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Environmental variables measured at multiple spatial scales exert uneven influence on fish assemblages of floodplain lakes

Daniel J. Dembkowski · L. E. Miranda

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Abstract We examined the interaction between environmental variables measured at three different scales (i.e., landscape, lake, and in-lake) and fish assemblage descriptors across a range of over 50 floodplain lakes in the Mississippi Alluvial Valley of Mississippi and Arkansas. Our goal was to identify important local- and landscape-level determinants of fish assemblage structure. Relationships between fish assemblage structure and variables measured at broader scales (i.e., landscape-level and lake-level) were hypothesized to be stronger than relationships with variables measured at finer scales (i.e., in-lake variables). Results suggest that fish assemblage structure in floodplain lakes was influenced by variables operating on three different scales. However, and contrary to expectations, canonical correlations between in-lake environmental characteristics and fish assemblage structure were generally stronger than correlations between landscape-level and lake-level

variables and fish assemblage structure, suggesting a hierarchy of influence. From a resource management perspective, our study suggests that landscape-level and lake-level variables may be manipulated for conservation or restoration purposes, and in-lake variables and fish assemblage structure may be used to monitor the success of such efforts.

Keywords Fish assemblage structure · CAP analysis · Floodplain lake · Mississippi Alluvial Valley · Depth

Introduction

Floodplain lakes created by the meandering of rivers are dynamic systems with unique and diverse habitats and environmental conditions (Baker et al., 1991; Sabo & Kelso, 1991). Thus, floodplain lakes are excellent systems for examining relationships between abiotic and biotic factors and fish assemblage structure. Floodplain lakes and other extra-channel habitats are important components of river–floodplain ecosystems in view of the fact that floodplain habitats support reproduction, growth, and recruitment of many channel-dwelling fishes (Welcomme, 1979; Penczak et al., 2003; Zeug et al., 2005; Nunn et al., 2007). Moreover, floodplain lakes support their own unique fish assemblages and species. Thus, there is a direct relationship between fish assemblage characteristics in floodplain habitats and fish assemblage characteristics in the

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main channel (Welcomme, 1979), and a river system's gamma diversity. Recognition of these important linkages and identification of variables influencing fish assemblage structure in floodplain lakes can aid in conservation, restoration, and management of floodplain lakes and their respective river systems.

Previous studies have identified a variety of environmental variables as determinants of floodplain lake fish assemblages (e.g., Winemiller et al., 2000; Miranda & Lucas, 2004; Penczak et al., 2004; Tales & Berrebi, 2007). Environmental variables that determine floodplain lake fish biodiversity (e.g., richness, diversity, and evenness metrics) and assemblage composition (e.g., taxa and functional guilds) frequently originate from multiple spatial scales (e.g., Allen & Starr, 1982; Imhof et al., 1996; Dembkowski & Miranda, 2012). Relative importance of deterministic variables may change as a function of spatial scale, suggesting that fish assemblage determinants at a given scale may be the result of processes occurring at other, usually larger, spatial scales (i.e., show a hierarchy of influence; Syms, 1995; Brind'Amour et al., 2005). For example, a study may identify variables at the local and landscape-level scales as deterministic of fish assemblage structure, when in fact the local variables may be mediated by the landscape-level variables. Understanding the influence of fish assemblage determinants functioning on multiple spatial scales can foster the development of a more efficient and holistic approach to floodplain ecosystem conservation and restoration. Conditional upon a hierarchy of influence, conservation and management efforts can be focused on landscape-level variables, which mediate in-lake variables, which ultimately mediate fish assemblage structure.

We examined the interactions between three classes of environmental variables (i.e., landscape, lake, and in-lake levels) and fish assemblage structure across a range of floodplain lakes in the Mississippi Alluvial Valley of Mississippi and Arkansas. Each class of variables fell onto a gradient of resolution where landscape-level variables represented the coarsest resolution (i.e., broadest scale) and in-lake variables represented the finest resolution. Variables measured on a broader scale (e.g., landscape- and lake-level variables) have been identified by other authors as deterministic of variables measured on a finer scale, such as in-lake processes, biodiversity, and fish assemblage composition in standing bodies of water

(e.g., Lucas, 1985; Magnuson et al., 1998; Tejerina-Garro et al., 1998; Dembkowski & Miranda, 2012). The specific objective of our study was to identify important local- and landscape-level determinants of fish assemblage structure in floodplain lakes. Also of interest were relationships between landscape, lake, and in-lake descriptors and frequency of occurrence of selected taxonomic and feeding guilds. Relationships between fish assemblage structure and variables measured at broader scales (i.e., landscape- and lake-levels) were expected to be stronger than relationships between fish assemblage structure and variables measured at finer scales (i.e., in-lake variables). We also hypothesized strong relationships among the three classes of environmental variables based on previous hierarchical theory (e.g., Allen & Starr, 1982).

Methods

Site description

The alluvial valley of the lower Mississippi River extends from near Cairo, Illinois south to the confluence of the Mississippi and Atchafalaya rivers in east-central Louisiana (Fig. 1; Killgore et al., 2007). Within the states of Mississippi and Arkansas, major tributary streams to the Mississippi River include the Yazoo, White, Arkansas, and Ouachita rivers, each with extensive tributary networks. Hundreds of floodplain lakes are situated along these tributary streams. Most of the lakes are oxbows, resulting from river channel abandonment due to sediment deposition or anthropogenic channel alterations (Biedenharn et al., 2000). Fifty-three floodplain lakes within the Yazoo, White, Arkansas, and Ouachita River basins were investigated from July 2006 to August 2010 (Fig. 1). These lakes were channel remnants of the extant or ancient rivers that flow or had once flowed through the valley. Although there are many floodplain lakes in the region that are channel remnants of the present Mississippi River, those lakes are larger and were not considered for this study. Forty 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, White, and Ouachita 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 the Delta National Forest, Mississippi. Lakes were selected based on diverse representation of landscape and basin characteristics, and accessibility. Efforts were made to select lakes along perceived gradients of environmental variables including depth, surface area, degree of connectivity with the closest rivers, and riparian and watershed land-cover compositions.

