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Fish Biodiversity in Floodplain Lakes of the Mississippi Alluvial Valley

Daniel Jay Dembkowski

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FISH BIODIVERSITY IN FLOODPLAIN LAKES OF THE
MISSISSIPPI ALLUVIAL VALLEY

By

Daniel Jay Dembkowski

A Thesis
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Master of Science
in Wildlife, Fisheries and Aquaculture Science
in the Department of Wildlife, Fisheries and Aquaculture

Mississippi State, Mississippi

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MISSISSIPPI ALLUVIAL VALLEY

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Fish assemblages from 54 oxbow lakes in the Mississippi Alluvial Valley were sampled to identify relationships among environmental variables and fish biodiversity in floodplain lake ecosystems. Environmental variables deterministic over fish biodiversity showed a hierarchical organization and were classified as primary or secondary depending on if one variable was considered to govern another. Primary variables included depth, surface area, surrounding land use, and degree of lake-river interconnectedness. Secondary variables included suites of water quality and primary productivity variables. Maximum depth and percentage of agricultural land surrounding lakes showed strongest relationships with other ecosystem components, significantly influencing water quality, primary productivity, and fish biodiversity. I found contrasting results regarding effect of lake-river interconnectedness on fish biodiversity, but maintain that connectivity is nonetheless an important floodplain lake ecosystem component and suggest that floodplain lake management efforts focus on depth, percentage of agricultural land, and restoration of connectivity.

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CHAPTER I

INTRODUCTION

The alluvial valley of the Lower Mississippi River (LMR) begins just upstream of Cairo, Illinois and extends south to the confluence of the Mississippi and Atchafalaya rivers in east-central Louisiana (Killgore et al. 2007). The floodplain of the LMR widens significantly within the alluvial valley, ranging in width from 40 to 200 km, making it one of the largest floodplains in the world (Baker et al. 1991; Biedenharn et al. 2000). In the states of Arkansas and Mississippi, the alluvial valley is locally referred to as the “Delta.” Prior to human settlement, most of the alluvial valley was covered with a dense bottomland hardwood forest that was inundated intermittently with flood waters 4-5 months (Smith 1954). Much of the valley has a layer of rich, fluvial soil, and at present, has been cleared for agricultural purposes (King and Keeland 1999).

The alluvial valley is strewn with hundreds of floodplain lakes situated adjacent to the Mississippi River and its tributaries which include the Arkansas, White, and Yazoo rivers, among others. These lakes are mostly oxbows, created when river bends are cutoff or abandoned resulting from sediment deposition or anthropogenic alteration (Biedenharn et al. 2000; Dodson 2005). Oxbow lakes are characteristic water bodies of meandering rivers that flow in poorly defined channels. Oxbow lakes and other extra-channel habitats are important components of floodplain-river ecosystems, in that

undisturbed floodplain habitats support reproduction and growth of most channel-dwelling fishes (Welcomme 1979). Thus, there is a direct relationship between fish community characteristics in floodplain habitats and fish community characteristics in the main channel. Undisturbed floodplain habitats constitute a large part of the flood-pulse concept (Junk et al. 1989) and are thus highly productive, heterogeneous, and dynamic environments (Winemiller et al. 2000). Consequently, unmodified oxbow lakes harbor unique and diverse fish assemblages (Sparks 1995). These fish assemblages are integral components of floodplain ecosystems and help maintain proper ecosystem function and resilience (Holmlund and Hammer 1999).

The Southeast is the most fish species-rich region in the U.S. (Warren and Burr 1994). It is likely not a coincidence that the Southeast also has the largest concentration of floodplain rivers and oxbow lakes in the nation. Several large floodplain rivers (e.g., Yazoo, Sunflower, Coldwater, and White) and hundreds of oxbow lakes are located within the Mississippi Alluvial Valley alone. Mississippi and Arkansas are the fifth and sixth most fish species-rich states in the country, respectively (Warren and Burr 1994). High species richness and diversity of floodplain lake fishes were maintained historically by heterogeneous and dynamic floodplain-river processes such as periodic inundation by flood waters (Baker et al. 1991; Galat et al. 1998). Increased regulation of free-flowing rivers, however, has essentially disconnected rivers from their floodplains and hindered the ability of natural ecological processes to maintain high fish species richness and diversity in floodplain-lake ecosystems (Bayley 1995; Rodríguez and Lewis 1997).

To protect urban developments and agricultural investments in the region, a variety of federally-sponsored flood-control and river-regulation projects involving the

LMR and its tributaries were instituted beginning in 1937. The system of levees, meander cutoffs, bank stabilization structures, and other channel containment structures are among the most notable channel modification features in the region and represent the single greatest perturbation (anthropogenic or natural) to the LMR in the past several hundred years (Biedenharn et al. 2000). These disturbances have altered floodplain-river processes such as meandering and flooding; processes that are essential in the production and maintenance of floodplain lakes (Miranda 2005). Furthermore, existing oxbow lakes are subject to varying levels of degradation and Aycock (2008) found that biotic integrity (as measured with fish community metrics) was impaired in most floodplain lakes in the Mississippi Alluvial Valley.

Metrics of species richness and diversity lie at the heart of many indices of biotic integrity (IBI; Karr 1981; Angermeier and Karr 1986; Angermeier and Schlosser 1988). Indices of species richness and diversity are relatively simple to estimate and often provide a rapid indication of the overall ecological welfare of a given environment (Magurran 1988; Magurran 2004). Spatial variability in species richness and diversity is one of the oldest and most important patterns in ecology (Hawkins 2001). Not only are species richness and diversity valuable in describing and comparing communities, but they also can serve as a baseline to assess the success of conservation and management strategies (Amarasinghe and Welcomme 2002).

Because biotic integrity was found to be impaired in most oxbow lakes in the Mississippi Alluvial Valley (Aycock 2008) and fish species richness and diversity were key metrics used in the IBI, the next logical step in preservation and restoration of oxbow lakes and their fish assemblages is to emphasize preservation or enhancement of fish

biodiversity. To accomplish this, it is first necessary to identify primary variables (e.g., depth, surface area, percentage of agriculture surrounding each lake, and degree of lake-river interconnectedness) that control characteristics of the aquatic environment in which fish live; that is, distinguish variables that have a controlling effect over a multitude of water quality and primary productivity variables (secondary variables). We must then examine how fish species richness and diversity (tertiary variables) change in response to variations in the primary variables, identify which conditions promote the highest levels of fish biodiversity, and design management plans to specifically address them.

Therefore, the objectives of this study were to (1) estimate relative importance of primary variables in controlling variation in suites of secondary variables and fish biodiversity, as well as the relation between the secondary variables and fish biodiversity across a range of floodplain lakes in the Mississippi Alluvial Valley, and (2) examine how fish assemblages are affected by periodic connection (a primary variable) between floodplain lakes and their parent rivers.

This thesis is structured so as to address each objective in manuscript form. Each manuscript houses its own introduction, methods, results, and discussion. The first objective is addressed in Chapter 2, where I begin with a discussion of the classification of the hierarchy of environmental variables and how certain variables (i.e., primary) are determinants of others (i.e., secondary and tertiary). The chapter progresses towards an explanation of primary and secondary variable selection and collection procedures followed by a description of the fish biodiversity variables. The focal point of Chapter 2 synthesizes relationships between each of four primary variables and suites of secondary variables and fish biodiversity, as well as between suites of secondary variables and fish

biodiversity. The second objective is addressed in Chapter 3 and was motivated by the marked disturbance to floodplain-river ecosystems afforded by channel containment features and the resultant disconnect between rivers and floodplain lakes. This chapter examined the interaction between lateral connectivity, one of the four primary variables considered in chapter 2, and fish species richness, diversity, and assemblage composition in two disjoined segments of a floodplain lake connected to and isolated from the Yazoo River. An overall conclusion summarizing and synthesizing pertinent findings and suggesting direction for future research is provided in chapter 4.

CHAPTER II
RELATIONSHIPS AMONG ENVIRONMENTAL VARIABLES AND FISH
BIODIVERSITY METRICS IN FLOODPLAIN LAKE ECOSYSTEMS

Introduction

Floodplain rivers are among the most biologically diverse ecosystems in the world (Tockner and Stanford 2002). Most of this biological diversity is supported by the dynamic nature and diverse environmental conditions inherent to floodplain river ecosystems (Baker et al. 1991; Sabo and Kelso 1991). Environmental factors determine aquatic community organization by acting as filters that affect capacity of a species to occupy a given area (Tonn et al. 1990). Fish species distributions and community composition can be affected by environmental factors directly via limits on physiological tolerance or indirectly via constraints on biotic interactions (Miranda and Lucas 2004).

Environmental variables that determine fish community composition are likely to show a hierarchical organization. Thus, variables may be classified as primary, secondary, or tertiary depending on whether one variable may be considered to govern another. Lake physical characteristics (primary variables) may influence lake water quality and primary productivity characteristics (secondary variables). Likewise, lake water quality, primary productivity, and physical characteristics (primary and secondary variables) may influence the fish assemblage (tertiary variables). For example, vertical

stratification of temperature and dissolved oxygen concentrations are controlled largely by depth (Dake and Harleman 1969), whereas presence of a fish species may be controlled by temperature, oxygen, and diversity of habitat afforded by depth (Miranda, in press). Similarly, lake acidity is influenced by the relative position of the lake within the landscape; lakes over carbonate-based sediments show less impact of acidification than lakes over granite-based sediments (Jackson et al. 2001), affecting species composition through water chemistry and through the shape of the land surface.

Numerous studies have identified environmental variables as determinants of floodplain lake fish communities (e.g., Winemiller et al. 2000; Miranda and Lucas 2004; Penczak et al. 2004; Tales and Berrebi 2007). These studies have sometimes confounded primary and secondary variables in their analyses. As a result, a study might conclude that land-use and chlorophyll-*a* are key variables, when in fact these variables represent disparate scales and chlorophyll-*a* (the secondary variable) may be governed by land-use (the primary variable). Additional studies are needed because (1) relatively little information is available about how variables representing different scales interact in floodplain lakes; (2) understanding hierarchy of variables can foster the development of a more holistic approach to floodplain ecosystem conservation and restoration; and (3) hierarchy of variables should be considered in management with primary variables probably being the focus of conservation and restoration strategies because these are often variables that managers can actually manipulate; secondary and tertiary variables may instead be useful for monitoring results of conservation and restoration efforts.

I examined the interaction between primary environmental variables descriptive of floodplain lake large-scale features, suites of secondary variables descriptive of water

quality and primary productivity, and a set of tertiary variables descriptive of fish biodiversity across a range of floodplain lakes in the Mississippi Alluvial Valley of Mississippi and Arkansas. Lake depth, surface area, degree of connectivity with parent river, and land-use around the lake were considered as primary variables. These variables have been identified by other authors as the driving forces for many processes in standing bodies of water (e.g., Lucas 1985; Junk et al. 1989; Magnuson et al. 1998; Tejerina-Garro et al. 1998). The specific objective of this study was to estimate relative importance of each primary variable in controlling variation in the suites of secondary and tertiary variables, and relation between secondary and tertiary variables. I hypothesized that suites of secondary variables would be more important in controlling variation in the tertiary variables because fish biodiversity is likely affected on a more proximate level by water quality and primary productivity variables than by large-scale primary variables; however, primary variables also may have a strong indirect effect on fish biodiversity.

Methods

Study lakes

Fifty-four floodplain lakes were sampled from July 2006 to August 2010 (Figure 2.1). Lakes were chosen from select river basins in Mississippi and Arkansas. Forty-six lakes were sampled twice each and 8 lakes were sampled once. Forty-one lakes were situated adjacent to the Yazoo River and its major tributaries (the Coldwater, Sunflower, Yalobusha, and Tallahatchie rivers) and 13 lakes were within the Arkansas and White

river basins. Eight lakes from the White River Basin were located within the White River National Wildlife Refuge, Arkansas. Three lakes from the Yazoo River Basin were located within Delta National Forest. Lakes were selected based on ease of accessibility and diverse representation of physical and chemical habitat characteristics. In particular, efforts were made to select lakes along gradients of depth, surface area, degree of connectivity with parent rivers, and watershed composition.

Primary variable selection and collection

Maximum depth, surface area, fluvial lake-river interconnectedness, and percentage of watershed agricultural land were selected *a priori* as primary environmental variables. They were selected on the basis that they seem to be the driving forces behind the variation in other lake water quality and primary productivity variables and because they are often identified as fundamental to many processes in floodplain dynamics (Junk et al. 1989; Baker et al. 1991; Miranda 2005; Lubinski et al. 2008). Thus, the primary (fundamental) environmental variables were selected based on the premise that they act independently and collectively to shape floodplain lake water quality, primary productivity, and fish biodiversity characteristics.

Maximum depth was defined as the deepest point detected by depth soundings taken with a handheld (DF2200PX, NorCross Marine, Orlando, Florida) or boat-mounted (X126 DF Sonar, Lowrance Electronics, Tulsa, Oklahoma) depth finder in a zig-zag pattern along the former thalweg between the two ends of each lake. Maximum depth was selected as a primary variable as opposed to mean depth because it better

characterizes the planform and cross-sectional morphology of fluvial lakes (former river channels) than mean depth.

Surface area and land-use composition surrounding each lake were calculated using spatial analyst tools in the Arc-GIS software package. Aerial photography and satellite images for lakes within Mississippi were available from the National Agricultural Imagery Program (NAIP) and were obtained from the Mississippi Automated Resource Information System (MARIS). Images of the 14 lakes in Arkansas were obtained from the United States Geological Survey (USGS) Southeast Gap Analysis Project (SEGAP) database. Lakes were treated as polygons, and those not already identified as water bodies in Arc-GIS were digitized as such.

