Fish Diversity and Abundance in Relation to Interannual and Lake-Specific Variation in Abiotic Characteristics of Floodplain Lakes of the Lower Kaskaskia River, Illinois

DANIEL E. SHOUP*[1] AND DAVID H. WAHL

Kaskaskia Biological Station, Illinois Natural History Survey,
Rural Route 1, Box 157, Sullivan, Illinois 61951, USA

Abstract.—The importance of floodplain lakes to tropical river systems is well established, but little is known about the function of these habitats in temperate river systems. We examined fish diversity, abundance, and reproduction within six oxbow lakes of the Kaskaskia River, Illinois, over 5 years and their relationship to 11 abiotic environmental variables. The lakes were hydrologically dynamic within and among years, varying in the time connected with the main stem (0–22 weeks/year) and the frequency of low (<0.3-m) water (0–23 weeks/year). Differences were found both among years and lakes. All measured limnological variables (dissolved oxygen, Secchi disk depth, conductivity, and temperature) varied temporally, but only conductivity and Secchi disk depth varied among lakes. Fish species differed among lakes and between adjacent lotic habitats, and species-specific abundance varied among years, seasons, and lakes. This variation was related to several environmental variables. Diversity was positively related to the distance between the oxbow lake and the river but not to any variables that had interannual variation. Seine catch per unit effort (CPUE) was negatively related to mean water level and Secchi disk depth. Total electrofishing CPUE was not related to any variables; however, that of bluegills *Lepomis macrochirus* was positively related to maximum depth and that of warmouths *L. gulosus* was positively related to vegetated area. Across all lakes, evidence of reproduction was found for five species and was negatively related to the mean water level and frequency of low water and positively related to flood periodicity. The oxbow lakes have the potential to contribute to the fish community of the main river by providing spawning and nursery habitat for several fish species as well as helping maintain several less abundant main-stem species. However, when considering management options to maintain or restore these ecosystem functions, interannual variation in environmental variables, particularly those related to flood periodicity, should be considered.

Main river channels, backwater habitats, and oxbow lakes are believed to be highly integrated and interdependent within river ecosystems (Welcomme 1979; Bayley 1995; Sparks 1995; Winemiller et al. 2000; Herwig et al. 2004, 2007). Periodically rivers have variable flood pulses that produce a dynamic edge or "moving littoral" zone (Junk et al. 1989) in the floodplain where the aquatic and terrestrial habitats meet. This moving littoral zone increases nutrient cycling (Junk et al. 1989), enhances growth rates of some species (Wahl and Nielsen 1985; Gutreuter et al. 1999), and provides corridors for fish migration between the main river channel and oxbow lakes (Amoros and Bornette 2002), which in turn, can increase biodiversity. As a result of this periodic connection between oxbow lakes and main river channels, oxbows are thought to provide fish in the

main river with important spawning and nursery habitat (Welcomme 1979; Sheaffer and Nickum 1986; Sabo and Kelso 1991; Turner et al. 1994) or overwinter habitat (Dettmers et al. 2001a). However, the importance of oxbow habitats and the resulting fish composition probably varies with the attributes of the individual lakes and rivers.

Tropical floodplain systems have been well studied (see review by Welcomme 1979), but little is known about floodplain systems in the north temperate zone (Winemiller et al. 2000). Relative to tropical systems, temperate river systems experience larger seasonal temperature fluctuations, less distinct rainy and dry seasons (leading to less predictable flooding cycles), and more seasonally variable light regimes (Junk 1999; Tockner et al. 2000; Wahl et al. 2008). Temperate rivers also have experienced stronger disturbances in their paleoclimatic history leading to lower species diversity than have tropical river systems (Junk 1999). The interaction between temperature and flooding cycles may also lead to differences in ecosystem processes in temperate systems (Tockner et al. 2000). A few studies have investigated the environmental factors related to larval and juvenile fish abundance in

* Corresponding author: dshoup@okstate.edu
[1] Present address: Department of Natural Resource Ecology and Management, Oklahoma State University, 008c Ag Hall, Stillwater, Oklahoma 74078, USA.

North American temperate oxbow lakes (Sheaffer and Nickum 1986; Sabo and Kelso 1991; Sabo et al. 1991; Turner et al. 1994). Even fewer studies have considered the relationship between environmental conditions and adult fish populations in these systems (Winemiller et al. 2000; Miranda and Lucas 2004). Because none of these studies used repeated measurements from the same lakes, variables related to interannual weather variation (e.g., water level, frequency of desiccation events, and amount of time connected with the main stem) and their effect on fish reproduction in oxbow lakes could not be considered. It has been suggested that this interannual variation is important in maintaining floodplain fish diversity (Sparks 1995; Lasne et al. 2007) but there is disagreement in the literature (Pegg et al. 2006). Therefore, more information is needed to understand the factors controlling interannual and lake-specific fish abundance, diversity, and richness of these hydrologically dynamic systems to make informed management decisions.

We examined fish species diversity, richness, abundance, and reproduction during a 5-year period in six oxbow lakes along the Kaskaskia River, Illinois, a low gradient fifth-order river. We related these variables to physical and chemical characteristics of the oxbow lakes and to the abundance of fish in the main stem. Specifically, we examined lake-specific as well as interannual differences in oxbow morphology, location, water chemistry, and hydrology to assess the factors that most strongly influence fish abundance in these temperate oxbow lakes. These variables may all affect the contribution of these lakes as nursery and spawning areas and, ultimately, their contribution to fish populations in the main-stem river. Understanding the relationships between oxbow lakes and fish abundance has strong implications for management of floodplain river ecosystems.

Methods

Study region.—The Kaskaskia River originates in Champaign County, Illinois, and flows into the Mississippi River near Moro Island (Mississippi River kilometer 188 [mile 117], as measured from the confluence of the Ohio and Mississippi rivers). Many oxbow lakes were naturally created along the length of the river before it was impounded and channelized. The Kaskaskia River has two large upstream impounds (Lake Shelbyville and Carlyle Lake) and has been channelized from the Mississippi River upstream to Fayetteville, Illinois. Six lakes were chosen for study along an unchannelized reach of the Kaskaskia River between Fayetteville and Okawville, Illinois (38°25′08″–38°27′34″N, 89°37′05″–89°44′41″W), which is below the most downstream impoundment

(Figure 1). Lakes were chosen that varied with respect to distance from the river and several morphological attributes (Table 1).

Abiotic sampling.—Water level gauges were placed in each of the lakes and levels recorded weekly, with additional daily recordings taken during major rain events. These gauge readings were used to determine the timing and duration of low-water periods (<30 cm average depth). Timing and duration of connections between the oxbow lakes and the main stem were determined using water level data for the Kaskaskia River at Venedy Station (site 05594100; Figure 1) obtained from the U.S. Geological Survey (USGS). During a spring flood event (May 2002) water depths in the oxbow lakes, the floodplain, and the river were recorded to determine the river level at which each oxbow first connected with the main river. This information was then used in conjunction with data from the USGS water level gauge on the Kaskaskia River to determine when flood connection events occurred in each oxbow during the entire study period.

Digital orthophoto quadrangle (DQQ) images from the Illinois State Geological Survey were used to measure lake surface areas using Scion Image Beta 3b (Scion Corporation, Frederick, Maryland) and the distance between each oxbow and the Kaskaskia River using MrSid Viewer version 2.0.0.50 (International Land Systems, Inc., Silver Spring, Maryland). Depth-mapping was conducted on all oxbow lakes during early September 2002 when water levels were similar to those on the date the DOQ images were taken (we considered these "full pool" lake levels for the purpose of defining lake metrics). Lakes were mapped by measuring water depth every 10 m along parallel transects spaced at 30-m intervals along the length of the lake. Percent area covered by submerged and emergent vegetation was also recorded during these surveys. Vegetation coverage each year was very similar in each lake (D. E. Shoup, personal observation).

Physical and chemical conditions were recorded at all lakes during each fish sampling period (spring and fall) at a fixed site in the deepest part of the lake. Temperature and dissolved oxygen (DO) profiles and surface conductivity were measured with a YSI meter (Yellow Springs Instruments). Because temperature and DO typically were not stratified, only surface values were used for analysis. Secchi disk depth (nearest 1 cm) also was measured and was always smaller than the maximum depth.

