Response of Brazos River Oxbow Fish Assemblages to Patterns of Hydrologic Connectivity and Environmental Variability

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Abstract.—Three oxbow lakes with different connection frequencies and an adjacent reach of the middle Brazos River, Texas, were surveyed quarterly from summer 1993 to summer 1996 to examine the effects of hydrology and physicochemical attributes on fish assemblage structure. During flood events, oxbows usually were colonized by about 20 fish species from the river channel, and several fluvial specialists were rarely or never sampled from oxbows. Multivariate analyses of seine samples revealed divergent patterns of assemblage structure during periods of isolation that also were associated with a gradient of maximum water depth, temperature, and conductivity. In contrast, analysis of gill-net samples that targeted large fishes revealed low between-site and temporal variation in assemblage structure among oxbow lakes but significant differences in the structure of oxbow versus channel assemblages. The shallowest oxbow (which dried out with greatest frequency) had the most variable fish assemblage across seasons and was dominated by small colonizing species, whereas deeper oxbows and the river channel tended to have higher species richness and more stable assemblages. Despite large differences in connection frequency and distance from the river channel, the deepest oxbows had the most similar fish assemblage structure across all seasons. Multiple regression analysis suggested that the timing and frequency of flood events (yielding colonization) in the most frequently connected oxbow interact with predator abundance (yielding mortality) to influence the abundance of common lotic-adapted minnows (red shiner *Cyprinella lutrensis* and bullhead minnow *Pimephales vigilax*) that periodically dominated the species assemblage of that oxbow after floods. Our results suggest that current hydrologic and geomorphologic dynamics in the middle Brazos River produce oxbow lakes with a range of physical characteristics yielding different disturbance and colonization regimes that strongly influence fish species assemblages.

Floodplain rivers are dynamic ecosystems characterized by high biological diversity, productivity, spatial complexity, and flow variability (Sparks 1995). Ecological processes in these systems are dominated by hydrology (Poff and Allan 1995), and conceptual models emphasize flood dynamics as a primary factor influencing fish productivity and recruitment (Junk et al. 1989; Humphries et al. 1999). Periodic inundation provides opportunities for aquatic organisms to access productive off-channel floodplain habitats, such as oxbow lakes that function as spawning and nursery areas for many fish species, provide aquatic organisms with refuge from disturbances in the river channel, and contribute to the biodiversity of the river–floodplain system as a whole (Halyk and Balon 1983; Sabo and Kelso 1991; Sabo et al. 1991; Hoover and Killgore 1998; Swales et al.

1999; Ward et al. 1999). Periodic connection to the river channel facilitates faunal exchange and tends to homogenize fish assemblages spatially (Rodriguez and Lewis 1997). As habitats become isolated, biotic interactions and physicochemical characteristics appear increasingly important in structuring fish assemblages (Tejerina-Garro et al. 1998; Winemiller et al. 2000).

Modified river–floodplain systems have received comparatively little attention despite changes in fish distribution, abundance, and assemblage structure associated with the alteration of natural hydrologic regimes (Moyle and Light 1996; Tockner and Stanford 2002; Feyrer and Healey 2003). Proposed restoration strategies include increasing the connection between rivers and their floodplains and reestablishing a relatively natural hydrologic regime (Bayley 1991; Trexler 1995; Amoros and Bornette 2002). A major challenge for restoration efforts is to determine the ecological function of these systems under natural flow regimes (Bayley 1995; Richter et al. 1997; Michener and Haeuber 1998). Floodplain rivers exhibit a wide range of flow dynamics, and variable responses of aquatic fauna are expected

TABLE 1.—Means (SDs) of physical characteristics and connectivity estimates for the Brazos River (BR) and three types of oxbows: one deep and frequently connected oxbow (DF); one deep and rarely connected oxbow (DR); and one shallow oxbow with an intermediate connection frequency (SI).

Characteristic	DF	DR	SI	BR
Depth (cm)	95 (33.0)	93 (48.2)	54 (26.4)	232 (56.9)
Secchi depth (cm)	16.5 (5.1)	17.4 (7.6)	14.3 (5.0)	30.5 (21.0)
Temperature (°C)	23.9 (7.4)	22.5 (8.3)	25.5 (6.1)	23 (6.7)
Dissolved oxygen (mg/L)	7.6 (2.4)	9.3 (2.2)	8.3 (2.6)	9.5 (1.4)
pH	8.2 (0.7)	8.8 (0.7)	8.2 (0.7)	8.1 (0.9)
Conductivity (μS)	348 (79.2)	418 (61.6)	349 (55.3)	939 (300.0)
Chlorophyll a (μg/L)	59 (54.6)	85 (115.0)	37 (47.2)	23 (12.8)
Area (ha)	20.5	28.1	14.3	42
Shoreline perimeter (m)	7,187.1	5,000.1	3,559	
Distance from the river (m)	214	1,035	536	
Number of connections	14	0	4	
Days connected	30	0	10	

(Puckridge et al. 1998; Humphries et al. 1999). Although few opportunities exist to study unmodified North American systems, the structure and function of an unmodified reach can remain intact, provided river regulation upstream allows sufficient hydrologic variation (Sparks et al. 1990; Poff et al. 1997; Richter et al. 1997).