Individual lake watersheds were not defined due to lack of sufficient topographic relief in the region (Baker et al. 1991). Instead, concentric bands (50, 500, 1,000, and 5,000 m) were drawn around each lake. Percentages of land-use classifications available from the MARIS and SEGAP databases were calculated within each band. Percentage of row-crop agriculture was selected as a fundamental variable over other land-use classifications because of the notable historical influences agricultural practices have had on the lower Mississippi Alluvial Valley ecoregion (Smith 1954; King and Keeland 1999). Preliminary analyses using pairwise comparisons of mean percent coverage indicated no statistically significant increases in percentage of row-crop agriculture beyond the 1,000 m band; thus, percentage agriculture in the 1,000 m band was used for all subsequent analyses.

Interconnectedness between each fluvial lake and its parent river was measured using effective distance, defined as the stream channel distance between each lake and its

parent river. Other indices of lake-river interconnectedness include counts of inlets/outlets and area of neighboring water bodies (Miyazono et al. 2010), qualitative indices (Miranda 2005; Lubinski et al. 2008), and comparisons of direct field observations of flooding with river discharge levels (Zeug et al. 2005). The methods of Zeug et al. (2005) are possibly the most precise; however, direct field observation of flooding at all study lakes included in the present study was impractical given time and personnel constraints. Differences in elevation between oxbow lakes and their parent rivers are important in affecting connectivity; however, available elevation data had relatively low resolution and agricultural practices have likely altered the landscape to the point where elevation data find use only in limited settings. Because of the limited utility of elevation data within the study region and other time and personnel limitations, effective distance was used as a proxy for other more involved measurements. Effective distance is measured easily and should suitably index connectivity in that lakes closer to their parent rivers (i.e., have a shorter effective distance) are thought to be connected on a more frequent basis than lakes with farther effective distances.

Secondary variable selection and collection

All secondary variables (lake water quality and primary productivity characteristics) collected herein are frequently included in the standard suite of lake measurements collected by aquatic scientists. Turbidity (nephelometric turbidity units; NTU), pH, dissolved oxygen (DO; mg L⁻¹), DO saturation (%), temperature (°C), water transparency (cm), and concentrations of chlorophyll-*a* and phycocyanin (fluorescence units; FU) were measured at each lake. I also considered the chlorophyll-*a*:phycocyanin

ratio because it reportedly reflects availability of nitrogen and phosphorous (nitrogen-limited lakes would tend to have greater ratios; Foy 1993). Turbidity, pH, DO and DO saturation, and temperature were measured in situ with a Eureka Manta™ multiprobe (Eureka Environmental Engineering, Austin, Texas). Water transparency was measured using a Secchi disk (20 cm diameter). Concentrations of chlorophyll-*a* and phycocyanin were measured in situ using an *Aquafluor*™ handheld fluorometer (Turner Designs, Sunnyvale, California). All water quality variables were measured in summer (June-August) from the epilimnion at a single point near the deepest point in each lake.

Although considered to be secondary in nature, variables indexing primary productivity (i.e., chlorophyll-*a*, phycocyanin, and the chlorophyll-*a*:phycocyanin ratio) were treated as a separate data matrix because they largely index biotic characteristics, whereas variables such as DO, turbidity, and temperature largely index abiotic characteristics, although DO is partly determined by algae photosynthesis. Additionally, primary variables may differentially influence the water quality variables versus the primary productivity variables.

Fish collections

Fish were collected diurnally by a boat electrofisher equipped with a GPP 7.5 Smith-Root™ pulsator unit (Smith-Root, Inc., Vancouver, Washington). Pulsed DC electricity was cycled at 60 Hz with voltage output adjusted according to the specific conductance of each lake to maintain a constant output of 6-8 A. Individual samples consisted of 0.25 h of continuous electrofishing along random shoreline areas. Sampling lasted 0.5 – 2.0 h depending on lake area. Fish were netted from the bow of the boat by

two netters equipped with 2.7 m dip nets with 0.4 cm bar mesh. Fish were identified to species and counted before release near the site of capture. Those species difficult to identify in the field were preserved in a 10% formalin solution and transported to the lab for positive identification with taxonomic keys (Ross 2001).

Fish biodiversity metrics

Fish assemblage descriptors were classified as tertiary variables on the basis that they are likely affected either directly or indirectly by primary and secondary variables. Species richness and diversity metrics were calculated using diversity modules available in the PAST™ and PRIMER-E™ ecological software packages (Hammer et al. 2001; Clarke and Gorley 2006). Collections of threadfin shad (*Dorosoma petenense*) and gizzard shad (*Dorosoma cepedianum*) did not accurately reflect their true abundance in the study lakes due to their fleeting behavior in response to energized water. Hence, they were excluded from the calculation of metrics sensitive to species abundance (i.e., diversity, dominance, and evenness metrics) but were included in metrics of species richness. Species richness metrics included raw species richness (S_{raw}), rarefied species richness (S_{rare}), Margalef's species richness (S_{Margalef}), and Menhinick's species richness ($S_{\text{Menhinick}}$). The Margalef and Menhinick indices are standardized by number of individual fish collected at each lake, but the Menhinick index is more sensitive to sample size and highly abundant species than the Margalef index (Wilhm 1967; Peet 1974; Danilov and Ekelund 2001). Rarefaction is a standardization method that asks how many species would be found if sampling effort (expressed as number of individuals) was fixed (Magurran 1988; Gotelli and Colwell 2001). Rarefaction estimates were fixed to

the smallest observed sample size (97 individuals). Diversity metrics included the Shannon-Wiener diversity index (H') and Fisher's alpha (F_α), differing mainly in that the Shannon-Wiener index is especially influenced by abundant species (Southwood and Henderson 2000). Dominance was measured with a variant of the Simpson's diversity index (D), hereafter referred to as Simpson's dominance ($1-D$) and the Berger-Parker index (d). Simpson's dominance is greatly weighted towards the most abundant species and is less sensitive to species richness than the Berger-Parker index (Magurran 2004). Evenness was measured with Buzas and Gibson's evenness index (E) and Pielou's evenness index (J); they differ in that Buzas and Gibson's index is highly dependent on the relationship between number of species and number of individuals and Pielou's index is inherently biased in that it is based on total number of species in the lake (Buzas and Hayek 2005), which is unknown and substituted with sample estimates of species richness. Dominance and evenness metrics are related inversely, but both index overall equitability of individuals among taxa (Hammer et al. 2001).

The aforementioned species richness and diversity metrics have traditionally been used in a univariate sense, examining trends in individual metrics in response to variation in other characteristics. For example, Ludsin et al. (2001) examined the relationship between system productivity and fish species richness in Lake Erie (USA) fish communities using simple univariate linear regression. Similarly, Lubinski et al. (2008) assessed relationships between fish species richness, diversity, and evenness measures and lake-specific environmental variables using ordinary least-squares linear regression. For the purposes of this study, all species richness and diversity indices were grouped to

create a multi-index matrix. This matrix was thought to be representative of all facets of overall fish biodiversity: richness, diversity, and equitability.

Statistical analysis

Relationships among secondary variables and among fish biodiversity metrics were assessed with nonmetric multidimensional scaling (NMS). The NMS procedure is an indirect gradient analysis ordination technique in which similar variables and metrics are plotted close together in ordination space and dissimilar variables and metrics are plotted far apart. The NMS procedure allows the use of various distance measures and has no assumptions of linearity (McCune and Grace 2002). The NMS procedure was applied using PRIMER-E statistical software with a Pearson correlation similarity measure obtained from correlations among the secondary variables and correlations among the fish biodiversity metrics. Because the ordination is based upon a correlation-type similarity matrix, the relative distances apart of the secondary variables and fish biodiversity metrics reflect the Pearson pairwise correlations between each variable or metric (Clarke and Gorley 2006).

Canonical analysis of principal coordinates (CAP) was used to examine relationships between each individual primary variable and suites of secondary and tertiary variables, as well as the relationships between secondary and tertiary variables. The CAP procedure is a multivariate data reduction technique that identifies axes running through a cloud of data points that have the strongest correlation with another set of variables (Anderson and Robinson 2003). Because the CAP analysis essentially ordinated one data matrix in consideration of another, it is a constrained analysis that uses

an *a priori* hypothesis to construct correlations between matrices. Furthermore, it is flexible and meaningful in that it can be performed using any ecological distance measure (Anderson and Willis 2003). The CAP approach to constrained ordination is essentially a three-step process that includes a principal coordinates analysis (PCO), selection of m principal coordinate axes, and an ensuing canonical correlation analysis based on a matrix of explanatory variables. When relating a multivariate matrix to a single variable matrix, the CAP analysis produces a single canonical correlation representing the strength of the association between the canonical (i.e., CAP) axis and the explanatory variable. When relating two multivariate matrices, multiple canonical correlations are produced so as to represent the strength of the association between multiple axes maximizing the linear correlation between data matrices (M.J. Anderson, University of Auckland, personal communication).

Separate CAP analyses were applied to examine correlations between primary and secondary variables, and between secondary and tertiary variables. The CAP analysis sought to find correlations between axes representing most of the variation in water quality, primary productivity, and fish biodiversity matrices relative to each individual primary variable, with the constraint that secondary and tertiary matrices were thought to be responses of explanatory variables. In relating suites of secondary variables to fish biodiversity metrics, the CAP analysis sought to find correlations with the constraint that fish biodiversity metrics responded to suites of secondary variables. All CAP analyses were performed using the PERMANOVA+ add-on for PRIMER statistical software package (PRIMER-E Ltd, Plymouth, United Kingdom; Clarke and Gorley 2006) with a Euclidean distance measure. Euclidean distance is a generic distance measure that is well

suiting for non-zero environmental data and is easily interpreted in that it is essentially the straight-line distance between two variables in multidimensional space (McGarigal et al. 2000).

Results

Primary variables

The study lakes varied greatly in their representation of primary environmental variables (Table 2.1). Maximum depth ranged from 0.5 to 8.6 m (mean = 2.8 m), degree of lake-river interconnectedness ranged from 0 to 14 km (mean = 2.5 km), and percentage of row-crop agriculture ranged from 0 to 77% (mean = 47%). Lake surface area ranged from 0.01 to 5.7 km² (mean = 0.74 km²). Lakes within the Delta National Forest and the White River National Wildlife Refuge were surrounded primarily by bottomland hardwood forest (mean percentage agriculture in 1,000 m band = 1.4%), whereas lakes outside protected areas were surrounded primarily by agricultural land (mean percentage agriculture in 1000 m band = 59%).

Secondary variables

Study lakes also varied in their representation of water quality and primary productivity variables (Table 2.1). Chlorophyll-*a* and phycocyanin fluorescence averaged 286 (range = 65 – 964) and 2.5 (range = 0.25 – 9.6), respectively. The chlorophyll-*a*:phycocyanin ratio averaged 160 (range = 19 – 426). Secchi visibility and turbidity, both indexes of overall water transparency, averaged 50 cm (range = 15 – 105)

and 29 NTU (range = 4.7 – 113), respectively. DO concentration and DO saturation averaged 6.2 mg l⁻¹ (range = 1.5 – 11) and 82% (range = 19 – 147), respectively. Water temperature averaged 29°C (range = 26 – 34). pH was variable across lakes (range = 5.2 – 9.5) but averaged slightly alkaline (7.2). The NMS plot demonstrated that secondary variables were primarily situated along a gradient of water transparency, with the extremities contrasting Secchi visibility against turbidity and chlorophyll-*a* (Figure 2.2). A second axis contrasted dissolved oxygen levels against algal concentrations.

The overall matrices of water quality variables and primary productivity variables were correlated significantly ($m = 2$; $P < 0.01$). The CAP procedure identified two canonical axes that captured most of the association between water quality variables and primary productivity variables. The first and second canonical correlations, indicating strength of the association between the matrix of water quality variables and the matrix of primary productivity variables, were $\delta_1 = 0.50$ and $\delta_2 = 0.29$, respectively.

Fish collections

Over the multiyear sampling period, over 93,100 fish representing 71 species were collected during 128 hours of electrofishing. Analyses were conducted with data from different years combined after a permutation analysis of variance (PERMANOVA; Anderson 2001) with a Bray-Curtis similarity measure indicated no significant among-year differences in assemblage composition for lakes sampled across years ($P = 0.31$). Excluding threadfin shad and gizzard shad, bluegill (*Lepomis macrochirus*) were collected most frequently (34% of the catch by number), followed by longear sunfish (*Lepomis megalotis*; 10%), orangespotted sunfish (*Lepomis humilis*; 9%), smallmouth

buffalo (*Ictiobus bubalus*; 7%), largemouth bass (*Micropterus salmoides*; 7%), brook silverside (*Labidesthes sicculus*; 5%), and bigmouth buffalo (*Ictiobus cyprinellus*; 4%).

Fish biodiversity metrics

Metrics of species richness and diversity were highly variable across study lakes (Table 2.1). Columbus Lake had the greatest observed S_{raw} (44), whereas Enterprise Lake had the least S_{raw} (12). Bobber Lake was the most even in terms of Buzas and Gibson's evenness index (0.62) and Anthrax Lake was the least even (0.12). All other richness and diversity metrics are derived from these basic measurements of raw species richness and evenness and thus show similar patterns of variability.

The biodiversity metric NMS plot demonstrated that metrics emphasizing each facet of fish biodiversity (i.e., species richness, species diversity, and equitability) were generally similar to each other (Figure 2.3). The horizontal extremities of the NMS configuration contrasted metrics of species evenness and species richness, with other intermediary metrics being a mixture of these two components (Figure 2.3). For example, because the Shannon-Wiener index of diversity is computed in consideration of species richness and species evenness, it is situated midway between the richness and evenness extremities in multidimensional space. Vertically, E , S_{raw} , S_{rare} , and S_{Margalef} were contrasted against d , $1-D$, and $S_{\text{Menhinick}}$. Menhinick's species richness may be correlated with dominance measures because it is sensitive to highly abundant (dominant) species (Wilhm 1967).

