

**THE INFLUENCE OF ENVIRONMENTAL FACTORS ON SPATIAL AND  
TEMPORAL VARIATION OF FISH ASSEMBLAGES IN THE LOWER BRAZOS  
RIVER, TEXAS**

A Thesis

by

RAYMOND Y. LI

Submitted to the Office of Graduate Studies of  
Texas A&M University  
in partial fulfillment of the requirements for the degree of  
MASTER OF SCIENCE

December 2003

Major Subject: Wildlife and Fisheries Sciences

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December 2003

Major Subject: Wildlife and Fisheries Sciences

**ABSTRACT**

The Influence of Environmental Factors on Spatial and Temporal Variation of Fish Assemblages

in the Lower Brazos River, Texas. (December 2003)

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Large floodplain rivers are spatially heterogeneous and temporally dynamic ecosystems. However, few studies have quantified the variation or species-environment relationships of fish assemblages in the main-channel of large rivers. Fishes were collected along a 10-km reach of the lower Brazos River, a large floodplain river in Texas. Collections targeted the 15<sup>th</sup>, 30<sup>th</sup>, and 50<sup>th</sup> percentile discharge rates of summer and winter seasons. My objectives were: (1) to compare fish assemblage structure in shallow river-margins versus deepwater habitats, (2) to evaluate the spatial and temporal variability of fish assemblages in these two habitats, (3) to identify species-environment relationships that likely structure these assemblages, and (4) to quantify the relative variation in assemblage structure as related to environmental versus seasonal sources.

A total of 41 species and 28,469 individual fishes were collected. Assemblages were less variable than levels typically reported for streams and had weak species-environment relationships. Temporal variability of the shallow river-margin fish assemblage was primarily the result of juvenile recruitment, displacement of individuals following spates, or seasonal immigration by *Mugil cephalus*. Among the deepwater assemblages, increased movement associated with reproductive activities increased temporal variation. Spatial variation was detected only among deepwater assemblages and was related to velocity. Eighteen commonly collected species were evaluated for relationships with environmental variables and season.

Shallow river-margin assemblages were dominated by habitat-generalists and were most strongly differentiated by season, discharge and conductivity. Deepwater samples were dominated by *Lepisosteus osseus* and *L. oculatus* and were most strongly differentiated by velocity. For shallow river-margin and deepwater assemblages, environmental variables uniquely explained more of the total variation than season. Results of this study point to biotic factors as probably explaining a large proportion of the unexplained variation.

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## INTRODUCTION

Throughout the world, large floodplain rivers are highly productive landscapes (Bayley 1995) that support diverse fish assemblages (Sparks 1995). In their natural state, these systems are dominated by fluvial processes that create spatially heterogeneous and temporally dynamic habitats. The continual flow of water, via sediment erosion and deposition, ultimately shapes channel morphology (Leopold et al. 1992) and thus the variety of physical habitats available for fish. In addition, temporal fluctuation in discharge influences environmental variability (Grossman et al. 1998) and hydraulic connectivity of secondary and floodplain habitats (Amoros & Bornette 2002).

Most rivers in the U.S. have been anthropogenically modified (Benke 1990) resulting in dramatic declines to native fishes (Moyle & Williams 1990). River engineering to accommodate navigation, alleviate flooding, generate hydropower, and provide water for municipal and agricultural uses has greatly homogenized floodplain river habitats. River channelization and inundation reduces the physical habitat complexity, flow variability, and discharge fluctuation required to sustain diverse fish assemblages.

Community ecologists commonly seek to identify and understand abiotic processes, sources of spatial and temporal variability, and their relationships to biotic community structure. However, few studies have explored the spatial and temporal variability of floodplain river-fish assemblages or compared the relationship of various abiotic factors to assemblage structure (Lobb & Orth 1991, Dettmers et al. 2001). Such information is essential for the successful implementation of management, mitigation, and restoration strategies to protect floodplain rivers and their fish assemblages.

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This thesis follows the style and format of Environmental Biology of Fishes.

Abiotic processes at both the landscape and local levels influence fish assemblages (Angermeier & Winston 1998). Across the landscape, both longitudinal and lateral processes play significant roles in structuring river-fish assemblages. However, as rivers are distinguished from lentic systems by their unidirectional flow (Ryder & Pesendorfer 1989), lotic studies have traditionally emphasized longitudinal patterns. The river continuum concept postulates that longitudinal transitions in physical processes produce a predictable distribution pattern of the river biota (Vannote et al. 1980). Downstream increases in species richness and trophic diversity of fish assemblages are typical of most watersheds and usually relate to increasing habitat heterogeneity and stability (e.g., Sheldon 1968, Horwitz 1978, Paller 1994).

Ecologists also acknowledge the role of lateral processes in structuring river-fish assemblages (Minshall et al. 1985, Ward 1989). Floodplains are large sources of nutrients and organic matter for river biota (Sparks et al. 1990). According to the flood-pulse concept, floodplains along large river systems are the primary habitats for growth and production of most river fishes; whereas functions of the main-river channel are limited to use as transient habitats for movement and migration (Junk et al. 1989). During baseflow river conditions, fishes use fringing floodplain lakes for reproduction (Hohausova' 2000) and feeding (Kwak 1988). Even in the absence of hydrological connection to the main-river channel, isolated floodplain lakes may provide a significant source of episodic recruitment to the river-fish assemblage (Winemiller et al. 2000). During elevated riverflow, fishes exploit inundated floodplains as they migrate between floodplain lakes (Rodriguez & Lewis 1994) and the river channel to find reproductive, nursery, and foraging habitats (Welcomme 1979), and refuge from strong river currents (Ross & Baker 1983).

Studies evaluating the influence of local factors on fish assemblages have been largely limited to headwater streams and wadeable rivers. Streams are comprised of geomorphic riffle

and pool mesohabitats, each with characteristic depths and current velocities and supporting distinct assemblages (Vadas & Orth 1997, Taylor 2000). Within mesohabitats, structural complexity created by substrate heterogeneity (Schlosser 1982), the presence of macrophytes (Lobb & Orth 1991) and large woody debris (Angermeier & Karr 1983) contributes to local sources of spatial variability among fish assemblages.

Stream-fishes are exposed to considerable temporal changes in their environments. Particularly among headwater and mid-order streams, wide and unpredictable fluctuations in discharge can greatly influence physicochemical conditions. Extreme changes in water temperature, dissolved oxygen and salinity are strongly related to fish assemblage structure in some streams (Matthews 1987, Ostrand & Wilde 2001). Flood and drought are common, but unpredictable events that are strongly related to the structure of stream-fish assemblages (Resh et al. 1988). During floods, fishes move to lateral habitats to avoid strong current velocities and displacement downstream (Ross & Baker 1983). Elevated discharge may also displace less adapted exotic fishes and reduce their competitive effects on native species (Gido et al. 1997). Conversely, during droughts, desiccating riffles may induce temporal variability among pool-fish assemblages (Gelwick 1990, Grossman et al. 1998). Theoretically, such stochastic and frequent fluctuations of stream systems should deter fish assemblages from attaining equilibrium, and therefore reduce the role of biotic processes on assemblage structure (Grossman et al. 1982, Schlosser 1987, Grossman et al. 1998).

In contrast to streams, environmental conditions of large rivers are less variable, and their fish assemblages are theorized to be structured by combinations of both biotic and abiotic factors (Schlosser 1987, Paller 1994). In the tropics, the relative influences of biotic and abiotic factors on floodplain river-fishes appear to be strongly correlated with seasonal flood-pulse dynamics. During high water periods, floods expand the range of available aquatic habitats and

fishes become randomly distributed across the floodplain (Saint-Paul et al. 2000). Conversely, during low water seasons aquatic habitats are reduced to isolated floodplain lakes and the river channel, within which predictable outcomes of competition and predation structure fish assemblages (Rodriguez & Lewis 1994). Outside the tropics, large floodplain rivers undergo less predictable flood regimes. Additionally, environmental conditions such as water temperature and dissolved oxygen may dramatically fluctuate across diel, daily and seasonal time periods.

Despite such contrasts between large rivers and small streams, inferences regarding the spatial and temporal patterns of large-river fish assemblages are adopted primarily from studies of headwater streams and wadeable rivers (Stalnaker et al. 1989, Dettmers et al. 2001). Moreover, patterns of habitat-use by fishes in large rivers and small streams can substantially differ (Lobb & Orth 1991). Therefore, in order to increase the knowledge and understanding of fishes in floodplain rivers, my study was focused on sources of spatial and temporal variability of fish assemblages in a 10-km reach of the lower Brazos River in east-central Texas. My objectives were: (1) to compare fish assemblage structure in shallow river-margins versus deepwater habitats, (2) to evaluate the spatial and temporal variability of fish assemblages in these two habitats, (3) to identify species-environment relationships that likely structure these assemblages, and (4) to quantify the relative variation in assemblage structure as related to environmental versus seasonal sources.

Drawing from prevailing models (Schlosser 1987, Matthews et al. 1988), I expected environmental conditions of the lower Brazos River to be less variable and more predictable than conditions of headwater systems, but less predictable than those characterizing tropical lowland rivers. Accordingly, I hypothesized fish assemblages of the lower Brazos River would show moderate levels of temporal variation that would be largely related to physicochemical and

hydrologic conditions. Moreover, because the reach was located 195 km from coastal waters, I expect the abundance of estuarine species to increase during springtime migrations and reproductive periods. I hypothesized spatial variation of current velocities among mesohabitats would be correlated with structure of fish assemblages. Geomorphic mesohabitats form a gradient of depth and flow conditions, along which the greatest differences are between more lotic conditions in riffles and lentic conditions in backwaters and pools. Therefore, I hypothesized that limnophilic taxa would be associated with more lentic backwaters, tributary confluences, and pools whereas rheophilic taxa would be associated with more lotic riffles and runs (Aadland 1993). Moreover, I expected assemblage structure to be related to spatial variability in physicochemical conditions associated with specific mesohabitat types.

## MATERIALS AND METHODOLOGY

### *Study Reach*

The lower Brazos River is a warmwater, meandering, floodplain river. Sinuosity, calculated as the ratio of river length to valley length from USGS 1:20,000 topographic maps (Rosgen 1996), was 2.16. Several flood control dams and water supply reservoirs are located along the upper reaches of the watershed, but the lower Brazos River remains one of few large-river systems in Texas and the USA that has a relatively unregulated flow regime (Figure 1). The study reach was located within the Western Gulf Coastal Plain physiographic province between Sealy and Simonton, Texas (29°40'N and 96°01'W) and drains approximately 72,000 km<sup>2</sup> (Figure 2). The reach began 600 m above the river confluence with Allens Creek and ended 10-km downriver. Lateral point bars dominated the shoreline. Range and crop agriculture were the primary land uses and a gallery forest of willow *Salix sp.*, eastern cottonwood *Populus deltoides*, and sycamore *Platanus occidentalis* extended along both banks for most of the reach. This river segment was selected because it contained representative habitats of the lower Brazos River and it also was the site for concurrent hydrologic studies by the Texas Water Development Board (TWDB) for a proposed municipal water supply reservoir on Allens Creek.

