

DEMOGRAPHIC AND TROPHIC DYNAMICS OF FISHES IN RELATION TO
HYDROLOGIC VARIATION IN CHANNEL AND FLOODPLAIN HABITATS OF
THE BRAZOS RIVER, TEXAS

A Dissertation

by

STEVEN CHRISTOPHER ZEUG

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

August 2007

Major Subject: Wildlife and Fisheries Sciences

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Chair of Committee, Kirk Winemiller
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Stephen Davis
Lee Fitzgerald
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ABSTRACT

Demographic and Trophic Dynamics of Fishes in Relation to Hydrologic Variation in Channel and Floodplain Habitats of the Brazos River, Texas. (August 2007)

Steven Christopher Zeug, B.S. Humboldt State University

Chair of Advisory Committee: Dr. Kirk Winemiller

Large rivers in North America have been subjected to a variety of hydrologic alterations that have negatively impacted aquatic fauna. These impacts have triggered restoration efforts, including management of flows, to restore or maintain ecological integrity. Ecological data relevant to flow management and habitat restoration is scarce, and conceptual models of ecosystem function have been widely applied to large rivers despite a lack of quantitative evaluation of these models. Here, I examine demographic and trophic dynamics of fishes with divergent life histories and trophic guilds in relation to habitat heterogeneity and flow variability in a relatively unaltered floodplain system: the Brazos River, Texas. Reproductive activity of fishes with three divergent life history strategies was positively associated with long-term river hydrology, although species with alternate strategies exploited different portions of the hydrograph (peak flow versus increasing flow). Despite the positive association with hydrology, low-flow periods were favorable for recruitment, and food resources for larvae and juveniles were denser during these periods. Some species used both oxbow and channel habitats during some point in their life cycle, whereas other species appeared to be almost entirely restricted to one habitat type.

Terrestrial C₃ macrophytes accounted for a significant fraction of the biomass of most consumer species examined. Small-bodied species in oxbow lakes assimilated large fractions of biomass from benthic algae, whereas this pattern was not observed in the river channel. Frequent flow variations in the river channel may reduce algal standing stocks, and significant contributions from autochthonous algal sources may only occur during low-flow periods. Trophic positions of detritivores indicated that terrestrial carbon sources were assimilated, for the most part, via invertebrates rather than by direct consumption. My results indicate that current conceptual models are too vague to provide accurate predictions for restoration strategies in rivers with variable flow regimes. Flow and habitat management strategies that focus on reproducing key features of historical fluvial dynamics are likely to be more successful than strategies that focus on single indicator species or flow dynamics that differ from the historical hydrograph.

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CHAPTER I

INTRODUCTION

Floodplain rivers are widely recognized as areas of high biological productivity and diversity associated with their large size, spatial heterogeneity, and flow variability (Sparks 1995). Floodplains provide a variety of ecosystem services, and per-unit-area, have greater economic value than most other ecosystem types (Constanza et al. 1997). Despite the high ecological and economic value of floodplains, these ecosystems are among the most threatened on a global scale (Tockner and Stanford 2002). River impoundment, water extraction, and levee construction have significantly altered the natural flow regimes of many large rivers. Hydrology is the primary driver of ecological dynamics in lotic systems and aquatic fauna are adapted to natural flow regimes (Poff et al. 1997). River modifications have been associated with reduced fish productivity, diversity and invasions by exotic species (Moyle and Light 1996; Bunn and Arthington 2002; Tockner and Stanford 2002). Restoration strategies for these systems have focused on management of instream flows to maintain ecological integrity; however, ecological data necessary to support these strategies are lacking (Naiman et al. 1995; Richter et al. 1997).

Conceptual models of ecological function in large rivers can be useful as guides for flow management but require evaluation with empirical data (Thorp et al. 2006). Currently, conceptualization of ecosystem function in rivers has outpaced empirical evaluation, and few studies have tested hypotheses drawn from model predictions.

This dissertation follows the style of Ecology.

These models are often assumed to apply to rivers with flow regimes that deviate significantly from the river systems used to formulate conceptual models (Humphries et al. 1999). Worldwide, large rivers display a range of flood timing, duration, and frequency that have the potential to influence aquatic fauna (Puckridge et al. 1998). Additionally, fish populations possess a diversity of life history strategies. Environmental conditions that optimize recruitment are strongly associated with life history traits, and flow conditions that benefit one strategy may be detrimental to species with a different suite of traits (Sparks 1995; Olden et al. 2006).

The general objectives of this study were to: 1) quantitatively evaluate how reproduction and recruitment of fish populations with divergent life history strategies are influenced by habitat heterogeneity and flow variability using the framework of current conceptual models, and 2) identify the relative importance of terrestrial and aquatic production sources supporting aquatic consumers in different trophic guilds within main channel and floodplain habitats.

My study system was the middle Brazos River located in east-central Texas. The Brazos is the 11th longest river in the United States, and the longest river contained entirely within the borders of Texas. Fewer hydrologic modifications are present throughout the Brazos River-floodplain relative to other North American systems, making it highly suitable for evaluation of reproduction, recruitment and trophic dynamics under relatively natural conditions. Three dams are present on the main-stem Brazos in and above the city of Waco, however, flows below Waco appears to be primarily influenced by regional precipitation with flows approximating historical

conditions (Zeug et al. 2005). Additionally, there are few levees on the middle-lower Brazos allowing for channel-floodplain connections and a meandering and dynamic channel. Below I briefly describe conceptual models related to fish reproduction, recruitment and trophic dynamics and the objectives of each chapter in relation to examining the predictions of these models for the Brazos River.

MODELS RELATED TO FISH REPRODUCTION AND RECRUITMENT

The flood pulse concept (FPC) (Junk et al. 1989) is probably the most widely cited conceptual model describing ecological dynamics in floodplain rivers. This model emphasizes the importance of lateral connectivity for biomass production. Flood pulses stimulate release of inorganic nutrients and entry of carbon sources into the aquatic realm from adjacent terrestrial areas resulting in blooms of primary and secondary production. Fish reproduction generally coincides with high flow periods that allow placement of offspring in to productive floodplain habitats. The main channel is viewed as a “highway” for fishes to travel between important floodplain habitats and provides relatively little organic carbon to support the aquatic fauna. In temperate zone rivers, optimal conditions for fish reproduction and recruitment occur when high flows coincide with rising spring-time temperatures. The absence of a flood pulse or alteration in timing and/or duration is predicted to reduce recruitment success (Bayley 1991).

The FPC was developed largely from observations of tropical river systems where flood pulses are predicable within and between years. Many rivers have flow regimes that do not conform to the optimal set of conditions described by the FPC, and several studies have found that the main channel of large rivers can support diverse

aquatic communities, challenging the highway analogy of the FPC (Winemiller 1996; Dettmers et al. 2001). Humphries et al. (1999) formulated the low-flow recruitment hypothesis (LFR) to describe fish population dynamics in large rivers with flood regimes that are relatively unpredictable or that occur during periods when temperatures are not optimal for reproduction. Floodplain use in these systems is risky, because fish may become stranded during rapidly declining water levels. Further, if floods are of short duration, there may be insufficient time for fish reproduction, juvenile rearing, and movement back to the channel. This model proposes that fish reproduction and recruitment can occur in the main channel and are optimized during periods of low-flow when temperatures are warm and food resources for larvae and juveniles become concentrated.

Chapter II develops statistical models of reproductive activity for seven species representing three divergent life history strategies. These models employ biotic and abiotic variables drawn from predictions of the FPC and LFR models. I used an information theoretic model selection technique that allowed each candidate model to be considered a working hypothesis, and averaged model estimates to determine which predictor variables had good support. The abundance of adults of each species was compared among main channel and floodplain habitats to identify areas that are profitable for reproduction of species with different life history strategies. The results of the modeling exercise and abundance comparisons are then discussed in relation to predictions of each conceptual model and life history theory.

In chapter III, I examined the recruitment success and demographic characteristics of the same seven species in different habitat units (channel vs. floodplain) and hydrologic periods (wet vs. dry years). The two year study included a relatively dry period (year 1) when floodplain-river channel connections were infrequent and habitats were isolated for most of the year, and a wet period (year 2) when floodplain and channel habitats experienced frequent hydrologic connections that provided opportunities for faunal exchange between habitats. Recruitment of each species was measured by comparing juvenile abundance, and the proportion of juveniles in populations of each species between habitats and hydrologic periods. Additionally, data for a suite of environmental variables was compiled to identify characteristics associated with optimal recruitment of each species.

MODELS RELATED TO TROPHIC DYNAMICS

The river continuum concept (RCC) (Vannote et al. 1980) predicts that transported carbon leaked from tributaries and upstream areas due to processing inefficiencies is the primary source of carbon supporting consumers in large rivers. Recently, several studies have concluded that upstream-downstream food web linkages are actually rather weak (Thorp et al. 1998; Hury et al. 2002), therefore this model was not considered in the current study. The flood-pulse concept proposes that terrestrial carbon originating on the floodplain supports the majority of consumer biomass in the main channel as described above, emphasizing the importance of lateral rather than longitudinal connectivity. Thorp and DeLong (1994) proposed the riverine productivity model (RPM) that suggests autochthonous algal carbon is more easily assimilated than

either transported particulate carbon or terrestrial carbon originating on the floodplain. According to the RPM, algae may be the primary source of carbon supporting aquatic consumers despite its lower abundance in the channel environment.

I used stable isotopes of carbon and nitrogen in the IsoSource mixing model to determine the relative contribution of four terrestrial and aquatic production sources to aquatic consumers in the Brazos River main channel and two oxbow lakes. Because they provide a measure of material that is actually assimilated by consumers and integrates feeding history over relatively long time periods (weeks to months), stable isotopes are an effective tracer of different production sources in aquatic food webs. Estimation of the relative importance of different production sources has been complicated in previous studies, because carbon isotope ratios of algae and terrestrial C_3 macrophytes often overlap and two end-member mixing models are unable to distinguish between these sources. The IsoSource model provides a method for modeling source contributions when the number of sources is too great for a unique solution (number of sources $>$ number of isotopes + 1). Nitrogen ratios were used to calculate the trophic positions of aquatic consumers, and results were compared among the three habitats surveyed.

Chapter VI summarizes the results of chapters II - IV and suggests future directions for research in large river systems. My results provide quantitative data for the Brazos River against which the predictions of the aforementioned models can be evaluated. Consideration of life history strategies and trophic guilds as a framework for data analysis provides a way for these results to be applied to other large river systems

with different taxa. Quantitative evaluation of conceptual models is essential to advance understanding of ecological dynamics in large rivers, and my study represents an important step to elucidating how flow variability and habitat heterogeneity influence aquatic fauna in these diverse and productive ecosystems.

