Relationships between Floodplain Lake Fish Communities and Environmental Variables in a Large River–Floodplain Ecosystem

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Abstract.—Floodplain lakes of large river systems contain fish habitats that are not found elsewhere within the river, and these lakes have a diversity of environmental conditions that vary in space and time. Our objective was to examine relationships between floodplain lake fish communities and environmental variables associated with lake morphology, water chemistry, and river–floodplain connectivity in a large river–floodplain ecosystem. Multivariate direct-gradient analyses indicated that lake surface area, lake depth, water clarity, and (to a lesser extent) dissolved oxygen were the most important factors in the structuring of lake fish communities. Results further suggested that floodplain lakes could be placed into groups that contained distinctive fish communities. Fish community structure was not strongly related to river–floodplain connectivity, though fish species richness in individual lakes was positively correlated with degree of flooding in those lakes. Fish species diversity in lakes was positively correlated with linear distance between lakes and the main river channel; lakes that were furthest from the main river channel had more diverse fish communities. The diversity of environmental conditions in floodplain lakes is essential for maintaining net ecosystem diversity in large river ecosystems.

Modern-day large rivers are subject to a variety of environmental impacts related to economic development and patterns of land use in many regions of the world. These practices include channel alignment, dredging, and bank stabilization for commercial navigation, construction of levee networks for flood control, and draining of wetlands and water withdrawal for agricultural purposes (Gore and Shields 1995; Stanford et al. 1996; Poff et al. 1997). These impacts have essentially eliminated many natural processes in rivers and are especially evident in floodplain habitats, where the effects of altered hydrology and associated nutrient exchange, sedimentation, and water withdrawal are most exacerbated (Knowlton and Jones 1997; Benke et al. 2000). The combined effects of these impacts have led to a net reduction in connectivity between the rivers and their floodplains (Ward and

Stanford 1995). The long-term ecological effects of these impacts on riverine ecosystems and their fish communities are not yet fully understood (Sparks 1995; Karr 1999).

The alluvial valley of the lower Mississippi River contains hundreds of fluvial lakes that are created naturally from channel meandering, braiding, and associated processes (Miranda 2005). Floodplain lakes are dynamic environments with unique habitats that are not found elsewhere in the river, and they contain a diversity of environmental conditions that vary in space and time (Baker et al. 1991; Sabo and Kelso 1991). Unfortunately, these lakes are no longer being created naturally in most river systems and are undergoing “terrestrialization” as they age, fill with sediment, become smaller and shallower, and progressively disconnect from adjacent rivers (Miranda 2005). Channel degradation occurring in some rivers in response to regulation schemes further exacerbates this process by lowering river channel bottoms (as distance above mean sea level), which increases the seasonal flows needed to reconnect floodplains (Biedenharn and Watson 1997). The dynamic nature of floodplain lakes is driven largely by seasonal flood pulses, which affect

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many aspects of their ecology. Floods provide periodic connections between the lake and the main river channel that facilitate nutrient exchange between the river and floodplain, affect sediment deposition in floodplain habitats, and homogenize fish communities by allowing passage between the river and floodplain (Miranda 2005; Schramm and Eggleton 2006). In terms of riverwide fish production and species diversity, seasonal connections between rivers and their floodplains are considered essential for healthy river ecosystems (Junk et al. 1989; Bayley 1995; Sparks 1995; Bowen et al. 2003).

The effects of humans on modern-day rivers and associated floodplain habitats are mostly irreversible. Understanding what factors are involved in the structuring of riverine fish communities is an important first step toward managing and conserving riverine fisheries in the remaining habitats. Thus, to effectively manage, conserve, or restore floodplain fish communities, it is essential to understand how these fish communities are influenced by their environment. The primary goal of this research was to examine empirical relationships between fish community structure and environmental conditions in floodplain lakes of a large river–floodplain ecosystem. We tested the hypothesis that predictable fish communities occur in association with environmental variables that reflect morphometry, water quality, and connectivity of floodplain lakes. Implications of this research are to provide an understanding of fish–environment relationships in large river–floodplain ecosystems. Results can further help guide future river management and aid resource managers in species conservation efforts in large river–floodplain ecosystems.

Methods

Study area.—The White River is the largest river basin in Arkansas in terms of drainage area (44,400 km² within Arkansas; 71,911 km² total in Arkansas and Missouri) and drains 34% of the state (Robison and Buchanan 1988). The White River forms in northwestern Arkansas, flows northward into Missouri, and then flows southward back into Arkansas. The White River flows almost the length of the state before flowing into the Mississippi River at river kilometer (rkm) 964 (rkm 0 = mouth of the Mississippi River), just north of the Arkansas River confluence. The upper White River in northern Arkansas and southern Missouri is impounded by four dams that create a series of large reservoirs (Beaver, Table Rock, Bull Shoals, and Norfork lakes). The lower 476 km of the river below Batesville, Arkansas, is free flowing, has an active floodplain, and typifies a lowland warmwater river. The U.S. Army Corps of Engineers maintains a navigation channel by

dredging throughout the lower 400 km of the river (2.4 m deep upstream through rkm 320; 1.4 m deep to rkm 400). This section of the river contains no entrainment structures, such as bank revetments or dike fields. The lower section of the river also has several large, free-flowing tributaries (e.g., Buffalo, Black, and Cache rivers) that moderate thermal effects of upstream dams (K. Shirley, Arkansas Game and Fish Commission, unpublished data). The White River National Wildlife Refuge (WRNWR) is located between rkm 16 and 161. The refuge contains about 65,000 ha of bottomland hardwood forest floodplain habitat and approximately 360 floodplain lakes with surface areas exceeding 0.2 km² (2 ha). The floodplain also contains hundreds of smaller (<0.2-km²) lakes and numerous interconnected sloughs and bayous. Seasonal flood pulses are the primary mechanism by which these floodplain lakes become seasonally connected to the White River; some lakes become highly connected to the main river channel and others do not (Lubinski 2004). The WRNWR is typically inundated with spring floodwaters from March to late April or May, although the duration varies among years.