Landscape variables

Landscape-level variables selected for analyses included descriptors of riparian and watershed land-

covers. Lake-specific watersheds could not be defined because of the 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. The 50-m band was designated as the riparian zone, and the 500-, 1,000-, and 5,000-m bands were considered descriptive of the encircling land-cover and a proxy to a lake’s watershed. Land-cover data (queried in 2009 and 2010) within each band was obtained from the National Agriculture Imagery Program (NAIP), Mississippi Automated Resource Information System (MARIS, 2011), Arkansas GeoStor (2009), and the U.S. Geological Survey

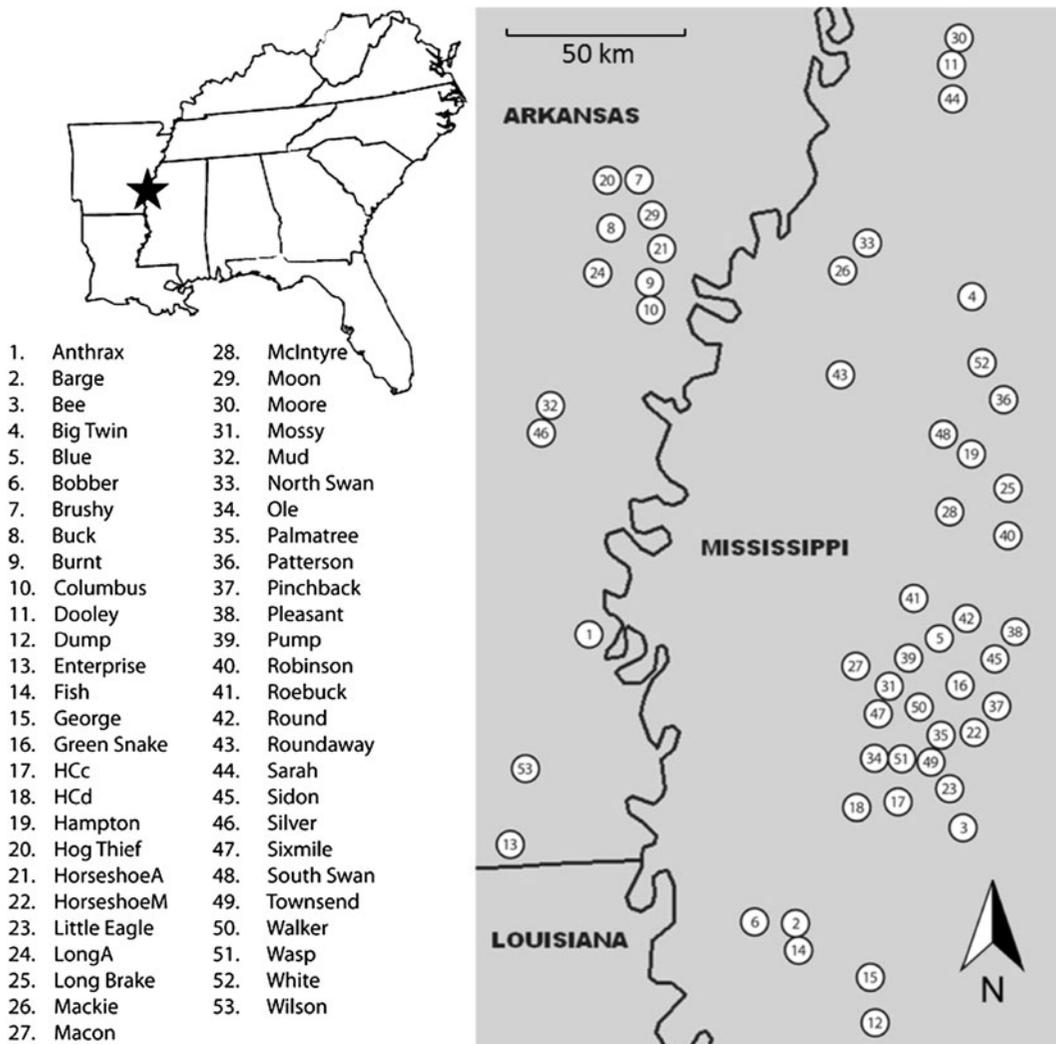


Fig. 1 Map of the lower Mississippi Alluvial Valley region of Mississippi and Arkansas, with names and locations of 53 floodplain lakes studied from 2006 to 2010. The inset identifies the location of the study region in the southeastern United States

(USGS) Southeast Gap Analysis Project (SEGAP) databases. Land-cover classes identified within the riparian zone consisted of row-crop agriculture, forest cover, wetlands, and human disturbance (e.g., urban development and impervious surfaces). Land-cover classes identified within the broader concentric bands were the same as those of the riparian zone, although a freshwater class that included other water bodies was also included. Percentages of the land-cover classes were calculated within each concentric band. All geospatial data were extracted with spatial analyst tools available in the Arc-GIS software package. Lakes were treated as polygons, and those that had not already been identified as water bodies in Arc-GIS were digitized and added.

Lake variables

Floodplain lake-main channel interconnectedness, maximum depth, and surface area were selected for analyses on the basis that these variables are often identified as fundamental to many other processes in floodplain dynamics (Junk et al., 1989; Baker et al., 1991; Miranda, 2005; Lubinski et al., 2008). In addition, Dembkowski & Miranda (2012) demonstrated the hierarchical influence of connectivity, depth, and surface area on fish biodiversity in a similar set of floodplain lakes in the Mississippi Alluvial Valley and, because biodiversity is an integral component of assemblage structure, these variables are thought to affect fish assemblage structure in a similar manner.