CHAPTER II

ECOLOGICAL CORRELATES OF FISH REPRODUCTIVE ACTIVITY IN

FLOODPLAIN RIVERS: A LIFE HISTORY-BASED APPROACH

INTRODUCTION

The critical role of hydrology to ecological dynamics in river-floodplain systems is well recognized (Poff et al. 1997; Bunn and Arthington 2002). Alteration of natural flow regimes due to dam and levee construction, water extraction, and channel modification has been associated with myriad impacts on aquatic fauna (Moyle and Light 1996; Tockner and Stanford 2002; Agostinho et al. 2004). In response to these impacts, instream flow recommendations have been developed to restore the ecological integrity of modified systems (Jowett 1997; Richter et al 1997). Most of these strategies focus on minimum base flows, flow variability, or habitat availability and may produce conflicting assessments depending on the method used (Jowett 1997). Ecological data relevant to restoration of modified river systems is often lacking (Naiman et al. 1995; Richter et al. 1997) and conceptual models of ecological function can be useful to guide restoration strategies (Trexler 1995). Large rivers exhibit a wide range of flow dynamics, and conceptual models should be evaluated before application to river management strategies (Thorp et al. 2006).

For over a decade, the flood pulse concept (FPC) (Junk et al. 1989) has been viewed as the best approximation of ecological function in large lowland rivers. The FPC emphasizes the importance of pulsed lateral connections to aquatic productivity and maintenance of biotic diversity. The timing of reproduction by fishes is predicted to

coincide with flood pulses that allow placement of offspring in floodplain habitats where they can exploit the high productivity associated with the aquatic/terrestrial transition zone (ATTZ). In temperate regions, optimal conditions for reproduction are predicted to occur when flooding coincides with appropriate temperatures, and lower recruitment is predicted when these conditions are not met (Bayley 1991). Humphries et al. (1999) proposed the low-flow recruitment hypothesis (LFR) for rivers in which flood dynamics are unpredictable or flood pulses do not coincide with rising temperature. This model recognizes the importance of lateral connectivity to ecological dynamics, but proposes that the timing of fish reproduction coincides with predictable low flows when temperatures are warm and food resources are concentrated.

Floodplain rivers support fish species with a diversity of life history strategies (Humphries et al. 1999; Winemiller et al. 2000; King et al. 2003). Environmental conditions that differentially affect reproduction and recruitment of species with different life history strategies (Magalhaes et al. 2003; Olden et al. 2006), and model predictions of reproduction (e.g. FPC) may only apply to a subset of species with a particular suite of traits. Flow management strategies that benefit one strategy may be detrimental to species that rely on alternate flow conditions (Sparks 1995; Scheerer 2002; Welcomme et al. 2006) or off-channel habitats that frequently are overlooked in instream flow management. Integration of conceptual models of reproduction with fish life history strategies can provide valuable information regarding flow management strategies necessary to support the diversity of fishes that occur in large rivers.

My goals for this study were to identify biotic and abiotic factors associated with reproductive activity of fishes with divergent life history strategies and compare patterns of fish reproductive activity and adult abundance within channel and floodplain habitats. I predicted that combinations of biotic and abiotic factors related to reproductive activity would be strongly associated with life history strategy and the value of habitats for reproduction by fishes with different life history strategies would primarily be associated with hydrologic connections among aquatic habitats.

METHODS

Study system

The main-stem Brazos River flows 1485 km from its origin near the Texas-New Mexico boarder to the Gulf of Mexico near Freeport, Texas. The current study was conducted on the middle Brazos between 30°25'N and 30°37'N (Figure 1). In this region the Brazos is a meandering low-gradient river bordered by forested and agricultural lands and drains a 76,361 km² catchment. Oxbow lakes are common on the middle Brazos floodplain, and hydrologic connections between oxbows and the channel are relatively unpredictable both within and among years (Winemiller et al. 2000; Zeug et al. 2005). The middle Brazos is less modified by dams and levees than other North American floodplain rivers, and although flow is partially regulated by dams in and above the city of Waco, Texas, current flow dynamics are relatively similar to pre-dam flows.

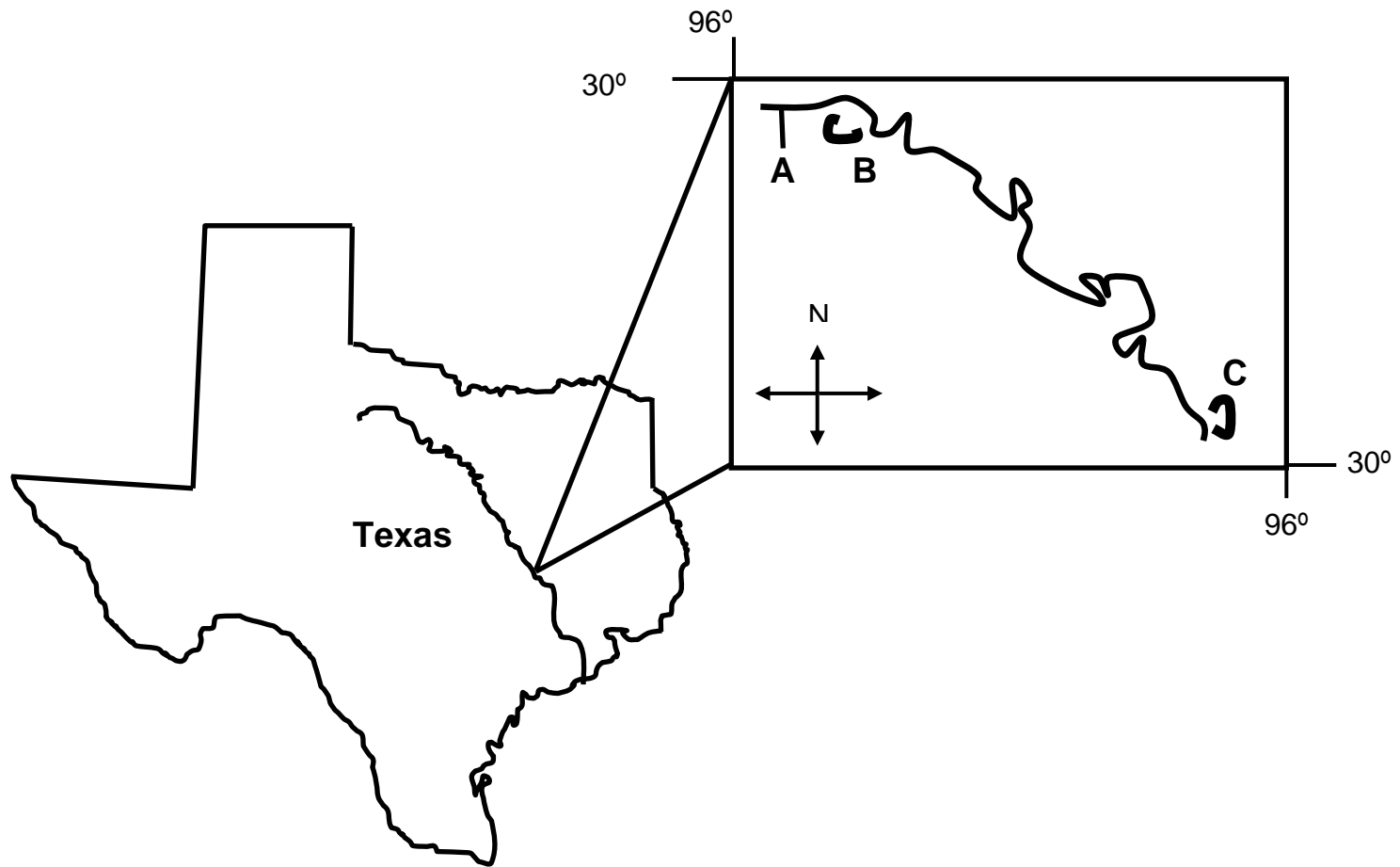


Figure 1. Map depicting the location of the Brazos River in Texas and the study reach on the middle Brazos. A = main channel survey site, B = rarely connected oxbow lake, C = frequently connected oxbow lake.

A previous survey of 10 Brazos oxbow lakes by Winemiller et al. (2000) found that oxbows with similar geomorphology had similar fish assemblages. Two of these oxbow lakes with different connection frequencies and a 7 km reach of the Brazos River were surveyed monthly from June 2003 to May 2005. One oxbow (OXFREQ) connects to the active channel relatively frequently at moderate levels of Brazos River discharge, and one oxbow (OXRARE) connects relatively rarely at high river discharge. The two oxbows were selected to span the range of oxbow connection frequencies based on the previous survey. Both oxbows were located on cattle ranches, however both lakes retained an unaltered riparian zone dominated by willow (*Salix sp.*). Oxbow substrates were composed primarily of mud and clay covered by leaf litter. Large woody debris was common in both habitats, and aquatic macrophytes were rare. Overbank flooding is the primary source of water for both oxbow lakes and extended periods of isolation result in oxbow desiccation. Mean maximum depth for OXFREQ and OXRARE during the study was 1.2 and 1.9 m, respectively. The surveyed reach of the Brazos River was selected based on boat access and proximity to the uppermost oxbow lake. Flows required for oxbow-river connections were estimated by surveys conducted by the Texas Water Development Board (TWDB) and were calibrated to a United States Geological Survey (USGS) gauge located near the Brazos River survey reach.

Abiotic predictor variables

Two variables representing flow regime were estimated to reflect different temporal scales to which species may respond. Floodplain connectivity during the current study period was measured as the days of habitat isolation calculated from

oxbow connectivity estimates provided by the Texas Water Development Board, and mean daily flow from USGS gauge 08108700. Given that the timing of reproduction could represent adaptation to the long-term hydrograph, the mean flow for each month of the year based on the previous 30 years of data was also included as a predictor variable. Temperature and dissolved oxygen were measured during each survey using a YSI 85 hand-held meter. Mean photoperiod in Brazos County during each month was obtained from the United States Naval Observatory, Astronomical Applications Department.

Biotic predictor variables

Zooplankton were collected using a 10-l Schindler trap with 80- μ m mesh in the cod end. Individuals were identified as rotifers, cladocerans or copepods, and densities were determined from two 1-ml sub-samples using a Sedgwick-Rafter counting cell. Predator abundance was estimated as the combined gillnet catch-per-unit effort (methodology described below) of alligator gar (*Atractosteus spatula*), spotted gar (*Lepisosteus oculatus*), longnose gar (*Lepisosteus osseus*), blue catfish (*Ictalurus furcatus*), channel catfish (*Ictalurus punctatus*), largemouth bass (*Micropterus salmoides*), spotted bass (*Micropterus punctulatus*), and white crappie (*Pomoxis annularis*).

