0	0.21	0.03	0	0	0	0.01
<i>Orthoptera</i>	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0
<i>Megaloptera</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Physidae</i>	0.01	0.01	0	0	0.01	0.01	0	0	0	0	0	0	0	0	0
<i>Diptera</i>	0	0	0	0	0	0.02	0.03	0	0	0.09	0.19	0.03	0	0.01	0.56
<i>Trichoptera</i>	0	0	0	0	0	0	0	0	0	0	0.03	0	0	0	0.01

Black crappie fed predominantly on palaemonid shrimp (75.9%) (Table 2.1), with amphipods, unidentified fish, ephemeropterans (mostly common burrowing mayflies, Ephemeraidae), and hemipterans (primarily water boatman, Corixidae) making up an additional 1.1 to 14.1% of the overall diet (Tables 2.1, 2.4). Warmouth diets also included unidentified fish (10.2%), but were dominated by invertebrates, particularly cambarid crayfishes (75.5%; Table 2.1). Several other invertebrates made up from 3.7% to 4.7% of the warmouth diet, including naucorid and belostomatid hemipterans, palaemonid shrimp, and larval and adult odonates (mostly Gomphidae, Libellulidae, and Coenagrionidae; Table 2.4).

Table 2.2: Mean dietary data presented as frequency of occurrence (O%), percent composition by number and weight (N%; W%), index of relative importance (IRI) and index of relative importance percentage (IRI%; bolded) for bluegill and redspotted sunfish in the ARB.

<i>Bluegill Sunfish (N=380)</i>						<i>Redspotted Sunfish (N=106)</i>				
	O%	N%	W%	IRI	IRI%	O%	N%	W%	IRI	IRI%
<i>Diptera</i>	0.55	0.53	0.14	0.37	69.92	0.22	0.14	0.02	0.04	15.52
<i>Ephemeroptera</i>	0.38	0.08	0.12	0.08	14.41	0.33	0.10	0.06	0.05	23.37
<i>Odonata</i>	0.08	0.01	0.13	0.01	1.97	0.08	0.01	0.03	0.003	1.27
<i>Coleoptera</i>	0.12	0.02	0.15	0.02	3.83	0.14	0.04	0.13	0.02	10.57
<i>Hymenoptera</i>	0.05	0.01	0.01	9E-04	0.18	0.09	0.02	0.08	0.01	3.99
<i>Hemiptera</i>	0.08	0.02	0.1	0.01	1.67	0.15	0.04	0.18	0.03	14.94
<i>Trichoptera</i>	0.14	0.04	0.01	0.01	1.26	0.11	0.03	0.004	0.003	1.47
<i>Plecoptera</i>	0.09	0.01	0.01	0.002	0.34	0.07	0.02	0.01	0.002	1.02
<i>Corbiculidae</i>	0.04	0.01	0.09	0.004	0.80	0.07	0.02	0.03	0.01	3.75
<i>Physidae</i>	0.03	0.003	0.02	6E-04	0.12	0.09	0.02	0.06	0.01	3.03
<i>Unionidae</i>	0	0	0	0	0	0	0	0	0	0
<i>Shell Fragments</i>	0	0	0	0	0	0	0	0	0	0
<i>Palaemonidae</i>	0.06	0.02	0.11	0.01	1.44	0.07	0.03	0.15	0.01	5.42
<i>Amphipoda</i>	0.16	0.08	0.02	0.02	2.98	0.14	0.11	0.01	0.02	7.25
<i>Unid. Fish</i>	0.02	0.002	0.08	0.002	0.35	0.04	0.01	0.15	0.01	2.68
<i>Fish Eggs</i>	0.02	0.17	0.01	0.004	0.71	0.03	0.41	0.01	0.01	5.33
<i>Other Prey</i>	0.03	0.01	0.01	1E-04	0.02	0.04	0.01	0.09	9E-04	0.41

Bluegill sunfish diets consisted predominantly of dipterans (69.92%), mostly midge larvae (family Chironomidae) and biting midge larvae (family Ceratopogonidae; Tables 2.2 and 2.4). Ephemeropterans represented 14.4% of bluegill diets, including minnow (Baetidae), squaregill (Caenidae), and common burrowing mayflies (Table 2.4). Several coleopterans were also commonly found in bluegill stomachs, including crawling water beetles (Haliplidae), predaceous diving beetles (Dytiscidae), whirligig beetles (Gyrinidae) and water scavenger beetles (Hydrophilidae), but these prey were not included in Table 2.4 because of their extensive deterioration in the stomachs of all of the centrarchid species. Numerous other invertebrates made up small percentages of the bluegill diet, including crustaceans (amphipods and palaemonid shrimp), naucorid Hemipterans, odonates (Gomphidae and Coenagrionidae), and trichopterans (mostly Hydropsychidae; Tables 2.2, 2.4).

Table 2.3: Mean dietary data presented as frequency of occurrence (O%), percent composition by number and weight (N%; W%), index of relative importance (IRI) and index of relative importance percentage (IRI%; bolded) for longear and redear sunfish in the ARB.

	<i>Longear Sunfish (N=94)</i>					<i>Redear Sunfish (N=68)</i>				
	O%	N%	W%	IRI	IRI%	O%	N%	W%	IRI	IRI%
<i>Diptera</i>	0.29	0.18	0.03	0.06	17.55	0.10	0.07	0.002	0.01	0.69
<i>Ephemeroptera</i>	0.43	0.14	0.28	0.18	50.41	0.32	0.03	0.06	0.03	2.88
<i>Odonata</i>	0.04	0.01	0.06	0.003	0.85	0.02	5E-04	5E-04	1E-05	0.001
<i>Coleoptera</i>	0.09	0.02	0.04	0.005	1.47	0.02	5E-04	0.001	3E-05	0.003
<i>Hymenoptera</i>	0	0	0	0	0	0.02	5E-04	1E-04	9E-06	9E-04
<i>Hemiptera</i>	0.03	0.01	0.03	0.001	0.33	0	0	0	0	0
<i>Trichoptera</i>	0.12	0.04	0.01	0.006	1.60	0.03	0.003	2E-04	9E-05	0.01
<i>Plecoptera</i>	0.11	0.03	0.01	0.004	1.26	0.02	5E-04	5E-05	8E-06	8E-04
<i>Corbiculidae</i>	0.16	0.04	0.15	0.031	8.55	0.68	0.44	0.47	0.61	59.45
<i>Physidae</i>	0.06	0.01	0.02	0.002	0.54	0.50	0.20	0.23	0.21	20.49
<i>Unionidae</i>	0	0	0	0	0	0.16	0.03	0.04	0.01	1.12
<i>Shell Fragments</i>	0	0	0	0	0	0.37	0.22	0.21	0.16	15.33
<i>Palaemonidae</i>	0.05	0.02	0.17	0.01	2.94	0.02	0.002	0.002	5E-05	0.01
<i>Amphipoda</i>	0.19	0.21	0.02	0.043	12.10	0.03	0.01	9E-05	1E-04	0.01
<i>Unid. Fish</i>	0.03	0.01	0.15	0.005	1.36	0	0	0	0	0
<i>Fish Eggs</i>	0.01	0.27	0.01	0.003	0.81	0	0	0	0	0
<i>Other Prey</i>	0.06	0.01	0.02	9E-04	0.25	0	0	0	0	0

Ephemeropterans were the most important prey item for redspotted sunfish (23.4%), and included baetid, caenid and ephemerid mayflies (Tables 2.2, 2.4). Dipterans (mostly chironomid and ceratopogonid larvae), hemipterans (mostly naucorids), and coleopterans (including halipids, dysticids, gyrinids and hydrophilids) all made up at least 15% of the diet, with lower percentages of crustaceans (amphipods and palaemonid shrimp). Redspotted sunfish also commonly consumed mollusks (the clam *Corbicula fluminea* and physid snails), fish eggs, and terrestrial insects, including ants (family Formicidae) and wasps (suborder Apocrita). Similar to redspotted sunfish, longear sunfish also preyed heavily on ephemeropterans (50.4%), primarily baetids, caenids and ephemerids (Tables 2.3, 2.4). Dipterans (mostly chironomids and ceratopogonids) made up 17.6% of the diet, which also included significant numbers of amphipods, *C. fluminea*, and palaemonid shrimp.

The redear sunfish diet consisted primarily of *C. fluminea*, which comprised 59.5% of their stomach contents (Tables 2.3, 2.4). Redear stomach contents also included physid snails, freshwater mussels (Unionidae), and unidentified shell fragments, which together represented an additional 37% of the diet of these trophically specialized invertivores.

Table 2.4: Prey families for selected macroinvertebrate orders found in bluegill (BG), redspotted (RSP), longear (LES), warmouth (WAR), and redear (RES) sunfishes, black crappie (BC), and largemouth bass (LMB) stomachs. Percentage of prey family of all consumed individuals within specific order is italicized and total prey numbers of respective families are in parentheses.

	BG	RSP	LES	WAR	RES	BC	LMB
<i>Order Ephemeroptera</i>							
<i>Baetidae</i>	34% (92)	17% (14)	25% (24)	25% (4)	3% (2)	24% (52)	0
<i>Caenidae</i>	44% (119)	49% (39)	38% (36)	13% (2)	5% (3)	13% (27)	0
<i>Ephemeridae</i>	13% (37)	20% (16)	31% (29)	37% (6)	87% (51)	55% (116)	100% (7)
<i>Other Ephemeroptera</i>	9%(24)	14% (11)	6% (6)	25% (4)	5% (3)	8% (17)	0
<i>Order Hemiptera</i>							
<i>Naucoridae</i>	68% (38)	78% (21)	100% (3)	42% (16)	0	2% (6)	10% (1)
<i>Corixidae</i>	28% (16)	15% (4)	0	11% (4)	0	98% (244)	20% (2)
<i>Belostomatidae</i>	4% (2)	7% (2)	0	47% (18)	0	0	70% (7)
<i>Order Odonata</i>							
<i>Gomphidae</i>	28% (11)	0	33% (2)	70% (33)	0	0	25% (1)
<i>Coenagrionidae</i>	47% (19)	75% (6)	67% (4)	26% (12)	50% (1)	33% (2)	50% (2)
<i>Libellulidae</i>	5% (2)	0	0	0	0	0	0
<i>Aeshnidae</i>	0	0	0	2% (1)	0	0	0
<i>Other Odonata</i>	20% (8)	25% (2)	0	2% (1)	50% (1)	67% (4)	25% (1)
<i>Order Diptera</i>							
<i>Chironomidae</i>	85% (1750)	89% (84)	91% (96)	86% (6)	83% (113)	79% (168)	0
<i>Ceratopogonidae</i>	9% (193)	8% (7)	9% (9)	0	17% (23)	20% (43)	0
<i>Sciomyzidae</i>	>1% (11)	0	0	0	0	0	0
<i>Stratiomyidae</i>	0	3% (3)	>1% (1)	14% (1)	0	1% (2)	0
<i>Other Diptera</i>	5% (95)	0	0	0	0	0	0

2.3.2 Niche Breadth and Diet Overlap

Values for Levin's standardized index of diet breadth range from near 0 to 1, with low values depicting specialist and higher values representing generalist diets. Overall diet breadth values indicated that largemouth bass, black crappie, warmouth and redear sunfish were

specialized foragers (Table 2.5). Conversely, bluegill, redspotted and longear sunfish diet breadth values were representative of generalist foraging tactics (Table 2.5). On the macrohabitat level, black crappie and warmouth diets were relatively more specialized in lakes, whereas values for bluegill, redspotted and longear were among the lowest in open canals (Table 2.5).

Table 2.5: Levin's standardized index values for diet breadth by percent composition of weight for largemouth bass (LMB), black crappie (BC), warmouth (WAR), bluegill (BG), redspotted (RSP), longear (LES), and redear (RES) sunfishes collected in dead end canal (DEC), lake, natural bayou (NB), open canal (OC) in the ARB, total number of prey taxa for each species (N).

	<i>LMB</i>	<i>BC</i>	<i>WAR</i>	<i>BG</i>	<i>RSP</i>	<i>LES</i>	<i>RES</i>
<i>DEC</i>	0.120	0.243	0.084	0.502	0.280	0.360	0.150
<i>Lake</i>	0.167	0.077	0.025	0.396	0.351	0.323	0.217
<i>NB</i>	0.086	0.187	0.071	0.384	0.337	0.306	0.234
<i>OC</i>	0.129	0.205	0.139	0.249	0.265	0.104	0.372
<i>Overall</i>	0.083	0.130	0.045	0.431	0.443	0.349	0.117
<i>N</i>	13	13	14	20	18	16	12

Table 2.6: Modified Morisita's diet overlap index values for percent composition by prey weight (W%) for largemouth bass (LMB), black crappie (BC), warmouth (WAR), bluegill (BG), redspotted (RSP), longear (LES), and redear (RES) sunfishes collected in the ARB.

W%	LMB	BC	WAR	BG	RSP	LES	RES
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	

Values for Morisita's diet overlap index range from 0 to 1 (complete similarity), and I considered index values greater than 0.5 to indicate high diet overlap, although this value represents a conservative interpretation (Matthews 1998). Dietary overlap based on both prey weights (Table 2.6) and prey numbers (Table 2.7) exceeded 0.5 for largemouth bass and

warmouth, as well as for bluegill-redspotted, bluegill-longear, and redspotted-longear sunfishes. Black crappie diet overlaps based on prey weights also exceeded 0.5 for redspotted and longear sunfishes, but not when overlaps were based on prey numbers. The diet of redear sunfish was substantially different than the other centrarchids, with no overlap values exceeding 0.38.

Table 2.7: Modified Morisita's diet overlap index values for percent composition by prey number (N%) for largemouth bass (LMB), black crappie (BC), warmouth (WAR), bluegill (BG), redspotted (RSP), longear (LES), and redear (RES) sunfishes collected in the ARB.

N%	LMB	BC	WAR	BG	RSP	LES	RES
LMB							
BC	0.32						
WAR	0.67	0.35					
BG	0.02	0.16	0.12				
RSP	0.05	0.22	0.15	0.60			
LES	0.05	0.36	0.17	0.70	0.90		
RES	0.01	0.02	0.02	0.15	0.11	0.17	

2.3.3 Diet Composition by Macrohabitat

Detrended correspondence analysis indicated that a linear model (PCA) was inappropriate for the diet data, and subsequent analyses by CCA and generalized linear mixed model analysis of scores were the most appropriate for the data. Results of the CCA revealed significant separation of diets among the seven sunfishes, given the co-variables region, macrohabitat and number of fishes ($F = 8.6516$, $P = 0.01$; Figure 2.3). Results of the generalized linear mixed model indicated that macrohabitat did not have an overall effect on diets ($F = 1.06$, $P = 0.3907$), however there were differences within individual species diets among the macrohabitats ($F = 2.52$, $P < 0.0001$). The scores indicated that bluegill in open canals consumed significantly more mayflies and less chironomids than in the other macrohabitats, whereas warmouth in dead end canals consumed substantially more odonates than the other macrohabitats.

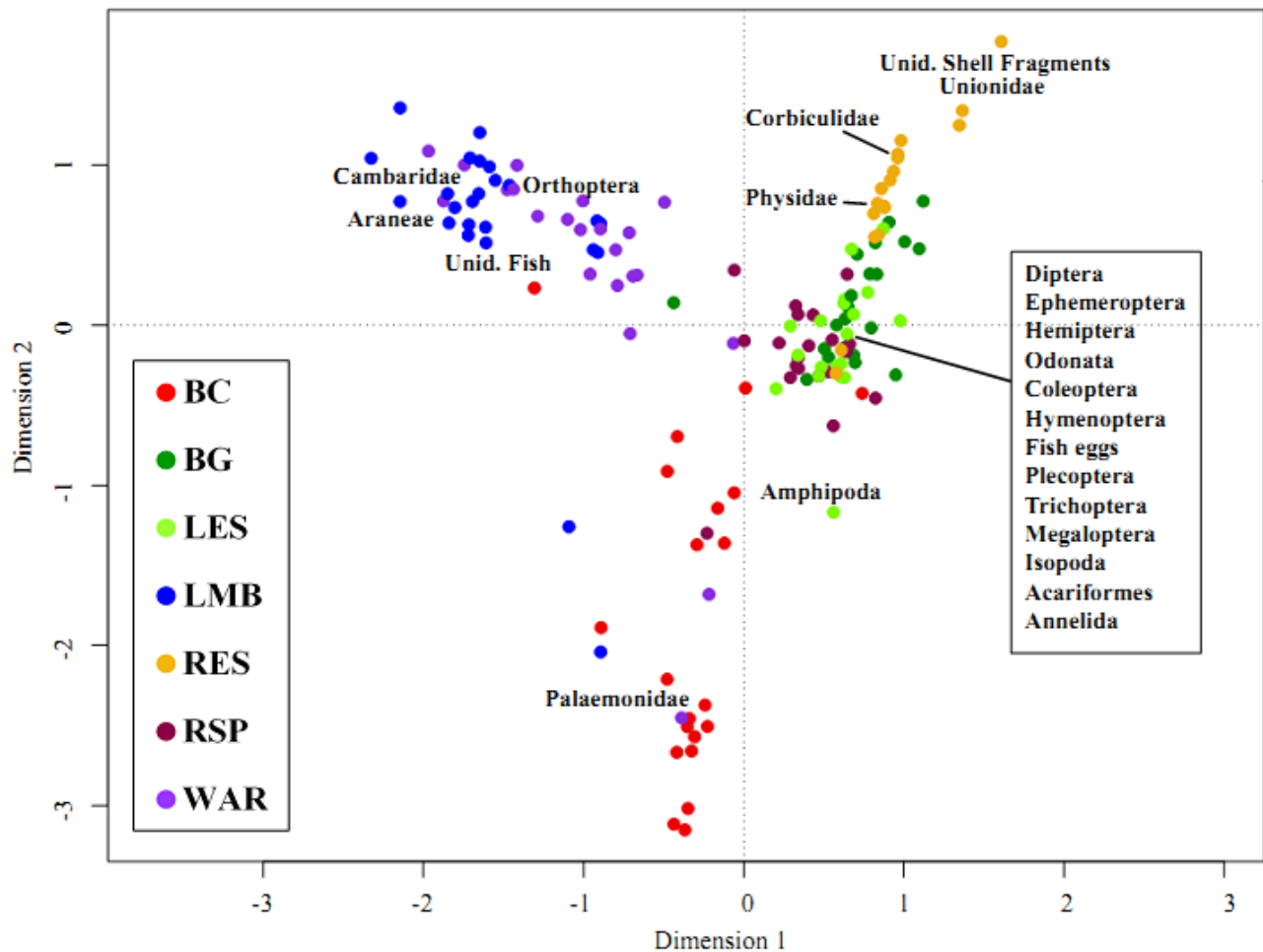


Figure 2.3: CCA depicting IRI% values for black crappie (BC), bluegill (BG), longear sunfish (LES), largemouth bass (LMB), redear sunfish (RES), redspotted sunfish (RSP) and warmouth (WAR), where the plotted prey are depicted in the ordination.