Fish sampling.—Fish were sampled once during the fall and following spring each year from fall 1998 to spring 2003. Kehrer and Round lakes were not sampled in fall 2000 due to an access problem. Each lake was

SHOUP AND WAHL
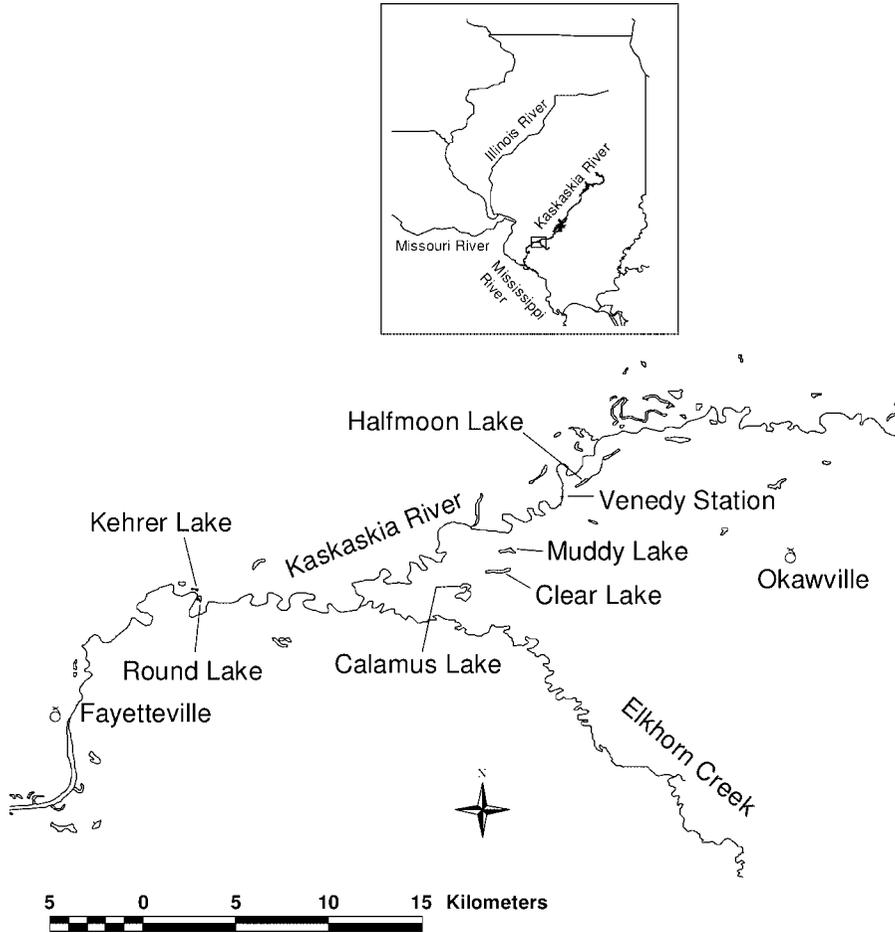
FIGURE 1.—Map of the study region in the Kaskaskia River floodplain showing the locations of the six oxbow lakes that were sampled in the fall and spring from 1998 to 2003.

divided into two transects (one on each side of the lake) and electrofished for a total of 30 min (where possible) with a boat-mounted AC electrofishing unit (three-phase, 9 A, 240 V). One seine haul (9 × 1.2 m seine

with a 1.2-m^3 bag having 3-mm delta mesh; average area sampled, 6 × 7 m) was also taken at two fixed sites per lake during 2000 through 2003 to better assess young-of-the-year (age-0) fish abundance. For both the

TABLE 1.—Morphometric data from six oxbow lakes in the Kaskaskia River floodplain. Surface area and distance from the river were calculated from digital orthophoto quadrangle (DOQ) images provided by the Illinois State Geological Survey. Depth and percent of area with submergent and emergent vegetation were measured on dates when the oxbows had water levels similar to those on the dates when the DOQ images were taken. The number of weeks with low water was based on the average depth less than 0.3 m. Values in a column without a letter in common are significantly different. ($P \leq 0.05$).

Lake	Surface area (ha)	Maximum depth (m)	Volume (100 m^3)	Distance from river (m)	Area with vegetation (%)	Weeks connected with river per year (SE)	Weeks with low water per year (SE)
Calamus	4.2	1.07	198.3	1,051	2	2.4 (1.3) y	0.2 (0.2) w
Clear	8.0	0.69	980.6	1,288	100	1.2 (0.7) x	7.0 (3.3) yx
Halfmoon	1.4	0.46	78.3	294	20	11.4 (1.8) z	23.0 (5.2) z
Kehrer	0.4	2.00	32.4	105	3	0.0 (0.0) x	0.0 (0.0) w
Muddy	11.3	0.33	225.2	454	12	21.8 (9.6) z	3.0 (2.9) xw
Round	1.0	1.69	19.9	57	5	0.0 (0.0) x	0.6 (0.6) w

electrofishing and seine catches, fish were identified, measured (nearest 1 mm TL) and returned to the lake. To compare with species composition in the oxbow lakes, similar samples obtained by means of a boat-mounted AC electrofisher (60 min/year, when possible) were collected in the main stem of the Kaskaskia River in the falls of 1996, 1999, 2001, and 2002 (R. Sauer, Illinois Department of Natural Resources, unpublished data). Electric seine samples using AC (150–200-m reach of stream, 20–40 min/year; Bayley et al. 1989) were also collected in the nearby Elkhorn Creek tributary of the Kaskaskia River (the closest connection point from the Kaskaskia River system to three of the six oxbow lakes) in the summers of 1996 and 2002.

Data analysis.—Fish species diversity was estimated by means of Simpson's diversity index (D), which is calculated as

$$D = \frac{1}{\sum (p_i^2)},$$

where p_i is the proportion of all individuals in the sample that belong to species i. All replicate electrofishing and seine samples from the same season and year were pooled for diversity calculations. Relative abundance of each species was determined as catch per hour by electrofishing and catch per square meter from seining (CPUE). The relative number of age-0 fish (based on TL) produced in each oxbow was estimated (present in $\geq 25\%$ of samples) from the fall seine samples.

Repeated-measures analysis of variance (ANOVA) was used to test for differences among years, seasons (fall and spring), and oxbow lakes in water quality, water level, connectivity parameters, and seine and electrofishing CPUE. Mean water level, number of weeks connected with the river, and low water level were calculated for the 6 months before seasonal sampling. Values were either natural-log transformed or square-root transformed as required to normalize the data (data already conformed to the homogeneity of variance assumption). Data showing significant differences from ANOVA procedures ($P < 0.05$) were subsequently analyzed with Tukey's tests.

To see whether temporal and lake-specific variation in abiotic environmental variables identified by the ANOVA analysis related to changes in individual biotic variables (diversity [D], total and species-specific seine and electrofishing CPUE, and total age-0 CPUE), we used linear multiple regression models (nonlinear methods were considered, but linear patterns were always a better fit to the data). Because lake morphometry variables by their nature are not temporally variable, we tested for relationships between these variables and the mean values of the biotic variables over the entire study. We constructed 15 a priori models among lakes (SAS Proc Mixed; SAS Institute 1999), consisting of all combinations of maximum depth, surface area, distance from river, and percent area with vegetation (a variable that showed no meaningful interannual variation). These variables were selected based on the role they play in the ecology of fishes (Savino and Stein 1982; Ney 1999; Lubinski et al. 2008). The most parsimonious of the 15 models were determined separately for each biotic response variable (species richness, D, total and species-specific seine and electrofishing CPUE, and total age-0 CPUE) using second-order Akaike's information criterion (AIC$_c$, because our ratio of observations to parameters was less than 40; Burnham and Anderson 2002). Models with AIC$_c$ values within two units of the model with the lowest AIC$_c$ were considered to have substantial support (Burnham and Anderson 2002). Within those parsimonious models, we further consider models with at least one slope that was significantly different from zero ($P < 0.10$) and some predictive power ($R^2 > 0.25$). For species-specific catch rates, we only analyzed the most abundant species (based on break points that existed in the data, we used species that were present in more than 20% of samples for seine or more than 50% for electrofishing data). We did not include lake volume because it is a function of lake area and depth.

For abiotic variables that were measured multiple times during the study and were expected to vary temporally, we used a repeated-measures univariate analysis to relate these with the biotic variables measured during each year and season (SAS Proc Mixed, SAS Institute 1999). We constructed 31 a priori repeated-measures models consisting of all combinations of mean water level, conductivity, Secchi disk depth, weeks connected with river, and weeks of low water based on the role these variables play in the ecology of fishes and river-floodplain systems (Copp 1989; Sabo et al. 1991; Bonner and Wilde 2002). The most parsimonious of the 31 models were determined separately for each biotic response variable (species richness, D, total and species-specific seine and electrofishing CPUE, and total age-0 CPUE) using second-order AIC$_c$. For this analysis, R^2 was calculated as the ratio between the variance explained by the model and the total amount of variance in a reduced model with no predicting variables (i.e., only fitting an intercept parameter; Kreft and De Leeuw 1998). Surface temperature and DO were not included in the models because biologically meaningful variation did not occur for these variables among years or oxbow lakes.
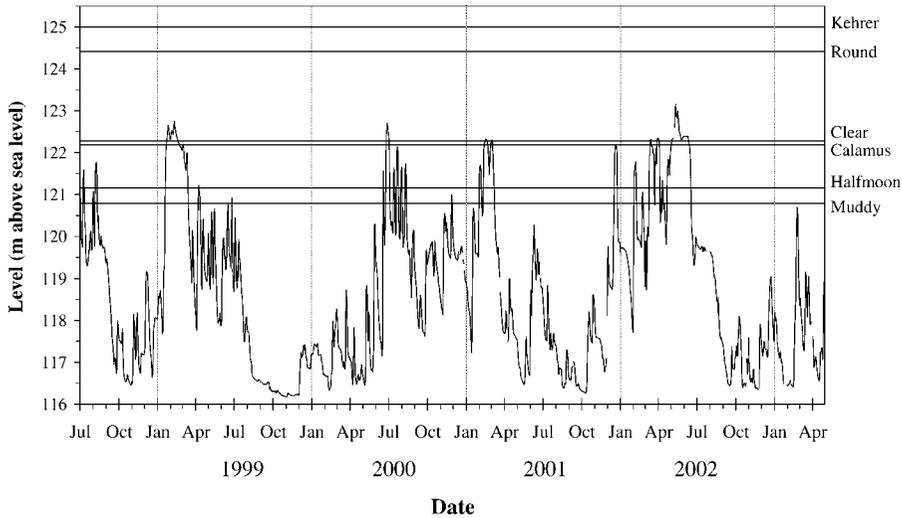
FIGURE 2.—Water level in the Kaskaskia River (Venedy Station [USGS gauging station 05594100]), July 1998–April 2003. The horizontal lines represent the depths at which the different oxbow lakes connect with the Kaskaskia River.