Hierarchical variable relationships

Statistically significant relationships existed between primary variables and respective matrices of secondary variables, and between primary variables and fish biodiversity (tertiary) variables (Figure 2.4). Significant relationships were detected also between matrices of secondary variables and fish biodiversity variables (Figure 2.4).

Water quality and primary productivity were correlated with primary variables. Depth showed the strongest correlation with water quality variables ($\delta = 0.79$; $P < 0.001$). Surface area ($\delta = 0.40$; $P < 0.01$) and percentage of agricultural land ($\delta = 0.41$; $P < 0.10$) also were correlated with the suite of water quality variables. However, degree of lake-river interconnectedness was not correlated significantly with water quality variables. In each case, the CAP procedure selected $m = 2$ to 6 principal coordinates that accounted for 67 -99% of the variability in the resemblance matrix constructed from normalized water quality variables. Depth was the only primary variable that was correlated significantly with primary productivity variables ($\delta = 0.68$; $P < 0.001$). In this case, the CAP procedure selected $m = 2$ principal coordinates that accounted for 94% of variability in resemblance matrix constructed from normalized primary productivity variables.

As for the relationship between each primary variable and the matrix of fish biodiversity variables, percentage of agricultural land showed the strongest correlation with fish biodiversity ($\delta = 0.85$; $P < 0.001$), followed by lake surface area ($\delta = 0.51$; $P < 0.05$) and depth ($\delta = 0.50$; $P < 0.05$). In each case, the CAP procedure selected $m = 1$ to 9 principal coordinates that accounted for 95 to 98% of variation in the resemblance matrix constructed from fish biodiversity variables. Fish biodiversity was generally greater in large, deep lakes with lesser proportions of watershed agricultural land. Contrary to my

expectations, overall degree of lake-river interconnectedness was not correlated significantly with fish biodiversity metrics, possibly due to an inadequate measure of connectivity.

Of the suites of secondary variables, only primary productivity variables were correlated significantly with fish biodiversity metrics ($m = 2$; $P < 0.05$). As primary productivity increased, fish biodiversity generally decreased. The CAP procedure identified two canonical axes that captured most of the association between primary productivity variables and fish biodiversity variables. The first and second canonical correlations, indicating strength of the association between the matrix of fish biodiversity variables and the matrix of primary productivity variables, were $\delta_1 = 0.51$ and $\delta_2 = 0.20$, respectively. The analysis found similar canonical correlations between water quality variables and fish biodiversity variables ($\delta_1 = 0.52$; $\delta_2 = 0.46$), but these correlations were not significant statistically.

Discussion

Results from this study suggest strongly that selected primary variables are important in controlling variation in suites of secondary (i.e., water quality and primary productivity) and tertiary (i.e., fish biodiversity) variables. Results did not meet my initial expectations as stronger correlations were found between the primary variables and fish biodiversity, than between secondary variables and fish biodiversity; however, this is not to say that secondary variables are not important in affecting fish biodiversity. Overall, maximum depth and percentage of agricultural land seem to be not only the most

important primary variables, but the most important overall variables, influencing water quality, primary productivity, and fish biodiversity variables.

Depth, secondary variables, and fish biodiversity

Maximum depth had the strongest and most significant correlation with suites of water quality and primary productivity variables, indicating that depth is a major determinant over abiotic community and thus likely a significant force in organization of floodplain lake fish assemblages. Water transparency is largely influenced by depth. Deeper lakes tend to have greater water transparency than shallow lakes because they are less at the mercy of wind and biologically-induced turbation (Schelske et al. 1995). Sediments and substrates that would otherwise remain in suspension in shallow systems are allowed to settle out and the increased depth dampens ability of wave action and benthivorous fishes to agitate benthic sediments (Shorman and Cotner 1997). Potential impacts of water transparency on the fish assemblage under the influence of depth are well-summarized by the piscivory-transparency-morphometry (PTM) model of Rodríguez and Lewis (1997). The PTM model predicts that relative abundance of sight-feeding piscivores and abundance of fishes with low-visibility tactile-feeding adaptations should vary predictably as water transparency declines following reductions in lake depth and subsequent resuspension of benthic sediments (Hamilton and Lewis 1990; Rodríguez and Lewis 1997). Variation in abundance of different groups of fishes may have a marked effect on metrics of species evenness, dominance, and diversity. Additionally, sight-feeding piscivores keep populations of forage fish in check, and a reduction in

predators may enable forage fish to become dominant, again affecting metrics of species evenness, dominance, and diversity.

Depth is largely responsible for the thermal, chemical, and light stratification of freshwater lakes (Dodson 2005). The relationship between density and temperature is responsible largely for vertical temperature stratification within freshwater systems (Dake and Harleman 1969). Because solubility of oxygen varies with temperature, dissolved oxygen profiles often mirror those of temperature (Brönmark and Hansson 2005).

Shallow lakes may experience large fluctuations in dissolved oxygen in part because resuspended sediments (due to wave action and bioturbation) can result in increases in water column and sediment respiration (Roozen et al. 2003). Maintenance of high water levels (i.e., increased depth) is an effective method to avoid unsuitable DO events in floodplain lakes (Miranda et al. 2001). Depth may limit algae production in deeper lakes because nutrients required for photosynthesis may be trapped below the euphotic zone barring lake turnover, ultimately resulting in a lesser summertime fluorescence of chlorophyll-*a*. Shallow lakes experience greater rates of planktonic photosynthesis because required nutrients remain within the euphotic zone (Nõges 2009). This property is related to the vertical stratification of light as different wavelengths are filtered out along depth gradients (Kirk 1985; Dodson 2005).

Aspects of fish biodiversity are likely directly and indirectly affected by depth and the forces that it exerts on secondary variables. Depth likely augments habitat heterogeneity in that deeper lakes may have a vertical stratification of complex habitats (Gorman 1987). A greater complexity of habitats could permit exploitation by a greater number of species. Deeper oxbow lakes provide greater environmental stability

(supporting a greater diversity of fishes) and habitat persistence and are usually exempt from adverse environmental conditions and periodic desiccation that may affect shallow lakes (Zeug et al. 2005; Shoup and Wahl 2009). Shallow lakes that experience periodic desiccation and frequently harsh environmental conditions likely have species-depauperate fish assemblages limited to species suited for rapid colonization such as orangespotted sunfish and mosquitofish (*Gambusia affinis*) and fishes tolerant of poor water quality. Conversely, deeper, more environmentally stable lakes may support stable fish assemblages (Jester et al. 1992).

Agriculture, secondary variables, and fish biodiversity

It was no surprise that percentage of watershed agricultural land was important in controlling variation in water quality variables and fish biodiversity variables. Numerous other studies have identified variables stemming from agricultural practices as influencing habitat degradation (e.g., Lucas 1985), water quality (e.g., Hall et al. 1999), and overall fish assemblage characteristics (e.g., Walser and Bart 1999). Unfortunately, most impacts of agricultural land on water quality variables are negative. Without proper watershed management, floodplain lakes may experience an increase in suspended sediment loads in the water column, followed by a decrease in water transparency. Suspended sediment loads can result in increased water column respiration, decreasing dissolved oxygen concentrations (Roozen et al. 2003). Physical effects of land development include increased suspended sediment loads, silt deposition, and increased nutrient loading (Cooper 1987; Cooper and McHenry 1989; Miranda et al. 2001; Schweizer and Matlack 2005). Sedimentation and its linked effects on water quality

variables are perhaps the most notable impact of agricultural use in floodplain-river systems. Floodplain lakes within the Mississippi Alluvial Valley experienced a 50-fold increase in sedimentation rates with the clearing of land for agricultural purposes (Wren et al. 2008). Percentage of agricultural land may couple with effects of depth to influence water quality variables in that increased sedimentation leads to an eventual reduction in depth. Thus, lakes with high sedimentation rates would experience accelerated lake-shallowing and eventually be subject to environmental conditions typical of shallow lakes (i.e., increased turbidity, large fluctuations in DO) and an unfavorable shift in fish assemblage characteristics (Miranda 2010). For example, homogenization of benthic substrates may eliminate species with substrate-specific spawning behaviors (e.g., lithophilic spawners, phytolithophilic spawners; Winemiller and Rose 1992). Negative effects of agricultural practices on water quality variables can be mitigated by simple implementation of best management practices (BMPs) designed to prevent influx of agricultural inputs into floodplain lakes.

Contrary to my expectations, percentage of agricultural land surrounding each lake was not correlated significantly with primary productivity variables. High concentrations of suspended sediments from agricultural runoff increase attenuation rate of light (Kirk 1985; Dodson 2005) and water column respiration (Roozen et al. 2003) and decrease photosynthetic capacity of primary producers (Wood and Armitage 1997). Runoff from agricultural fields may contain high concentrations of nitrogen and phosphorous-based pesticides and fertilizers, contributing to eutrophication of floodplain lakes as indexed by fluorescence of chlorophyll-*a* and phycocyanin and by the chlorophyll-*a*:phycocyanin ratio.

Surface area, secondary variables, and fish biodiversity

In my study, lake surface area was only weakly, but nonetheless significantly, correlated with water quality variables and fish biodiversity. Surface area may influence dissolved oxygen concentrations in that lakes with a larger surface area often have a larger fetch, allowing for wind action to agitate the epilimnion. Accordingly, a greater amount of atmospheric oxygen may become dissolved in the water (Dodson 2005). A larger surface area also provides a greater area for absorption of solar radiation, resulting in increased epilimnetic temperatures. Lake area also has been shown to affect pH (Rago and Wiener 1986; Matuszek and Beggs 1988). It is probable that additional correlations between surface area and the water quality variables and primary productivity variables are dampened by the combined effects of the other fundamental environmental variables. For example, reductions in surface area are typical of floodplain lakes undergoing successional processes of depth reduction and increased disconnection (Miranda 2005; Shields et al. 2010), thus, instead of having a significant individual effect, surface area may interact with other primary variables to have a significant collective effect on suites of secondary and tertiary variables.

The relationship between biodiversity and area is well-known and has had many ecological applications (e.g., the theory of island biogeography; MacArthur and Wilson 1967). In floodplain lakes, the species-area relationship is likely a function of lake area and a balance between immigration (colonization) and local extinction events. Area itself usually has no direct effect on organisms (Wright 1983), rather, greater area is correlated commonly with greater habitat complexity, and a lake with greater habitat heterogeneity is theoretically able to support more species with adaptations to exploit all available

habitats. Although surface area seems to be an important factor affecting fish biodiversity, it is likely of little concern to most aquatic scientists and biologists interested in floodplain restoration simply because it is difficult to manipulate; little can be done to alter direct effects of surface area on water quality variables, primary productivity variables, and fish biodiversity.

Connectivity, secondary variables, and fish biodiversity

Lake-river interconnectedness was an extremely influential component of floodplain ecosystem dynamics prior to major landscape modifications in the region (Junk et al. 1989). Previous studies have shown connectivity to affect water quality and primary productivity variables (Knowlton and Jones 1997; Galat et al. 1998), and to affect fish diversity and structure of fish assemblages (Miranda 2005; Zeug et al. 2005; Shoup and Wahl 2009; Miyazono et al. 2010). Therefore, connectivity was expected to be strongly and significantly associated with the suites of secondary habitat variables and with fish biodiversity. Nevertheless, among the selected primary variables, degree of lake-river interconnectedness was one of the least-correlated primary variables with the suites secondary and fish biodiversity variables.

It is probable that any linearity in effects of connectivity on floodplain lake water quality, primary productivity, and fish biodiversity variables is masked by effects of other primary variables or by an unsuitable index of lake-river interconnectedness. For example, as oxbow lakes become further-disconnected from their parent rivers, they undergo various successional changes in a trajectory towards terrestrialization (Shields et al. 2010). These changes typically include reductions in depth and surface area (Miranda

2005). Isolated oxbow lakes, especially those situated outside of protected areas, are surrounded primarily by agricultural land. Thus, an analysis looking at the individual effects of connectivity on habitat variables may actually be confounding effects of connectivity with the combined effects of other primary variables. Occasionally, due to anthropogenic alterations, lakes farther from the river may actually experience connection on a more frequent basis than lakes situated only a short distance from the river. Distance between a lake and its river also may be confounded by presence of the levee system or flood control structures. Thus, it is likely that effective distance is a useful index of connectivity up to some point beyond which it is confounded by other factors, limiting its overall utility and reliability as a measure of lake-river interconnectedness.

In some cases, effective distance may be a suitable measure of lake-river interconnectedness, and it may be that effects of connectivity are reflected more in fish assemblage composition than in fish biodiversity metrics. Fish biodiversity in a more-connected lake may be similar to that of an isolated lake; however, the fish assemblage structure itself may be substantially different. Fish assemblages in well-connected oxbows tend to include a greater representation of large-bodied riverine species (Miranda 2005; Zeug et al. 2005). Riverine species may simply replace lacustrine species in well-connected lakes, changing overall fish assemblage composition but generally leaving fish biodiversity unaffected, or affected minimally so that our sampling could not detect the change. The limited utility and general unreliability of effective distance as an index of lake-river interconnectedness; however, leaves much to be desired in terms of a measure of connectivity. In any case, further research is needed in understanding effects of

connectivity on fish biodiversity and overall assemblage composition, as well as in development of a high-utility index of lake-river interconnectedness.

