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Fish Assemblage Structure in Relation to Environmental Variation among Brazos River Oxbow Lakes

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Abstract.—Fish assemblages and habitat conditions of oxbow lakes and the main channel of the middle-lower Brazos River, a meandering lowland river in east central Texas, were investigated during summer 1994. All oxbows were eutrophic, with chlorophyll-*a* levels of up to 640 μg/L. Assemblage structure showed large between-lake variation that was explained by both physical and biotic variables, with combinations of water depth, dissolved oxygen, dissolved nutrients, turbidity, and plankton densities accounting for 45–59% of the variation in abundance of the dominant species. Water depth and dissolved nutrient concentrations were the best predictors of species diversity and fish abundance. Periodic desiccation of shallow, vegetated oxbows created harsh conditions that favored small fishes that are efficient colonizers. The two youngest oxbows were relatively deep and contained a high diversity and biomass of fishes. Of the 42 fish species collected, several were largely restricted to oxbow lakes, and others were either entirely restricted to or common only in the river channel. The flood dynamics of Brazos River floodplain habitats are less predictable (both intra- and interannually) than are those of large temperate rivers that receive runoff from snowmelt or predictable spring rainfall. As a result, Brazos River oxbow lakes remain separated from the river channel for many months or years, such that faunal exchange between oxbows to the channel should be pulselike and irregular.

A major challenge for fisheries managers is to gain a functional understanding of population and community response to environmental variation and disturbance at varying spatiotemporal scales. Virtually all aquatic habitats experience periodic disturbances at some scale of space and time (Resh et al. 1988; Sparks et al. 1990; Reice 1994), and disturbances of human origin are increasingly influential in ecosystems worldwide. River ecosystems are particularly dynamic, and variation in hydrology creates a patchwork mosaic of habitats at spatial scales that range from microhabitats to fluvial basins. Lowland rivers typically have broad floodplains that contain a variety of aquatic habitats, such as sloughs and oxbow lakes (the latter are sometimes referred to as lagoons or billabongs in regions outside of North America). The ecology of these floodplain habitats is believed to be closely integrated with their associated channel habitat, which supports the reproduction and growth of many—perhaps even the majority—of channel-dwelling fish populations (Welcomme 1979). The natural flood regimes of most North American rivers have been severely altered, which complicates current attempts to understand floodplain ecology and fish recruitment dynamics (Michener and Haeuber 1998).

Aquatic floodplain habitats have been investigated extensively in the tropics, often in areas where fish species richness and levels of taxonomic uncertainty are high (Lowe-McConnell 1964; Welcomme 1979; Junk et al. 1983; Smith and Bakowa 1994; Tejerina-Garro et al. 1998). Floodplains have been less-often studied in the northern temperate zone, even though these regions have a much longer history of ichthyological and fishery research. Investigations of lentic ecology have centered chiefly on northern lakes that are of glacial origin as well as on the numerous reservoirs constructed during this century. In relation to the ‘‘rough fishes’’ (e.g., gars, shad, and suckers) that dominate many natural floodplain ecosystems in North America, fishery resources of glacial lakes and reservoirs are widely perceived to be more valuable and hence more worthy of management (Scarnecchia 1992).

Systematic alteration of lowland river floodplains resulted in the gradual realization that biological diversity was being impoverished on a broad regional scale. Because floodplain habitats are highly productive, heterogeneous, and dynamic, they support a high degree of species diversity

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(Sparks 1995; Michener and Haeuber 1998). In floodplain rivers, erosion of the outer banks and deposition on the inside banks of channel curves leads to increasing channel meandering over time. A curve can become so large that the channel eventually comes into contact with itself and thereby cuts off the segment and creates an oxbow lake within the floodplain. Young oxbow lakes are steep-banked and are located near the river channel. Over many years of flooding and sediment deposition, oxbows fill in and become shallower, and bank erosion may cause the river channel to move a considerable distance away from the oxbow. As a result of the dynamic physical processes that create and ultimately destroy oxbows, these aquatic habitats show large between-lake variation in terms of geomorphology and the timing and magnitude of natural disturbance events. This large spatiotemporal variation poses both challenges and opportunities for fishes and other organisms. Desiccation results in catastrophic mortality, whereas flooding introduces colonists into highly productive areas that can serve as nursery habitats.

In this paper, we examine fish abundance and assemblage structure in 10 oxbow lakes and the river channel in the central Brazos River floodplain in east central Texas. Our objectives were to document species richness and relative abundance during summer and to seek patterns of association between fish assemblage structure and physicochemical and biotic variables. Such patterns are identified, and resulting inferences support a general model of population and community response to habitat heterogeneity and dynamics in temperate oxbow lakes. Conclusions from this comparative analysis have strong implications for the management of aquatic biodiversity in meandering lowland rivers.

Methods

Study region.—The Brazos River has its origin near the New Mexico–Texas border, and it flows southeast across Texas to the western Gulf of Mexico, near Freeport. In east central Texas, the Brazos River is a meandering lowland river that drains mostly nutrient-rich forested and agricultural land. The broad floodplain of the middle Brazos River contains numerous oxbow lakes (Figure 1). During the winter of 1991–1992, the middle and lower Brazos River experienced a centennial flood, at which time oxbows were filled to capacity and were accessed by the river fauna. During October 1993 and June 1994, we used aerial photography to survey 40 oxbow lakes between 28°59′N, 95°24′W, and 30°37′N, of which 10 were chosen for further study based on our ability to obtain landowner permission and to achieve coverage over a broad segment of the longitudinal gradient of the river. We also sampled a 6.5-km reach of the Brazos River channel at 30°37′N, 96°37′W using methods identical to those used in the oxbows. Located near Moehlman's Slough oxbow (see below), this channel site was selected based on boat access and its close proximity to College Station, Texas.

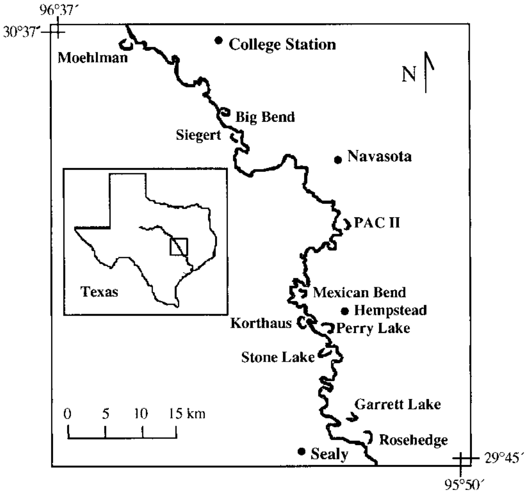

Figure 1.—Map of the Brazos River floodplain study region showing the location of the oxbow lakes that were surveyed during the summer of 1994.

Habitat sampling.—Three oxbow lakes (Moehlman's, Siegert's, and Big Bend lakes) were mapped with a geographic positioning system (GPS) with base station corrections and a geographic information system (ArcInfo), whereas the other seven oxbow lakes were mapped with recent aerial photos and U.S. Geological Survey topographic maps (1:24,000). The age of each oxbow lake was estimated by consulting old maps and aerial photographs and by interviewing landowners. The area of the 6.5-km reach of the river channel was estimated to be 42 ha. Each oxbow lake and the river channel were surveyed once during the period between June 13 and September 1, 1994. Three subsequent years of repeated sampling in three of these oxbows indicated that most species completed reproduction by mid-April (the principal exceptions were mosquitofish *Gambusia affinis,* inland silverside *Menidia beryllina,* and orangespotted sunfish *Lepomis humilis,* which reproduced throughout summer). All but one of these oxbow lakes were located on ranches, most of which had cattle grazing within or around the local watershed. PAC II Lake was surrounded by a vegetable farm that was operated by a state correctional facility. We interviewed landowners about land-use practices and any efforts to manage the oxbows. With the possible exception of Rosehedge (blue tilapia) and Perry Lakes (redear sunfish and largemouth bass), none of the lakes had been stocked with fishes, and none had been stocked at least within the past decade.