We examined the response of fish assemblages in three oxbow lakes and one river channel site along a relatively unmodified reach of the middle Brazos River, Texas, to patterns of hydrologic connectivity and physicochemical characteristics during isolation. Our goals were to describe fish assemblage structure in habitats with different connection frequencies and to examine the relative influence of connectivity and habitat characteristics on species assemblages. We predicted oxbows would share a similar assemblage structure after floods that facilitated faunal exchange (Rodriguez and Lewis 1997), and physicochemical characteristics would strongly influence divergent assemblages during periods of isolation (Halyk and Balon 1983; Rodriguez and Lewis 1997; Tejerina-Garro et al. 1998; Winemiller et al. 2000; Suarez et al. 2001; Feyrer et al. 2004). Connectivity to source populations is an important determinant of assemblage structure in aquatic systems (Taylor 1997; Lonzarich et al. 1998; Olden et al. 2001; Baber et al. 2002), and oxbows that connect to the main channel with greater frequency are expected to have species assemblages more similar to those of the river channel than would oxbows that remain isolated for long periods between flood events.

Study Site

The main stem of the Brazos River originates in Stonewall County, Texas, at the confluence of the Salt Fork and Double Mountain Fork. The river flows southeast for 1,485 km before entering the northern Gulf of Mexico. The present study was conducted on the middle Brazos River between 30°25′N and 30°37′N. The middle Brazos is a meandering lowland river with forest and agricultural lands dominating the 76,361 km² catchment. Oxbow lakes are common on the floodplain of the middle Brazos; more than 40 have been identified in aerial surveys (Winemiller et al. 2000). A once-in-100-years flood in the winter of 1991–1992 filled all oxbows to capacity and provided an opportunity for river fauna to access oxbow habitats. Three oxbows with different depths and connection frequencies were selected for quarterly surveys: one deep and frequently connected oxbow, one deep and rarely connected oxbow, and one shallow oxbow with an intermediate connection frequency, hereafter referred to as DF, DR, and SI, respectively. In addition, using identical methods, we surveyed a 6.5-km reach of the river channel (30°37′N, 96°37′W), selected based on boat access and proximity to the most upstream oxbow.

Methods

Habitat sampling.—All oxbows were mapped by using a Trimble GPS Pathfinder backpack unit with base-station corrections to obtain values for shoreline perimeter, area, and minimum distance from the river channel (Table 1). The area of the river channel site was estimated from U.S. Geological Survey topographic maps (1:24,000). Each oxbow and the river channel were sampled quarterly from summer 1993 to summer 1996 except for DF, which was omitted in the winter of 1994, and DR, which was omitted in the summer of 1996 because of desiccation. Sampling was terminated after summer 1996 surveys, when all oxbows dried out.

A suite of physicochemical parameters was measured at each site. Temperature (°C), dissolved oxygen (mg/L), conductivity (μS), and pH were measured with a Hydrolab Datasonde. Maximum depth and Secchi depth were recorded to the nearest centimeter. Chlorophyll concentrations were determined fluorometrically (Wetzel and Likens 1991) in the laboratory from water samples held on ice. Flow data for the Brazos River were obtained from U.S. Geological Survey gauge 08108700 at the Texas State Highway 21 bridge. The substrate of all oxbows was a clay–mud mixture with coarse detritus overlying some areas. The substrate of the river channel consisted primarily of clay, mud, and fine silt overlying sand and gravel.

The minimum flow required to inundate oxbow lakes was estimated by comparing direct field observations of flooding (rise and fall in oxbow water level, recent water marks on riparian vegetation) with peak discharge during the quarter that preceded field observations. The smallest peak discharge that yielded flooding was used as an estimate of the minimum flow required to connect each oxbow with the active channel (Figure 1).

Fish sampling.—Small-bodied fishes (<200-mm standard length [SL]) were sampled by using a 10-m × 2-m bag seine with 6.4-mm mesh in the wings and 3.2-mm mesh in the bag. Successive seine hauls were conducted at new locations within the habitat until no new species were collected. The distance covered by each seine haul was estimated, and the total distance seined per survey was recorded for calculating catch per unit effort (CPUE; number or biomass of each species per 10 m of seine haul).

Large-bodied fishes were sampled with two multifilament experimental gill nets. Each gill net consisted of three panels, each measuring 16.5 × 2 m, with 2.54-, 5.1-, and 7.6-cm-bar mesh. Gill nets were deployed between approximately 1600 hours and 1900 hours in each oxbow and between about 1600 hours to 0800 hours the next day at the river channel site. Additional gill-net effort was required in the channel because of greater transparency, flow, and the apparent lower density of large-bodied fishes in the river. Shallow water prevented use of gill nets in oxbow lakes on some dates. The duration in minutes of each gillnet set was recorded, and CPUE was calculated as number of individuals and biomass per gill-net hour.

All fishes collected were killed by immersion in tricaine methanesulfonate (MS-222). Small fishes were then fixed in 15% formalin solution, and large
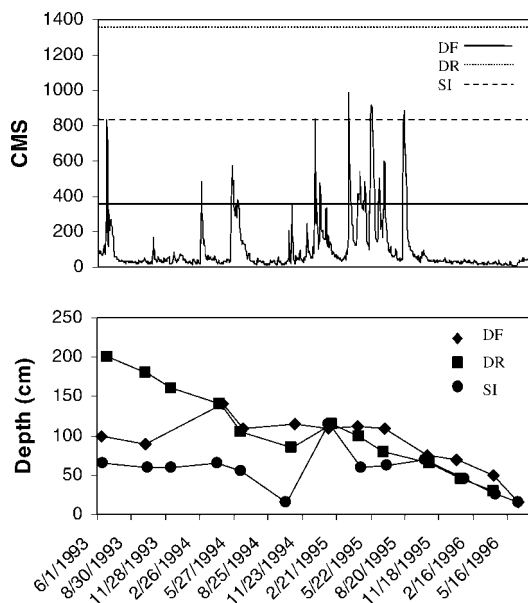

FIGURE 1.—Daily stream flow hydrograph (m³/s [CMS]) of the Brazos River at the Texas State Highway 21 bridge from June 1993 to June 1996 (top panel) and oxbow water depth measurements for each season (bottom panel). The horizontal lines on the hydrograph indicate estimates of the river flow required for oxbow connections. Abbreviations are as follows: DF = one deep and frequently connected oxbow; DR = one deep and rarely connected oxbow; and SI = one shallow oxbow with an intermediate connection frequency. Connectivity estimates for DR were provided by the Texas Water Development Board (TWDB 2004).

fishes were transported to the laboratory on ice and stored frozen for later analysis. Fishes were identified, measured (SL and total length [TL] to the nearest 1 mm), and weighed (nearest 0.1 g).