Examination of N%, W%, O%, IRI and IRI% values (Appendix A1-A7) corroborated results of the CCA, but also indicate several non-significant trends in the dataset. Largemouth bass and black crappie consumed more palaemonid prey in lakes relative to the other macrohabitats (Figure 2.4). Similarly, IRI values indicated consumption of fish by largemouth bass and warmouth was highest in natural bayous relative to lakes and the excavated canals. Despite the importance of dipterans in bluegill diets in all macrohabitats, IRI% values were at least 15% lower in open pipeline canals, with the opposite trend evident for ephemeropterans (Figure 2.5). Likewise, consumption of dipterans by redspotted, longear and redear sunfishes was

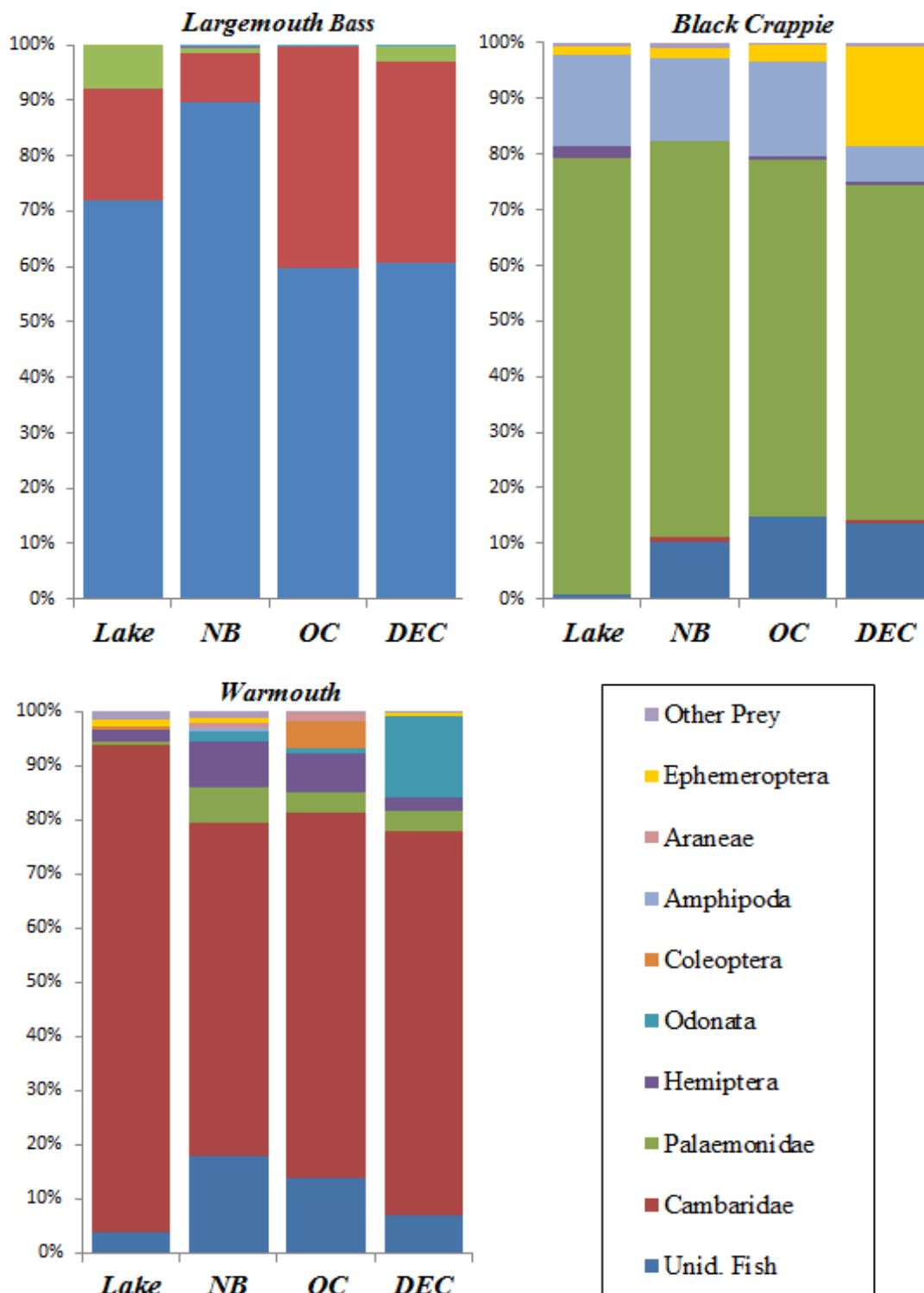


Figure 2.4: Dietary composition (IRI%) of Atchafalaya River Basin largemouth bass, black crappie and warmouth in lake, natural bayou (NB), open canal (OC) and dead-end canal (DEC) macrohabitats.

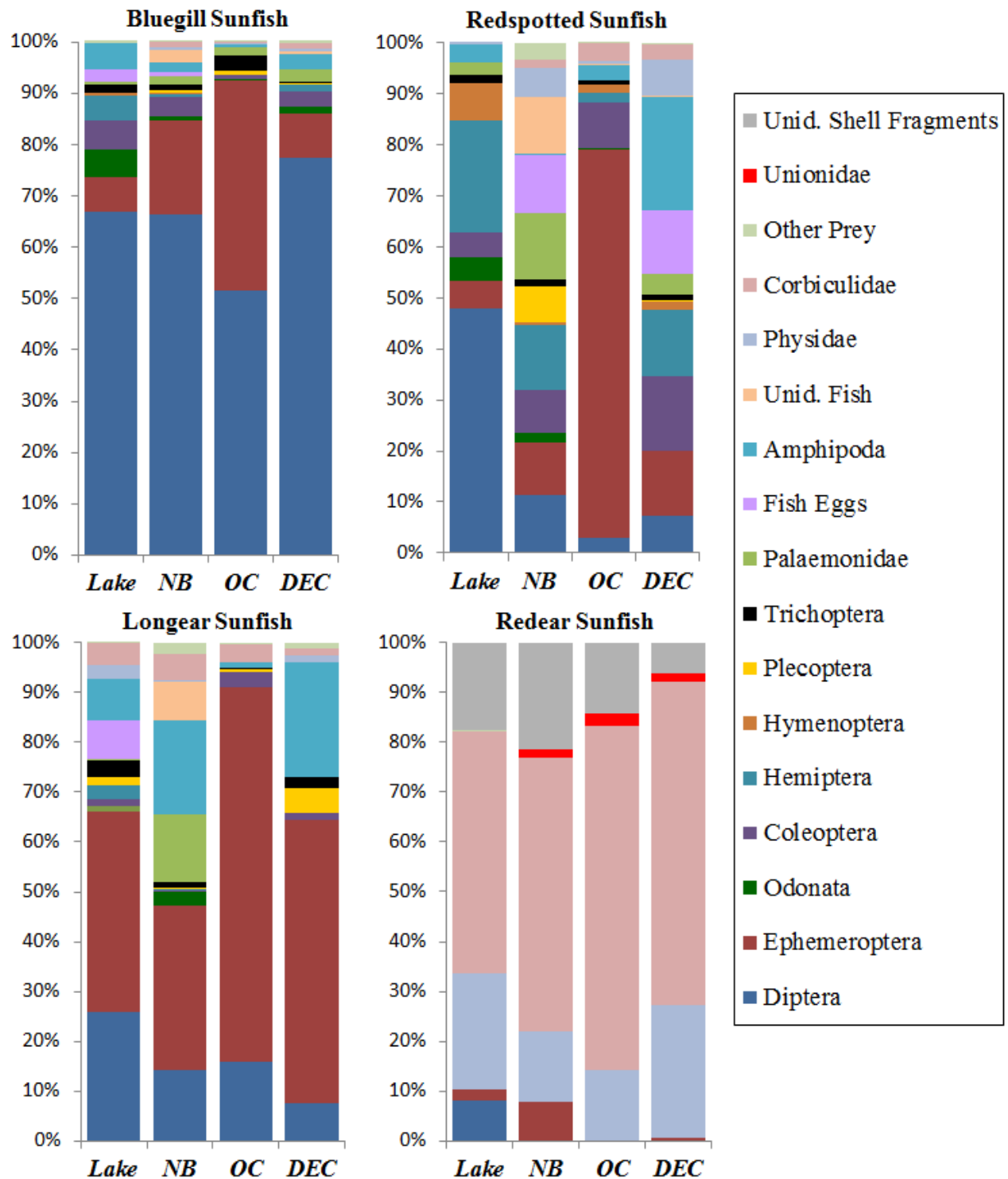


Figure 2.5: Dietary composition (IRI%) of Atchafalaya River Basin bluegill, longear, redspotted, and redear sunfishes in lake, natural bayou (NB), open canal (OC) and dead-end canal (DEC) macrohabitats.

highest in lakes, with ephemeropterans increasing in dietary importance in open pipeline canals for longear and redspotted sunfishes, the latter of which also exhibited increased consumption of hemipterans in lakes.

2.3.4 Stable Isotope Analysis

The bi-plot of mean $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ isotopes reflects the significantly different isotopic signatures of the seven ARB centrarchids ($P = 0.0007$; Figure 2.6). Mean isotope values were not different among macrohabitats ($P = 0.86$; Figure 2.7), although the plot suggests that the mean signature for open pipeline canals was more depleted for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ relative to the other macrohabitats. Mean $\delta^{15}\text{N}$ signatures were significantly different among species ($F = 24.29$, $P = 0.0001$), and the most enriched $\delta^{15}\text{N}$ signature was for largemouth bass (16.06‰), followed by black crappie, longear sunfish, redspotted sunfish, and bluegill, with the least enriched signatures exhibited by redear sunfish and warmouth (Table 2.8, Figure 2.8). Mean $\delta^{13}\text{C}$ signatures were also significantly different among species ($F = 2.76$, $P = 0.0147$) and indicated that the longear sunfish was the most enriched species (-28.38‰), followed by redspotted sunfish, largemouth bass, warmouth, and bluegill, with the most depleted species being redear sunfish and black crappie (Table 2.8; Figure 2.9).

Table 2.8: Mean stable isotope data for largemouth bass (LMB), black crappie (BC), warmouth (WAR), redear (RES), bluegill (BG), redspotted (RSP), and longear (LES) sunfishes collected in the Atchafalaya River Basin. Data presented for all individuals as well as by dead-end canal (DEC), lake, natural bayou (NB), and open canal (OC) macrohabitats.

	Overall (N=20)		DEC (N=5)		Lake (N=5)		NB (N=5)		OC (N=5)	
Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
LMB	-28.56	16.06	-28.69	15.90	-28.95	16.00	-27.99	16.08	-28.61	16.24
BC	-29.07	15.44	-29.04	15.55	-28.72	15.68	-29.09	15.92	-29.42	14.60
WAR	-28.67	14.38	-28.09	14.58	-28.65	14.48	-28.66	14.27	-29.31	14.20
RES	-29.32	14.17	-29.39	14.48	-28.78	14.17	-29.05	13.95	-30.08	14.08
BG	-28.94	14.66	-28.31	14.81	-29.1	14.90	-29.11	14.44	-29.26	14.51
RSP	-28.55	14.81	-28.51	14.93	-28.56	14.86	-28.22	14.80	-28.90	14.67
LES	-28.38	14.94	-28.43	15.02	-28.52	15.01	-27.98	14.87	-28.60	14.88

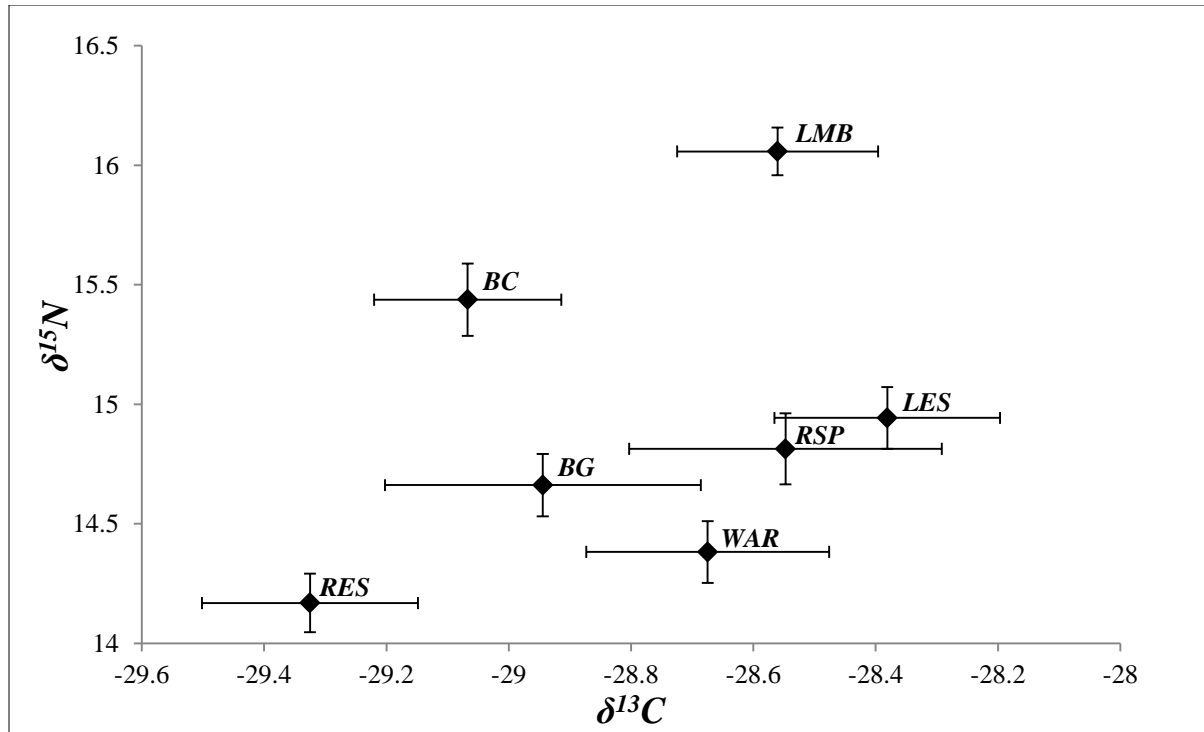


Figure 2.6: Overall carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope signatures for largemouth bass (LMB), black crappie (BC), longear sunfish (LES), redbottom sunfish (RSP), bluegill (BG), warmouth (WAR) and redear sunfish (RES) collected in the ARB (N=20 samples per species).

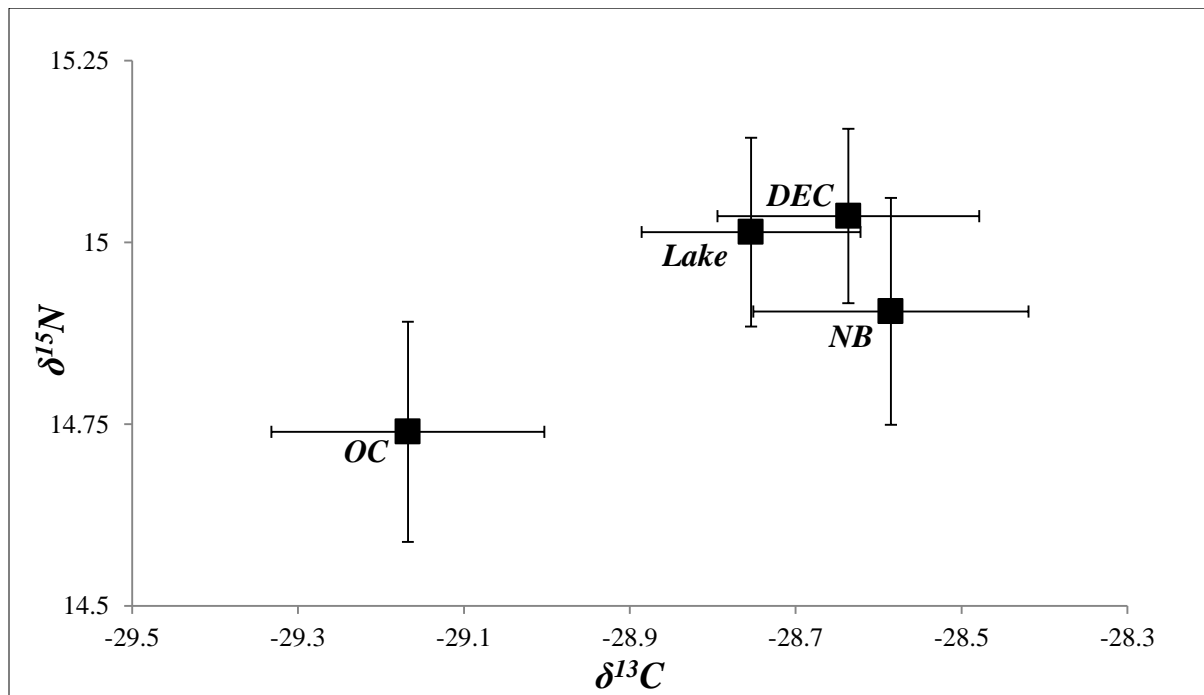


Figure 2.7: Overall carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) averages for fish sampled from open canals (OC), dead-end canals (DEC), natural bayous (NB), and lakes in the ARB (N=35 samples per macrohabitat).

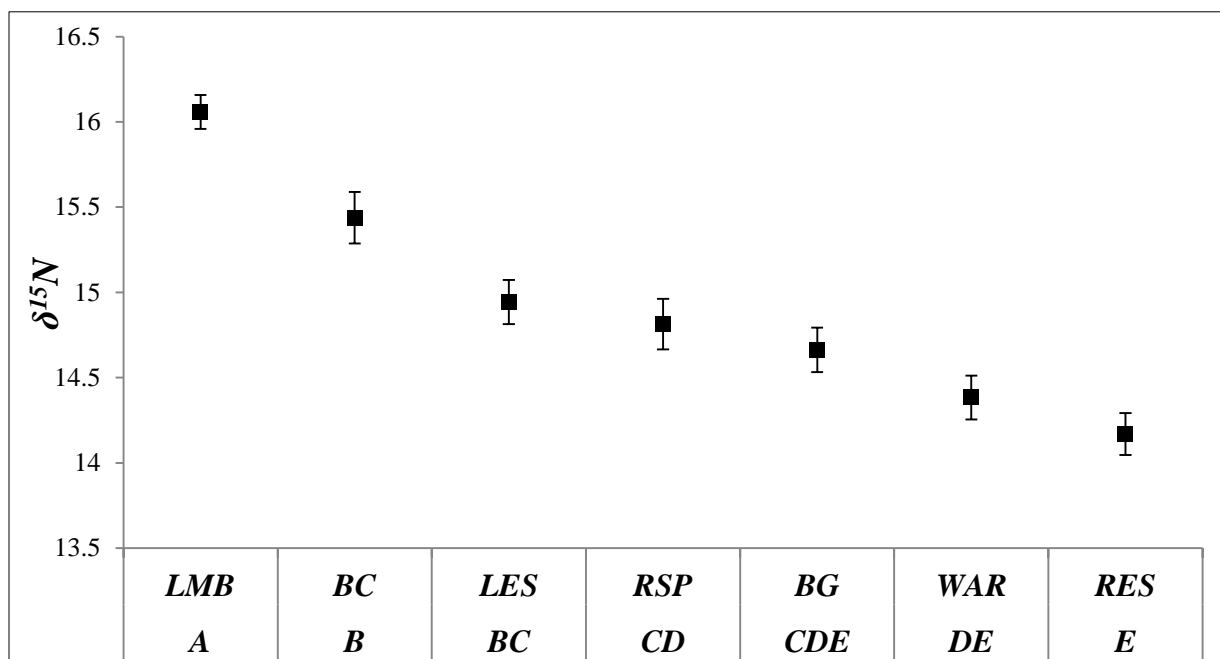


Figure 2.8: Mean nitrogen ($\delta^{15}\text{N}$) signatures and standard error with statistically significant differences depicted by alphabetical designations for largemouth bass (LMB), black crappie (BC), longear (LES), redspotted (RSP), bluegill (BG), warmouth (WAR), and redear (RES) sunfishes in the Atchafalaya River Basin.

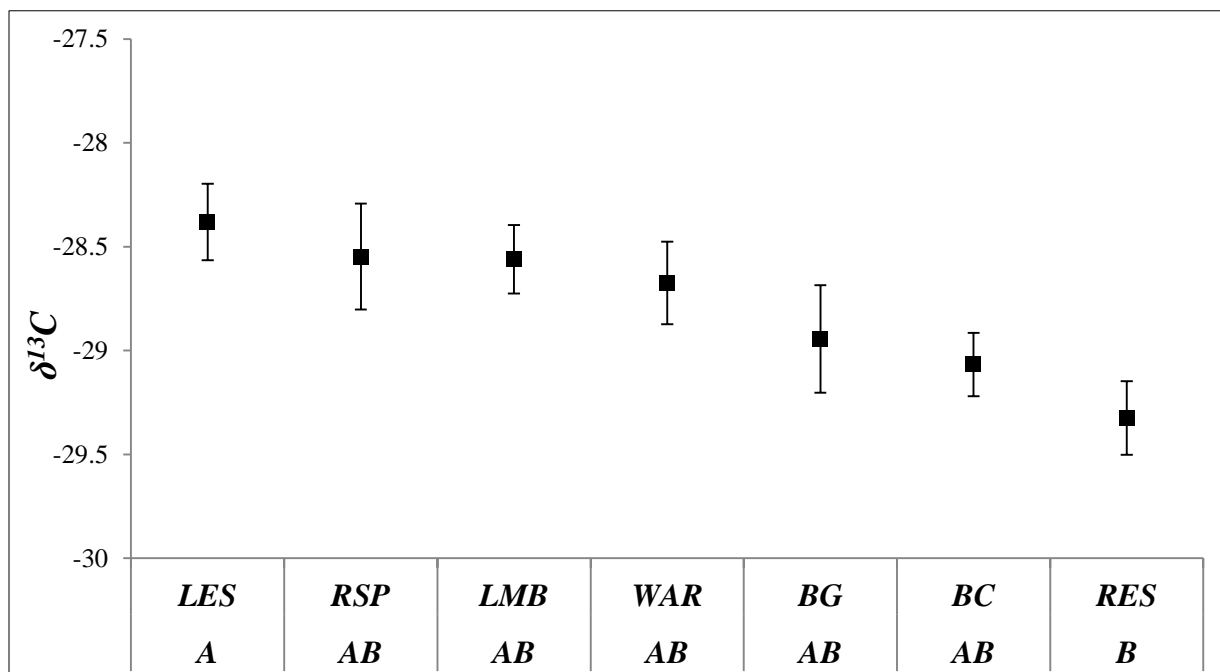


Figure 2.9: Mean carbon ($\delta^{13}\text{C}$) signatures and standard error with statistically significant differences depicted by alphabetical designations for largemouth bass (LMB), black crappie (BC), longear (LES), redspotted (RSP), bluegill (BG), warmouth (WAR), and redear (RES) sunfishes in the Atchafalaya River Basin.