A suite of physicochemical attributes was measured at each survey site. Maximum depth and Secchi depth were recorded. Temperature, pH, conductivity, and dissolved oxygen (DO) concentration were measured with a Hydrolab Datasonde. Dissolved nutrient concentrations (PO_4, total dissolved phosphorus, NH_4, NO_2, NO_3, and total dissolved nitrogen) were measured in the laboratory from water samples that were maintained on ice from the time they were collected in the field. Standard colorimetric methods were used to measure nutrients (Wetzel and Likens 1991). Chlorophyll *a* was determined fluorometrically (Wetzel and Likens 1991), and total dissolved phosphorus (TDP) and nitrogen (TDN) were measured spectrophotometrically following a simultaneous persulfate digestion (Hosomi and Sudo 1986).

Zooplankton samples were obtained with a Schindler trap (10 L) with an 83-μm mesh net and were preserved in 70% EtOH. Zooplankton were identified to the lowest possible taxon with a dissecting or light microscope and taxonomic keys in Pennak (1978). The density of each identified taxon was estimated from two 1-mL subsamples, and counting was performed with a Selgewick–Rafter cell. Carapace length of zooplankton in each subsample was measured with an ocular micrometer, and the mean size of four major zooplankton categories (copepods, copepod nauplii, cladocerans, and rotifers) was calculated.

We identified aquatic macrophytes and visually estimated the percentage of areal coverage at each site. The substrate of all oxbows consisted of a dense clay–mud mixture, which was occasionally overlaid with leaf litter. The substrate of the river channel consisted mostly of clay, mud, and fine silt. Areas of fine sand overlying gravel were also encountered in areas where flowing water removed silt, and large rocks were in some midchannel areas.

Fish sampling.—We sampled fishes using seines and gill nets. Electrofishing was also performed on most lakes, but because a few of the lakes were too shallow to permit entrance with a boat, no electrofishing data were analyzed for this study. Oxbow lakes tended to be shallow and turbid, so that seining and gillnetting consistently yielded high fish densities during daylight hours. Seine hauls were performed in the middle reaches of oxbows with a 10 × 2-m bag seine that had 0.64-cm mesh on the wings and 0.32-cm mesh in the bag. Seine hauls were perpendicular to the shoreline from deeper water to shore. In the river channel, hauls were made near gently sloping banks from a maximum depth of 1.75 m and at an angle following the flow of water. In the event that a snag hindered a seine haul, the haul was terminated, any captured fishes were released, and a new haul was initiated. Hauls were repeated along new transects until no additional small species or obvious variation in the relative abundances of species were observed (three to six hauls). Seining consistently captured grass shrimp *Palaemonetes kadiakensis* and small (<20 cm standard length [SL]) fishes, but capture of large fishes was infrequent using this method. The distance covered by each seine haul was estimated, and the number of hauls was recorded for calculation of catch-per-unit-effort (CPUE; number or biomass of each species per 10 m of seine haul) of fishes and grass shrimp captured in seine hauls.

In order to sample larger fishes, two multifilament experimental gill nets (each with three panels measuring 16.5 × 2 m, with 2.54-, 5.1-, and 7.6-cm bar mesh) were fished from approximately 1600 to 1900 h in each oxbow lake and from 1600 h until 0800 h the next day in the Brazos River. Again, because the lakes were shallow and turbid and because fish densities were high, late-afternoon gillnetting consistently resulted in high catch rates for many species, including gars, catfishes, suckers, and centrarchids. Greater gillnetting effort was required in the river channel because of its greater depth, flow, and transparency and because of its apparently lower density of large fishes. The actual minutes of each gill-net set were recorded, and catch data were recorded as number and biomass of each species captured per hour. Three years of subsequent quarterly sampling of three oxbows and the river channel confirmed that our seining and gillnetting protocols yielded fairly consistent estimates of species richness and relative abundances, especially for common species. The longer period for gill-net sets in the river channel did not result in more captures of large species (compared with the deeper oxbows) (Table 1).

TABLE 1.—The total number of individuals captured from oxbow lakes and the Brazos River (seine + gill-net samples). Site codes: BB = Big Bend, MO = Moehlman's Slough, SI = Siegert's Oxbow, GA = Garrett Lake, KH = Korthaus Bottom, MX = Mexican Bend, PA = PAC II, PR = Perry Lake, RH = Rosehedge Lake, ST = Stone Lake, and BR = Brazos River.

Taxon	BB	MO	SI	GA	KH	MX	PA	PR	RH	ST	BR	Total
Lepisosteidae												
Lepisosteus oculatus (spotted gar)	7	6	3		3	10		9		7	1	46
Lepisosteus osseus (longnose gar)		1									14	15
Clupeidae												
Dorosoma cepedianum (gizzard shad)	137	353		3	27	25		18		27	9	599
Dorosoma petenense (threadfin shad)	6	113			92	48		1,020		1,829	3	3,111
Cyprinidae												
Cyprinella lutrensis (red shiner)							552				1,623	2,176
Cyprinella venusta (blacktail shiner)											6	6
Cyprinus carpio (common carp)	6	2	1	2		7				24		42
Extrarius aestivalis (speckled chub)											16	16
Notemigonus crysoleucas (golden shiner)			111		8	69	9	1				198
Notropis buchanani (ghost shiner)											1	1
Notropis shumardi (silverband shiner)			10		3						52	65
Opsopoeodus emiliae (pugnose minnow)		298			139			146		78	6	667
Pimephales vigilax (bullhead minnow)											156	156
Catostomidae												
Carpiodes carpio (river carpsucker)	1	2									3[a]	6
Ictiobus bubalus (smallmouth buffalo)	7	14	13		2	10						46
Ictaluridae												
Ameiurus melas (black bullhead)				1	1	11	40	1		8		62
Ameiurus natalis (yellow bullhead)	1	1	1	1						4	8[a]	16
Ictalurus furcatus (blue catfish)	2						214				1	217
Ictalurus punctatus (channel catfish)	1	10					3			3	6	23
Noturus gyrinus (tadpole madtom)		1						4				5
Pylodictis olivaris (flathead catfish)											1[a]	1
Fundulidae												
Fundulus notatus (blackstripe topminnow)					40					1		41
Poeciliidae												
Gambusia affinis (mosquitofish)	49	492	1,142	3,083	5	85	337	4	4	247	4	5,452
Atherinidae												
Labidesthes sicculus (brook silverside)					13							13
Menidia beryllina (inland silverside)		45	35	124				121				325
Moronidae												
Morone chrysops (white bass)					1							1

TABLE 1.—Continued.

Taxon	BB	MO	SI	GA	KH	MX	PA	PR	RH	ST	BR	Total
Centrarchidae												
Lepomis cyanellus (green sunfish)					1		62				9	72
Lepomis gulosus (warmouth)	4	118	27	3	15	44	28	3	1	34		277
Lepomis humilis (orangespotted sunfish)		4	86	1	56		474			93		714
Lepomis macrochirus (bluegill sunfish)	7	119	9	18	87	457	120	300	5	98	2	1,222
Lepomis megalotis (longear sunfish)		18			23	3	13	25		1	12	95
Lepomis microlophus (redear sunfish)					25	3		24				52
Micropterus punctulatus (spotted bass)											3	3
Micropterus salmoides (largemouth bass)		23			14	2		28				67
Pomoxis annularis (white crappie)	146	1,367	28	1	214	236		18		68	2	2,080
Percidae												
Etheostoma chlorosomum (bluntnose darter)					9							9
Etheostoma gracile (slough darter)		2	1		3	4		3		9		22
Percina caprodes (logperch)		1						2				3
Percina macrolepida (bigscale logperch)		1			1	4						6
Percina sciera (dusky darter)											8	8
Sciaenidae												
Aplodinotus grunniens (freshwater drum)		1								1		2
Cichlidae												
Oreochromis aureus (blue tilapia)									2			2
Total number collected	374	2,992	1,467	3,237	782	1,018	1,852	1,727	12	2,532	1,946	17,939

[a] Electrofishing captures.

Electrofishing (pulsed DC from a handheld boat unit) at six of the sites also confirmed that gill-net data provided reliable indicators of the presence of large fishes in these systems. At a given site, scarcely any species were captured by electrofishing that were not captured either by gillnetting or seining. Of the total number of large fish species captured by the combined methods of gillnetting and electrofishing (in five oxbows and the river channel), an average of 73% were captured by gill nets alone. This percentage was lowest (50%) for the river channel site, where four large species were captured by electrofishing but not by gill nets. Of these four, one was also captured in our seine samples (the three remaining species that were not treated in our analysis were the river carpsucker, the yellow bullhead, and the flathead catfish). Additionally, the smallmouth buffalo was not captured during our summer 1994 survey of the river, but it was captured during later surveys.