### *Study Sites*

Sites within the study reach were individual riffle, run, pool, embayment, and tributary confluence habitats. Pools, runs, and riffles were delineated using water depth, current velocity, and visible water surface turbulence (Vadas & Orth 1998). Pool habitats had low current velocities (< 10 cm/s) and no visible surface water turbulence. Run habitats had small areas of turbulence (< 25%) and swift current velocities (10 to 25 cm/s). Riffle habitats had surface

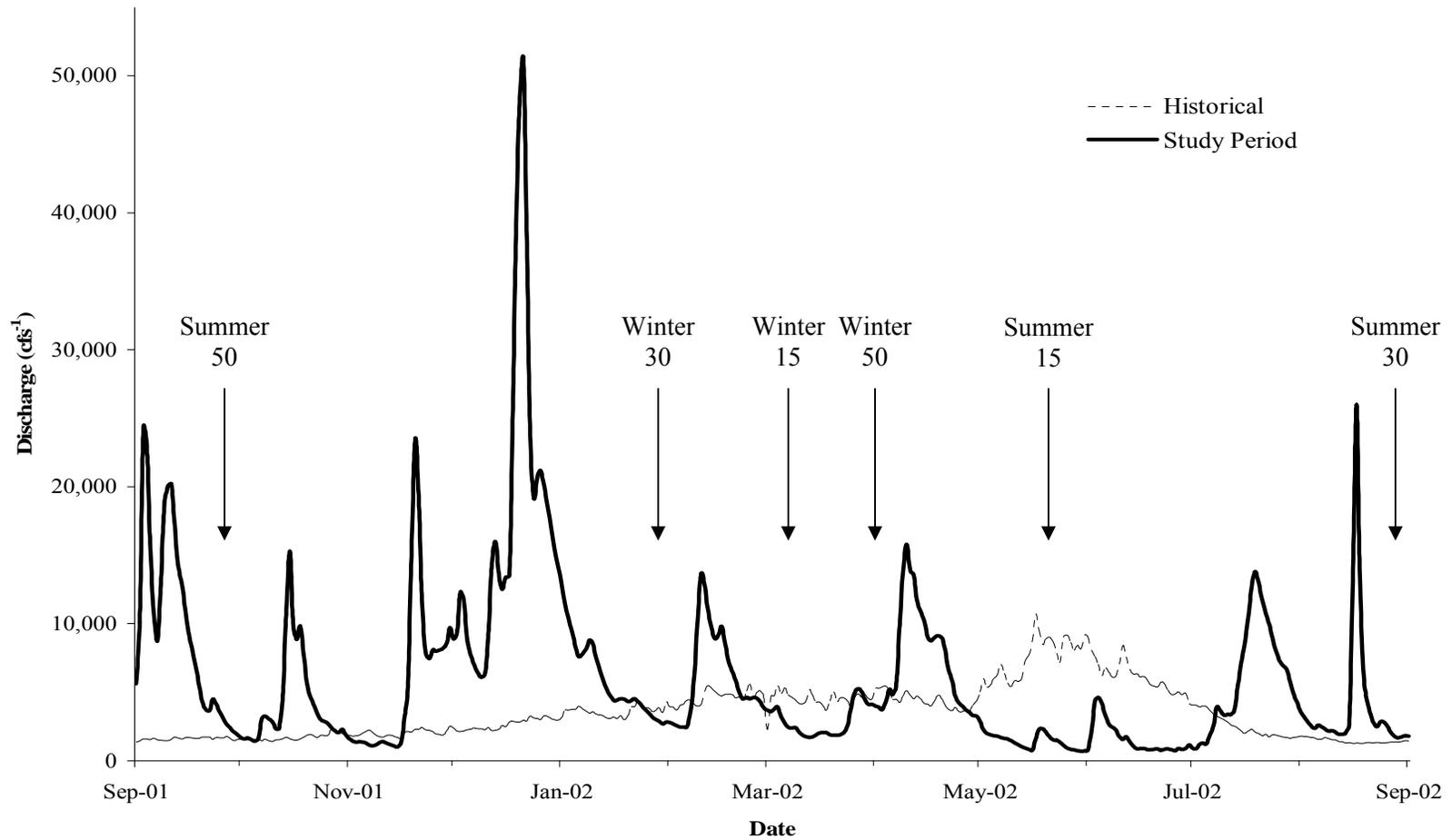


Figure 1. Historical (based upon 82 years of record) and mean daily discharge rates during study period (September 01, 2001 – August 31, 2002) of the lower Brazos River, Texas, as recorded by the U.S. Geological Service’s Brazos River at Simonton gage station (#: 08114000) located approximately 48 km downriver of the study reach. Arrows indicate collection dates and targeted percentile discharge rates.



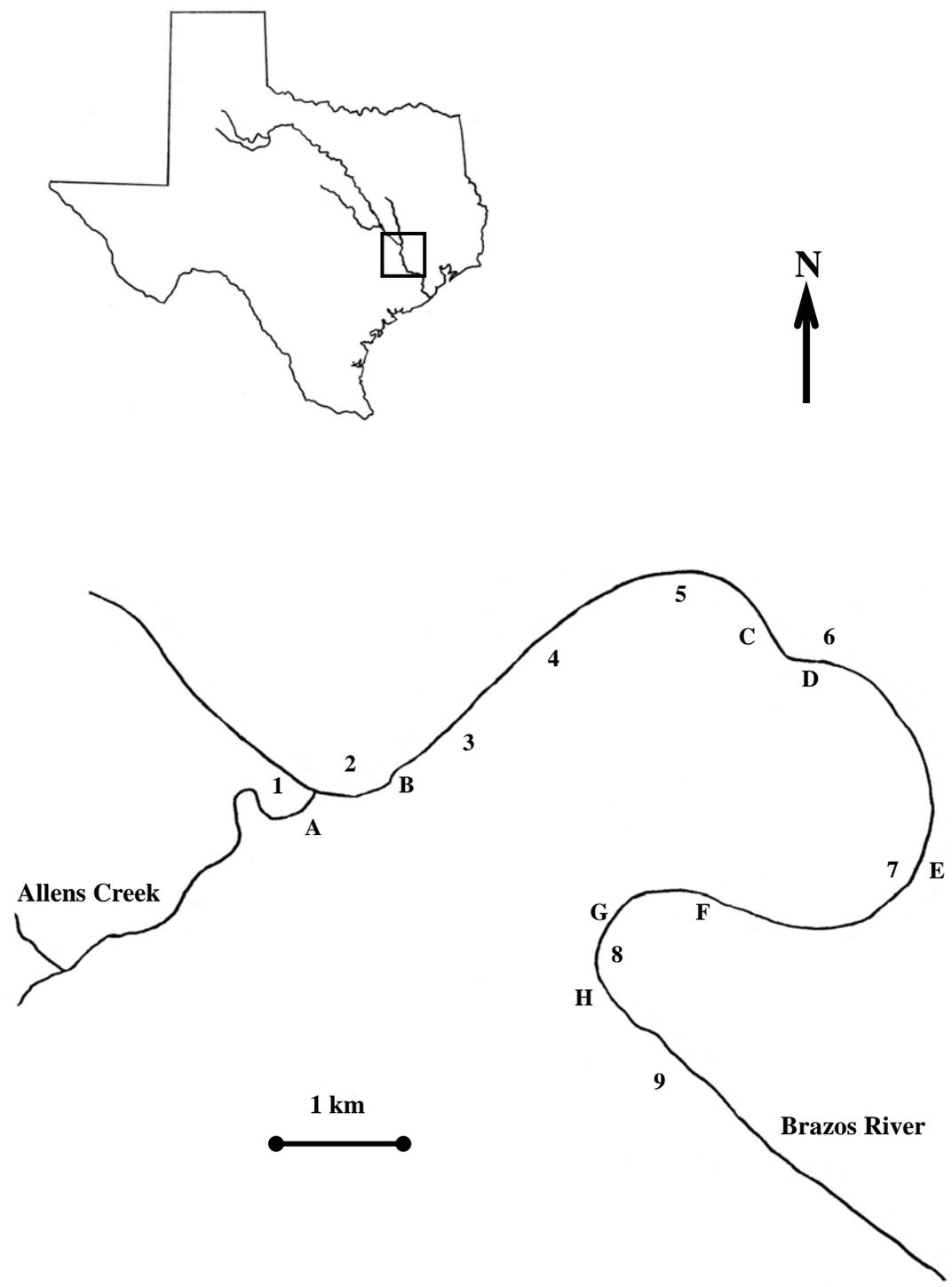


Figure 2. Map of the lower Brazos River study reach, Texas. Shallow river-margin sites are designated by numbers and deepwater sites are designated by letters in ascending order from upstream to downstream.

turbulence across more than 25% of the surface area. Embayments were lateral habitats enclosed along three sides and partially isolated from faster currents of the main-river channel (Armantrout 1998). The confluence of Allens Creek, an intermittent adventitious stream, comprised the only tributary confluence habitat. Nine shallow (< 1 m) river-margin sites and eight deepwater (> 1 m) sites were established to represent the habitats present throughout the reach. Shallow river-margin study sites included four pools, two runs, one riffle, the tributary confluence of Allens Creek, and one embayment. Deepwater study sites included three pools, two embayments, two runs, and the tributary confluence of Allens Creek.

#### *Habitat Characterization*

Hydrologic conditions during each collection trip were characterized by the mean discharge (recorded hourly) and river-stage condition (rising, falling, or stable) as recorded by the U.S. Geological Service (USGS) gage station (#: 08114000) located approximately 48 km downriver of the study reach in Simonton, Texas and published at:

[http://waterdata.usgs.gov/tx/nwis/uv/?site\\_no=08114000&agency\\_cd=USGS](http://waterdata.usgs.gov/tx/nwis/uv/?site_no=08114000&agency_cd=USGS)

Physicochemical parameters were measured within the sampled area immediately following fish collections at each site. Temperature (°C), dissolved oxygen concentration (mg/L), and conductivity (uS/cm) were measured in the center of each area with a YSI-85 (Yellow Springs Instruments) multimeter. Following Vadas & Orth (1998), mean water depth and current velocity for each shallow river-margin site were calculated from measurements at three equidistant points along a diagonal bisecting the area sampled. For deepwater sites, water depth and current velocity were measured once in the center of the netted area. Water depths less than 150 cm were measured to the nearest centimeter using a graduated wading rod; those exceeding 150 cm were measured to the nearest ten centimeters using a Speedtech<sup>®</sup> sonar depth meter.

*Table 1.* Modified Wentworth classification scale of substrate particle size in the lower Brazos River, Texas. The scale was modified to distinguish between major classes of particle size. Diameter ranges represent the diameter across the intermediate axis.

Substrate Classification:	Diameter Range (mm):
Clay	<0.062 mm, consolidated
Silt	<0.062 mm, unconsolidated
Sand	0.062 – 2.0
Gravel	2.0 – 64.0
Cobble	64.0 – 256.0
Boulder	256.0 – 2048.0
Bedrock	> 2048.0

Velocity was measured to the nearest centimeter per second at 0.6 times the water depth using a Marsh-McBirney Flowmate 2000 electromagnetic flow meter. The dominant particle size of substrate along shallow river-margin sites was tactilely classified according to a modified Wentworth scale (Rosgen 1996; Table 1).

### *Fish Collections*

Collections were made from September 2001 through August 2002 and targeted the 15<sup>th</sup>, 30<sup>th</sup>, and 50<sup>th</sup> percentiles of the mean daily discharge rate across summer (April to October) and winter seasons (November to March; Table 2). Mean daily discharge rates were calculated by the TWDB based on the 60 years of record prior to 2001, which was collected by the USGS gage station.

No single methodology can effectively sample an entire river-fish assemblage across all depth and flow conditions (Casselman et al. 1990). Therefore methods were selected as appropriate for each habitat. Shallow river-margin sites were sampled using seines, and deepwater sites using gillnets. Each shallow river-margin site wholly comprised a single mesohabitat type and was sampled during daylight hours using a 5-m long x 1.2-m x 1.2-m bag seine of 4.5-mm mesh. For each site, three contiguous 15-m seine hauls were made parallel to shore. Deepwater sites were sampled with a 38.1-m x 1.8-m experimental monofilament gillnets comprised of five panels, one each of 2.5-, 3.8-, 5.1-, 6.3-, and 7.6-cm bar mesh. Gillnets were typically deployed with one end anchored to a riverbank or large woody debris and set at a 45° angle from the direction of current. Gillnets were allowed to fish overnight for approximately 16 hours. Fishes that were state or federally listed as rare, threatened, or endangered and large individuals of common species were recorded and returned alive to the river. All other fishes

*Table 2.* Targeted and actual discharge rates of the lower Brazos River during collection periods. Discharge rates were calculated from riverflow data collected by the USGS Brazos River at Richmond, Texas gage station (#: 08114000).

Season	Collection Dates	Target Discharge (cfs)	Actual Discharge (mean)
Summer 50 <sup>th</sup>	20 – 23 Sept 2001	2,630	4,043
Summer 30 <sup>th</sup>	27 – 30 Aug 2002	1,410	1,477
Summer 15 <sup>th</sup>	13 – 16 May 2002	924	886
Winter 50 <sup>th</sup>	29 Mar – 01 Apr 2002	3,460	4,185
Winter 30 <sup>th</sup>	02 – 05 Feb 2002	1,710	2,623
Winter 15 <sup>th</sup>	08 – 11 Mar 2002	1,000	2,228

were euthanized in tricane (MS-222) and fixed in 10% formalin in the field. In the lab, fishes were sorted and identified using regional keys (Robison & Buchanan 1987, Hubbs et al. 1991, Ross 2001), and voucher specimens of representative sizes for each species were cataloged and deposited into the Texas Cooperative Wildlife Collections of Texas A&M University.

#### *Fish Assemblage Characterization*

Due to known catch biases associated with different sampling methods, data for samples in shallow river-margins were analyzed separately from those in deepwater habitats. Metrics for total catch, species abundance, and three components of species diversity (richness, heterogeneity, and evenness) were calculated for comparisons between shallow river-margin and deepwater sites. Species richness was calculated as the number of species collected. Heterogeneity was calculated as Simpson's index of diversity, and evenness as Simpson's measures of evenness following Krebs (1999):

Simpson's Index of Diversity (1-D):

$$D = \sum(p_i)^2$$

D: Simpson's index

$p_i$ : Proportion of species abundance  $i$  in total sample

Simpson's Measure of Evenness (E):

$$E = \frac{1/D}{s}$$

D: Simpson's index

s: Number of species in the sample

To characterize the assemblage of the entire reach, totals across sites and collections for abundance and species richness were calculated for each gear. Because sampling effort within gears was equal (area seined, or time for gillnets), abundances were not further standardized.