Results

Environmental Conditions

All oxbow lakes except Kehrer and Round connected to the Kaskaskia River several times during the 5-year study period (Table 1; Figure 2). Connection events typically occurred in winter or early spring but had substantial interannual variability (Figure 2). The number of weeks connected varied among years ($F_{5, 25}$ = 2.81, P < 0.04) and oxbow lakes ($F_{5, 38}$ = 9.75, P < 0.01), ranging from 0 to over 21 weeks/year (Figure 2). All oxbow lakes (except for Kehrer Lake) also had periods of very low water (Table 1). The number of weeks with water depths less than 0.3 m varied among years ($F_{5, 21}$ = 3.65, P < 0.02) and lakes ($F_{5, 38}$ = 18.03, P < 0.01), ranging from 0 to 23 weeks/year (Table 1). Only Halfmoon Lake dried entirely such that no fish survived (winter 1999 and fall–winter 2000). Periods of lowest water depth in all oxbow lakes occurred between the spring and fall samples ($F_{1, 21}$ = 30.14, P < 0.01).

Substantial variation in physical and chemical variables existed among years, seasons, and lakes. Secchi disk depths ($F_{1, 23}$ = 1.12, P = 0.04), temperature ($F_{1, 25}$ = 2.89, P = 0.03), and DO ($F_{1, 25}$ = 2.81, P = 0.04) had significant year × season interaction indicating considerable interannual variation. Dissolved oxygen also varied interannually ($F_{5, 25}$ = 2.81, P = 0.04), but did not vary by season ($F_{1, 5}$ = 0.39, P = 0.56) or among lakes ($F_{5, 45}$ = 1.69, P = 0.16). However, these temporal differences probably were not biologically important as hypoxic conditions (DO < 4.0 mg/L) occurred infrequently (<15% of

samples; Figure 3). Secchi disk depths ($F_{5, 35}$ = 2.67, P = 0.04) and conductivity ($F_{5, 34}$ = 7.63, P < 0.01) also varied among oxbow lakes (Figure 3).

Fish Communities

We found a total of 38 species across all oxbow lakes (31 in seine and 33 in the electrofishing samples; mean D ± SE = 3.4 ± 0.37, averaged across seasons, years, and lakes) and 44 species in the adjacent Kaskaskia River sites (Table 2; D = 7.1 ± 1.2, averaged across years). In general, the species-specific abundances in the oxbow lakes were different from those in the main stem and tributaries of the Kaskaskia River (Table 2). Only 17% of the species were found in both habitats and at similar relative abundances, including several species of Cyprinidae, one species each of Catostomidae, Centrarchidae, and Percidae, and all of the Atherinidae and Poeciliidae species collected. Many species (26%) were found only in the main-stem and tributary habitats and included several species of Cyprinidae, Ictaluridae, and Percidae and one species each of Catostomidae and Lepisosteidae. Several species (17%) were only found in the oxbow lakes (including all species of Amiidae and Petromyzontidae sampled), although these species do occur elsewhere in the river drainage (R. Sauer, Illinois Department of Natural Resources, personal communication). Several of the species (25%) found in both habitats were more abundant in the main-stem and tributary habitats, including two species of Centrarchidae, Cyprinidae, and Ictaluridae, one species of Catostomidae, and all of the Aphredoderidae, Esocidae, Moronidae, and Sciae-
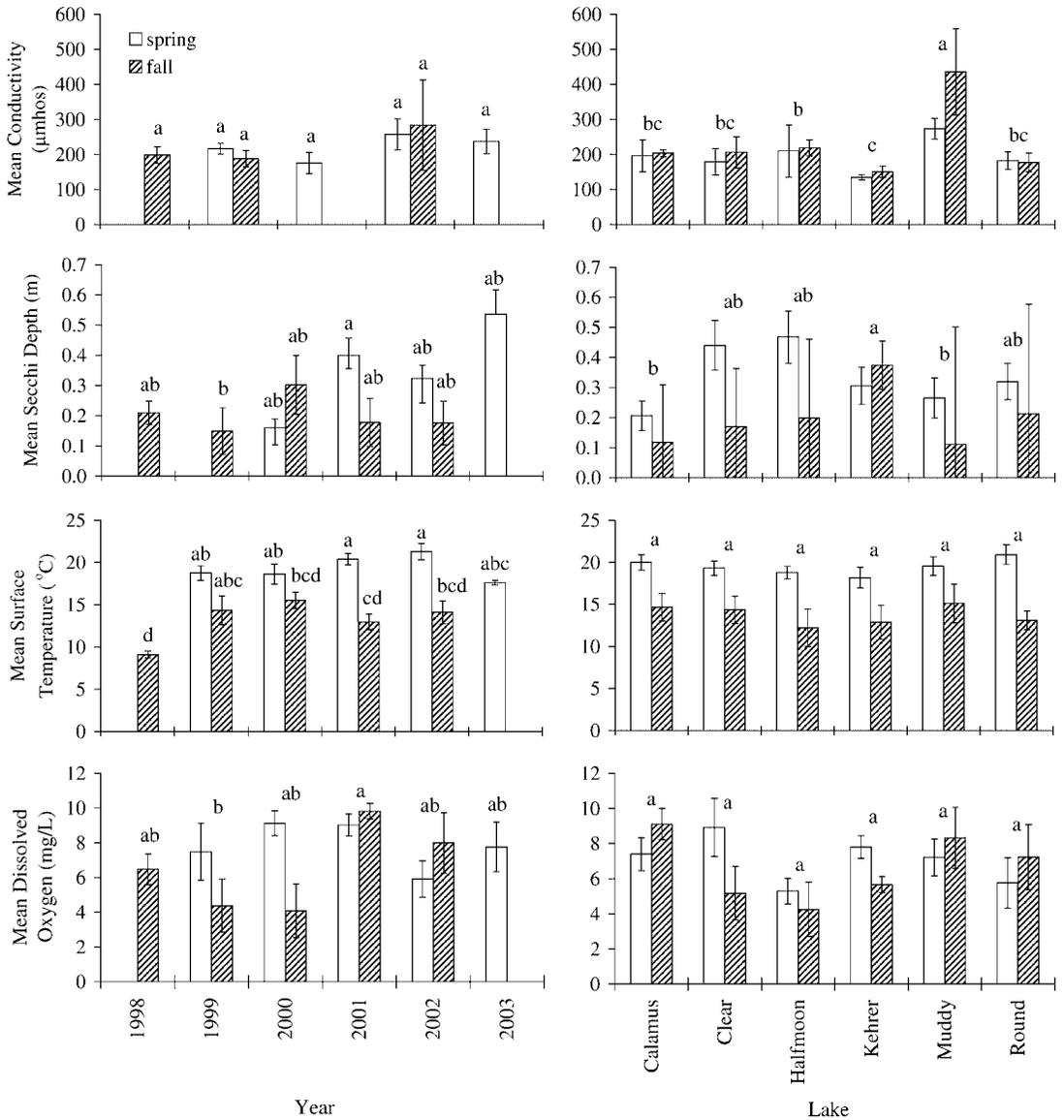
FIGURE 3.—Physical and chemical conditions in six oxbow lakes in the Kaskaskia River floodplain. Values are the means of spring and fall samples taken from 1998 to 2003; the error bars represent SEs. In the column on the left, different letters indicate significant differences ($P < 0.05$) among lake–season combinations as determined by Tukey's test except for dissolved oxygen, for which they indicate differences among years only. In the column on the right, different letters indicate differences among lakes as determined by Tukey's test (though there were differences between seasons for Secchi disk depth and temperature, there were no significant interactions).

nidae collected. Eight species (five Centrarchidae, two Catastomidae, and all of the Clupeidae species collected) found in both oxbow and river habitats were more abundant in the oxbow lakes. For the most part, species occurred in the habitats with which they generally are most commonly associated (i.e., lentic verses lotic; see review by Lee et al. 1980). However,

pirate perch, mud darter, bluntnose darter, and western mosquitofish are backwater or lake species that occurred exclusively or in greater abundance in the main-stem and tributary habitats. All of these species except pirate perch were only rarely collected in either habitat.

Diversity varied among lakes and seasons, but

TABLE 2.—Electrofishing (number/h) and seine (number/m^2, in parentheses) CPUE for all species of fish in six oxbow lakes and two lotic sites (Venedy Station on the main stem and Elkhorn Creek tributary) in the Kaskaskia River basin drainage. Occurrence is indicated as being found in both habitats (B), only found in the main stem (M), only found in oxbows (O), and found in both habitats but more abundant in the main stem (AM) or oxbows (AO).