Fishes and grass shrimp were sacrificed by immersion in MS-222 and were then preserved in 15% formalin or were transported to the laboratory, where they were stored frozen. All fishes were identified, weighed (to the nearest 0.1 g), and measured [both SL and total length (TL), to the nearest 1 mm].

Data analysis.—Species richness (S) and diversity (Shannon's H′) were calculated for each seine and gill-net sample based on species numerical and biomass CPUEs. Relationships between all possible combinations of environmental variables and fish CPUE and species diversity were examined with Pearson's product-moment correlation of log-transformed ($\log_e[x + 1]$) values. Statistical significance was assessed at $\alpha < 0.05$, and P values

TABLE 2.—Physicochemical parameters measured at 10 oxbow lakes and the Brazos River. Nutrient concentrations are given in μM/L. Abbreviations are Cond. = conductivity, DO = dissolved oxygen, TDP = total dissolved phosphorus, TP = total phosphorus, TDN = total dissolved nitrogen, TN = total nitrogen.

Water body	Area (ha)	Depth (cm)	Secchi (cm)	Temperature (°C)	pH	Cond. (μS/cm)	DO (mg/L)	PO_4	TDP	TP	NH_4	NO_2	NO_3	TDN	TN
Big Bend	20.5	100	13	30.0	7.8	400	6.0	0.28	1.2	5.0	5.00	0.12	0.49	48.4	55
Garrett Lake	19.6	20	5	38.2	10.1	218	11.1	4.16	8.1	38.8	3.40	0.35	0.32	88.7	841
Korthaus Bottom	4.5	150	30	32.1	8.5	326	7.0	0.30	0.8	1.5	2.80	0.10	0.02		
Mexican Bend	5.6	80	7	37.0	8.9	300	11.5	0.41	1.7	10.2	0.05	0.11	5.40	42.0	98
Moelhman's Slough	28.0	85	9	31.0	7.9	450	3.0	0.44	1.0	8.5	2.90	0.08	0.30	34.0	132
PAC II Lake	17.3	100	10	32.0	8.8	208	7.7	0.78	1.6	11.4	1.50	0.15	5.40	62.0	88
Perry Lake	35.3	110	27	32.4	9.0	251	9.8	0.98	2.1	7.1	0.30	0.04	0.60	39.0	53
Rosehedge Lake	5.6	100	50	28.9	6.9	361	0.1	1.42	3.1	5.7	8.10	0.16	0.20	150.0	204
Siegert's Oxbow	14.2	26	26	33.0	6.7	360	2.9	0.64	1.7	6.4	5.20	0.15	1.00	41.0	61
Stone Lake	6.1	75	10	34.0	8.7	280	6.0	3.70	4.5	10.9	4.00	0.16	1.30	47.0	62
Brazos River	42.0	300	12	31.5	7.2	780	8.3	0.51	1.9	4.3	6.80	0.43	10.27	52.6	57

were adjusted for multiple comparisons with the Bonferroni algorithm.

Patterns of association between oxbow lakes and environmental and fish abundance data were explored with canonical correlation analysis (CCA), which identifies relationships between two sets of variables by finding the linear combinations of the variables in the first set that are most highly correlated with the linear combinations of the variables in the second set (Lebart et al. 1984). After derivation of canonical vectors, correlations of the original variables with these vectors ('loadings') were examined. The resulting canonical structure served as the basis for biological interpretations. Bartlett's test for the equality of eigenvalues was used to test the significance of canonical correlations; a pair of canonical vectors was considered significant if the test of equality of the remaining eigenvalues (squared canonical correlation coefficients) was significant at $P < 0.05$.

Two separate CCAs were performed with seine data and two different sets of environmental data, one containing variables associated with physical factors and one containing variables associated with productivity. In order to ordinate oxbows in relation to fish assemblages and the physical attributes, CCA was performed on log-transformed numerical CPUEs (from seine samples for the seven fish species that were obtained at the greatest number of sites), lake area, lake depth, Secchi depth, DO, and pH. In order to ordinate oxbows in relation to fish assemblages and variables related to productivity and food supply, a second CCA was performed with the same fish data set and TDP, TDN, chlorophyll *a*, zooplankton density, and rotifer density. In order to gain further insight regarding fish assemblage response to recent and current habitat conditions, collective length–frequency distributions were plotted for each sample (seine + gill net) and were compared using the Kolmogorov–Smirnov two-sample test (K-S).

Results

Habitat Features

We were able to determine the precise ages of Big Bend (1975) and Korthaus Bottom (1986) lakes, but it was not possible to determine dates of formation for the other oxbows (all have existed since at least 1940). All of the oxbows have small watersheds, and all were flooded during the 1991–1992 winter flood, with the possible exception of PAC II oxbow. PAC II has dried out only once during the past 50 years, and although rarely flooded by the river, it receives subsurface inflow of water (D. Matthews, Texas Department of Criminal Justice, PAC II Unit, personal communication).

Compared with oxbow lakes, habitats in the main river channel were characterized by (in addition to flowing water) greater depth, more heterogeneous substrate, and a scarcity of emergent and submerged aquatic macrophytes. Dissolved oxygen concentrations in oxbow lakes ranged from supersaturation (Mexican Bend) to severe hypoxia

TABLE 3.—Concentration of chlorophyll (Chl) *a* (μg/L) densities (Den, number/L) and mean sizes (μm) of zooplankton and phytophankton, shrimp catch per unit effort (CDUE, number/10 m seine haul), fish seine CPUE numeric abundance (number/10 m seine haul) and biomass (g/10 m seine haul) and fish gill-net CPUE numeric abundance (number$\cdot$m$^{-1}\cdot$h^{-1}) and biomass (g$\cdot$m$^{-1}\cdot$h^{-1}) in 10 oxbow lakes and the Brazos River channel.

water body	Chl *a* (μg/L)	Copepods				Cladocera		Rotifers		Phyto-plankton size	Shrimp CPUE	Fish seine CPUE		Fish gill-net CPUE	
		Adult		Nauplii								Numeric	Biomass	Numeric	Biomass
		Den	Size	Den	Size	Den	Size	Den	Size						
Big Bend	21.5	220	600	145.0	145	50.0	650	2,405	205	23	10.8	52.0	165.0	8.1	4,102
Garrett Lake	640.0	0		0		10.0	430	95	75	54	93.2	539.2	146.6	4.0	10,000
Korthaus Bottom	15.5	0		7.0	140	3.5	250	312	120	12	5.8	113.5	194.4	6.0	2,072
Mexican Bend	73.0	390	850	965.0	180	560.0	605	5,390	195	380	53.8	162.2	251.7	16.9	15,212
Moelhman's Slough	70.0	2	460	35.0	170	0		1,299	145	21	39.5	185.1	205.8	5.2	5,243
PAC II Lake	99.0	200	880	440.0	153	425.0	600	2,170	180	135	2.5	295.7	1,252.2	5.1	1,845
Perry Lake	140.0	8	910	7.0	185	10.0	435	424	110	24	7.7	239.5	508.6	5.3	1,773
Rosehedge Lake	26.7	45	690	145.0	205	0		1,540	135	450	0	3.3	105.5	4.0	3,843
Siegert's Oxbow	44.0	50	920	115.0	155	280.0	295	90	170	100	1,004.5	364.2	74.2	2.2	1,002
Stone Lake	88.0	0		7.5	170	2.0	460	328	105	17	35.6	308.9	739.4	9.6	8,090
Brazos River	22.5	3.3	925	3.3		0		40			1.3	245.1	138.1	0.5	495

(Rosehedge), whereas DO in the river channel was near saturation (Table 2). Dissolved oxygen concentration was not correlated with depth ($r = 0.11$, $P = 0.75$). Afternoon water temperatures were uniformly high during summer (Table 2). The most turbid oxbows were Garrett, Mexican Bend, and Moehlman's, and the least turbid was Rosehedge, a relatively deep oxbow that was blanketed by a thick layer of aquatic macrophytes. Based on high concentrations of total nitrogen and phosphorus (Table 2), all 11 sites can be characterized as eutrophic or hypereutrophic. Phytoplankton density, as indicated by chlorophyll-*a* concentration, was lowest in Korthaus Bottom, the youngest oxbow, and highest in Garrett Lake, the shallowest oxbow (Table 3). Rotifer densities were low in the two shallowest oxbows (Siegert's and Garrett), and density was even lower in the river channel (Table 3). Cladoceran densities were relatively low in all systems except Siegert's, PAC II, and Mexican Bend. Adult copepod densities were low except for those of PAC II, Mexican Bend, and Big Bend. Densities of copepod nauplii showed a pattern similar to that of adults; however, Siegert's and Rosehedge oxbows showed moderately high densities (Table 3). Grass shrimp density was at least 10-fold greater in Siegert's oxbow compared with the other habitats (Table 3). Grass shrimp were uniformly small (<25 mm), as evidenced by the high correlation between shrimp biomass and numeric density in seine samples ($r = 0.998$, $P < 0.0001$).