The degree of connectivity between floodplain lakes and the nearest river is likely influenced by the linear distance between the connection points, the change in elevation from the floodplain lake to the river channel, and anthropogenic modifications such as levees and channelization. Several methods of measuring lake–river interconnectedness have been developed, including 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). Direct observation of connection events and comparison with river discharge levels is likely the most precise index of connectivity; however, direct observation of flooding at all the studied lakes included in the present research was impractical. Also, available

elevation data in the study regions were of relatively low resolution. Furthermore, agricultural practices, leveeing, and ditching have altered the hydrology of the study region to the point where elevation data have limited utility. Because of the general unreliability of other connectivity indices and the limited utility of elevation data, we used effective distance, defined as channel distance between each lake and the nearest river, as an index of lake–river interconnectedness. The channels were sinuous ephemeral streams connecting each floodplain lake to the nearest river. Effective distance is easily measured and should index connectivity as the lakes closer to the nearest rivers are expectedly connected on a more frequent basis than lakes with farther effective distance.

Maximum depth was defined as the deepest point detected by soundings taken with a handheld (DF2200PX, NorCross Marine,¹ Orlando, Florida) or boat-mounted (X126 DF Sonar, Lowrance Electronics, Tulsa, Oklahoma) depth finder. The depth finders were operated from a boat navigating in a zig-zag pattern along the former thalweg between the two ends of each lake. Maximum depth was selected over mean depth because it better characterizes the cross-sectional morphology of channel remnants than mean depth (Dembkowski & Miranda, 2012). Lake surface area was estimated using spatial analysis tools available in the Arc-GIS software package.

In-lake variables

In-lake variables selected for this study were grouped into two classes representative of water quality and primary productivity. Turbidity (nephelometric turbidity units; NTU), pH, dissolved oxygen (DO; mg l⁻¹), DO saturation (%), temperature (°C), and water transparency (cm) represented lake water quality. Water quality variables were measured twice at each lake during daytime hours in the summer (June–August) from the epilimnion at a single point near the deepest point in each lake. Turbidity, pH, DO, DO saturation, and temperature were measured in situ using a Eureka Manta multiprobe (Eureka Environmental Engineering, Austin, Texas). Water

¹ The use of trade, product, industry, or firm names or products or software is for informative purposes and does not constitute an endorsement by the U.S. government or U.S. Geological Survey.

transparency was measured using a Secchi disk (20 cm diameter).

The concentration of chlorophyll *a* (fluorescence units; FU) was used to index lake primary productivity. Chlorophyll *a* was also measured in the summer from the epilimnion at a single point near the deepest point in each lake using an *Aquafluor*TM handheld fluorometer (Turner Designs, Sunnyvale, California).

Fish collections

Fish were collected during daytime hours by a boat electrofisher equipped with a GPP 7.5 Smith-RootTM 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 indiscriminate shoreline areas. We collected 2–16 samples per lake depending on lake area. Fish were netted from the bow of the boat by two netters equipped with 2.7-m long dip nets with 0.4-cm bar mesh. Fish were identified to species and counted before release near the site of capture. Transects were located far enough apart so that fish released at one site would not influence catches in the adjacent transect. Those species too 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). Although electrofishing does collect small fishes, it is biased against small-bodied species and juveniles of large-bodied species (Reynolds, 1996; Dolan & Miranda, 2003). Thus, our collections reflected a skewed representation of the fish assemblages, yet were adequate to describe differences across lakes (Miranda, 2011).

Statistical analysis

Fish assemblage structure was represented as fish percentage compositional data of species present in at least 90% of the studied lakes. Removal of species present in less than 10% of the studied lakes may improve the signal-to-noise ratio in a dataset and frequently enhances the detection of relationships between biotic assemblage structure and environmental drivers (Cao et al., 2001; Legendre & Gallagher, 2001; McCune & Grace, 2002; Miranda & Lucas,

2004). Collections of threadfin shad *Dorosoma petenense*, gizzard shad *Dorosoma cepedianum*, and western mosquitofish *Gambusia affinis* did not reflect true abundance because of shad fleeing behavior in response to electrofishing, and mosquitofish insusceptibility to electrofishing. Hence, these species were also excluded from analyses (Miranda, 2011; Demkowski & Miranda, 2012).

Multivariate sets of landscape (i.e., riparian and watershed land-cover variables) and in-lake variables (i.e., water quality and primary productivity variables) were reduced into smaller sets of unrelated and more easily interpretable univariate variables using principal components analysis (PCA; McCune & Grace, 2002). Before PCA, environmental variables were log-transformed to reduce skewness and standardized (mean = 0; SD = 1) to place all variables in the same scale. Principal component axes with eigenvalues larger than 1 were interpreted and retained for subsequent analyses (Johnson, 1998; McCune & Grace, 2002).

Relationships between and among the environmental variables and fish assemblage structure were examined using canonical analysis of principal coordinates (CAP; Anderson & Willis, 2003). 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 an external variable (Anderson & Robinson, 2003). Because the CAP analysis essentially ordines one data matrix in consideration of another, it is a constrained analysis that uses an a priori hypothesis to construct correlations between sets of variables. 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 (δ) representing the strength of the association between the *m* principal coordinate axes and the explanatory variable (M. J. Anderson, University of Auckland, personal communication). Canonical correlations were not corrected to maintain experiment-wise error rates because this would have resulted in significance levels too conservative to draw our interests.

Separate CAP analyses were applied to examine correlations between each level of environmental variables (i.e., landscape, lake, and in-lake) and fish assemblage structure. The CAP analysis sought to find correlations between axes representing most of the variation in the fish assemblage matrix relative to each respective environmental variable. We also examined relationships between specific aspects of the fish assemblage and environmental variables. Fishes were grouped into taxonomic and feeding guilds, and CAP was used to assess relationships between guilds and environmental variables. Specifically, we examined relationships between environmental variables and frequency of occurrence of buffalos, catfishes, gars, and sunfishes because these fish were collected in most studied lakes and were of special interest. Fishes were grouped according to feeding guilds as proposed by Balon (1990), Killgore & Hoover (1992), and Goldstein & Simon (1999) and as implemented by Killgore & Hoover (1992), Miyazono et al. (2010), and Dembkowski & Miranda (2011). Feeding guilds representing less than 5% of the total catch by number were not included in analyses. All analyses between the fish assemblage and external variables were performed with Bray–Curtis dissimilarities calculated from fourth-root-transformed percentage compositional data. The fourth-root transformation was selected because it reduced skewness of the fish assemblage data better than other transformations. All PCA and CAP analyses were performed using the PERMANOVA+ add-on for PRIMER statistical software package (PRIMER-E Ltd, Plymouth, United Kingdom; Clarke & Gorley, 2006). Significance levels for all statistical procedures were designated at $\alpha = 0.05$. All analyses were conducted with data from different years combined after a permutational multivariate analysis of variance (PERMANOVA; 999 permutations; Anderson, 2001) indicated no significant year effect on assemblage composition ($P = 0.32$).