### *Spatial and Temporal Variation in Assemblage Structure*

Correspondence analyses (CA) were performed on matrices of species abundance by samples using the CANOCO software program (ter Braak & Smilauer 1998). CA uses weighted averaging to maximize the covariance among species' sample scores (here the relative abundance of species across samples), from which one can infer environmental gradients related to species' distributions across samples. CA is particularly appropriate for unimodal response models, such as species-environment relationships (Sheldon 1911). To reduce the influence of species that had highly skewed distributions or were rarely collected, species' abundances were  $\log(x+1)$  transformed and the option to down-weight rare species was chosen. Sample scores were assigned to groups based on site and seasonal percentile discharge and then labeled in ordination plots along with commonly collected species to illustrate inferred spatial and temporal patterns along ecological gradients. Scales for CA axes were in average standard deviations (SD) of species turnover, for which a 50% turnover in species composition occurs within approximately 1 SD and a complete species turnover, within approximately 4 SD (Gauch 1982).

For shallow river-margin data, repeated-measures analyses of variance (ANOVA) were performed on CA axes I and II sample scores as the dependent variables using SPSS (version 11.0 for Windows). Samples scores were  $\log(x+10)$  transformed to approximate a normal distribution with uniform variance. Tests of spatial variation were based on hydraulic (i.e. lotic versus lentic) habitat-types, which comprised the between-subjects effect. Sites located in runs or riffles were classified as lotic habitats; sites in pools, embayments, or tributary confluences were classified as lentic habitats. Tests of temporal variation were based on six periods of discharge (15<sup>th</sup>, 30<sup>th</sup>, and 50<sup>th</sup> percentiles in each of summer and winter) and comprised the within-subjects effect. For significant ( $P < 0.05$ ) repeated-measures ANOVA test results,

Bonferroni multiple pair-wise comparisons were used to identify significant ( $P < 0.05$ ) differences among independent (between-subjects) variables.

For deepwater sites, zero catch occurred for some samples (see results section). Therefore, no components of variance could be calculated and these samples were omitted from CA. Thus data for deepwater sites violated the balanced design requirement for repeated-measures ANOVA. However, zero catches can provide important insight for interpreting patterns of spatial and temporal variability in assemblage structure and species-environment relationships. Therefore, Kendall's coefficient of concordance (Kendall's  $W$ ) was used to analyze spatial and temporal variation among deepwater fish assemblages. Ranks for species' abundances in all samples and then samples without zero catch were compared in tests ( $P < 0.05$ ) of concordance among categories within each of the following groups: collection, season, site, and habitat-type.

#### *Species-environment Relationships*

Canonical correspondence analysis (CCA) was run using the CANOCO software program to identify species-environment relationships. CCA is a direct gradient analysis that combines the weighted averaging technique of CA with multiple regression in order to find a linear combination of environmental variables that maximizes the dispersion of species' abundances (Jongman et al. 1995). Again, species' abundances were analyzed separately for shallow river-margin and deepwater datasets. Rare species typically have a minor influence on results of multivariate statistics, but can be perceived as outliers in ordinations (Gauch 1982). Therefore, species whose abundance made up less than 0.1% of the total catch in a dataset were omitted from that CCA. To reduce the influence of highly skewed distributions, species-abundances were  $\log(x+1)$  transformed.



For shallow river-margin samples, water temperature, dissolved oxygen, depth, current velocity, and discharge comprised the continuous environmental variables used in the CCA. Nominal variables were created for each category of the following environmental variables: river-stage condition, dominant substrate particle size, mesohabitat-type, and season. To quantify variation in species' distributions that were uniquely correlated with environmental variables, a partial CCA (Bocard et al. 1992) was run with summer and winter as covariables. Conversely, to quantify variation due uniquely to seasons, a second partial CCA was run with environmental variables as covariables. To test significance ( $P < 0.05$ ) of variation explained by the canonical axes, a Monte Carlo randomization test was run on each partial-CCA model. Variables having high multicollinearity (variance inflation factors  $> 3$ ) were removed and Monte Carlo randomizations (199 permutations using a split-plot design to account for repeated samples across sites) were run on the first canonical axis in order to test significance of a singular environmental gradient, and on the combination of all canonical axes to test significance of the overall species-environment relationship.

For deepwater samples, a similar suite of environmental variables was used in the CCA. However, because substrate particle size was not characterized and depth of gillnets was constant, substrate and water depth variables were omitted from analysis of deepwater datasets. As described for shallow river-margin samples, partial CCA's were run to quantify the variation in deepwater species' distributions that was due uniquely to environmental variables and season. As earlier noted, elimination of deepwater samples with zero catch violated the balanced design requirement of split-plot designed statistical tests. Therefore, Mantel tests were used to test significance of correlations among samples based on their species' abundances, as compared to correlations based on values for their environmental variables and season. Mantel tests evaluate the correlation patterns between similarity matrices by comparing a Z statistic for permuted

data with that of a test statistic. Using PC-ORD for Windows (McCune & Mefford 1997), Mantel tests were run between matrices based on species abundance and environmental variables, and species abundance and season. Tests were first run using all samples and then with zero catch samples omitted to determine the effect of zero catch samples. Euclidean distance was selected to calculate similarity matrices. Monte Carlo randomization tests (1000 permutations) were used to determine the significance ( $P < 0.05$ ) of matrix correlations. Using CANOCO, a canonical variates analysis (CVA) also referred to as Fisher's linear discriminate analysis was performed to determine the combination of measured environmental variables that best distinguish samples with zero catch from positive catch samples.

## RESULTS

### *Catch Abundance and Species Richness*

A total of 28,469 individuals representing 41 taxonomic species and 13 families was collected (Appendix A). Across shallow river-margin samples, 28,210 individuals representing 38 species and 12 families were collected. Two cyprinids—red shiner (*Cyprinella lutrensis*) and bullhead minnow (*Pimephales vigilax*)—dominated the shallow river-margin assemblage (Table 3). Other species commonly collected (relative abundance > 0.1%) along the river-margin were (in decreasing order of relative abundance) silverband shiner *Notropis shumardi*, mosquitofish *Gambusia affinis*, ghost shiner *Notropis buchmanii*, striped mullet *Mugil cephalus*, threadfin shad *Dorosoma petenense*, speckled chub *Macrhybopsis aestivalis*, gizzard shad *Dorosoma cepedianum*, inland silverside *Menidia beryllina*, and silver chub *Macrhybopsis storeriana*. Simpson's index of species diversity for the shallow river-margin assemblage was 0.530 and Simpson's measure of evenness was 0.050.

Across all shallow river-margin collections grouped by season (Table 4), 34 species were captured in summer and 22 in winter. Across summer collections, species richness increased (16, 19, and 27) with increasing discharge rate, whereas across winter collections species richness followed a triangular distribution (13, 16, and 13) having its high point during the 30<sup>th</sup> percentile discharge rate. By contrast to species richness, catch abundance across all shallow river-margin sites grouped by collection period, peaked in March (during the winter 15<sup>th</sup> and 50<sup>th</sup> percentile collections), then generally declined through the remainder of the year, and dropping lowest in August (summer 30<sup>th</sup> percentile collection). With regard to spatial distribution of fishes along shallow river-margins, species richness ranged from 9 to 30 and catch abundance from 1,132 to 6,309 individuals. For both species richness and catch

Table 3. Species commonly collected (> 0.1% of total catch) in shallow river-margin samples during summer and winter seasons for the 50<sup>th</sup>, 30<sup>th</sup>, and 15<sup>th</sup> percentile discharge rates in the lower Brazos River, Texas. Species codes are those used to designate species in ordinations.

Scientific Name	Common Name	Species Code	Summer			Winter			Total abundance	% Relative Abundance
			50	30	15	50	30	15		
<i>Menidia beryllina</i>	inland silverside	Men ber	19	3	6	1	0	1	27	0.106
<i>Dorosoma cepedianum</i>	gizzard shad	Dor cep	36	1	0	3	0	1	41	0.145
<i>Dorosoma petenense</i>	threadfin shad	Dor pet	46	68	2	3	8	2	129	0.457
<i>Cyprinella lutrensis</i>	red shiner	Cyp lut	1,744	886	2,777	4,720	1,578	6,909	18,614	65.984
<i>Macrhybopsis aestivalis</i>	speckled chub	Mac aes	11	8	0	33	11	10	73	0.259
<i>Macrhybopsis storeriana</i>	silver chub	Mac sto	27	1	2	0	1	0	31	0.110
<i>Notropis buchanani</i>	ghost shiner	Not buc	71	0	39	293	49	316	768	2.722
<i>Notropis shumardi</i>	silverband shiner	Not shu	221	10	78	776	30	626	1,741	6.172
<i>Pimephales vigilax</i>	bullhead minnow	Pim vig	723	237	103	1,879	166	1,518	4,626	16.398
<i>Mugil cephalus</i>	striped mullet	Mug cep	0	0	6	612	1	0	619	2.194
<i>Gambusia affinis</i>	western mosquitofish	Gam aff	359	173	732	71	21	39	1,395	4.945

Table 4. Species richness and total abundance of shallow river-margin sites in the lower Brazos River, Texas.

Site	Summer					
	50		30		15	
	Abundance	Species Richness	Abundance	Species Richness	Abundance	Species Richness
1	447	16	440	15	1,027	10
2	502	11	268	7	350	7
3	92	5	224	5	338	4
4	41	5	71	6	457	4
5	162	9	28	1	400	5
6	762	17	88	6	193	8
7	659	9	71	4	208	6
8	400	7	113	3	259	6
9	261	6	106	5	526	2
Total	3,326	27	1,409	16	3,758	19

Site	Winter					
	50		30		15	
	Abundance	Species Richness	Abundance	Species Richness	Abundance	Species Richness
1	904	11	116	7	3,375	14
2	1,537	7	317	5	488	4
3	217	5	47	4	214	5
4	1,294	8	141	8	3,033	6
5	1,585	6	300	4	90	3
6	477	6	285	4	1,082	4
7	484	7	30	3	462	5
8	1,019	6	239	5	109	2
9	886	4	401	5	585	5
Total	8,403	16	1,876	13	9,438	16

Site	Summer		Winter		Total	
	Abundance	Species Richness	Abundance	Species Richness	Abundance	Species Richness
1	1,914	26	4,395	17	6,309	30
2	1,120	16	2,342	8	3,462	17
3	654	8	478	6	1,132	10
4	569	9	4,468	11	5,037	14
5	590	11	1,975	6	2,565	13
6	1,043	21	1,844	6	2,887	23
7	938	12	976	8	1,914	15
8	772	10	1,367	7	2,139	12
9	893	8	1,872	6	2,765	9
Total	8,493	34	19,717	22	28,210	41

abundance, values were lowest in collections for site 3 (riffle) and highest in site 1 (tributary confluence of Allens Creek).

After low catch abundances were encountered in deepwater samples during the first collection period (summer 50<sup>th</sup> percentile discharge rate), deepwater sites were amended to target more-lentic habitats in order to increase catch abundance. Six sites in lentic habitat types (three embayments, two pools and one tributary confluence) and two in more-lotic habitats were chosen for sampling during the remaining five collections. With sampling data from the first collection period omitted, 259 individuals representing 11 species and six families were collected. Of those species, longnose gar *Lepisosteus osseus* dominated the assemblage (Table 5). Other commonly collected species were (in decreasing order of relative abundance) spotted gar *Lepisosteus oculatus*, gizzard shad, river carpsucker *Carpioides carpio*, blue catfish *Ictalurus furcatus*, smallmouth buffalo *Ictiobus bubalus*, channel catfish *Ictalurus punctatus*, freshwater drum *Aplodinotus grunniens*, striped mullet, and skipjack herring *Alosa chrysochloris*. One species, common carp *Cyprinus carpio*, contributed < 0.1% to overall abundance. Simpson's index of species diversity was 0.619 and Simpson's measure of evenness was 0.147.

Among deepwaters, spatial distribution of gillnet catches differed between lentic and more lotic habitats. Across the 30 samples in lentic habitats, 255 individuals representing 13 species and six families (Table 6) were collected. By contrast, seven of 10 samples in lotic habitats caught no fish while the remaining three samples caught a total of only four individuals—three longnose gar and one spotted gar. Species richness across lentic sites ranged from five to 10 and catch abundance ranged from 12 to 89 individuals. Deepwater assemblages also differed within and between seasons. The two summer collections captured 136 individuals comprising 11 species, whereas 123 individuals comprising 9 species were captured across the

Table 5. Species richness and total abundance of deepwater sites in the lower Brazos River, Texas. \*Summer 50<sup>th</sup> percentile collections were not listed due to revised sampling locations.