Data analysis.—Species richness for each quarterly sample was estimated as the number of species collected in each gill net or seine sample. Electrofishing was used to verify estimates of species richness and generally collected a subset of the species that were captured by seines and gill nets. The blackstripe topminnow *Fundulus notatus* was the only species collected by electrofishing that was not collected with seines or gill nets. This species was represented by one individual taken during the summer 1995 survey of DR. Pearson product moment correlations were calculated for all possible combinations of environmental parameters, numeric and biomass CPUE, and species richness. Except for pH, all values were log transformed [$\log_{10}(x + 1)$] before correlation analysis. Correlations were calculated for seine and gill-net

data separately. Statistical significance was assessed at α = 0.05 and P-values were adjusted for multiple comparisons by using the Bonferroni correction (critical P = 0.0011).

Multivariate analysis.—Correspondence analysis (CA) was performed on matrices of species CPUE × site for quarterly gill-net and seine samples. This form of analysis uses reciprocal averaging to simultaneously ordinate sample and species scores based on turnover of the relative abundance of species. The significance of site, season, and year groupings were tested by multiresponse permutation procedures (MRPP), where sample scores from axis 1 and 2 were the response variables, and site, season, or year was the categorical variable. When significant groupings were detected, pairwise comparisons between groups were conducted, and P-values were Bonferroni-adjusted for multiple comparisons. Canonical correspondence analysis (CCA) was used to explore relationships between species CPUE and environmental parameters and to examine environmental gradients among sites. Canonical correspondence analysis is a direct gradient technique that ordinates species and sample scores along environmental gradients. Correspondence and canonical correspondence analyses were conducted with CANOCO (version 4; Microcomputer Power), and MRPP was performed with PC-ORD (version 4; MJM Software).

Multiple regression analysis was used to identify variables related to connectivity and predation that potentially influenced the abundance of red shiner *Cyprinella lutrensis* and bullhead minnow *Pimephales vigilax* in the deep, frequently connected oxbow (DF). These species dominated the postflood seine samples that grouped with the river channel in CA ordinations but were rarely collected during other surveys or in less frequently connected oxbows. The combined CPUE of red shiners and bullhead minnow in each quarter was the dependent variable, and independent variables were numerical CPUE of small piscivores (white crappie *Pomoxis annularis* and warmouth *Lepomis gulosus*) in seine samples, days of isolation, days of connectivity in the previous quarter, and number of connections in the previous quarter. Because gill-net samples were lacking on some dates, large piscivores were not examined as an independent variable. All values were log-transformed to meet the assumption of normality, and all possible permutations of one-, two-, three-, and four-variable models were constructed. When additional variables improved the adjusted R^2 by <0.10, the re-

duced model was used. Regressions were run with NCSS (2000 edition; Number Cruncher Statistical Systems).

Results

Habitat

Oxbow features were generally more similar to each other than to the river channel (Table 1). Site scores on CCA axis 1 described an oxbow–river channel gradient in which high scores associated with the river channel site were correlated with greater depth, conductivity, and lower temperatures. Axis 2 described a seasonal gradient, where high scores corresponding primarily to winter surveys were correlated with lower values for depth, temperature, and pH and higher dissolved oxygen concentrations. Summer sample scores were low on axis 2, and fall and spring scores were generally intermediate (Figure 2).

Connectivity estimates indicated that DR did not connect to the active channel during the study, whereas SI connected on 4 occasions for 10 d and DF connected on 14 occasions for a total of 30 d (Table 1).

Species Richness and Abundance

Our samples yielded 48 fish species representing 13 families (Appendix). The river channel produced 42 species, and 37, 33, and 27 species were collected in DF, DR, and SI, respectively. Species richness in quarterly seine samples ranged from 1 in SI to 20 in DF; collections typically produced 8–13 species (Table 2). Depth was significantly and positively correlated with species richness in seine collections across all seasons (r = 0.48, P < 0.001). Individual gill-net samples typically yielded 4–7 species, and richness ranged from 0 (on three occasions in the river channel) to 9 (DF and DR; Table 2). Conductivity was negatively correlated with richness in gill-net samples (r = −0.46, P < 0.001), and conductivity values in the river channel were double those of the oxbow lakes during most surveys (Table 1).