Results of the MANOVA indicated statistically significant differences in ^{15}N and ^{13}C values across the centrarchid assemblage among macrohabitats (Wilks' Lambda). However, neither ^{15}N or ^{13}C values individually differed among the four macrohabitats ($F = 1.06$, $P = 0.3971$ and $F = 1.00$, $P = 0.4695$), although these values did differ among species ($F = 24.54$, $P < 0.0001$, and $F = 2.76$, $P = 0.0154$).

2.4 DISCUSSION

2.4.1 Resource Partitioning

Resource partitioning promotes coexistence between two or more species through segregation along a resource axis, ameliorating competition and facilitating coexistence by reducing interspecific interactions (Matthews 1998; Wheeler and Allen 2003). Ross (1986) reported that on average, there was more resource partitioning between fish species within genera relative to more distantly related taxa, with resource segregation along food, habitat, or foraging time axes (Ross 1986; Matthews 1998). Sympatric centrarchids have been documented to show evidence of trophic resource partitioning in other systems (George and Hadley 1979; Laughlin and Werner 1980; Wheeler and Allen 2003), with differences in feeding ecology influenced by competition, trophic specialization and prey availability (Bootsma et al. 1996). Within the ARB, stomach content analyses revealed distinct prey preferences among the cohabiting sunfishes, suggesting limited potential for interspecific competition within this diverse assemblage.

Although centrarchids generally prefer littoral zone habitat and exhibit considerable spatial overlap that could promote competitive interactions among species, these interactions can be strongly influenced by habitat structure and predation vulnerability (Mittelbach 1984, 1986; Osenberg et al. 1988). Lepomid sunfishes have been documented to minimize predation risk and

maximize foraging opportunities by alternating periods of movement through vegetated and non-vegetated habitat (Dewey and Jennings 1992). The littoral zone of the ARB often supports dense beds of floating, submerged, and emergent aquatic macrophytes, which serve as spawning and nursery habitat for fish populations in riverine backwaters (Holland and Huston 1985; Dewey and Jennings 1992). Together with submerged baldcypress stumps and roots, this underwater structural complexity may contribute to species coexistence by providing a range of microhabitats at both the individual and species level (Schoener 1974; Durrell 2000).

Micropterus spp. are often designated as the keystone species in aquatic ecosystems due to their predatory influence on prey habitat usage, community structure and trophic-level biomass (Power et al. 1996; Schindler et al. 1997; Jackson 2002; Miranda and Dibble 2002). Although generally considered to be piscivorous, largemouth bass prey upon an assortment of aquatic organisms (Heidinger 1975; Ross 2000; Warren 2009), and crayfish can comprise a large portion of the diet in selected environments (Schramm and Maceina 1986; Sammons and Maceina 2006). Largemouth bass was the only predominately piscivorous species among the seven centrarchids I analyzed, although crayfishes were often encountered in stomachs and likely accounted for the elevated diet overlaps with warmouth. *P. clarkii* is abundant within the southeastern region of the ARB (Bonvillain 2012), but fluctuates in availability to predators based on water levels during the annual flood-pulse. My study was conducted during the low-water season, when many *P. clarkii* had returned to burrows, and probably contributed to the high proportions of fish in the largemouth bass diet. It is likely that the dietary proportion of crayfish in largemouth bass increases during high water, but an increase in diet similarity with warmouth would likely not be indicative of increased competition, but rather both species exploiting an abundant resource.

Described as a solitary and opportunistic predator, warmouth exhibit a substantially larger gape size relative to other lepidomids and are able to capture larger prey such as crayfishes and small fishes (Ross 2000). In the ARB, warmouth periodically consumed fish but fed predominantly on red swamp crayfish (*P. clarkii*), with smaller dietary proportions of large belostomatid hemipterans and odonates, which is consistent with previous diet studies (Germann et al. 1975; Guillory 1978). In addition to the increased gape size, warmouth diet composition may be related to their use of submerged baldcypress logs and stumps rather than macrophytes as foraging habitat (personal observation). Warmouth habitat associations and food habits thus minimize trophic interactions with other ARB lepidomids, promoting coexistence of this trophically intermediate (between largemouth bass and the small-mouthed *Lepomis* spp.) species in the shallow-water centrarchid assemblage.

Black crappie are primarily midwater invertivores with a varied diet of insect larvae, amphipods, freshwater shrimp, and fish (Ellison 1984; Keast 1985b; Liao et al. 2002; Warren Jr. 2009). Benthic prey items function as a transitional food for crappie during the ontogenetic dietary shift from zooplankton to fish (Tuten et al. 2008), the latter of which increases in dietary importance when crappies attain a total length of 140-200 mm (Maceina et al. 1991; Muoneke et al. 1992; Mittelbach and Persson 1998). Piscivory in black crappie can depend on the availability of fish prey, as well as the relationship between predator and prey size (Ellison 1984; Hodgson et al. 1997), but can increase the potential for trophic competition with other piscivores in the aquatic community.

Interestingly, although numerous prey fishes are present in the ARB, the black crappie diet was composed almost exclusively of freshwater shrimp and amphipods. Amphidromous river shrimp (*Macrobrachium ohione*) may be particularly vulnerable to crappie, as they are

abundant in the ARB (Truesdale and Mermilliod 1979), their migrations peak in summer, and juveniles move only at night (Bauer and Delahoussaye 2008). Black crappie are considered to be among the most active nocturnal foragers within the centrarchid assemblage, with both crepuscular and nocturnal feeding peaks (Guy et al. 1992; Keast and Fox 1992; Shoup et al. 2004), and the similarity between predator and prey behavior may play an important role in the apportionment of resources between crappie and the other ARB centrarchids. Ager (1976) also reported that mysid shrimp comprised a majority of the diet for black crappie from Lake Okeechobee, Florida, and their higher caloric value may provide superior forage and improved growth of black crappie in these systems (Tuten et al. 2008). Both mysid and palaemonid shrimp have a higher energy density than other macroinvertebrate prey such as ephemeropterans and dipterans (Cummins and Wuycheck 1971), and the increased net energy gains may explain the apparent preference for shrimp by black crappie in Florida and the ARB. The apparent nocturnal foraging behavior of black crappie may explain its predation on the common burrowing mayfly, as these nymphs also exhibit nocturnal movements (Leonard and Leonard 1962; Knopp and Cormier 1997).

The lack of piscivory in black crappie diets may result from potential competitive interactions with larger piscivores such as largemouth bass, bowfin (*Amia calva*), gars (*Lepisosteus* spp.) and catfishes (*Ictalurus* and *Ameiurus* spp.), all of which consume significant quantities of fish in the ARB (C. P. Bonvillain, unpublished data). The low degree of dietary overlap with other centrarchids reflects substantial partitioning of the invertebrate forage base, but whether it is an active process related to interspecific interactions, or a more passive process related to habitat use and the vulnerability of palaemonid shrimp to foraging crappie, is unknown. Low trophic overlap with cohabiting fishes can result in increased individual growth

in black crappie populations, as well as increased recruitment through a reduction in predation risk (Frankiewicz 1996; Post 1996; Tuten et al. 2008).

Bluegill sunfish have been described as insectivorous, planktivorous, omnivorous and piscivorous, and likely epitomize a generalist feeding strategy (Spotte 2007). Although they can exploit zooplankton prey in pelagic habitats, they feed primarily on vegetation-dwelling macroinvertebrates in littoral zones, and less so on benthic-dwelling taxa (Schramm and Jirka 1989; Dewey et al. 1997). The majority of bluegill stomachs in the ARB contained aquatic plant material, which was likely ingested along with the dipteran larvae, ephemeropterans, odonates, coleopterans, hemipterans and amphipods that comprised the majority of their diet. Bluegills are behaviorally flexible predators, and can alter their foraging behavior in response to variations in habitat structure, prey abundance, interspecific and intraspecific competition, and predation risk (Mittelbach 1981, 1984; Werner and Hall 1988; Mittelbach and Osenberg 1993; Shoup et al. 2003), often remaining in aquatic vegetation beds rather than foraging in energetically more profitable open water when piscivores are present (Dewey et al. 1997).

Redspotted sunfish proved to be even more of a generalist invertivore than bluegill in the ARB. Redspotted sunfish generally forage in aquatic macrophyte beds and bottom sediments (Warren 2009), feeding on a variety of adult and larval aquatic insects in both freshwater streams and oligohaline coastal environments (Desselle et al. 1978; Robison and Buchanan 1984). In the ARB, redspotted sunfish were the only centrarchid that lacked a specific prey item exhibiting an index of relative importance value greater than 50%. Interestingly, consumption of naucorid hemipterans by redspotted sunfish may have reflected interspecific differences in foraging ability (mouth gape) or foraging habitat preferences, and contrasted with warmouth, which ingested mostly belostomatids, and black crappie, which apparently focused on corixids. Although

elevated indices of dietary overlap existed between redspotted, bluegill, and longear sunfishes, the potential for significant trophic competition would seem to be minimal for redspotted sunfish given its diverse diet.

Longear sunfish have been described primarily as benthic predators, consuming a variety of larval midges, mayflies and caddisflies in other systems (Cooner and Bayne 1982; Shoup and Hill 1997; Warren 2009). Despite the prevalence of chironomids throughout the ARB ecosystem, longear sunfish foraged primarily on ephemeropterans, which limited diet overlap with the other cohabiting sunfishes. Mayflies may be more available to invertivorous fishes in southern ecosystems relative to coldwater streams (Berner and Pescador 1988), as higher water temperatures can lengthen development times and result in consistent rates of emergence throughout the year (Berner and Pescador 1988). Longear sunfish often inhabit areas of higher current velocity (Gunning and Sutkus 1990, Schaefer et al. 1999), which are also preferred by many mayfly taxa (Ciborowski 1983), exhibiting a potential relationship the availability of mayflies and the habitat preference of foraging longear sunfish.

Redear sunfish are among the most trophically specialized centrarchids, employing a unique jaw musculature to consume hard-bodied prey such as snails and small bivalves (Wainwright and Lauder 1992; Huckins 1997), although they will also consume dipterans and ephemeropterans (Desselle et al. 1978; Huckins 1997; VanderKooy et al. 2000). They are principally benthic feeders, and their almost exclusive diet of corbiculid clams and physid snails resulted in virtually no diet overlap with any of the co-occurring centrarchid species in the ARB. Redear sunfish also tend to inhabit deeper water than the other sunfishes, and the combination of habitat preference and diet specificity results in almost complete trophic partitioning between this species and other littoral sunfishes in this system.

The compromise between foraging profitability and predator avoidance largely defines lepomid habitat and resource utilization. Structural complexity varied substantially within the ARB macrohabitats that I sampled, ranging from dense macrophyte beds to moderately dense submerged woody debris accumulations and inundated cypress trees. Increased habitat complexity in macrophyte beds likely resulted in high macroinvertebrate abundances for foraging sunfishes (Colon-Gaud 2003), although the extremely high stem densities within hydrilla beds may have reduced foraging efficiency (Spotte 2007). Aquatic macrophytes support abundant and diverse macroinvertebrate communities, allowing for interspecific dietary specialization in resident fish assemblages (Keast 1968; Keast 1985a,b; Bryan and Scarnecchia 1992; Dewey et al. 1997). While providing a predation refuge for lepomid sunfishes, particularly juveniles (Weaver 1997), high invertebrate prey abundances in vegetation beds can also concentrate forage fish for piscivores such as largemouth bass, with predation efficiency dependent on stem density (Savino and Stein 1989).

Taken as a whole, results of my study indicate a lack of competition within the centrarchid assemblage in the ARB, despite moderately high values of dietary overlap between several cohabiting species. Elevated levels of dietary overlap can be indicative of competition if resources are limiting, but can also reflect abundant resources that are simply being exploited by a number of consumers (Matthews 1998). I believe the elevated overlap values between bluegill, longear and redspotted sunfishes are indicative of abundant prey and do not reflect strong competition among these species. Although comparable macroinvertebrate taxa were consumed, the dietary proportions of specific prey items varied among species, with much of the similarity related to the predominance of dipteran larvae in all three diets. Chironomids are often the most abundant macroinvertebrate taxa within most freshwater ecosystems (Courtney and Merritt

2008) and are ubiquitous and abundant in ARB macrophyte beds (Colon-Gaud 2003).

Chironomid-based diet similarity was also reported between cohabiting darters in two Ohio streams (Hlohowskyj and White 1983), and was also interpreted by the authors as multi-species exploitation of an abundant resource rather than evidence of trophic competition. Finally, the size of the ARB, the diversity of macro- and micro-habitat types, and the seasonally dynamic water levels associated with this flood-pulse ecosystem may also facilitate resource partitioning and minimize competition among cohabiting littoral fishes. Whereas stream-dwelling centrarchid assemblages may experience an increased probability of competitive interactions due to an imbalance between available prey and fish density (Matthews 1998), ARB sunfishes have a number of spatial and temporal axes on which to partition prey resources, and my data suggest that these seven species effectively minimize trophic interactions by exploiting different prey taxa, and for some species, different foraging habitats.

2.4.2 Macrohabitat Diet Trends

Results of the canonical correspondence analysis and subsequent general linear models indicated that the diets of centrarchid species were not significantly different among the selected macrohabitats. Despite variations in physicochemical factors and habitat structure within macrohabitat types, centrarchid prey selection was relatively consistent overall throughout the lower ARB. This consistency may be related to the hydrologic connectivity of all macrohabitats for extended periods (weeks to months) during the annual flood pulse (Alford and Walker 2011), i.e., the flood pulse may not only increase productivity within the ARB floodplain system (Junk et al. 1989; Bayley 1995), but may also result in similar fish encounter rates with prey items during high water stages, and more homogenous distributions of invertebrate and fish prey organisms when floodwaters recede.

Despite the overall lack of significant differences in prey consumption of centrarchids among macrohabitats, dietary indices revealed subtle trends in centrarchid prey consumption among macrohabitats. Bluegill consumed fewer chironomids and more ephemeropterans in open canals relative to other macrohabitats, although whether this was related to differences in habitat structure or anthropogenic disturbance (much higher boat traffic dislodging burrowing ephemeropterans) in these excavated canals is unknown. Overall dipteran consumption by bluegill, longear, redspotted and redear sunfish was generally among the highest in lacustrine environments, suggesting that lakes may provide the most suitable habitats for chironomid production. Largemouth bass consumed more crayfish in dead end and open canals, which may have been a function of increased cambarid abundance in these canals or reduced availability of forage fish. The diet of black crappie was almost exclusively made up of palaemonid shrimp in lakes, suggesting that ARB lakes may be important migratory habitats for these amphidromous crustaceans. Conversely, black crappie in dead-end canals consumed large numbers of burrowing mayflies, an important prey item in other systems (Siefert 1969), suggesting these canals provided more suitable substrates for ephemerids (Rasmussen 1988), and less so for palaemonids.

2.4.3 Trophic Relationships and Foraging Habitat

Stable isotope analysis has been used to assess resource partitioning in centrarchid assemblages of other systems (Paterson et al. 2006). Mean nitrogen signatures provide insight regarding a species foraging history and trophic position within the aquatic community (Post 2002), as predators become enriched in ^{15}N by 3.4‰ per trophic level (Minagawa and Wada 1984; Peterson and Fry 1987; Vander Zanden and Rasmussen 1999). Although examination of exact trophic position is necessary for comparisons across multiple ecosystems due to variability

at the base of the food web (Post 2002), my study focused solely on trophic relationships within the Atchafalaya River Basin and foraging history between the seven selected species.

As the top carnivore, $\delta^{15}\text{N}$ values were highest in largemouth bass, indicating that they likely represent the uppermost trophic position within the sampled centrarchid assemblage. As the trophic intermediate between *Micropterus* spp. and *Lepomis* spp., both in size and foraging ecology (Aday et al. 2009), black crappie nitrogen signatures were lighter than largemouth bass, yet heavier than the five lepidomid species. Furthermore, the $\delta^{15}\text{N}$ values for bluegill, redspotted and longear sunfish were not significantly different, which reflected the elevated levels of dietary overlap among these species. Warmouth had a relatively low nitrogen signature, suggesting a more herbivorous diet for its primary prey, *P. clarkii*. Redear sunfish $\delta^{15}\text{N}$ values were lowest among the centrarchid assemblage, emphasizing its highly specialized foraging ecology and the phytoplankton/periphyton diets of corbiculid clams and physid snails.

Carbon signatures reflect foraging habitat selection (Vander Zanden and Rasmussen 1999) as $\delta^{13}\text{C}$ values are enriched $<1\%$ between predator and prey (Wada et al. 1993; France 1995; Vander Zanden and Rasmussen 2001; Paterson et al. 2006). Consequently, distinct carbon signatures of specific foraging habitats can be traced through the aquatic food web (Gearing 1991, Clarke et al. 2005). Carbon production occurs from two primary sources, with levels of enrichment differing between littoral and pelagic production (France 1995). Carbon signatures in littoral zones, reflecting the carbon cycling of detritus and benthic algae, yield less $\delta^{13}\text{C}$ fractionation than phytoplankton, the base of the pelagic food web (France 1995; Hecky and Hesslein 1995; Vander Zanden and Rasmussen 1999; Paterson et al. 2006). Consequently, the carbon signatures of species foraging on pelagic prey are more depleted, whereas the values of littoral consumers will be relatively enriched.

Carbon signatures for the centrarchid assemblage of the ARB were similar, indicating a potential overlap in foraging habitat and lack of foraging habitat segregation. Longear and redspotted sunfish exhibited the most enriched carbon signatures, indicating extensive foraging on littoral zone prey such as ephemeropterans, which are common in submerged aquatic vegetation (Colon-Gaud et al. 2004; Waltz and Burian 2008) and are carbon enriched relative to chironomids (Vander Zanden and Rasmussen 1999). Largemouth bass and warmouth $\delta^{13}\text{C}$ values were also indicative of littoral habitat selection, reflecting the consumption of fishes and *P. clarkii* that are typically associated with littoral macrophytes (Troutman et al. 2007; Walls 2009).

Bluegill carbon signatures were slightly more depleted than those of redspotted and longear sunfish, a result that may be explained by the larger proportion of chironomid larvae in bluegill diets. Chironomids are common in benthic habitats (Courtney and Merrit 2008) and exhibit more depleted $\delta^{13}\text{C}$ values than other insects such as ephemeropterans (Vander Zanden and Rasmussen 1999). Black crappie carbon signatures were slightly more depleted than all other species except redear sunfish, perhaps reflecting the dietary importance of pelagic, planktivorous freshwater shrimp (Bauer and Delahoussaye 2008). Interestingly, the $\delta^{13}\text{C}$ values of molluscivorous redear sunfish were the most depleted in the assemblage. Clams and snails reside throughout the benthic zone of many aquatic habitats throughout the ARB, feeding primarily on phytoplankton and periphyton, respectively, and these trophic relationships are reflected in the carbon composition of their primary centrarchid predator. Overall, the lack of habitat segregation suggested by the $\delta^{13}\text{C}$ signatures of the seven ARB centrarchids further emphasizes the importance of taxonomic partitioning of sunfish diets as a means to reduce the potential for interspecific competition.

2.4.4 Foraging Ecology Summary and Future Investigations

Within the centrarchid assemblage of the Atchafalaya River Basin, stomach content analyses revealed distinct prey preferences among the sympatric sunfishes, suggesting limited potential for interspecific competition. Analysis of carbon and nitrogen stable isotope signatures corroborated these results, indicating trophic specialization despite potential spatial overlap within the littoral zone and lack of habitat segregation. Future research should include the less abundant centrarchids, such as spotted bass, white crappie, flier, green and orangespotted sunfish, as their trophic relationships may provide further understanding of this diverse assemblage and its interaction with the dynamic floodplain ecosystem.