Fish collection

Large-bodied fish (> 100 mm SL) were collected with two experimental gillnets that consisted of three panels measuring 16.5 X 2 m, with 25.4-, 76-, and 51-mm bar mesh. Gillnets were set between approximately 1700 h and 0700 h the next day. The

duration in hours of each set was recorded for calculation of species catch-per-unit effort (# species h⁻¹). Small-bodied fish (< 100 mm SL) were collected using a 10 X 2 m bag seine with 6.4 mm mesh in the wings and 3.2 mm mesh in the bag. A series of seine hauls was made perpendicular to shore along unique transects within the habitat until no new species were collected. The total distance traveled per survey was estimated, and CPUE was calculated as # species m⁻¹. Electrofishing was used to supplement samples of species associated with woody debris (bluegill, white crappie) that were not as easily captured with seines and gillnets. Collections were not made in the Brazos River during certain months due to high flows and oxbows were not sampled during November 2004 due to extensive flooding. All fishes were euthanized by immersion in tricaine methanesulfonate (MS222). Large fish were placed on ice, transported to the laboratory and stored frozen. Small fish were fixed in a 10% formalin solution and stored in 70% ethanol.

Based on their positions within the triangular life history continuum proposed by Winemiller and Rose (1992), seven species were selected for estimation of reproductive activity in relation to biotic and abiotic characteristics. Among Brazos River fishes, the western mosquitofish (*Gambusia affinis*) and red shiner (*Cyprinella lutrensis*) represent the opportunistic strategy, bluegill (*Lepomis macrochirus*) and white crappie (*Pomoxis annularis*) represent the equilibrium strategy, and gizzard shad (*Dorosoma cepedianum*), spotted gar (*Lepisosteus oculatus*) and longnose gar (*Lepisosteus osseus*) represent the periodic strategy. Opportunistic strategists are characterized by small adult size, short generation time, high reproductive effort, and extended breeding seasons. Species with

this strategy can quickly colonize disturbed or newly available habitats. Equilibrium strategists have characteristics (high juvenile survivorship, parental care, and large eggs) inferred to be adaptive in habitats where resources are limited and/or density dependence is strong. Periodic strategists are characterized by delayed maturation, large adult body size, high fecundity, and contracted breeding seasons. This strategy is predicted to perform well when resources for larvae are patchy in space or time (Winemiller and Rose 1993), and reproduction is synchronized with favorable periods that are relatively predictable between years. Two gar species were included here, because there is strong habitat partitioning between these species. Longnose gar are more abundant in the river channel and spotted gar are more abundant in oxbows (Winemiller et al 2000; Zeug et al. 2005).

To validate that species used for analysis represented the three endpoint strategies in the Winemiller-Rose life history model, correspondence analysis (CA) was performed on six life history characteristics estimated for each species (Figure 2). Characteristics included in CA were: minimum length at maturity (L_{\min}), maximum length (L_{\max}), mean fecundity, length of the reproductive period, mean egg size, and the presence or absence of parental care. Minimum length at maturity was defined as the smallest female observed with ripe gonads, and maximum length was defined as the largest female collected. Length of the reproductive period was estimated as the number of months when ripe females were collected. Females were classified as ripe based on the gonadosomatic index and presence of mature oocytes in ovaries. Mature oocytes were those \geq the greatest modal egg size observed during the reproductive period of

each species. Information regarding the presence or absence of parental care was obtained from literature.

Sample processing

Reproductive activity was estimated using the gonadosomatic index (GSI) for females [$100 * (\text{gonad mass}/\text{body mass})$] (Figures 3, 4, and 5). Individuals were measured to the nearest mm standard length (SL) and weighed to the nearest 0.01 g. Ovaries were removed, blotted dry, and weighed to the nearest 0.001 g on an analytical balance. Ovaries were stored in a 10% formalin solution buffered with sodium phosphate for later fecundity and egg size estimation. For most species, all individuals were processed. Large numbers of mosquitofish and red shiners were collected in monthly surveys (> 100 individuals) and for these species, individuals were placed into 5-mm size classes and 3 individuals from each size class were processed.

Red shiner and mosquitofish fecundity was estimated by direct count. Red shiner ovaries contained multiple batches of eggs based on size frequency distributions, and only the largest size class was used for fecundity estimation (batch fecundity). For all other species, a sub-sample of the anterior portion of the ovary was removed and fecundity calculated as:

$$F_{\text{total}} = (OW_{\text{total}} \times E_{\text{sub}}) / OW_{\text{sub}}$$

where OW_{total} is the total ovary weight, E_{sub} is the number of eggs in the sub-sample, and OW_{sub} is the weight of the sub-sample. Mean egg size was estimated by measuring the largest egg in the ovary or sub-sample and averaging values for all individuals of a species in the sample.

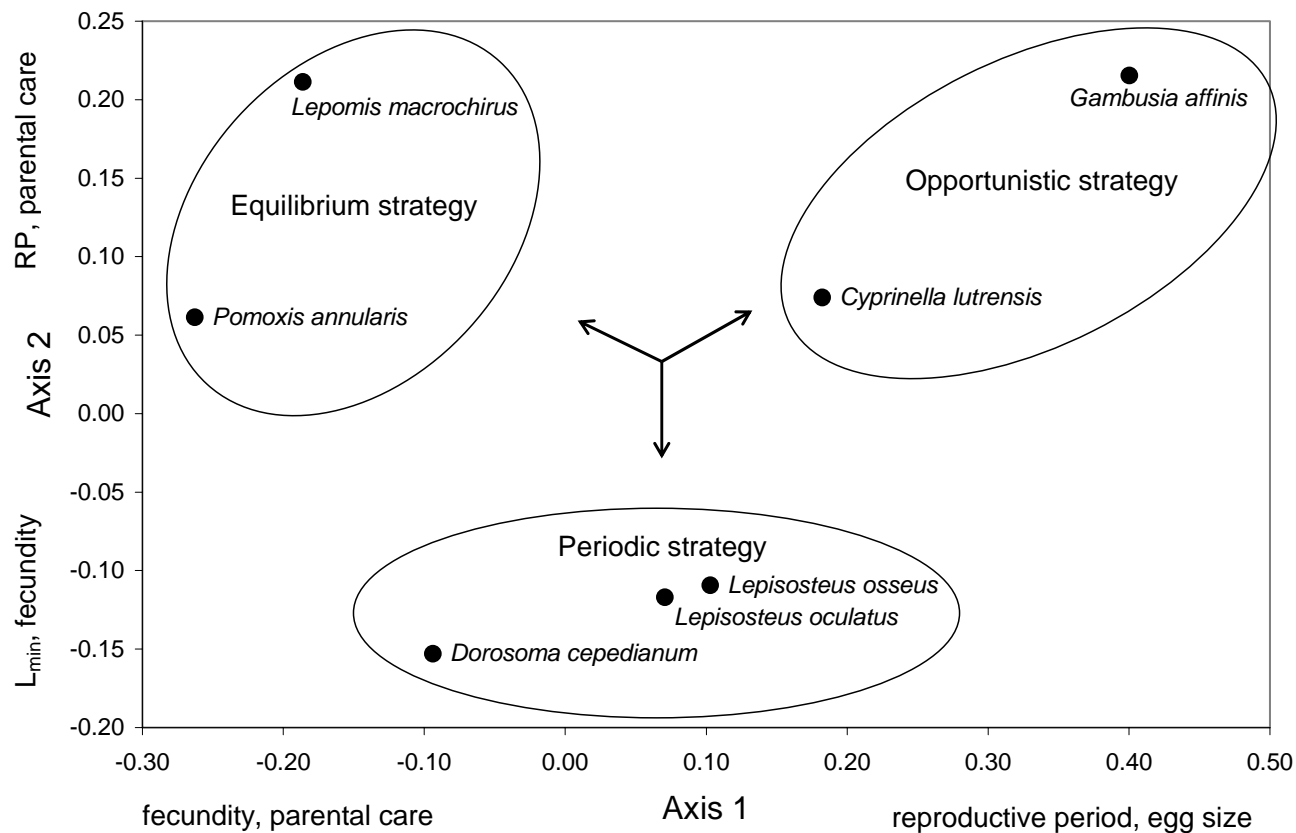


Figure 2. Ordination of species scores from correspondence analysis based on the six estimated life history characteristics. Axis 1 modeled 59.6 % of the total variation; axis 2 modeled 25.5 % of variation. Axis 1 variable loadings: $L_{\min} = 0.45$, $L_{\max} = 0.36$, reproductive period = 1.41, fecundity = -0.82, parental care = -6.19, egg size = 2.05. Axis 2 variable loadings: $L_{\min} = -0.27$, $L_{\max} = -0.03$, reproductive period = 2.40, fecundity = -0.48, parental care = 7.07, egg size = 0.29.

To determine if GSI was a sufficient predictor of reproductive activity, linear regressions were performed to test the null hypothesis of no difference between GSI and modal egg size for each species. For mosquitofish, embryo developmental stage was substituted for egg size (Haynes 1995). Additionally regressions were performed to determine if body size (standard length) within species was related to GSI. The relationship between GSI and egg size or developmental stage was positive and significant for all seven species indicating that GSI is an appropriate response variable (red shiner $R^2 = 0.48$, $P < 0.001$, mosquitofish $R^2 = 0.16$, $P < 0.001$, gizzard shad $R^2 = 0.50$, $P < 0.001$, spotted gar $R^2 = 0.10$, $P = 0.03$, longnose gar $R^2 = 0.48$, $P < 0.001$, white crappie $R^2 = 0.45$, $P < 0.001$, bluegill $R^2 = 0.21$, $P < 0.001$). Additionally, peaks in juvenile abundance closely followed periods of high GSI (Zeug unpublished data). The relationship between standard length and GSI was significant for mosquitofish ($R^2 = 0.10$, $P < 0.001$) and spotted gar ($R^2 = 0.11$, $P = 0.03$). For these species, residuals of the relationship between SL and GSI were used as the response variable in place of raw GSI.