Mean numeric and biomass CPUE from seine collections suggested that the river channel and SI had many small-bodied fishes, whereas DF and DR tended to have fewer but larger fishes (Table 2). All oxbows had greater mean values for numeric CPUE in gill-net collections than the river channel, and deep oxbows had greater values of numeric CPUE in gill-net collections than did the shallowest oxbow. Depth was negatively and significantly correlated with gill-net numeric CPUE across all seasons (r = −0.52, P < 0.001), and no correla-
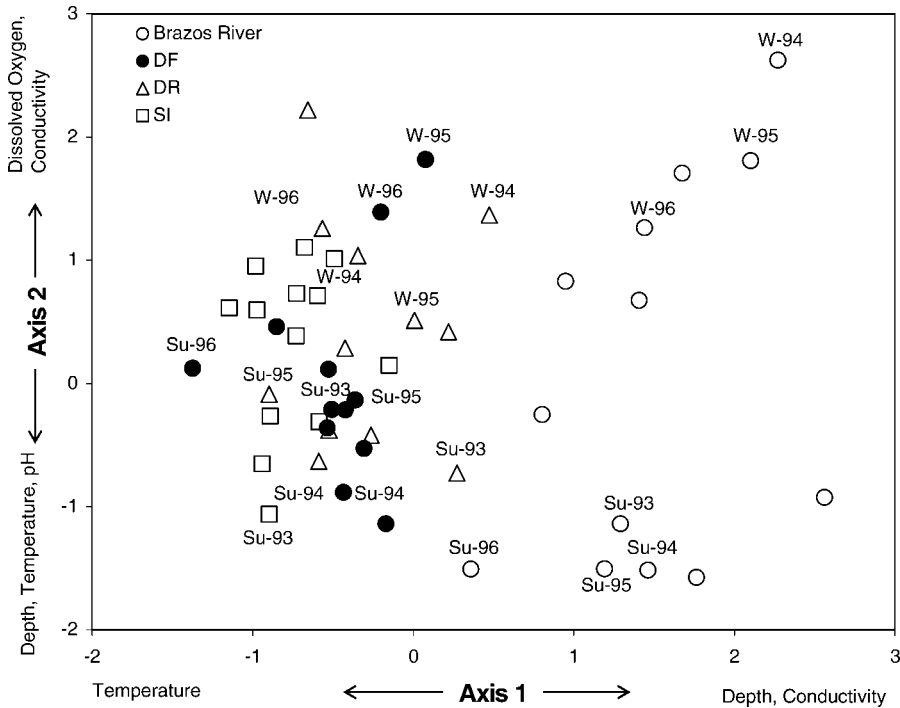
FIGURE 2.—Plot of site scores of environmental variables from canonical correspondence analysis for 1993–1996. Temperature, conductivity, and depth were significantly correlated with axis 1 (eigenvalue = 0.473). Temperature, dissolved oxygen, pH, conductivity, and depth were significantly correlated with axis 2 (eigenvalue = 0.092). All winter (W) and summer (Su) samples are labeled. See Figure 1 for abbreviations pertaining to oxbow types.

tions between CPUE and environmental variables among seine collections were significant.

Ordination of Fish Assemblages

Variation in fish assemblage structure was greater among sites than between years or seasons (Figure 3). Pairwise comparisons of site scores on CA axes 1 and 2 using MRPP revealed statistically significant differences in assemblage structure between sites (Table 3); however, year ($A = -0.01$, $P = 0.662$) and season ($A = -0.03$, $P = 0.923$) groupings were not significant. Axis 1 modeled 30.9% of the total variation and differentiated oxbow lake assemblages with greater abundances of catfish, shad, and sunfish from river channel assemblages, which contained lotic-adapted cyprinids (e.g., red shiners, bullhead minnow, and silverband shiner). Axis 2 modeled 9.9% of the total

TABLE 2.—Means (SDs) of estimates of species richness, catch per unit effort (CPUE), and effort for all quarterly surveys. Site abbreviations are given in Table 1.

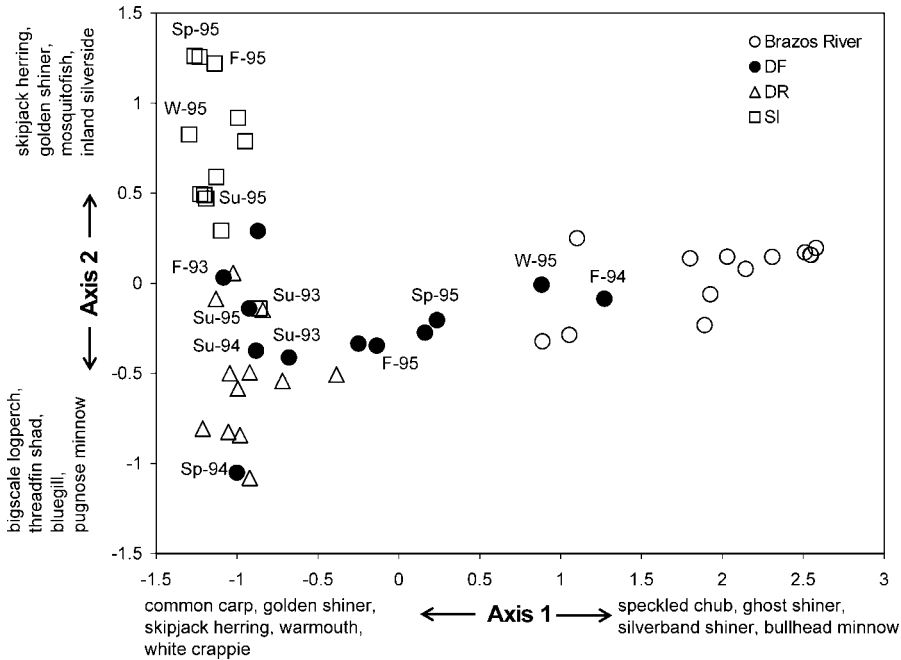|	Seine				Gill net			
Variable	DF	DR	SI	BR	DF	DR	SI	BR
Species richness	13	11	8	11	6	7	5	4
	(3.8)	(2.7)	(4.9)	(3.9)	(2.4)	(1.9)	(1.2)	(1.9)
CPUE								
Number	229.2	130.3	320.7	517.7	7.9	8.4	4.8	0.4
	(192.5)	(156.0)	(335.1)	(484.7)	(4.0)	(3.9)	(4.4)	(0.2)
Biomass (g)	632.3	249.6	142.2	230.5	4,392.1	6,098.1	3,996.8	559.7
	(530.1)	(158.18)	(121.2)	(217.7)	(3,236.8)	(4,139.7)	(4,255.9)	(608.2)
Effort[a]	39.3	58.8	37.3	52.7	4.8	5.9	4.2	29.4
	(15.0)	(27.2)	(10.4)	(12.0)	(1.7)	(1.5)	(1.3)	(16.0)