Fish Abundance and Diversity

Overall, 42 fish species were obtained from the surveys, with collections dominated by mosquitofish, gizzard shad, red shiner, white crappie, and bluegill sunfish (Table 1). Except for the red shiner, which essentially was confined to the channel and to one oxbow (PAC II), these abundant fishes occurred at nearly every site. By number, the red shiner greatly dominated the river channel sample, although gars (only 15 individuals) accounted for the greatest biomass (17.94 kg). Total fish biomass in samples varied from a low of 2.2 kg for Rosehedge Lake, the lake located farthest from the river channel (1,800 m), to highs of 42.8 and 43.7 kg for Stone Lake and Moehlman's Slough, respectively. Using comparable seine effort but a greater gill-net effort, a total of 20.3 kg of fishes was removed from the river channel survey reach, which is close to the mean total biomass for all sites (22.6 kg). Overall, biomass from gill nets was dominated by gizzard shad, smallmouth buffalo, carp, spotted gar, and white crappie. Two lakes were unusual in that none of these five fishes dominated numerically or in terms of biomass; the exotic blue tilapia dominated the biomass of Rosehedge Lake, and the blue catfish dominated the biomass of PAC II Lake. Rosehedge was almost hypoxic throughout, and very few fishes were collected.

In general, fish biomass in oxbow lakes was greater than that in the river channel. Biomass

TABLE 4.—Estimates of species richness (S), diversity (H′), and evenness (E) based on numeric and biomass catch-per-unit-effort from seine and gill-net samples in 10 oxbows and a Brazos River site.

Water body	Seine samples					Gill-net samples				
	Numeric			Biomass		Numeric			Biomass	
	S	H′	E	H′	E	S	H′	E	H′	E
Big Bend	7	1.27	0.65	0.81	0.42	7	1.56	0.80	1.43	0.73
Garrett Lake	9	0.22	0.10	0.72	0.33	1	0	0	0	0
Korthaus Bottom	19	2.16	0.73	1.86	0.63	6	1.45	0.81	1.46	0.81
Mexican Bend	13	1.57	0.61	1.52	0.59	6	1.71	0.95	1.47	0.82
Moelhman’s Slough	15	1.54	0.57	1.46	0.54	9	1.85	0.84	1.61	0.73
PAC II Lake	11	1.73	0.72	1.32	0.55	4	0.51	0.37	0.11	0.08
Perry Lake	14	1.14	0.43	1.75	0.66	6	1.45	0.81	1.15	0.64
Rosehedge Lake	3	0.94	0.86	0.06	0.05	1	0	0	0	0
Siegert’s Oxbow	11	0.90	0.37	1.73	0.72	5	1.19	0.74	1.24	0.77
Stone Lake	15	0.93	0.34	1.71	0.63	7	1.43	0.74	1.15	0.59
Brazos River	15	0.66	0.24	0.96	0.35	5	0.93	0.58	0.52	0.32

CPUE from seine samples was 138.1 g/10 m haul for the river and ranged from 74.2 to 1,252.2 g/10 m in the oxbow lakes (mean for oxbows = 364.3 g/10 m). Biomass CPUE from gill-net samples was 495 g · m^{-1} · h^{-1} from the river and from 1,002 to 15,212 g · m^{-1} · h^{-1} from the oxbow lakes (oxbow mean = 5,318 g · m^{-1} · h^{-1}). In terms of the numerical abundance of fishes, the river channel CPUE from seine samples was average (Table 3), whereas gill-net CPUE was lower than that of any of the oxbows. Seine samples from the channel were dominated by the red shiner, whereas mosquitofish usually were the most numerous species in seine samples from oxbows (Table 1).

Species richness and diversity in seine samples was lowest in Rosehedge Lake and greatest in Korthaus Bottom, the youngest oxbow (Table 4). Most oxbows and the river channel yielded between 10 and 20 species in seine samples. For numeric catch data, species evenness in seine samples was greatest for Rosehedge, but this involved low catches of only three species (Table 1). Korthaus and PAC II also had large values for evenness. Based on seine biomass data, evenness was greatest for Siegert’s oxbow and least for Rosehedge. Among gill-net samples, the greatest richness and diversity were recorded for Moehlman’s Slough (both for numeric and biomass data), but Mexican Bend (numeric and biomass) and Korthaus Bottom (biomass) had the greatest evenness (Table 4). As a result of domination by blue catfish, the gill-net numeric and biomass samples from PAC II had extremely low diversity and evenness.

When the river channel samples were excluded as outliers, numeric density of seine samples declined with depth, and gill-net numeric density tended to increase (Figure 2). Seine biomass CPUE showed no relationship with water depth (either excluding or including the channel sample), but gill-net biomass showed a negative relationship with water depth (Figure 2). Trends for gill-net data indicate that a greater density of fishes of smaller average size were encountered in deeper oxbows.

Some of the highest bivariate correlations described negative relationships between TDN and measures of species diversity (Table 5), which provides an indication that faunistically depauperate lakes were hypereutrophic (Tables 2, 3). Species diversity calculated from biomass data was strongly negatively associated with TDN for both seine and gill-net samples, with diversity falling to nearly zero above 65 μM/L (Figure 3). Species diversity calculated from numeric data was negatively associated with TDN, but the correlation for seine data was weak.

Fish numeric density from seine samples was positively correlated with temperature and chlorophyll *a*, and gill-net numeric density was positively correlated with TDP and total zooplankton density (Table 5). Warmer oxbows with more phytoplankton biomass were associated with greater numbers of small fishes. Oxbows with more TDP and zooplankton were associated with greater biomass of large fishes. Fish abundance and fish diversity were weakly associated (*r* values of 0.11 to −0.54).

Oxbow area and depth were strongly and positively correlated (Table 5). Positive correlations also were obtained for pH and DO, TDP and chlorophyll *a*, and rotifer density and total zooplankton density (Table 5), whereas Secchi depth and DO were negatively correlated. In addition, some of the lakes with low transparency (Garrett, Perry)

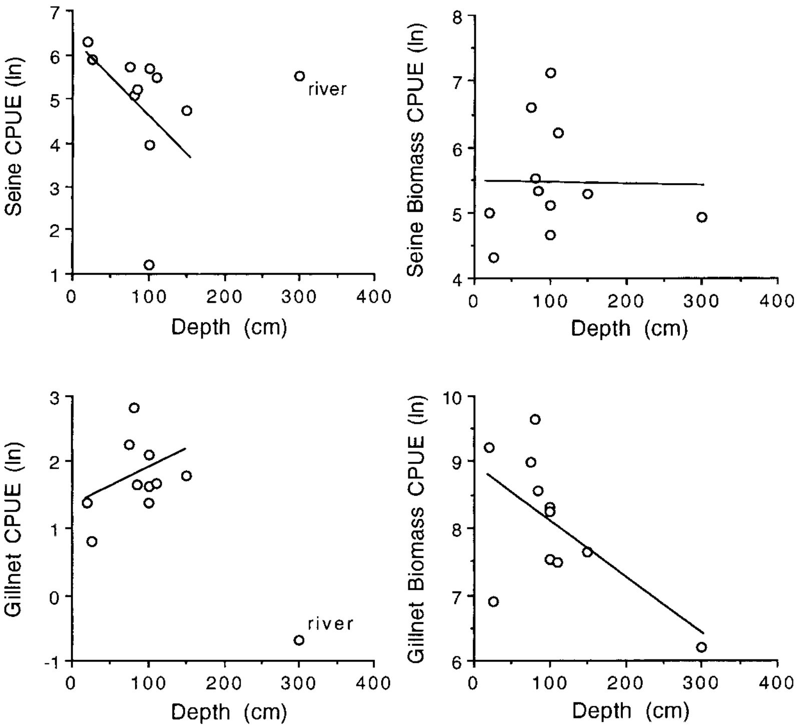

Figure 2.—Linear regressions for bivariate relationships between maximum depth and catch-per-unit-effort (CPUE; data were log-transformed) based on the number of individuals and the total biomass of fishes in seine and gill-net samples from 10 oxbows and a Brazos River site. The outlying river site was deleted from the linear regressions on the left. Regression equations and coefficients of determination were as follows: $\log_e$(seine CPUE) $= -0.016$(depth) $+ 6.3$, $r^2 = 0.18$; $\log_e$(seine biomass) $= 0.0002$(depth) $+ 5.5$, $r^2 = 0$; $\log_e$(gill-net CPUE) $= 0.005$(depth) $+ 1.3$, $r^2 = 0.13$; and $\log_e$(gill-net biomass) $= -0.008$(depth) $+ 8.9$, $r^2 = 0.37$.