Family	Species	Occurrence	Venedy Station	Elkhorn Creek	Oxbow lake Calamus	Clear
Atherinidae	Brook silverside *Labidesthes sicculus*	B	1.7		0.7 (0.002)	
Catastomida	Smallmouth buffalo *Ictiobus bubalus*	B	5.0		0.9	0.8
Catastomidae	Black buffalo *Ictiobus niger*	B	0.8		0.6	0.4
Centrarchidae	Flier *Centrarchus macropterus*	B		1.4	0.3	3.6 (0.006)
Clupeidae	Gizzard shad *Dorosoma cepedianum*	B	35.6	49.7	95.4	10.7
Catastomidae	River carpsucker *Carpiodes carpio*	B	3.0			
Catastomidae	Quillback *Carpiodes cyprinus*	B	0.8	0.7	0.2	
Cyprinidae	Golden shiner *Notemigonus crysoleucas*	B		7.9		3.9 (0.015)
Ictaluridae	Yellow bullhead *Ameiurus natalis*	B		3.5	0.3	(0.001)
Lepisosteidae	Shortnose gar *Lepisosteus platostomus*	B	1.9		0.4	
Percidae	Mud darter *Etheostoma asprigene*	B	0.5		(0.007)	
Poeciliedae	Western mosquitofish *Gambusia affinis*	B	0.3		(0.107)	0.6 (0.004)
Catastomidae	Shorthead redhorse *Moxostoma macrolepidotum*	M	1.4			
Cyprinidae	Red shiner *Cyprinella lutrensis*	M	39.2	5.1		
Catastomidae	Creek chubsucker *Erimyzon oblongus*	M		10.9		
Cyprinidae	Redfin shiner *Lythrurus umbratilis*	M		15.2		
Cyprinidae	Emerald shiner *Notropis atherinoides*	M	0.5			
Ictaluridae	Blue catfish *Ictalurus furcatus*	M	0.5			
Ictaluridae	Tadpole madtom *Noturus gyrinus*	M		9.7		
Ictaluridae	Freckled madtom *Noturus nocturnes*	M	0.8			
Ictaluridae	Flathead catfish *Pylodictis olivaris*	M	8.4			
Lepisosteidae	Longnose gar *Lepisosteus osseus*	M	0.3			
Percidae	Bluntnose darter *Etheostoma chlorosomum*	M		0.7		
Percidae	Slough darter *Etheostoma gracile*	M		0.7		
Percidae	Slenderhead darter *Percina phoxocephala*	M	0.3			
Percidae	Walleye *Sander vitreus*	M	1.6			
Amiidae	Bowfin *Amia calva*	O			7.2	2.8
Catastomidae	Golden redhorse *Moxostoma erythrurum*	O				
Centrarchidae	Redear sunfish *Lepomis microlophus*	O			0.7 (0.019)	0.8 (0.009)
Centrarchidae	Black crappie *Pomoxis nigromaculatus*	O			3.6	0.6 (0.037)
Ictaluridae	Black bullhead *Ameiurus melas*	O				3.4 (0.016)
Ictaluridae	Brown bullhead *Ameiurus nebulosus*	O				4.2 (0.009)
Lepisosteidae	Spotted gar *Lepisosteus oculatus*	O			0.8	0.3
Percidae	Johnny darter *Etheostoma nigrum*	O			(0.036)	
Petromyzontidae	Chestnut lamprey *Ichthyomyzon castaneus*	O				
Aphredoderidae	Pirate perch *Aphredoderus sayanus*	AM		20.3	0.5 (0.002)	0.4 (0.006)
Catastomidae	Spotted sucker *Minytrema melanops*	AM		13.9		
Centrarchidae	Green sunfish *Lepomis cyanellus*	AM	4.9	8.3		0.2 (0.001)
Centrarchidae	Longear sunfish *Lepomis megalotis*	AM	1.3	9.0	0.2	
Cyprinidae	Common carp *Cyprinus carpio*	AM	10.1	6.2	9.1	12.9 (0.006)
Cyprinidae	Bluntnose minnow *Pimephales notatus*	AM		14.3		
Cyprinidae	Bullhead minnow *Pimephales vigilax*	AM	11.4			
Esocidae	Redfin pickerel *Esox americanus*	AM		13.0		0.2 (0.006)
Ictaluridae	Channel catfish *Ictalurus punctatus*	AM	6.3	3.3	0.2	
Moronidae	White bass *Morone chrysops*	AM	2.8			
Fundulidae	Blackstripe topminnow *Fundulus notatus*	AM	0.6	43.0		0.2
Sciaenidae	Freshwater drum *Aplodinotus grunniens*	AM	19.9	1.6	0.3	
Catastomidae	Bigmouth buffalo *Ictiobus cyprinella*	AO	0.3	0.7	23.9	7.8
Centrarchidae	Warmouth *Lepomis gulosus*	AO	0.3	2.1	9.5 (0.010)	5.7 (0.066)
Centrarchidae	Orangespotted sunfish *Lepomis humilis*	AO		4.0	2.5 (0.221)	(0.013)
Centrarchidae	Bluegill *Lepomis macrochirus*	AO	11.6	45.1	42.3 (0.481)	27.8 (0.441)
Centrarchidae	Largemouth bass *Micropterus salmoides*	AO	0.9	2.1	2.1	3.3
Centrarchidae	White crappie *Pomoxis annularis*	AO	0.5		40.9 (0.047)	1.5 (0.059)

among-lake patterns were not consistent between seasons (lake × season interaction: $F_{5, 42} = 2.60$, $P = 0.04$; Figure 4). No significant year effect was found ($F_{5, 25} = 0.59$, $P = 0.21$). Species richness did not vary significantly across years ($F_{5, 25} = 2.00$, $P = 0.11$), seasons ($F_{5, 42} = 1.55$, $P = 0.22$), or lakes ($F_{5, 42} =$ 2.51, $P = 0.05$, all Tukey's tests: $P > 0.11$). For the most abundant species captured, CPUE from seines had a significant year × season interaction with higher CPUE in fall samples of some years than in others ($F_{3, 6} = 4.96$, $P = 0.04$). Electrofishing CPUE was higher in fall than spring samples ($F_{1, 48} = 4.64$, $P = 0.04$), but

TABLE 2.—Extended.

Family	Oxbow lake			
	Halfmoon	Kehrer	Muddy	Round
Atherinidae		1.9 (0.022)	0.3	0.1
Catastomida	1.8 (0.068)	3.1	0.5	0.9
Catastomidae	(0.057)	6.8	0.8	
Centrarchidae	(0.031)		(0.001)	0.3
Clupeidae	39.3 (0.115)	29.5	123.9	18.1 (0.001)
Catastomidae			(0.001)	
Catastomidae			1.2	
Cyprinidae	(0.069)	0.4 (0.003)	(0.191)	1.1
Ictaluridae	0.3 (0.003)		0.4	
Lepisosteidae	0.8 (0.010)	0.2	0.5	0.4
Percidae	(0.013)			(0.001)
Poeciliedae	(0.101)	0.2	(0.440)	0.3
Catastomidae				
Cyprinidae				
Catastomidae				
Cyprinidae				
Cyprinidae				
Ictaluridae				
Ictaluridae				
Ictaluridae				
Ictaluridae				
Lepisosteidae				
Percidae				
Percidae				
Percidae				
Percidae				
Amiidae	1.3 (0.097)	2.0	4.9	4.1
Catastomidae	0.5			
Centrarchidae	0.3	2.8 (0.006)		1.7 (0.001)
Centrarchidae	6.0	1.6 (0.009)	1.2	13.8 (0.009)
Ictaluridae	0.5 (0.066)			
Ictaluridae	0.8			
Lepisosteidae	1.0	0.2	0.2	0.4
Percidae	(0.016)	(0.014)	(0.006)	
Petromyzontidae	(0.003)			
Aphredoderidae	(0.018)	0.1		
Catastomidae		0.2		
Centrarchidae	1.0	0.2	0.3	0.4
Centrarchidae		0.4		
Cyprinidae	6.8 (0.005)	5.1	7.0 (0.002)	6.6
Cyprinidae			(0.002)	
Cyprinidae		(0.009)	(0.003)	
Esocidae	1.5			
Ictaluridae			1.0	
Moronidae		0.2	0.2	
Fundulidae	(0.010)	4.8 (0.011)		
Sciaenidae			6.4	
Catastomidae	1.5 (0.057)	26.9	4.0	4.0
Centrarchidae	3.5 (0.063)	2.6	(0.002)	12.3 (0.026)
Centrarchidae	0.5	1.8 (0.059)	1.5 (0.228)	(0.002)
Centrarchidae	67.0 (0.298)	109.8 (0.549)	4.4 (0.076)	134.9 (0.316)
Centrarchidae	16.8 (0.005)	5.1 (0.026)	0.5 (0.006)	4.7 (0.051)
Centrarchidae	5.5	12.2	6.2 (0.003)	10.9 (0.034)

did not vary by year ($F_{5, 24} = 1.32$, $P = 0.29$). Fish were probably concentrated by low water levels that occurred in the fall. Western mosquitofish and bluegills were typically the most abundant species in the seine samples in all lakes, except Round and Kehrer lakes where western mosquitofish were not detected (Table 2). Orangespotted sunfish were also seasonally abundant in Calamus, Kehrer, and Muddy lakes. Bluegills and gizzard shad were the most abundant species in electrofishing samples in all lakes. Common carp were present in all lakes, but most abundant in Clear Lake.
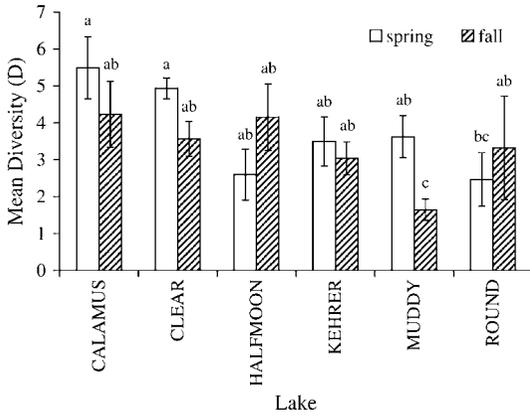
FIGURE 4.—Mean values of Simpson's diversity index (D) for spring and fall samples in the six oxbow lakes in the Kaskaskia River floodplain, 1998–2003. The error bars represent SEs; different letters indicate significant differences ($P < 0.05$) as determined by Tukey's test.