Primary productivity, water quality, and fish biodiversity

Of the suites of secondary variables, only primary productivity variables were correlated significantly with fish biodiversity. The observed trend of decreasing fish biodiversity in lakes with higher trophic states was surprising given the relationship between productivity and biodiversity. The relationship between primary productivity and fish biodiversity is best characterized by the species-energy hypothesis, which asserts that energy availability generates and maintains gradients of species richness and diversity (Hawkins et al. 2003). In general, biodiversity of a given community is limited by the energy supply supporting that community. Similar to the species-area relationship (MacArthur and Wilson 1967), the greater the total resource base, the greater the likelihood that there will be a greater variety of resource types, thus theoretically supporting a greater diversity of species (Wright 1983). In a review of broad-scale patterns of species richness and diversity, Hawkins et al. (2003) found that in most empirical studies, most of the variance in vertebrate species richness was explained by water energy, as measured either directly or indirectly as primary productivity.

However, it is important to note that many of the study lakes are likely situated at a higher trophic status than those of most other studies. For example, in an analysis of biotic integrity in relation to lake productivity, Schulz et al. (1999) classified lakes along a gradient of trophic status from oligotrophic to hypereutrophic. Lakes classified as hypereutrophic had a mean Secchi visibility of 119 cm, whereas mean Secchi visibility of

lakes included in this study was 50 cm. Thus, by these standards, lakes included in this study are beyond hypereutrophic and fish biodiversity within them may be limited by too much productivity as opposed to too little productivity. Similar reductions in species numbers and abundance as a function of extreme hypereutrophication also have been noted in other studies (Kautz 1982; Lee et al. 1999).

Because patterns of local diversity depend on local abiotic characteristics (Tales and Berrebi 2007), I expected strong and significant correlations between the water quality variables and fish biodiversity. Instead, I observed a relatively weak and non-significant interaction. The lack of a stronger interaction could have been a function of sampling design. Some of the measured water quality variables have wide diurnal fluctuations, thus, some of the variance in the water quality matrix is likely due to variation in timing of sample collection. Increased variability in the water quality matrix could have distorted relationships with fish biodiversity. For example, there are often notable diurnal changes in DO concentration, DO saturation, and temperature, especially in shallow systems (Dodson 2005; Miranda 2005). The variability cannot be avoided even when water quality samples are collected at fixed stations or times because day-to-day changes in cloud cover and wind action can change local conditions. The greater temporal consistency of the primary productivity variables also may have contributed to their having a stronger correlation with fish biodiversity. It is likely, however, that the water quality variables collected are sufficient; had they been inadequate, the significant correlations between the primary variables and water quality variables probably would not have been observed. Magnitudes of correlations were similar between water quality variables and fish biodiversity, as between primary productivity variables and fish

biodiversity, but the former correlations were not significant statistically. Although not significant statistically, these results should be interpreted with ecological discretion.

Ecological applications

Results herein provide the framework for a conceptual model that identifies individual and collective influences of variables from different scales on each other and ultimately on oxbow lake fish biodiversity. This conceptual model is centered on the relationships between depth and secondary and tertiary variables and between percentage of agricultural land and secondary and tertiary variables. Although hierarchically distant from fish biodiversity compared to suites of water quality variables and primary productivity variables, depth and percentage of agricultural land should become the focus of floodplain lake management schemes. In addition to suggesting a conceptual model, the results also can be viewed as a circular model of floodplain lake management in that primary variables can be manipulated for conservation and restoration purposes and secondary and tertiary variables can be used to monitor success of such efforts. Similarly, the model may be useful in adaptive management of floodplain ecosystems. Results will encourage aquatic ecologists to consider interactions of ecosystem components in making decisions regarding management schemes. Although I have taken a reductionist approach to the analysis by examining interactions between individual ecosystem components, results will ultimately foster development of a more holistic approach to floodplain ecosystem conservation and management.

Table 2.1. Descriptive statistical properties of primary variables, secondary variables, and fish biodiversity variables collected from 54 oxbow lakes in the Mississippi Alluvial Valley, 2006-2010.¹

Variable	Mean	SD	CV	Min	25 th	Median	75 th	Max
<i>Primary</i>								
Depth (m)	2.8	1.7	61	0.50	1.6	2.3	3.9	8.6
Surface area (km ²)	0.74	1.2	159	0.01	0.1	0.22	0.73	5.7
Agriculture (%)	47	26	56	0	32	54	68	77
Connectivity (km)	2.5	2.9	120	0	0.2	1.7	3.5	14
<i>Secondary</i>								
Secchi (cm)	50	21	43	15	35	49	66	105
Temperature (°C)	29	1.7	5.7	26	28	30	31	34
DO (mg l ⁻¹)	6.2	1.9	31	1.5	5	5.9	7.1	11
DO saturation (%)	82	25	30	19	67	78	97	147
pH	7.2	0.64	9	5.2	6.8	7.1	7.6	9.5
Turbidity (NTU)	29	23	81	4.7	14	24	32	113
Chlorophyll- <i>a</i>	286	187	66	65	174	238	361	964
Phycocyanin	2.5	2.1	84	0.25	1.1	1.7	3.2	9.6
Chl- <i>a</i> :Phyco	160	97	60	19	93	145	207	426
<i>Fish Biodiversity</i>								
S _{raw}	25	7.8	32	12	19	24	28	44
S _{rare}	13	3.1	24	6	11	13	15	23
S _{Margalef}	3.7	1.2	31	1.9	2.9	3.4	4.3	6.7
S _{Menhinick}	1.2	0.38	32	0.44	0.89	1.2	1.4	2.1
H'	2.1	0.40	20	0.63	1.8	2.1	2.3	2.8
F _α	5.5	2.1	39	2.3	4.1	5.3	6.6	12
E	0.35	0.11	30	0.12	0.27	0.34	0.43	0.62
J	0.65	0.11	17	0.23	0.58	0.66	0.73	0.82
d	0.41	0.15	36	0.21	0.30	0.36	0.51	0.88
1-D	0.25	0.12	47	0.12	0.17	0.21	0.33	0.77

¹ SD = standard deviation; CV = coefficient of variation; Min = minimum; 25th = 25th quantile; 75th = 75th quantile; Max = maximum. Of the secondary variables, Secchi = Secchi visibility, DO = dissolved oxygen, and Chl-*a*:Phyco = chlorophyll-*a*:phycocyanin ratio. Chlorophyll-*a* and phycocyanin were measured in relative fluorescence units. Fish biodiversity metrics included raw species richness (S_{raw}), rarefied species richness (S_{rare}), Margalef's species richness (S_{Margalef}), Menhinick's species richness (S_{Menhinick}), Shannon-Wiener diversity (H'), Fisher's diversity (F_α), Buzas and Gibson's evenness (E), Pielou's evenness (J), Berger-Parker dominance (d), and Simpson's dominance (1-D).

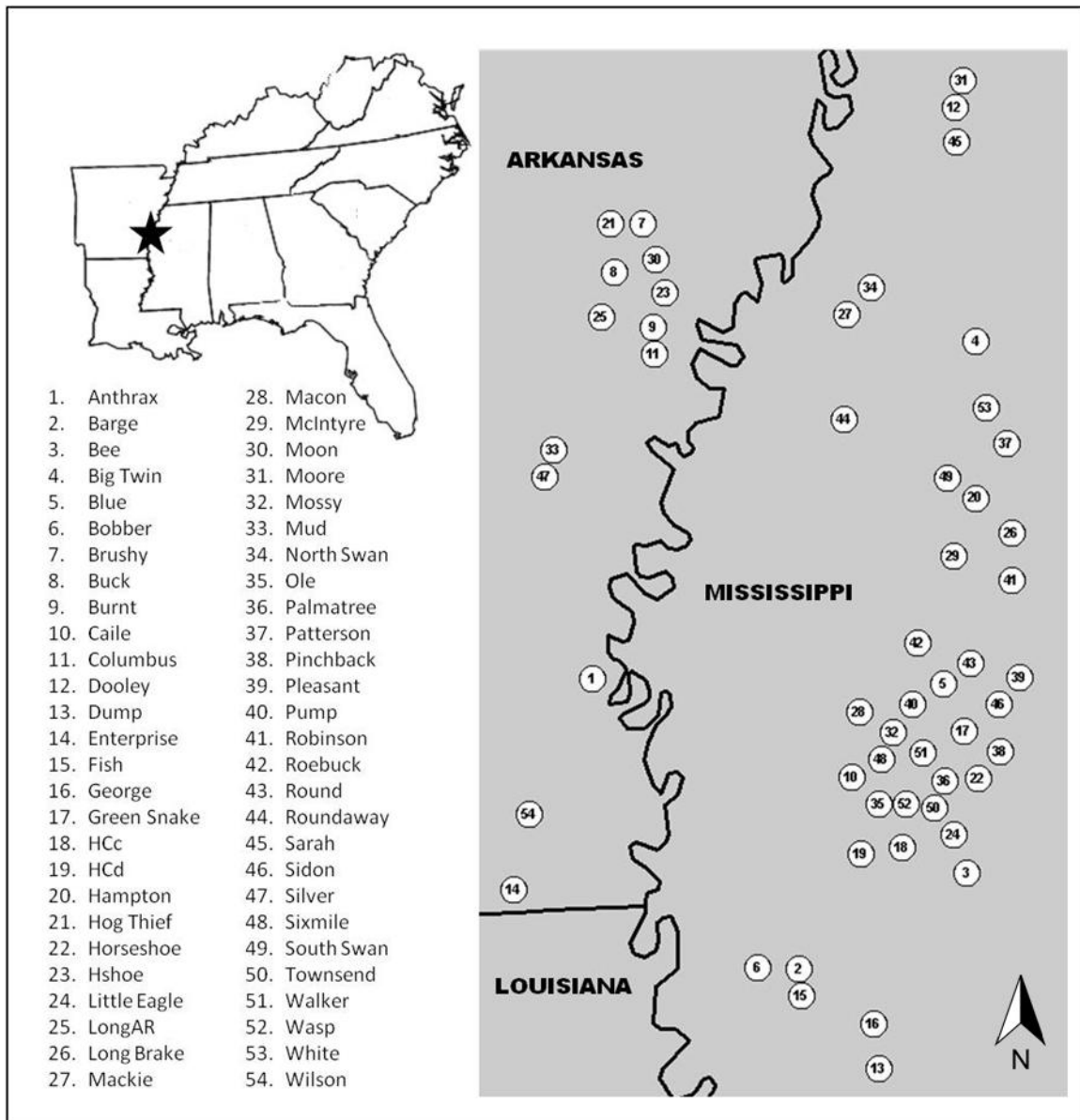
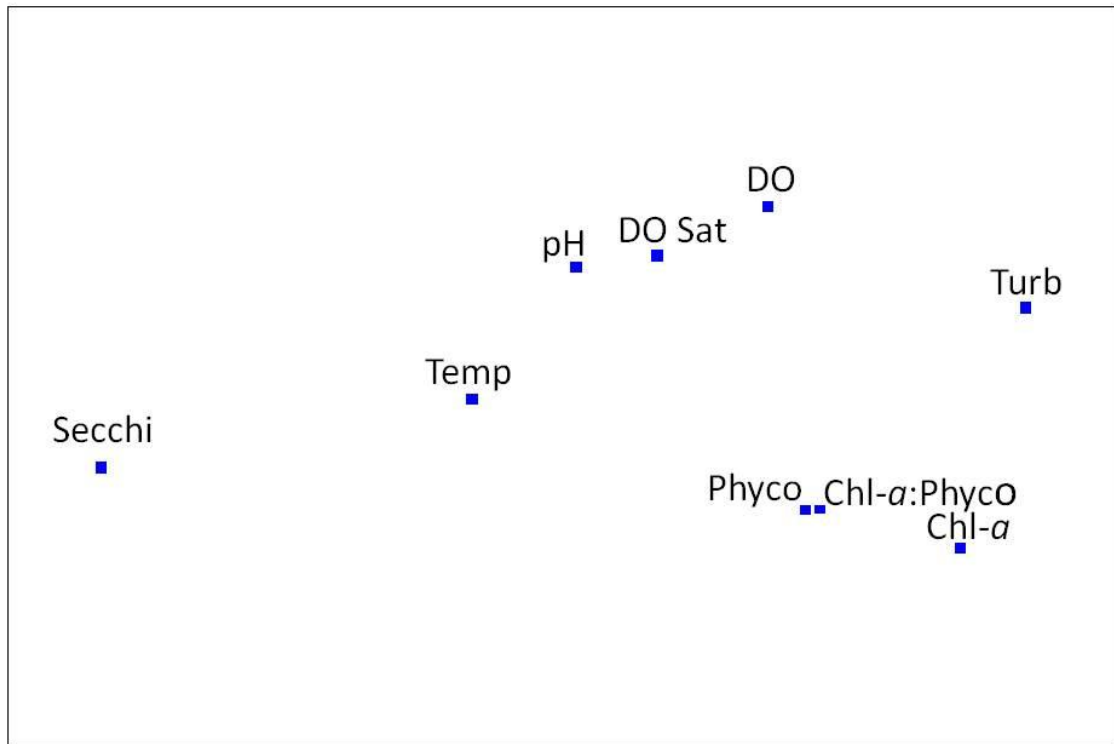
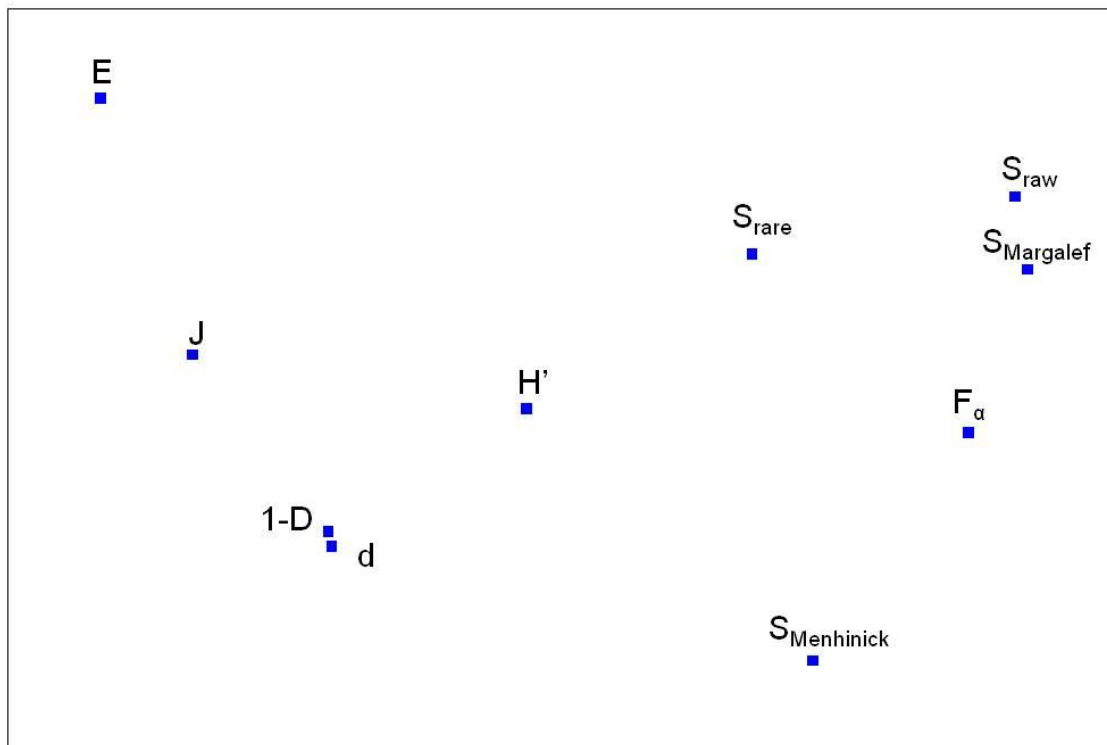