Lake selection.—A total of 16 floodplain lakes within the WRNWR were selected for this study (Figure 1). Floodplain lakes were emphasized because they are important floodplain habitats and support a major proportion of the riverine fish fauna. In this study, 64 of 95 species recorded from the lower White River (Robison and Buchanan 1988; Arkansas Game and Fish Commission, unpublished data) were collected. Lake selection was based on several factors that included lake size and boat access for sampling. Although fewer than 50 of the refuge's lakes were accessible by boat, selection of study areas was done randomly from these lakes. Based on examination of refuge maps and consultation with WRNWR personnel, selected lakes were judged to be representative of all lakes present in the system. We did consider that the selected lakes potentially represented a biased subset of all lakes because they were boat accessible and subject to angling effort differing from that in nonaccessible lakes. However, on-site observations indicated that at least some angling effort occurred in nearly all lakes, even those without road or boat access.

Fish collections.—To better depict the overall lake fish communities, sampling was conducted with three gear types: mini-fyke nets, experimental gill nets, and boat-mounted electrofishers (nighttime). Four modified mini-fyke nets were fished per lake during summer (July–August) 2002 for approximately 24 h. Mini-fyke nets had 3-mm bar mesh and were fished in littoral-zone areas less than 10 m from shore to target small-bodied littoral-zone fishes (Gutreuter et al. 1995; Clark

FIGURE 1.—Map showing the locations of selected floodplain lakes sampled for fish community diversity and environmental variables in the lower White River system, Arkansas (scale: 1 cm = 2 km; RKM = river kilometer). Scale: 1 cm = 2 km (1 in = 5 mi).

et al. 2007). Also during summer 2002, three monofilament experimental gill nets (8.1 m long; 2.4 m deep) were fished per lake. Gill nets were fished concurrently with the mini-fyke nets in each lake and deployed in limnetic-zone areas up to several meters deep. Gill nets targeted larger-bodied limnetic and benthic species. The nets had five different equal-area mesh sizes (2.54, 3.81, 5.08, 6.35, and 7.62 cm²) to reduce fish size selectivity (Hubert 1996). Gill nets were fished for 4 h in the morning from approximately 0700 to 1100 hours; 4-h sets were used instead of overnight sets to help reduce fish mortality from stress and predator impacts (e.g., turtles and American alligators *Alligator mississippiensis*). Boat-mounted nighttime electrofishing was conducted during fall (October–November) 2002 with a pulsed-DC Smith-Root 7.5 generator-powered pulsator electrofisher (Smith-Root, Inc., Vancouver, Washington). Six 10-min electrofishing samples were taken in each lake; three samples were taken at 15 Hz and three were taken at 60 Hz to target the widest variety of scaled and scaleless fishes (Schramm and Pugh 2000). Nighttime

electrofishing was conducted from approximately 1 h after sunset to 1 h before sunrise in littoral-zone areas only. Electrofishing output settings were standardized based on water temperature and conductivity to achieve an approximately standard power output of 3,000 W during all sampling (Burkhardt and Gutreuter 1995). In combination, the three gear types were expected to adequately sample the lake fish communities in terms of species composition and size structure.

Environmental data.—Environmental variables that were expected to affect fish communities were measured or estimated concurrently with fish sampling. Lake morphometric variables were estimated once and assumed to be constant throughout the study. Mean depth measurements of each lake were determined by traveling zigzag patterns across each lake with a portable depth finder and recording depth every 10 s. Maximum depth in each lake was determined from these measurements. A length:width ratio for each lake was calculated as the lake length (longest axis) divided by the lake width (perpendicular to this axis), as determined from topographic maps in Delorme 3-D TopoQuads mapping software (Delorme, Yarmouth, Maine). In interpreting length:width ratios, 1.0 represented a lake that was perfectly round. Lake distance from the main river channel was also determined with Delorme 3-D TopoQuads software. Lake surface areas were determined from a geographic information systems database maintained by the WRNWR. Degree of flooding was a qualitative estimate of river–floodplain connectivity based on a rating method similar to that of Miranda (2005). The WRNWR field personnel working in refuge lakes were asked to classify each lake on a three-point scale in which 1 represented a lake that flooded infrequently, 3 represented a lake that flooded frequently, and 2 represented an intermediate lake. Morphoedaphic index (MEI) values for each lake were calculated by dividing the total dissolved solids (TDS) measure by lake mean depth following the methods of Ryder et al. (1974). Lakes also were classified according to their location in the south unit (scored as 1) or north unit (scored as 2) of the refuge; a highway causeway (Arkansas State Highway 1) served as the dividing boundary between units. This boundary is not arbitrary because the causeway affects flooding patterns in the refuge, both from downstream flows in the White River proper and backflows from the Mississippi River.

During summer and fall sampling in each lake, dissolved oxygen (DO; mg/L), temperature (°C; vertical profile at 0.5-m increments), and conductivity (µS/cm) measurements were taken with a handheld YSI (Yellow Springs, Ohio) Model 85 multiprobe field meter at three randomly selected sites per lake. The

level of TDS (mg/L) was measured with an Oakton Instruments (Vernon Hills, Illinois) deluxe conductivity–TDS meter Model WD-35607-69 at the same three sites. The DO, temperature, conductivity, and TDS measurements were taken during summer concurrently with fykenetting and gillnetting and were collected between 0700 and 1100 hours; values from 0.5-m depth were reported. Water quality measures taken during fall concurrently with electrofishing were recorded between 1800 and 0000 hours. Water clarity (cm) was measured with a standard Secchi disk at the same three sites during summer sampling only.