Seine and electrofishing CPUE for the most abundant species had high temporal variability. Year effects were only significant for orangespotted sunfish sampled by seines ($F_{1, 11} = 3.93$, $P = 0.03$), but we detected significant seasonal variation in catch rates of bluegills sampled by seines ($F_{1, 19} = 5.93$, $P = 0.02$); and bluegills ($F_{1, 33} = 5.01$, $P = 0.03$), bowfins ($F_{1, 33} = 4.54$, $P = 0.04$), and white crappies ($F_{1, 33} = 5.19$, $P = 0.03$) sampled by electrofishing (Table 3). Mosquito-fish catch rates also varied seasonally, but the pattern was not consistent among lakes (lake × season interaction $F_{5, 19} = 3.09$, $P = 0.03$). Catch rates differed among lakes for white crappies ($F_{5, 19} = 2.84$, $P = 0.04$) and orangspotted sunfish ($F_{5, 19} = 4.03$, $P = 0.01$) sampled by seines and bluegills ($F_{5, 33} = 4.96$, $P < 0.01$), bigmouth buffaloes ($F_{5,33} = 9.32$, $P < 0.01$), bowfin ($F_{5, 33} = 4.15$, $P < 0.01$), and white crappies ($F_{5, 33} = 3.75$, $P < 0.01$) sampled by electrofishing (Table 3).

The presence of age-0 size-classes in fall seine samples (including samples from lakes that did not connect with the river during or after the spawning season) indicated that the oxbow lakes were being used for spawning and nursery habitat, or both, by at least some individuals of some species. However, the presence of age-0 fish varied by species and years among oxbows (Table 4). Age-0 bluegills were detected in all lakes in 2002 and all but Halfmoon and Muddy lakes in 2001. Detection of age-0 fish of other species was more lake-specific. In both years, age-0 western mosquitofish were found in Muddy Lake, but not in any other oxbow. Age-0 orangespotted sunfish were found in Calamus Lake in both years and

Muddy Lake in 1 year. Age-0 warmouth were found in Clear Lake in both years, and Calamus and Round lakes in one of the 2 years.

Relationships between Environmental Variables and Fish Communities

Given the interannual, seasonal, and lake-specific variability measured, we tested to see whether fish community and population characteristics were related to abiotic conditions both spatially and temporally. We found that at least some community-level metrics were related to changes in environmental conditions. Fish diversity was positively related to distance to the river (adjusted $R^2 = 0.81$; Table 5), an abiotic factor with lake-specific, but not interannual variation. Among the other parsimonious models predicting diversity (testing interannual variation or lake-specific differences), no variables had significant slopes, indicating that diversity was more affected by interlake (distance to the river) than temporally variable conditions. The AIC_c analysis identified one parsimonious model for predicting species richness; however, this model did not have significant slopes (all $P > 0.20$). Total seine CPUE was best explained by a negative relationship with both mean water level and Secchi disk depth (both variables that varied temporally), but only Secchi depth had a significant slope ($R^2 = 0.45$; Table 6). Total electrofishing CPUE was best explained by one parsimonious model that included lake-specific differences and two models that included variables with interannual variation. Among lakes, maximum depth was positively related with total CPUE ($R^2 = 0.83$; Table 5). For variables with interannual variation, a negative relationship with mean water level and Secchi disk depth and a positive relationship with conductivity was found in both models. The second model with interannual variation also included a negative relationship with weeks connected to the main stem of the river. However, in both of these models, only Secchi depth had a significant slope (Table 6). Total CPUE for age-0 fish was best described by two models (using variables that varied temporally) that explained substantial variation (Table 6). The first model included negative relationships with mean water level, weeks of low water, and conductivity; and a positive relationship for weeks connected with river ($R^2 = 0.55$). The second model included the same variables except conductivity, but explained a similar amount of the variation in the data (adjusted $R^2 = 0.53$), indicating that conductivity was not adding much predictive power to the first model. Therefore, both interannual and among-lake variation appeared to be important factors determining total CPUE metrics.

Several species-specific metrics also had strong

TABLE 3.—Abundance of the most common fish species from electrofishing samples (number/h) taken from six oxbow lakes in the lower Kaskaskia River floodplain during spring and fall over a 5-year period.

Lake	1998 Fall	1999 Spring	1999 Fall	2000 Spring	2000 Fall	2001 Spring	2001 Fall	2002 Spring	2002 Fall	2003 Spring
Bigmouth buffalo										
Calamus	52.0	8.0	24.0	16.0	26.0	20.0	34.0	24.0	8.0	4.5
Clear	0.0	8.0	0.0	2.0	8.0	6.3	0.0	12.0	36.0	2.5
Halfmoon	0.0	2.0	0.0	0.0	0.0	6.0	0.0	4.0	0.0	0.0
Kehrer	26.0	6.0	46.0	28.0	0.0	4.0	2.0	16.0	58.0	28.4
Muddy	0.0	4.0	0.0	6.0	1.0	3.0	0.0	2.0	0.0	9.5
Round	0.0	12.0	12.0	0.0	0.0	8.0	0.0	0.0	2.3	2.0
Bluegill										
Calamus	74.0	148.0	68.0	52.0	32.0	28.0	2.0	12.0	12.0	2.0
Clear	0.0	12.0	0.0	10.0	42.0	22.6	0.0	12.0	120.0	29.5
Halfmoon	94.0	0.0	0.0	0.0	150.0	48.0	0.0	0.0	0.0	0.0
Kehrer	74.0	108.0	130.0	30.0	0.0	96.0	130.0	48.0	272.0	96.2
Muddy	8.0	14.0	0.0	2.0	2.0	4.6	0.0	0.0	0.0	2.5
Round	316.0	14.0	30.0	0.0	0.0	404.0	52.0	16.0	138.1	115.5
Bowfin										
Calamus	2.0	10.0	4.0	4.0	16.0	6.0	4.0	2.0	8.0	10.0
Clear	0.0	2.0	0.0	16.0	0.0	6.3	0.0	2.0	6.0	0.0
Halfmoon	4.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0
Kehrer	2.0	2.0	0.0	2.0	0.0	2.0	2.0	4.0	0.0	4.7
Muddy	2.0	6.0	0.0	16.0	1.0	4.6	0.0	0.0	0.0	18.0
Round	6.0	4.0	6.0	0.0	0.0	4.0	4.0	2.0	0.0	5.0
Common carp										
Calamus	2.0	8.0	10.0	20.0	12.0	6.0	4.0	4.0	10.0	7.5
Clear	0.0	4.0	0.0	8.0	8.0	24.9	0.0	10.0	66.0	7.0
Halfmoon	6.0	0.0	0.0	0.0	16.0	8.0	0.0	2.0	0.0	0.0
Kehrer	14.0	4.0	4.0	0.0	0.0	14.0	2.0	2.0	2.0	2.7
Muddy	2.0	4.0	0.0	6.0	3.0	9.9	0.0	2.0	0.0	10.0
Round	4.0	4.0	24.0	0.0	0.0	4.0	12.0	2.0	4.5	4.0
Gizzard shad										
Calamus	646.0	4.0	10.0	60.0	24.0	0.0	14.0	10.0	100.0	16.0
Clear	0.0	20.0	0.0	0.0	40.6	4.0	0.0	0.0	0.0	0.0
Halfmoon	116.0	10.0	0.0	0.0	18.0	16.0	0.0	20.0	0.0	0.0
Kehrer	106.0	18.0	18.0	18.0	0.0	86.0	8.0	8.0	6.0	4.7
Muddy	106.0	286.0	0.0	40.0	219.0	0.0	0.0	26.0	0.0	2.5
Round	0.0	4.0	24.0	0.0	0.0	36.0	48.0	26.0	2.3	27.0
White crappie										
Calamus	94.0	22.0	102.0	32.0	40.0	20.0	12.0	34.0	36.0	1.5
Clear	0.0	2.0	0.0	0.0	4.0	4.3	0.0	0.0	0.0	2.0
Halfmoon	22.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kehrer	14.0	20.0	26.0	18.0	0.0	2.0	8.0	4.0	10.0	6.7
Muddy	16.0	6.0	0.0	6.0	1.0	9.9	0.0	0.0	0.0	10.0
Round	14.0	0.0	6.0	0.0	0.0	20.0	44.0	4.0	4.5	4.5

relationships with environmental conditions. These models included a mix of variables with and without interannual variation. Catch per unit effort of bluegills in seines was best explained by a positive relationship with maximum depth ($R^2 = 0.48$; Table 5) that varied among lakes. Other parsimonious models did not have significant slopes (Table 5). Catch per unit effort of warmouth in seines was well described by a positive relationship with the percent of vegetated area ($R^2 = 0.70$; Table 5). While vegetation can vary annually, this was not the case in the lakes during the time of our study. One parsimonious model was identified relating variables with interannual variation with seine CPUE

of warmouth, but slopes were not significant. Models were also tested for CPUE of white crappies and orangespotted sunfish in seines, but the most parsimonious models for these species did not have significant slopes and explained little of the variation in the data ($R^2 < 0.20$). Variation in CPUE of age-0 bluegills was well described by two models (Table 6). The first model included negative relationships with mean water level, weeks of low water, and conductivity; and a positive relationship with weeks connected with river ($R^2 = 0.64$). All of these variables showed significant interannual variation except conductivity. The second model had the same variables, but added a positive

TABLE 4.—Age-0 fish densities (number/m^2) from seine samples in six oxbow lakes in the Kaskaskia River floodplain during fall 2001 and 2002.