Results

Landscape, lake, and in-lake variables

The studied lakes varied greatly in their landscape, lake, and in-lake variables (Table 1). Ranges of landscape- and lake-level variables reflected our

efforts to select diverse lakes along gradients of depth, surface area, connectivity, and riparian and watershed land-covers. Maximum depth ranged from 0.5 to 8.6 m, surface area from 0.01 to 5.7 km², connectivity between floodplain lakes and the nearest river from 0 to 13.5 km, and riparian and watershed land-covers from primarily agriculture and human disturbance to primarily freshwater and bottomland hardwood forest. Water quality and primary productivity variables showed similar variation.

Riparian land-cover variables were reduced to a single principal component axis (hereafter, “riparian PC1”) representative of 63% of the total variance within the dataset. The percentage of agricultural land and human disturbance displayed positive loadings on the axis, whereas the percentage of forested land displayed negative loadings (Table 2). Watershed land-cover variables were reduced into two principal component axes cumulatively representative of 72% of the total variance within the dataset. The first axis (hereafter, “watershed PC1”) explained approximately 53% of the variance; the percentage of forested land displayed positive loadings, and the percentage of agricultural land and human disturbance displayed negative loadings (Table 3). The second axis (hereafter, “watershed PC2”) explained an additional 19% of the total variance; the percentage of freshwater displayed positive loadings and the percentage of wetlands displayed negative loadings. Water quality variables were also reduced into two principal component axes cumulatively representative of 68% of the total variance. The first axis (hereafter, “water quality PC1”) explained 41% of the total variance; negative values were indicative of higher DO, DO percent saturation, pH, and water temperature. The second axis (hereafter, “water quality PC2”) explained an additional 27% of the total variance and represented a gradient of water transparency, where negative values represented greater transparency (Table 4).

Fish collections

In the multiyear sampling period, over 92,300 fish representing 71 species and 19 families were collected during 118 h of electrofishing (Table 5). Excluding shads, the minimum and maximum numbers of species collected across all studied lakes were 11 and 43, respectively. The most common species were bluegill *Lepomis macrochirus* (34% of the total catch by

Table 1 Descriptive statistical properties of landscape, lake, and in-lake-level variables collected from 53 floodplain lakes in the Mississippi Alluvial Valley, 2006–2010

Variable	Mean	CV	Min	Max
Landscape				
Watershed—5,000-m band (%)				
Agriculture	50	53	1	83
Forest-cover	28	169	1	91
Wetlands	4	123	0	14
Human disturbance	4	123	1	11
Freshwater	5	77	0	17
Watershed—1,000-m band (%)				
Agriculture	47	57	0	77
Forest-cover	31	114	2	100
Wetlands	6	153	0	38
Human disturbance	5	63	0	12
Freshwater	3	116	0	17
Watershed—500-m band (%)				
Agriculture	45	60	0	81
Forest-cover	31	41	0	100
Wetlands	7	116	0	52
Human disturbance	5	97	0	16
Freshwater	2	70	0	13
Riparian zone (%)				
Agriculture	23	80	0	57
Forest-cover	43	92	0	100
Wetlands	18	145	0	89
Lake				
Depth (m)	2.8	61	0.50	8.6
Surface area (km ²)	0.74	159	0.01	5.7
Connectivity (km)	2.50	120	0	14
In-lake				
Secchi (cm)	50.5	43.1	15	105
Temperature (°C)	29.6	5.5	26.2	34
DO (mg l ⁻¹)	6.2	31.8	1.5	11.4
DO saturation (%)	82.1	30.5	19	147
pH	7.2	8.9	5.2	9.5
Turbidity (NTU)	26.7	74.3	4.7	107
Chlorophyll <i>a</i> (FU)	292	65	65	964

All values are raw values before reduction by principal components analysis; see “[Methods](#)” for details

number), longear sunfish *Lepomis megalotis* (10%), orangespotted sunfish *Lepomis humilis* (9%), small-mouth buffalo *Ictiobus bubalus* (7%), largemouth bass *Micropterus salmoides* (7%), brook silverside *Labidesthes sicculus* (5%), and bigmouth buffalo

Table 2 Component loadings for the first principal component (PC) axis for riparian land-cover variables measured in a 50-m band surrounding floodplain lakes

Variable estimated	PC1
% Row-crop agriculture	0.64
% Forest cover	-0.58
% Human disturbance	0.50
Eigenvalue	1.8
Percent variance	63

Eigenvalues and percent variance explained are denoted at the bottom of the table

Table 3 Component loadings for the first two principal component (PC) axes for watershed land-cover variables measured in 500-, 1,000-, and 5,000-m bands surrounding floodplain lakes

Variable estimated	PC1	PC2
500-m band (%)		
Agriculture	-0.32	0.11
Forest-cover	0.34	0.07
Human disturbance	-0.24	0.27
Wetlands	-0.14	-0.50
Freshwater	-0.10	0.26
1,000-m band (%)		
Agriculture	-0.32	0.11
Forest-cover	0.34	0.04
Human disturbance	-0.28	0.16
Wetlands	-0.14	-0.52
Freshwater	-0.12	0.18
5,000-m band (%)		
Agriculture	-0.32	0.10
Forest-cover	0.34	0.02
Human disturbance	-0.26	0.05
Wetlands	-0.17	-0.45
Freshwater	-0.13	-0.07
Eigenvalue	7.9	2.8
Percent variance	53	19