Data analysis.—Species richness was estimated as the number of species present. Species diversity was estimated using Simpson's reciprocal diversity index (Simpson 1949; Washington 1984). Evenness was computed by dividing the observed Shannon diversity index (H') by the theoretical maximum diversity ($H_{\max}$), which is equivalent to $\log_{10}(\text{species richness})$ (Magurran 2004). Relationships between fish species diversity, richness, and evenness measures and lake-specific environmental variables were assessed with ordinary least-squares linear regression. Significance level for all statistical analyses was set at 0.05.

Canonical correspondence analysis (CCA; ter Braak 1986) was used to examine relationships between fish communities and environmental variables measured. These analyses were designed to identify statistically significant environmental gradients within floodplain lake fish communities and provide a basis for classifying lakes into groups with similar characteristics and fish communities. The CCA is a direct gradient analysis that ordines a species $\times$ sample data matrix within the constraint that resulting site scores must be linear combinations of the environmental variables measured (Palmer 1993). Significance of the fish–environment association was assessed by comparing observed eigenvalues from the first three ordination axes with those generated from randomization of the species $\times$ lake data matrix (10,000 iterations) using a simple Monte Carlo reshuffling algorithm. Rejection of this test meant that observed eigenvalues were greater than those expected by chance (i.e., eigenvalues generated from randomized data), which indicated a significant association between fish communities and environmental variables. Significance level for Monte Carlo analyses was set at 0.05.

In an attempt to examine community structure in a more holistic manner, fish community data were combined for all gears. Because units of catch per unit effort (CPUE) varied across gears, data were converted from raw species-specific CPUE data into ranked abundances for each gear, where the species-specific ranks were averaged across gears. All species were

used in this ranking procedure; the most abundant species received a rank of 64 (64 species were collected overall), the second most abundant species received a rank of 63, and so forth. In cases where a species was not collected with a particular gear, ranks were considered tied and the mean rank was used. For instance, if a gear collected 44 of the 64 species present (meaning 20 species were not collected), the 20 uncollected species were assigned a mean rank of 10.5. Because ordination analyses can be sensitive to high numbers of rare species in various ways (ter Braak 1995), one CCA was constructed using ranked abundances of all 64 collected species and another CCA was constructed using only those species that constituted more than 0.05% of all collected fishes. This latter CCA contained the 42 most common (i.e., highly ranked) species, which represented 99.7% of all collected fishes. Our elimination of rare species was consistent with studies by Miranda and Lucas (2004) and Miranda (2005), who did similar research, and is sometimes warranted in ordination analyses (McCune and Grace 2002). Gido et al. (2002), Eggleton et al. (2005), and Falke and Gido (2006) represent other ordination examples where rare species were eliminated. However, rare species were included in analyses involving richness, diversity, and evenness.

All CCA calculations and associated Monte Carlo tests were conducted with PC-ORD software (McCune and Mefford 1999). To interpret the ordination axes, we examined the intraset correlations as recommended by ter Braak (1986). Intraset or environment–axis correlations are the correlation coefficients between the environmental variables and the ordination axes. By examining signs and relative magnitudes of these correlation coefficients, one can infer the relative importance of each environmental variable for predicting the community composition along the respective ordination axis (ter Braak 1986).

To assess relationships between individual fish species and environmental variables, we examined Pearson's product-moment correlation coefficients that reflected associations between individual lake (i.e., sample) scores and individual species scores from the CCA ordination (McCune and Grace 2002). A negative correlation represented an inverse relationship between fish species and lakes (and, hence, the environmental variables associated with those lakes). Similarly, positive correlations represented direct associations between species and lakes. A correlation coefficient near zero signified the absence of a species–lake relationship, meaning that the species in question was sufficiently general and found across a wide range of environmental conditions.

TABLE 1.—Lake morphometric variables from 16 floodplain lakes in the lower White River system, Arkansas 2002. Values are considered constant for summer and fall sampling periods.

Variable	Mean	SE	Minimum	Maximum
Average depth (m)	2.2	0.3	0.6	4.7
Degree of flooding	2.3	0.2	1.0	3.0
Maximum depth (m)	3.5	0.5	1.0	7.9
Morphoedaphic index	76	10	28	171
Distance from main channel (km)	1.7	0.3	0.03	4.5
Length : width	17	2	2	33
Lake surface area (km ²)	0.21	0.04	0.03	0.48

Results

Floodplain Lake Environmental Characteristics

Maps used for lake morphometric determinations (i.e., surface area and length : width ratio) assumed base flow conditions; thus, values computed for all lakes reflect disconnection from the main river. The selected lakes had surface areas ranging from 0.03 to 0.48 km² (mean $\pm$ SE = 0.21 $\pm$ 0.04 km²), length : width ratios ranging from 2 to 33 (17 $\pm$ 2), depths ranging from 0.6 to 4.7 m (2.2 $\pm$ 3.3 m), and distances from the main channel ranging from 0.03 to 4.50 km (1.7 $\pm$ 0.4 km; Table 1). Water quality variables fluctuated between summer and fall months. During summer, DO levels averaged 6.19 $\pm$ 0.29 mg/L and ranged from 4.3 to 7.9 mg/L. Fall DO levels were greater on average (8.92 $\pm$ 0.48 mg/L; Table 2) than summer DO levels. Summer water temperatures averaged 29.4 $\pm$ 0.3°C and ranged from 26.7°C to 30.8°C, whereas fall water temperatures were lower (17.8 $\pm$ 0.9°C; Table 2). Secchi depth measurements taken during summer averaged 65 $\pm$ 6 cm. Also, fall water quality measures were more variable than those of summer. Conductivity and TDS levels were high during both summer and fall, suggesting that floodplain lake waters were generally hard (Table 2). No other data sets were available that

TABLE 2.—Mean environmental variables from 16 floodplain lakes in the lower White River system, Arkansas 2002.