Lake	Year	Species Bluegill	Western mosquitofish	Orangespotted sunfish	Warmouth	Total age-0 fish production
Calamus	2001	0.36		0.01		0.371
	2002	2.25		0.29	0.08	2.63
Clear	2001	0.17			0.02	0.18
	2002	0.22			0.08	0.31
Halfmoon	2001					0.00
	2002	1.06				1.06
Kehrer	2001	0.06				0.06
	2002	1.25				1.25
Muddy	2001		0.21			0.21
	2002	0.50	0.17	0.17		0.83
Round	2001	0.08			0.02	0.09
	2002	0.50				0.50

relationship with Secchi disk depth (a variable with significant interannual variation) and explained somewhat more variation ($R^2 = 0.74$). Other parsimonious models had slopes that were not significant and did not include any variables not already in the two stronger models (Table 6).

Several species-specific relationships were also identified for electrofishing CPUE. Bigmouth buffalo

TABLE 5.—Models relating lake-specific variability in morphometry and mean fish community variables from six oxbow lakes in the Kaskaskia River drainage. The most parsimonious of the 15 models (consisting of all combinations of maximum depth, surface area, distance from the river, and percent area with vegetation) were selected using the second-order Akaike information criterion (AIC$_c$). Only models with at least one significant slope ($P < 0.10$) were considered further. The adjusted-R^2 was used to determine which of these parsimonious models had strong predictive power ($R^2 > 0.25$). Values were square-root transformed or arcsin transformed as necessary to normalize the data. Significant models with strong predictive power are denoted by bold italics.

Model	Adjusted R^2	AIC$_c$	ΔAIC$_c$	w_i	Model parameter	Estimate	P
				Diversity D			
1	*0.81*	*21.0*	*0.00*	*0.99*	Distance to river	*0.95*	*0.01*
					Intercept	*−3.56*	*0.08*
				Bluegill seine CPUE (number/m^2)			
1	*0.48*	*−0.9*	*0.00*	*0.66*	Maximum depth	*0.10*	*0.08*
					Intercept	*0.73*	*<0.01*
2	0.28	1.1	1.99	0.24	Lake surface area	−0.01	0.16
					Intercept	0.88	0.00
				Warmouth seine CPUE (number/m^2)			
1	*0.70*	*−14.9*	*0.00*	*0.95*	% Vegetation	*0.06*	*0.02*
					Intercept	*0.62*	*<0.01*
				Total electrofishing CPUE (number/h)			
1	*0.83*	*46.0*	*0.00*	*0.98*	Maximum depth	*9.98*	*<0.01*
					Intercept	*11.46*	*<0.01*
				Bigmouth buffalo electrofishing CPUE (number/h)			
1	*0.63*	*30.1*	*0.00*	*0.92*	Distance to river	*1.33*	*0.04*
					Intercept	*−7.05*	*0.10*
				Bluegill electrofishing CPUE (number/h)			
1	*0.77*	*40.7*	*0.00*	*0.94*	Maximum depth	*5.37*	*0.01*
					Intercept	*0.61*	*0.72*
				Common carp electrofishing CPUE (number/h)			
1	*0.92*	*20.9*	*0.00*	*1.00*	% Vegetation	*2.30*	*<0.01*
					Intercept	*1.71*	*<0.01*
				Gizzard shad electrofishing CPUE (number/h)			
1	*0.76*	*28.3*	*0.00*	*0.89*	% Vegetation	*−2.37*	*0.01*
					Intercept	*4.83*	*<0.01*

CPUE was positively related with distance from the river ($R^2 = 0.63$; Table 5), a variable with no interannual variation. We also found five parsimonious models that related bigmouth buffalo electrofishing CPUE with variables that had interannual variation (Table 6). All five models included a negative relationship with mean water level and a positive relationship with conductivity. Some models also included a negative relationship with the number of weeks of low water, Secchi disk depth, the number of weeks connected with the main stem of the river, or a combination of these factors. All models explained between 64% and 71% of the variation in bigmouth buffalo electrofishing CPUE (Table 6), suggesting that most of the variation was related to changes in mean water level and conductivity and only a small amount of additional variation was being explained by the other variables. Bluegill electrofishing CPUE was positively related with maximum depth ($R^2 = 0.89$; Table 5), a variable with lake-specific but not interannual variation. None of the parsimonious models relating bluegill electrofishing CPUE with variables exhibiting interannual variation had significant slopes. Common carp electrofishing CPUE was positively related to percent of vegetated area ($R^2 = 0.92$; Table 5), and gizzard shad electrofishing CPUE was negatively related to percent of vegetated area ($R^2 = 0.76$; Table 5). Vegetation coverage in the oxbow lakes did not exhibit interannual variation. No models for common carp or gizzard shad electrofishing CPUE using variables that exhibited interannual variation had significant slopes. Models with and without variables exhibiting interannual variation were also tested for the electrofishing CPUE of bowfins and white crappies. However, none of these models had significant slopes.

Discussion

The oxbow lakes of the Lower Kaskaskia River are diverse and temporally variable habitats. By examining multiple years, we found large differences through time in variables related to hydrology, water chemistry, and lake morphometry among oxbow lakes. Many of these differences correlated with fish diversity and abundance; however, not all fish variables responded to the same environmental conditions. Our study illustrates the importance of the interannual variation in hydrology and water chemistry in these habitats, similar to previous work outside North America (Armor0s and Bornette 2002; De Graaf 2003; King et al. 2003). Individual species have their own specific habitat requirements and therefore are likely to use floodplain habitats under different conditions. At any point in time, individual oxbow lakes will have different habitat conditions that may be either suitable or intolerable for a particular species. Therefore, the entire floodplain should be viewed as a single functioning unit with no particular habitat being more important to the fish community than another (Dettmers et al. 2001b). We found high interannual variation within six oxbow lakes. As a result, future studies of large river ecosystems and their associated oxbow lakes should include multiyear assessments.

We found the relative abundances of fish species in oxbow lakes were, in some cases, very different from the main-stem and tributary habitats. This is consistent with studies of floodplain fish communities in the tropics (Meschiatti et al. 2000) and Europe (Grift et al. 2001; Slavik and Bartos 2001). Fish abundances did not appear to follow any major taxonomic divisions between habitats, but rather appeared related to species preference for lentic versus lotic habitat (as described by Lee et al. 1980 and citations therein), as has been observed in European floodplain ecosystems (Slavik and Bartos 2001; Lasne et al. 2007). Some studies suggest that oxbow lakes maintain main-stem populations of some species through periodic immigration of individuals from these subpopulations, which increases productivity and diversity of river systems (Sheaffer and Nickum 1986; Molls 1999; Amoros and Bornette 2002). Consistent with this hypothesis, we found high abundance of several species in the main stem and tributaries of the Kaskaskia River that are typically associated with lentic habitats. We found evidence of spawning for several of these species in oxbow habitats. However, our data suggest not all main-stem species use oxbow habitat. There were substantial differences in relative abundances of fish species among oxbow lakes. Individual oxbow lakes differed greatly in the amount of time they both experienced low water levels and were connected to the river. Periodic flood events may be important to floodplain ecosystem function by allowing periodic migration of species among oxbows, even if these species are not using the main-stem habitat. Flood events may also transport larval fish between oxbows lakes and enhance recruitment by minimizing the chance that a catastrophic event in a single oxbow lake could eliminate all fish produced.

We found that fish diversity in oxbow lakes was positively related to the distance from the river, similar to the results of Lubinski et al. (2008). While oxbow lakes are inherently unstable environments with frequent disturbance, those farther away from the main river channel are more stable because they experience fewer and less severe flood events, assuming they are sufficiently deep to avoid desiccation. Therefore, it is possible that only species that are adapted to frequent severe flooding do well in oxbow lake habitats closest

TABLE 6.—Models relating the interannual variation of environmental conditions and fish community variables from six oxbow lakes in the Kaskaskia River drainage. The models used repeated measures to account for the variation between spring and fall samples during 5 years (2 years for age-0 fish production). The second-order Akaike information criterion was used to select the most parsimonious models of the 31 models tested (all combinations of mean water level, conductivity, Secchi disk depth, weeks connected with the river, and weeks of low water). Only models with at least one significant slope ($P < 0.10$) were considered further. See Table 5 for additional details.