had high concentrations of chlorophyll *a* and high DO.

Length–frequency distributions for all fishes did not significantly differ among eight of the lakes (K-S, $P > 0.05$). Most lakes had a mode between 30 and 50 mm TL. Two sites (Garrett, Siegert's) had greater proportions of small fishes relative to the other sites, whereas Rosehedge was skewed toward a greater proportion of large fishes (Figure 4). Garrett and Siegert's were the shallowest oxbows, and they were dominated by mosquitofish. Rosehedge was deeper yet extremely hypoxic, and it was dominated by sunfishes and tilapia.

Ordination of Oxbow Assemblages

Canonical correlation analysis of the seven dominant fishes and five physical factors yielded two canonical axes that modeled 44.7% of the total variation (Table 6). The first axis described a gradient that differentiated shallow oxbows with low DO and domination by mosquitofish from deep, well-oxygenated oxbows with few mosquitofish

TABLE 5.—List of the significant ($P < 0.05$, Bonferroni adjusted) Pearson's product-moment correlations between and among environmental and catch-per-unit-effort (CPUE) data (log transformed) from 10 oxbows and a Brazos River site.

Comparison	*r*
Lake area × lake maximum depth	0.82
Secchi depth × dissolved oxygen	−0.63
pH × Dissolved oxygen	0.79
Total dissolved phosphorus × chlorophyll *a*	0.88
Total zooplankton density × rotifer density	0.90
Temperature × seine numeric CPUE	0.71
Temperature × gill-net biomass CPUE	0.72
Total dissolved phosphorus × gill-net numeric CPUE	0.66
Total dissolved phosphorus × H′ seine numeric CPUE	−0.74
Total dissolved phosphorus × H′ gill-net numeric CPUE	−0.62
Total dissolved nitrogen × H′ seine biomass CPUE	−0.87
Total dissolved nitrogen × H′ gill-net numeric CPUE	−0.81
Total dissolved nitrogen × H′ gill-net biomass CPUE	−0.78
Chlorophyll *a* × seine numeric CPUE	0.74
Total zooplankton density × gill-net numeric CPUE	0.79
Total zooplankton density × gill-net biomass CPUE	0.60

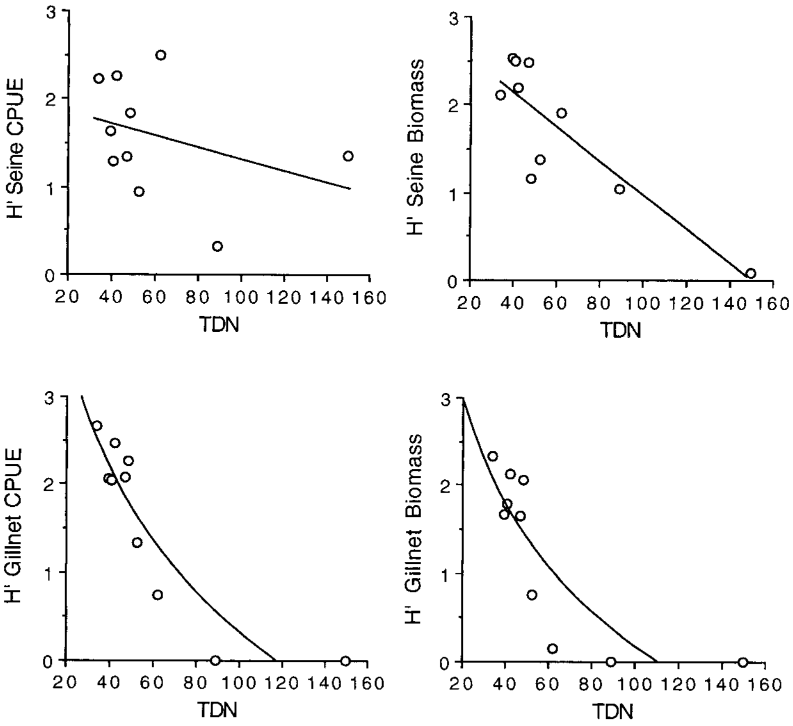

Figure 3.—Linear regressions for bivariate relationships between total dissolved nitrogen and H′ based on number of individuals and total biomass of fishes in seine and gill-net samples from 10 oxbows and a Brazos River site. Regression equations and coefficients of determination were as follows: H′ seine catch-per-unit-effort (CPUE) = $-0.007(\text{TDN}) + 1.97$, $r^2 = 0.13$; H′ seine biomass = $-0.020(\text{TDN}) + 2.92$, $r^2 = 0.74$; H′ gill-net CPUE = $-4.675 \times \log(\text{TDN}) + 9.675$, $r^2 = 0.84$; and H′ gill-net biomass = $-4.067 \times \log(\text{TDN}) + 8.31$, $r^2 = 0.72$.

but many sunfishes and shad. This first axis ordinated sites with the Brazos River at one end and the two shallowest oxbows (Garrett, Siegert's) and Rosehedge (hypoxic) at the other. High scores on the second axis were associated with higher DO, lower transparency, lower pH, and more bluegill and longear sunfish but fewer gizzard shad and white crappie (Figure 5). The second axis positioned the Brazos River and Moehlman's Slough at one end (shad and crappie dominated) and Mexican Bend, Perry Lake, and Korthaus Bottom at the other. The overall pattern of site ordination indicates a gradient from the river channel to relatively deep oxbows, with more oxygen and fewer aquatic macrophytes, to shallow oxbows and those with low DO concentrations.

Canonical correlation analysis of the seven dominant fishes and five environmental factors associated with basal food-web production yielded two canonical axes that modeled 59.1% of the total variation (Table 7). The first axis described a gradient that contrasted oxbows with high TDN and high densities of phytoplankton, zooplankton, and mosquitofish with those having high rotifer densities, high TDP, and more gizzard shad and crappie. This CCA axis positioned Big Bend and Moehlman's at one extreme and the two shallow oxbows (Garrett, Siegert's), Rosehedge, and PAC II at the other. The gradient described by the second axis differentiated oxbows with high TDP and threadfin shad abundance with those having more TDN, chlorophyll *a*, rotifers, gizzard shad, crappie, and bluegill and longear sunfish (Figure 5). The second axis positioned Rosehedge at one end (high TDN) and Stone Lake (high threadfin shad abundance) at the other. In this case, the Brazos River was near the centroid on both CCA axes.