Eigenvalues and percent variance explained are denoted at the bottom of the table

Ictiobus cyprinellus (4%). Among taxonomic guilds, centrarchids (i.e., sunfishes) were collected most frequently (70% of the total catch by number), followed by catostomids (suckers; 11%), cyprinids (minnows; 5%), atherinids (silversides; 5%), lepisosteids (gars; 5%), and sciaenids (drum; 1%). Among feeding guilds, invertivores were collected most

Table 4 Component loadings for the first two principal component (PC) axes for water quality variables measured from the studied lakes

Variable estimated	PC1	PC2
Secchi depth	0.30	-0.60
Turbidity	-0.24	-0.60
Water temperature	-0.29	-0.38
DO	-0.47	0.05
DO % saturation	-0.54	-0.21
pH	-0.47	-0.26
Eigenvalue	2.4	1.6
Percent variance	41	27

DO dissolved oxygen concentration

Eigenvalues and percent variances explained are denoted at the bottom of the table

frequently (62% of the total catch by number), followed by invertivore–piscivores (18%), invertivore–detritivores (14%), and piscivores (5%).

Fish assemblage–environment relationships

Statistically significant relationships were found among all levels of environmental variables, and between the landscape, lake, and in-lake level variables and fish assemblage structure (Table 6).

Lake surface area and watershed PC2 were significantly correlated with water quality PC1 ($\delta = 0.39$; $P = 0.01$ and $\delta = 0.30$; $P = 0.03$, respectively). Lake depth was significantly correlated with water quality PC2 ($\delta = 0.63$; $P = 0.001$) and chlorophyll *a* concentration ($\delta = 0.67$; $P = 0.001$).

Excluding the degree of lake–river interconnectedness, all landscape- and lake-level variables (i.e., depth, surface area, riparian PC1, watershed PC1, and watershed PC2) were significantly correlated with fish assemblage structure (δ range = 0.46–0.79; all $P < 0.05$; Table 6). All in-lake variables (i.e., water quality PC1, water quality PC2, and chlorophyll *a* concentration) were also significantly correlated with fish assemblage structure (δ range = 0.74–0.91; all $P < 0.05$; Table 6).

Relationships between taxonomic guilds, feeding guilds, and environmental variables

The studied lakes displayed various canonical correlations between the selected taxonomic guilds and each

level of environmental variables, but no strong patterns relative to the hierarchy of environmental factors were evident (Table 6). Buffalo frequency of occurrence was significantly correlated with riparian PC1 ($\delta = 0.29$; $P = 0.03$), depth ($\delta = 0.45$; $P = 0.004$), and water quality PC2 ($\delta = 0.38$; $P = 0.02$), suggesting that buffalo representation in the fish assemblage generally increases with shallow water, riparian disturbances, and turbidity. Gar frequency of occurrence was significantly correlated with riparian PC1 ($\delta = 0.34$; $P = 0.01$), watershed PC1 ($\delta = 0.34$; $P = 0.01$), and water quality PC2 ($\delta = 0.38$; $P = 0.02$), suggesting that gar representation in the fish assemblage generally increases with watershed and riparian disturbances and turbidity. Sunfish frequency of occurrence was significantly correlated with watershed PC2 ($\delta = 0.39$; $P = 0.01$), suggesting that sunfish representation in the fish assemblage generally increases in lakes with a greater percentage of freshwater within their watershed. Catfish frequency of occurrence was not significantly correlated with any of the landscape, lake, or in-lake variables.

Although there were significant relationships between feeding guilds (except catfishes) and various landscape, lake, and in-lake variables, the relationships were not consistent (i.e., feeding guilds were not related to only 1 or 2 environmental variables; Table 6). Invertivore–piscivore frequency of occurrence was significantly correlated with riparian PC1 ($\delta = 0.48$; $P = 0.001$), the degree of lake–river interconnectedness ($\delta = 0.49$; $P = 0.004$), and water quality PC1 ($\delta = 0.29$; $P = 0.04$), suggesting that their representation in the fish assemblage generally decreases with lake–river disconnection and low DO, pH, and temperature, but increases with riparian disturbance. Invertivore frequency of occurrence was also significantly correlated with water quality PC1 ($\delta = 0.43$; $P = 0.03$), suggesting a concurrent decrease in representation with decreasing DO, pH, and water temperature. Invertivore–detritivore frequency of occurrence was significantly correlated with watershed PC2 ($\delta = 0.32$; $P = 0.02$), depth ($\delta = 0.46$; $P = 0.01$) and water quality PC2 ($\delta = 0.34$; $P = 0.01$), suggesting a general increase in representation with depth reductions and low water transparency. Piscivore frequency of occurrence was significantly correlated with the degree of lake–river interconnectedness and water quality PC2 ($\delta = 0.38$; $P = 0.02$ and $\delta = 0.36$; $P = 0.01$, respectively),

Table 5 Common and scientific names, and taxonomic guild (i.e., family) and feeding guild classifications of species collected from 53 floodplain lakes in the Mississippi Alluvial Valley, 2006–2010