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CHAPTER 3: EFFECTS OF PHYSICOCHEMICAL PROPERTIES AND MACROHABITAT ON THE CONDITION (W_r) OF THE CENTRARCHID ASSEMBLAGE WITHIN THE ATCHAFALAYA RIVER BASIN, LOUISIANA

3.1 INTRODUCTION

Condition indices, which compare individual fish weights to the standard weight of that species for corresponding lengths (Murphy et al. 1991), have been widely used in fisheries management to monitor the health (physiological well-being, or robustness) of freshwater fish populations (Blackwell et al. 2000; Neumann et al. 2012). Condition indices reflect the cumulative effects of environmental variability on fish physiology, providing insights into potential problems with habitat suitability, prey availability and competition (Pope and Kruse 2007). Relative to fish in poor condition, fish with higher condition values can exhibit increased growth, enhanced reproduction, and increased survival (Blackwell et al. 2000; Neumann et al. 2012), which may result in increased individual fitness (Bolger and Connolly 1989). As a non-invasive technique, this method remains an important part of fish assessment protocols, and can provide a reliable index of chronic stress (Neumann et al. 2012).

Although historical assessments of fish health were often based on Fulton's (K) or LeCren's relative (K_n) condition factors (Blackwell et al. 2000), recent studies have used relative weight (W_r) as the standard measure of condition (Pope and Kruse 2007) for comparisons between fish of various lengths and from multiple populations (Wege and Anderson 1978). As an assessment metric, W_r has been shown to be related to fish growth in centrarchids (Wege and Anderson 1978; Guy and Willis 1995), as well as tissue energy content in piscivorous crappie, walleye and striped bass (Rose 1989; Brown and Murphy 1991; Neumann and Murphy 1991). Several studies have examined the impacts of environmental factors on W_r , and have shown fish condition to be positively related to water quality and habitat (DiCenzo et al. 1995) and prey

availability (Busacker et al. 1990; Flickinger and Bulow 1993; Ney 1993; Liao et al. 1995; Paukert and Rogers 2004).

The studies cited above indicate that assessments of condition can provide a relatively sensitive measure of environmental influences on fish foraging ecology and physiology. These assessments might be particularly interesting in an environmentally complex system such as the Atchafalaya River Basin (ARB) in south-central Louisiana, providing insight into the relative suitability of the various aquatic habitats that support ARB floodplain fishes and invertebrates. Littoral areas within these habitats are often dominated by centrarchid fishes, including abundant populations of largemouth bass (*Micropterus salmoides*), black crappie (*Pomoxis nigromaculatus*), warmouth (*Lepomis gulosus*), bluegill (*L. macrochirus*), redspotted (*L. miniatus*), longear (*L. megalotis*) and redear sunfish (*L. microlophus*), as well as rarer species such as spotted bass (*Micropterus punctulatus*), white crappie (*P. annularis*), orangespotted sunfish (*L. humilis*), and flier (*Centrarchus macropterus*). This relatively diverse and widely distributed centrarchid assemblage provides a unique opportunity to assess habitat effects on the overall health (Pope and Kruse 2007) of fishes inhabiting an environmentally complex ecosystem (Alford and Walker 2011; Kaller et al. 2011). In this study, I investigated physicochemical and macrohabitat effects on the condition of ARB centrarchids inhabiting lakes, natural bayous, open excavated canals and dead-end excavated canals. Each of these macrohabitats are characterized by differences in aquatic macrophyte coverage, water quality, habitat variables, water velocity, channel width and depth, all of which can potentially affect the physiology and foraging ecology of resident fishes, and may be reflected in habitat-specific condition indices.

3.2 METHODS

3.2.1 Site Description and Selection

As one of the largest bottomland hardwood swamps in North America, the Atchafalaya River Basin is comprised of an extensive network of natural bayous, shallow lakes and dredged oil and gas canals (Ruess 1988, 2004; Perret et al. 2010). A primary feature of this floodplain system is the Atchafalaya River (mean discharge 5,179 m³/s; Iseri and Langbein 1974), the largest tributary of the Mississippi River that carries 30% of the combined flows of the Mississippi and Red rivers (Rutherford et al. 2001) to the Gulf of Mexico. This floodway system stretches approximately 275 km from its source near Simmesport, Louisiana to the Gulf of Mexico, and averages 25-35 km in width (Figure 3.1; Ford and Nyman 2011).

The ARB supports substantial fisheries production associated with the annual flood pulse of the Atchafalaya River (Bryan and Sabins 1979; Rutherford et al. 2001; Alford and Walker 2011), with water levels typically rising 4-5 m in the spring and declining throughout late summer (Lambou 1990; Fontenot et al. 1997). The flood pulse inundates the southern ARB, resulting in extensive areas of submerged and connected floodplain habitat (Snedden et al. 1999). Conversely, canals, bayous and lakes represent distinct habitats during low water stages that differ in littoral habitat structure, ranging from beds of hydrilla (*Hydrilla verticillata*), coontail (*Ceratophyllum demersum*), fanwort (*Cabomba caroliniana*), water hyacinth (*Eichhornia crassipes*), common salvinia (*Salvinia minima*) and bulltongue (*Sagittaria lancifolia*) to brush piles and submerged large woody debris and root wads derived from baldcypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*) and black willow (*Salix nigra*).

There are several issues currently affecting aquatic habitat quality the ARB, including sedimentation, reduced floodplain circulation related to canal spoil banks, and poor water quality

(Sabo et al. 1999a,b; Podey et al. 2006; Hupp et al. 2008; Kaller et al. 2011). Seasonal hypoxia related to floodplain inundation and detrital decomposition can detrimentally affect nekton assemblages during elevated and declining river stages (Bryan and Sabins 1979; Hern et al. 1980; Rutherford et al. 2001; Kaller et al. 2011), with similar impacts caused by invasive aquatic plants (particularly floating taxa) during low water (Colon-Gaud et al. 2004).

3.2.2 Field Sampling

My study area encompassed a 900 km² area in the southeastern portion of the lower ARB bounded on the east by the Gulf Intracoastal Waterway (and accompanying guide levee) and on the west by the main stem of the Atchafalaya River (Figure 3.1). I randomly selected four sites to represent lake, natural bayou, dead-end canal and open canal habitats within Flat Lake, Murphy Lake and East Grand Lake regions of the lower ARB. Sites were selected such that macrohabitat characteristics were as consistent as possible among the regions, e.g., all lakes were shallow with moderate flow and water circulation, whereas pipeline canals had unimpeded straight line flow for more than five kilometers. I sampled 12 sites in both 2011 and 2012 (4 macrohabitats in each of 3 regions; Figure 3.1) with 2 of the original 12 sites moved in 2012 because of inaccessibility due to low water levels throughout the ARB.

3.2.3 Fish Collections

I conducted sampling efforts at 24 fish collection sites from 1 August to 16 September 2011, and 28 May to 11 July 2012 (Figure 3.1). These collection dates reflected water level conditions suitable for electrofishing, as catch per unit effort (CPUE) in the southeastern ARB declines when the river stage at the Butte La Rose gauge (USGS 07381515) exceeds 3 m (fishes move out of confined channels and onto the floodplain; Perret et al. 2010). Sampling was delayed in 2011 following an extensive flood event that kept the water stage between 3.34-7.03

m for the duration of the summer. Sampling was conducted between river stages 1.34-2.36 m in 2011 and 0.91-1.77 m in 2012 (Butte La Rose, USGS 07381515).

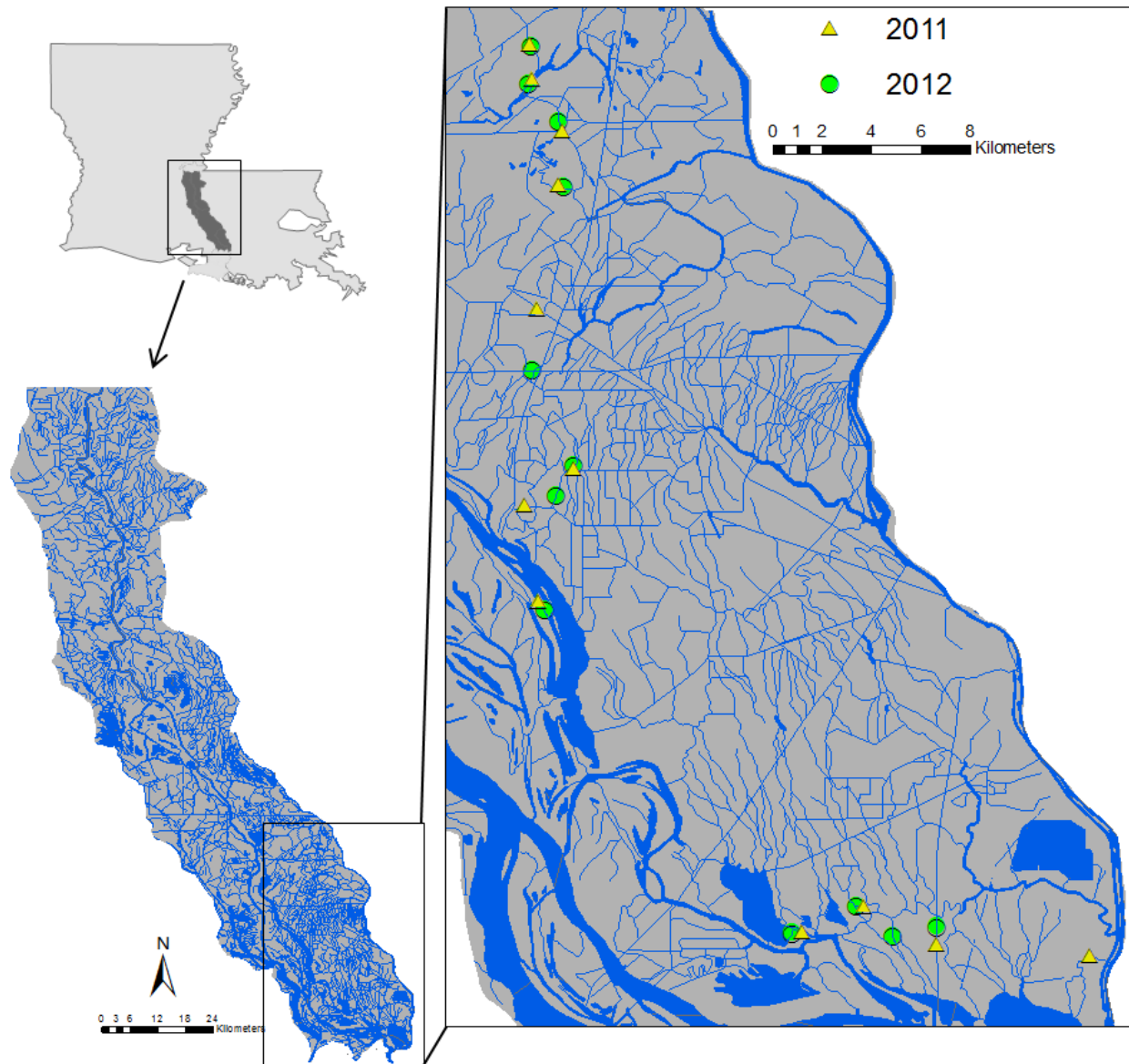


Figure 3.1: Location of the Atchafalaya River Basin and the fish collection sites sampled during 2011 (triangles, N=12) and 2012 (circles, N=12) in the Flat Lake, Murphy Lake and East Grand Lake regions of the lower Atchafalaya River Basin, Louisiana.

I collected fishes with standardized electrofishing techniques using a boat-mounted direct current (DC) electrofishing unit with a driver and two netters. Fishes were collected for a total of 1500 sec (on-time) between 0800 and 1200 hours from all microhabitats along 200 m of

shoreline at each site. Common microhabitats within each transect included aquatic vegetation mats, live trees, deadfalls and stumps. All fish sampling was confined to mid-morning to reduce the potential for diel variability in diets within species. All adult centrarchids were netted, placed in an ice slurry, and transported to the School of Renewable Natural Resources, LSU AgCenter, Baton Rouge, Louisiana (LSU AgCenter IACUC A2011-16). Minimum sizes of retained individuals were >150 mm (*Micropterus* spp.), >125 mm (*Pomoxis* spp.), and >80 mm (*Lepomis* spp.).

3.2.4 Water Quality and Habitat Measurements

Water quality data was taken at three points along the littoral zone sampling transect at each respective site. I used a hand held probe (YSI, Inc., Yellow Springs, OH) to record water quality data, including water temperature (°C), surface dissolved oxygen concentration (DO; mg/L), turbidity (NTU), pH and specific conductance (uhms/cm). Bottom dissolved oxygen concentration (DO; mg/L) was also recorded in order to determine dissolved oxygen differential (DODiff), which is calculated as the difference between surface and bottom DO. These measurements were taken 3 meters from the shoreline along the electrofishing transect at a depth of 0.5 m. I also measured current velocity (cm) at each transect with a handheld velocimeter, (Sontek Flowtracker Handheld ADV). Channel width (m) was estimated with a laser rangefinder (Bushnell Corporation, Overland Park, KS), and depth was recorded with a portable sonar and GPS unit (Eagle Electronics ®, Catoosa, OK).

Littoral zone habitat characteristics were evaluated with a series of 30 transects at locations oriented perpendicular to the shoreline. Any presence of aquatic vegetation or wood structure was identified and estimated as percent coverage. Aquatic vegetation was classified as submerged, emergent, or floating and identified to species. Woody debris was classified as live

trees, root wads, cypress knees, deadfalls and stumps. Means of estimated percent coverage for each transect were calculated for all fish collection sites and included in subsequent quantitative analyses.

3.2.5 Relative Weight (W_r) Comparisons

Total lengths (TL; mm) and weights (W; g) were recorded for all centrarchids collected from each of the sample locations. Relative weight (W_r) was calculated as:

$$W_r = (W/W_s) * 100,$$

with W representing the weight of an individual fish and W_s representing the standard weight for each species calculated from regressions based on the 75th percentile weights at a specific length (Murphy et al. 1990; Neumann et al. 2012). Standard weight slopes and intercepts have been published for five of the seven species that I studied (Table 3.1; Hillman 1982; Henson 1991; Neumann and Murphy 1991; Pope et al. 1995; Bister et al. 2000). I used the standard curve for bluegill to calculate W_r for redspotted and longear sunfish, as I was interested in differences in condition of these fishes among macrohabitats and associations with physicochemistry, and not on the actual W_r values themselves. I chose the bluegill standard weight equation because of similarities in size, robustness and morphometric characteristics between these species.

Table 3.1: Intercepts and slopes of standard weight (W_s) equations used to calculate relative weights of ARB centrarchids.

Species	Intercept (a')	Slope (b)	Min. TL (mm)
<i>Black Crappie</i>	-5.618	3.345	100
<i>Bluegill</i>	-5.374	3.316	80
<i>Largemouth Bass</i>	-5.528	3.273	150
<i>Redear Sunfish</i>	-4.968	3.119	70
<i>Warmouth</i>	-5.18	3.241	80

3.2.6 Statistical Analyses

I used analysis of variance (ANOVA) and marginal means with the Tukey-Kramer *post hoc* adjustment to compare the W_r values of the seven centrarchids among the four ARB macrohabitats (PROC GLM; SAS Institute Inc., Cary, N.C.). I then investigated macrohabitat physicochemistry with an exploratory principal components analysis, and concluded that individual site measurements were better suited for inclusion into the subsequent general linear model, as overall water quality trends were not apparent across all macrohabitat designations. The general linear model examined potential associations between the W_r of each centrarchid species (dependent variable) and physicochemical measurements at each site (PROC GLM; SAS Institute Inc., Cary, N.C.). Because of multicollinearity among the variables, the final model included surface dissolved oxygen, dissolved oxygen differential (surface minus bottom), water temperature, pH, turbidity, specific conductance, current velocity, and channel width, as well as the littoral zone coverage (%) of submerged (SAV), floating (FAV) and emergent (EAV) aquatic vegetation, as well as woody debris coverage.

3.3 RESULTS

3.3.1 Relative Weight (W_r) and Macrohabitat

I collected 2,036 centrarchid fishes during the summers of 2011 and 2012, including 407 largemouth bass, 304 black crappie, 330 warmouth, 563 bluegill, 162 redspotted, 198 longear and 72 redear sunfish. I calculated mean relative weights (W_r) for each individual (Table 3.2), and evaluated potential trends in relative weight with fish size by plotting individual W_r values by total length for each species (Appendix C).

Table 3.2: Relative weight (W_r) marginal means with standard errors for largemouth bass (LMB), black crappie (BC), warmouth (WAR), bluegill (BG), longear (LES), redspotted (RSP) and redear (RES) sunfishes sampled in respective macrohabitats in the ARB with corresponding sample sizes.

	DEC		Lake		NB		OC	
	N	Mean +- SE	N	Mean +- SE	N	Mean +- SE	N	Mean +- SE
LMB	71	117.07±0.87	134	116.75±0.92	121	117.07±0.79	81	116.13±0.96
BC	94	107.67±0.66	99	109.77±0.73	46	106.26±0.93	65	107.44±0.89
WAR	115	113.04±0.77	40	112.54±1.46	126	109.58±0.70	49	110.10±1.19
BG	173	112.00±0.70	167	109.68±0.79	125	111.61±0.81	98	109.03±0.78
LES	32	125.82±1.60	47	124.39±1.45	71	122.27±1.08	48	119.26±1.34
RSP	43	135.91±1.66	28	132.81±1.81	57	134.98±1.07	34	127.17±1.71
RES	24	107.61±1.52	27	108.08±1.76	10	107.12±1.68	11	107.52±1.37

Mean W_r for largemouth bass ($F_{3,403} = 0.20$, $P = 0.8960$) and redear sunfish ($F_{3,68} = 0.04$, $P = 0.9873$) were not significantly different among macrohabitats (Table 3.2; Figure 3.2). Similarly, although the bluegill W_r model was significant ($F_{3,559} = 3.27$, $P = 0.0210$), *post hoc* analysis indicated no differences in W_r among macrohabitats. In contrast, W_r differed among macrohabitats for black crappie ($F_{3,300} = 3.40$, $P = 0.0181$;), warmouth ($F_{3,326} = 4.16$, $P = 0.0066$), redspotted sunfish ($F_{3,158} = 6.36$, $P = 0.0004$), and longear sunfish ($F_{3,194} = 3.93$, $P = 0.0094$), although patterns were not consistent among the four species (Table 3.2; Figure 3.2). Black crappie and longear sunfish W_r values were highest in lakes, whereas warmouth W_r was highest in dead end canals, and redspotted sunfish W_r was highest in dead end canals and natural bayous (Figure 3.2).