Site	Summer					
	50*		30		15	
	Abundance	Species Richness	Abundance	Species Richness	Abundance	Species Richness
A	--	--	0	0	1	1
B	--	--	0	0	0	0
C	--	--	4	4	52	7
D	--	--	1	1	3	2
E	--	--	8	4	52	6
F	--	--	0	0	2	1
G	--	--	9	7	3	3
H	--	--	0	0	1	1
Total	--	--	22	9	114	9

Site	Winter					
	50		30		15	
	Abundance	Species Richness	Abundance	Species Richness	Abundance	Species Richness
A	9	4	1	1	15	5
B	0	0	1	1	0	0
C	52	1	6	4	4	2
D	3	2	5	3	10	2
E	52	2	9	3	12	4
F	2	0	0	0	1	1
G	3	2	6	4	5	3
H	1	4	0	0	1	1
Total	47	7	28	7	48	8

Site	Summer*		Winter		Total	
	Abundance	Species Richness	Abundance	Species Richness	Abundance	Species Richness
A	1	1	25	6	26	6
B	0	0	1	1	1	1
C	56	8	18	5	74	8
D	4	2	25	6	29	7
E	60	7	29	5	89	7
F	2	1	1	1	3	1
G	12	7	13	6	25	10
H	1	1	11	4	12	5
Total	136	11	123	9	259	11

Table 6. Species commonly collected (> 0.1% of total catch) in deepwater samples during summer and winter seasons for the 50<sup>th</sup>, 30<sup>th</sup>, and 15<sup>th</sup> percentile discharge rates in the lower Brazos River, Texas. Codes are those used to designate species in ordinations. Summer 50<sup>th</sup> percentile collections were not listed due to revised sampling locations.

Scientific Name	Common Name	Species Code	Summer			Winter			Total Abundance	% Relative Abundance
			50	30	15	50	30	15		
<i>Carpoides carpio</i>	river carpsucker	Car car	--	5	5	1	2	3	16	6.178
<i>Ictiobus bubalus</i>	smallmouth buffalo	Ict bub	--	2	3	1	3	1	10	3.861
<i>Alosa chrysochloris</i>	skipjack herring	Alo chr	--	2	0	0	0	0	2	0.772
<i>Dorosoma cepedianum</i>	gizzard shad	Dor cep	--	0	2	6	7	3	18	6.950
<i>Ictalurus furcatus</i>	blue catfish	Ict fur	--	2	3	0	6	4	15	5.792
<i>Ictalurus punctatus</i>	channel catfish	Ict pun	--	1	2	0	1	1	5	1.931
<i>Lepisosteus oculatus</i>	spotted gar	Lep ocu	--	5	2	14	1	8	30	11.583
<i>Lepisosteus osseus</i>	longnose gar	Lep oss	--	2	94	23	8	27	154	59.460
<i>Mugil cephalus</i>	striped mullet	Mug cep	--	0	1	1	0	1	3	1.158
<i>Aplodinotus grunniens</i>	freshwater drum	Apl gru	--	2	2	1	0	0	5	1.931



*Table 7.* Summary of correspondence analysis (CA) of shallow river-margin fish assemblages in the lower Brazos River, Texas.

	Axis I	Axis II
Total Inertia: 1.002		
Eigenvalue	0.216	0.121
Percent of species variation explained	21.6	12.1
Cumulative percent explained	21.6	33.7

three winter collections. Summer 30<sup>th</sup> percentile collections had the highest catch abundance (114 individuals), and summer 15<sup>th</sup> percentile collections had the lowest catch abundance (22 individuals). Within winter collections, 47, 28, and 48 individuals were captured during the 50<sup>th</sup>, 30<sup>th</sup> and 15<sup>th</sup> percentiles.

#### *Spatial and Temporal Variation in Assemblage Structure*

Across shallow river-margin samples, total inertia—the eigenvalue for variation in species distribution among all samples—was 1.002 (Table 7). Results from the CA are plotted for axes I and II (Figure 3). Axes I and II had eigenvalues of 0.216 and 0.121, and together explained 33.7% of the total variation in species distribution. Sample scores on axis I spanned 1.84 SD units, indicating slightly greater than 50% turnover in assemblage composition. Axis I revealed a seasonal gradient, as sample scores differed significantly between seasons ( $F = 15.940$ ,  $df = 1$ ,  $P = 0.005$ ). Centroids for winter samples (but for few species) are located towards the left on axis I, whereas those for summer samples (and most species) had higher axis I scores and are located generally to the right of the plot (Figure 3). Axis II was related to a gradient for discharge rate ( $F = 5.061$ ,  $df = 5$ ,  $P = 0.001$ ). Samples made during the 15<sup>th</sup> and 30<sup>th</sup> percentile discharges had higher axis II scores (toward the top in Figure 3) and in the winter (upper left in Figure 3) were associated with bullhead minnow, red shiner, speckled chub, silver chub, and channel catfish, whereas in summer (upper right in Figure 3) were associated with redear sunfish *Lepomis microlophus*, ribbon shiner *Lythrurus fumeus*, spotted gar, river carpsucker, warmouth *Lepomis gulosus*, pirate perch *Aphredoderus sayanus*, and white crappie *Pomoxis annularis*. Samples within the 50<sup>th</sup> percentile discharge had low axis II scores (toward the bottom in Figure 3), and were more strongly associated with striped mullet.

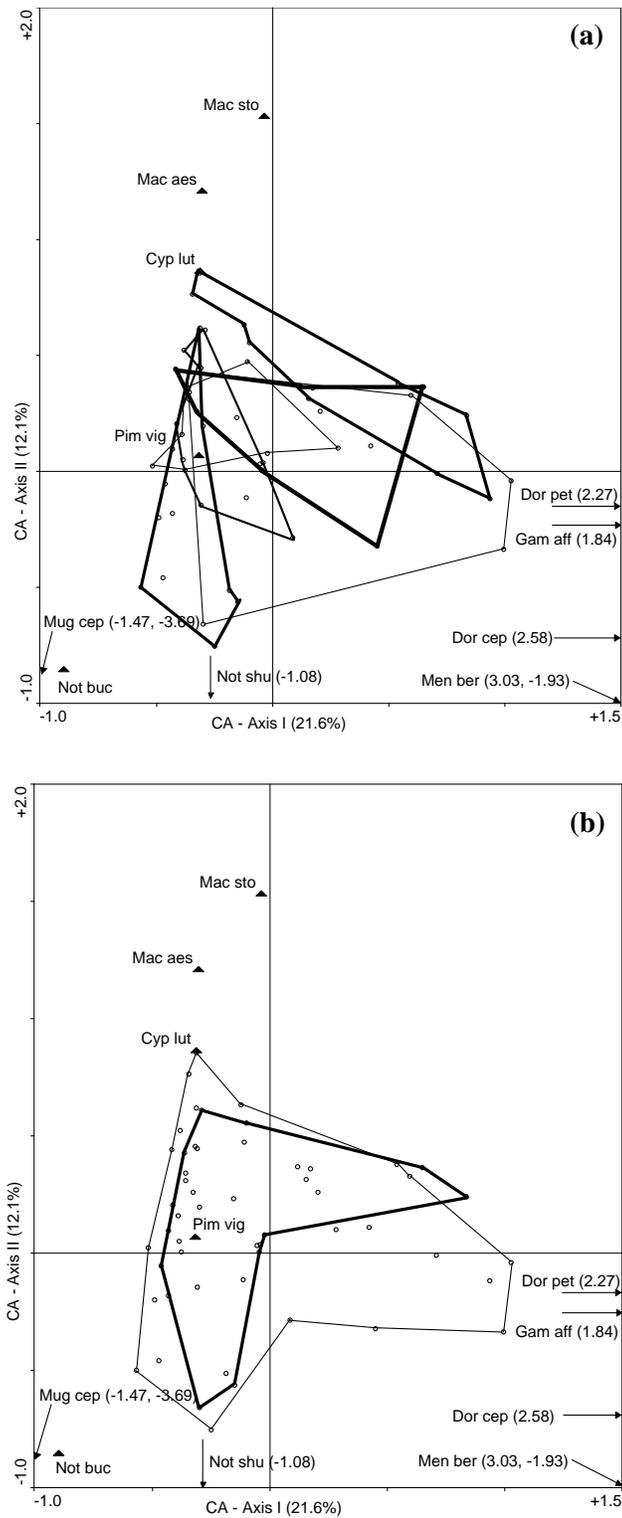


Figure 3. Correspondence analysis (CA) plots of shallow river-margin fish assemblages in the lower Brazos River, Texas. Sample scores are grouped by discharge rate (a) and habitat-type (b). Triangles represent scores of common species and circles represent sample scores. Species codes are listed in Table 3.

*Table 8.* Repeated-measures ANOVA test by discharge rate and habitat-type based on correspondence analysis axes I and II shallow river-margin sample scores of the lower Brazos River, Texas. For axes with significant differences in sample scores, Bonferroni pair-wise comparisons test were used to identify where the differences occurred. Underscores represent samples that were not significantly different.

Discharge Rate								
	F-Ratio	<i>P</i> – value	Summer 50	Summer 30	Summer 15	Winter 50	Winter 30	Winter 15
Axis I	8.328	< 0.001						
Axis II	5.061	0.001						
Site								
	F-Ratio	<i>P</i> – value	Lentic			Lotic		
Axis I	0.439	0.529						
Axis II	0.021	0.889						

ANOVA tests of CA scores for shallow river-margin samples showed differences among discharge rates and seasons, but not habitat-types (Table 8). A temporal effect was identified along both axis I ( $F = 8.328$ ,  $df = 5$ ,  $P < 0.001$ ) and axis II ( $F = 5.061$ ,  $df = 5$ ,  $P = 0.001$ ) indicating that fish assemblages varied across seasons (from winter to summer, primarily from left to right on axis I) and discharge rates (from 50<sup>th</sup> to 15<sup>th</sup> to 30<sup>th</sup>, primarily from bottom to top on axis II). Bonferroni multiple comparisons revealed significant pair-wise differences along axis I between summer 50<sup>th</sup> percentile samples and winter samples for both 15<sup>th</sup>, and 50<sup>th</sup> percentiles, and differences along axis II between samples during summer 30<sup>th</sup> and winter 15<sup>th</sup> percentiles. Samples during the summer 50<sup>th</sup> percentile were distinguished by strong associations on axis I with species in the lower right of the plot (sharpnose shiner *Notropis oxyrhynchus*, brook silverside *Labidesthes sicculus*, flathead catfish *Pylodictus olivaris*, blue catfish *Ictalurus furcatus*, small unidentified *Lepomis* juveniles, white crappie, river carpsucker, gizzard shad, threadfin shad, speckled chub and silver chub). Samples within summer 30<sup>th</sup> percentile were strongly associated with threadfin shad and speckled chub. By contrast, both winter 15<sup>th</sup> and 50<sup>th</sup> percentile samples were strongly associated with red shiner, bullhead minnow, silverband shiner, and ghost shiner. Winter 50<sup>th</sup> percentile samples were further distinguished from other samples by the presence of striped mullet. Significant spatial variation between habitat-types was not detected along either axis I ( $F = 0.439$ ,  $df = 1$ ,  $P = 0.529$ ) or II ( $F = 0.021$ ,  $df = 1$ ,  $P = 0.889$ ) as measured by differences between assemblages in lentic versus lotic habitat-types.

Because samples with zero catch were omitted, CA of the deepwater assemblage reflected only fishes captured in the remaining 30 samples. Total inertia of these 30 samples was 1.907 (Table 9). The first two CA axes had eigenvalues of 0.424 and 0.359 and together explained 41.1% of the species distribution for deepwater assemblages. Sample scores

*Table 9.* Summary of correspondence analysis (CA) of deepwater fish assemblages in the lower Brazos River, Texas.