Model	Adjusted R^2	AIC_c	ΔAIC_c	w_i	Model parameter	Estimate	P
				Seine CPUE (number/m^2)			
1	*0.45*	*58.3*	*0.00*	*0.50*	Mean water level	*−0.001*	*0.85*
					Secchi depth	*−1.988*	*0.00*
					Intercept	*3.903*	*0.01*
				Electrofishing CPUE (number/h)			
1	*0.67*	*158.8*	*0.0*	*0.50*	Mean water level	*−0.113*	*0.06*
					Conductivity	*4.055*	*0.06*
					Secchi depth	*−14.895*	*<0.01*
					Intercept	*15.886*	*0.54*
1	0.68	159.5	0.68	0.35	Mean water level	−0.083	0.17
					Weeks connected with river	−1.618	0.21
					Conductivity	4.443	0.31
					Secchi depth	−13.877	<0.01
					Intercept	13.669	0.58
				Western mosquitofish seine CPUE (number/m^2)			
1	*0.28*	*−32.0*	*0.00*	*0.51*	Weeks connected with river	*0.071*	*0.01*
					Conductivity	*−0.003*	*0.96*
					Intercept	*0.633*	*0.10*
				Total age-0 production (number/m^2)			
1	0.20	48.67	0.00	0.23	Mean water level	0.008	0.24
					Secchi depth	−0.894	0.22
					Intercept	−0.333	0.70
2	0.24	49.51	0.83	0.15	Mean water level	0.010	0.12
					Conductivity	−1.036	0.14
					Intercept	4.516	0.30
3	*0.55*	*50.0*	*1.29*	*0.12*	Mean water level	*−0.010*	*0.18*
					Weeks of low water	*−0.663*	*0.02*
					Weeks connected with river	*0.632*	*0.01*
					Conductivity	*−1.161*	*0.05*
					Intercept	*6.520*	*0.09*
4	*0.53*	*50.4*	*1.74*	*0.10*	Mean water level	*−0.012*	*0.17*
					Weeks of low water	*−0.787*	*0.01*
					Weeks connected with river	*0.602*	*0.02*
					Intercept	*0.234*	*0.75*
				Age-0 bluegill production (number/m^2)			
1	0.39	51.65	0.00	0.24	Mean water level	0.006	0.35
					Conductivity	−2.087	0.01
					Intercept	10.381	0.07
2	*0.64*	*51.8*	*0.16*	*0.22*	Mean water level	*−0.016*	*0.06*
					Weeks of low water	*−0.788*	*0.01*
					Weeks connected with river	*0.634*	*0.01*
					Conductivity	*−2.134*	*<0.01*
					Intercept	*12.255*	*0.02*
3	*0.74*	*52.3*	*0.65*	*0.17*	Mean water level	*−0.014*	*0.06*
					Weeks of low water	*−0.883*	*<0.01*
					Weeks connected with river	*0.889*	*<0.01*
					Conductivity	*−5.204*	*<0.01*
					Secchi depth	*1.572*	*0.04*
					Intercept	*27.492*	*0.01*
4	0.08	53.4	1.76	0.10	Mean water level	0.001	0.85
					Secchi depth	−0.834	0.32
					Intercept	−0.209	0.84
				Bigmouth buffalo electrofishing CPUE (number/h)			
1	*0.70*	*87.76*	*0.00*	*0.23*	Mean water level	*−0.030*	*0.01*
					Weeks of low water	*−0.544*	*0.05*
					Conductivity	*2.537*	*0.01*
					Secchi depth	*−1.460*	*0.07*
					Intercept	*−7.728*	*0.15*
2	*0.64*	*87.91*	*0.14*	*0.21*	Mean water level	*−0.028*	*0.02*
					Conductivity	*2.332*	*0.01*

TABLE 6.—Continued.

Model	Adjusted R^2	AIC_c	ΔAIC_c	w_i	Model parameter	Estimate	P
					Secchi depth	−2.021	0.02
					Intercept	−6.564	0.23
3	0.66	88.15	0.39	0.19	Mean water level	−0.022	0.06
					Weeks connected with river	−0.309	0.21
					Conductivity	2.406	0.01
					Secchi depth	−1.827	0.03
					Intercept	−6.988	0.20
4	0.66	89.12	1.35	0.11	Mean water level	−0.027	0.02
					Weeks of low water	−0.718	0.01
					Conductivity	2.430	0.01
					Intercept	−8.600	0.12
5	0.71	89.45	1.68	0.10	Mean water level	−0.026	0.03
					Weeks of low water	−0.490	0.07
					Weeks connected with river	−0.214	0.36
					Conductivity	2.568	<0.01
					Secchi depth	−1.381	0.08
					Intercept	−7.907	0.14

to the river; however, further research is needed to test this hypothesis. Oxbows that are far from the main stem or that are in heavily disturbed areas (e.g., behind constructed levees) may rarely flood. These types of oxbows would be expected to have lower diversity because these systems tend toward geographical and temporal uniformity that does not offer the variety of habitat types that occurs on the more frequently flooded portion of the floodplain (Tockner et al. 1998).

We found that several environmental conditions were important in influencing the abundance of some fish species. Total fish abundance, as indicated by seine catches across oxbow lakes, was best explained by a negative relationship with water level and transparency (as measured by Secchi disk depth), two variables that showed significant interannual variation. These variables were also important in models predicting bigmouth buffalo electrofishing CPUE. Similar variables have been related to differences in fish communities in tropical oxbow lakes (Rodriguez and Lewis 1997; Tejerina-Garro et al. 1998) and in North American systems where year-to-year variation was not explicitly considered (Winemiller et al. 2000; Miranda and Lucas 2004). Bluegill abundances (both electrofishing and seine data) in our lakes were also strongly related to maximum depth as has been reported by Lubinski et al. (2008). Fish abundance has been suggested to increase because deep lakes are more resistant to desiccation (Winemiller et al. 2000; Zeug et al. 2005). Turbidity may influence fish abundance by reducing foraging ability (Bonner and Wilde 2002) and predation risk (Reid et al. 1999), altering predator–prey interactions and the resulting species composition. Turbidity may also indicate increased sedimentation rates leading to eventual decreased lake depth, lower DO concentrations and increased temperatures (USEPA 1993). In

addition to turbidity, vegetation can affect predation rates in fish (Savino and Stein 1982; Gotceitas 1990). Warmouth, common carp, and gizzard shad abundances were strongly related to percent of vegetated area; these relationships are consistent with previous studies (Pflieger 1975; Parkos et al. 2003; Michaletz and Bonneau 2005; Penne and Pierce 2008). Distance from the river, weeks of low water, weeks connected to the river, and conductivity were also important in predicting bigmouth buffalo abundance. These variables relate to the stability of the oxbow lakes, suggesting that this species is more abundant in habitats with shallow but stable water levels.

Several studies have suggested that North American oxbow lakes function as spawning and nursery habitat for fish that later contribute to the main river populations (Sheaffer and Nickum 1986; Sabo and Kelso 1991; Turner et al. 1994). These conclusions are based on the presence of age-0 fish from a single year of sampling. We found evidence of fish reproduction in all of the oxbow lakes, but also found that there is a high degree of interannual variation. Total age-0 fish CPUE was strongly related to mean water depth, as well as time with low water, and connections with the river. These variables are all related to annual stability of oxbow lakes and the creation of corridors needed for movement of fish between the oxbows and the river. Similar types of variables have also been shown to influence floodplain production of juvenile fish in Europe (Copp 1989); however, we found higher age-0 bluegill CPUE correlated with greater connectivity to the main river, which is opposite to the pattern found previously by Zeug and Winemiller (2008). In addition to these variables, conductivity and water transparency also influenced age-0 bluegill CPUE. Conductivity is probably related to oxbow stability, as salinity tends to

increase as desiccation occurs. The effect of water transparency probably reflects the predation refuge that is afforded by high turbidity (Reid et al. 1999). Abundance of age-0 fish in European systems is thought to be more a function of extinction than colonization (Tales and Berrebi 2007) and it is possible this was the case in our study. However, further research will be needed to differentiate these two mechanisms. Previous single-year studies have found total larval production is highest in oxbow lakes that are large with complex shorelines and heterogeneous bottom contours (Sabo and Kelso 1991) as well as low total organic carbon levels and high DO, conductivity, and turbidity (Sabo et al. 1991). Our results highlight the additional importance of annual variation in hydrologic cycles. The dynamic nature of age-0 fish production and connections between habitats may lead to high variability in year-class strength of some species in river-floodplain ecosystems that depend on oxbow lakes for spawning or nursery habitat. Frequent flooding may reduce survival by flushing age-0 fish from the backwater nursery habitats, but long periods without floods could also reduce recruitment if age-0 fish run out of food or are trapped in an oxbow that dries before reconnecting with the main stem of the river.

The species for which we documented reproduction in oxbow lakes (*Lepomis* spp. and mosquitofish) were similar to those found by other studies (Sheaffer and Nickum 1986; Sabo and Kelso 1991; Turner et al. 1994). None of these species are obligate riverine species (although they were commonly found in the main-stem river samples), and are probably best characterized as intermediate between riverine and lacustrine (Lee et al. 1980). Reproduction by *Dorosoma* spp., inland silversides *Menidia beryllina*, *Pomoxis* spp., darters, and shiners has also been documented in North American backwater habitats (Sheaffer and Nickum 1986; Sabo and Kelso 1991; Turner et al. 1994). These species appear to reproduce in both the lotic and lentic habitats of the river floodplain (Sheaffer and Nickum 1986; Turner et al. 1994), suggesting that the backwater habitat is supplemental rather than obligatory for most fish inhabiting North American rivers.

Oxbows appear to contribute to the fish community of river ecosystems by providing reproductive habitat for several species as well as by providing subpopulations for maintaining less abundant main-stem fish and invertebrate species used as food by fish (Welcomme 1979; Sheaffer and Nickum 1986; Sabo and Kelso 1991; Turner et al. 1994; this study). However, for oxbow lakes to contribute to river fish populations, flood patterns must exist that allow the oxbow lakes to connect with each other and with the main river at appropriate intervals. Large river systems throughout the world, including North America, have been altered through channelization, levees, impoundments, and land-use practices. Two of the oxbow lakes we examined, Round and Kehrer lakes, no longer connect to the Kaskaskia River due to down-cutting of the main river channel. Isolation of oxbow lakes on the floodplain would probably have several negative effects in these ecosystems (Ward 1995; Miranda and Lucas 2004; Lasne et al. 2007), and therefore should be considered in floodplain restoration efforts.

Where possible, river restoration efforts should include improvements in degraded oxbow habitats. In situations where this is not possible, managers should focus on maintaining existing oxbow habitat to ensure the functioning of the large river ecosystem. Channelization and flood control measures often limit the creation of new oxbow lakes and destroy existing habitats (Ward 1995), and therefore should be avoided whenever possible. Spring floods improve growth rates of some species (Gutreuter et al. 1999) and provide corridors for fish movement (Amoros and Bornette 2002) that may allow oxbow lakes to function as spawning and nursery habitat for some species. Flood events also appear important in preventing harsh environmental conditions (e.g., low water levels) that would eliminate many fish species from oxbow lakes. Flood pulses may maintain high diversity in oxbow lakes (Bayley 1995), and our results support that conclusion. Water control management should take into account the importance of flood events to river ecosystem function. Our results indicate oxbow lakes are diverse and variable, and that the abundance of fish in these systems is related to a variety of environmental factors, some of which are variable from year to year. As a result, we suggest that individual oxbow lakes are each valuable and preservation measures should not be focused on any single lake or subset of lakes. Rather, restoration should focus on the interconnectedness of oxbow habitats to maintain fish diversity in floodplain systems. Further, we suggest that future studies of floodplain systems should consider interannual variation to fully understand the functioning of these ecosystems.