[a] Seine = meters, gill net = hours.

FIGURE 3.—Plot of site scores on correspondence analysis axes 1 and 2 (Hill's scaling) from seine samples for 1993–1995. Oxbow samples collected after a connection with the main channel in the previous quarter are labeled with the season and year. Season abbreviations are as follows: Sp = spring, Su = summer, F = fall, and W = winter; see Figure 1 for abbreviations pertaining to oxbow types.

variation and differentiated the three oxbow lakes from each other (Figure 3). Negative scores on axis 2 corresponding to DR were associated with more threadfin shad, bluegill, and pugnose minnow. Positive scores corresponding to SI were associated with more western mosquitofish, inland silverside, and golden shiner. Correspondence analysis scores for DF were generally intermediate between those of the other two oxbows; however, two surveys had scores similar to those of the river channel. These two samples had an abundance of red shin-

ers and bullhead minnow, species that dominate river channel samples.

Depth, temperature, and conductivity were the most important environmental variables associated with species distributions. Axis 1 described a gradient from species characteristic of the river assemblage (greater depth and conductivity, lower temperature) to species that were common in oxbows (shallower water, lower conductivity, higher temperature). Axis 2 generally described seasonal differences in species abundance in the river channel correlated with temperature, depth, and dissolved oxygen.

Assemblages of large fish captured in gill nets were more similar among oxbows than were assemblages of small fish captured in the seine (Figure 4). Pairwise comparisons of CA site scores indicated that the assemblage of large fish in the river channel was structured differently from those in oxbows. Further, among oxbows, the SI assemblage was different from the other two oxbows (Table 3). Year ($A = -0.01$, $P = 0.479$) and season ($A = -0.01$, $P = 0.656$) groupings were not significant. Axis 1 modeled 18.6% of the total variation and differentiated oxbow lakes, containing

TABLE 3.—Effect size (A) and P-values from pairwise comparisons of correspondence analysis sample scores using multiresponse permutation procedures. Significance was assessed at $P = 0.008$ (Bonferroni corrected). Site abbreviations are given in Table 1.

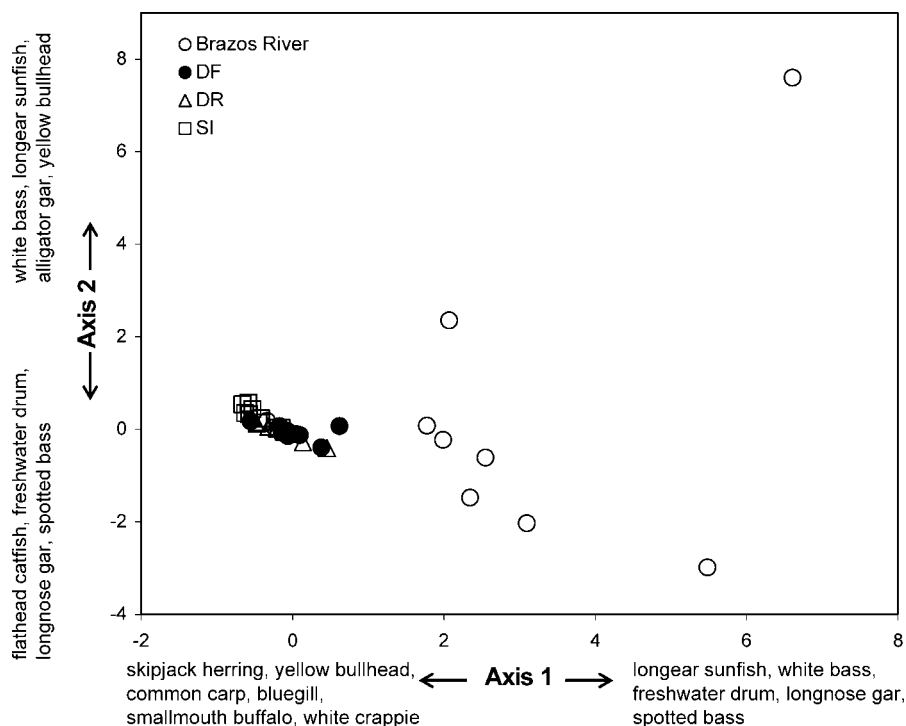| Comparison	Seine		Gill net	
	A	P	A	P
BR × DF	0.45	<0.001	0.20	<0.001
BR × DR	0.66	<0.001	0.21	<0.001
BR × SI	0.68	<0.001	0.24	<0.001
DF × DR	0.12	0.004	0.01	0.328
DF × SI	0.31	<0.001	0.33	<0.001
DR × SI	0.44	<0.001	0.30	<0.001

FIGURE 4.—Plot of site scores on correspondence analysis axes 1 and 2 (Hill's scaling) from gill-net samples. See Figure 1 for abbreviations pertaining to oxbow types.

greater abundances of white crappie, smallmouth buffalo, and bluegill, from the river channel, which had relatively more longear sunfish and gar. Axis 2 modeled 13.2% of the total variation and described seasonal variation in river channel assemblages (Figure 4).