	Axis I	Axis II
Total Inertia: 1.907		
Eigenvalue	0.424	0.359
Percent of species variation explained	22.3	18.8
Cumulative percent explained	22.3	41.1

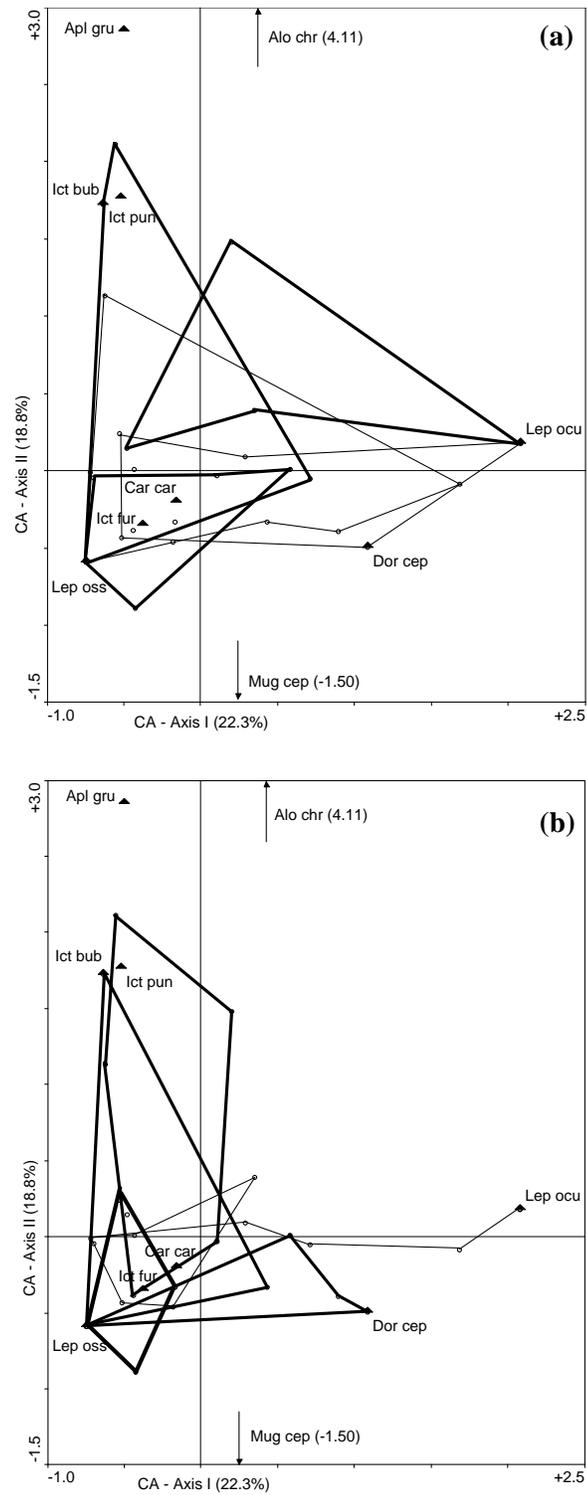


Figure 4. Correspondence analysis (CA) plots of deepwater fish assemblages in the lower Brazos River, Texas. Sample scores are grouped by discharge rate (a) and site (b). Triangles represent scores of common species and circles represent sample scores. Species codes are listed in Table 6.

extended along 3.00 SD (Figure 4), indicating relatively greater species variation across samples than did scores for shallow river-margin assemblages. As observed for shallow river-margin assemblages, season and discharge rate were stronger gradients on the first two axes than were spatial differences among sites. The lower left of the plot represents a deepwater core assemblage of longnose gar, blue catfish, river carpsucker, and striped mullet during the winter 15<sup>th</sup> percentile collections. This assemblage continued to be associated mainly with runs, even as the assemblage composition expanded during winter 30<sup>th</sup> and 50<sup>th</sup> percentile collections, and again during summer 30<sup>th</sup> and 15<sup>th</sup> percentile collections. Embayments samples are distributed along axis I from winter 50<sup>th</sup> to summer 30<sup>th</sup> and 15<sup>th</sup> percentile collections and were associated with spotted gar and gizzard shad. Centroids for pool samples during winter 50<sup>th</sup> and summer 15<sup>th</sup> percentiles extended along axis II and were associated with freshwater drum, channel catfish, and smallmouth buffalo, whereas samples during summer 30<sup>th</sup> percentile were associated with skipjack herring and common carp.

Tests of deepwater assemblages using Kendall's  $W$  indicated various levels of concordance among species' rank abundances based on temporal and spatial groups (Table 10). However, concordance of groups was equal between all samples and samples without zero catch. Species' rank abundances were concordant across the five assemblages for samples grouped by collection ( $W = 0.605$ ,  $df = 10$ ,  $P = 0.001$ ) and across the three groups of winter samples ( $W = 0.756$ ,  $df = 10$ ,  $P = 0.012$ ), but not across the two groups of summer samples ( $W = 0.742$ ,  $df = 10$ ,  $P = 0.138$ ). Species rank abundances for the eight assemblages were concordant across samples grouped by site ( $W = 0.517$ ,  $df = 10$ ,  $P < 0.001$ ). Although concordance for two assemblages across samples grouped as either lentic or lotic habitat was high, it was not significant ( $W = 0.813$ ,  $df = 10$ ,  $P = 0.092$ ), nor was it significant across samples grouped as either Allens Creek or Brazos River sites ( $W = 0.833$ ,  $df = 10$ ,  $P = 0.082$ ).



*Table 10.* Summary of Kendall's  $W$  tests evaluating temporal and spatial concordance between scores on canonical correspondence axes I and II versus fish species abundances, grouped across samples in deepwater habitats of the lower Brazos River, Texas.

	Without zero catch		All samples	
	Kendall's $W$	$P$ - value	Kendall's $W$	$P$ - value
Temporal Groups:				
5 total collections	0.605	0.001	0.605	0.001
3 winter collections	0.756	0.012	0.756	0.012
2 summer collections	0.742	0.138	0.742	0.138
Spatial Groups:				
8 sites	0.517	< 0.001	0.517	< 0.001
lentic and lotic	0.813	0.092	0.813	0.092
Allens Creek and Brazos River	0.833	0.082	0.833	0.082

### *Species-environment Relationships*

In the CCA plots, centroids represent nominal environmental variables and species, whereas arrows represent continuous environmental variables. The length and direction of arrows indicate the range and direction of positively increasing variation, with smaller angles between environmental variables and a canonical axis indicating stronger correlations. Arrows also extend in the negative direction, but for simplicity are not shown. Scaling of the plot was chosen so that environmental centroids located closer to an axis represents a greater correlation with that canonical axis, and species' centroids are at the center of the species' distribution with respect to values for environmental variables across samples. Thus, species' centroids plotted at the extreme end of an environmental variable indicate species' abundances that are more strongly correlated with that variable than species whose centroids are near the origin.

Total variation among shallow river-margin species assemblages was 0.713.

Eigenvalues of the first two CCA axes were 0.148 and 0.075, which together explained 31.2% of the variation in fish species' distribution (Table 11). Summer samples and water depth significantly explained species' distributions and were positively correlated with axis I (Table 11, Figure 5); whereas current velocity significantly explained species' distributions and was negatively correlated with axis I. Summer samples significantly explained species' distributions and were positively correlated with axis II; whereas tributary confluence samples and silt substrates significantly explained species' distributions and were inversely correlated with axis II. Near the origin are centroids for bullhead minnow, silverband shiner, ghost shiner, red shiner, speckled chub, silver chub, and western mosquitofish indicating either their weak association with specific environmental conditions, or their strong association with intermediate values of these variables (Figure 5). In shallow river-margin samples, most of these species

*Table 11.* Summary of canonical correspondence analysis (CCA) of environmental variables for shallow river-margin fish assemblage composition in the lower Brazos River, Texas. Canonical coefficient values in bold indicate environmental variables with significant t-values ( $> |2.1|$ ) with axis I or II. Correlation values in bold indicate environmental variables with strong correlations ( $r > |0.4|$ ) with axis I or II. ‡ indicates environmental variables of low multicollinearity in the model when summer and winter were included as covariables.

Total Inertia		0.713		
	Axis I	Axis II		
Eigenvalue	0.148		0.075	
Percent of variation explained	20.7		10.5	
Cumulative percent explained	20.7		31.2	
Species-environment correlations	0.902		0.832	
Environmental Variable	Canonical coefficients		Correlation with axes	
	Axis I	Axis II	Axis I	Axis II
Summer	<b>1.2186</b>	<b>1.2391</b>	<b>0.6635</b>	0.2122
Winter	0	0	<b>-0.6635</b>	-0.2122
‡ Discharge	0.2654	-0.1439	-0.1572	<b>-0.5958</b>
‡ Stable	0.0383	0.2676	-0.1980	0.2537
‡ Falling	0	0	0.1980	-0.2537
Pool	-0.0697	0.2404	-0.2421	0.1145
‡ Run	0.0173	0.0599	-0.0779	0.0831
Riffle	-0.1218	0.1365	-0.1902	0.2155
Tributary confluence	0.2562	<b>-0.7291</b>	<b>0.4784</b>	-0.2830
‡ Backwater	0	0	0.0543	-0.1185
Temperature	-0.2661	-0.7621	<b>0.5490</b>	-0.0416
Dissolved oxygen	0.3045	0.4512	-0.3750	0.2968
Conductivity	-0.0319	0.1784	0.0404	<b>0.4970</b>
‡ Depth	<b>0.2802</b>	0.0555	0.3300	0.0643
‡ Velocity	<b>-0.2623</b>	0.1488	-0.3374	0.2753
‡ Silt	0.1503	<b>0.6301</b>	<b>0.4097</b>	-0.2410
Sand	0	0	-0.3089	0.1212
‡ Gravel	0	0	-0.0399	0.1103
Significance Tests of Canonical Axes:		Season	Environmental Variables	
Axis I		N/A	0.0200	
All Axes		0.0050	0.0400	

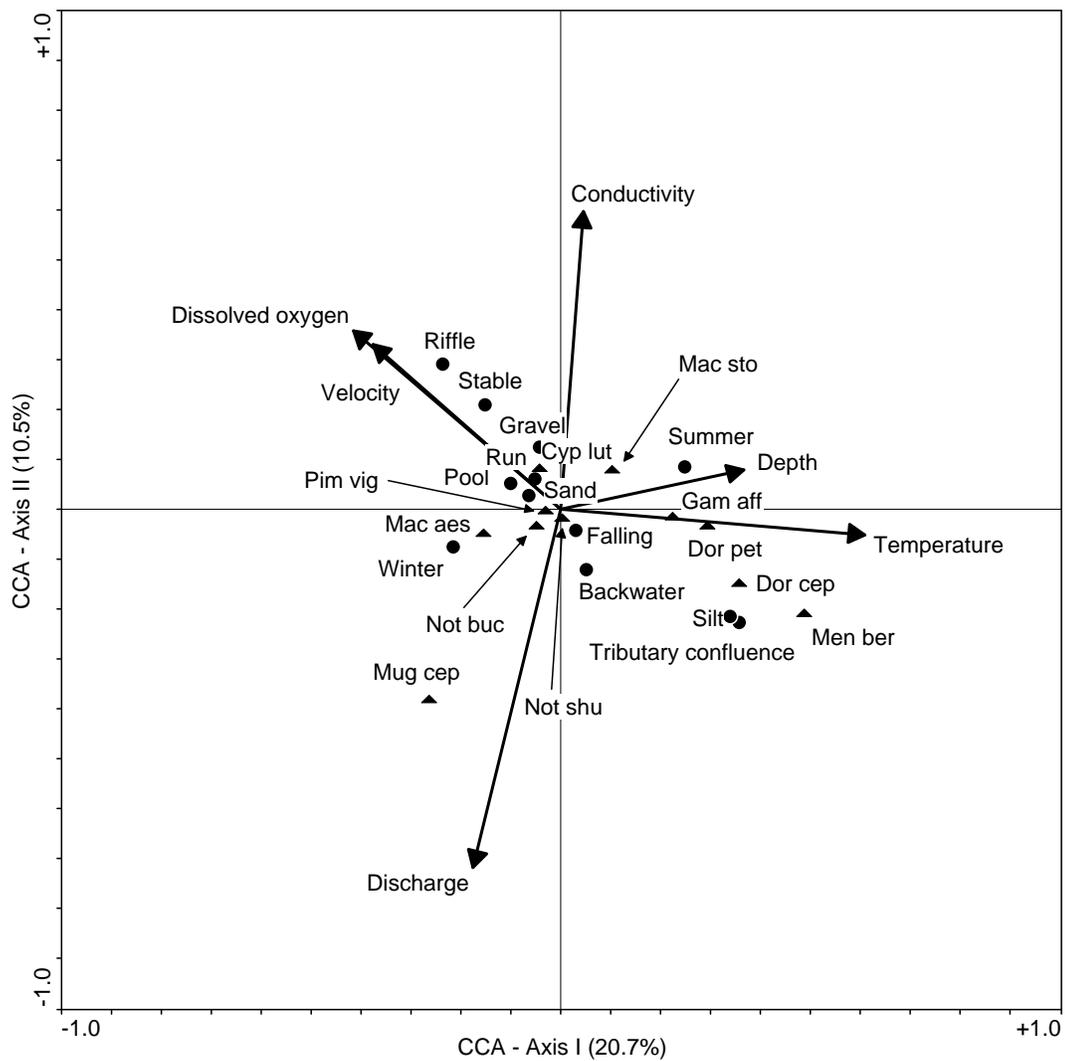


Figure 5. Canonical correspondence analysis (CCA) plot of results for fish assemblages sampled in shallow river-margins along the lower Brazos River, Texas. Triangles represent species centroids. Circles represent nominal explanatory variables. Arrows represent continuous explanatory variables. Species codes are listed in Table 3.