Figure 2.1. Map of the Lower Mississippi Alluvial Valley region of Mississippi and Arkansas, with names and locations of 54 lakes sampled from 2006-2010. The inset identifies location of the study region in the southeastern United States.



Variable	Phyco	Chl- <i>a</i>	Chl- <i>a</i> :Phyco	Secchi	Turb	Temp	DO	DO Sat
Phyco								
Chl- <i>a</i>	0.42							
Chl- <i>a</i> :Phyco	0.86	0.81						
Secchi	-0.29	-0.56	-0.50					
Turb	0.17	0.39	0.33	-0.70				
Temp	0.02	-0.13	-0.07	0.07	-0.07			
DO	0.21	0.10	0.18	-0.37	0.22	0.10		
DO Sat	0.15	0.02	0.10	-0.25	0.06	0.41	0.54	
pH	0.18	-0.15	0.01	-0.14	0.06	0.35	0.32	0.66

Figure 2.2. Nonmetric multidimensional scaling configuration of water quality and primary productivity variables including Secchi visibility (Secchi), temperature (Temp), pH, dissolved oxygen (DO), dissolved oxygen saturation (DO Sat), turbidity (Turb), phycocyanin fluorescence (Phyco), chlorophyll-*a* fluorescence (Chl-*a*), and ratio of chlorophyll-*a* to phycocyanin (Chl-*a*:Phyco) for 54 oxbow lakes in the Mississippi Alluvial Valley, 2006-2010. Similar variables are plotted close together, whereas dissimilar variables are plotted far apart. The table below is the Pearson correlation coefficient matrix from which the ordination similarity measure was obtained.



Metric	S_{raw}	S_{rare}	1-D	H'	E	$S_{Menhinick}$	$S_{Margalef}$	J	F_{α}
S_{raw}									
S_{rare}	0.81								
1-D	-0.41	-0.70							
H'	0.62	0.88	-0.94						
E	-0.25	0.27	-0.69	0.57					
$S_{Menhinick}$	0.62	0.73	-0.61	0.76	0.27				
$S_{Margalef}$	0.96	0.85	-0.46	0.68	-0.14	0.73			
J	0.13	0.58	-0.92	0.85	0.90	0.54	0.23		
F_{α}	0.91	0.85	-0.53	0.74	-0.02	0.88	0.95	0.34	
d	-0.38	-0.64	0.96	0.91	-0.70	-0.63	-0.44	-0.89	-0.53

Figure 2.3. Nonmetric multidimensional scaling configuration of fish biodiversity metrics including raw species richness (S_{raw}), rarefied species richness (S_{rare}), Margalef's species richness ($S_{Margalef}$), Menhinick's species richness ($S_{Menhinick}$), Shannon-Wiener diversity (H'), Fisher's diversity (F_{α}), Buzas and Gibson's evenness (E), Pielou's evenness (J), Berger-Parker dominance (d), and Simpson's dominance (1-D) for 54 oxbow lakes in the Mississippi Alluvial Valley, 2006-2010. Similar metrics are plotted close together, whereas dissimilar metrics are plotted far apart. The table below is the Pearson correlation coefficient matrix from which the ordination similarity measure was obtained.

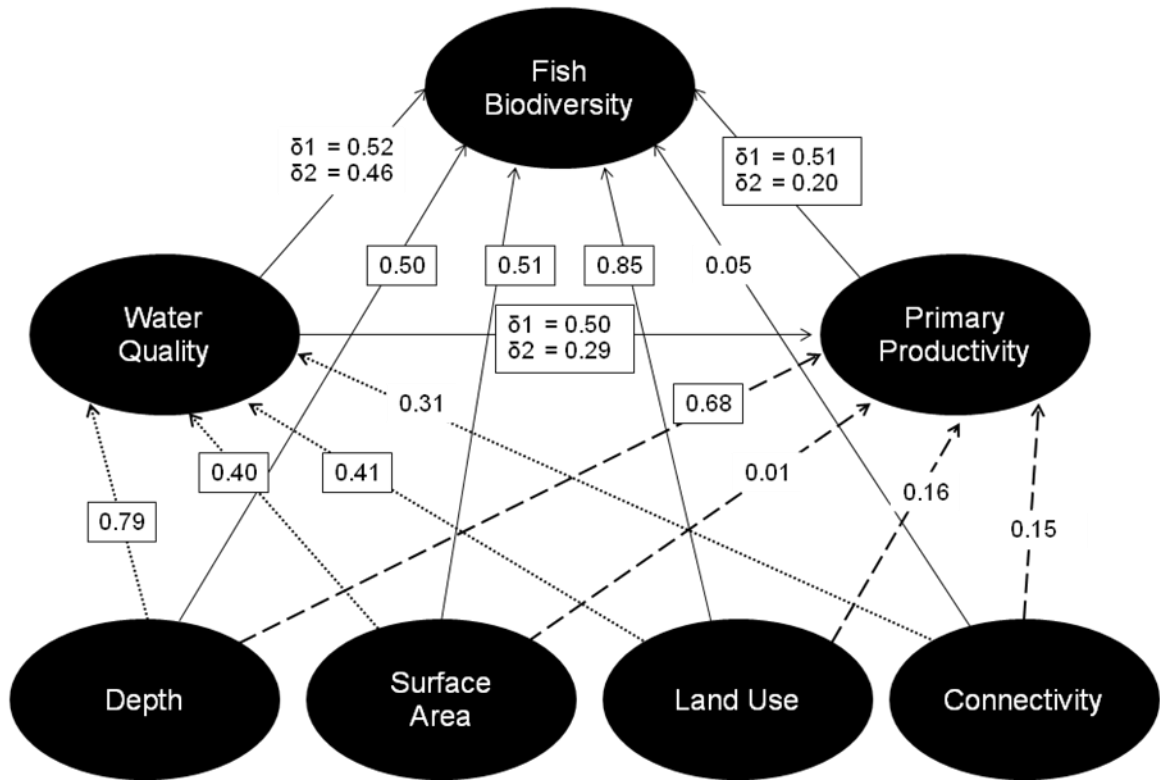


Figure 2.4. Canonical correlations between hierarchical oxbow lake ecosystem components. Depth, surface area, land use, and connectivity were assigned as primary variables. Suites of water quality variables (temperature, Secchi visibility, dissolved oxygen concentration, dissolved oxygen saturation, turbidity, and pH) and primary productivity variables (phycocyanin fluorescence, chlorophyll-*a* fluorescence, and ratio of chlorophyll-*a* to phycocyanin) were assigned as secondary variables. Fish biodiversity variables (raw species richness, rarefied species richness, Margalef's species richness, Menhinick's species richness, Shannon-Wiener diversity, Fisher's diversity, Berger-Parker dominance, Simpson's dominance, Buzas and Gibson's evenness, and Pielou's evenness) were assigned as tertiary variables. Dotted lines show correlations between primary variables and the suite of water quality variables. Dashed lines show correlations between primary variables and the suite of primary productivity variables. Solid lines show correlations between primary variables and fish biodiversity, between groups of secondary variables, and between secondary variables and fish biodiversity. Relationships between variables were assessed using canonical analysis of principal coordinates. Boxed correlations are statistically significant at $\alpha = 0.10$.

CHAPTER III
FISH ASSEMBLAGES IN TWO DISJOINED SEGMENTS OF AN OXBOW LAKE
CONNECTED TO AND ISOLATED FROM THE YAZOO RIVER

Introduction

Connectivity has long been recognized as a fundamental concept in ecology (MacArthur and Wilson 1967; Merriam 1984; Taylor et al. 1993). Connectivity is most often referred to as the degree to which the environment promotes or impedes movement of organisms among resource patches (Taylor et al. 1993; Tischendorf and Fahrig 2000), although numerous disciplines have adopted varying definitions on the same theme (Magnuson et al. 1998; Ward et al. 1999; Tetzlaff et al. 2007). Connectivity and its inverse, isolation, may affect ecosystem attributes such as species richness and biodiversity by influencing colonization and extinction rates (Lindborg and Eriksson 2004). A highly connected site may exhibit greater species richness and diversity because colonization variables (i.e., among-site variables) may exert a greater influence on the system than extinction variables (i.e., within-site variables). Although various factors contribute to augmentations and reductions in species richness and biodiversity (Chapin and Walker 1997; Vitousek and Mooney 1997), specific mechanisms behind fluxes in ecosystem attributes remain obscure (Harrison and Bruna 1999). Understanding the role of connectivity in influencing species richness and biodiversity is especially

important because of the degree to which connectivity has been anthropogenically altered (Pringle 2003).

River systems are perhaps the most anthropogenically altered ecosystems in the world (Dynesius and Nilsson 1994). Regulation of lotic systems has altered riverine connectivity along vertical, temporal, longitudinal and lateral dimensions (Ward 1989). Vertical connectivity incorporates interactions between the river channel and groundwater within the hyporheic zone. The temporal dimension implies that lotic systems and their attributes are dynamic through time. For fish, longitudinal connectivity in terms of upstream and downstream migration is probably the most well-recognized dimension (Calles and Greenberg 2009), but the lateral dimension is extremely important for fulfilling fish life history requirements and providing other lotic ecosystem services. Lateral connectivity in lotic systems is best characterized by the flood-pulse concept (Junk et al. 1989), in which seasonal high water periodically inundates the floodplain, providing a linkage between the channel and extra-channel habitats (of which floodplain lakes are prominent). In many floodplain river systems, lateral connectivity has been interrupted by levees, revetted banks, and other channel modification projects initiated to protect urban areas and agricultural investments. A small number of lakes remain inside the levees, but a vast majority have lost their riverine component. Alteration to the connectivity regime has ultimately resulted in hindrance of productivity of natural resources and disruption of natural processes that structure fish assemblages and maintain fish biodiversity in floodplain lakes (Bayley 1995; Rodríguez and Lewis 1997).

Construction of channel containment features has prevented river systems from evolving; that is, floodplain lakes are being created far less often than when rivers were

unregulated (Matthes 1947). Furthermore, disconnected lakes are subject to ecological succession to terrestrial environments and thus biotic integrity, as measured with fish assemblage metrics, may be compromised. To protect and improve biotic integrity of these relict ecosystems, an understanding of the influence of connectivity on fish species richness, diversity, and assemblage composition is essential.

I examined the interaction between connectivity and fish species richness, diversity, and assemblage composition in Hard Cash Lake, a floodplain lake of the Yazoo River in north-central Mississippi, USA. The lake is bisected by the Yazoo River levee system, effectively leaving part of the lake connected to the river and part of the lake disconnected. Earlier studies of the effect of connectivity on fish assemblages have relied on multiple lakes with differing levels of connection from adjacent rivers (Miranda 2005; Zeug et al. 2005; Shoup and Wahl 2009; Miyazono et al. 2010). As lakes become progressively disconnected, they undergo various successional environmental changes in a trajectory towards terrestrialization (Shields et al. 2010). Hence, earlier studies have confounded loss of connectivity with other effects of lake aging. My study represents a unique experimental situation because by splitting the lake with a levee, both segments are the same age. Thus, confounding a loss of connectivity with effects of environmental changes associated with succession was avoided and effects of connectivity were isolated. Results were expected to provide ecological insight that may aid in future management actions designed to restore and maintain fish assemblage attributes and overall biotic integrity in floodplain lakes.