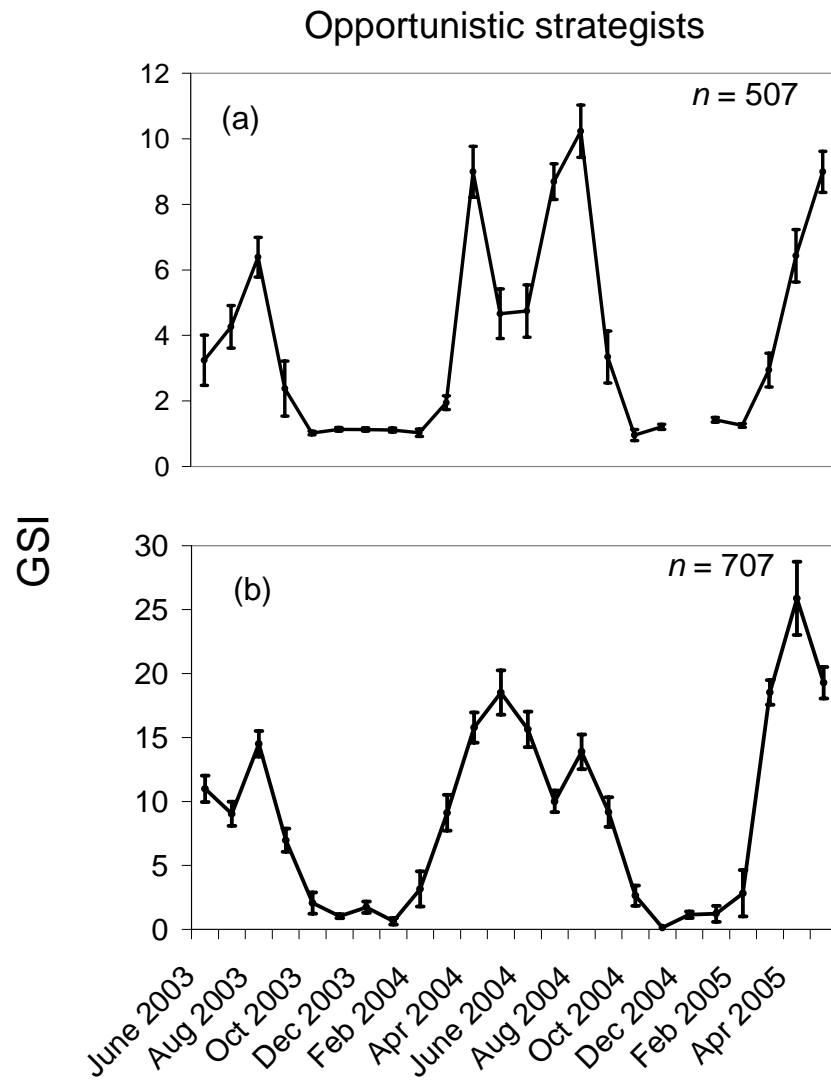


Figure 3. Plot of mean GSI values over the 2-year study period for the two opportunistic strategists. Species in each panel are as follows (a) = red shiner, (b) = mosquitofish.

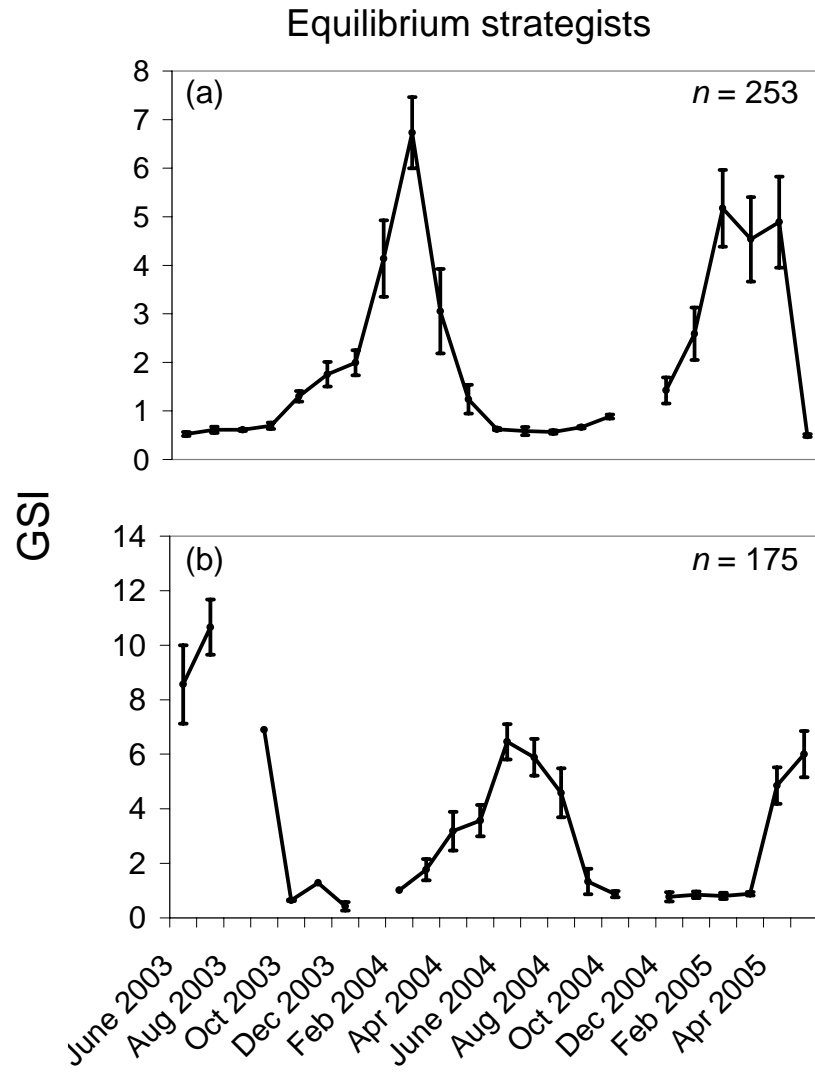


Figure 4. Plot of mean GSI values over the 2-year study period for the two equilibrium strategists. Species in each panel are as follows (a) = white crappie, (b) = bluegill.

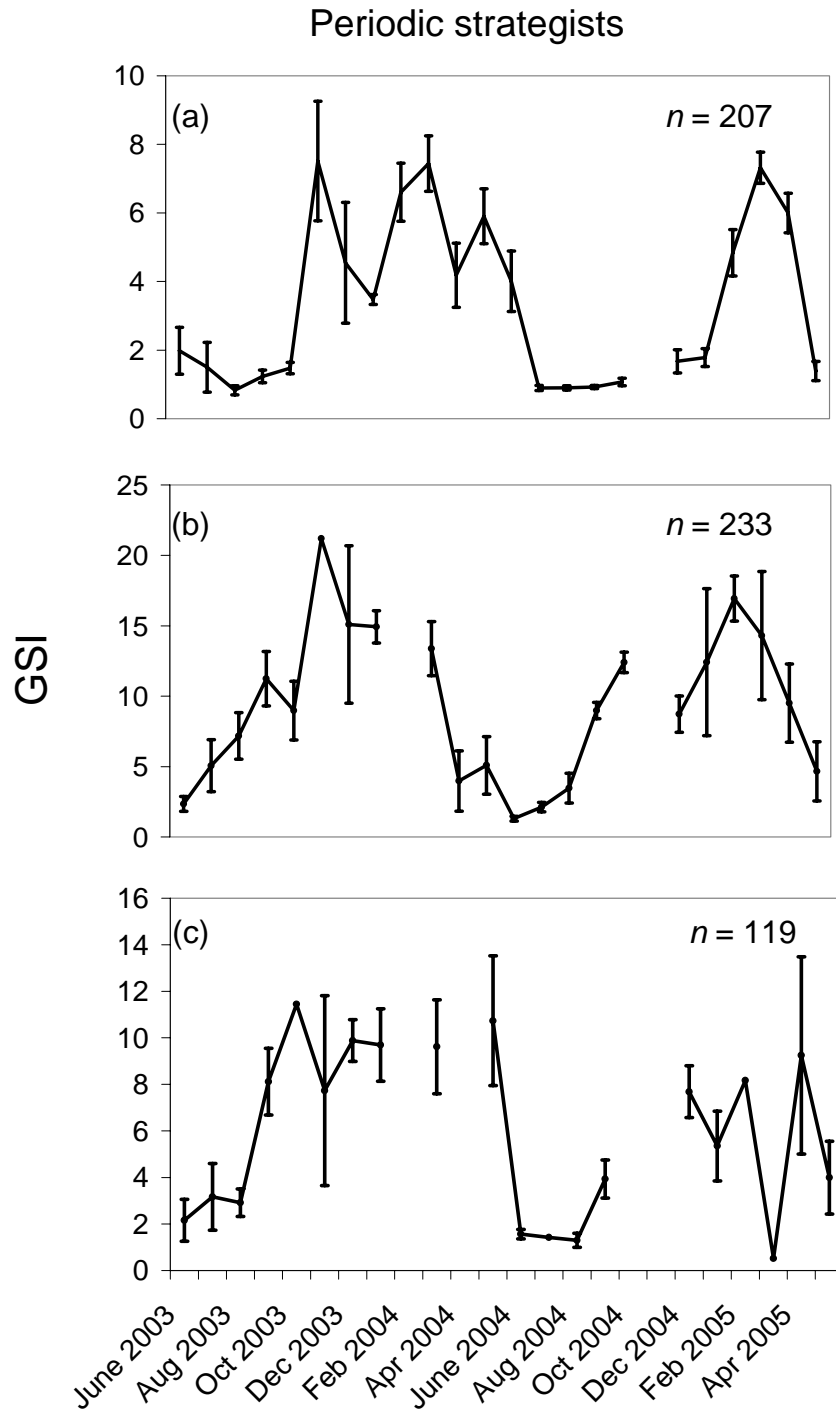


Figure 5. Plot of mean GSI values over the 2-year study period for the three periodic strategists. Species in each panel are as follows (a) = gizzard shad, (b) = spotted gar and (c) = longnose gar.

Model construction and selection

Model sets were constructed for each species based on biotic and abiotic factors predicted by conceptual models (FPC, LFR) to influence fish reproductive activity. Both conceptual models predict associations between reproductive activity, flood dynamics, temperature and larval food resources. The density of predators of early life stages also can be influenced by water level (Copp 1992) and was included as a predictor variable. Measured variables considered for inclusion in models of reproductive activity included, mean monthly river discharge (calculated for the previous 30-years of record), days of floodplain isolation, temperature, photoperiod, rotifer density, copepod density, cladoceran density, and predator abundance.

Correlation analysis was performed on independent variables to identify potential sources of multicollinearity. Temperature was significantly and positively correlated with rotifer density and photoperiod. Temperature was retained, and rotifer density and photoperiod were excluded from the analysis. Temperature was retained because of its predicted importance in conceptual models. Cladoceran and copepod densities were combined into the variable “microcrustacean density”. Tests for normality were performed on dependent variables (GSI or residuals) prior to model construction. When the assumption of normality was not met, data were log transformed as $\log_{10}(x + 1)$. Surveys in the Brazos River produced few crappie and bluegill, thus these species models included samples from oxbows only. Additionally, the longnose gar model was calculated using samples exclusively from the Brazos River.