Variable	Mean	SE	Minimum	Maximum
Summer				
Dissolved oxygen (mg/L)	6.19	0.29	4.34	7.90
Water temperature (°C)	29.4	0.3	26.7	30.8
Total dissolved solids (mg/L)	134.8	4.2	102.5	182.7
Conductivity (µS/cm)	230.4	4.7	175.2	248.1
Secchi depth (cm)	65.1	6.1	15.0	110.0
Fall				
Dissolved oxygen (mg/L)	8.92	0.48	6.10	14.01
Water temperature (°C)	17.8	0.9	13.0	25.5
Total dissolved solids (mg/L)	124.7	3.7	95.7	156.3
Conductivity (µS/cm)	209.5	6.8	158	256.2

TABLE 3.—Descriptive statistics for community metrics averaged across 16 floodplain lakes in the lower White River system, Arkansas 2002. Mean species richness (number of species present) was determined for all gear types pooled. Simpson's reciprocal diversity index and evenness (Shannon diversity index/theoretical maximum diversity) were averaged across the four gear types.

Measure	Mean	SE	Minimum	Maximum
Species richness	37	0.8	30	42
Simpson's index	5.205	0.031	2.173	9.045
Evenness	0.560	0.006	0.424	0.655

could be used to assess similarities and differences between study lakes and all other WRNWR lakes.

Some significant correlations were detected among the environmental variables from floodplain lakes, but not as many as expected. Distance from the main river channel tended to be the most important factor. Lake surface area was negatively correlated to distance from the main river channel ($r = -0.56$, $P = 0.02$), as was water clarity (i.e., Secchi depth; $r = -0.60$, $P = 0.01$). Average lake depth was not significantly correlated with distance from the main river channel ($r = -0.391$, $P = 0.13$). The MEI values also were greatest in small, shallow lakes and were correlated with several of these same variables. Results suggested that floodplain lakes located farthest from the main river channel tended to be smaller, shallow, and turbid and have high MEI values. Lake proximity to the main river channel did not appear to be related to flooding patterns. Degree of flooding was not correlated with lake distance from the main river channel ($r = 0.10$, $P = 0.70$), as lakes typically flooded through interconnected sloughs and bayous and other low-elevation areas in the floodplain. In other words, close proximity of a lake to the main river channel did not necessarily infer immediate flooding in that lake as river stages began to increase.

Floodplain Lake Fish Communities

Species richness, diversity, and evenness.—Fish collections from the three gears encompassed 42,065 fishes representing 64 species. However, one fyke net from one lake containing 14,868 Mississippi silvery minnow *Hybognathus nuchalis* was excluded from further analysis because it tended to skew all analyses. Species richness pooled across gears averaged 37 species/lake and ranged from 30 to 42 species/lake (Table 3). Electrofishing sampling recovered the most species (mean $\pm$ SE = 21.6 $\pm$ 0.8 species/lake). Fyke nets and gill nets collected an average of 18.8 $\pm$ 0.8 and 8.5 $\pm$ 0.7 species/lake, respectively.

The most abundant species from floodplain lakes in terms of percent abundance of all fishes collected were

TABLE 4.—Mean rank and composition of fish species (in alphabetical order) captured with four gears in 16 floodplain lakes in the lower White River system, Arkansas, 2002. Codes are used in ordination diagrams (Figures 2, 3).

Species code	Common name	Scientific name	Mean rank ^b	Percent composition ^c
BKBF	Black buffalo	<i>Ictiobus niger</i>	33.8	0.13
BKCP	Black crappie ^a	<i>Pomoxis nigromaculatus</i>	41.9	0.47
BKSS	Brook silverside ^a	<i>Labidesthes sicculus</i>	38.8	6.4
BLGL	Bluegill ^a	<i>Lepomis macrochirus</i>	53.9	9.5
BMBF	Bigmouth buffalo	<i>Ictiobus cyprinellus</i>	33.6	0.25
BNDR	Bluntnose darter	<i>Etheostoma chlorosoma</i>	28.8	0.22
BPTM	Blackspotted topminnow	<i>Fundulus olivaceus</i>	26.3	0.25
BWFN	Bowfin	<i>Amia calva</i>	30.6	0.10
CARP	Common carp	<i>Cyprinus carpio</i>	32.4	0.16
CNCF	Channel catfish ^a	<i>Ictalurus punctatus</i>	41.0	0.35
CYMW	Cyprress minnow	<i>Hybognathus hayi</i>	30.9	0.94
DLSF	Dollar sunfish	<i>Lepomis marginatus</i>	27.6	0.21
ERSN	Emerald shiner ^a	<i>Notropis atherinoides</i>	40.2	22.4
FWDM	Freshwater drum ^a	<i>Aplodinotus grunniens</i>	45.2	1.7
GDSN	Golden shiner	<i>Notemigonus crysoleucas</i>	28.4	0.26
GZSD	Gizzard shad ^a	<i>Dorosoma cepedianum</i>	53.0	5.9
LESF	Longear sunfish	<i>Lepomis megalotis</i>	37.6	0.99
LGPH	Logperch	<i>Percina caprodes</i>	37.8	0.64
LMBS	Largemouth bass ^a	<i>Micropterus salmoides</i>	47.3	1.04
LNGR	Longnose gar	<i>Lepisosteus osseus</i>	32.5	0.12
MMSN	Mimic shiner	<i>Notropis volucellus</i>	29.9	4.9
MQTF	Western mosquitofish	<i>Gambusia affinis</i>	24.7	0.07
OSSF	Orangespotted sunfish ^a	<i>Lepomis humilis</i>	48.9	3.6
PDSN	Pallid shiner	<i>Hybopsis amnis</i>	26.4	0.10
PGMW	Pugnose minnow	<i>Opsopoeodus emiliae</i>	34.4	12.0
PRPH	Pirate perch	<i>Aphredoderus sayanus</i>	27.8	0.08
RESF	Redear sunfish ^a	<i>Lepomis microlophus</i>	40.6	0.63
RVCS	River carpsucker	<i>Carpionodes carpio</i>	28.6	0.08
SJHR	Skipjack herring	<i>Alosa chrysochloris</i>	26.7	0.08
SLDR	Slough darter	<i>Etheostoma gracile</i>	26.5	0.09
SMBF	Smallmouth buffalo ^a	<i>Ictiobus bubalus</i>	42.8	0.71
SPSK	Spotted sucker	<i>Minytrema melanops</i>	37.4	0.48
STGR	Spotted gar ^a	<i>Lepisosteus oculatus</i>	49.3	0.79
SVMW	Mississippi silvery minnow	<i>Hybognathus nuchalis</i>	27.2	0.22
TFSD	Threadfin shad ^a	<i>Dorosoma petenense</i>	42.4	1.1
TLSN	Taillight shiner	<i>Notropis maculatus</i>	30.0	1.3
WDSN	Weed shiner	<i>Notropis texanus</i>	33.4	16.6
WRMH	Warmouth	<i>Lepomis gulosus</i>	48.8	1.9
WTBS	White bass	<i>Morone chrysops</i>	29.7	0.16
WTCP	White crappie ^a	<i>Pomoxis annularis</i>	46.8	1.3
YLBH	Yellow bullhead	<i>Ameiurus natalis</i>	27.0	0.06
YWBS	Yellow bass	<i>Morone mississippiensis</i>	42.5	0.81