Study Site

Hard Cash Lake (30°07'52.12"N, 90°30'39.80"W) is an oxbow lake of the Yazoo River located in Humphreys County, Mississippi, USA (Figure 3.1). Oxbow lakes are created naturally when bends of a meandering river are cut off and abandoned resulting from sediment deposition or artificially due to anthropogenic alteration (Biedenharn et al. 2000). Hard Cash Lake was created artificially when the Yazoo River levee system was completed in the 1890s (R. Easley, Yazoo-Mississippi Delta Levee Board, personal communication). The levee bisects the lake into two segments, one of which is connected to the river and one of which is isolated. The connected segment will hereafter be referred to as Hard Cash connected (HCc), while the isolated segment will be referred to as Hard Cash disconnected (HCd). HCc retains connectivity to the Yazoo River by way of a connection channel on its northernmost end (Figure 3.1). The connection channel is approximately 60 m long and 2.5 m wide during low water. HCd is isolated from both HCc and the Yazoo River by the levee and is periodically stocked by the Mississippi Department of Wildlife, Fisheries and Parks (MDWFP).

The two segments are similar in their local environmental attributes. The most notable difference between the two, aside from the marked difference in connectivity, is a large difference in surface area. HCc is the smaller of the two segments with a surface area of approximately 5 ha, length of 0.70 km, and mean width of 67 m. HCd has a surface area of approximately 31 ha, length of 4.5 km, and mean width of 77 m. Both segments have a maximum depth of 5.2 m. Mean fluorescence of chlorophyll-a (fluorescence units; FU) was similar in both segments (131 FU and 123 FU in HCc and

HCd, respectively) and land use surrounding both segments is dominated by row-crop agriculture (60% and 70% in 500 m buffer surrounding HCc and HCd, respectively).

Methods

Connectivity with Yazoo River

Frequency and duration of connectivity between HCc and the Yazoo River was estimated using river stage data and elevation of the connection channel. River stage data were available from the U.S. Army Corps of Engineers gage station (Station ID #CE48D3CO; USACE 2010) approximately 5.5 river kilometers upstream from the connection channel. The highest elevation point on the channel connecting the Yazoo River with HCc was identified onsite with a Trimble GeoXT™ handheld GPS unit (Trimble Navigation Limited, Sunnyvale, California). Elevation data were adjusted to account for a small difference in elevation between the gage station and the connection channel. Whenever river stage elevation exceeded the highest elevation point in the connection channel, HCc was assumed to be connected to the river.

Fish collections

Fish assemblages in the Hard Cash lakes were estimated on four occasions from June 2007 through June 2010. HCd was sampled in 2007, 2009, and 2010 and HCc in 2009 and 2010. Access constraints allowed matching sampling periods only in 2009 and 2010. Sampling of HCc occurred during periods of disconnection. Fish were collected during daytime hours by a boat electrofisher equipped with a GPP 7.5 Smith-Root™

pulsator unit (Smith-Root, Inc., Vancouver, Washington). Pulsed DC electricity was cycled at 60 Hz with voltage output adjusted according to the specific conductivity of each segment to maintain a constant output of 6-8 A. Individual samples consisted of 0.25 h of continuous electrofishing along random shoreline areas. Sampling lasted 0.75 – 1.5 h depending on lake area. Fish were netted from the bow of the boat by two netters equipped with 2.7 m dip nets with 0.4 cm bar mesh. Fish were identified to species and counted before release near the site of capture. Those species difficult to identify in the field were preserved in a 10% formalin solution and transported to the lab for positive identification with taxonomic keys (Ross 2001).

Fish assemblage descriptors

Differences in fish assemblage descriptors between HCc and HCd were examined using the compare-diversities module available with the PAST™ statistical software package (Hammer et al. 2001). The module computed several diversity indices (i.e., dominance, evenness, richness, diversity) for each lake segment and compared segments using a bootstrap randomization procedure. The bootstrap procedure creates 1,000 random replicate datasets by resampling the original dataset with replacement (Efron 1979; Hammer et al. 2001). Thus, confidence intervals and significance values can be computed to test the null hypothesis that there is no difference in fish species richness and assemblage composition between HCc and HCd.

To examine differences in fish functional group characteristics between the lakes, species were grouped into life-history guilds, micro-reproductive guilds, and trophic guilds prior to analysis as proposed by Balon (1990), Killgore and Hoover (1992),

Winemiller and Rose (1992), and Goldstein and Simon (1999), and implemented by Killgore and Hoover (1992), Aycock (2008) and Miyazono et al. (2010; Table 3.1). Life history classifications included periodic, equilibrium, and opportunistic strategists. Periodic strategists included long-lived, late-maturing, large-bodied, and highly fecund fish taxa. Equilibrium strategists included taxa of intermediate size, with moderate fecundity, high parental care, and moderate longevity. Opportunistic strategists included rapidly-maturing small-bodied fishes with low longevity and low fecundity. Micro-reproductive guilds classified fish taxa into groups according to specific spawning behavior. Pelagophilic spawners included egg-scattering fishes with buoyant eggs. Phytophilic spawners included those that deposit adhesive eggs on submerged woody debris or aquatic vegetation. Similarly, phytolithophilic spawners included those that deposit eggs on or near submerged aquatic vegetation; however, for phytolithophilic spawners the vegetative-spawning behavior is facultative. Lithophilic and lithopelagophilic spawners deposit eggs over rock or gravel substrata; lithophils have benthic larvae and lithopelagophils have pelagic larvae. Polyphilic spawners are generalists, depositing eggs over any available substrate. Speleophilic spawners deposit eggs in crevices, under rocks, or in any other hollow cavity. Viviparous spawners are live-bearers, with eggs typically developing within the mouth of the adult fish (mouth-brooders). Trophic guilds classified fish taxa into groups according to major dietary components. Trophic guilds included piscivores, detritivores, invertivores, planktivores, and herbivores. Combinations of trophic guilds were used to classify the feeding habits of fishes occupying various feeding guilds throughout different life stages. Chi-square tests for equal proportions (SAS Institute 2010, Cary, North Carolina) were used to assess

differences in frequencies of individuals within various functional groups between the two segments of the lake. Principal sources of differentiation between HCc and HCd were identified with the cell chi-square option, which computes the relative contribution of each guild class to the total chi-square statistic.

Results

Connectivity with Yazoo River

Annual river stage data (1944-2009) coupled with field measurements indicated that HCc is connected to the Yazoo River whenever river stage exceeds 7.65 m. The Yazoo River has been connected to HCc at least once per year since 1944, except 1963, 1967, 1981, and 1986. Connection occurred at a mean annual frequency of 1.94 (range 0-7 times per year). Individual periods of consecutive connection ranged from 1 to 203 days (mean = 47.2; SD = 53.6) but most periods of inundation lasted 50 days or less (Figure 3.2). The longest individual period in which HCc was continuously connected to the river occurred from 1982 to 1983 (203 days). Periods of connectivity strongly reflect regional precipitation events, with connection occurring most frequently in early spring (day of year 1 – day of year 150; Figure 3.3).

Fish collections

Over the multiyear sampling period, 4,276 fish representing 33 species (HCd = 22, HCc = 26) were collected during 7 h of electrofishing. Analyses were conducted with data from different years combined after preliminary analysis with a permutation analysis

of variance (PERMANOVA; Anderson 2001) and Bray-Curtis similarity measure indicated no significant among-year differences in samples taken in the connected segment ($P = 0.795$) or the isolated segment ($P = 0.851$). Twenty-two samples (yielding 3,567 individuals) were taken from HCd whereas 6 samples (yielding 709 individuals) were taken from HCc, for an effort of 18 min/ha in HCc and 11 min/ha in HCd. Collections of threadfin shad and gizzard shad did not accurately reflect their true abundance in either segment due to their fleeting behavior in response to energized water. Hence, they were excluded from analyses sensitive to species abundances (i.e., diversity, evenness, and dominance metrics) and from functional group compositional analyses. Seven species were collected only in HCd, and 11 species were collected only in HCc (Table 3.2). Silver carp *Hypophthalmichthys molitrix* and paddlefish *Polyodon spathula* were observed in HCc but evaded the electrical field and were not captured and therefore not counted as part of the collections.

Fish assemblage descriptors

The indices examined with the compare-diversities module were significantly ($P < 0.05$) different between HCc and HCd. Greater species diversity, richness, and evenness were observed at HCc (Table 3.3). Greater dominance was observed at HCd (Table 3.3); that is, relatively few species (i.e., bluegill, largemouth bass, and smallmouth buffalo) dominated the assemblage and composed the bulk of the fish collected. Chi-square tests indicated that there were significant ($P < 0.05$) differences in functional group percentage compositional data between HCc and HCd. Abundance of life history strategists differed significantly between the lakes ($\chi^2 = 68.9$; $P < 0.001$). Much of the

difference can be attributed to the larger proportion of periodic strategists in HCc as compared to HCd (Figure 3.4). Abundance of individuals within micro-reproductive guilds also differed significantly between HCc and HCd ($\chi^2 = 166.1$; $P < 0.001$). A larger proportion of individuals within the lithophilic reproductive guild was collected in HCc. Individuals within the pelagophilic reproductive guild were observed only in HCc (Figure 3.4). Western mosquitofish was the only viviparous fish observed during the study period, and was only collected in HCd (Figure 3.4). Frequencies of individuals within trophic guilds also differed significantly between HCc and HCd ($\chi^2 = 190.6$; $P < 0.001$). Piscivores were more abundant in HCc whereas detritivores were more abundant in HCd (Figure 3.4). Individuals within the planktivore-detritivore feeding guild were present only in HCc, whereas members of the invertivore-herbivore feeding guild were present only in HCd.

Discussion

Connectivity plays a substantial role in shaping fish assemblage attributes in floodplain lakes. Loss of stochastic flood events and habitat heterogeneity has resulted in reductions of species diversity, species richness, and species evenness in HCd that are otherwise maintained possibly at historic levels in HCc by means of frequent connection to the Yazoo River. Disregarding the connectivity variable, greater species richness and diversity would be expected at HCd in accordance with the species-area relationship (MacArthur and Wilson 1967; Gilbert 1980; Brown 1981). With a surface area roughly six times the size of HCc, HCd would be expected to have greater spatial and resource heterogeneity, thus theoretically supporting a greater diversity of fishes than its smaller

counterpart. However, despite a large difference in surface area, the smaller, frequently connected segment of the lake supported a more diverse, rich, and even fish assemblage. This observation counters the relationship that would be expected under the species-area relationship and suggests that connectivity is a key variable influencing fish species richness, diversity, and assemblage structure in floodplain lakes.

My findings are consistent with results of previous studies examining fish assemblage attributes among oxbow lakes. In a study of fish assemblage structure among oxbow lakes of the Brazos River (USA) species richness, diversity, and evenness were greatest in the most-connected oxbow lake (Winemiller et al. 2000). Miranda (2005) noted that more species were observed in oxbow lakes that connect to the Mississippi River (USA) than in lakes permanently separated from the river. Similarly, Galat et al. (1998) and Petry et al. (2003) observed greater species richness in connected floodplain water bodies of the Missouri (USA) and Paraná (Brazil) rivers, respectively, than in isolated floodplain water bodies. Miranda (2005) hypothesized that the greater species richness and diversity of fishes in frequently connected oxbow lakes may be attributable to the fish assemblages consisting of riverine and lacustrine species that are periodically mixed during inundation. Increased habitat heterogeneity in terms of lotic and lentic components in connected lakes also may facilitate maintenance of a more rich, diverse, and even fish assemblage. Periodic inundation allows for homogenization of river and floodplain fish assemblages and “rejuvenation” of the fish assemblage, thereby maintaining species richness and diversity.

The species observed only in HCc (e.g., black buffalo, longnose gar, river carpsucker spotted sucker, white bass) are typically riverine and are periodic life history

strategists. Because most floodplain river fishes are adapted to inhabit the lotic and lentic components of a river (Fernando and Holčík 1982), these fishes are well-suited for the dynamic environment of HCc. All species collected only in HCc migrate upstream for spawning and may benefit from the riverine conditions of HCc during high water. During periods of high water, the connection channel provides a pathway for ichthyofaunal exchange from the main river channel into HCc. Kwak (1988) found increases in lateral movement of fishes between the river channel and floodplain habitats in response to increasing river discharge, thus, colonization of HCc likely occurs annually in early spring when frequency and duration of connection is greatest. This ichthyofaunal exchange continually refreshes the fish assemblage of HCc; however, further study is needed to quantify species turnover rates and patterns of movement between the river channel and HCc. Moreover, although much of the substrate of HCc is silt and clay, periodic strategists with lithophilic spawning behavior likely exploit rock or gravel substrata that becomes available from the scouring action of flood waters (Trush et al. 2000).

The species observed only in HCd are typically lacustrine-adapted and are more generalistic in their life-history, micro-reproductive, and feeding tendencies than fishes collected solely in HCc. I observed a greater degree of species dominance in HCd than in HCc, likely attributed to the establishment and propagation of fishes well-adapted to lacustrine conditions (e.g., bluegill, largemouth bass). Dominance of largemouth bass is likely assisted by periodic stocking (MDWFP stocked fingerling largemouth bass twice since 2000; MDWFP unpublished stocking records). Decreased habitat complexity in HCd due to a lack of riverine stimuli may be a foundation for high species dominance

because of greater exploitation by generalist fishes. Because HCd is isolated from the Yazoo River, colonization by riverine species is unlikely, barring any anthropogenic-induced introductions, thus, species richness can only decrease. Shoup and Wahl (2009) hypothesized that species diversity may be less in oxbow lakes outside constructed levees because they do not have the habitat heterogeneity afforded by flood events. Isolated oxbow lakes such as HCd experience fewer and less severe flood events and thus have greater stability than frequently connected lakes such as HCc (Shoup and Wahl 2009). Increased stability of isolated lakes compared to connected lakes promotes limnological conditions ideal for reproductive habits of equilibrium strategists (Miyazono et al. 2010), but eliminates riverine conditions needed for successful reproduction of periodic strategists.