Discussion

Oxbow lakes of the Brazos River vary greatly with respect to size, depth, and virtually every physicochemical parameter that we measured. Perhaps not surprisingly, the fish assemblage structure of these lakes also varied greatly, but more importantly, strong physicochemical associations with assemblage structure were evident. These

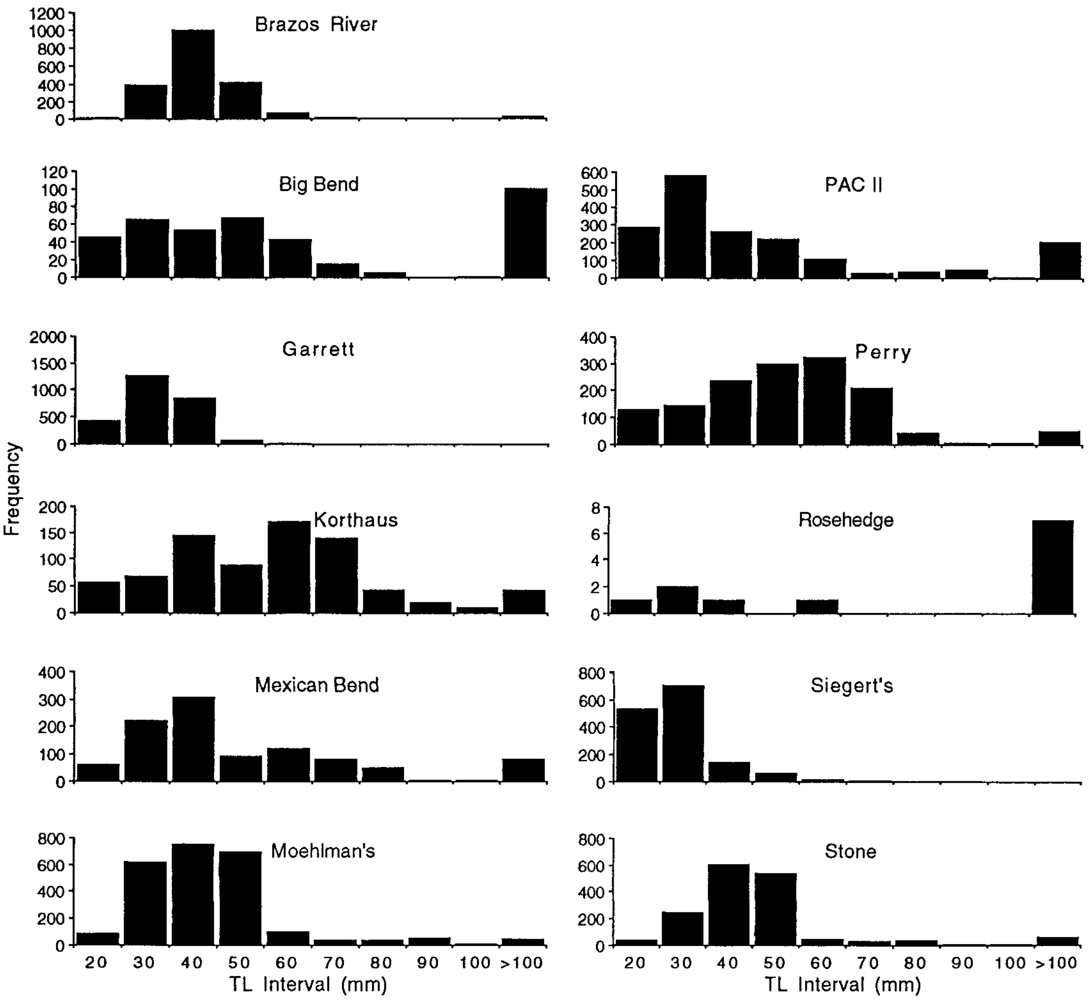

Figure 4.—Length–frequency histograms based on all fishes captured during summer 1994 (by seine and gill net) for 10 oxbows and a Brazos River site.

trends reveal an environmental gradient of aquatic habitat stability–harshness. Because shallower oxbows are likely to dry out with greater frequency, maximum water depth serves as a good indicator of habitat stability. At the high stability end of the gradient, the river channel has large surface area, greater maximum depth, higher DO, and high species richness. Species evenness was relatively low in the river channel as a result of domination by species such as the red shiner and bullhead minnow. Shallow oxbows that undergo periodic hypoxia and desiccation represent the low-stability endpoint of the gradient. The great density of macrophytes covering the surface of old, shallow oxbows probably reduced wind mixing and phytoplankton production, thereby resulting in clearer water and lower DO (Rosehedge, Siegert's). Deeper oxbows have physical and biotic attributes that are intermediate, although fish species diversity and evenness tended to be highest in these systems. The response of fishes to this oxbow harshness–stability continuum is analogous to that described by Rahel (1984) for a bog lake successional gradient in northern Wisconsin.

The lotic channel tended to have higher DO and a more speciose fish fauna than did most of the oxbows (including several species never collected from oxbows). Several fishes were only collected from the river channel during our survey (e.g., blacktail shiner, speckled chub, bullhead minnow, and spotted bass), whereas others were common in oxbows but were apparently absent or rare in

TABLE 6.—Statistics associated with the first two canonical axes from canonical correlation analysis performed on seven common species and five physical environmental features of 10 oxbow lakes and a Brazos River channel site based on catch-per-unit-effort (CPUE) (number of individuals) of seine samples.

Statistics, habitat, or species	Axis 1	Axis 2
Canonical correlation	0.61	0.19
Percent of variance explained	34.00	10.70
Standardized correlation with environmental axis		
Habitat feature		
Area	0.13	0.12
Depth	−0.85	−0.09
Secchi depth	0.18	0.34
pH	0.19	−0.21
Dissolved oxygen	−0.32	0.64
Scores that are linear combinations of environmental axis		
Species		
Dorosoma cepedianum	−1.28	−2.28
Dorosoma petenense	−0.85	−0.66
Gambusia affinis	0.92	−0.01
Lepomis gulosus	−0.69	−1.12
Lepomis macrochirus	−1.37	1.77
Lepomis megalotis	−2.29	0.86
Pomoxis annularis	−1.17	−2.14

the river channel (e.g., golden shiner, black bullhead, and inland silverside). Two large species that were not collected during our summer 1994 study, the alligator gar and the smallmouth buffalo, were collected from the river channel (using the same methods we used) during three subsequent years of quarterly sampling. Beyond these additions, cumulative species richness scarcely increased with additional sampling over a prolonged period. During 3 years of surveys in the Brazos River channel, Moehlman's Slough, Big Bend, and Siegert's oxbow, we rarely encountered the alligator gar in oxbows, even though the spotted and longnose gars were common there. Smallmouth buffalo are common in the channel and some oxbow lakes, where their benthic foraging suspends sediments, which, in turn, increases turbidity and rates of nutrient regeneration (Shormann and Cotner 1997). Only two exotic species were collected, one of which was stocked (blue tilapia in Rosehedge Lake) and one of which is ubiquitous (European carp). These species can influence community composition via competition or habitat alteration. Carp are benthivorous feeders that suspend bottom sediments and may compete with native fishes (Laird and Page 1996). Tilapia aggression may interfere with nesting by native fishes (Noble and Germany 1986), and their foraging on macrophytes may change habitat structure and primary production (Courtney and Robbins 1973).

Because they display less accumulation of alluvial sediments, young oxbows are deeper, larger, and, hence, more stable in terms of desiccation and hypoxia than are older oxbows. Oxbows with the lowest DO had dense macrophyte cover on the water surface (e.g., *Lotus* sp.) that shaded the water column and decreased turbulent mixing and transfer of O_2 from the atmosphere. Maximum depth was the best predictor of fish abundance. The youngest oxbows, Korthaus and Big Bend, lie close to the river channel from which they had recently been cut off (264 and 240 m, respectively), and their natural levees tend to be less developed in the area of channel cut-off, so they should be more frequently flooded than are older oxbows. In some cases, old oxbows are located near the river channel, a consequence of long histories of erosion that have moved the river channel away and subsequently back to them. Pac II, Garrett, and Perry Lake are old oxbows located near the river channel (144–192 m). However, because many decades of sedimentation (during floods) have created natural levees along the river margins, these oxbows probably are flooded less frequently than are young oxbows. The manager of the PAC II farm recounted how the oxbow at PAC II did not receive floodwaters during the century flood of 1991–1992. The PAC II oxbow was very unusual in that it was undoubtedly very old yet relatively deep (possibly receiving subsurface inflow; Matthews, personal communication), and it contained an unusual fish assemblage. With red shiners numerically dominant and green sunfish plus catfishes of the genus *Ictalurus* as common piscivores, the PAC II assemblage was more similar to the Brazos River assemblage than to those of other oxbows.