Assemblage Structure and Hydrology

The effect size parameters from MRPP analysis reflected among-habitat variations in depth, connectivity, and their interactions. All pairwise site comparisons were significant except for large-fish assemblages in the two deep oxbows (Table 3). Effect size parameters (A) for small-fish assemblages between the river channel and oxbows were smallest for the deep and frequently connected oxbow (DF; Table 3). Among oxbows, the two deepest oxbows (DF, DR) were more similar to each other than to SI and the greatest effect size occurred between the shallow, intermediately connected oxbow (SI) and the deep, infrequently connected oxbow (DR). Effect sizes for large-fish assemblages were approximately equal between the river channel and all oxbow lakes; among oxbows, the two deep oxbows had the lowest effect size (Table 3).

The abundance of red shiners and bullhead minnow in DF during different seasons was associated with hydrologic regime and predator abundance. Days of isolation (β_1), number of connections in the previous period (β_2), and numerical CPUE of small piscivores in seine samples (β_3) explained 70.5% of variation in the numerical CPUE of red shiners and bullhead minnow ($F_{3,11} = 6.36$, $P = 0.016$; $y = -2.06\beta_1 - 3.11\beta_2 - 1.07\beta_3 + 6.76$). Abundance of these lotic-adapted species was negatively correlated with piscivore abundance, days of isolation, and flood connections during the previous quarter.

Discussion

Fish assemblage structure was associated with both macrohabitat features (e.g., depth) and the frequency of floods that connect oxbows with the river channel. Although postflood assemblages in the shallowest oxbow (SI) contained species similar to other oxbows, relatively long periods of isolation resulted in assemblages dominated by small species that were tolerant of periodically harsh environmental conditions (e.g., western mosquitofish and orangespotted sunfish). River flooding introduced colonists after oxbow desic-

cation; however, channel-adapted species (e.g., red shiners, bullhead minnow, and silverband shiners) that were relatively common in the most frequently connected oxbow were rarely collected from SI after floods. SI is located more than 300 m farther from the river than DF is, and the dispersal ability of these species may have interacted with connectivity to influence colonization (Taylor 1997). The two deepest oxbows had the most similar species assemblages across all seasons despite a large difference in connection frequency (14 versus 0 occasions) and distance from the channel (214 m versus 1035 m), thus indicating that depth was a strong influence on assemblage structure. Olden et al. (2001) found that isolation and geomorphology factors operated relatively independently of each other in determining the assemblage structure of northern drainage lakes, and our results indicated similar patterns in Brazos oxbows.

The effect of variable inundation frequency on assemblage structure in Brazos oxbows contrasts with studies of floodplain lakes in other systems. In those systems, the type of lake isolation (Tejerina-Garro et al. 1998) and distance from the channel (Rodriguez and Lewis 1997; Tejerina-Garro et al. 1998) had no effect on assemblage structure, but their flood dynamics were more predictable. The stochastic flood dynamics of the Brazos River may partially explain the difference (Winemiller 1996). In the Brazos, variation in flood magnitude yielded different frequencies of flood connections in different oxbows, and variation in flood timing appeared to influence the ability of some species to colonize and persist in oxbow habitats. Petry et al. (2003) found significant differences in species richness, density, and biomass of fishes in connected and isolated floodplain lagoons of the upper Paraná River, Brazil, during a year when drought combined with hydrologic regulation altered normal flood dynamics. Connectivity also influenced assemblages in off-channel habitats of a regulated river in Oregon (Scheerer 2002). Additionally, connectivity is an important factor influencing species assemblages in other aquatic systems (Taylor 1997; Lonzarich et al. 1998; Magnuson et al. 1998; Schlosser and Kallemeyn 2000; Olden et al. 2001; Baber et al. 2002).

Variation in species CPUE among habitats was mostly associated with a gradient of water depth, conductivity, and temperature. Deep oxbows tend to have greater species richness than the warmest, shallowest oxbow, which was dominated by small species (e.g., western mosquitofish and inland silverside) with traits well suited for rapid coloni-

zation (Winemiller and Rose 1992). The river channel had a greater maximum depth, higher conductivity, and cooler temperatures than oxbow lakes, and the river assemblage was dominated by lotic-adapted cyprinids. Similar relationships between assemblage structure and physicochemical characteristics during isolation have been described for 10 Brazos River oxbow lakes (Winemiller et al. 2000), Canadian floodplain pools (Halyk and Balon 1983), Californian floodplain ponds (Feyrer et al. 2004), and neotropical floodplain lakes (Rodriguez and Lewis 1997; Tejerina-Garro et al. 1998; Suarez et al. 2001).

Patterns of seasonal variation in assemblage structure were generally weak, and no MRPP seasonal groupings were significant. Although variation in dissolved oxygen and pH were significant in CCA, variation in these parameters did not appear to greatly affect species composition. Seasonal variation in dissolved oxygen and pH is less extreme in Brazos oxbows than in more northern freshwater habitats, where these parameters can be important factors structuring fish assemblages (Tonn and Magnuson 1982; Rahel 1984; Schlosser and Kallemeyn 2000).