Independent variables used in models included: 30-year hydrograph, isolation days, microcrustacean density, temperature, and predator abundance. To insure that models reflected biological reality as closely as possible, some variable combinations were excluded from consideration. For example, predator abundance is predicted to be greater during low-water periods and lower during high-water periods when aquatic habitats are expanded (Copp 1992). The variable isolation days reflected this change in water level during the study, whereas the 30-year hydrograph was not linked to conditions during the study when predator abundance was estimated. Therefore predator abundance was considered in conjunction with isolation days but not with the 30-year hydrograph. Twenty-one candidate models were evaluated. Generalized linear models were constructed for mosquitofish, red shiner, longnose gar, spotted gar and bluegill, whereas autoregressive models were constructed for shad and white crappie due to first-order autocorrelation in model residuals. Both modeling techniques utilized maximum likelihood to estimate model parameters. All models were constructed using SAS (Version 9.1.3)

Best approximating models were selected using an information-theoretic approach. Because it allows the evaluation of evidence in data for multiple working hypotheses, this methodology is superior to traditional hypothesis testing when using observational data (Burnham and Anderson 2002; Hobbs and Hilborn 2006). In the present study, each candidate model was considered a working hypothesis. This methodology has been successfully used to evaluate models for a wide range of ecosystems (Harig and Faush 2002; Sztatecsny et al. 2004; Torgersen and Close 2004).

Akaike's Information Criterion corrected for small sample size (AIC_c) was used to select best approximating models from the candidate set. Models were ranked using ΔAIC_c values, AIC_c weights (w_i), and evidence ratios. Model weights are interpreted as the probability that the model would be selected as the "best model" after many repetitions of model selection (Hobbs and Hilborn 2006). Evidence ratios estimate support in the data for two models based on model weights. Ratios were computed as w_i/w_j , where w_i is the model weight for the best model in the candidate set. Models with $\Delta AIC_c < 2.00$ and evidence ratios < 2.70 were considered competing models. To reduce model selection uncertainty, model averaged estimates of regression coefficients and unconditional standard errors were calculated from the entire model set. Model averaging can reduce model bias and increase precision of regression coefficient estimates (Burnham and Anderson 2002). Unconditional 95% confidence intervals were used to determine the level of support for regression coefficients. When confidence intervals included zero, the coefficient was assumed to have little support.

Species abundance

Catch-per-unit effort of adults of each species was compared among habitats using generalized estimating equations (GEE). Abundance estimates were log transformed ($\log_{10} x + 1$) in order to meet assumptions of the GEE procedure. The variable "month" was included as the repeated variable in the model, and an autoregressive correlation structure among months was specified. When significant differences were detected, pairwise tests were conducted. Because the same response

variable was used in multiple tests, P -values were corrected using the Bonferroni correction ($\alpha_{\text{adjusted}} = 0.013$).

RESULTS

Life history classification

Correspondence analysis produced two axes that explained 85.1% of the variation in species life history characteristics (Figure 2). Three end-point strategies were well differentiated in the CA ordination. Axis one contrasted opportunistic species (red shiner and mosquitofish) that had longer reproductive periods and small body size from equilibrium species (bluegill and crappie) that had greater body size, fecundity and parental care. Axis two contrasted periodic species (shad, spotted gar, and longnose gar) that had greater fecundity, body size at maturity, and maximum length, from equilibrium and opportunistic species that had more developed parental care and longer reproductive periods.

Flood dynamics

Multiple flood events connected oxbow and channel habitats during the 2-year study period (Figure 6). Flow dynamics did not appear to follow a seasonal pattern and floods occurred in all four seasons. Nine flood events connected OXFREQ with the river channel for a total of 56 days of connectivity. Four flood events connected OXRARE with the river channel for a total of 10 days of connectivity. The 30-year hydrograph indicated mean flows were greatest in May and June and lowest in August and September.

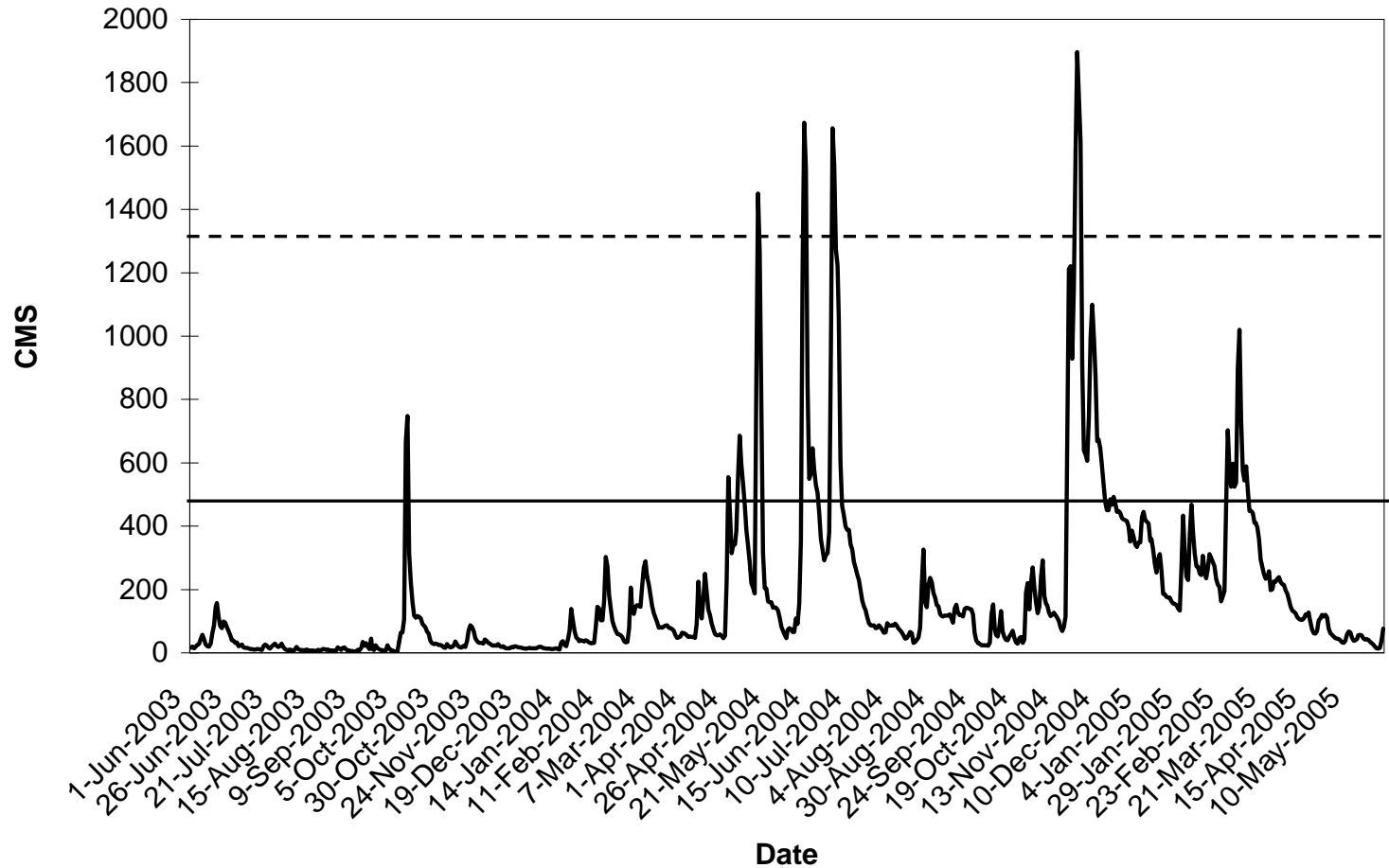


Figure 6. Daily stream flow hydrograph of the Brazos River during the two year study period. The solid horizontal line represent flows required to connect OXFREQ with the river channel and the dashed line represent flows required to connect OXRARE.

Opportunistic strategists

The best approximating model for mosquitofish indicated positive associations between GSI, the 30-year hydrograph and temperature (Table1). The next best model was more than two times less likely (evidence ratio 2.35) and included variables from the best model with the addition of microcrustacean density. Model averaged parameter estimates and confidence intervals indicated microcrustacean density had little support (Table 2). The best model selected for red shiner had positive associations between GSI, the 30-year hydrograph and temperature (Table1). Three competing models contained the two variables from the best model as well as combinations of microcrustacean density (negative association), isolation days (positive association) and predator abundance (negative association) (Table 1). Model averaged parameter estimates indicated that only the 30-year hydrograph, temperature and predator abundance had support (Table 2).

Periodic strategists

The best gizzard shad model contained positive associations between GSI, the 30-year hydrograph and microcrustacean density, and negative associations between GSI, days of habitat isolation and predator abundance. The second best model was 2.57 times less likely and consisted of the previous parameters with the addition of temperature (negative association). Model averaged estimates indicated little support for isolation days and temperature (Table 2). The highest ranked model for spotted gar included negative associations between GSI and temperature (Table 1). The competing model included temperature and the 30-year hydrograph (negative association) and both

variables had good support (Table 2). The best longnose gar model indicated negative associations between GSI and temperature. The next best model (evidence ratio = 2.58) included temperature and a positive association with the 30-year hydrograph although the hydrograph had little support.

Equilibrium strategists

Two competing models were selected for bluegill (Table 1). The best model contained temperature and the 30-year hydrograph as predictors, and both associations were positive. The competing model contained the two predictor variables from the best model and a negative association with microcrustacean density, however only the predictors from the best model had good support (Table 2). The best model selected for white crappie included negative associations with GSI and temperature, and positive associations with GSI and microcrustacean density (Table 1). The next best crappie model included the variables from the best model and a positive association with the 30-year hydrograph. This model was 3.41 times less likely compared with the best model and the 30-year hydrograph had little support.

Table 1. Best approximating model(s) for each species based on ΔAIC_c values model weights and evidence ratios. K = the number of parameters estimated for each model and ER = evidence ratio. β_1 = 30-yr hydrograph, β_2 = temperature, β_3 = microcrustacean density, β_4 = isolation days, β_5 = predator abundance, β_6 = autocorrelation correction parameter.