The best predictor of species diversity was dissolved nutrient concentrations (Table 5). Based on nutrient and chlorophyll-*a* concentrations, all of the systems that we studied were eutrophic; some were best described as hypereutrophic. Chlorophyll-*a* concentration at Garrett Lake was extremely high (640 μg/L), and this lake was slowly drying up during the summer of 1994. Rates of nutrient recycling measured at the water–sediment interface of Big Bend and Moehlman's Slough were among the highest reported for freshwater ecosystems (J. B. Cotner, unpublished data). Total dissolved nitrogen was inversely correlated with species diversity, an indication that the most nutrient-rich oxbows also were relatively harsh aquatic habitats in which many species were unable to persist. Somewhat paradoxically, ammonium con-

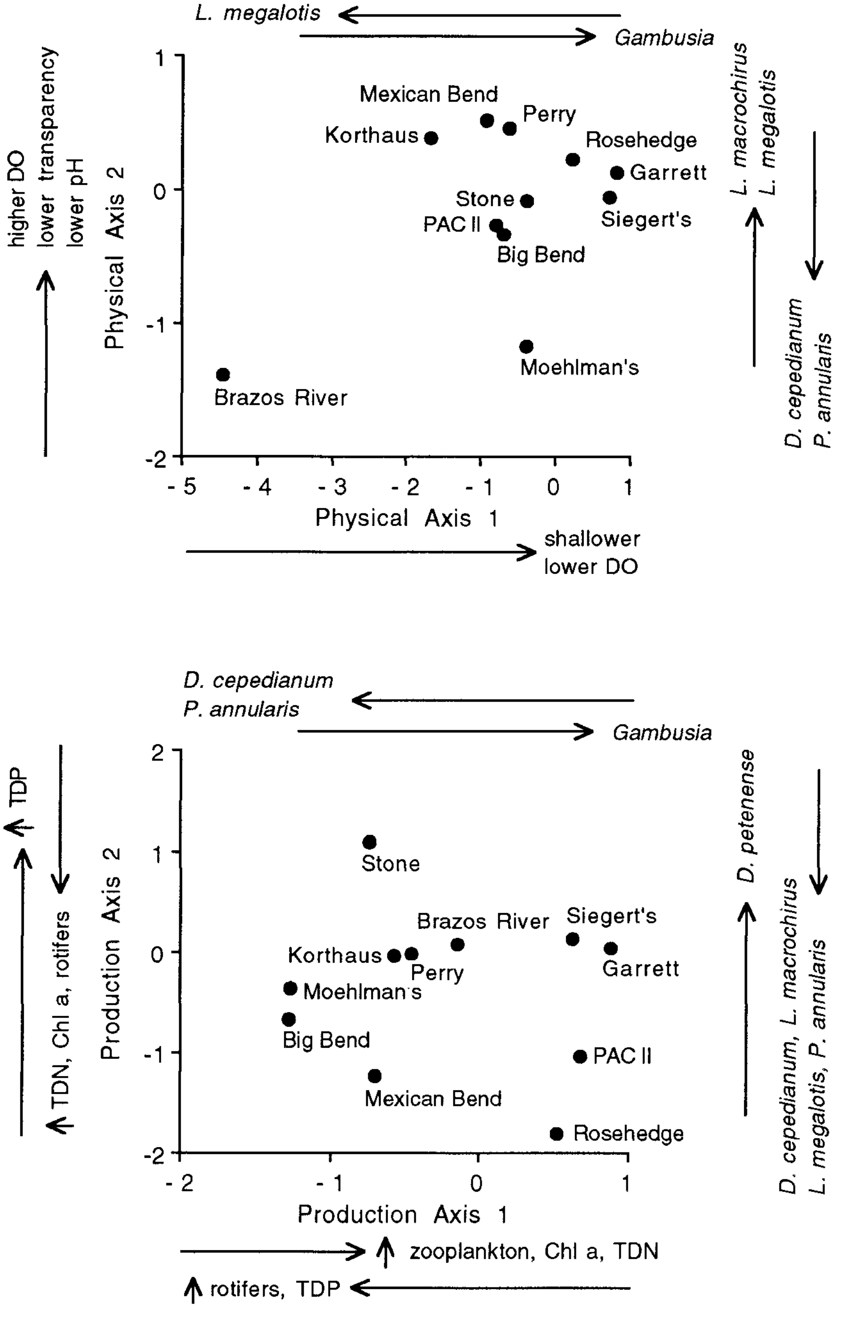

Figure 5.—Plots of site scores on the first two axes from canonical correlation analyses based on the environmental data matrix. Vectors indicate the relationships of dominant environmental variables and fish species on the gradients modeled by the canonical axes. The top plot is derived from an environmental data set that included five physicochemical variables (see Table 6 for associated statistics); the bottom plot is derived from an environmental data set that contained five variables related to productivity (see Table 7 for associated statistics). The same seven dominant fish species were used in each analysis.

TABLE 7.—Statistics associated with the first two canonical axes from canonical correlation analysis performed on seven common species and five environmental features associated with resource production of 10 oxbow lakes and a Brazos River channel site based on catch-per-unit-effort (CPUE) (number of individuals) of seine samples.

Statistic, habitat, or species	Axis 1	Axis 2
Canonical correlation	0.66	0.395
Percent of variance explained	36.90	22.20
Standardized correlation with environmental axis		
Habitat feature		
Total dissolved phosphorus	−0.43	1.29
Total dissolved nitrogen	−0.40	−0.47
Chlorophyll *a*	0.57	−0.86
Zooplankton density	1.18	−0.03
Rotifer density	−1.28	−0.32
Scores that are linear combinations of environmental axis		
Species		
Dorosoma cepedianum	−1.68	−1.39
Dorosoma petenense	−0.97	1.46
Gambusia affinis	0.92	−0.02
Lepomis gulosus	−0.52	−1.30
Lepomis macrochirus	−0.66	−1.87
Lepomis megalotis	−0.48	−0.71
Pomoxis annularis	−1.46	−1.11

centrations were greatest in old oxbows (Rosehedge, Siegert's), the river channel, and one of the youngest oxbows (Big Bend). The highest correlations obtained for ammonium were with pH ($r = -0.71$) and conductivity ($r = 0.53$). Although photosynthesis increases pH and consumes NH_4, there seems to be no simple model to account for between-site variation in NH_4. The watershed-to-lake area ratios of these oxbows are very small (<10), so that nutrient regeneration should be dominated by recycling and other internal processes, such as sediment suspension by benthivorous fishes.

Ordination based on a subset of the common fishes and two alternative subsets of environmental parameters yielded a general gradient of shallow, often hypoxic lakes dominated by mosquitofish versus deeper lakes and the river channel, which supported a more even distribution of species. Analysis of the body length distributions of the fish assemblages reinforced this pattern; shallow oxbows were strongly dominated by small fishes. Grass shrimp also were most abundant in the shallowest oxbows. Unlike tropical regions, where fishes with accessory respiratory adaptations are common in floodplain habitats (Junk et al. 1983; Winemiller 1989), few fishes of the Brazos River possess such adaptations. Only gars are known to have accessory aerial respiration, yet even gars tended to be uncommon or absent in the oxbows with the lowest DO levels. Small fishes, such as mosquitofish, probably survive by occupying microhabitats near the surface—microhabitats that contain slightly elevated DO—or, alternatively, they may be more efficient in using aquatic surface respiration (Lewis 1970; Kramer and McClure 1982). Among the 34 Missouri fish species that Smale and Rabeni (1995) tested for hypoxia tolerance, 8 of the 10 most-tolerant species were inhabitants of Brazos oxbows (the other two species do not occur in the region). These fishes were able to tolerate critical DO concentrations between 0.49 and 0.73 mg/L.

Even though water depth and quality were strong predictors of assemblage structure, food resources influenced patterns of species abundance as well. Chlorophyll *a*, zooplankton density, and rotifer density had the highest loadings on the dominant CCA axis, which also included TDP and TDN. Chlorophyll *a* and zooplankton density were positively correlated with fish abundance in seine and gill-net samples, respectively, which suggests that fish production was influenced by resource availability. In a comparison of the abundance of various trophic groups and nutrients of three oxbow lakes (Big Bend, Moehlman's, and Siegert's) and the Brazos River, Winemiller (1996) described food-web patterns that suggested predator control and trophic cascades. In our analysis of 11 sites, the positive correlation between chlorophyll *a* and the numeric density of small, mostly zooplanktivorous fishes (as indexed by seine numeric CPUE) supports this view. Likewise, the positive correlation between density of large fishes caught in gill nets and zooplankton density suggests that larger predatory fishes, such as crappie and gar, may depress the densities of small invertebrate feeders. Crappie were particularly abundant predators in most of the oxbows. The correlation between grass shrimp numeric and biomass CPUEs and crappie seine numeric and biomass CPUEs were -0.125 and -0.28, respectively ($P > 0.05$). The fact that fish densities were strongly negatively correlated with dissolved nutrient concentrations also reveals a potential influence of predation on fish densities during the study period (i.e., increased inorganic nutrients is not associated with greater fish biomass density). The influence of predation on food-web structure is probably secondary to, and interacts with, variation in the physicochemical environment, particularly at the hypereutrophic end of the productivity continuum observed among these oxbows.