3.3.2 Macrohabitat Characteristics

Physicochemical parameters recorded at the sample sites during 2011 and 2012 varied not only among macrohabitat types, but also among sites within macrohabitats (Tables 3.4, 3.5). Surface DO values were highest in lakes and lowest in open canals (although none of the values recorded at mid-morning during the two years were hypoxic), whereas DO differential was generally higher in dead end canals. Turbidity was lowest in dead end canals and highest in lakes, although the relative contributions of biogenic and abiogenic sources of turbidity were

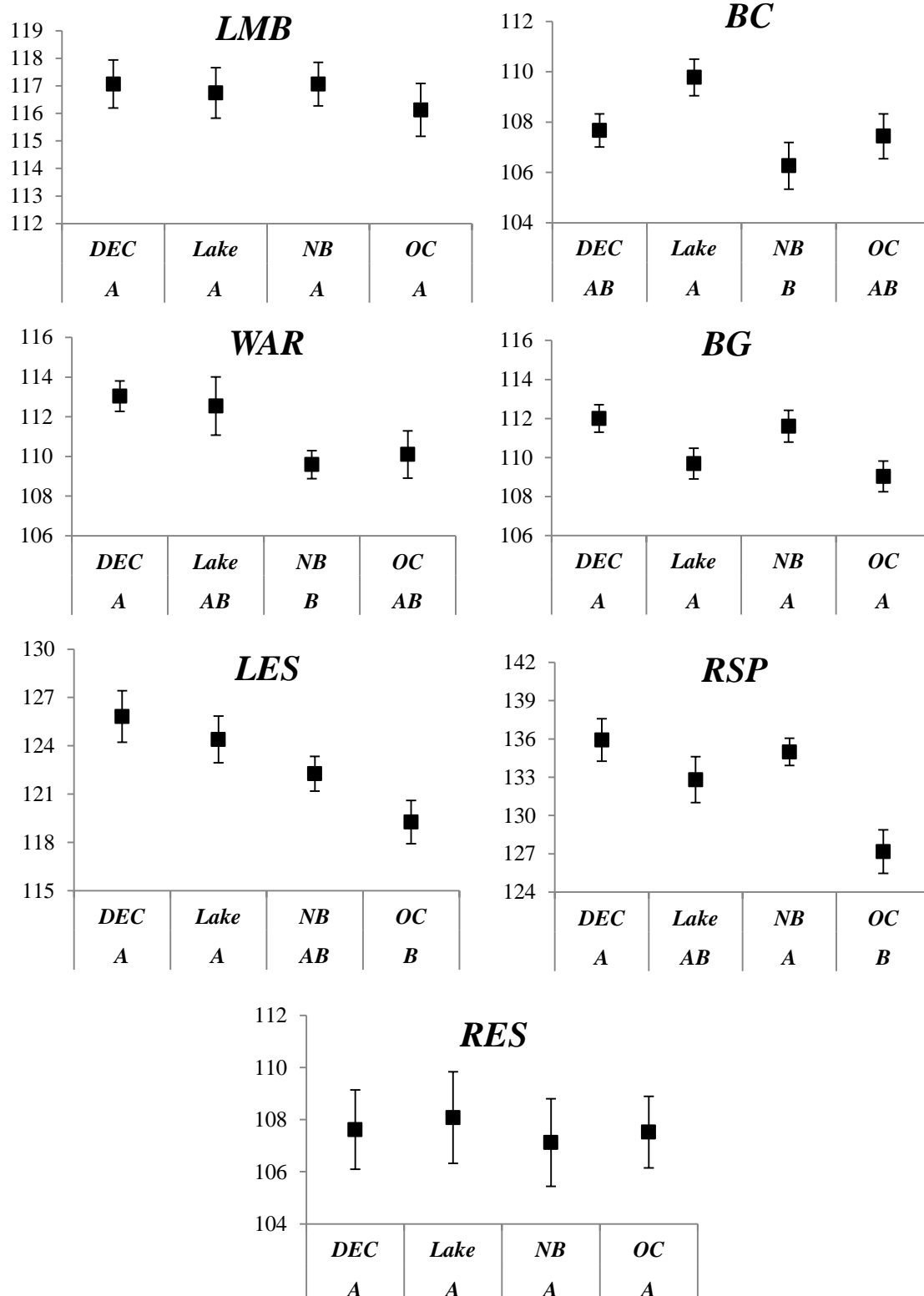


Figure 3.2: Centrarchid relative weight (W_r) marginal means by macrohabitat with standard error bars for largemouth bass (LMB), black crappie (BC), warmouth (WAR), bluegill (BG), longear (LES), redspotted (RSP) and redear sunfish (RES).

not assessed. Mean depth, water temperature, specific conductivity and pH were generally similar between all macrohabitats, although pH was relatively higher in lakes. Current velocity was non-existent in dead end canals, and was highest in open canals. Lakes had the greatest channel widths, with similar values among dead end canals, natural bayous and open canals. Lakes and open canals had the highest ratios of total habitat coverage, although mean values were generally consistent amongst all macrohabitats (Table 3.5). Open and dead end canals exhibited the highest percentage of submerged aquatic vegetation habitat. Macrophyte coverage was much lower in lakes, although between-year variability was very evident, e.g., submerged macrophyte coverage at lake site ML02 increased by a factor of nine between the two years (Table 3.5). The abundance of woody debris habitat was highest in lakes and natural bayous.

3.3.3 Relative Weight (W_r) and Physicochemical Properties

Of the physicochemical parameters in the model, DO differential was positively associated with W_r values of four species, including largemouth bass, black crappie, redspotted sunfish, and redear sunfish (Table 3.3). Specific conductance was positively associated with W_r of largemouth bass and warmouth, as was channel width, although both species along with redspotted sunfish exhibited lower W_r values with greater coverage of floating (largemouth bass) or submerged (warmouth) macrophytes. In contrast, emergent macrophyte coverage was positively related to W_r values of black crappie and longear sunfish, with black crappie W_r also showing a positive relationship with turbidity. Current velocity was positively and negatively associated with W_r of longear sunfish and redspotted sunfish, respectively, with redspotted sunfish W_r also related positively to pH, and negatively to water temperature and woody debris coverage (Table 3.3).

Table 3.3: Associations between largemouth bass (LMB), black crappie (BC), warmouth (WAR), redspotted (RSP), longear (LES) and redear (RES) sunfish relative weights and physicochemical variables at individual ARB fish collection sites. *P*-values, parameter estimates and *F* values are included in the table.

<i>Species</i>	<i>Physicochemical Property</i>	<i>Parameter</i>	<i>F</i>	<i>P- value</i>
LMB	DO Differential	1.761	7.09	0.0081
	Specific Conductance	53.97	4.24	0.0401
	Channel Width	0.026	6.16	0.0135
	FAV Coverage	-0.197	5.69	0.0175
BC	DO Differential	1.163	3.94	0.0480
	Turbidity	0.178	4.78	0.0295
	EAV Coverage	1.425	10.63	0.0012
WAR	Specific Conductance	71.81	5.31	0.0219
	Channel Width	0.044	12.05	0.0006
	SAV Coverage	-0.151	5.25	0.0227
RSP	DO Differential	2.256	4.61	0.0335
	Water Temperature	-3.052	6.05	0.0151
	pH	18.074	5.31	0.0226
	Current Velocity	113.054	4.22	0.0417
	SAV Coverage	-0.268	7.84	0.0058
	FAV Coverage	-0.442	5.59	0.0193
	Wood Coverage	-0.622	7.46	0.0071
LES	Current Velocity	-113.247	4.55	0.0343
	EAV Coverage	1.814	6.25	0.0133
RES	DO Differential	3.806	4.30	0.0425

3.4 DISCUSSION

3.4.1 Influence of Macrohabitat on Centrarchid Condition

In general, macrohabitat influences on W_r reflected macrohabitat trends in food habits of the seven ARB sunfishes (Chapter 2). Stomach content analysis revealed no difference in prey consumption among the different macrohabitats for largemouth bass, bluegill, or redear sunfish, and W_r analyses suggest that there is adequate forage in all of these macrohabitat types to maintain condition in these species. Black crappie exhibited the highest mean W_r values in lakes,

Table 3.4: Individual site water quality measurements and macrohabitat means (with standard errors) within the littoral zones of ARB sampling locations, including dead end canals (DEC), lakes, natural bayous (NB) and open canals (OC). Physicochemical parameters include surface (DO-S), bottom (DO-B) and differential (DOD) dissolved oxygen, water temperature (Tmp), pH, turbidity (Turb), specific conductance (SC), channel velocity (CV) and channel width (CW).

<i>Hab</i>	<i>Year</i>	<i>Site</i>	<i>Depth</i>	<i>DO-S</i>	<i>DO-B</i>	<i>DOD</i>	<i>Tmp</i>	<i>pH</i>	<i>Turb</i>	<i>SC</i>	<i>CV</i>	<i>CW</i>
DEC	2011	EGL54	155.67	5.62	1.88	3.74	31.83	7.41	12.43	0.479	0.001	46.33
DEC	2012	EGL54	153	6.82	3.34	3.48	29.04	7.59	11.73	0.358	0	43
DEC	2011	FL25	110	2.94	1.5	1.44	31.29	7.52	7.13	0.467	0.002	22.33
DEC	2012	FL25	140	6.83	4.57	2.26	30.59	7.21	6.867	0.397	3E-04	24
DEC	2011	ML04	85.33	4.02	2.82	1.2	29.76	7.54	17.03	0.523	0	36.33
DEC	2012	ML04	211	8.73	3.62	5.11	28.84	7.26	23.93	0.442	3E-04	41.67
DEC	MEAN		<i>1.43</i>	<i>5.83</i>	<i>2.96</i>	<i>2.87</i>	<i>30.22</i>	<i>7.42</i>	<i>13.19</i>	<i>0.44</i>	<i>6E-</i>	<i>35.61</i>
	(SE)		<i>(0.18)</i>	<i>(0.86)</i>	<i>(0.47)</i>	<i>(0.62)</i>	<i>(0.5)</i>	<i>(0.06)</i>	<i>(2.64)</i>	<i>(0.02)</i>	<i>04(0)</i>	<i>(4.15)</i>
Lake	2011	EGL32	119.33	7.8	5.99	1.81	33.97	7.92	16.13	0.454	0.002	346.3
Lake	2012	EGL32	89	7.17	6.85	0.31	29.2	7.98	27.2	0.387	0.07	334
Lake	2011	FL34	113.67	6.16	5.23	0.93	31.71	8.08	27.93	0.542	0.027	142.3
Lake	2012	FL34	145	11.2	10.2	0.92	29.74	8	32.6	0.432	0.064	114.7
Lake	2011	ML02	118.33	7.18	2.41	4.77	32.33	7.35	29.57	0.446	0.046	193
Lake	2012	ML02	78	7	5.98	1.02	29.62	7.69	46.13	0.498	0.012	182.3
LAKE	MEAN		<i>1.11</i>	<i>7.74</i>	<i>6.12</i>	<i>1.63</i>	<i>31.10</i>	<i>7.84</i>	<i>29.93</i>	<i>0.46</i>	<i>0.04</i>	<i>218.78</i>
	(SE)		<i>(0.1)</i>	<i>(0.72)</i>	<i>(1.03)</i>	<i>(0.66)</i>	<i>(0.77)</i>	<i>(0.11)</i>	<i>(3.97)</i>	<i>(0.02)</i>	<i>(0.01)</i>	<i>(40.1)</i>
NB	2011	EGL13	176	7.43	2.56	4.87	31.98	7.48	4.57	0.438	0.036	77.67
NB	2012	EGL13	185	4.44	2.98	1.46	30.43	7.54	10.53	0.432	0.021	65.67
NB	2011	FL13	136.33	6.07	4.82	1.25	31.69	7.93	22.5	0.546	0.026	20.67
NB	2012	FL13	151	5.15	4.7	0.45	32.19	7.33	19.8	0.439	0.106	42.67
NB	2011	ML03	95	6.84	5.77	1.07	30.6	7.85	35.2	0.527	0.006	45.67
NB	2012	ML03	136	7.66	6.95	0.71	26.96	7.42	50.7	0.44	0.034	48.33
NB	MEAN		<i>1.47</i>	<i>6.26</i>	<i>4.63</i>	<i>1.63</i>	<i>30.64</i>	<i>7.59</i>	<i>23.88</i>	<i>0.47</i>	<i>0.04</i>	<i>50.11</i>
	(SE)		<i>(0.13)</i>	<i>(0.52)</i>	<i>(0.68)</i>	<i>(0.66)</i>	<i>(0.79)</i>	<i>(0.1)</i>	<i>(6.87)</i>	<i>(0.02)</i>	<i>(0.01)</i>	<i>(8.06)</i>
OC	2011	EGL51	94	6.47	6.12	0.35	30.88	7.69	13.3	0.496	0.007	40.67
OC	2012	EGL51	148	6.77	6.16	0.61	30.49	7.7	34.13	0.516	0.055	48.33
OC	2011	FL17	85.33	3.13	2.65	0.48	31.35	7.6	32.5	0.484	0.052	25.33
OC	2012	FL17	129	5.21	4.31	0.9	31.48	7.28	18.63	0.447	0.116	27
OC	2011	ML01	151	7.47	1.62	5.85	32.07	7.36	11.4	0.457	0.042	37.33
OC	2012	ML01	147	4.93	4.28	0.65	30.41	7.53	24.43	0.484	0.005	35.33
OC	MEAN		<i>1.26</i>	<i>5.66</i>	<i>4.19</i>	<i>1.47</i>	<i>31.11</i>	<i>7.53</i>	<i>22.4</i>	<i>0.48</i>	<i>0.05</i>	<i>35.67</i>
	(SE)		<i>(0.12)</i>	<i>(0.64)</i>	<i>(0.74)</i>	<i>(0.88)</i>	<i>(0.26)</i>	<i>(0.07)</i>	<i>(3.92)</i>	<i>(0.01)</i>	<i>(0.02)</i>	<i>(3.51)</i>

Table 3.5: Individual site littoral zone physical structure measurements and macrohabitat means (with standard errors) of ARB sampling locations, including dead end canals (DEC), lakes, natural bayous (NB) and open canals (OC). Measurements include percentage of total habitat coverage (Total Hab), percentage of open water coverage (Open Water), percentages of submerged, floating and emergent vegetation coverage (SAV Cov; FAV Cov; EAV Cov) and percentage woody debris coverage (Wood Cov).

<i>Hab</i>	<i>Year</i>	<i>Site</i>	<i>Total Hab</i>	<i>SAV Cov</i>	<i>FAV Cov</i>	<i>EAV Cov</i>	<i>Wood Cov</i>
DEC	2012	EGL54	68	42.17	21.2	0.3	4.33
DEC	2011	EGL54	64.25	35.5	26.3	2	0.5
DEC	2011	FL25	62.08	38.33	16.7	2.9	3.96
DEC	2012	FL25	21.97	6.818	10.6	0.6	3.94
DEC	2011	ML04	56.2	21.2	4	0	31
DEC	2012	ML04	41.89	24.59	0.68	0	18.51
DEC	MEAN		<i>50.27</i>	<i>26.98</i>	<i>12.04</i>	<i>0.83</i>	<i>10.80</i>
	(SE)		<i>(2.11)</i>	<i>(1.95)</i>	<i>(0.97)</i>	<i>(0.22)</i>	<i>(1.02)</i>
Lake	2012	EGL32	45.33	5.333	6.33	0	33.67
Lake	2011	EGL32	41.75	8.75	1.75	0	32
Lake	2012	FL34	47.97	1.25	10.3	4.2	32.19
Lake	2011	FL34	52	5.75	8.75	2.3	35.25
Lake	2011	ML02	66.5	7.75	29.5	0.5	28.5
Lake	2012	ML02	99.5	65.67	31.8	0	2
LAKE	MEAN		<i>59.77</i>	<i>17.20</i>	<i>14.97</i>	<i>1.25</i>	<i>26.41</i>
	(SE)		<i>(2.23)</i>	<i>(2.10)</i>	<i>(1.21)</i>	<i>(0.32)</i>	<i>(1.62)</i>
NB	2012	EGL13	50.69	21.11	6.81	0	22.78
NB	2011	EGL13	68.75	29	26.5	1.5	11.75
NB	2012	FL13	54.22	28.75	14.2	5.8	5.47
NB	2011	FL13	86.25	77.25	1	3.8	4.25
NB	2011	ML03	40.8	12.4	0.2	0	28.2
NB	2012	ML03	37	16	1.5	0	19.5
NB	MEAN		<i>51.69</i>	<i>23.96</i>	<i>7.57</i>	<i>0.86</i>	<i>19.29</i>
	(SE)		<i>(1.91)</i>	<i>(2.09)</i>	<i>(0.89)</i>	<i>(0.27)</i>	<i>(1.40)</i>
OC	2011	EGL51	60.5	36.75	18.3	1.3	4.25
OC	2012	EGL51	72.86	33.29	11.4	0	28.14
OC	2012	FL17	44.21	9.868	11.4	1.1	21.84
OC	2011	FL17	59	39.75	14	3.5	1.75
OC	2012	ML01	55.28	28.61	6.67	0	19.72
OC	2011	ML01	53.5	13.5	29.5	1.8	8.75
OC	MEAN		<i>59.72</i>	<i>30.15</i>	<i>14.29</i>	<i>1.93</i>	<i>13.28</i>
	(SE)		<i>(1.77)</i>	<i>(1.63)</i>	<i>(0.99)</i>	<i>(0.45)</i>	<i>(1.29)</i>

which may have been related to the apparent abundance of palaemonids in lake habitats and their dietary importance for lake-dwelling black crappie. River shrimp migrate through wide channelled lakes in the ARB during their amphidromous life-history (Bauer and Delahoussaye 2008), and these lakes may provide optimal foraging conditions for these more pelagic (Warren 2009) predators. Warmouth mean relative weights were highest in dead end canals and lakes. Warmouth residing in blackwater, dead-end canals within the ARB exhibit a tolerance for hypoxia that may allow them to exploit habitats that exclude other, less tolerant species of invertivorous fishes, yet still may support moderate densities of, their dominant prey (*P. clarkii*), similar to hypoxia tolerant gar (*Lepisosteus* spp.; Pollard et al. 1983; Lambou 1990; Shenoi 1996; Snedden et al. 1999; Rutherford et al. 2001; Bonvillain 2012).

Both longear and redspotted sunfishes exhibited the lowest W_r values in open pipeline canals. This may reflect differences in the abundance of preferred invertebrate forage for these two sunfishes, as open canals are subject to considerable boat traffic and wave-induced disturbance. Interestingly, both species consumed much higher proportions of mayflies in open canal habitats (particularly redspotted sunfish; Chapter 2), and reduced condition could reflect reduced chironomid densities (Liao et al. 1995) or increased energetic costs associated with foraging on mayflies.

3.4.2 W_r and ARB Physicochemistry

Fish condition has been used as an index of environmental suitability (Blackwell et al. 2000), as well as an indicator of species health (Neumann et al. 2012), and the responses of fish populations to biotic and abiotic factors (Cone 1989; Blackwell et al. 2000). Within freshwater ecosystems, biotic and abiotic effects may function to impact community structure (Power et al. 1985; Matthews 1998; Schaefer et al. 1999), although the ability of fishes to tolerate or avoid

physicochemical stress may be more influential on individual condition than biotic factors or habitat complexity (Matthews 1998). Interestingly, bluegill condition was not associated with any of the physicochemical properties included in the model, suggesting that this species may be particularly well suited for the environmentally dynamic nature of this floodplain ecosystem. Not surprisingly, bluegill are often the most abundant and prolific centrarchids in lacustrine ecosystems (Alfermann and Miranda 2013). Among the sunfishes, they are considered to be the most tolerant to adverse conditions (Beitinger et al. 2000; Miranda et al. 2000; Killgore and Hoover 2001), which is consistent with the lack of differences in bluegill food habits or condition among the macrohabitats that I studied.

Largemouth bass typically occupy littoral macrophyte beds and submerged woody debris (Sammons and Bettoli 1999; Schultz et al. 2008), and their condition reflects both the abundance and availability of prey abundance in these structurally complex habitats. Within the ARB, macrophyte beds support a diversity of potential prey resources for largemouth bass, which include all of the sunfishes collected in this study as well as western mosquitofish (*Gambusia affinis*), least killifish (*Heterandria formosa*), and sailfin molly (*Poecilia latipinna*) (Troutman et al. 2007). Although largemouth bass use all types of submerged structure for cover, foraging, and spawning (Heggenes and Traaen 1988; Matthews 1998), bass condition and growth have been reported to be negatively associated with aquatic vegetation (Colle and Shireman 1980; Cailteux et al. 1998; Pothoven et al. 1999; Brown and Maceina 2002) reflecting reductions in foraging efficiency with increasing stem densities (Savino and Stein 1982; Savino and Stein 1989; Shaefer et al. 1994; Gotceitas and Colgan 1989; Valley and Bremigan 2002) as aquatic macrophyte density may influence diet through the regulation of piscivory (Bettoli et al. 1992; Dibble and Harrel 1997). Largemouth bass condition was positively associated with greater

channel widths (=lakes), which typically had lower levels of macrophyte coverage than the other macrohabitats, and may reflect greater prey availability in lake habitats.

Dissolved oxygen differential was positively related to the W_r of largemouth bass, black crappie, redspotted sunfish, and redear sunfish, indicating better condition in more stratified habitats. Despite being tolerant of low dissolved oxygen levels, both largemouth bass and black crappie are known to avoid extreme hypoxic conditions (Burleson et al. 2001; Killgore and Hoover 2001; Rutherford et al. 2001; Knights et al. 2005; Aday et al. 2009), and exposure to chronic hypoxia can significantly alter fish metabolism (Heath 1991; Furimsky et al. 2003), reproductive efforts (Coutant 1975), and presumably, condition. Inundated backwaters of the ARB floodplain are often hypoxic, with low DO water spreading to permanent waterbodies as river stages fall (Bryan and Sabins 1979; Sabo et al. 1999a,b). In many areas of the ARB, benthic strata remain hypoxic, even after normoxic conditions have returned to the upper water column (Table 3.4). Interestingly, Rutherford et al. (2001) reported a positive association between DO differential and the abundance of largemouth bass, black crappie, redspotted and redear sunfish abundances in the ARB. The additional relationship with W_r for these species suggests that stratified littoral habitats offer increased prey availability, perhaps forcing hypoxia-intolerant invertebrates to move from benthic areas to more normoxic habitats in the upper water column where they are more available to foraging fishes.

The relative weights of largemouth bass and warmouth, the two most piscivorous species that I collected, were both positively associated with specific conductance. Similar abundance relationships reported by Rutherford et al. (2001) may reflect increased aquatic productivity in habitats exhibiting higher specific conductance values (Cole 1994). Furthermore, higher specific conductance in the ARB may be indicative of influxes of distributary or main channel water,

which may continue to bring nutrients into permanent floodplain waterbodies even after the peak of the flood pulse. Additional relationships between warmouth W_r values and ARB physicochemistry were contradictory, with greater condition exhibited in areas characterized by greater channel widths, which correlates with greater condition in lakes, but not dead end canals, which were of moderate channel width. Warmouth exhibit a tolerance for hypoxic conditions (Killgore and Hoover 2001) and prefer low turbidity levels (Alfermann and Miranda 2013), and were found to be abundant in blackwater ARB habitats characterized by low turbidity, dissolved oxygen, pH, and current velocity (Rutherford et al. 2001). Given the predominantly stenophagous diet of this species, perhaps warmouth condition is mostly associated with the distribution and abundance of *P. clarkii*, and is much less related to the effects of ARB physicochemistry on the fish themselves.