Species	Model(s)	ΔAIC_c	AIC_c weight	ER	K
mosquitofish (<i>Gambusia affinis</i>)	β_1, β_2	0.00	0.42	1.00	4
	$\beta_1, \beta_2, \beta_3$	1.72	0.18	2.35	5
red shiner (<i>Cyprinella lutrensis</i>)	β_1, β_2	0.00	0.37	1.00	4
	$\beta_1, \beta_2, \beta_4$	1.60	0.17	2.24	5
	$\beta_1, \beta_2, \beta_3$	1.64	0.16	2.29	5
gizzard shad (<i>Dorosoma cepedianum</i>)	$\beta_1, \beta_2, \beta_4, \beta_5$	1.90	0.14	2.60	6
	$\beta_1, \beta_3, \beta_4, \beta_5, \beta_6$	0.00	0.67	1.00	7
	$\beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \beta_6$	2.57	0.19	3.61	8
spotted gar (<i>Lepisosteus oculatus</i>)	β_2	0.00	0.27	1.00	3
	β_1, β_2	0.11	0.26	1.05	4
longnose gar (<i>Lepisosteus osseus</i>)	β_2	0.00	0.46	1.00	3
	β_1, β_2	2.58	0.13	3.63	4
bluegill (<i>Lepomis macrochirus</i>)	β_1, β_2	0.00	0.42	1.00	4
	$\beta_1, \beta_2, \beta_3$	1.57	0.19	2.18	5
white crappie (<i>Pomoxis annularis</i>)	$\beta_2, \beta_3, \beta_6$	0.00	0.43	1.00	5
	$\beta_1, \beta_2, \beta_4, \beta_6$	2.47	0.13	3.41	6

Table 2. Model averaged estimates of regression coefficients with unconditional 95 % confidence intervals. Asterisks indicate parameters that were found to have little support following calculation of unconditional confidence intervals. β_1 = 30-yr hydrograph, β_2 = temperature, β_3 = microcrustacean density, β_4 = isolation days, β_5 = predator abundance, β_6 = autocorrelation correction parameter.

Species	β_1	β_2	β_3
mosquitofish	0.55 (0.37 - 0.74)	1.74 (1.45 - 2.02)	-0.03* (-0.01 - 0.07)
red shiner	0.49 (0.33 - 0.64)	1.56 (1.32 - 1.79)	-0.03* (-0.06 - 0.00)
gizzard shad	0.41 (0.28 - 0.54)	-0.03* (-0.30 - 0.24)	0.12 (0.09 - 0.16)
spotted gar	-0.31 (-0.52 - -0.10)	-1.04 (-1.37 - -0.71)	-0.01* (-0.07 - 0.04)
longnose gar	0.24* (0.00 - 0.49)	-0.94 (-1.28 - -0.60)	-0.04* (-0.12 - 0.40)
bluegill	0.40 (0.24 - 0.55)	1.36 (1.12 - 1.60)	-0.05* (-0.09 - 0.00)
white crappie	0.10* (-0.14 - 0.34)	-0.69 (-0.99 - -0.40)	0.15 (0.09 - 0.21)

Table 2. Continued

Species	β_4	β_5	β_6
mosquitofish	-0.02* (-0.08 - 0.04)	0.53 (0.18 - 0.89)	- -
red shiner	0.05* (0.00 - 0.10)	-0.40 (-0.68 - -0.13)	- -
gizzard shad	-0.03* (-0.08 - 0.03)	-0.69 (-0.94 - -0.43)	-0.32 (-0.48 - -0.16)
spotted gar	-0.01* (-0.08 - 0.07)	-0.20* (-0.63 - 0.23)	- -
longnose gar	0.08* (-0.05 - 0.21)	-0.51* (-1.13 - 0.11)	- -
bluegill	0.03* (-0.03 - 0.08)	-0.15* (-0.50 - 0.19)	- -
white crappie	-0.04* (-0.02 - 0.10)	-0.30* (-0.66 - 0.06)	-0.48 (-0.65 - -0.32)

Adult abundance

Significant differences among habitats were detected for all species with the exception of mosquitofish (Table 3). Among oxbow lakes, species abundances were similar with the exception of gizzard shad that were significantly more abundant in OXFREQ than the other two habitats (Table 3). Red shiners were more abundant in the river channel than oxbows (Figure 7). Spotted gars were more abundant in oxbows, and longnose gars were more abundant in the river (Figure 7). Bluegills were more abundant in OXRARE than the river channel, and white crappies were more abundant in oxbows relative to the river channel (Figure 7).

DISCUSSION

Model selection indicated that temperature and the 30-year hydrograph had strong support as factors associated with reproductive activity of species with divergent life history strategies. Five of the seven species examined had competing models that included well supported associations with the 30-year hydrograph, whereas isolation days during the study period had little support in data for any species. This suggests that a subset of Brazos River fishes have reproductive ecologies adapted to long-term hydrologic dynamics which supports FPC model that stresses the importance of predictable flow periods to fish reproductive activity (Junk et al. 1989; Bayley 1991). The advantage of floodplain inundation should be greater when floods coincide with optimal temperatures (Gutreuter et al. 1999; Winemiller 2005; Schramm and Eggleton 2006). Over the 2-year study period, some floods occurred outside of species'

Table 3. Results of generalized estimating equations comparing abundance of adults between habitats. Significance was assessed at $\alpha = 0.013$ (Bonferroni corrected).

Species	All habitats		BR x OF		BR x OR		OF x OR	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
mosquitofish	3.20	0.202	-	-	-	-	-	-
red shiner	14.50	< 0.001	14.19	< 0.001	13.99	< 0.001	2.24	0.135
gizzard shad	18.14	< 0.001	17.45	< 0.001	4.29	0.038	13.80	< 0.001
spotted gar	12.64	0.002	7.85	0.005	12.91	< 0.001	3.12	0.077
longnose gar	12.89	0.002	13.05	0.002	13.32	< 0.001	0.11	0.735
bluegill	11.04	0.004	3.69	0.055	8.27	0.004	6.08	0.014
white crappie	17.69	< 0.001	11.87	0.001	13.42	< 0.001	2.92	0.087

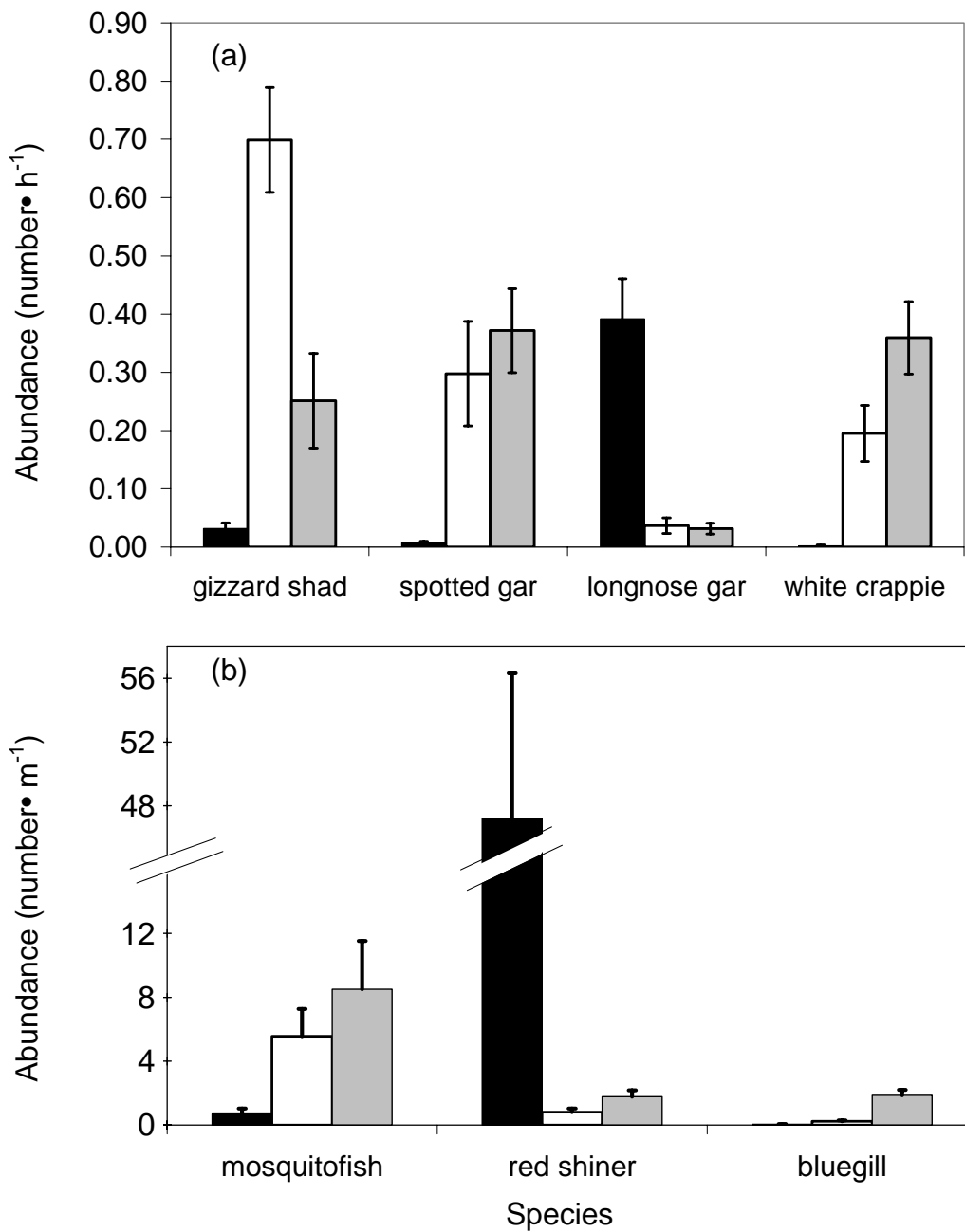


Figure 7. Mean abundances and standard errors for adults of the seven selected species in each habitat. The top panel (a) contains abundances of large species captured in gillnets and the bottom panel (b) contains small species captured with seines. Closed bars = Brazos River, open bars = OXFREQ and gray bars = OXRARE.

reproductive periods (winter and fall), and this may have influenced the weak support for the short-term hydrologic predictor variable (isolation days).

Relationships between GSI and temperature suggested that species with different life history traits may exploit floods differently. Negative relationships between GSI and temperature were associated with species (longnose gar, gizzard shad and white crappie) that had greater fecundity (mean fecundity $> 13,000$) and maximum body size (maximum SL > 250 mm). Reproductive activity of these species was greatest in spring as the 30-year hydrograph was increasing. This strategy would allow early life stages to move into slack-water floodplain habitats that are important nursery areas for some species (Sabo and Kelso 1991; Killgore and Baker 1996; Pease et al. 2006). Species with positive associations between GSI and temperature (mosquitofish, red shiner and bluegill) had small adult sizes (maximum SL < 110 mm) and extended reproductive periods (5-7 months). Reproductive activity of these species coincided with peak flows that may allow them to colonize off-channel floodplain habitats and exploit them for reproduction during low-flow periods. King et al. (2003) reported that mosquitofish were one of the few species that revealed an increase in juvenile abundance in response to flooding in an Australian floodplain river. Only spotted gar had a negative association with the 30-year hydrograph. Adults of this species are common in backwater habitats and may reproduce during low flow-periods as described in the LFR model (Humphries et al. 1999).