Common name	Scientific name	Taxonomic guild	Feeding guild	N_{Fish}	N_{Lakes}
American eel	<i>Anguilla rostrata</i>	Anguillidae	IP	2	2
Paddlefish	<i>Polyodon spathula</i>	Polyodontidae	PLANK	1	1
Bowfin	<i>Amia calva</i>	Amiidae	P	317	40
Longnose gar	<i>Lepisosteus osseus</i>	Lepisosteidae	P	136	19
Shortnose gar	<i>Lepisosteus platostomus</i>	Lepisosteidae	P	125	27
Spotted gar	<i>Lepisosteus oculatus</i>	Lepisosteidae	P	1,882	52
Chain pickerel	<i>Esox niger</i>	Esocidae	IP	17	7
Mooneye	<i>Hiodon tergisus</i>	Hiodontidae	I	1	1
Skipjack herring	<i>Alosa chrysochloris</i>	Clupeidae	IP	4	1
Gizzard shad	<i>Dorosoma cepedianum</i>	Clupeidae	D	12,954	53
Threadfin shad	<i>Dorosoma petenense</i>	Clupeidae	D	26,485	41
Bighead carp	<i>Hypophthalmichthys nobilis</i>	Cyprinidae	PLANK	2	1
Common carp	<i>Cyprinus carpio</i>	Cyprinidae	ID	374	43
Blacktail shiner	<i>Cyprinella venusta</i>	Cypinidae	I	134	9
Bullhead minnow	<i>Pimephales vigilax</i>	Cyprinidae	ID	10	5
Cypress minnow	<i>Hybognathus hayi</i>	Cyprinidae	HD	38	3
Grass carp	<i>Ctenopharyngodon idella</i>	Cyprinidae	H	3	3
Golden shiner	<i>Notemigonus crysoleucas</i>	Cyprinidae	I	529	33
Pallid shiner	<i>Hybopsis amnis</i>	Cyprinidae	I	1	1
Pugnose minnow	<i>Opsopoeodus emiliae</i>	Cyprinidae	ID	957	41
Ribbon shiner	<i>Lythrurus fumeus</i>	Cyprinidae	ID	86	7
Silver carp	<i>Hypophthalmichthys molitrix</i>	Cyprinidae	PLANK	7	5
Taillight shiner	<i>Notropis maculatus</i>	Cyprinidae	ID	410	20
Emerald shiner	<i>Notropis atherinoides</i>	Cyprinidae	PLANK	100	5
Creek chubsucker	<i>Erimyzon oblongus</i>	Catostomidae	ID	2	2
Smallmouth buffalo	<i>Ictiobus bubalus</i>	Catostomidae	ID	3,696	44
Bigmouth buffalo	<i>Ictiobus cyprinella</i>	Catostomidae	ID	1,875	49
Black buffalo	<i>Ictiobus niger</i>	Catostomidae	ID	59	21
Blacktail redhorse	<i>Moxostoma poecilurum</i>	Catostomidae	I	13	8
Quillback carpsucker	<i>Carpiodes cyprinus</i>	Catostomidae	I	10	5
River carpsucker	<i>Carpiodes carpio</i>	Catostomidae	I	125	11
Spotted sucker	<i>Minytrema melanops</i>	Catostomidae	I	186	12
Brook silverside	<i>Labidesthes sicculus</i>	Atherinidae	I	2,457	48
Inland silverside	<i>Menidia beryllina</i>	Atherinidae	I	66	5
Tadpole madtom	<i>Noturus gyrinus</i>	Ictaluridae	IP	2	1
Black bullhead	<i>Ameiurus melas</i>	Ictaluridae	IP	23	13
Yellow bullhead	<i>Ameiurus natalis</i>	Ictaluridae	IP	91	27
Blue catfish	<i>Ictalurus furcatus</i>	Ictaluridae	IP	39	13
Channel catfish	<i>Ictalurus punctatus</i>	Ictaluridae	IP	234	34
Flathead catfish	<i>Pylodictis olivaris</i>	Ictaluridae	IP	59	18
Western mosquitofish	<i>Gambusia affinis</i>	Poeciliidae	I	186	29
Blackspotted topminnow	<i>Fundulus olivaceus</i>	Fundulidae	I	215	29
Blackstripe topminnow	<i>Fundulus notatus</i>	Fundulidae	I	39	9
Golden topminnow	<i>Fundulus chrysotus</i>	Fundulidae	I	7	2

Table 5 continued

Common name	Scientific name	Taxonomic guild	Feeding guild	N_{Fish}	N_{Lakes}
Northern starhead topminnow	<i>Fundulus dispar</i>	Fundulidae	I	1	1
White bass	<i>Morone chrysops</i>	Moronidae	IP	44	9
Yellow bass	<i>Morone mississippiensis</i>	Moronidae	IP	255	10
Pirate perch	<i>Aphredoderus sayanus</i>	Aphredoderidae	IP	25	10
Flier	<i>Centrarchus macropterus</i>	Centrarchidae	I	2	1
Dollar sunfish	<i>Lepomis marginatus</i>	Centrarchidae	I	13	5
Green sunfish	<i>Lepomis cyanellus</i>	Centrarchidae	IP	135	26
Longear sunfish	<i>Lepomis megalotis</i>	Centrarchidae	I	5,291	43
Orangespotted sunfish	<i>Lepomis humilis</i>	Centrarchidae	I	4,829	46
Redspotted sunfish	<i>Lepomis miniatus</i>	Centrarchidae	I	224	11
Bluegill	<i>Lepomis macrochirus</i>	Centrarchidae	I	17,971	53
Redear sunfish	<i>Lepomis microlophus</i>	Centrarchidae	IP	560	32
Warmouth	<i>Lepomis gulosus</i>	Centrarchidae	IP	1,778	52
Spotted bass	<i>Micropterus punctulatus</i>	Centrarchidae	IP	315	11
Largemouth bass	<i>Micropterus salmoides</i>	Centrarchidae	IP	3,487	51
Black crappie	<i>Pomoxis nigromaculatus</i>	Centrarchidae	IP	292	35
White crappie	<i>Pomoxis annularis</i>	Centrarchidae	IP	1,895	49
Banded pygmy sunfish	<i>Elassoma zonatum</i>	Elassomatidae	I	1	1
Bluntnose darter	<i>Etheostoma chlorosomum</i>	Percidae	I	10	7
Cypress darter	<i>Etheostoma proeliare</i>	Percidae	I	1	1
Mud darter	<i>Etheostoma asprigene</i>	Percidae	I	3	3
Speckled darter	<i>Etheostoma stigmaeum</i>	Percidae	I	7	4
Swamp darter	<i>Etheostoma fusiforme</i>	Percidae	I	1	1
Logperch	<i>Percina caprodes</i>	Percidae	I	383	10
Sauger	<i>Sander canadense</i>	Percidae	IP	2	2
Blackside darter	<i>Percina maculata</i>	Percidae	I	30	6
Freshwater drum	<i>Aplodinotus grunniens</i>	Sciaenidae	IP	846	40

Only species with ' N_{Lakes} ' values greater than six were retained for fish assemblage analyses

N_{Fish} total number of fish collected, N_{Lakes} number of lakes in which species was collected, *D* detritivore, *H* herbivore, *HD* herbivore–detritivore, *I* invertivore, *ID* invertivore–detritivore, *IP* invertivore–piscivore, *P* piscivore, *PLANK* planktivore

suggesting an increase in representation in the fish assemblage with lake–river disconnection and turbidity.