Robinson and Tonn (1989), Rodríguez and Lewis (1997), and Lewis et al. (2000) suggested that piscivory, under the influence of water transparency, may be a proximal factor in eliminating fishes intolerant to predation, thereby structuring fish assemblages. Relative abundance of strictly piscivorous fishes (i.e., bowfin, gars) in HCd; however, was negligible, and, although largemouth bass compose a large percentage of the fish assemblage in HCd, the turbid nature of floodplain lakes in the Yazoo River basin (Cooper 1987; Cooper and McHenry 1989) likely limits the foraging efficiency of sight-feeding piscivores (Tejerina-Garro et al. 1998; Reid et al. 1999; Miranda and Lucas 2004), lessening effect of piscivores on fish assemblage structure.

Oxbow lakes are important components of floodplain-river ecosystems. Many fishes use oxbow lakes as refugia and as spawning and nursery areas (Sabo and Kelso 1991; Bayley 1995). Separation of floodplain and riverine habitats has ultimately led to

an impairment of biotic integrity in relict oxbow lakes. Results herein suggest that connectivity significantly affects fish assemblage attributes, many of which (e.g., species richness, diversity, evenness, dominance) are used as common metrics with which to measure biotic integrity. Decisions concerning oxbow lake restoration efforts need to consider effects of periodic connection on the fish assemblage. Management plans should attempt to incorporate restoration of connection between oxbow lakes and their parent rivers. However, I caution against mindless restoration of connection between rivers and floodplain lakes. The process of disconnection occurs naturally as lakes age and become further separated from their parent rivers (Shields et al. 2010). Older lakes are typically situated farther from the main river channel and have become senescent; nonetheless, older lakes harbor unique fish assemblages of their own. At the same time, channel modifications have prevented the formation of new lakes (Matthes 1947), resulting in a disproportionate amount of senescent oxbow lakes. Special attention should be brought upon restoring connectivity to evolutionarily younger oxbow lakes whose natural connectivity has been disrupted by anthropogenic processes. Restoration of connectivity to such lakes will not only aid in maintenance of diversity within fish assemblages, but also in maintenance of diversity among fish assemblages.

Table 3.1. Common and scientific names, and life history, reproductive, and trophic guild classifications of species collected in the Hard Cash lakes, 2007-2010.

Name		Guild		
Common	Scientific	Life history	Reproductive	Trophic
Bigmouth buffalo	<i>Ictiobus cyprinellus</i>	Periodic	Phytolithophilic	Planktivorous-detritivorous
Black buffalo	<i>Ictiobus niger</i>	Periodic	Phytolithophilic	Invertivorous-detritivorous
Black bullhead	<i>Ameiurus melas</i>	Equilibrium	Speleophilic	Invertivorous-piscivorous
Blue catfish	<i>Ictalurus furcatus</i>	Equilibrium	Speleophilic	Invertivorous-piscivorous
Bluegill	<i>Lepomis macrochirus</i>	Equilibrium	Polyphilic	Invertivorous
Bluntnose darter	<i>Etheostoma chlorosomum</i>	Opportunistic	Phytophilic	Invertivorous
Bowfin	<i>Amia calva</i>	Equilibrium	Phytophilic	Piscivorous
Brook silverside	<i>Labidesthes sicculus</i>	Opportunistic	Phytolithophilic	Planktivorous-invertivorous
Channel catfish	<i>Ictalurus punctatus</i>	Equilibrium	Speleophilic	Invertivorous-piscivorous
Common carp	<i>Cyprinus carpio</i>	Periodic	Phytolithophilic	Invertivorous-planktivorous
Dollar sunfish	<i>Lepomis marginatus</i>	Opportunistic	Polyphilic	Invertivorous
Freshwater drum	<i>Aplodinotus grunniens</i>	Periodic	Pelagophilic	Invertivorous-piscivorous
Gizzard shad	<i>Dorosoma cepedianum</i>	Periodic	Lithopelagophilic	Herbivorous-detritivorous
Golden shiner	<i>Notemigonus crysoleucas</i>	Periodic	Phytophilic	Invertivorous-herbivorous
Green sunfish	<i>Lepomis cyanellus</i>	Equilibrium	Polyphilic	Invertivorous-piscivorous
Largemouth bass	<i>Micropterus salmoides</i>	Equilibrium	Polyphilic	Invertivorous-piscivorous
Longear sunfish	<i>Lepomis megalotis</i>	Equilibrium	Polyphilic	Invertivorous
Longnose gar	<i>Lepisosteus osseus</i>	Periodic	Phytolithophilic	Piscivorous
Orangespotted sunfish	<i>Lepomis humilis</i>	Opportunistic	Lithophilic	Invertivorous
Pugnose minnow	<i>Opsopoeodus emiliae</i>	Opportunistic	Phytophilic	Detritivorous
Redear sunfish	<i>Lepomis microlophus</i>	Equilibrium	Lithopelagophilic	Invertivorous
Ribbon shiner	<i>Lythrurus fumeus</i>	Opportunistic	Lithopelagophilic	Invertivorous-detritivorous
River carpsucker	<i>Carpiodes carpio</i>	Periodic	Polyphilic	Planktivorous-detritivorous
Shortnose gar	<i>Lepisosteus platostomus</i>	Periodic	Phytophilic	Piscivorous
Smallmouth buffalo	<i>Ictiobus bubalus</i>	Periodic	Phytolithophilic	Invertivorous-detritivorous
Spotted gar	<i>Lepisosteus oculatus</i>	Periodic	Phytophilic	Piscivorous
Spotted sucker	<i>Minytrema melanops</i>	Periodic	Lithopelagophilic	Invertivorous
Threadfin shad	<i>Dorosoma petenense</i>	Opportunistic	Phytophilic	Planktivorous
Warmouth	<i>Lepomis gulosus</i>	Equilibrium	Lithophilic	Invertivorous-piscivorous
Western mosquitofish	<i>Gambusia affinis</i>	Opportunistic	Viviparous	Invertivorous
White bass	<i>Morone chrysops</i>	Periodic	Phytolithiphilic	Invertivorous-piscivorous
White crappie	<i>Pomoxis annularis</i>	Equilibrium	Phytophilic	Invertivorous-piscivorous
Yellow bullhead	<i>Ameiurus natalis</i>	Equilibrium	Speleophilic	Invertivorous-piscivorous

Table 3.2. Total counts of species collected in Hard Cash connected (HCc) and Hard Cash disconnected (HCd). Numbers in parentheses represent the percentage composition of each species in the assemblage. Blank spaces indicate that the species was not detected.

Species	HCc	HCd
Bigmouth buffalo	26 (3.66)	
Black buffalo	4 (0.56)	
Black bullhead		1 (0.02)
Blue catfish	1 (0.14)	
Bluegill	232 (32.7)	1081 (30.31)
Bluntnose darter		1 (0.02)
Bowfin	4 (0.56)	
Brook silverside	39 (5.5)	138 (3.86)
Channel catfish	2 (0.28)	
Common carp	29 (4.1)	1 (0.02)
Dollar sunfish		2 (0.05)
Freshwater drum	22 (3.1)	
Gizzard shad	22 (3.1)	719 (20.15)
Golden shiner		10 (0.28)
Green sunfish	3 (0.42)	15 (0.42)
Largemouth bass	110 (15.5)	415 (11.63)
Longear sunfish	46 (6.48)	150 (4.21)
Longnose gar	2 (0.28)	
Orangespotted sunfish	56 (7.89)	43 (1.21)
Pugnose minnow	8 (1.12)	102 (2.85)
Redear sunfish		17 (0.47)
Ribbon shiner		5 (0.14)
River carpsucker	15 (2.12)	
Shortnose gar	2 (0.28)	
Smallmouth buffalo	28 (3.94)	221 (6.19)
Spotted gar	25 (3.52)	34 (0.95)
Spotted sucker	1 (0.14)	
Threadfin shad	5 (0.71)	565 (15.84)
Warmouth	8 (1.13)	13 (0.36)
Western mosquitofish		2 (0.05)
White bass	7 (0.98)	
White crappie	11 (1.55)	31 (0.86)
Yellow bullhead	1 (0.14)	1 (0.02)
All	709 (100)	3567 (100)

Table 3.3. Fish assemblage descriptors and significance values computed by the compare-diversities module in Hard Cash connected (HCc) and Hard Cash disconnected (HCd). P represents the probability of the observed differences occurring by random chance. All calculations indicated significant differences at the 0.05 level of significance.

Index	HCc	HCd	P
Berger-Parker Dominance	0.16	0.28	< 0.001
Buzas and Gibson's Evenness	0.42	0.28	0.008
Shannon Diversity	2.3	1.74	< 0.001
Fisher's Alpha Diversity	4.84	3.02	< 0.001
Menhinick Richness	0.92	0.41	< 0.001
Margalef Richness	3.53	2.45	0.003

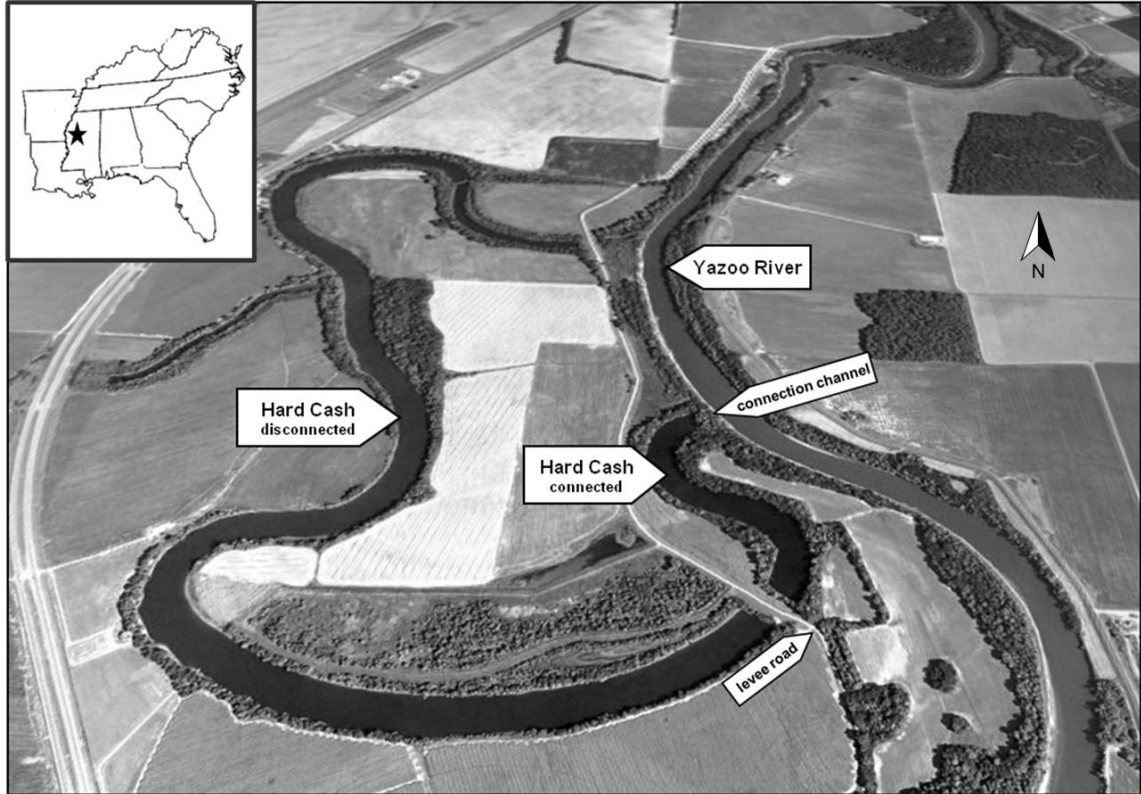


Figure 3.1. Aerial photograph showing the Hard Cash lakes as bisected by the Yazoo River levee, Humphreys County, Mississippi. The inset identifies the location of the lake in the southeastern United States.

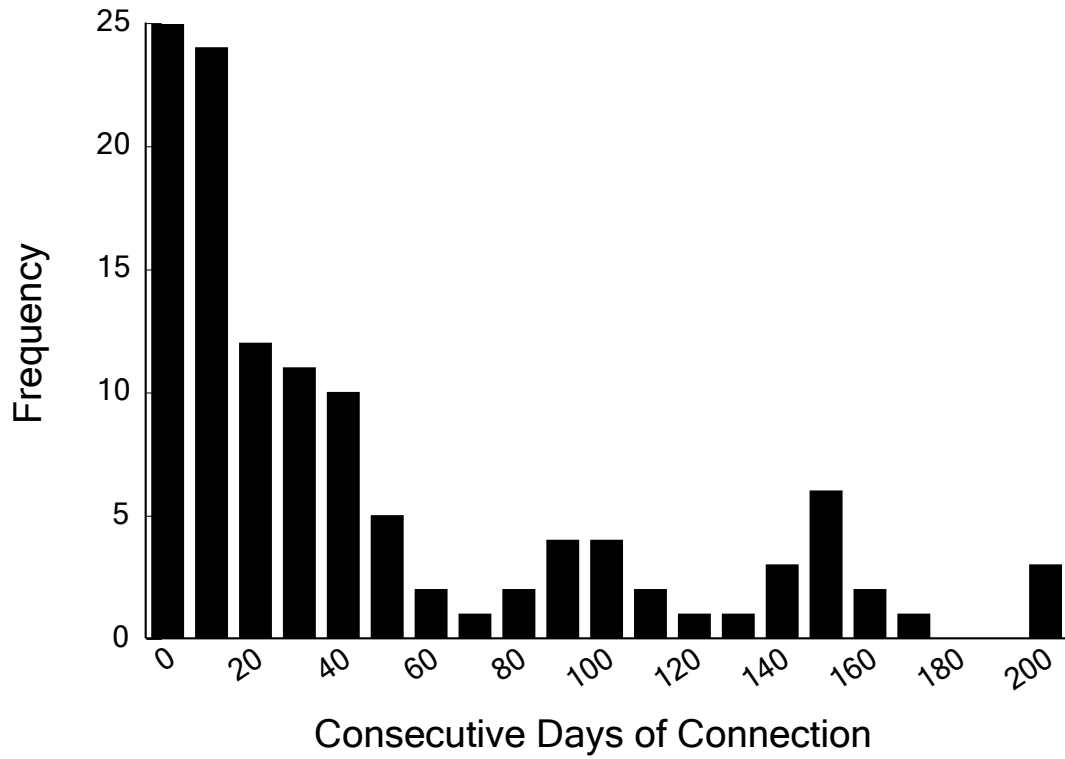


Figure 3.2. Frequency of individual periods of consecutive connection between Hard Cash connected and the Yazoo River, 1944-2009. Periods of connection were grouped into 10-day bins for graphical representation.