Biotic predictor variables tended to have less support for most species and may have a greater effect on young-of-the-year survival whereas abiotic variables had a

greater influence on reproductive activity. Despite this pattern, several well supported associations with biotic predictors were identified. Crappie and shad had positive associations with microcrustacean density that were strongly supported by data. The density of food resources for larvae is important to the production of strong year classes for species that produce many small offspring (Winemiller and Rose 1993), and shad and crappie had the greatest mean fecundity and smallest eggs of the seven species examined. Gizzard shad and red shiner had negative associations with predator abundance, whereas mosquitofish had a positive association. Zeug et al. (2005) found that red shiner abundance was significantly influenced by predator abundance in a Brazos oxbow, and juvenile gizzard shad are a common food item of Brazos predators (Zeug unpublished data). Mosquitofish are able to exploit shallow habitats that may allow them to reproduce successfully despite greater predator abundance.

Copp (1989) suggested that patterns of adult abundance are good indicators of the reproductive function of a habitat. Evaluation of adult abundance patterns in the Brazos River suggested that oxbow lakes were particularly important for equilibrium strategists (crappie, bluegill) that were rarely collected in the main channel where frequent sub-bankfull flows may disrupt reproductive activity. Crappie and bluegill are nest building brood guarders, and reproduction in the channel may be less successful during flood conditions. Bonvechio et al. (2005) found negative associations between flow rate and year class strength of equilibrium species (centrarchids) in Florida rivers. Periodic species were abundant in Brazos River channel and floodplain habitats. The larger size and greater longevity of periodic species allow them to survive during sub-

optimal periods, and although some reproduction probably occurs every year (Humphries et al. 2002), strong year classes may be produced only when floods coincide with optimal temperatures (Sommer et al. 2001; Halls and Welcomme 2004). Opportunistic strategists were abundant in all habitats, and these species may be able to reproduce successfully in a variety of habitats and under a wide range of environmental conditions (Winemiller 1989; Spranza and Stanley 2000). Some species may use multiple habitats during their life cycle (Schiemer 2000), however among the seven species surveyed in the Brazos, there was no obvious segregation between adult and juvenile habitats.

Observed patterns of reproductive activity and habitat occupancy suggest that both flood dynamics and habitat heterogeneity were important for fish reproduction in rivers. Pease et al. (2006) found that both flood timing and low velocity off-channel habitats were important for larval and juvenile fishes in the Rio Grande, New Mexico. Instream flow methodologies that focus on historical flow characteristics, such as the range of variability approach (RVA) proposed by Richter et al. (1997), may be superior to other methodologies (Jowett 1997) because fish reproductive ecologies appear to be adapted to long-term hydrologic dynamics. Off-channel floodplain habitats, such as oxbow lakes, sloughs and marshes, provide valuable spawning and nursery areas for many fish species (Sabo and Kelso 1991; Killgore and Baker 1996; Swales et al. 1999) and appear to be particularly important for equilibrium-type species (Kwak 1988; Scott and Nielsen 1989). Most instream flow strategies focus on in-channel or seasonally flooded habitats (Jowett 1997), however perennial-slack water areas also require

consideration. Construction of levees or alteration of fluvial processes that drive the creation and succession of off-channel habitats would likely result in reduced productivity of species associated with these habitats (Aarts et al. 2004; Schiemer et al. 2003).

Species responses to flow regulation and flood management strategies may be predicted in the context of life history-environment relationships (Olden et al. 2006), however, caution should be used in the application of these results. Only seven of 45 species collected (16%) were included in our study. The three endpoint model of Winemiller and Rose (1992) describes a gradient, and certain species have characteristics that would place them at intermediate positions between endpoint strategies. Some species have highly specific physicochemical or other habitat requirements for reproduction that may be obscured by analyses at the level of life history strategy. Only three habitats were surveyed for adult abundance estimates over the two year study however, a previous survey of 10 Brazos oxbows by Winemiller et al. (2000) indicated that habitats with similar geomorphic characteristics supported similar abundances of species with similar life history traits.

Large rivers display a wide range of hydrologic dynamics and spatial habitat units that influence aquatic fauna (Puckridge et al. 1998; Thorp et al. 2006). Alteration of either of these components can significantly reduce fish populations adapted to natural fluvial dynamics (Moyle and Light 1996; Aarts et al. 2004). Consideration of how alternative life history strategies respond to flow and habitat features of fluvial

systems can increase the utility of conceptual models as guides for flow management and habitat restoration strategies.

CHAPTER III

RELATIONSHIPS BETWEEN HYDROLOGY, SPATIAL HETEROGENEITY, AND

FISH RECRUITMENT DYNAMICS IN A TEMPERATE FLOODPLAIN RIVER.

INTRODUCTION

Flood dynamics are predicted to be the primary environmental factor influencing fish recruitment in large rivers (Sparks, 1995; Agostinho et al. 2004; Winemiller, 2005). The flood pulse concept (FPC; Junk et al. 1989) suggests that annual floodplain inundation triggers blooms of primary and secondary production, and fish in these systems have reproductive ecologies adapted to exploit this pulse of production. In temperate zone rivers, flood pulses that coincide with optimal temperatures have been associated with greater growth and survival of some species (Gutreuter et al. 1999; Sommer et al. 2001; Schramm and Eggleton 2006) and are predicted to increase fish recruitment, whereas the absence of a flood pulse or lack of synchronization between temperature and over-bank flooding reduces recruitment success (Bayley, 1991; Halls and Welcomme 2004). Despite widespread acceptance of the FPC model, recent studies suggest that in rivers where flood dynamics do not exhibit the optimum described in the FPC, fish can recruit successfully during low-flow periods (Humphries et al. 1999; Humphries et al. 2002; King et al 2003). Humphries et al. (1999) described this recruitment strategy as part of a low flow recruitment hypothesis (LFR) proposed to explain fish population dynamics in rivers with less predictable flow regimes.

Habitat heterogeneity also has a significant impact on fish recruitment, and loss of certain habitat types due to hydrologic modification and floodplain disconnection may

be the primary cause of reduced recruitment in modified rivers (Aarts et al. 2004). Fluvial dynamics create a mosaic of habitats within river-floodplain systems including off-channel habitats such as oxbow lakes, sloughs and other slack water areas (Amoros and Bornette 2002). These habitats serve a variety of ecological functions including spawning and nursery areas and refuge from high flows in the main channel (Sabo and Kelso 1991; Humphries et al. 2006; Pease et al. 2006). Physicochemical attributes of different habitat units have a strong influence on local species assemblages (Tejerina-Garro et al. 1998; Winemiller et al. 2000; Suarez et al. 2004) and interactions between flood dynamics and habitat characteristics influence the value of different habitats for spawning, feeding or refuge (Feyrer et al. 2006).

Attempts to elucidate optimal conditions for recruitment are complicated by the diversity of reproductive tactics displayed by fishes in large rivers. Flow and habitat characteristics that benefit one strategy may be detrimental to others (Sparks, 1995; Scheerer, 2002), and recruitment dynamics may not be synchronized among species with divergent strategies (Welcomme et al. 2006). Because the performance of populations with particular suites of life history traits has been associated with both hydrologic dynamics (Merigoux et al. 2001; Magalhaes et al. 2003; Olden et al. 2006) and habitat characteristics (Persat et al. 1994; Townsend and Hildrew 1994; Winemiller, 1996), life history theory provides a good framework for evaluating environmental influences on recruitment dynamics.

My goals for this study were to evaluate the relative influence of hydrology and habitat characteristics on recruitment of species with divergent life history strategies, and

to associate recruitment dynamics of each species with environmental characteristics in each habitat and hydrologic period. I predicted that conceptual models of recruitment would apply to fish in the Brazos River and that hydrologic and habitat characteristics that maximize recruitment would be strongly associated with life history strategy.

METHODS

Study system

The Brazos River is a meandering low-gradient river that flows southeast > 1400 km from the Texas-New Mexico border to the Gulf of Mexico 2 km south of Freeport, Texas. The current study was conducted on the middle Brazos River in east-central Texas (Figure 1). The middle Brazos is partially regulated by dams near the city of Waco, Texas; however, flow dynamics are primarily driven by regional precipitation with contemporary fluvial dynamics approximating historical conditions based on historical USGS flow data. Oxbow lakes are common on the Brazos floodplain and connections between oxbows and the active river channel occur at irregular intervals in response to flow magnitude and oxbow geomorphology. For additional study site details see Winemiller et al. (2000) and Zeug et al. (2005).

Two oxbow lakes with different connection frequencies and a 7 km reach of the Brazos River channel located near the most upstream oxbow were surveyed monthly from June 2003 to May 2005. These oxbow lakes were selected to represent a range of connection frequencies from rare to frequent. One oxbow (OXFREQ) connected frequently at moderate levels of river discharge and the other oxbow (OXRARE) connected rarely at high levels of river discharge. Flows required to connect oxbows

with the river channel were determined by surveys conducted by the Texas Water Development Board and calibrated to a United States Geological Survey (USGS) flow gauge located near the Brazos River survey reach.

Biotic and abiotic characteristics

Environmental variables measured during each survey were selected based on predictions of conceptual models of fish recruitment in floodplain rivers (FPC, LFR). Temperature and dissolved oxygen were measured using a YSI 85 meter. Maximum depth of each oxbow and the main channel site was recorded to the nearest 1 cm. Days of isolation (i.e. no connection with the river) were calculated using daily stream flow data from USGS gauge and TWDB estimates of oxbow connection thresholds.

Zooplankton were collected using a 10 l Shindler trap with an 80 μm mesh cod end.

Organisms were identified as rotifers or microcrustaceans (copepods and cladocerans) and densities were estimated from two 1-ml sub-samples using a Sedgewick-Rafter counting cell. Predator abundance was estimated as the combined gillnet catch-per-unit effort of alligator gar (*Atractosteus spatula*), spotted gar (*Lepisosteus oculatus*), longnose gar (*Lepisosteus osseus*), blue catfish (*Ictalurus furcatus*), channel catfish (*Ictalurus punctatus*), largemouth bass (*Micropterus salmoides*), spotted bass (*Micropterus punctulatus*), and white crappie (*Pomoxis annularis*).

Fish collection

Fishes were collected using a combination of standardized seine hauls and gillnet sets. Small-bodied species and juveniles of large-bodied species were collected with a 10 x 2-m bag seine composed of 6.4-mm mesh in the wings and 3.2-mm mesh in the

bag. A series of seine hauls was made perpendicular to shore along unique transects within the habitat until no additional species were added to the cumulative list. The total distance traveled with the seine was recorded for calculation on catch-per-unit effort (CPUE). In order to collect large-bodied fishes, two multifilament gillnets were deployed between approximately 1700 h and 0700 h the next day. Each gillnet contained three panels measuring 16.5 x 2 m with 25.4-, 76-, and 51-mm bar mesh. The total hours of each set was recorded for CPUE calculations. During certain months, samples were not collected in the Brazos River due to high flows.