As previously mentioned, black crappie W_r values were much higher in lake macrohabitats, and were positively associated with turbidity and emergent aquatic vegetation coverage. Previous studies in the ARB have indicated that black crappie abundance is highest in green-water habitats, such as lakes (Rutherford et al. 2001). Although turbidity was typically highest in the lake macrohabitats that I studied (Table 3.4), I did not assess the relative contributions of abiotic and biogenic sources to turbidity. However, it is likely that phytoplankton production in the study lakes contributed to the higher turbidity levels, and this increase in primary production in lake habitats resulted in greater prey abundance and increased black crappie foraging profitability. Although emergent vegetation was not generally higher in lakes, the coverage of emergent macrophytes in Duck Lake Pass (Site FL34; Table 3.5) was among the highest encountered; interestingly, black crappie were particularly abundant at this site relative to the other sampling locations.

General life-history studies suggest longear sunfish prefer higher flow velocities (Gunning and Suttkus 1990), although they may also be abundant in lentic habitats (Berra and Gunning 1972; Page and Burr 1991; Warren 2009). Rutherford et al. (2001) indicated that longear sunfish distributions were associated with highly turbid brown water sites in lotic regions of the ARB near the Atchafalaya River and Intracoastal Waterway. In my study, longear sunfish W_r was negatively associated with current velocity, but current velocities at all of the sites were extremely low (Table 3.4), and I did not sample until well after the flood pulse had subsided.

Redspotted sunfish W_r was associated with seven physicochemical and habitat parameters, including positive associations with DO differential, pH and current velocity, as well as negative associations with water temperature, floating and submerged macrophyte coverage, and woody debris coverage. In an extensive examination of centrarchid assemblages in floodplain lakes of the Mississippi alluvial valley, Alfermann and Miranda (2013) noted that redspotted sunfish assemblages were correlated with Secchi depth and maximum depth, indicating preferences for deep, clearer-water habitats. In the ARB, redspotted sunfish are not as common as other littoral centrarchids (or are less vulnerable to littoral electrofishing), and, at least based on their W_r values, are apparently less structure-associated than the other sunfishes and exhibit better condition in relatively cooler, higher velocity (albeit on a small scale) habitats with a well oxygenated upper water column.

Despite the spatial overlap of the littoral ARB centrarchids that I collected, patterns of W_r among macrohabitats and physicochemical characteristics differed substantially among several species, suggesting that condition analyses can reflect differences in habitat suitability in an environmentally complex system like the ARB. Taken together with the interspecific differences in diet composition described in Chapter 2, these analyses not only show how this assemblage is

partitioning trophic resources, but also how subtle differences in habitat structure and water quality can influence prey assemblage composition and the robustness of fish inhabiting different macrohabitat types.

3.4.3 Management Implications and Future Directions

Trends in centrarchid condition suggest that although habitats within the ARB differ regarding their overall suitability as sunfish foraging habitat, all of the species are generally able to flourish in all of the permanent waterbodies on the ARB floodplain. However, water quality and physical habitat characteristics differed among macrohabitats, as well as between sites within macrohabitats, indicating that water management activities that create or modify lakes, canals, and bayous in the ARB may alter habitat suitability for one or more species. Although the shallow lakes sampled in my study were generally well suited as centrarchid habitat, dead end canals varied in their effect on centrarchid condition, suggesting that water management projects aimed at improving conditions for fishes need to address not only macrohabitats, but also the physicochemical and structural characteristics within these macrohabitats. Unfortunately, variability in the annual flood pulse (Alford and Walker 2011) complicates all of these analyses, i.e., habitat modifications might be beneficial in one year, but not in another because of overriding effects of flooding on water quality.

Despite these complexities, several conclusions were apparent in my analyses. First, condition values among the centrarchid species were uniformly high relative to the standard curves, suggesting that overall foraging conditions are excellent in the ARB. However, on a finer scale, fish abundance (Rutherford et al. 2001), food habits, and W_r values all indicated that lake habitats are most suitable for black crappie, and lake habitats in general should probably be a point of emphasis for restoration/protection. Also, as a monitoring tool, my study can provide a

benchmark for future studies of centrarchid condition associated with management activities designed to improve fish habitat (Neumann et al. 2012). Moreover, as the annual flood pulse inundates the ARB, water quality, particularly DO levels, may fluctuate substantially among habitat types (Bryan and Sabins 1979; Sabo et al. 1999), and assessment of centrarchid condition may provide a simple (compared to other methods such as RNA/DNA ratios; Aday et al. 2009) yet effective measure of water quality impacts on ARB fishes over relatively short time frames. Finally, future investigations of condition and food habits of less abundant lepomis, particularly orangespotted and green sunfishes, as well as spotted bass, white crappie and flier, might clarify the reasons for their extremely patchy distribution and further the trophic relationships within the diverse centrarchid assemblage of the ARB.

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APPENDIX A: STOMACH CONTENT MACROHABITAT DATA

Table A1: Largemouth bass (*Micropterus salmoides*) dietary data (FO%, N%, W%, IRI, IRI%) by macrohabitat.

	<i>Dead End Canal (N=46)</i>					<i>Lake (N=68)</i>					<i>Natural Bayou (N=58)</i>					<i>Open Canal (N=48)</i>				
	FO%	N%	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%	FO%	N %	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%
Unid. Fish	0.5	0.38	0.58	47.88	60.67	0.6	0.46	0.59	63.2	72.06	0.72	0.53	0.73	90.78	89.79	0.58	0.55	0.26	47.28	59.64
Cambaridae	0.41	0.27	0.42	28.61	36.25	0.31	0.18	0.39	17.5	19.91	0.21	0.17	0.25	8.756	8.66	0.29	0.35	0.73	31.7	39.99
Palaemonidae	0.09	0.25	0	2.155	2.73	0.21	0.32	0.01	6.93	7.91	0.05	0.18	0.01	0.961	0.95	0	0	0	0	0
Araneae	0	0	0	0	0	0.03	0.01	0.01	0.06	0.071	0.02	0.01	0	0.02	0.02	0.02	0.02	0	0.049	0.061
Hemiptera	0.02	0.01	0	0.025	0.031	0.01	0.01	0	0.01	0.012	0.07	0.06	0.01	0.427	0.422	0	0	0	0	0
Physidae	0	0	0	0	0	0	0	0	0	0	0.03	0.02	0.01	0.104	0.103	0	0	0	0	0
Odonata	0.04	0.02	0	0.098	0.124	0.01	0.01	0	0.01	0.012	0	0	0	0	0	0.02	0.02	0	0.041	0.052
Ephemeroptera	0.02	0.02	0	0.05	0.063	0.01	0.01	0	0.02	0.024	0.02	0.01	0	0.019	0.019	0.04	0.04	0	0.166	0.209
Hymenoptera	0.02	0.01	0	0.024	0.031	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera	0.02	0.01	0	0.025	0.031	0	0	0	0	0	0.02	0.01	0	0.019	0.019	0	0	0	0	0
Plecoptera	0.02	0.02	0	0.049	0.062	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megaloptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0.02	0	0.041	0.052
Orthoptera	0	0	0	0	0	0	0	0	0	0	0.02	0.01	0	0.02	0.019	0	0	0	0	0

Table A2: Black crappie (*Pomoxis nigromaculatus*) dietary data (FO%, N%, W%, IRI, IRI%) by macrohabitat.

	<i>Dead End Canal (N=52)</i>					<i>Lake (N=91)</i>					<i>Natural Bayou (N=58)</i>					<i>Open Canal (N=28)</i>				
	FO%	N%	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%
Palaemonidae	0.53	0.43	0.4	0.44	60.2	0.89	0.47	0.74	1.1	78.61	0.72	0.46	0.46	0.67	71.26	0.67	0.51	0.37	0.59	64.15
Unid. Fish	0.25	0.02	0.36	0.1	13.55	0.11	0	0.1	0	0.796	0.28	0.01	0.34	0.1	10.36	0.26	0.01	0.52	0.14	14.77
Amphipoda	0.14	0.33	0.01	0.05	6.311	0.44	0.44	0.08	0.2	16.53	0.29	0.45	0.03	0.14	14.86	0.33	0.41	0.05	0.16	17.04
Ephemeroptera	0.53	0.13	0.12	0.13	18.11	0.36	0.02	0.04	0	1.445	0.28	0.02	0.04	0.02	1.638	0.37	0.03	0.04	0.03	3.052
Hemiptera	0.12	0.03	0.01	0	0.683	0.43	0.04	0.02	0	1.982	0.14	0.01	0	0	0.199	0.26	0.02	0.01	0.01	0.678
Diptera	0.1	0.04	0	0	0.511	0.26	0.02	0	0	0.569	0.19	0.04	0	0.01	0.946	0.11	0.02	0	0	0.285
Cambaridae	0.04	0	0.1	0	0.535	0.03	0	0.01	0	0.018	0.05	0	0.12	0.01	0.672	0	0	0	0	0
Odonata	0.02	0	0	0	0.007	0.04	0	0.01	0	0.041	0	0	0	0	0	0	0	0	0	0
Trichoptera	0.04	0.01	0	0	0.068	0.01	0	0	0	2E-04	0.07	0	0	0	0.032	0	0	0	0	0
Coleoptera	0	0	0	0	0	0.02	0	0	0	0.003	0	0	0	0	0	0.04	0	0	0	0.008
Hymenoptera	0	0	0	0	0	0.01	0	0	0	3E-04	0.03	0	0	0	0.007	0	0	0	0	0
Megaloptera	0	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0.001	0	0	0	0	0
Plecoptera	0.02	0.01	0	0	0.022	0	0	0	0	0	0.07	0	0	0	0.035	0.07	0	0	0	0.021

Table A3: Warmouth (*Lepomis gulosus*) dietary data (FO%, N%, W%, IRI, IRI%) by macrohabitat.

	<i>Dead End Canal (N=48)</i>					<i>Lake (N=27)</i>					<i>Natural Bayou (N=56)</i>					<i>Open Canal (N=25)</i>				
	FO%	N%	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%
Cambaridae	0.43	0.19	0.78	0.41	70.92	0.62	0.35	0.91	0.77	90.25	0.31	0.18	0.72	0.28	61.81	0.38	0.25	0.68	0.35	67.32
Unid. Fish	0.15	0.11	0.16	0.04	7.029	0.19	0.11	0.06	0.03	3.714	0.27	0.17	0.12	0.08	17.81	0.21	0.14	0.21	0.07	13.89
Araneae	0	0	0	0	0	0	0	0	0	0	0.05	0.03	0.06	0	1.082	0.08	0.06	0.05	0.01	1.714
Odonata	0.23	0.33	0.04	0.09	14.77	0.04	0.02	0	0	0.101	0.11	0.07	0	0.01	1.673	0.08	0.06	0.01	0.01	1.013
Hemiptera	0.13	0.1	0.02	0.02	2.623	0.15	0.11	0.02	0.02	2.238	0.18	0.13	0.08	0.04	8.44	0.17	0.19	0.03	0.04	7.307
Palaemonidae	0.11	0.19	0.01	0.02	3.652	0.04	0.09	0.01	0	0.44	0.15	0.18	0.02	0.03	6.549	0.13	0.14	0.02	0.02	3.763
Coleoptera	0	0	0	0	0	0.08	0.04	0	0	0.395	0.02	0.01	0	0	0.044	0.17	0.14	0.01	0.02	4.773
Ephemeroptera	0.11	0.05	0	0.01	0.896	0.12	0.11	0	0.01	1.492	0.07	0.07	0	0	1.052	0	0	0	0	0
Plecoptera	0	0	0	0	0	0.04	0.04	0	0	0.195	0.07	0.05	0	0	0.88	0.04	0.03	0	0	0.225
Hymenoptera	0.02	0.02	0	0	0.07	0	0	0	0	0	0.02	0.01	0	0	0.044	0	0	0	0	0
Diptera	0	0	0	0	0	0.08	0.13	0	0.01	1.17	0.02	0.01	0	0	0.045	0	0	0	0	0
Amphipoda	0	0	0	0	0	0	0	0	0	0	0.04	0.07	0	0	0.526	0	0	0	0	0
Physidae	0	0	0	0	0	0	0	0	0	0	0.02	0.01	0	0	0.045	0	0	0	0	0
Orthoptera	0.02	0.01	0	0	0.037	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A4: Redear sunfish (*Lepomis microlophus*) dietary data (FO%, N%, W%, IRI, IRI%) by macrohabitat.

	<i>Dead End Canal (N=22)</i>					<i>Lake (N=26)</i>					<i>Natural Bayou (N=6)</i>					<i>Open Canal (N=14)</i>				
	FO%	N%	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%	FO%	N%	W%	IRI	IRI%
Corbiculidae	0.55	0.34	0.35	0.375	48.5	0.65	0.44	0.43	0.57	54.92	0.83	0.48	0.66	0.96	69.07	0.86	0.51	0.57	0.92	64.95
Phsyidae	0.36	0.2	0.29	0.179	23.16	0.46	0.16	0.16	0.15	14.07	0.67	0.15	0.14	0.2	14.26	0.71	0.25	0.27	0.38	26.54
Unionidae	0.05	0.01	0.01	0	0.079	0.19	0.04	0.04	0.02	1.497	0.33	0.05	0.05	0.03	2.51	0.21	0.05	0.06	0.02	1.621
Shell Fragments	0.27	0.19	0.31	0.136	17.59	0.42	0.28	0.24	0.22	21.51	0.5	0.25	0.14	0.19	14.09	0.36	0.17	0.08	0.09	6.282
Ephemeroptera	0.32	0.03	0.03	0.018	2.376	0.46	0.06	0.12	0.08	7.917	0	0	0	0	0	0.21	0.02	0.02	0.01	0.609
Diptera	0.27	0.22	0.01	0.062	8.059	0	0	0	0	0	0.17	0.01	0	0	0.074	0	0	0	0	0
Palaemonidae	0	0	0	0	0	0.04	0.01	0	0	0.037	0	0	0	0	0	0	0	0	0	0
Trichoptera	0.05	0	0	0	0.021	0.04	0.01	0	0	0.022	0	0	0	0	0	0	0	0	0	0
Odonata	0.05	0	0	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera	0	0	0	0	0	0.04	0	0	0	0.02	0	0	0	0	0	0	0	0	0	0
Plecoptera	0	0	0	0	0	0.04	0	0	0	0.006	0	0	0	0	0	0	0	0	0	0
Hymenoptera	0.05	0	0	0	0.012	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda	0.09	0.01	0	0.001	0.18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A5: Bluegill sunfish (*Lepomis macrochirus*) dietary data (FO%, N%, W%, IRI, IRI%) by macrohabitat.

	<i>Dead End Canal (N=115)</i>					<i>Lake (N=113)</i>					<i>Natural Bayou (N=88)</i>					<i>Open Canal (N=64)</i>				
	<i>FO%</i>	<i>N%</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>	<i>FO%</i>	<i>N%</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>	<i>FO%</i>	<i>N%</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>	<i>FO%</i>	<i>N%</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>
Ephemeroptera	0.27	0.05	0.11	0.05	8.56	0.36	0.05	0.05	0.04	6.74	0.41	0.1	0.1	0.08	18.4	0.58	0.18	0.4	0.34	41.2
Diptera	0.5	0.67	0.14	0.41	77.6	0.64	0.44	0.15	0.38	66.9	0.5	0.51	0.09	0.3	66.3	0.53	0.62	0.17	0.42	51.5
Odonata	0.07	0.01	0.08	0.01	1.21	0.12	0.01	0.24	0.03	5.53	0.06	0.01	0.05	0	0.76	0.03	0	0.02	0	0.09
Coleoptera	0.11	0.02	0.13	0.02	3.16	0.19	0.02	0.14	0.03	5.56	0.08	0.02	0.2	0.02	3.85	0.06	0.02	0.11	0.01	0.99
Hymenoptera	0.03	0	0	0	0.03	0.09	0.01	0.02	0	0.53	0.06	0.01	0.01	0	0.21	0.02	0	0	0	0.01
Hemiptera	0.08	0.01	0.07	0.01	1.27	0.13	0.02	0.18	0.03	4.77	0.06	0.01	0.03	0	0.57	0.03	0	0.01	0	0.04
Trichoptera	0.07	0.02	0	0	0.31	0.19	0.04	0.01	0.01	1.59	0.1	0.04	0.01	0	1	0.22	0.08	0.03	0.02	3.02
Plecoptera	0.07	0.01	0.01	0	0.23	0.1	0.01	0	0	0.22	0.08	0.02	0.01	0	0.46	0.13	0.02	0.02	0.01	0.62
Physidae	0.05	0.01	0.04	0	0.47	0.03	0	0.01	0	0.07	0.05	0.01	0.04	0	0.44	0.06	0.01	0.05	0	0.43
Corbiculidae	0.04	0.02	0.14	0.01	1.31	0.01	0	0.01	0	0.03	0.03	0.02	0.11	0	1.03	0.02	0	0.01	0	0.02
Palaemonidae	0.07	0.02	0.15	0.01	2.28	0.04	0.01	0.07	0	0.49	0.06	0.03	0.1	0.01	1.68	0.08	0.02	0.16	0.01	1.75
Unid. Fish	0.03	0	0.1	0	0.52	0.01	0	0.01	0	0.01	0.05	0.01	0.23	0.01	2.37	0	0	0	0	0
Fish Eggs	0.01	0.04	0	0	0.07	0.04	0.28	0.02	0.01	2.42	0.02	0.14	0.01	0	0.75	0	0	0	0	0
Orthoptera	0	0	0	0	0	0.02	0	0.03	0	0.11	0	0	0	0	0	0	0	0	0	0
Araneae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0.01	0	0.02
Amphipoda	0.14	0.1	0.01	0.02	2.95	0.22	0.1	0.03	0.03	5.05	0.14	0.06	0.01	0.01	2.06	0.09	0.03	0	0	0.37
Annelid Worm	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0.01	0	0	0	0	0
Isopoda	0.03	0.01	0	0	0.05	0	0	0	0	0	0.01	0	0	0	0.01	0	0	0	0	0
Water Mite	0.01	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0.01
Megaloptera	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0.01	0	0	0	0	0

Table A6: Longear sunfish (*Lepomis megalotis*) dietary data (FO%, N%, W%, IRI, IRI%) by macrohabitat.

	<i>Dead End Canal (N=16)</i>					<i>Lake (N=23)</i>					<i>Natural Bayou (N=32)</i>					<i>Open Canal (N=23)</i>				
	<i>FO%</i>	<i>N%</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>	<i>FO%</i>	<i>N%</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>	<i>FO%</i>	<i>N%</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>	<i>FO%</i>	<i>N%</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>
Ephemeroptera	0.44	0.29	0.46	0.33	56.7	0.39	0.05	0.28	0.13	40	0.38	0.19	0.12	0.12	32.9	0.52	0.32	0.72	0.54	75
Diptera	0.19	0.16	0.08	0.04	7.64	0.39	0.15	0.06	0.08	26	0.22	0.21	0.02	0.05	14.3	0.35	0.3	0.03	0.11	15.9
Trichoptera	0.13	0.07	0.02	0.01	2.08	0.22	0.04	0.02	0.01	3.47	0.09	0.04	0	0	1.08	0.04	0.04	0	0	0.25
Coleoptera	0.06	0.01	0.12	0.01	1.46	0.09	0.01	0.04	0	1.39	0.06	0.02	0.01	0	0.47	0.13	0.06	0.12	0.02	3.15
Palaemonidae	0	0	0	0	0	0.04	0.01	0.01	0	0.31	0.13	0.07	0.31	0.05	13.6	0	0	0	0	0
Plecoptera	0.25	0.07	0.05	0.03	5.11	0.13	0.02	0.02	0	1.52	0.03	0.02	0.01	0	0.27	0.09	0.04	0.01	0	0.55
Physidae	0.13	0.03	0.04	0.01	1.59	0.13	0.01	0.06	0.01	2.89	0.06	0.01	0.01	0	0.4	0	0	0	0	0
Corbiculidae	0.06	0.03	0.09	0.01	1.26	0.04	0.02	0.3	0.01	4.31	0.16	0.04	0.08	0.02	5.24	0.13	0.09	0.1	0.03	3.56
Limpet	0	0	0	0	0	0	0	0	0	0	0.13	0.02	0.04	0.01	2.17	0	0	0	0	0
Hemiptera	0	0	0	0	0	0.09	0.01	0.1	0.01	2.87	0.03	0.01	0.02	0	0.25	0	0	0	0	0
Cambaridae	0.06	0.01	0.1	0.01	1.26	0	0	0	0	0	0.03	0.01	0.01	0	0.17	0.04	0.02	0.01	0	0.17
Unid. Fish	0	0	0	0	0	0	0	0	0	0	0.09	0.02	0.27	0.03	7.75	0	0	0	0	0
Amphipoda	0.38	0.32	0.03	0.13	22.9	0.17	0.13	0.03	0.03	8.29	0.19	0.33	0.02	0.07	18.7	0.09	0.09	0	0.01	1.19
Isopoda	0	0	0	0	0	0.04	0	0	0	0.07	0	0	0	0	0	0.04	0.04	0	0	0.24
Fish Eggs	0	0	0	0	0	0.04	0.54	0.03	0.02	7.71	0	0	0	0	0	0	0	0	0	0
Odonata	0	0	0	0	0	0.04	0.01	0.07	0	1.1	0.09	0.02	0.09	0.01	2.76	0	0	0	0	0
Water Mite	0	0	0	0	0	0.04	0	0	0	0.06	0	0	0	0	0	0	0	0	0	0

Table A7: Redspotted sunfish (*Lepomis miniatus*) dietary data (FO%, N%, W%, IRI, IRI%) by macrohabitat.