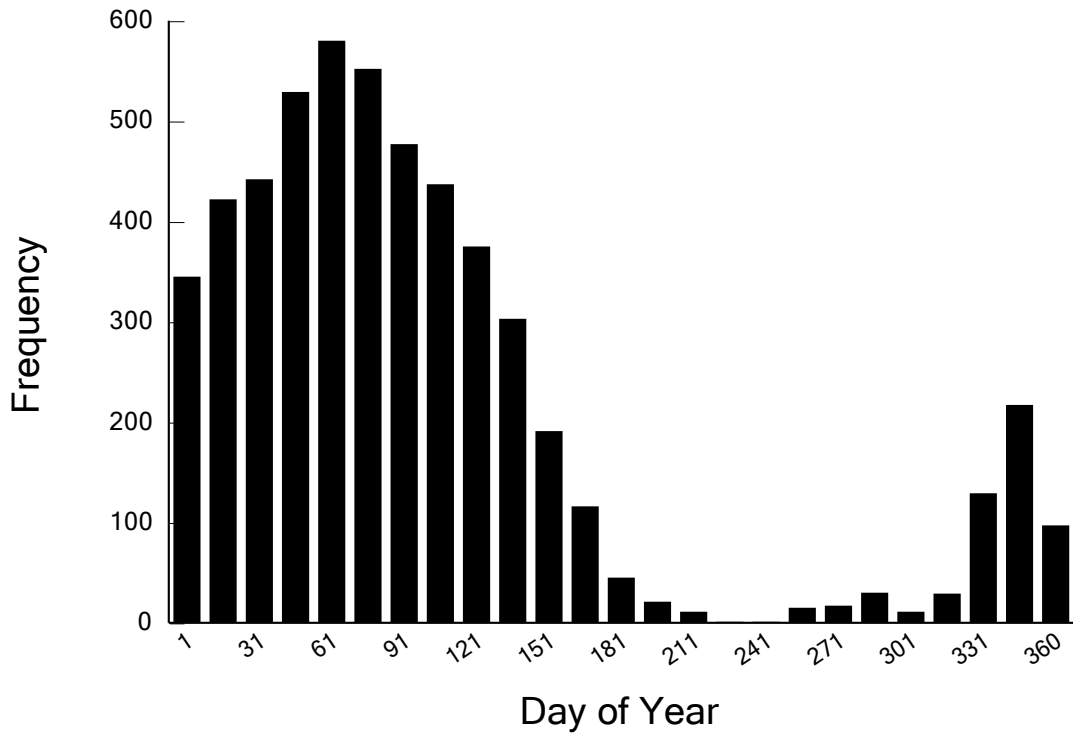


Figure 3.3. Annual cycle of connection between Hard Cash connected and the Yazoo River, 1944-2009. Connection events occur most frequently between day of year 1 and day of year 150, reflecting regional precipitation events. Days of year were grouped into 15-day bins for graphical representation.

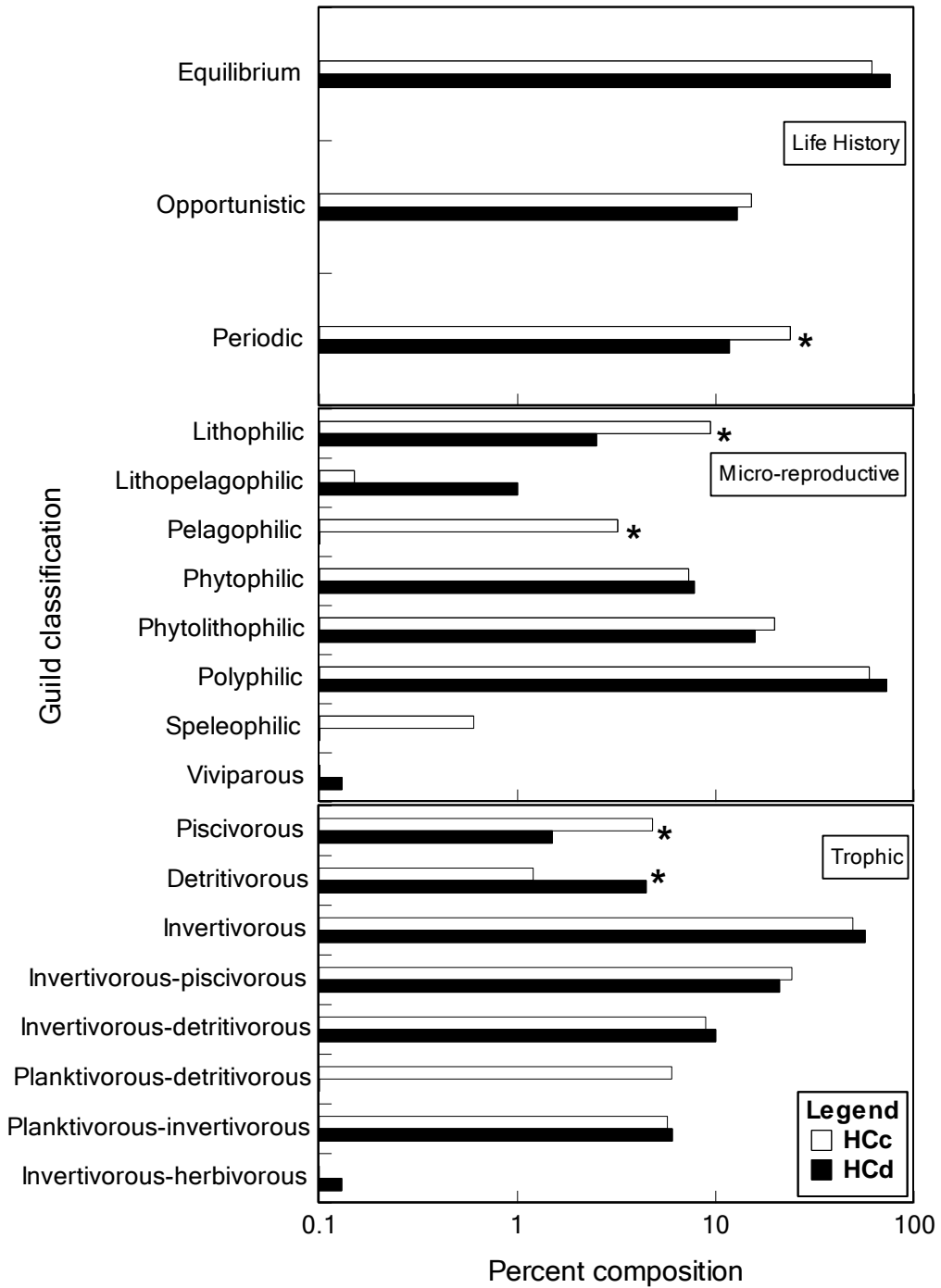


Figure 3.4. Functional group percentage compositional data for fishes collected from Hard Cash connected (HCC) and Hard Cash disconnected (HCD). A chi-square test indicated significant differences ($P < 0.001$) between HCC and HCD for all three guild classifications; * indicate individual guilds that are responsible for a large proportion of the overall chi-square statistic.

CHAPTER IV

SUMMARY AND CONCLUSIONS

This study was designed so as to provide fisheries ecologists and aquatic scientists with greater insight to floodplain lake fish community ecology. The objective of Chapter 2 was to estimate the relative importance of each of four primary variables in controlling the variation in suites of secondary variables and fish biodiversity, as well as the relationship between suites of secondary variables and fish biodiversity. Above all others, maximum depth and percentage of agricultural land surrounding lakes were identified as the most important primary variables, significantly influencing water quality, primary productivity, and fish biodiversity variables. Surprisingly, degree of lake-river interconnectedness was not related linearly to suites of water quality, primary productivity, or fish biodiversity variables. The objective of Chapter 3 was to examine how fish biodiversity and assemblage structure was affected by periodic connection between floodplain lakes and their parent rivers. Fish assemblage attributes were compared in two disjoined segments of an oxbow lake connected to and isolated from the Yazoo River. Greater species richness, diversity, and evenness were observed in the connected segment. Additionally, the connected segment had a greater abundance of piscivores and periodic life-history strategists. All fishes collected solely in the connected segment were typically riverine in nature, whereas those fishes collected only

in the disconnected segment were more lacustrine-adapted. In contrast to the results of Chapter 2, results of Chapter 3 indicate that periodic connection is important for structuring the fish assemblage and maintaining fish biodiversity.

Although my study has ultimately identified several variables that should become the focal point of floodplain lake management efforts, contrasting results regarding effects of connectivity on fish biodiversity beg for further explanation. I assert that connectivity is indeed deterministic over fish biodiversity and assemblage structure. In chapter 2, degree of lake-river interconnectedness as measured along a distance gradient was not correlated significantly with fish biodiversity. Contrastingly, in Chapter 3, fish biodiversity and assemblage composition differed significantly from the connected segment to the disconnected segment. This more than likely indicates that the index of connectivity used in Chapter 2 (effective distance from lake to parent river) is unsuitable.

Each chapter used a different index of connectivity, which may be limiting power of my analyses to capture the actual effect of connectivity on the fish assemblage. In Chapter 2, I indexed connectivity with effective distance from each lake to its parent river, whereas in Chapter 3, connectivity was indexed by coupling river and oxbow elevation data with river stage data to obtain frequency and duration of connection events for the connected segment. Although the methods used in Chapter 3 are likely more precise than many others, the Hard Cash lakes represent an extremely unique experimental situation and the application of such an index of connectivity is probably limited to use in lakes with morphological characteristics similar to those of the Hard Cash lakes. At greater distances from the river, connectivity may become confounded by presence of the levee system or flow diversion channels and utility of indices using

Euclidean distance or effective distance will likely decrease. The most accurate index of connectivity couples personal observations of connection events with river stage data (e.g., Zeug et al. 2005), but this demands large investments of time and personnel. In any case, there is a need for the development of a high-utility index of connectivity.

Another facet of this study that implores further questioning is lack of a significant correlation between the water quality variables and fish biodiversity. Because local abiotic characteristics often dictate local biodiversity (Tales and Berrebi 2007), it seems odd that water quality was found to be relatively unimportant. Had water quality sampling been standardized at fixed times and locations, it is possible that a significant correlation would have been observed. Although not significant statistically, magnitude of correlations between water quality and fish biodiversity were similar to those between primary productivity and fish biodiversity, which were significant statistically. In this instance, I believe that dependence on statistical significance should be lessened and that these results should be interpreted as ecologically significant.

Alternatively, the water quality variables measured herein may not be suitable to reflect fish biodiversity. Although local abiotic characteristics dictate local biodiversity (Tales and Berrebi 2007), the water quality variables may function at too small of a temporal and spatial scale to accurately reflect fish biodiversity within the study lakes. Primary productivity variables may be reflective of processes occurring at larger temporal and spatial scales, hence their stronger correlation with fish biodiversity. Water quality variables were only measured in the epilimnion. Fish biodiversity may not be affected by epilimnetic water quality because fish have the ability to move to find areas with suitable water quality. To fully encompass lake-wide trends in water quality, water

quality sampling effort would need to be expanded to multiple depths and to multiple littoral and limnetic areas. Additionally, the scale of water quality sampling could be modified to encompass long-term patterns by using data-loggers placed in various locations throughout each lake. It is likely that fish biodiversity is better reflected by long-term means and variability in water quality variables than by values collected on only one or two occasions throughout the sampling period. Additional variables that could have potential utility in reflecting long-term water quality trends include various sediment nutrient concentrations.

By design, my study did not incorporate fish assemblage composition into the analysis in Chapter 2. Although Chapter 3 indicates that fish assemblage composition is influenced by periodic connection, correlations between fish assemblage composition and depth, surface area, and percentage of agriculture surrounding lakes are lacking. These correlations are missing links in floodplain lake fish community ecology and should provide direction for future research. An additional primary variable that was not considered for my study was lake age. Effects of lake age are likely encompassed by depth, surface area, degree of lake-river interconnectedness, and amount of surrounding agricultural land. For example, as floodplain lakes take on a trajectory towards terrestrialization, they often experience reductions in depth, surface area, and connectivity with their parent river, and an increase in surrounding agricultural land (Shields et al. 2010). Thus, it is probable that little, if any, pertinent information is lost by the exclusion of lake age as a primary variable.

Although it seems as if this study has raised more questions than it has answered, such is the nature of science. Results herein have filled a critical gap in the knowledge

base of floodplain lake ecosystems. Specific objectives were fulfilled in that deterministic primary variables were identified, and relationships among ecosystem components functioning at different scales were quantified. Biologists interested in floodplain lake restoration and preservation should focus on management of depth, percentage of agricultural land surrounding lakes, and restoration of connectivity. Questions regarding the connectivity conundrum and effects of primary and secondary variables on overall fish assemblage composition that were left unanswered by this study should be addressed in future research ventures.

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