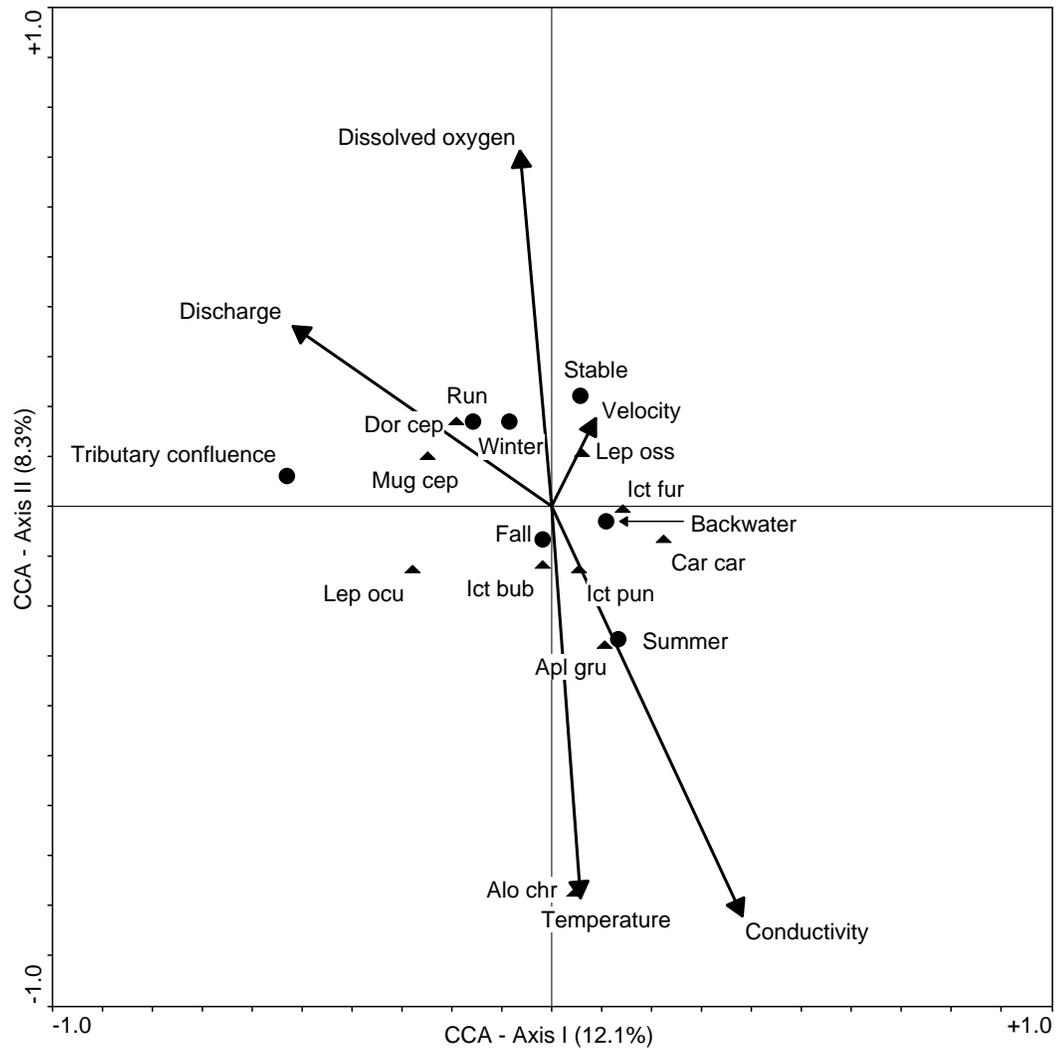
were collected across a wide range of conditions, thus most were weakly associated with the measured environmental variables. Gizzard shad and inland silversides were strongly associated with silt substrates, higher temperatures, and the tributary confluence site. Threadfin shad and western mosquitofish were also associated with higher temperatures. Striped mullet were associated with higher discharge rates and winter samples. Although a large range of values was measured for dissolved oxygen, conductivity, water temperature, and discharge rate these environmental variables were not strongly associated with species' distribution.

With summer and winter included as covariables, the 16 environmental variables combined uniquely explained 32.8% of the variation in species' distributions across shallow river-margin samples. Monte Carlo randomizations indicated significant relationships between species' distributions and selected environmental variables along the first, as well as all combined canonical axes together. By contrast, summer and winter uniquely explained only 6.7% of the variation in species' distributions. Monte Carlo randomizations indicated a significant relationship between species' distributions and season for all canonical axes. An additional 6.7% of the variation in species' distributions could be equally explained by either of these variable groups (seasonal or environmental variables).

Total variation among deepwater species assemblages was 1.886. Eigenvalues of the first two CCA axes were 0.227 and 0.154, which together explained 20.4% of the variation in fish species' distributions (Table 12). Summer samples and water temperature were significant and positively correlated with axis I, whereas discharge rate was significant and negatively correlated with axis I (Table 12, Figure 6). Discharge rate was significant and positively correlated with axis II, whereas summer samples and water temperature were significant and negatively correlated with axis II. Skipjack herring was strongly associated with higher

*Table 12.* Summary of canonical correspondence analysis (CCA) of environmental variables for deepwater fish assemblage composition in the lower Brazos River, Texas. Canonical coefficient values in bold indicate environmental variables with significant t-values ( $> |2.1|$ ) with axis I or II. Correlation values in bold indicate environmental variables with strong correlations ( $r > |0.4|$ ) with axis I or II.

Total Inertia		1.886		
	Axis I	Axis II		
Eigenvalue	0.227	0.154		
Percent of variation explained	12.1	8.3		
Cumulative percent explained	12.1	20.4		
Species-environment correlations	37.5	63.1		
Environmental Variable	Canonical coefficients		Correlation with axes	
	Axis I	Axis II	Axis I	Axis II
Summer	<b>4.5296</b>	<b>4.6926</b>	0.2450	<b>-0.4442</b>
Winter	0	0	-0.2450	<b>0.4442</b>
Discharge	<b>2.3760</b>	<b>2.3702</b>	<b>-0.4051</b>	0.2515
Stable	1.8252	0.8756	0.0725	0.2528
Falling	0	0	-0.0725	-0.2528
Run	-0.2719	-0.0453	-0.1205	0.1159
Tributary confluence	-0.6338	-0.0970	<b>-0.4792</b>	0.0494
Backwater	0	0	<b>0.4702</b>	-0.1216
Temperature	<b>-3.7657</b>	<b>-2.4776</b>	0.0454	<b>-0.5467</b>
Dissolved oxygen	-1.1312	0.5311	-0.0491	<b>0.4959</b>
Conductivity	0.8903	-0.5925	0.2979	<b>-0.5726</b>
Velocity	0.2263	0.1440	0.0689	0.1227



*Figure 6.* Canonical correspondence analysis (CCA) plot of results for fish assemblages sampled in deepwaters along the lower Brazos River, Texas. Triangles represent species centroids. Circles represent nominal explanatory variables. Arrows represent continuous explanatory variables. Species codes are listed in Table 6.

*Table 13.* Mantel tests for deepwater samples evaluating the correlations between similarity matrices based on species abundances and matrices based on either environmental variables or season.  $r$  represents the standardized Mantel statistic.

Samples	Environmental Variables		Season	
	$r$	$P$ – value	$r$	$P$ – value
All 40 samples	0.0693	0.192	0.0717	0.151
Samples without zero catch	0.0827	0.188	0.1313	0.098



temperatures. Freshwater drum were positively associated with conductivity and strongly associated with summer samples. River carpsucker and blue catfish were strongly associated with backwater samples. Spotted gar was negatively associated with current velocity. Longnose gar, gizzard shad, and striped mullet were associated with winter samples. Current velocity was not identified by CCA as having a strong correlation to species' distributions. However, this was likely due to the large numbers of zero catch samples in fast current velocities which were excluded from ordination analysis.

With summer and winter included as covariables, the 10 environmental variables uniquely explained 27.1% of the variation in species' distributions across deepwater samples. By contrast, summer and winter uniquely explained only 2.3% of the variation in species' distributions. An additional 3.0% of the variation in species' distributions could be equally explained by either of these variable groups. When all samples (including zero catches) were analyzed, Mantel tests showed no significant correlation between similarity matrices for species' abundances and matrices for environmental variables ( $r = 0.0693$ ,  $P = 0.192$ ) or for seasons ( $r = 0.0717$ ,  $P = 0.151$ ; Table 13). However, both tests indicated stronger concordance when samples with zero catch were excluded (environmental variables:  $r = 0.0827$ ,  $P = 0.188$ ; season:  $r = 0.1313$ ,  $P = 0.098$ ). CVA identified current velocity as the environmental variable significantly distinguishing between zero catch samples from samples with positive catch (Table 14, Figure 7). Additionally, dissolved oxygen and conductivity were nearly significant in distinguishing between these two sample groups.

*Table 14.* Summary of canonical variates analysis (CVA) performed on deepwater samples grouped as zero catch and positive catch samples in the lower Brazos River, Texas. Canonical coefficient values in bold indicate environmental variables with significant t-values ( $> |2.1|$ ) with axis I or II. Correlation values in bold indicate environmental variables with strong correlations ( $r > |0.4|$ ) with axis I or II.

Total Inertia		1.000		
	Axis I		Axis II	
Eigenvalue	0.657		0.343	
Percent of variation explained	65.7		34.3	
Cumulative percent explained	65.7		100.0	
Species-environment correlations	0.811		0.000	
Environmental Variable	Canonical coefficients		Correlation with axes	
	Axis I	Axis II	Axis I	Axis II
Summer	2.8426	0	0.1179	0
Winter	0	0	-0.1179	0
Discharge	2.9922	0	-0.0082	0
Stable	0.2095	0	-0.1443	0
Falling	0	0	0.1443	0
Run	0.1743	0	<b>0.6261</b>	0
Tributary confluence	0.2543	0	-0.0436	0
Backwater	0	0	<b>-0.5774</b>	0
Temperature	-0.7118	0	0.1978	0
Dissolved oxygen	1.6261	0	-0.065	0
Conductivity	1.7376	0	0.2488	0
Depth	-0.2008	0	-0.2568	0
Velocity	<b>1.1065</b>	0	<b>0.6948</b>	0

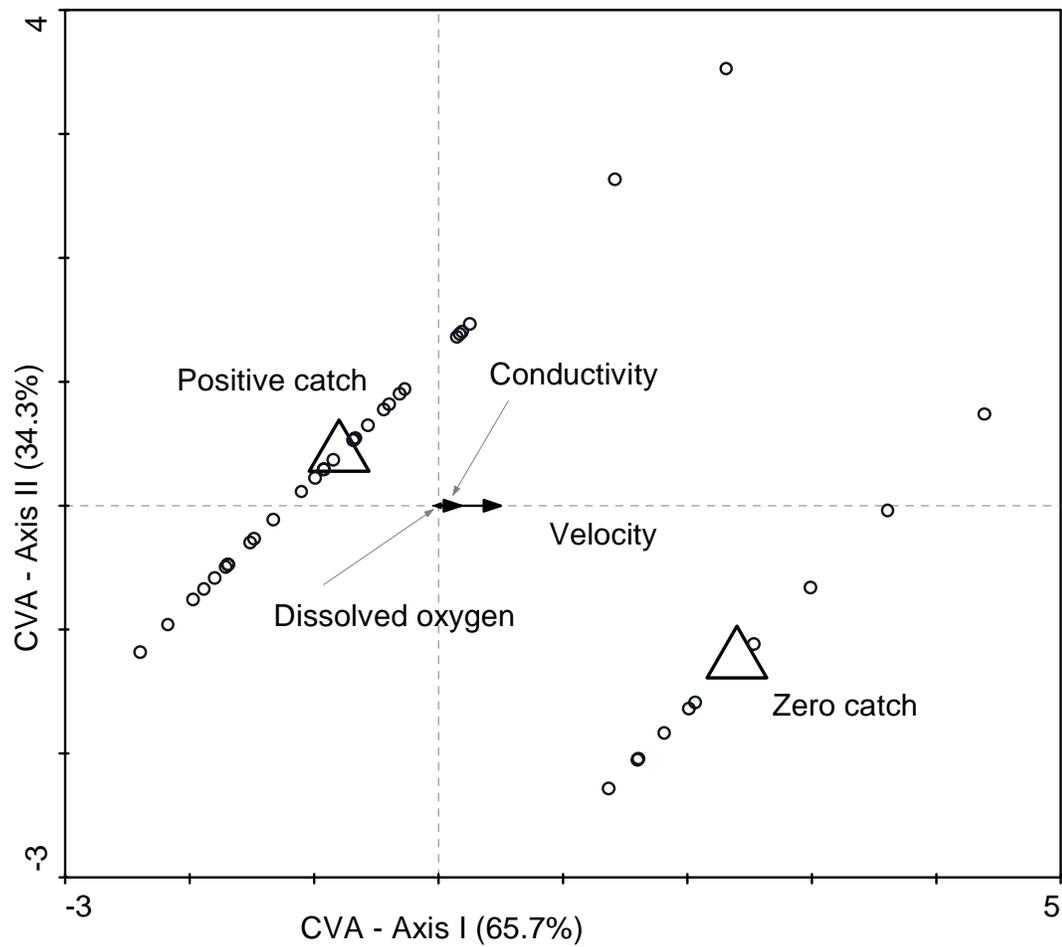


Figure 7. Canonical variates analysis (CVA) plot of positive catch and zero catch samples in the lower Brazos River, Texas. Circles represent individual samples and triangles represent centroids of positive catch and zero catch samples. Arrows represent continuous explanatory variables contributing significantly to axis I or II.