Discussion

Fish assemblage structure and taxonomic guilds were associated with landscape, lake, and local in-lake environmental characteristics. Fish assemblage structure was correlated with depth, surface area, and riparian and watershed land-covers. Although taxonomic and feeding guilds were correlated with various

environmental variables, these canonical correlations showed no consistent patterns relative to a hierarchical relationship with landscape, lake, and in-lake level variables. Results partially support our initial hypotheses in view of the fact that depth and riparian and watershed land-covers were significant determinants of fish assemblage structure. However, the degree of lake–river interconnectedness was not. In addition, we found stronger correlations between in-lake variables and fish assemblage structure than between landscape-level and lake-level variables and fish assemblage structure.

Table 6 Canonical correlations between floodplain lake landscape-level variables, lake-level variables, in-lake-level variables, fish assemblage structure, and selected taxonomic and feeding guilds

Variable	Water quality PC1	Water quality PC2	Chlorophyll <i>a</i>	Assemblage structure	Gars	Buffalos	Catfishes	Sunfishes	Invertivores	Invertivore–piscivores	Intervivore–detritivores	Piscivores
Landscape												
Riparian PC1	0.26	0.13	0.06	0.72	0.34	0.29	0.05	0.25	0.25	0.48	0.26	0.12
Watershed PC1	0.25	0.15	0.11	0.77	0.34	0.22	0.35	0.06	0.18	0.16	0.16	0.08
Watershed PC2	0.30	0.02	0.02	0.79	0.14	0.27	0.21	0.32	0.26	0.12	0.32	0.15
Lake												
Depth	0.27	0.63	0.67	0.71	0.11	0.46	0.01	0.14	0.07	0.02	0.46	0.23
Surface area	0.39	0.05	0.12	0.46	0.05	0.04	0.14	0.10	0.31	0.04	0.05	0.11
Connectivity	0.10	0.04	0.01	0.48	0.31	0.22	0.21	0.21	0.21	0.49	0.27	0.38
In-lake												
Water quality PC1				0.91	0.07	0.30	0.04	0.34	0.43	0.29	0.34	0.18
Water quality PC2				0.86	0.38	0.39	0.10	0.22	0.24	0.15	0.34	0.36
Chlorophyll <i>a</i>				0.74	0.04	0.33	0.25	0.29	0.21	0.12	0.29	0.01

Blanks indicate that the canonical correlation was not computed. Bold values indicate statistical significance at $\alpha = 0.05$

Land-cover and fish assemblage structure

Riparian and watershed land-covers exerted similar influences on water quality, primary productivity, and fish assemblage structure in our studied lakes. The importance of proper riparian and watershed management is well recognized (e.g., Tebo, 1955; Ritchie, 1972; Walser & Bart, 1999). Nonetheless, sedimentation and nutrient loading resulting from poor riparian and watershed practices continues to plague aquatic resources (Shields et al., 2010). Land-cover practices surrounding floodplain lakes may influence fish assemblage structure directly via physiological harm (Ritchie, 1972; Brunton, 1985) or indirectly via habitat or water quality degradation (Lucas, 1985; Cooper & McHenry, 1989; Hall et al., 1999; Roozen et al., 2003).

Lakes with high levels of riparian and watershed disturbances may experience high sedimentation rates (upwards of 7 cm year⁻¹; McHenry et al., 1982; Cooper & McHenry, 1989), which can accelerate reductions in depth. Thus, fish assemblages in lakes with riparian- and watershed-scale disturbances may be subject to unfavorable shifts in fish assemblage characteristics, as seen in extremely shallow lakes (Miranda, 2011). Similarly, the piscivory-transparency-morphometry model (PTM; Rodríguez & Lewis, 1997) may act to structure fish assemblages in lakes subject to large riparian and watershed disturbances, with sight-feeding piscivores eventually replaced by low-visibility tactile-feeders. Alternatively, because of the influence of suspended sediments and high nutrient loads on water quality characteristics, changes in fish assemblage structure relative to riparian and watershed land-covers may be more reflected in tolerance guilds than taxonomic guilds. However, our analysis was not designed to detect these changes. Moreover, watershed disturbances resulting from practices designed to support agriculture (e.g., clear-cutting, leveeing, ditching, channelization, and impoundments) can change hydrology and the water table, thereby affecting patterns in lake water level fluctuations (Foley et al., 2004).

Depth and fish assemblage structure

Depth has previously been recognized as a deterministic factor influencing the abiotic environment and fish assemblages in floodplain lakes. Depth is largely responsible for thermal, chemical, and light

stratification and for patterns of water transparency and planktonic photosynthesis dynamics in freshwater lakes (Scheffer, 2004; Nöges, 2009). Thus, fish assemblage structure is likely directly and indirectly influenced by depth and the forces it exerts on water quality and primary productivity, similar to the effects of surrounding land-cover. For example, Miranda (2011) found strong associations between depth and physicochemical characteristics and depth and fish assemblage structure and hypothesized that correlations between fish assemblage structure and physicochemical variables may be totally or partially regulated by depth.