Assemblages of large fishes captured in gill nets were more similar among sites than were small-fish (seine sample) assemblages across all seasons. Lonzarich et al. (1998) found that large fishes (>100 mm TL) colonized new habitats more rapidly than small fishes did, which may partially explain the observed similarity in oxbow assemblages. The deepest oxbows showed no differences in large-fish assemblages, probably related to greater persistence of aquatic habitat. Periodic desiccation of the shallowest oxbow may have prevented juveniles produced in situ from growing to sizes susceptible to gill nets.

In surveys conducted after several flood events, small-fish assemblages in DF were more similar to those in the river channel than to those in other oxbows. Multiple regression analysis suggested that interactions between connectivity and predation may influence colonization by lotic-adapted cyprinids characteristic of river channel assemblages. Predation seems to be a strong determinant of assemblage composition in neotropical floodplain lakes (Rodriguez and Lewis 1997; Suarez et al. 2001). Periods of extended oxbow isolation yielding enhanced recruitment of white crappie and warmouth are likely to hinder the establishment of lotic-adapted cyprinids (i.e., red shiners, bullhead minnow). Frequent flood connections may allow these small cyprinids to return to the

river channel, where they dominate the species assemblage.

The current study reinforces the view that oxbow lakes are important sources of fish production and biodiversity in the Brazos River–floodplain system. Although cumulative species richness was highest in the river channel, six species collected in oxbow lakes were never taken in river channel surveys. Conversely, seven species collected in the river channel were never taken in oxbow lakes (Appendix). Several species that were rare in river channel samples were particularly abundant in oxbow lakes (white crappie, bluegill, and threadfin shad). Floodplain habitats have been shown to be important for centrarchids (Kwak 1988; Raibley et al. 1997) and can provide profitable foraging areas for catfishes (Flotemersch and Jackson 2003). The importance of natural flow regimes for the maintenance of ecological processes in lotic systems is well recognized (Sparks 1995; Poff et al. 1997; Bunn and Arthington 2002; Bowen et al. 2003). Alteration of fluvial processes that form oxbows and drive floodplain geomorphic succession and lateral floodplain connectivity in the middle Brazos River would reduce fish production and biodiversity.

References

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

Baber, M. J., D. L. Childers, K. J. Babbitt, and D. H. Anderson. 2002. Controls on fish distribution and abundance in temporary wetlands. Canadian Journal of Fisheries and Aquatic Sciences 59:1441–1450.

Bayley, P. B. 1991. The flood pulse advantage and the restoration of river–floodplain systems. Regulated Rivers: Research and Management 6:75–86.

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

Bowen, Z. H., K. D. Bovee, and T. J. Waddle. 2003. Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. Transactions of the American Fisheries Society 132:809–823.

Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492–507.

Feyrer, F., T. R. Sommer, S. C. Zeug, G. O'Leary, and W. Harrell. 2004. Fish assemblages of perennial floodplain ponds of the Sacramento River, California (USA) with implications for the conservation of native fishes. Fisheries Management and Ecology 11:335–344.

Feyrer, F., and M. Healey. 2003. Fish community structure and environmental correlates in the highly altered southern Sacramento–San Joaquin Delta. Environmental Biology of Fishes 66:123–132.

Flotemersch, J. E., and D. C. Jackson. 2003. Seasonal foraging by channel catfish on terrestrially burrowing crayfish in a floodplain–river ecosystem. Ecohydrology and Hydrobiology 3:61–70.

Halyk, L. C., and E. K. Balon. 1983. Structure and ecological production of the fish taxocene of a small floodplain system. Canadian Journal of Zoology 61:2446–2464.

Hoover, J. J., and K. J. Killgore. 1998. Fish communities. Pages 237–260 in M. G. Messina and W. H. Conner, editors. Southern forested wetlands: ecology and management. CRC Press, Boca Raton, Florida.

Humphries, P., A. J. King, and J. D. Koehn. 1999. Fish, flows, and flood plains: links between freshwater fishes and their environment in the Murray–Darling River system, Australia. Environmental Biology of Fishes 56:129–151.

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.

Kwak, T. J. 1988. Lateral movement and use of floodplain habitat by fishes of the Kankakee River, Illinois. American Midland Naturalist 120:241–249.

Lonzarich, D. G., M. L. Warren, and M. R. E. Lonzarich. 1998. Effects of habitat isolation on the recovery of fish assemblages in experimentally defaunated stream pools in Arkansas. Canadian Journal of Fisheries and Aquatic Sciences 55:2141–2149.

Magnuson, J. J., W. M. Tonn, A. Banerjee, J. Toivonen, O. Sanchez, and M. Rask. 1998. Isolation vs. extinction in the assembly of fishes in small northern lakes. Ecology 78:2941–2956.

Michener, W. K., and R. A. Haeuber. 1998. Flooding: natural and managed disturbances. BioScience 48:677–680.

Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation 78:149–161.

Olden, J. D., D. A. Jackson, and P. R. Peres-Neto. 2001.

Spatial isolation and fish communities in drainage lakes. Oecologia 127:572–585.

Petry, A. C., A. A. Agostinho, and L. C. Gomes. 2003. Fish assemblages of tropical floodplain lagoons: exploring the role of connectivity in a dry year. Neotropical Ichthyology 1:111–119.

Poff, L. N., and D. J. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76:606–627.

Poff, L. N., D. J. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. BioScience 47:769–784.

Puckridge, J. T., F. Sheldon, K. F. Walker, and A. J. Boulton. 1998. Flow variability and the ecology of large rivers. Marine and Freshwater Research 49: 55–72.

Rahel, F. J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. Ecology 65: 1276–1289.

Raibley, P. T., K. S. Irons, T. M. O'Hara, K. D. Blodgett, and R. E. Sparks. 1997. Winter habitats used by largemouth bass in the Illinois River, a large river–floodplain ecosystem. North American Journal of Fisheries Management 17:401–412.