## DISCUSSION

According to the flood-pulse concept (Junk et al. 1989), the main channel of floodplain rivers is of limited value as fish habitat. Therefore, studies evaluating the spatial and temporal dynamics of large-river fish assemblages have traditionally emphasized those fishes occupying aquatic floodplain habitats (e.g., Kwak 1988, Saint-Paul et al. 2000, Slavik & Bartos 2000). However, recent studies suggest that the main-channel of large rivers support a speciose and abundant resident-fish assemblage (Dettmers et al. 2001, Stewart et al. 2002). Consistent with results from other studies of the lower Brazos River (Winemiller & Gelwick, Texas A&M University, unpublished report, Winemiller et al. 2000), 41 species and 13 families were captured in this study.

Strong patterns of habitat partitioning by fishes between shallow river-margin and deepwater habitats were observed. Collections in shallow river-margins were dominated by small-bodied species and juveniles of larger fishes, whereas deepwaters contained mostly adults of large-bodied fishes. Although size selectivity of sampling gears contributed to these patterns, additional samples by electrofishing (a less habitat-biased method) indicated that fish distribution between shallow river-margin and deepwater assemblages followed the same pattern of habitat partitioning among fishes based on their body size (Gelwick & Li, Texas A&M University, unpublished report). Characterized by shallow water depths and slow current velocities, shallow river-margins provide small-bodied fishes with refuge from strong river currents and large piscivorous fishes (Schlosser 1985, Bain et al. 1988). By contrast, large-bodied fishes are restricted to deepwater habitats as these areas provide protection from terrestrial and avian predators (Angermeier & Karr 1983, Power et al. 1989, Harvey & Stewart 1991). Such habitat partitioning suggests that these assemblages are structured by different environmental variables and should therefore exhibit differences in their relative levels of spatial

and temporal variation. This study included sampling methods, statistical analyses, and scales of abundance that differed between shallow river-margin and deepwater assemblages. Therefore, interpretations will emphasize broad-scale assemblage patterns within each habitat, rather than direct comparisons between them.

As indicated by standard deviations among CA sample scores, fish assemblages of the lower Brazos River were less variable than those reported for headwater streams and wadeable rivers in this region (e.g., Gelwick 1990, Herbert 1999). In my study, temporal variations were strongly correlated with seasonal population fluctuations and natural disturbance events. By contrast, spatial variation was low and probably related to the short study reach (Fuselier & Edds 1996). Spatial variation was detected only for deepwater assemblages, for which current velocity was the variable most strongly related to the presence or absence of fish.

#### *Shallow River-margin Assemblages*

Temporal variability of the shallow river-margin fish assemblage was strongly correlated with natural population fluctuations due to juvenile recruitment, seasonal migrations, and displacement or mortality of individuals following spate. Spring recruitment of juveniles can greatly influence temporal variation of fish assemblages (Turner et al. 1994, Taylor et al. 1996). Fish abundances are typically highest during the spring recruitment period and gradually reduce over the remainder of the year. A similar pattern of temporal variability was observed in the lower Brazos River during my study. Fish abundances were highest during the winter 15<sup>th</sup> and 50<sup>th</sup> percentile collections, which coincided with spring reproduction of most fishes in the region (Robison & Buchanan 1988). Although lengths of individuals were not measured, young-of-the-year fishes were abundant during those collections (personal observation) and probably increased temporally variability of the assemblage.

Movement by fishes across large distances can strongly influence temporal variability of assemblage structure within a single reach. Particularly in streams and rivers where environmental conditions frequently fluctuate, individuals must continually shift from less hospitable to more preferable habitat conditions (Angermeier & Schlosser 1989). Similarly, seasonal migrations can contribute to temporal variability of fish assemblages. For example, captures of striped mullet in the Brazos River were common only during the winter 50<sup>th</sup> percentile collections which increased temporal variation among assemblages during my study. Striped mullet is a schooling fish species primarily inhabiting coastal waters, but seasonally migrating into freshwater rivers (Hubbs et al. 1991).

Spates exceeding 24,000 cfs were recorded at the gage station just prior to summer 50<sup>th</sup> and 30<sup>th</sup> percentile collections, in which total catch abundances were particularly low. Spates are unpredictable periods of extreme discharge and capable of severely disrupting the composition of stream communities (Resh et al. 1988). Among fishes, spates can induce high mortality and downstream displacement of individuals, thereby reducing species richness and abundance (Ross & Baker 1983, Schlosser 1985, Harvey & Stewart 1991). Although overall catch was lower during those collection periods, catches for species of shad and chub were higher. Increased catch abundance of gizzard shad and threadfin shad might have been caused by displacement from floodplain habitats and reservoirs into the main-river channel during elevated discharge. Gizzard shad and threadfin shad are numerically abundant in oxbow lakes along the Brazos River (Winemiller et al. 2000) as they provide important reproductive and nursery habitats for both species (Robison & Buchanan 1988, Turner et al. 1994). Threadfin shad and gizzard shad are commonly stocked into reservoirs as prey species (Gido & Matthews 2000), so their high abundances might have also been the result of downstream displacement from reservoirs. Speckled chub and silver chub are benthic invertivores and have fusiform shaped bodies that are

morphologically adapted to withstand strong river currents. Thus their higher abundance following spates was probably related to their low vulnerability to both downstream displacement and mortality during high discharge conditions.

Previous studies have documented strong spatial separation of stream-fish assemblages among riffle, run, and pool mesohabitats (Gorman & Karr 1978, Schlosser 1982, Taylor 2000). In the headwaters of the Brazos River, spatial variation of fish assemblages is related to current velocity and water depth conditions (Ostrand & Wilde 2002). By contrast, shallow river-margin fish assemblages in my study were similar among sites and might be attributable to several factors. Perceptions of variability depend on the spatial scale being evaluated. Studies across broad geographic regions (e.g., Rahel & Hulbert 1991, Waite & Carpenter 2000) include a wide range of environmental conditions and therefore greater spatial variation among assemblages (Taylor et al 1996). By contrast, my study sites were located along a contiguous 10-km reach of the lower Brazos River, and environmental conditions were largely consistent across sampling sites within each collection period. In addition, selection of sites that could be seined along the river-margin might also have reduced variability of water depths and current velocities among samples and hence variation among fish assemblages. For example, at sampling sites along the shallow river-margin, water depth were consistently less than 1 m and current velocities rarely greater than 30 cm/s.

Despite spatial consistency of their environmental conditions, shallow river-margins are extremely sensitive to river-stage fluctuations (Bain et al. 1988). Because river discharge rates are rarely stable, river-margin fishes must relocate in response to fluctuating water levels to maintain themselves at appropriate water depths. Consequently, fishes must shift laterally to avoid strong current velocities and piscivorous fishes associated with deep waters, while also avoiding stranding in shallow waters (Schlosser 1985, Bain et al. 1988). In such variable

environments, habitat-generalist species typically dominate the assemblage composition (Poff & Allan 1995, Jepsen 1997), and likely contributed to the spatial homogeneity of shallow river-margin assemblages in the lower Brazos River. For example, red shiners accounted for two-thirds of my catch in shallow river-margin sites. Tolerant of a wide range of environmental conditions and physical habitat types, red shiners are generalist species and capable of exploiting a broad range of habitats (Marsh-Matthews & Matthews 2000). Additionally, red shiners quickly reach sexual maturity and are able to spawn several times a year, facilitating their rapid recruitment and population growth (Gido et al. 1997).

Fishes were not routinely classified into life stages during my study. However, ontogenetic shifts in resource use was probably common among the species I sampled (Polis 1984). Such shifts in habitat use have been documented among river-fish species similar to those I collected, and can provide insight into patterns of spatial and temporal variability otherwise concealed in assessments limited to taxonomic levels (Gelwick 1990, Lobb & Orth 1991, Aadland 1993). Incorporating ontogenetic shifts in habitat use might be particularly important to identify spatial patterns related to use of nursery and juvenile habitats along shallow river-margins and tributary confluences (Gorman 1986).

Although CA ordination scores were not statistically different between lentic and lotic habitat-groups, differences were clearly evident between the tributary confluence and river sites. Higher species richness and numerical abundances in the tributary confluence site were probably related to upstream movements by river fishes and downstream movements by stream fishes (Whiteside & McNatt 1972, Osborne & Wiley 1992). For instance, the capture of three species—green sunfish, largemouth bass and slough darter—was largely restricted to Allens Creek in my study, and other lateral habitats in that of others (Winemiller et al. 2000, Linam et al., Texas Parks and Wildlife Department, unpublished report). Species richness and catch



abundances were much lower in the riffle site. With the exception of speckled chub, most species captured within the Allens Creek confluence avoid faster current velocities, thus contributing to lower species richness and catch abundances in river samples.

### *Deepwater Assemblages*

In contrast to fish assemblages of the shallow river-margin, deepwater assemblages showed considerable spatial and temporal variation. Analogous to the separation between riffle and pool fishes typical of streams (Vadas & Orth 1997, Taylor 2000), deepwater fish of the lower Brazos River were spatially segregated between lotic and lentic assemblages. Like streams, large rivers are comprised of lotic and lentic habitat types along a gradient of depth and current velocity. The faster current velocities and shallower water depths make lotic habitats generally less inhabitable by large-bodied fishes (Matthews et al. 1994). Conversely, pools contain higher abundances of large-bodied fishes due to the buffering capacity of large volumes of water on extreme environmental fluctuations (Aadland 1993). For example, temperature in deep pools may be stratified, even during periods when riffle temperatures are fluctuating with those of ambient air (Matthews 1987).

Temporal variability of environmental conditions can influence fish assemblages in neighboring habitats. Pool assemblages undergo temporal change due to emigration and recolonization dynamics of riffle-dwelling fishes during drought (Gelwick 1990). In the lower Brazos River, stronger associations of less frequently captured species (freshwater drum, smallmouth buffalo, channel catfish, and common carp) with deeper pools alongside shallow runs might have indicated fish movement between these habitats under changing conditions, especially across discharge rates.

Adventitious tributaries are headwater streams that flow directly into large rivers, and the stability of their fish assemblages are strongly influenced by seasonal upstream-migrations by river-fishes (Gorman 1986). In the lower Missouri River, migrations of river-fishes into adventitious tributaries were strongly influenced by water temperatures and depths of confluences (Braaten & Guy 1999). Use of Allens Creek confluence habitats by river-fishes was similarly influenced. As Allens Creek and Brazos River water levels fluctuated, sediments were continually deposited or eroded, thereby affecting water depths within the confluence site. During the winter 15<sup>th</sup> and 50<sup>th</sup> percentile collections water depths exceeded 1 m, which enabled even large-bodied fishes to move between Allens Creek and the Brazos River. Conversely, formation of a sediment bar across the confluence decreased water depths during the remaining collections such that movement by large-bodied fishes was probably impeded or highly constrained. In addition, winter 15<sup>th</sup> and 50<sup>th</sup> percentile collections were during February and March, which coincided with warming water temperatures in the region. Like headwater streams, adventitious tributaries have low volumes of water and warm more rapidly than do main-river channel habitats (Whiteside & McNatt 1972). Therefore, larger catches in the confluence might have represented fish moving towards warmer water in Allens Creek. Furthermore, Allens Creek stream-flow is heavily supplemented by effluent from a wastewater treatment facility (McKone et al., Freese and Nichols Inc., unpublished report) and might further warm the stream during winter.

The reproductive role of habitats in adventitious streams may be another factor contributing to the higher catch of fish in the confluence site. Adventitious streams are particularly important habitats for spawning river-fishes (Brown & Coon 1994, Taylor et al. 1996). The 'low flow recruitment hypothesis' suggests river-channel backwaters are important reproductive and nursery habitats for fishes in lowland rivers that lack a regular and predictable

flood-pulse (Humphries et al. 1999). Accordingly, fish spawn during low discharge periods, which allow larvae to exploit high concentrations of prey that have accumulated in backwaters. Although the discharge regime of the lower Brazos River is largely unregulated, flooding is rare (USGS gage data) due to flood control and water supply reservoirs located upstream. Longnose gar was especially abundant in catches during winter 15<sup>th</sup> and 50<sup>th</sup> percentile collections and coincided with 19° C water temperatures—the temperature at which longnose gar initiate spawning (Robison & Buchanan 1988). Captures of young-of-the-year and juvenile longnose gar in Allens Creek during subsequent summer collections reinforced the likelihood that tributary confluences function as reproductive and nursery habitats for river species.

Similar to tributary confluences, embayments provide backwater habitats for reproductive adults and resulting juvenile fishes. In my study, catches were particularly high among embayment areas with woody snags or riprap debris. Such structure enhances invertebrate-prey production, and provides shelter for small fish from predators and strong river currents (Angermeier & Karr 1983, Madejczyk et al. 1998). Woody snags and riprap debris can also provide structure for adhesive eggs and larvae of lepisosteids (Robison & Buchanan 1988). As in the confluence site, I collected several young-of-the-year and juveniles of longnose gar, both in and near these structurally complex embayment sites, further reinforcing the theory of their role as reproductive and nursery habitats.