	<i>Dead End Canal (N=34)</i>					<i>Lake (N=19)</i>					<i>Natural Bayou (N=34)</i>					<i>Open Canal (N=22)</i>				
	<i>FO%</i>	<i>N %</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>	<i>FO%</i>	<i>N%</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>	<i>FO%</i>	<i>N %</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>	<i>FO%</i>	<i>N%</i>	<i>W%</i>	<i>IRI</i>	<i>IRI%</i>
Ephemeroptera	0.32	0.07	0.03	0.03	12.8	0.26	0.07	0.02	0.02	5.38	0.24	0.04	0.03	0.02	10.5	0.55	0.4	0.42	0.45	76
Diptera	0.19	0.07	0.03	0.02	7.3	0.42	0.45	0.05	0.21	48	0.18	0.09	0.01	0.02	11.3	0.14	0.11	0.01	0.02	2.97
Hymenoptera	0.1	0.01	0.03	0	1.52	0.11	0.03	0.27	0.03	7.19	0.06	0.01	0	0	0.6	0.14	0.04	0.02	0.01	1.54
Coleoptera	0.1	0.03	0.36	0.04	14.6	0.16	0.06	0.07	0.02	4.69	0.15	0.03	0.06	0.01	8.45	0.18	0.07	0.22	0.05	9.11
Trichoptera	0.1	0.02	0.01	0	1.17	0.16	0.04	0	0.01	1.56	0.12	0.02	0	0	1.36	0.09	0.04	0.01	0	0.78
Hemiptera	0.16	0.03	0.19	0.03	13.1	0.21	0.1	0.36	0.1	22.1	0.15	0.02	0.11	0.02	12.8	0.09	0.06	0.06	0.01	1.8
Odonata	0	0	0	0	0	0.21	0.04	0.06	0.02	4.74	0.09	0.01	0.02	0	1.71	0.05	0.01	0.02	0	0.28
Plecoptera	0.06	0.01	0.01	0	0.31	0	0	0	0	0	0.15	0.06	0.02	0.01	7.1	0	0	0	0	0
Physidae	0.1	0.03	0.16	0.02	6.97	0.05	0.01	0	0	0.17	0.12	0.03	0.05	0.01	5.76	0.05	0.01	0.05	0	0.47
Corbiculidae	0.13	0.02	0.04	0.01	3.11	0	0	0	0	0	0.06	0.02	0.02	0	1.5	0.09	0.09	0.13	0.02	3.35
Palaemonidae	0.1	0.04	0.06	0.01	3.89	0.05	0.04	0.16	0.01	2.44	0.09	0.03	0.2	0.02	12.8	0	0	0	0	0
Amphipoda	0.29	0.17	0.03	0.06	22.2	0.11	0.15	0.01	0.02	3.75	0.03	0.01	0	0	0.23	0.14	0.13	0.01	0.02	3.14
Unid. Fish	0.03	0	0.02	0	0.35	0	0	0	0	0	0.06	0.01	0.29	0.02	11.1	0.05	0.01	0.03	0	0.38
Fish Eggs	0.06	0.48	0.02	0.03	12.4	0	0	0	0	0	0.03	0.61	0.01	0.02	11.6	0	0	0	0	0
Cambaridae	0	0	0	0	0	0	0	0	0	0	0.03	0	0.17	0.01	3.3	0	0	0	0	0
Arguloida	0.03	0	0	0	0.06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megaloptera	0.03	0.01	0.01	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Annelid Worm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.01	0	0	0.14

APPENDIX B: STABLE ISOTOPE DATA

Table B1: Isotope values (^{13}C & ^{15}N) for individual centrarchids sampled in the ARB, with corresponding total length (mm) and weight (g).

<i>Species</i>	<i>Habitat</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	<i>TL(mm)</i>	<i>Weight(g)</i>
LMB	Lake	-28.568	16.871	354	667.8
LMB	Lake	-29.239	15.783	338	628.3
LMB	Lake	-28.548	16.12	322	547.6
LMB	Lake	-29.032	15.617	327	604.6
LMB	Lake	-29.367	15.63	315	528
LMB	DEC	-28.816	16.153	357	706.2
LMB	DEC	-29.375	15.401	280	415.9
LMB	DEC	-28.27	15.507	309	524.9
LMB	DEC	-27.887	16.43	327	587.1
LMB	DEC	-29.082	16.016	261	270.3
LMB	NB	-27.402	16.301	295	468.1
LMB	NB	-27.19	16.343	247	252.2
LMB	NB	-28.206	16.123	345	593.6
LMB	NB	-28.398	15.789	332	578.9
LMB	NB	-28.761	15.86	281	359.7
LMB	OC	-29.029	15.693	324	570.2
LMB	OC	-29.277	16.241	315	507.4
LMB	OC	-29.584	15.642	301	463.8
LMB	OC	-27.201	16.789	322	524.1
LMB	OC	-27.977	16.847	283	356.7
BC	Lake	-27.54	16.109	255	304.2
BC	Lake	-29.407	15.833	206	151.6
BC	Lake	-29.12	16.029	236	219.8
BC	Lake	-28.569	15.48	234	212.1
BC	Lake	-28.958	14.966	229	208
BC	DEC	-30.234	15.133	218	178.8
BC	DEC	-29.487	15.591	218	194.1
BC	DEC	-28.615	15.26	207	144.5
BC	DEC	-28.356	15.332	206	141.8
BC	DEC	-28.534	16.424	213	168
BC	NB	-28.553	15.863	251	247.2
BC	NB	-30.032	15.425	215	163.8
BC	NB	-29.176	16.357	225	178.4
BC	NB	-28.987	15.693	224	182.6
BC	NB	-28.692	16.247	218	167.2
BC	OC	-29.971	15.139	224	189.5
BC	OC	-29.462	14.303	228	208.6
BC	OC	-30.127	14.081	222	192.4

BC	OC	-28.811	15.19	216	149.4
BC	OC	-28.715	14.299	214	148.5
WAR	Lake	-27.94	15.209	169	117.8
WAR	Lake	-29.353	14.262	192	173.8
WAR	Lake	-28.856	14.36	183	159.2
WAR	Lake	-29.354	14.425	172	135.5
WAR	Lake	-27.734	14.147	210	249.4
WAR	DEC	-29.192	13.895	179	169.9
WAR	DEC	-27.703	15.078	168	130.6
WAR	DEC	-27.545	14.875	165	103.3
WAR	DEC	-28.002	14.205	182	140.7
WAR	DEC	-27.987	14.847	191	183.3
WAR	NB	-28.696	14.918	170	136.8
WAR	NB	-28.002	14.336	199	209.6
WAR	NB	-28.482	13.898	189	182
WAR	NB	-28.782	14.419	184	166.8
WAR	NB	-29.334	13.778	187	152
WAR	OC	-29.861	14.045	173	119.4
WAR	OC	-30.134	13.493	162	111.5
WAR	OC	-29.37	13.932	167	105
WAR	OC	-30.033	13.75	189	171.2
WAR	OC	-27.133	15.781	170	126.8
RES	Lake	-29.026	14.266	193	182.1
RES	Lake	-28.836	14.418	201	168.5
RES	Lake	-28.29	14.056	221	199.3
RES	Lake	-29.218	14.093	209	175.9
RES	Lake	-28.517	14.009	192	157.9
RES	DEC	-28.983	14.314	195	152.2
RES	DEC	-29.507	14.355	203	197.7
RES	DEC	-28.847	15.127	208	217.2
RES	DEC	-28.679	14.159	210	200.2
RES	DEC	-30.939	14.432	212	226.4
RES	NB	-29.414	13.751	217	207.5
RES	NB	-29.299	13.8	206	199.8
RES	NB	-28.582	14.862	165	94.8
RES	NB	-29.927	14.403	194	157.9
RES	NB	-28.032	12.926	198	161.7
RES	OC	-30.143	12.834	195	154.1
RES	OC	-30.873	14.144	212	212.7
RES	OC	-29.883	14.692	208	206.8
RES	OC	-29.605	14.449	192	148.4
RES	OC	-29.9	14.291	218	236.6

BG	Lake	-27.633	15.016	183	153.4
BG	Lake	-27.992	15.323	148	79.5
BG	Lake	-29.74	14.411	173	125.9
BG	Lake	-29.672	14.929	183	145.9
BG	Lake	-30.475	14.811	170	106.5
BG	DEC	-28.967	13.72	170	130.4
BG	DEC	-28.541	14.56	163	112.4
BG	DEC	-27.41	15.413	164	106.9
BG	DEC	-28.292	15.968	177	129.7
BG	DEC	-28.356	14.366	170	120.6
BG	NB	-29.381	14.369	187	156.9
BG	NB	-31.469	13.567	165	120.3
BG	NB	-27.72	14.623	183	160.6
BG	NB	-27.895	14.7	172	133.1
BG	NB	-29.062	14.939	184	148
BG	OC	-30.08	13.823	173	118.4
BG	OC	-29.482	14.474	161	97.1
BG	OC	-30.732	14.405	174	108.9
BG	OC	-27.707	14.684	169	132.8
BG	OC	-28.277	15.139	177	141.9
RSP	Lake	-26.824	16.517	127	57.8
RSP	Lake	-28.915	14.598	131	60.1
RSP	Lake	-28.701	14.217	127	52.7
RSP	Lake	-29.624	14.875	135	65
RSP	Lake	-28.749	14.092	125	52.6
RSP	DEC	-30.21	14.696	116	42.3
RSP	DEC	-30.628	13.96	126	54.5
RSP	DEC	-27.4	15.335	141	77.8
RSP	DEC	-27.046	15.525	133	61.8
RSP	DEC	-27.247	15.112	151	87.1
RSP	NB	-29.154	14.871	140	76.2
RSP	NB	-29.116	14.501	115	38.5
RSP	NB	-27.857	14.424	154	97.4
RSP	NB	-27.174	15.698	148	86.4
RSP	NB	-27.812	14.526	151	100.6
RSP	OC	-29.688	14.34	147	85.6
RSP	OC	-29.224	14.14	124	55.6
RSP	OC	-29.313	14.32	127	58.2
RSP	OC	-29.107	14.746	143	72.6
RSP	OC	-27.162	15.782	149	83.3
LES	Lake	-29.406	14.649	124	41.5
LES	Lake	-29.467	15.268	123	44.8

LES	Lake	-28.412	14.636	129	56.7
LES	Lake	-27.974	15.584	139	64.1
LES	Lake	-27.328	14.892	139	59.5
LES	DEC	-28.599	14.532	114	36.5
LES	DEC	-28.151	14.788	112	33.7
LES	DEC	-27.931	15.767	150	85
LES	DEC	-29.182	14.705	132	56.3
LES	DEC	-28.275	15.286	130	51.5
LES	NB	-26.376	15.954	121	42
LES	NB	-26.928	15.203	143	75.2
LES	NB	-28.573	15.193	133	57.2
LES	NB	-28.698	14.363	128	51.9
LES	NB	-29.321	13.652	127	50.2
LES	OC	-29.292	14.302	122	40.2
LES	OC	-28.474	14.256	143	65.7
LES	OC	-28.79	15.473	119	38.9
LES	OC	-28.588	14.925	128	56.2
LES	OC	-27.857	15.44	145	67.6

APPENDIX C: RELATIVE WEIGHT (W_r) PLOTS

Figure C1: Scatter plot depicting largemouth bass relative weights and total lengths among macrohabitats within the Atchafalaya River Basin, including dead end canals (DEC), lakes, natural bayous (NB) and open canals (OC).

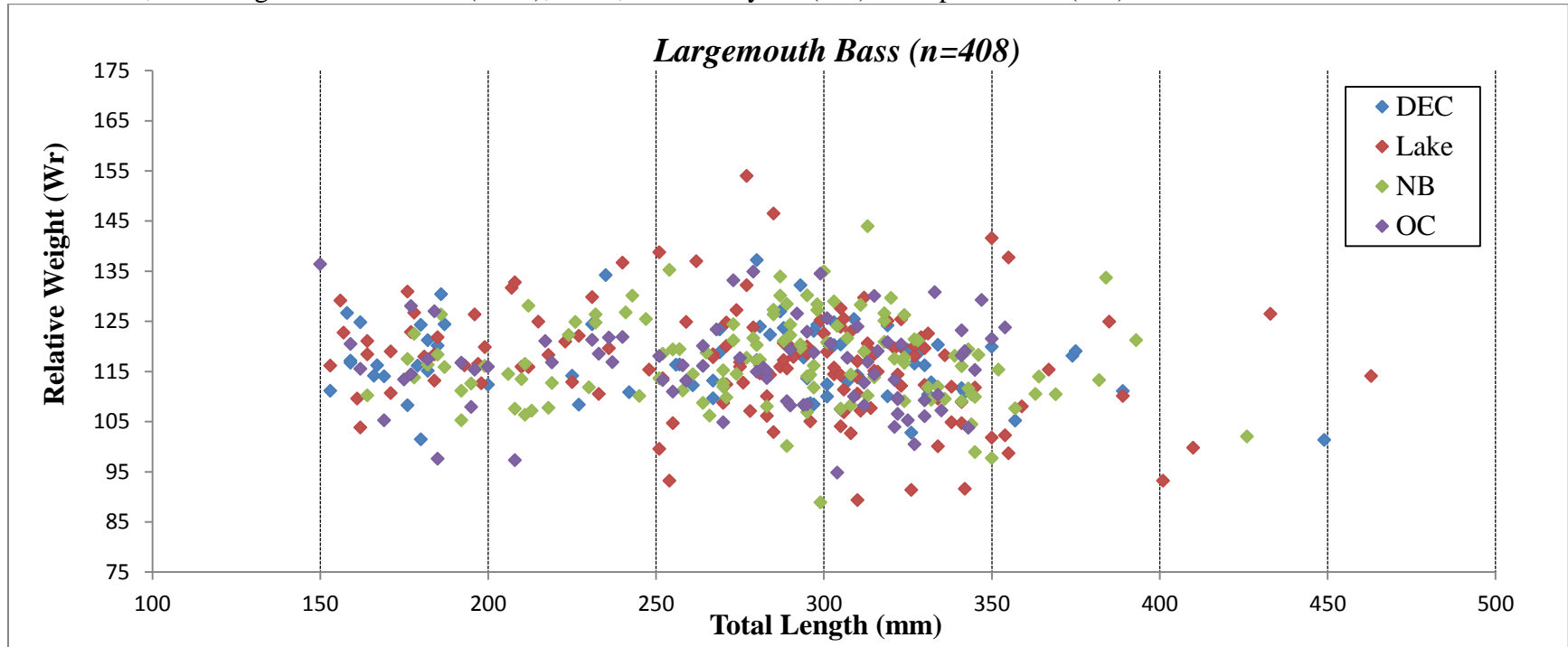


Figure C2: Scatter plot depicting black crappie relative weights and total lengths among macrohabitats within the Atchafalaya River Basin, including dead end canals (DEC), lakes, natural bayous (NB) and open canals (OC).

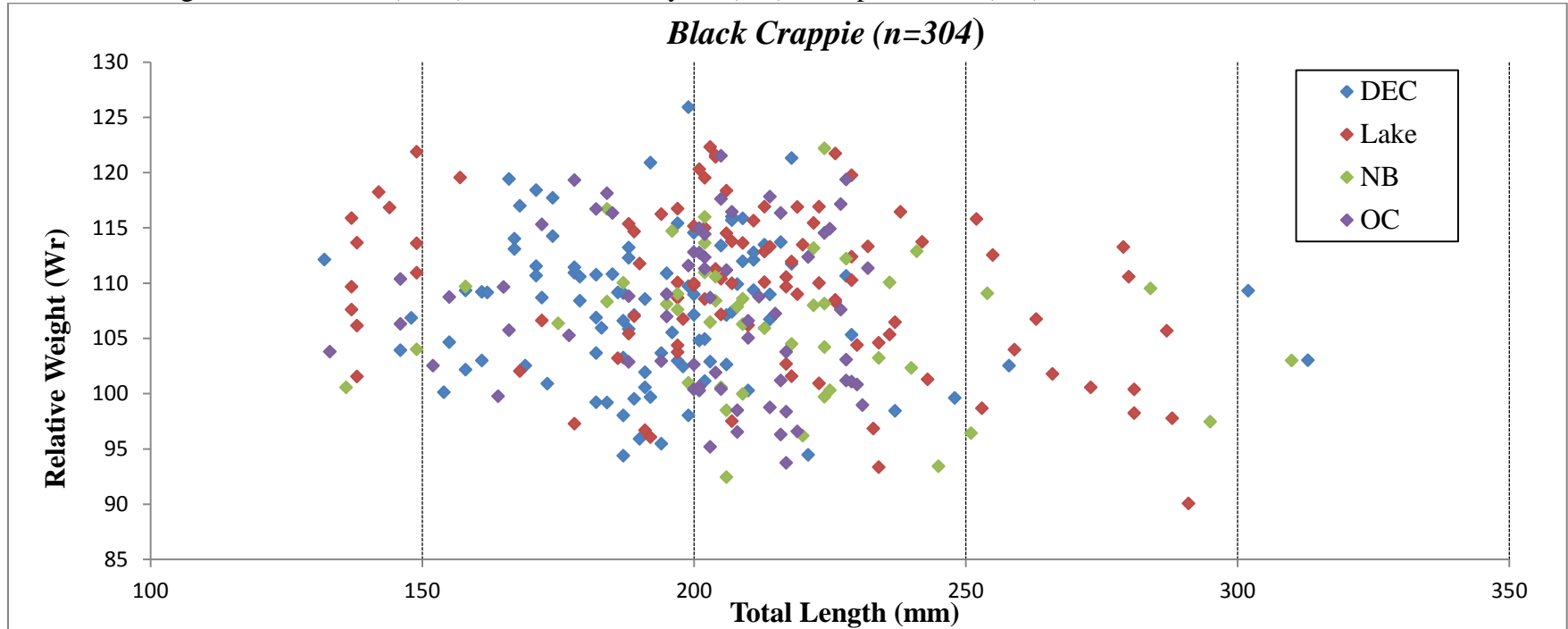


Figure C3: Scatter plot depicting warmouth relative weights and total lengths among macrohabitats within the Atchafalaya River Basin, including dead end canals (DEC), lakes, natural bayous (NB) and open canals (OC).