Richter, B. D., J. V. Baumgartner, R. Wigington, and D. P. Braun. 1997. How much water does a river need? Freshwater Biology 37:231–249.

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

Sabo, M. J., and W. E. Kelso. 1991. Relationships 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 A. 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.

Scheerer, P. D. 2002. Implications of floodplain isolation and connectivity on the conservation of an endangered minnow, Oregon chub, in the Willamette River, Oregon. Transactions of the American Fisheries Society 131:1070–1080.

Schlosser, I. J., and L. W. Kallemeyn. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. Ecology 81: 1371–1382.

Sparks, R. E., P. B. Bayley, S. L. Kohler, and L. L. Osborne. 1990. Disturbance and recovery of large floodplain rivers. Environmental Management 14: 699–709.

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

Suarez, Y. R., M. Petrere, and A. C. Catella. 2001. Factors determining the structure of fish communities in Pantanal lagoons (MS, Brazil). Fisheries Management and Ecology 8:173–186.

Swales, S., A. W. Storey, I. D. Roderick, and B. S. Figa. 1999. Fishes of floodplain habitats of the Fly River system, Papua New Guinea, and changes associated with El Nino droughts and algal blooms. Environmental Biology of Fishes 54:389–404.

Taylor, C. M. 1997. Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position. Oecologia 110:560–566.

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., and J. A. Stanford. 2002. Riverine flood plains: present state and future trends. Environmental Conservation 29:308–330.

Tonn, W. M., and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63: 1149–1166.

Trexler, J. C. 1995. Restoration of the Kissimmee River: a conceptual model of past and present fish communities and its consequences for evaluating restoration success. Restoration Ecology 3:195–210.

Ward, J. V., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research and Management 15:125–139.

Wetzel, R. A., and G. E. Likens. 1991. Limnological analyses, 2nd edition. Springer-Verlag, New York.

Winemiller, K. O. 1996. Factors driving temporal and spatial variation in aquatic floodplain food webs. Pages 298–312 in G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196–2218.

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.

Appendix: Frequencies of Occurrence

TABLE A.1.—Frequency of occurrence for all species collected in the Brazos River and three types of oxbows: one deep and frequently connected oxbow (DF); one deep and rarely connected oxbow (DR); and one shallow oxbow with an intermediate connection frequency (SI).

Species	DF	DR	SI	BR
Alligator gar *Atractosteus spatula*	1	0	0	4
Spotted gar *Lepisosteus oculatus*	8	10	8	7
Longnose gar *L. osseus*	3	3	0	7
Skipjack herring *Alosa chrysochloris*	0	0	6	1
Gizzard shad *Dorosoma cepedianum*	12	12	1	8
Threadfin shad *D. petenense*	5	6	1	4
Red shiner *Cyprinella lutrensis*	9	0	2	13
Blacktail shiner *C. venusta*	1	0	0	5
Common carp *Cyprinus carpio*	9	7	1	1
Mississippi silvery minnow *Hybognathus nuchalis*	0	0	0	1
Shoal chub *Macrhybopsis hyostoma*	0	0	0	8
Golden shiner *Notemigonus crysoleucas*	0	2	7	0
Blackspot shiner *Notropis atrocaudalis*	0	1	0	0
Smalleye shiner *N. buccula*	1	0	0	2
Ghost shiner *N. buchanani*	0	0	0	7
Sharpnose shiner *N. oxrhynchus*	0	0	0	4
Chub shiner *N. potteri*	0	0	0	4
Silverband shiner *N. shumardi*	3	1	1	12
Mimic shiner *N. volucellus*	0	0	0	3
Pugnose minnow *Opsopoeodus emiliae*	9	11	5	3
Bullhead minnow *Pimephales vigilax*	8	2	3	13
River carpsucker *Carpiodes carpio*	3	9	1	5
Smallmouth buffalo *Ictiobus bubalus*	11	11	9	3
Black bullhead *Ameiurus melas*	4	0	0	0
Yellow bullhead *A. natalis*	1	1	3	0
Blue catfish *Ictalurus furcatus*	4	4	1	3
Channel catfish *I. punctatus*	9	9	4	6
Tadpole Madtom *Noturus gyrinus*	1	1	0	1
Flathead catfish *Pylodictis olivaris*	1	0	0	1
Pirate perch *Aphredoderus sayanus*	2	0	0	0
Western mosquitofish *Gambusia affinis*	12	11	13	7
Striped mullet *Mugil cephalus*	1	0	0	1
Inland silverside *Menidia beryllina*	5	10	10	2
White bass *Morone chrysops*	3	0	0	4
Green sunfish *Lepomis cyanellus*	1	1	4	1
Warmouth *L. gulosus*	11	8	11	1
Orangespotted sunfish *L. humilis*	11	12	8	5
Bluegill *L. macrochirus*	9	12	8	2
Dollar sunfish *L. marginatus*	0	2	1	0
Longear sunfish *L. megalotis*	3	7	2	11
Spotted bass *Micropterus punctulatus*	0	0	0	3
Largemouth bass *M. salmoides*	3	7	0	3
White crappie *Pomoxis annularis*	11	12	11	2
Bluntnose darter *Etheostoma chlorosoma*	2	0	2	0
Slough darter *E. gracile*	5	7	5	1
Bigscale logperch *Percina macrolepida*	0	8	0	1
Dusky darter *P. sciera*	0	0	0	4
Freshwater drum *Aplodinotus grunniens*	1	4	0	1