^a Species was collected in all 16 lakes.
^b An average rank of 64 would indicate that the species was the most abundant species captured in all four gear types.
^c Represents percent composition of all fish collected in all gear types (total *n* = 21,197).

emerald shiners *Notropis atherinoides*, weed shiners *N. texanus*, pugnose minnows *Opsopoeodus emiliae*, bluegills *Lepomis macrochirus*, brook silversides *Labidesthes sicculus*, and gizzard shad *Dorosoma cepedianum* (Table 4). Each of these species contributed more than 5% of the fish community samples by number. These were smaller-bodied species collected in high abundances, mostly in fyke nets. In terms of ranked abundances averaged across gear types, the most abundant species were bluegills, gizzard shad, spotted gars *Lepisosteus oculatus*, orangespotted sunfish *Lepomis humilis*, warmouths *Lepomis gulosus*,

largemouth bass *Micropterus salmoides*, white crappies *Pomoxis annularis*, freshwater drum *Aplodinotus grunniens*, smallmouth buffalo *Ictiobus bubalus*, and yellow bass *Morone mississippiensis* (Table 4). These were larger-bodied species collected from electrofishing and gillnetting. Of the 64 species, 14 were collected in all 16 floodplain lakes (Table 4).

Separate least-squares linear regressions were conducted to relate fish species richness, diversity, and evenness to environmental variables. Degree of flooding was the only variable that was significantly related to species richness ($r^2 = 0.32$, slope = 1.81, $P = 0.02$).

Results suggested that greater fish community richness was associated with lakes that underwent greater degrees of flooding. Species richness exhibited no relationship with any other morphometric, physical, or water quality variable. Species diversity was related only to linear distance from the main channel ($r^2 = 0.26$, slope = 0.00049, $P = 0.04$), which indicated that fish community diversity was greater in lakes located furthest from the main river channel. Evenness exhibited significant relationships only with DO ($r^2 = 0.20$, slope = 0.07, $P < 0.001$) and water temperature ($r^2 = 0.29$, slope = -0.03 , $P < 0.001$).

Fish community–environment relationships.—The initial CCA that contained all 64 fish species and 11 environmental variables collected during summer and fall 2002 yielded three canonical axes that explained 46% of the total variation. However, although many species–axis correlations were high, none of the CCA axes was judged to be statistically significant (all $P > 0.05$). Thus, interpretations of patterns in community structure were limited, and this analysis was discarded. The CCA containing the 44 most abundant species (i.e., those contributing $>0.05\%$ of total abundance) and 11 environmental variables explained 48% of the variation and contained marginal significance on one axis. However, two medium-ranked species (spotted bass *Micropterus punctulatus* and shortnose gar *Lepisosteus platostomus*) were extreme outliers in the analysis because of high catches restricted to one lake (East Moon Lake for shortnose gars; Green Lake for spotted bass). These catches produced inflated average ranks for these species and greatly distorted the overall analysis. The two species were subsequently excluded from further analysis, and 42 species contributing 27,197 fishes (99.7% of all fish collected) were included in the final CCA. The final CCA model indicated significant associations between fish community structure and environmental variables in floodplain lakes. Significance was observed on two of three CCA axes (axis 1: $P = 0.004$; axis 2: $P = 0.654$; axis 3: $P = 0.039$). This CCA yielded three canonical axes that explained 43% of the total variation; axis 1, 2, and 3 accounted for 18, 13, and 12% of the variation in community structure, respectively.

Correlations between environmental variables and canonical axis 1 depicted a significant gradient involving lake size and, to a lesser extent, water clarity and DO levels (Table 5). The MEI values also appeared to be important in the structuring of fish communities, but the index's importance was probably due to its inclusion of lake depth, which was an important factor (notice that MEI and lake depth are strongly inversely related). Axis 1 differentiated lakes with high MEI, low

TABLE 5.—Intrasets correlations between 11 environmental variables and the first three canonical axes from canonical correspondence analysis performed using 42 fish species captured in 16 floodplain lakes in the lower White River system, Arkansas, 2002. Bold type indicates environmental variables with the greatest correlation to the respective ordination axis and, thus, the most important variables structuring the fish communities along that axis.