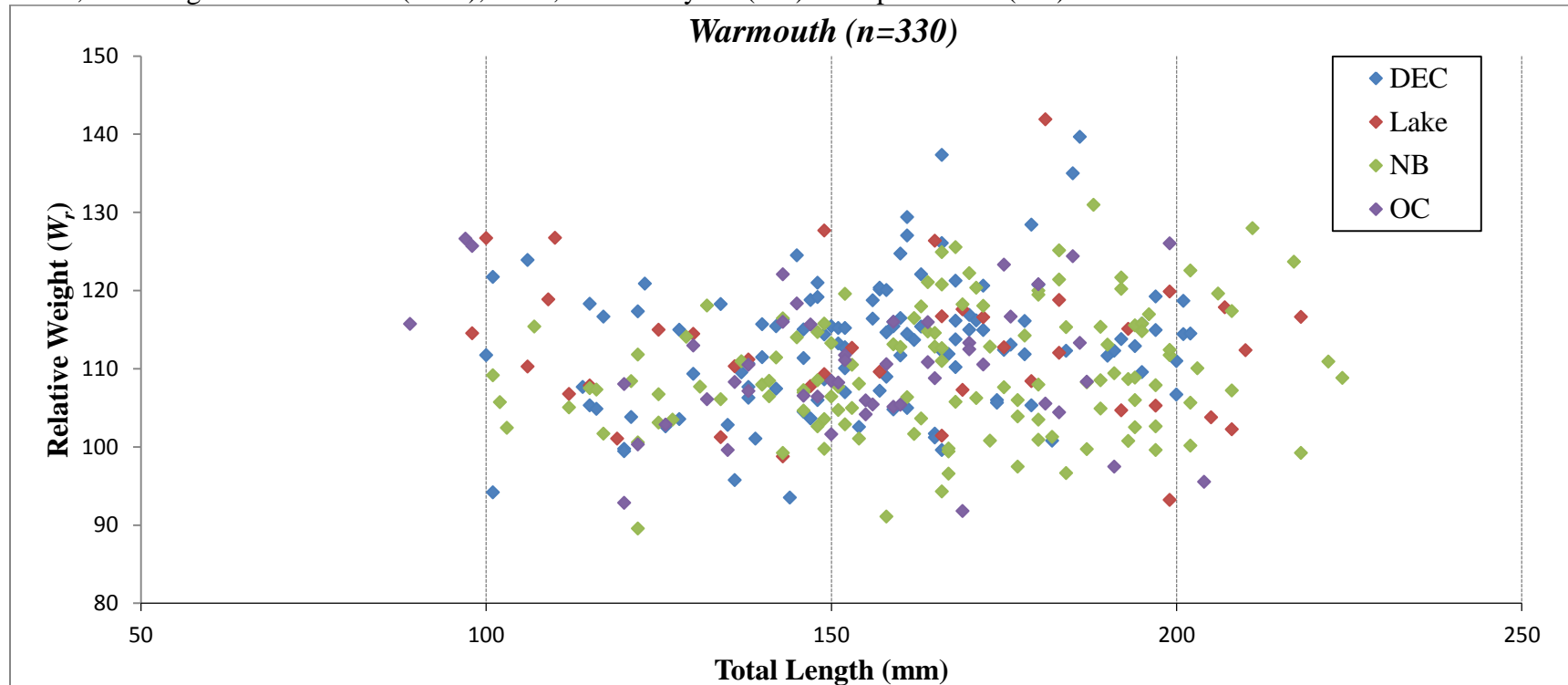


Figure C4: Scatter plot depicting bluegill sunfish relative weights and total lengths among macrohabitats within the Atchafalaya River Basin, including dead end canals (DEC), lakes, natural bayous (NB) and open canals (OC).

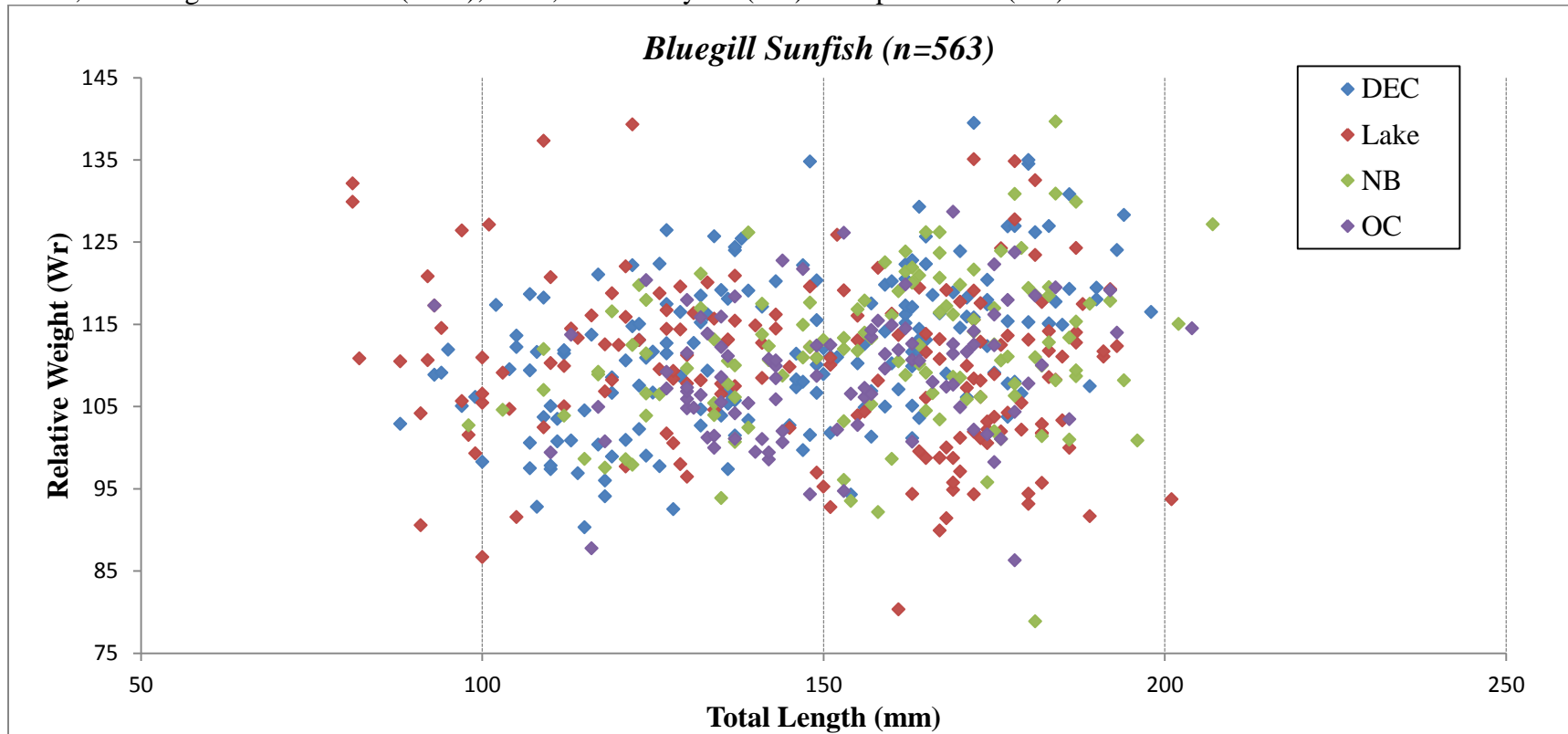


Figure C5: Scatter plot depicting longear sunfish relative weights and total lengths among macrohabitats within the Atchafalaya River Basin, including dead end canals (DEC), lakes, natural bayous (NB) and open canals (OC).

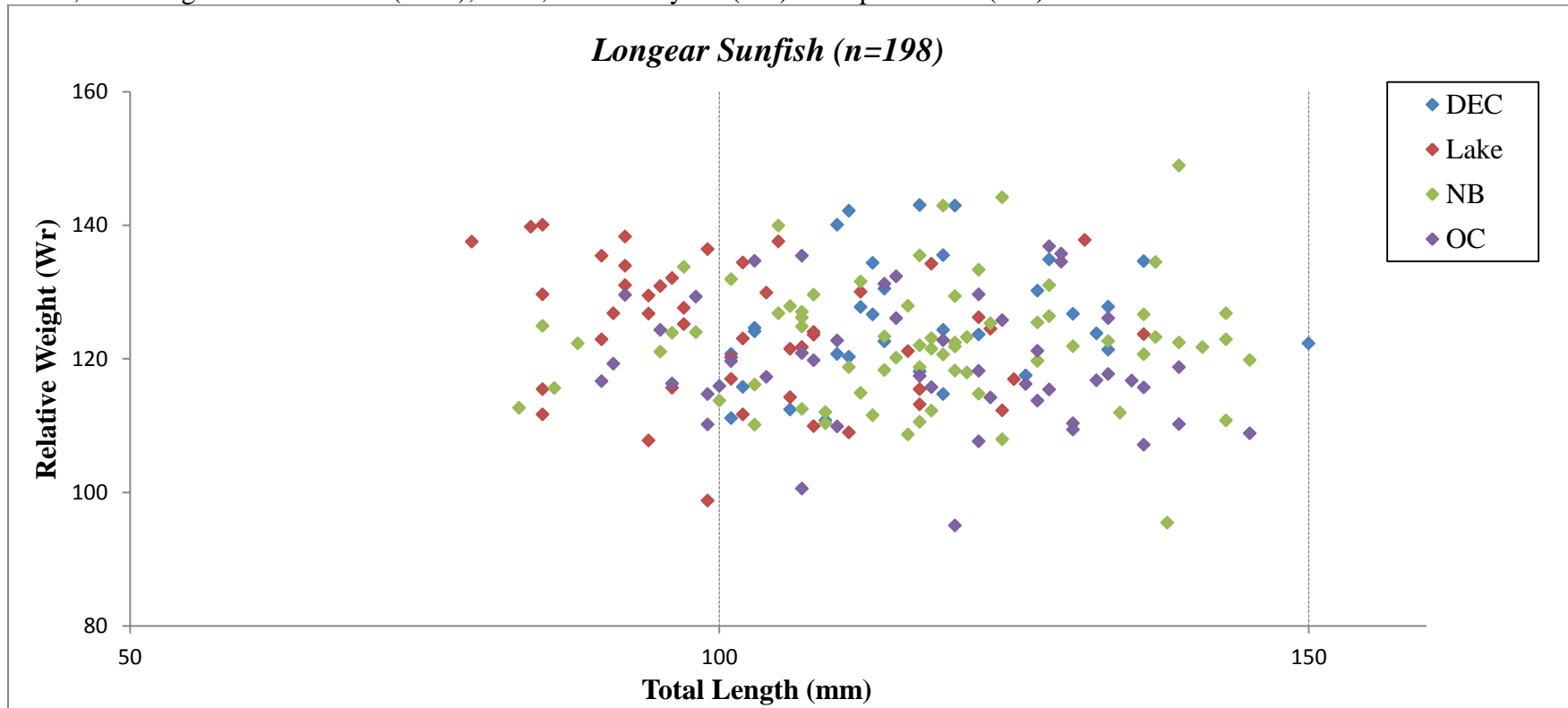


Figure C6: Scatter plot depicting redspotted sunfish relative weights and total lengths among macrohabitats within the Atchafalaya River Basin, including dead end canals (DEC), lakes, natural bayous (NB) and open canals (OC).

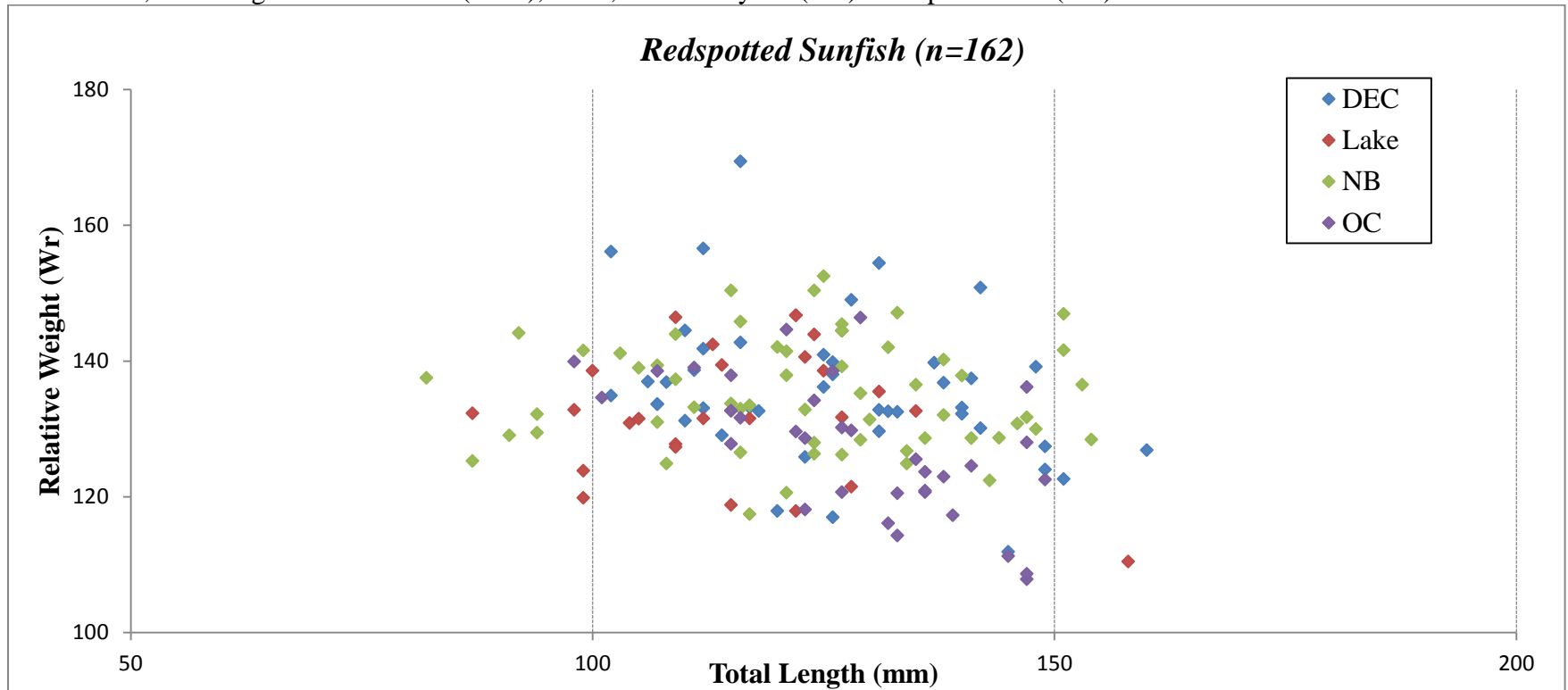
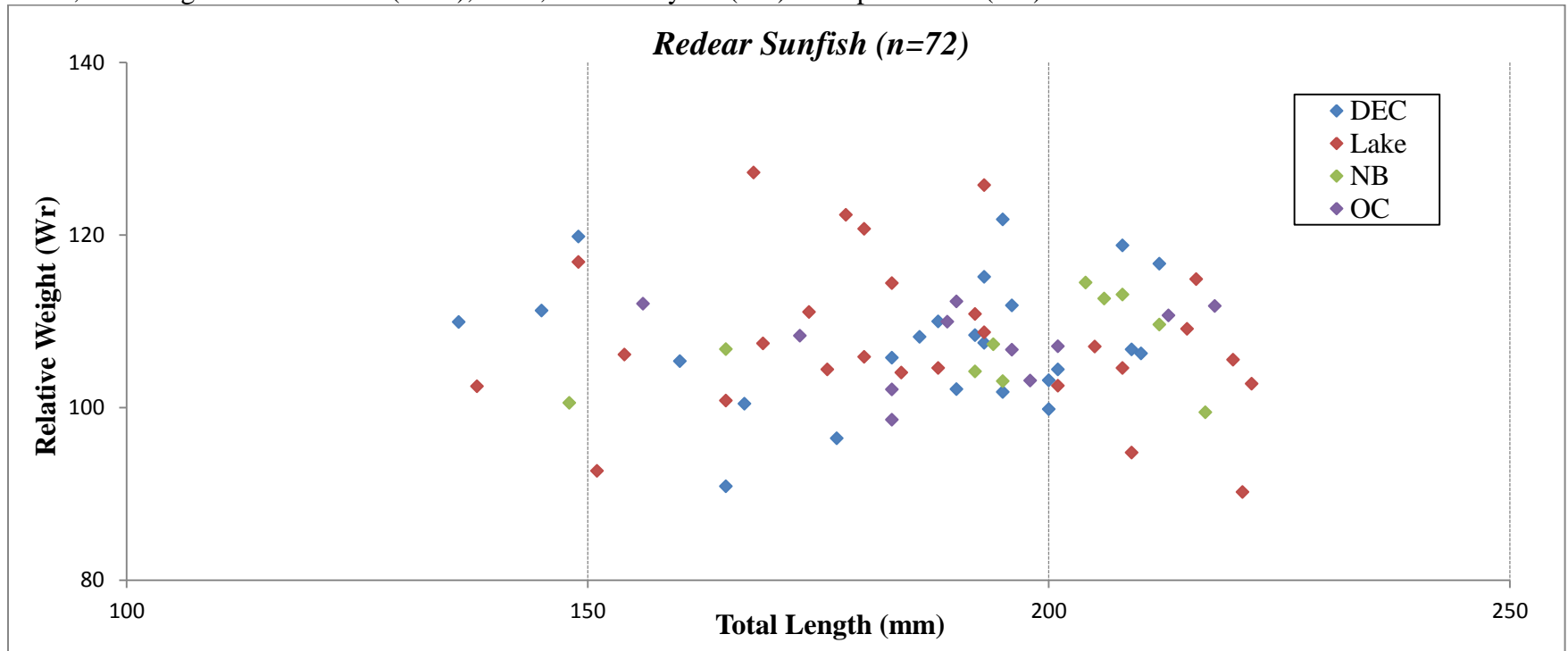


Figure C7: Scatter plot depicting redear sunfish relative weights and total lengths among macrohabitats within the Atchafalaya River Basin, including dead end canals (DEC), lakes, natural bayous (NB) and open canals (OC).



APPENDIX D: FISH SURVEY DATA

Table D1: Black crappie (BC), bluegill (BG), largemouth bass (LMB), longear (LES), redear (RES), redspotted (RSP) and warmouth (WAR) collection totals at individual sites, with corresponding GPS locations.

<i>2011 Fish Collection Sites</i>	<i>BC</i>	<i>BG</i>	<i>LMB</i>	<i>LES</i>	<i>RES</i>	<i>RSP</i>	<i>WAR</i>
N 30°03.985', W 091°22.568'	61	53	21	19	10	7	38
N 30°05.355', W 091°22.646'	12	16	21	22	0	9	11
N 30°06.403', W 091°23.222'	0	5	13	3	2	0	0
N 30°06.837', W 091°23.198'	0	1	29	0	0	1	3
N 29°47.977', W 091°14.419'	0	1	4	4	0	7	13
N 29°47.155', W 091°10.758'	7	3	9	4	2	2	3
N 29°47.631', W 091°17.070'	13	32	9	11	5	8	6
N 29°48.323', W 091°16.078'	4	39	19	0	6	0	6
N 29°57.850', W 091°22.333'	3	15	11	1	1	2	3
N 30°01.734', W 091°23.588'	3	14	14	20	3	5	0
N 29°54.891', W 091°23.049'	15	59	46	21	1	10	13
N 29°57.071', W 091°23.475'	8	30	23	4	0	5	10
<i>2012 Fish Collection Sites</i>	<i>BC</i>	<i>BG</i>	<i>LMB</i>	<i>LES</i>	<i>RES</i>	<i>RSP</i>	<i>WAR</i>
N 29°57.018', W 091°23.531'	12	58	29	6	4	21	67
N 29°54.765', W 091°22.970'	5	35	46	5	6	5	10
N 29°59.965', W 091°23.418'	17	42	21	11	3	10	6
N 29°57.893', W 091°22.341'	5	7	8	1	3	7	9
N 29°47.946', W 091°15.371'	31	14	17	13	1	13	25
N 29°47.918', W 091°14.412'	9	9	23	7	6	7	18
N 29°48.322', W 091°16.131'	3	8	10	7	3	14	29
N 29°47.661', W 091°17.203'	44	21	7	7	5	4	8
N 30°07.075', W 091°23.258'	4	22	13	0	2	4	12
N 30°06.403', W 091°23.222'	22	14	36	0	8	1	3
N 30°05.355', W 091°22.646'	5	10	26	28	0	7	6
N 30°03.985', W 091°22.568'	18	52	23	4	1	13	30

VITA

Brett Andrew Miller was born in 1986, in Iowa City, Iowa to Dr. Jeff and Chris Miller and after spending much of his childhood in the Texas hill country, he graduated from St. Stephen's Episcopal School in Austin, Texas in May 2005. Brett attended Rhodes College in Memphis, Tennessee, where he graduated in May 2009 with a major in Biology and minors in History and Environmental Science, followed by a year spent in the Alaskan Bering Sea working as a NOAA fisheries observer and northern fur seal research assistant. Brett enrolled in graduate school at Louisiana State University in the fall of 2010, where he examined the centrarchid assemblage of the Atchafalaya River Basin under the direction of Dr. William E. Kelso and Dr. Michael Kaller, and graduated magna cum laude with a Master's of Science in Renewable Natural Resources in the summer of 2013. Brett will attend the Texas A&M University School of Law at Texas Wesleyan University, Fort Worth, Texas, in the fall of 2013 and will pursue a career in water and environmental law.