Temporal variation of catch data for deepwater samples might be related to seasonal changes in fish behavior. Because gillnets are a passive capture gear, catch is highly selective for mobile species, and individuals that are active or less cautious (Hubert 1996). The higher summer catch rates in deepwater sites appear to be related to increased fish movements and migrations. During warmer seasons, fishes are more active as they seek reproductive habitats in spring and foraging habitats in summer (Gido & Matthews 2000). Conversely, captures in

winter typically decrease as fish activity declines with colder water temperatures. For example, Bodensteiner & Lewis (1992) reported large aggregations of fishes that over-wintered in the warm thermal refuge provided by deep backwaters.

### *Species-environment Relationships*

Species distributions in the lower Brazos River were only weakly related to measured in-stream variables. Shallow river-margin assemblages were largely dominated by cyprinids and western mosquitofish, all of which showed low associations with measured environmental variables. With the exception of ghost shiner and silverband shiner, these species are habitat generalists that can tolerate a broad range of environmental conditions (Bayer et al., Texas Parks and Wildlife Department, unpublished report). Although considered intolerant species, ghost shiner and silverband shiner are schooling species and generally restricted to large rivers with turbid water (Robison & Buchanan 1988, Ross 2001), such as the lower Brazos River.

Weak species-environment relationships were probably also related to the low spatial variation of environmental conditions associated with my short study reach. Sampling sites were located entirely on the Western Gulf Coastal Plain physiographic province. Latitude, drainage area, riparian land-use, and river gradient were consistent along the study reach, thus eliminating environmental variability associated with geographic and regional scales (Angermeier & Winston 1998, Marsh-Matthews & Matthews 2000). Most in-stream aquatic factors were also spatially consistent. Given the influence of diel fluctuations, measurements of water temperature and dissolved oxygen were relatively consistent across sites within each collection period (Appendix B). Streamflow from tributaries can dramatically disrupt physicochemical gradients along a river reach (Vannote et al. 1980). However, Allens Creek was the only tributary confluent with my study reach, and did not appear to alter discharge or measured environmental

variables of nearby habitats in the Brazos River. Thus, over the span of my study, species-environment relationships were dominated by temporal variation in environmental conditions. Two of three species that showed strong relationships with environmental variables were threadfin shad and striped mullet. However, this was probably because their catches were largely restricted to two collection periods. Therefore, their catch abundances were not conclusively related to environmental factors, but rather could have been coincidental occurrences related to spates or spring migrations.

Of the four species associated with strong current velocities along the shallow river-margin, two—silver chub and speckled chub—are behaviorally and morphologically adapted for such currents. Red shiners are habitat-generalists that tolerate a wide range of current velocities. Bullhead minnow is a benthic omnivore, and like the chubs, probably takes advantage of reduced-flow habitats associated with the interstitial space between substrate.

Due to the elimination of zero catch samples by CCA, current velocity was not identified as having a strong affect on deepwater assemblage composition. However, CVA indicated zero catch samples were primarily distinguished from positive catch samples by fast current velocities. The higher metabolic cost of rheotaxis under strong current conditions probably limited the distribution of large-bodied fishes in fast flowing habitats. Alternatively, if fishes tend to follow deeper channels, where velocities are lower compared to surface waters (Gordon et al. 1992), then they might have avoided gillnets, all of which were set 1 m below the surface.

Fish assemblages in the lower Brazos River varied seasonally, but not strongly. Seasonal variability of stream-fish assemblages largely depends on the climatic region. Temperate regions in the northern USA exhibit discrete seasons that profoundly influence seasonal composition of fish assemblages (Jackson et al. 2001). In contrast, the lower Brazos River is located at 29°40' N, where seasons are less discrete and variable. Summers are warm

and winters mild, therefore the influence of environmental conditions outweighed seasonal variation among fishes (Ostrand & Wilde 2002, Herbert & Gelwick 2003).

The low spatial and temporal variation of fish assemblages and weak species-environment relationships in this study are consistent with prevailing models developed for large river systems from headwater streams and wadeable rivers (Schlosser 1987, Matthews et al. 1988). Because sites were located along a short study reach, environmental conditions were consistent across sites during each collection and therefore species-environment relationships were largely related to temporal variations in environmental conditions across sites. In large rivers, such as the lower Brazos River, environmental conditions are more stable than streams and hence biotic processes contribute greatly to the structure of fish assemblages (Schlosser 1987). The role of biotic processes in fish assemblage variation was not evaluated in this study. However, the large percentage of variation left unexplained by environmental variables and season might represent the influence of biotic processes, as well as unexplained stochasticity. Although fish assemblages are assumed to be structured by a combination of biotic and abiotic factors, the temporal schedule of such influences is not necessarily constant (Weins 1986). Thus, spatial and temporal variation exhibited by assemblages over smaller spatial or temporal scales may appear stochastic and represent random habitat associations. For instance, fish assemblages of tropical rivers are randomly distributed during floods (Saint-Paul et al. 2000) but deterministically structured during low-water (Rodriguez & Lewis 1997). Since flood frequency of the lower Brazos River is low and collections were conducted during baseflow conditions, fish assemblages during this study showed low levels of variation and were comparable to those assemblages having more deterministic—as compared to stochastic—organizational patterns.

## CONCLUSIONS

Since most large floodplain rivers have been extensively modified, their fish assemblages have experienced drastic declines. Contrary to earlier theories and prevailing perceptions about large rivers, the main-river channel of the lower Brazos River contained a speciose and abundant resident-fish assemblage. Across three summer and three winter collections during baseflow conditions, 28,468 individuals representing 41 species and 13 families were captured across both shallow river-margin and deepwater habitats within a 10-km reach.

Despite the spatial heterogeneity and temporal dynamics of environmental variables in the lower Brazos River, fish assemblages exhibited distributions that were less variable than levels typically reported for headwater streams and wadeable rivers. Moreover, fishes revealed weak species-environment relationships. Temporal variations of the fish assemblage appeared to be primarily related to juvenile recruitment, displacement of individuals following spates, or seasonal immigration by striped mullet. Low spatial variability seemed to be associated with fairly constant environmental conditions across the study reach. Geographic, regional, and local scale environmental variables were each consistent across sites during each collection period. Therefore, species-environment relationships were largely related to temporal variation in physicochemical conditions. Spatial variation in species assemblage structure was most influenced by current velocity, which was strongly related to the presence or absence of large-bodied fishes. Future studies should incorporate broader spatial-scales that include a greater range of environmental conditions when assessing variation and species-environment relationships of fish assemblages in main-channel habitats of large rivers.

A 142,892 acre-feet municipal water supply reservoir is planned for Allens Creek. With water diversions proposed from the Brazos River to the reservoir, potential impacts to the

river-fish assemblage will undoubtedly depend on the timing, frequency, and duration of those diversions. In this study, I documented the spatial and temporal variation of fish assemblages in the lower Brazos River and identified the species-environment relationships responsible for assemblage variation over a one-year period of typical discharge. This information provides a baseline for future monitoring that could help detect and mitigate impacts associated with water diversions, and discriminate between effects of anthropogenic disturbances versus those due to natural assemblage fluctuations.



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**APPENDIX A**

*Appendix A.* List of all fish species collected in shallow river-margin samples along the lower Brazos River, Texas. Species abundances are grouped by collection period. Percent relative abundance represents the relative abundance of species across the six collections. Species codes are abbreviations used in ordination plots.

Species (common name)	Species Code	Summer			Winter			Total Number	Relative Abundance (%)
		50	30	15	50	30	15		
<i>Aphredoderidae</i>									
Aphredoderus sayanus (pirate perch)		1	0	0	0	0	0	1	< 0.10
<i>Atherinidae</i>									
Labidesthes sicculus (brook silverside)		4	0	0	0	0	0	4	< 0.10
Menidia beryllina (inland silverside)	Men ber	19	3	6	1	0	1	30	0.11
<i>Catostomidae</i>									
Carpionides carpio (river carpsucker)	Car car	13	6	5	1	2	3	30	0.11
Ictiobus bubalus (smallmouth buffalo)	Ict bub	0	3	3	1	3	1	11	< 0.10
<i>Centrarchidae</i>									
Lepomis cyanellus (green sunfish)		0	0	0	0	0	3	3	< 0.10
Lepomis gulosus (warmouth)		1	0	0	0	0	0	1	< 0.10
Lepomis humilis (orangespotted sunfish)		2	5	0	0	1	2	10	< 0.10
Lepomis macrochirus (bluegill sunfish)		1	2	1	1	0	6	11	< 0.10
Lepomis megalotis (longear sunfish)		2	2	0	1	0	0	5	< 0.10
Lepomis microlophus (redecor sunfish)		4	4	0	0	0	0	8	< 0.10
Lepomis hybrid (hybrid sunfish)		0	0	0	0	1	0	1	< 0.10
Lepomis sp. (juvenile sunfish TL < 20mm)		11	3	0	0	0	0	14	< 0.10
Micropterus punctulatus (spotted bass)		0	0	1	2	0	0	3	< 0.10
Micropterus salmoides (largemouth bass)		0	1	0	0	0	0	1	< 0.10

Appendix A. Continued.

Species (common name)	Species Code	Summer			Winter			Total Number	Relative Abundance (%)
		50	30	15	50	30	15		
Pomoxis annularis (white crappie)		4	1	0	0	0	0	5	< 0.10
Clupeidae									
Alosa chrysochloris (skipjack herring)	Alo chr	0	0	0	0	0	2	2	< 0.10
Dorosoma cepedianum (gizzard shad)	Dor cep	36	1	0	3	0	1	59	0.21
Dorosoma petenense (threadfin shad)	Dor pet	46	68	2	3	8	2	129	0.45
Cyprinidae									
Cyprinella lutrensis (red shiner)	Cyp lut	1,744	886	2,777	4,720	1,578	6,909	18,614	65.38
Cyprinella venusta (blacktail shiner)		0	2	1	1	0	1	5	< 0.10
Cyprinus carpio (common carp)		0	1	0	0	0	0	1	< 0.10
Lythrurus fumeus (ribbon shiner)		2	0	0	0	0	0	2	< 0.10
Macrhybopsis aestivalis (speckled chub)	Mac aes	11	8	0	33	11	10	73	0.26
Macrhybopsis storeriana (silver chub)	Mac sto	27	1	2	0	1	0	31	0.11
Notropis buchanani (ghost shiner)	Not buc	71	0	39	293	49	316	768	2.70
Notropis oxyrhynchus (sharpnose shiner)		3	0	0	0	0	0	3	< 0.10
Notropis shumardi (silverband shiner)	Not shu	221	10	78	776	30	626	1,741	6.12
Opsopoeodus emiliae (pugnose minnow)		1	0	1	0	0	0	2	< 0.10
Pimephales vigilax (bullhead minnow)	Pim vig	723	237	103	1,879	166	1,518	4,626	16.25
Fundulidae									
Fundulus notatus (blackstripe topminnow)		0	0	1	0	0	1	2	< 0.10

Appendix A. Continued.

Species (common name)	Species Code	Summer			Winter			Total Number	Relative Abundance (%)
		50	30	15	50	30	15		
Ictaluridae									
Ictalurus furcatus (blue catfish)	Ict fur	6	2	3	0	6	4	21	< 0.10
Ictalurus punctatus (channel catfish)	Ict pun	10	1	4	6	9	3	33	0.12
Noturus gyrinus (tadpole madtom)		0	0	0	1	1	0	2	< 0.10
Pylodictis olivaris (flathead catfish)		1	0	0	0	0	0	1	< 0.10
Lepisosteidae									
Lepisosteus oculatus (spotted gar)	Lep ocu	3	5	2	14	1	8	33	0.12
Lepisosteus osseus (longnose gar)	Lep oss	0	2	100	23	8	27	160	0.56
Mugilidae									
Mugil cephalus (striped mullet)	Mug cep	0	0	7	613	1	1	622	2.18
Percidae									
Etheostoma gracile (slough darter)		0	0	0	0	0	1	1	< 0.10
Poeciliidae									
Gambusia affinis (mosquitofish)	Gam aff	359	173	732	71	21	39	1395	4.90
Sciaenidae									
Aplodinotus grunniens (freshwater drum)	Apl gru	0	2	2	1	0	0	5	< 0.10

**APPENDIX B**

*Appendix B.* Range of physicochemical values across shallow river-margin and deepwater sampling sites during each of collection periods in the lower Brazos River, Texas.

Collection Period	Water Temperature (°C)		Dissolved Oxygen (mg/L)		Conductivity (µS/cm)	
	Min	Max	Min	Max	Min	Max
Summer 50	26.8	32.7	5.09	6.47	318.9	520.0
Summer 30	30.3	34.3	6.08	7.90	439.0	1129.0
Summer 15	24.3	30.1	7.15	10.91	696.0	902.0
Winter 50	19.7	24.2	7.14	9.64	401.0	556.0
Winter 30	10.3	17.4	9.19	12.77	11.6	814.0
Winter 15	15.7	20.6	8.87	13.00	527.0	620.0

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