Variable	Axis 1	Axis 2	Axis 3
Dissolved oxygen (mg/L)	0.365	−0.489	−0.140
Water temperature (°C)	0.327	−0.065	0.408
Total dissolved solids (mg/L)	0.299	−0.010	0.536
Secchi depth (cm)	0.470	−0.104	0.553
Average depth (m)	0.679	0.279	0.029
Degree of flooding	0.193	0.151	−0.172
Morphoedaphic index	−0.603	−0.471	−0.327
Distance from main channel (km)	−0.221	−0.257	−0.248
Length : width	0.411	−0.066	−0.165
Surface area (km ²)	0.707	−0.286	0.235
Location (north or south unit)	−0.229	−0.050	0.214

average depth, and small surface area (low axis 1 scores) from lakes with low MEI, high average depth, and large surface area (high axis 1 scores; Figure 2). Lakes that were most associated with low MEI values, small area, and low depth were East Moon, Little Moon, Upper Swan, and Buck lakes, while those associated with high MEI values, large area, and greater depth were Cooks, Moon, and Green lakes (Figure 2). Species–axis correlations indicated that the species having the strongest association with small, shallow lakes were golden shiners *Notemigonus crysoleucas*, yellow bullheads *Ameiurus natalis*, spotted suckers *Minytrema melanops*, bowfins *Amia calva*, spotted gars, cypress minnow *Hybognathus hayi*, and redear sunfish *Lepomis microlophus*, as evidenced by the large negative correlations on axis 1 (Table 6). Species associated with large, deep lakes were longear sunfish *Lepomis megalotis*, common carp *Cyprinus carpio*, and white bass *Morone chrysops*, as indicated by the high positive correlations on axis 1 (Table 6).

Correlations between environmental variables and canonical axis 2 suggested the presence of a weak gradient that contrasted lakes with low and high DO concentrations (Table 5). East Moon, Escronges, Moon, and Cooks lakes were most associated with greater DO levels (low axis 2 score), whereas Upper Swan, Buck, and Big White lakes were characterized by lower DO levels (high axis 2 scores). Longnose gars *Lepisosteus osseus* and river carpsuckers *Carpoides carpio* showed some association with greater-DO lakes (Figure 2), but because axis 2 was nonsignificant, the interpretations of species–environment associations were limited.

FIGURE 2.—Scatterplot of canonical correspondence analysis (CCA) scores for floodplain lake fish communities in the lower White River system, Arkansas, 2002. Scores for axes 1 and 2 are plotted for individual lakes (top panel) and fish species (bottom panel; codes are defined in Table 4) and are based on rank-ordered abundances as described in Methods. Group numbers are defined in Discussion. Environmental variables are average lake depth (ADEP; m), lake surface area (AREA; km²), water clarity (SECCHI; Secchi depth, cm), dissolved oxygen (DO; mg/L), and morphoedaphic index (MEI). Vectors were rescaled by a factor of 2.

TABLE 6.—Correlations between 42 fish species (codes defined in Table 4) captured in 16 floodplain lakes in the lower White River system, Arkansas, 2002 and the first three canonical axes from canonical correspondence analysis performed using 11 environmental variables. Bold type indicates species with the greatest correlations to the respective ordination axis.

Species code	Axis 1	Axis 2	Axis 3
BKBF	-0.369	0.051	0.434
BKCP	-0.252	-0.478	0.305
BKSS	0.048	0.389	0.600
BLGL	0.152	0.404	0.023
BMBF	-0.037	0.381	-0.582
BNDR	0.412	0.326	-0.065
BPTM	-0.146	0.058	-0.672
BWFN	-0.624	-0.063	-0.540
CARP	0.536	0.055	-0.023
CNCF	0.202	0.459	-0.181
CYMW	-0.514	-0.521	0.117
DLSF	0.112	0.296	0.016
ERSN	0.428	-0.299	0.397
FWDM	-0.027	-0.386	-0.463
GDSN	-0.785	-0.212	0.000
GZSD	0.404	-0.194	0.331
LESF	0.645	0.362	0.042
LGPH	0.090	0.466	0.546
LMBS	-0.120	0.126	0.152
LNGR	0.487	-0.671	-0.188
MMSN	0.225	0.142	-0.374
MQTF	-0.320	-0.004	-0.681
OSSF	0.293	0.143	0.351
PDSN	0.386	-0.561	0.313
PGMW	-0.470	0.070	0.458
PRPH	-0.170	0.219	0.477
RESF	-0.513	0.299	0.058
RVCS	0.218	-0.595	-0.151
SJHR	0.414	0.264	-0.419
SLDR	-0.405	0.202	-0.007
SMBF	0.469	-0.358	0.429
SPSK	-0.649	0.072	0.156
STGR	-0.601	-0.555	0.096
SVMW	0.169	-0.133	-0.577
TFSD	-0.205	-0.320	0.414
TLSN	-0.142	0.056	0.610
WDSN	0.120	0.323	-0.181
WRMH	0.261	0.379	0.426
WTBS	0.533	-0.335	0.155
WTCP	0.169	-0.508	-0.535
YLBH	-0.753	-0.007	-0.029
YWBS	-0.423	-0.409	0.463

Correlations between environmental variables and canonical axis 3 depicted a significant gradient involving water clarity, TDS, and, to a lesser extent, water temperature (Table 5). The range of TDS in the 16 lakes was relatively narrow (96–156 mg/L; one lake at 182 mg/L) and may not have been biologically significant. However, water clarity values (Secchi depth) were more meaningful, ranging over sevenfold across lakes from 15 to 110 cm. Lakes associated with a high clarity (high axis 3 scores) were Cooks, Moon, Little Moon, and Escronges lakes, whereas those most associated with low clarity were East Moon and Columbus lakes (low axis 3 scores; Figure 3). Species

associated with clearer lakes were mostly small bodied, such as taillight shiners *Notropis maculatus*, brook silversides, and logperch *Percina caprodes* (Figure 3). Many other species showed tendencies toward association with clearer lakes, but relationships were weaker. Species associated with more turbid lakes were western mosquitofish *Gambusia affinis*, blackspotted topminnow *Fundulus olivaceus*, bigmouth buffalo *Ictiobus cyprinellus*, Mississippi silvery minnow, bowfins, and white crappies (Figure 3).