The major trophic guilds in oxbows were phytoplankton, zooplankton, algivore/detritivores (grass shrimp and gizzard shad), zooplanktivore/insectivores (threadfin shad, mosquitofish, and sunfishes), and piscivores (spotted gar, ictalurid catfishes, and white crappie). Zooplankton typically were dominated by small rotifers, with the exceptions being the two shallowest oxbows and the Brazos River. Rotifer density was low in Garrett Lake, whereas Siegert's had a low density of rotifers but a relatively high density of larger Cladocera. The river channel had the lowest rotifer density (40 rotifers/L), and copepods and cladocerans were rare. Because it interferes with movement and foraging, turbulence probably had a negative influence on zooplankton in the river channel.

As discussed by Winemiller (1996), there are particular life history strategies associated with the abundance patterns of organisms inhabiting these oxbow lakes. Shallow oxbows, such as Siegert's, are dominated by small, opportunistic species with attributes that are well-suited for rapid colonization of recently disturbed habitats (Winemiller and Rose 1992). Zooplankton, grass shrimp, mosquitofish, inland silversides, and orangespotted sunfish have opportunistic life history attributes, and these species tended to be abundant in all oxbows but were especially abundant in the shallowest ones. Equilibrium-type (lower reproductive effort, brood care, and protracted spawning seasons) species (sunfishes, crappie, and ictalurid catfishes) tended to dominate the biomass of deeper oxbows, such as Korthaus, Moehlman's, PAC II, and Perry Lake. Fishes with attributes of the periodic strategy (delayed maturation, greater longevity, high fecundity, no parental care, and high interannual variance in recruitment) were present at almost all sites but tended to be most common in the river channel and deeper oxbows. Gars, gizzard shad, carp, and smallmouth buffalo were the principal periodic strategists in these ecosystems, and their biomass dominated several gill-net samples. Evidence of successful reproduction in oxbows was observed for virtually all common opportunistic and equilibrium fishes, but the gizzard shad appeared to be the only periodic strategists that spawned in great numbers within oxbows during the spring of 1994 (K. O. Winemiller, unpublished data).

Our study has established that oxbows of the Brazos River are highly productive habitats that are colonized by a variety of fishes during floods. For several species, oxbows appear to provide conditions that are more favorable for growth, survival, and reproduction than those associated with the river channel. However, our study only represents a snapshot in time, and conditions in oxbows certainly are dynamic and are influenced by variance in precipitation and floodplain hydrology. Flooding of these systems cannot be predicted (Winemiller 1996), and oxbows probably serve as source habitats for fish recruitment to the river channel only during unusual years. Yet, for certain species, this periodic recruitment from oxbows to the channel may be important for maintaining populations. For example, some of the large periodic strategists, such as gar and buffalo, may only have good recruitment during those years in which favorable springtime conditions are followed by flooding, which allows young-of-the-year fishes to move from oxbows to the river. Similarly, some equilibrium strategists, such as crappie, were uncommon in the river channel, and periodic flooding probably augments their channel populations when individuals emigrate from densely populated oxbows.

Floodplain habitats appear to be particularly important for nest-building fishes, such as centrarchids (Kwak 1988; Scott and Nielsen 1989; Raibley et al. 1997).Turner et al. (1994) described the phenology of larval fish production in floodplain habitats of the Tallahatchie River (Mississippi), with gizzard shad, crappie, and darters dominating spring samples and sunfishes, mosquitofish, and minnows dominating during summer. Sheaffer and Nickum (1986) found that shad, drums, and cyprinids (periodic-type fishes) made up 90% of the total catch of larval fishes in backwaters of the upper Mississippi River, and they concluded that backwaters functioned as sources for recruitment to downstream channel sites. Galat et al. (1998) described how connected floodplain habitats of the Missouri River contained more periodic-type fishes (e.g., goldeyes [Hiodontidae], suckers, drums, and minnows) when compared with isolated basins that were dominated by sunfishes. In excavated floodplain ponds along the lower Mississippi River, morphometry may influence access of spawning adults and affect larval survival and growth (Sabo and Kelso 1991). In addition, larval fish density was positively correlated with DO, conductivity, and turbidity (Sabo et al. 1991). Most major lowland rivers of the eastern and central United States are now leveed, and fish movement between floodplain habitats and the river channel is infrequent. As a result, the early life stages of many river fishes now depend heavily on lentic habitats of backwaters and tributary mouths (Brown and Coon 1994).

The Brazos River is essentially unleveed, and flow in the middle-lower reach (>600 km) is partially regulated via flood-control dams located in and above the city of Waco, Texas. The flood dynamics of the Brazos River are less predictable than those of other large temperate rivers that receive runoff from snowmelt and/or predictable spring rainfall. Brazos River oxbow lakes remain isolated from the river channel, except during those floods of relatively short duration (a few days to several weeks) that now occur approximately two times per year in an unpredictable manner. As a result, there is a large potential for interspecific variation in colonization, survival, growth, spawning, and recruitment among oxbows.

Temporal variation in environmental conditions in oxbows creates communities and food webs with variable structures (Power et al. 1995; Winemiller 1996). Species diversity at the landscape level is enhanced by this variation within the floodplain corridor. For example, the value for H', which is based on species biomass CPUE summed across all 11 sites, was 2.47, a value that is considerably higher than 1.86, the largest value reported for any individual site (Table 4). Whereas floods tend to homogenize regional diversity, the gradual desiccation and isolation of geomorphologically variable oxbows results in a divergence of habitat attributes and community structure. In a study of floodplain pools of a Canadian creek, Halyk and Balon (1983) concluded that extinction during periods of isolation had a greater influence on species richness than did colonization during spring floods. During isolation, individual species respond to local conditions in accordance with their life histories and other ecological attributes, such as feeding niche and ability to withstand hypoxia and predation. The result is a landscape mosaic of local habitats that supports varied communities, which, when integrated, increase regional diversity and moderate regional population fluctuations (Junk et al. 1989; Bayley 1995; Sparks 1995; Winemiller 1996; Poff et al. 1997). A very similar situation was described recently for beaver ponds in the southeastern United States, in which the dynamics of pond creation and destruction resulted in high between-site variation in habitats and assemblages and an enhancement of regional fish diversity (Snodgrass and Meffe 1998). If the oxbow lakes of the Brazos River were eliminated or degraded by adverse land usage, lentic-adapted species such as white crappie would become less abundant, which in turn would result in a reduction in the evenness component of species diversity. When rivers are leveed and separated from oxbow lakes, reduction in recruitment is anticipated, particularly during high flood years that produce the strongest year-classes in periodic-type fishes.

In addition to their positive influence on regional aquatic biodiversity and their potential role as nursery habitats, Brazos River oxbows have other important functions. During high floods, oxbows and other floodplain depressions retain large volumes of water, thus decreasing the velocity and height of the flood over adjacent terrestrial landscapes (Sparks 1993). In addition, oxbows trap sediments as the velocity of floodwaters declines during the process of retention. Nutrient mineralization rates are extremely high in oxbows (Shormann and Cotner 1997; J. B. Cotner, University of Minnesota, unpublished data), so these systems have the potential to remove some of the excess nutrients in terrestrial runoff while producing harvestable fish biomass (e.g., crappie, channel catfish). As described for other regions (Junk et al. 1989; Sparks et al. 1990; Trexler 1995; Galat et al. 1998), those practices that alter the natural flow regime (removal of terrestrial vegetation, channelization, and dams) or inhibit periodic flooding of oxbows (levees) affect not only regional biodiversity but also beneficial ecosystem processes.

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