The PTM model (Rodríguez & Lewis, 1997) provides a case where fish assemblage structure may be mediated by depth via water transparency. The PTM model predicts that relative abundance of fishes with low- and high-visibility feeding adaptations should vary predictably as water transparency declines following reductions in depth and subsequent resuspension of sediments (Hamilton & Lewis, 1990; Rodríguez & Lewis, 1997). Shifts in fish assemblage structure in response to changes in water transparency may be exacerbated in lakes experiencing high sedimentation rates, which experience increased lake-shallowing and would eventually be subject to environmental conditions typical of shallow lakes (i.e., increased turbidity and large fluctuations in DO). In addition, depth is often associated with environmental stability, with deeper lakes providing greater stability than shallower lakes (e.g., Zeug et al., 2005; Shoup & Wahl, 2009; Miranda, 2011).

Surface area and fish assemblage structure

Lake surface area was weakly, albeit significantly correlated with fish assemblage structure. Surface area showed the strongest correlation with water quality and no correlation with primary productivity. It is probable that the correlation between surface area and fish assemblage structure is confounded by the combined effects of depth and surrounding land-cover. For example, reductions in surface area are typical of floodplain lakes undergoing depth reduction via increased sedimentation, which is commonly linked with surrounding land-cover (Miranda, 2005; Wren et al., 2008; Shields et al., 2010).

Relationships between lake surface area and fish assemblage structure are more obscure than

relationships between surface area and fish biodiversity (e.g., MacArthur & Wilson, 1967; Eadie et al., 1986; Amarasinghe & Welcomme, 2002). In accordance with the species-area relationship, biodiversity scales positively with surface area (MacArthur & Wilson, 1967; Browne, 1981). Greater surface area may be correlated with greater habitat complexity, and a lake with greater habitat heterogeneity can theoretically support more species that are able to exploit all available habitats. Relationships between surface area and biodiversity can likely be extended to fish assemblage structure in view of the fact that larger lakes with more exploitable niche space and more fishes to fill these niche spaces may have different assemblage structure than smaller lakes.

Connectivity and fish assemblage structure

Before major landscape modifications in the region, lake–river connectivity was an extremely influential component of floodplain ecosystem dynamics (Junk et al., 1989; Baker et al., 1991). In addition, previous studies have demonstrated that connectivity is a driving force behind floodplain lake fish assemblage structure (Miranda, 2005; Zeug et al., 2005; Shoup & Wahl, 2009; Miyazono et al., 2010). Thus, we expected significant correlations between fish assemblage structure and the degree of lake–river interconnectedness. Nonetheless, connectivity was not correlated with fish assemblage structure as a whole.

It is probable that any actual relationships between fish assemblage structure and the degree of lake–river interconnectedness were diluted by the coarseness of our method of measuring connectivity. Dembkowski & Miranda (2012) found no association between floodplain lake fish biodiversity and the degree of lake–river interconnectedness in a similar set of floodplain lakes and hypothesized that the effects of connectivity may influence fish assemblage structure more than fish biodiversity. There is clearly scope for further research in understanding the effects of lake–river interconnectedness on fish assemblage structure in floodplain lakes, as well as in the development of a more accurate measure of lake–river connectivity, especially in regions with minimal topographic relief where leveeing, ditching, and channelization of nearby rivers might have altered natural connection routes. An ideal index of lake–river interconnectedness should probably include not only linear distance

of the connection channel, but also physical attributes of the connection channels (e.g., width, depth, and presence of fish passage barriers).

Water quality, primary productivity, and fish assemblage structure

Water quality and primary productivity showed stronger relationships with fish assemblage structure than any of the landscape-level or lake-level variables we considered. Although we expected stronger correlations between landscape- and lake-level variables and fish assemblage structure, the observed trend is not surprising given that local abiotic conditions are a filter operating on the origin and maintenance of fish assemblages as proposed by Tonn (1990) and modified by Tonn et al. (1990) and Wootton (1992). Whereas most of the landscape- and lake-level variables influence fish assemblage structure through direct or indirect pathways, water quality and primary productivity variables likely function to structure fish assemblages directly via physiological tolerance or thresholds. For example, fish assemblages in extremely turbid lakes may be dominated by tactile-feeding species because of the inability of sight-feeding piscivores to survive. Aside from turbidity, variables such as water temperature (Magnuson et al., 1979; Shuter et al., 1980), DO (Zalewski & Naiman, 1984), nutrient loading (Ryder, 1982; Rempel & Colby, 1991), and their diel and seasonal fluxes affect certain fish physiological attributes and have been demonstrated to affect assemblage structure. It should also be noted that fish assemblages themselves may influence water quality and primary productivity (e.g., bioturbation from foraging activities of benthic fishes; Scheffer, 2004; Mormul et al., 2012), but the potential for fish assemblages to influence environmental variables was not investigated in this study. Although water quality and primary productivity influence fish assemblage structure through direct pathways, it is important to note that they are both influenced to a certain degree by landscape-level and lake-level variables. Results of this study suggest that water quality was influenced by lake surface area, watershed land-cover, and depth, and that primary productivity was influenced by depth, but future research should be directed at further-elucidating these relationships to grasp a better understanding of the influence of landscape-level and lake-level variables on in-lake processes.

Ecological applications

Results of this study demonstrate that fish assemblage structure in floodplain lakes of the Mississippi Alluvial Valley was influenced by variables operating on three different scales, but in-lake variables showed stronger relationships with fish assemblage structure than did landscape-level or lake-level variables, suggesting a hierarchy of influence. Thus, in theory, depth, surface area, and riparian and watershed land-covers can be manipulated for conservation and (or) restoration purposes and water quality and primary productivity variables and fish assemblage structure can be used to monitor the success of such efforts. However, lake depth appears to be a “common denominator” for all landscape-level and lake-level variables because lakes subject to losses in surface area and to riparian- and watershed-scale disturbances exhibit abiotic characteristics and shifts in fish assemblage structure similar to lakes undergoing depth reductions. Deeper lakes provide greater environmental stability and may attenuate the negative effects of surface area reduction and sedimentation resulting from riparian and watershed disturbances.

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