Discussion

Fish Community Structure and Environmental Variables

Fish abundance and community structure variation were related to environmental variables in floodplain lakes of the lower White River. Furthermore, the diversity of environmental conditions in the lakes produced somewhat distinctive fish communities. Major environmental gradients related to the structuring of fish communities involved lake depth, lake surface area, water clarity, and TDS; DO played a lesser role. Using these characteristics along the first and second CCA axes, floodplain lakes could be allocated among three main community types. One community type (group 1) came from small, shallow, turbid lakes and was typified by spotted gars, spotted suckers, golden shiners, yellow bullheads, yellow bass, bowfins, white crappies, and cypress minnows. These communities and lakes tended toward the left of the CCA diagram (Figure 2). The second community type (group 2) came from larger lakes with greater water clarity but only medium depth. These lakes contained greater abundances of white bass, common carp, smallmouth buffalo, and emerald shiners and lesser abundances of longnose gars and river carsuckers. Group 2 communities and lakes tended toward the right side of the CCA diagram (Figure 2). The third community type (group 3) predominated in lakes of intermediate size, greater depth, and high turbidity (i.e., turbidity was similar to that in lakes containing group 1). Species most associated with the third group of lakes were longear sunfish, redear sunfish, common carp, brook silversides, and pugnose minnow. These communities and lakes tended toward the upper middle portion of the CCA diagram (Figure 2). Along the third CCA axis, lakes separated into two main groups distinguished mostly by water clarity (Figure 3). Gizzard shad, threadfin shad *Dorosoma petenense*, bluegills, largemouth bass, channel catfish *Ictalurus punctatus*, and freshwater drum were found in all lakes and showed no tendency toward association with any particular lake group.

Similar fish community–environment relationships have been identified in other studies assessing fish

FIGURE 3.—Scatterplot of canonical correspondence analysis (CCA) scores from floodplain lake fish communities in the lower White River system, Arkansas, 2002. Scores for axes 1 and 3 are plotted for individual lakes (top panel) and fish species (bottom panel); codes are defined in Table 4) and are based on rank-ordered abundances as described in Methods. Group numbers are defined in the Discussion. Environmental variables are average lake depth (ADEP; m), lake surface area (AREA; km²), water clarity (SECCHI; Secchi depth, cm), dissolved oxygen (DO; mg/L), and morphoedaphic index (MEI). Vectors were rescaled by a factor of 2.

community structure in river–floodplain ecosystems. In floodplain lakes of the Brazos River, Texas, water depth, DO, dissolved nutrients, turbidity, and plankton densities accounted for 45–59% of the variation in abundance of the dominant species (Winemiller et al. 2000). Lake fish communities were structured along a primary gradient that discriminated between deep, well-oxygenated lakes (dominated by sunfishes, especially longear sunfish) and shallow lakes with low DO (dominated by western mosquitofish). Similar to the Brazos River oxbows, lake depth played an important role in the structuring of floodplain lake fish communities in this study, and DO was secondarily important. Deeper floodplain lakes in this study were characterized by fish communities consisting of several sunfish species, white bass, and common carp. Deeper lakes also tended to be clearer and larger, and the dominant species were several sight-feeding and schooling predators (e.g., sunfishes and white bass; Robison and Buchanan 1988). Shallower lakes, which also tended to be small and turbid, contained higher abundances of white crappies, spotted gars, spotted suckers, golden shiners, yellow bullheads, bowfins, and several small-bodied minnow species. Many of these species are fairly omnivorous in their feeding or specialize on bottom feeding (Robison and Buchanan 1988). Although DO was considered secondarily important in fish community structure, this latter list includes several species that are tolerant to low-DO conditions (e.g., spotted gars, golden shiners, yellow bullheads, and bowfins) and suggests that smaller, more shallow floodplain lakes periodically contain hypoxic conditions. A more thorough characterization of floodplain lake environmental conditions that includes seasonal and diel components would be required to better assess this possibility.

Miranda and Lucas (2004) examined fish communities in lower Mississippi River floodplain lakes and generated findings that are partially comparable with ours. Their results emphasized the importance of lake morphometric measures in that lake fish communities varied mostly with respect to lake area, lake elongation (length:width ratio), and, to a lesser extent, water clarity. Lake depth was not used in their analysis. In these Mississippi River lakes, redear sunfish, warmouths, and gars *Lepisosteus* spp. were best represented in clear, short, small lakes. Temperate basses *Morone* spp. were dominant in clear, short, large lakes, while black crappies *Pomoxis nigromaculatus* and largemouth bass tended to be better represented in clear, short, mid-sized lakes. Fishes that were common in turbid lakes included buffaloes *Ictiobus* spp., white crappies, channel catfish, and orangespotted sunfish. In our study, although lake area and depth were important

in structuring fish communities and some similar fish–environment relationships were observed, length:width ratios of lakes were only moderately correlated with axis 1 and were not correlated with the second or third axes. We suspect that in the Mississippi River study by Miranda and Lucas (2004), lake depth (which was not measured) was strongly related to length:width ratio in those lakes.