Acknowledgments

References

Amoros, C., and G. Bornette. 2002. Connectivity and biocomplexity in water bodies of riverine floodplains. Freshwater Biology 47:761–776.

Bayley, P. B. 1995. Understanding large river–floodplain ecosystems. BioScience 45:153–158.

Bayley, P. B., R. W. Larimore, and D. C. Dowling. 1989. Electric seine as a fish sampling gear in streams. Transactions of the American Fisheries Society 118:447–453.

Bonner, T. H., and G. R. Wilde. 2002. Effects of turbidity on prey consumption by prairie stream fishes. Transactions of the American Fisheries Society 131:1203–1208.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer, New York.

Copp, G. H. 1989. The habitat diversity and fish reproductive function of floodplain ecosystems. Environmental Biology of Fishes 26:1–27.

De Graaf, G. 2003. The flood pulse and growth of floodplain fish in Bangladesh. Fisheries Management and Ecology 10:241–247.

Dettmers, J. M., S. Gutreuter, D. H. Wahl, and D. A. Soluk. 2001a. Patterns in abundance of fishes in main channels of the upper Mississippi River system. Canadian Journal of Fisheries and Aquatic Sciences 58:933–942.

Dettmers, J. M., D. H. Wahl, D. A. Soluk, and S. Gutreuter. 2001b. Life in the fast lane: fish and food web structure in the main channel of large rivers. Journal of the North American Benthological Society 20:255–265.

Gotceitas, V. 1990. Variation in plant stem density and its effects on foraging success of juvenile bluegill sunfish. Environmental Biology of Fishes 27:63–70.

Grift, R. E., A. D. Buijse, J. G. P. K. Breteler, W. L. T. Van Densen, M. A. M. Machiels, and J. J. G. M. Backx. 2001. Migration of bream between the main channel and floodplain lakes along the lower River Rhine during the connection phase. Journal of Fish Biology 59:1033–1055.

Gutreuter, S. J., A. D. Bartels, K. Irons, and M. B. Sandheinrich. 1999. Evaluation of the flood pulse concept based on statistical models of growth of selected fishes of the upper Mississippi River system. Canadian Journal of Fisheries and Aquatic Sciences 56:2282–2291.

Herwig, B. R., D. A. Soluk, J. M. Dettmers, and D. H. Wahl. 2004. Trophic structure and energy flow in backwater lakes of two large-floodplain rivers assessed using stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 61:12–22.

Herwig, B. R., D. H. Wahl, J. M. Dettmers, and D. A. Soluk. 2007. Spatial and temporal patterns in the food web structure of a large-floodplain river assessed using stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 64:495–508.

Junk, W. J. 1999. The flood pulse concept of large rivers: learning from the tropics. Archiv für Hydrobiologie 3(Supplement 115):261–280.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river–floodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences 106:110–127.

King, A. J., P. Humphries, and P. S. Lake. 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. Canadian Journal of Fisheries and Aquatic Sciences 60:773–786.

Kreft, I., and J. De Leeuw. 1998. Introducing multilevel modeling. Sage Publications, London.

Lasne, E., S. Lek, and P. Laffaille. 2007. Patterns in fish assemblages in the Loire floodplain: the role of hydrological connectivity and implications for conservation. Biological Conservation 139:258–268.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Publication 1980-12, Raleigh.

Lubinski, B. J., J. R. Jackson, and M. A. Eggleton. 2008. Relationships between floodplain lake fish communities and environmental variables in a large river–floodplain ecosystem. Transactions of the American Fisheries Society 137:895–908.

Meschiatti, A. J., M. S. Arcifa, and N. Fenerich-Verani. 2000. Fish communities associated with macrophytes in Brazilian floodplain lakes. Environmental Biology of Fishes 58:133–143.

Michaletz, P. H., and J. L. Bonneau. 2005. Age-0 gizzard shad abundance is reduced in the presence of macrophytes: implications for interactions with bluegills. Transactions of the American Fisheries Society 134:149–159.

Miranda, L. E., and G. M. Lucas. 2004. Determinism in fish assemblages of floodplain lakes of the vastly disturbed Mississippi alluvial valley. Transactions of the American Fisheries Society 133:358–370.

Molls, F. 1999. New insights into the migration and habitat use by bream and white bream in the floodplain of the River Rhine. Journal of Fish Biology 55:1187–1200.

Ney, J. J. 1999. Practical use of biological statistics. Pages 167–192 in C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Parkos, J. J., III, V. J. Santucci, Jr., and D. H. Wahl. 2003. Effects of adult common carp (Cyprinus carpio) on multiple trophic levels in shallow mesocosms. Canadian Journal of Fisheries and Aquatic Sciences 60:182–192.

Pegg, M. A., K. S. Irons, T. M. O'Hara, and M. A. McClelland. 2006. Initial response of a floodplain lake fish community to water level stabilisation. Ecology of Freshwater Fish 15:40–47.

Penne, C. R., and C. L. Pierce. 2008. Seasonal distribution, aggregation, and habitat selection of common carp in Clear Lake, Iowa. Transactions of the American Fisheries Society 137:1050–1062.

Pflieger, W. L. 1975. The fishes of Missouri. Missouri Department of Conservation, Jefferson City.

Rodriguez, M. A., and W. M. Lewis, Jr. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. Ecological Monographs 67:109–128.

Reid, S. M., M. G. Fox, and T. H. Whillans. 1999. Influence of turbidity on piscivory in largemouth bass (*Micropterus salmoides*). Canadian Journal of Fisheries and Aquatic Sciences 56:1362–1369.

Sabo, M. J., and W. E. Kelso. 1991. Relationship between morphometry of excavated floodplain ponds along the Mississippi River and their use as fish nurseries. Transactions of the American Fisheries Society 120:552–561.

Sabo, M. J., W. E. Kelso, C. F. Bryan, and D. A. Rutherford. 1991. Physicochemical factors affecting larval fish densities in Mississippi River floodplain ponds, Louisiana (U.S.A.). Regulated Rivers: Research and Management 6:109–116.

SAS Institute. 1999. SAS/STAT user's guide, version 8. SAS Institute, Cary, North Carolina.

Savino, J. F., and R. A. Stein. 1982. Predator–prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111:255–266.

Sheaffer, W. A., and J. G. Nickum. 1986. Backwater areas as nursery habitats for fishes in Pool 13 of the upper Mississippi River. Hydrobiologia 136:131–140.

Slavik, O., and L. Bartos. 2001. Spatial distribution and temporal variance of fish communities in the channelized and regulated Vltava River (central Europe). Environmental Biology of Fishes 61:47–55.

Sparks, R. E. 1995. Need for ecosystem management of large rivers and their floodplains. BioScience 45:168–182.

Tales, E., and R. Berrebi. 2007. Controls of local young-of-the-year fish species richness in flood plain water bodies: potential effects of habitat heterogeneity, productivity and colonization–extinction events. Ecology of Freshwater Fish 16:144–154.

Tejerina-Garro, F. L., R. Fortin, and M. A. Rodriguez. 1998. Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon basin. Environmental Biology of Fishes 51:399–410.

Tockner, K., F. Malard, and J. V. Ward. 2000. An extension of the flood pulse concept. Hydrological Processes 14:2861–2883.

Tockner, K., F. Schiemer, and J. V. Ward. 1998. Conservation by restoration: the concept for a river–floodplain system on the Danube River in Austria. Aquatic Conservation: Marine and Freshwater Ecosystems 8:71–86.

Turner, T. F., J. C. Trexler, G. L. Miller, and K. E. Toyer. 1994. Temporal and spatial dynamics of larval and juvenile fish abundance in a temperate floodplain river. Copeia 1994:174–183.

USEPA (U.S. Environmental Protection Agency). 1993. Guidance specifying management measures for sources of nonpoint pollution in coastal waters. USEPA, EPA 840-B-92-002, Cincinnati, Ohio.

Wahl, D. H., J. Goodrich, M. A. Nannini, J. M. Dettmers, and D. A. Soluk. 2008. Exploring riverine zooplankton in three habitats of the Illinois River ecosystem: where do they come from? Limnology and Oceanography 53:2583–2593.

Wahl, D. H., and L. A. Nielsen. 1985. Feeding ecology of the sauger (*Stizostedion canadense*) in a large river. Canadian Journal of Fisheries and Aquatic Sciences 42:120–128.

Ward, J. V. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regulated Rivers: Research and Management 11:105–119.

Welcomme, R. L. 1979. The fisheries ecology of floodplain rivers. Longman Press, London.

Winemiller, K. O., S. Tarim, D. Shormann, and J. B. Cotner. 2000. Fish assemblage structure in relation to environmental variation among Brazos River oxbow lakes. Transactions of the American Fisheries Society 129:451–468.

Zeug, S. C., and K. O. Winemiller. 2008. Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. River Research and Applications 24:90–102.

Zeug, S. C., K. O. Winemiller, and S. Tarim. 2005. Response of Brazos River oxbow fish assemblages to patterns of hydrologic connectivity and environmental variability. Transactions of the American Fisheries Society 134:1389–1399.