Rare species that were eliminated from the final CCA were judged to have no biological significance for community structure interpretations. Of the 22 species omitted from the final CCA, half were single-specimen catches; these species represented only 0.3% of the total number of fish collected. Deletion of rare species is commonly done in ordination analyses and often enhances the detection of community–environment relationships with several ordination methods (e.g., Austin and Greig-Smith 1968; Day et al. 1971; Callahan et al. 1979; McCune and Grace 2002). Such appeared to be true here, as the initial CCA of all 64 species depicted fish–environment relationships that were identical to those of the reduced analysis of 42 species. The only difference between the analyses was that the latter was significant. Thus, inclusion of rare species appeared only to have a dampening effect on the overall analysis. Further, it appeared that analysis of only the more highly abundant fish species was sufficient to detect the existing community–environment relationships, as suggested by Cao et al. (2001). Although deletion of rare species can be debated on the grounds of “losing good information,” this determination largely is based on the criterion used to define “good” information (McCune and Grace 2002). Conversely, richness and diversity analyses reported here included all species, as recommended by Cao et al. (1998).

Role of River–Floodplain Connectivity

Degree of flooding, which was a surrogate measure of river–floodplain connectivity in this study (Lubinski 2004), was not strongly related to fish community composition. In 2002, the magnitude and duration of spring flooding in the lower White River was above long-term averages, although summer and fall conditions were more typical (Clark 2006). Miranda (2005) reported strong relationships between fish communities and lake connectivity in the lower Mississippi River using an ordinal scale to quantify connectivity. Our degree of flooding variable was not a strong-scaled measure and may have been inadequate for depicting true connectivity of these lakes with the main river. The lower White River does have stream gauges, but none has been calibrated to accurately depict seasonal flooding patterns in floodplain habitats. Subsequent studies in these lakes have acquired better stage data

and have used remote monitors to detect lake-specific flood periodicity. This approach may provide better insights into the relationship between fish communities and river–floodplain connectivity.

Species richness was the only variable in this study that had a significant relationship with degree of flooding, suggesting that more frequently connected lakes tended to have more fish species. This is consistent with the results of Galat et al. (1998), who reported twice as many fish species in connected floodplain scours than in isolated scours in the lower Missouri River. Miranda (2005) reported similar results in that oxbow lakes that were permanently disconnected from the lower Mississippi River by levee systems consistently had fewer fish species than lakes with at least some connection to the river. Increased richness in more frequently connected lakes also is consistent with the idea that periodic flood pulses allow homogenization or “reshuffling” of fish communities between the river channel and floodplain lakes. Miranda (2005) hypothesized that lakes with higher degrees of connectivity (i.e., greater flooding) would be expected to contain a lotic and lentic species that are periodically mixed during flood pulses, whereas lakes with lower degrees of connectivity would contain mostly lentic species. There was some evidence of this possibility from the present study. For example, skipjack herring *Alosa chrysochloris*, a mostly lotic species, were found exclusively in floodplain lakes with high degrees of flooding (e.g., Brushy, Columbus, Green, Hog Thief, Horseshoe, and Moon lakes). Similarly, saugers *Sander canadensis*, another lotic species, were only collected in Brushy Lake, which had a higher degree of flooding. Longnose gars, smallmouth buffalo, and white bass, which are more riverine species, were weakly associated with lakes that had higher degrees of flooding. Conversely, results suggested that lentic species, such as yellow bullheads, spotted gars, bowfins, and several minnows, were more associated with lakes exhibiting lower degrees of flooding. Continued research in this area may gain insight into the possibility of whether lake fish communities can be used to ascertain flooding patterns and periodicity in floodplain lakes.

The maintenance of river–floodplain connectivity through flooding also helps maintain diverse riverine communities (Bayley 1995; Galat et al. 1998). Fish species diversity in White River floodplain lakes was significantly related to lake distance from the main river channel. Lakes that were located farthest from the White River main channel that flooded less frequently may have been more stable through time. Greater stability may have allowed for development of greater levels of fish community diversity, although this is an untested ecological theory. Lakes located farthest from

the main river channel tended to be shallower and more turbid and have higher TDS levels and smaller surface areas than lakes situated closer to the river. However, there was no correlation between lake distance from the main river channel and degree of flooding ($r = 0.10$, $P = 0.70$), as flooding in these lakes occurred through numerous chutes, side channels, and floodplain ditches that connect these habitats with each other and the main river channel. Future studies using better measures of connectivity for individual lakes may be better able to address this hypothesis.

Among all the drainages in the western Mississippi River basin, the White River has the most distinctive fish communities. In 1989, the Cache River–Lower White River floodplain gained status as “Wetlands of International Significance” and is 1 of only 22 such listed sites in the United States (Arkansas Wildlife Federation 2002). The basin contains over 150 native species of fishes and 13 endemic forms (Cross et al. 1986; Buchanan 1997). Fifty-eight species of freshwater mussels also are known from the White River, and three of these species are endemic. Although peer-reviewed scientific literature is mostly lacking, natural resource agencies and private conservation organizations, such as the Arkansas Natural Heritage Commission and The Nature Conservancy, regard the lower White River as a major center of biodiversity for the state of Arkansas because of its diversity of aquatic habitats, lack of high levels of regulation, and mostly intact hydrology (Arkansas Wildlife Federation 2002). Results of this study suggest that fish communities in floodplain lakes of the lower White River are structured by multiple environmental variables and that a diversity of floodplain lake conditions is critical for maintaining net ecosystem diversity. Nevertheless, the lower White River is the target of pending and proposed navigation and irrigation projects to support economic development in the Arkansas Delta region. Given that new floodplain lakes are no longer being created naturally in the lower White River, as in the lower Mississippi River (Miranda 2005), understanding fish–environment relationships in river–floodplain ecosystems is an important first step toward managing and conserving riverine fisheries. Results of this study can help guide future river management and aid resource managers in species conservation efforts in this and other large river–floodplain ecosystems.

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