Collected specimens were euthanized with tricaine methanesulfonate (MS222). Small individuals collected with the seine were then fixed in a 10% formalin solution and transferred to 70% ethanol for storage. Large fish were placed on ice, returned to the lab, and stored frozen. All individuals were identified, measured to the nearest mm standard length (SL), and weighed to the nearest gram.

Data analysis

Species were classified by life history strategy using the triangular model of fish life history evolution proposed by Winemiller and Rose (1992). Species with similar life history strategies are predicted to have similar population responses to environmental variation including flow variation in lotic systems (Winemiller 1989; Humphries et al. 1999). Seven species representing three endpoint strategies (periodic, equilibrium and opportunistic) were selected for analysis of spatial and temporal recruitment variation. Periodic strategists have characteristics (delayed maturation, high fecundity, and large adult size) that are adaptive in environments where resources for larvae and juveniles are

patchy in space and time. Species with this strategy usually have contracted breeding seasons synchronized with favorable periods that are relatively predictable between years. Equilibrium strategists are characterized by greater parental investment per offspring and relatively low interannual variation in recruitment. This strategy is proposed to be associated with resource limitation and/or high threat of predation mortality for early life stages. Opportunistic strategists have characteristics (small adult size, extended breeding seasons, high reproductive output) that allow them to quickly colonize new habitats. The western mosquitofish (*Gambusia affinis*) and red shiner (*Cyprinella lutrensis*) represent the opportunistic strategy, bluegill (*Lepomis macrochirus*) and white crappie (*Pomoxis annularis*) represent the equilibrium strategy, and gizzard shad (*Dorosoma cepedianum*), spotted gar (*Lepisosteus oculatus*) and longnose gar (*Lepisosteus osseus*) represent the periodic strategy. Zeug and Winemiller (*Unpublished manuscript*) found that the life history characteristics of these species were concordant with the three endpoint strategies described by the Winemiller and Rose (1992) model. Two gar species were included here, because there is strong habitat partitioning with longnose gar more abundant in the river channel and spotted gar more abundant in oxbows (Robertson et al. *Unpublished manuscript*).

Specimens were classified as adults or juveniles based on minimum size-at-maturity estimates for each species (Chapter II). Variation in recruitment of each species was evaluated spatially among two oxbow lakes and the Brazos River channel, and temporally between the two years each habitat was surveyed. Year 1 was relatively dry and oxbow-river channel connections were infrequent, whereas year 2 was relatively

wet with frequent hydrologic connections among habitats (Figure 1). Differences in juvenile abundance among habitats and years were tested using generalized estimating equations (GEE). These models contained individual habitats and years as main effects and “month” was specified as the repeated variable with an autoregressive correlation structure. When significant differences were detected, pairwise comparisons were made using Bonferroni corrected *P*-values to correct for the use of the same response variable in multiple tests.

To provide a measure of recruitment independent of adult standing stock, species recruitment among habitats and years also was evaluated by comparing the ratio of juvenile-to-adult individuals using the log-likelihood test. When significant differences were detected, pairwise comparisons for all possible habitat combinations ($n = 3$) were conducted. Probability values for pairwise tests were corrected using the Bonferroni algorithm ($\alpha_{\text{adjusted}} = 0.025$). Additionally, size-frequency distributions were constructed for each species and year to examine changes in population size structure through time. The GEE models were performed in SAS version 9.1 and log-likelihood tests were performed in NCSS 2000 version.

Principle components analysis (PCA) was performed on the sample x environmental variable matrix of monthly data in order to associate variation in biotic and abiotic characteristics with variation in recruitment. Prior to PCA, all variables were log transformed [$\log_{10}(x + 1)$] in order to meet the assumption of normality. PCA was conducted using CANOCO (Version 4, Microcomputer Power)

RESULTS

Environmental characteristics

Principle components analysis produced 2 axes that explained 82.5% of the variation in environmental characteristics (Figure 8). Axis 1 modeled 59.5% of the total variation and described a gradient between the most frequently connected oxbow (OXFREQ) that had greater microcrustacean densities, rotifer densities, and predator abundance, from the river channel that had greater depth and dissolved oxygen concentrations (Table 4). Sample scores for the rarely connected oxbow (OXRARE) had intermediate values on axis one. Axis two modeled 23.0% of the total variation and described differences between periods of hydrologic connectivity and isolation in oxbow lakes. Low scores on axis two were associated with greater isolation days, rotifer density, and predator abundance. High scores on axis two were associated with greater depth and microcrustacean density (Table 4).

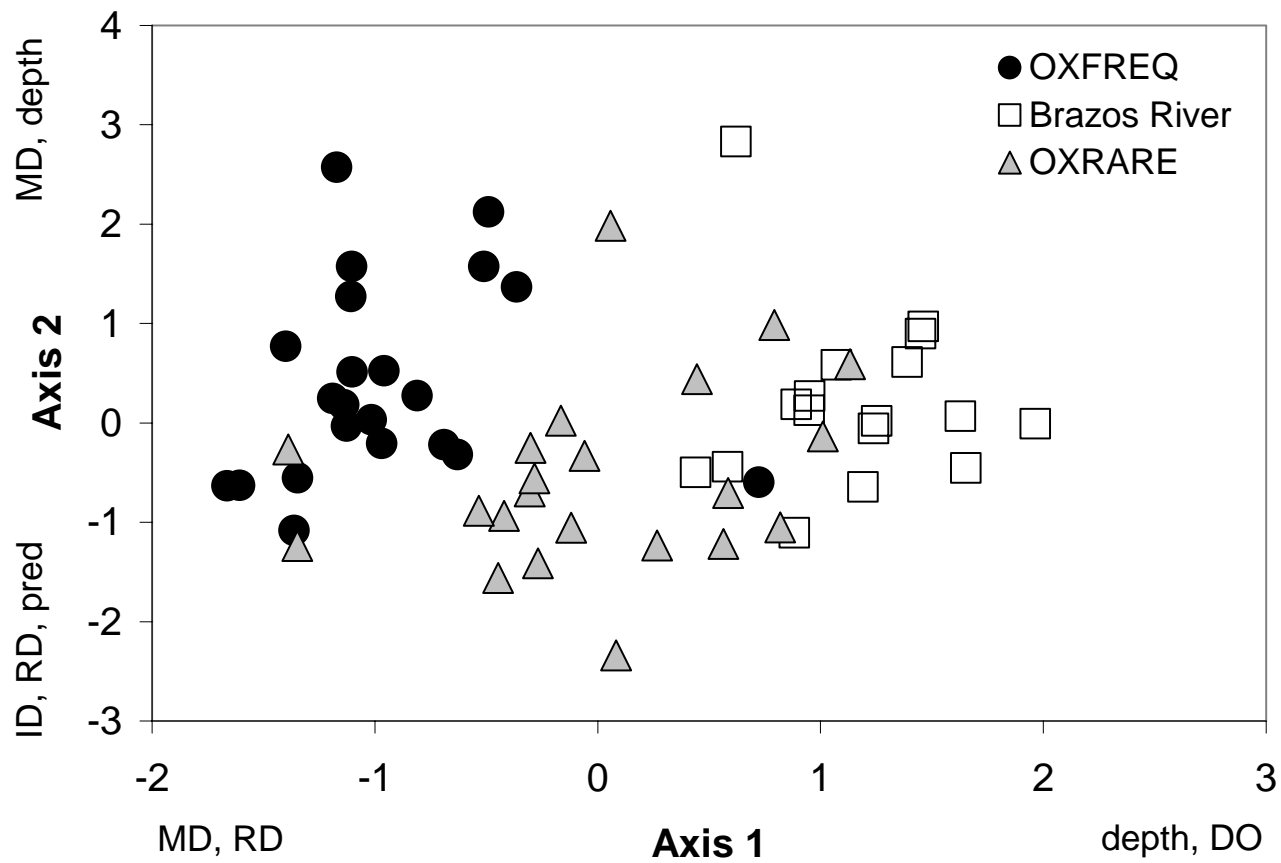


Figure 8. Sample scores of environmental variables from principle components analysis. Abbreviations are as follows: ID = isolation days, MD = microcrustacean density, RD = rotifer density, DO = dissolved oxygen and pred = predator abundance. Variable loadings are listed in Table 4.

Table 4. Variable loadings on the first two axes from PCA and means with standard deviations (in parentheses) of environmental variables measured in the three habitats surveyed.

Parameter	Loadings		OXFREQ	OXRARE	Brazos
	Axis 1	Axis 2			
Temperature (°C)	-0.032	-0.033	22.6 (7.0)	23.6 (7.7)	22.3 (7.0)
Dissolved oxygen (mg l ⁻¹)	0.303	-0.442	6.75 (2.48)	7.41 (1.97)	9.05 (1.71)
Depth (cm)	0.696	0.329	120 (29)	188 (53)	310 (193)
Rotifer density (# l ⁻¹)	-0.796	-0.314	537 (642)	388 (606)	28 (35)
Microcrustacean density (# l ⁻¹)	-0.939	0.215	181 (179)	26 (56)	2 (3)
Isolation days	-0.077	-0.921	75 (65)	161 (128)	-
Predator abundance (# h ⁻¹)	-0.110	-0.291	0.52 (0.40)	0.82 (0.46)	0.44 (0.28)

Equilibrium strategist recruitment

Surveys in the Brazos River yielded few juvenile white crappie ($n = 5$) or bluegill ($n = 39$), and the river channel was only included in comparisons of juvenile abundance for these species. Significant differences in white crappie abundance were detected among habitats, and multiple comparisons indicated that abundance was greater in the most frequently connected oxbow than any other habitat (Tables 5 and 6). The ratio of juvenile-to-adult crappie was also greatest in this habitat (Table 7). Crappie abundance was similar among years; however, juvenile-to-adult ratios were significantly different with a greater ratio in the dry year (Tables 5 and 7). Size frequency distributions indicated that the OXFREQ white crappie population was dominated by juveniles during both years; however, the year 2 (wet year) distribution suggested good recruitment of juveniles produced during year 1 (dry year) with an increase in the proportion of age-1 individuals (Figure 9). The OXRARE population was dominated by adults during the dry year (year 1) with two distinct peaks corresponding to age-1 and age-2 + individuals (Figure 9). The lack of juvenile production in OXRARE during the dry year was reflected in the reduction of the proportion of age-1 crappie during the subsequent wet year.

Bluegill abundance was significantly greater in the rarely connected oxbow relative to the other two habitats, and abundance was not significantly different between years (Tables 5 and 6). The bluegill juvenile-to-adult ratio was not significantly different among habitats or years (Table 7). Size frequency distributions suggested that

bluegill populations in both oxbow lakes were dominated by juveniles with little between-year variation in size structure (Figure 10).

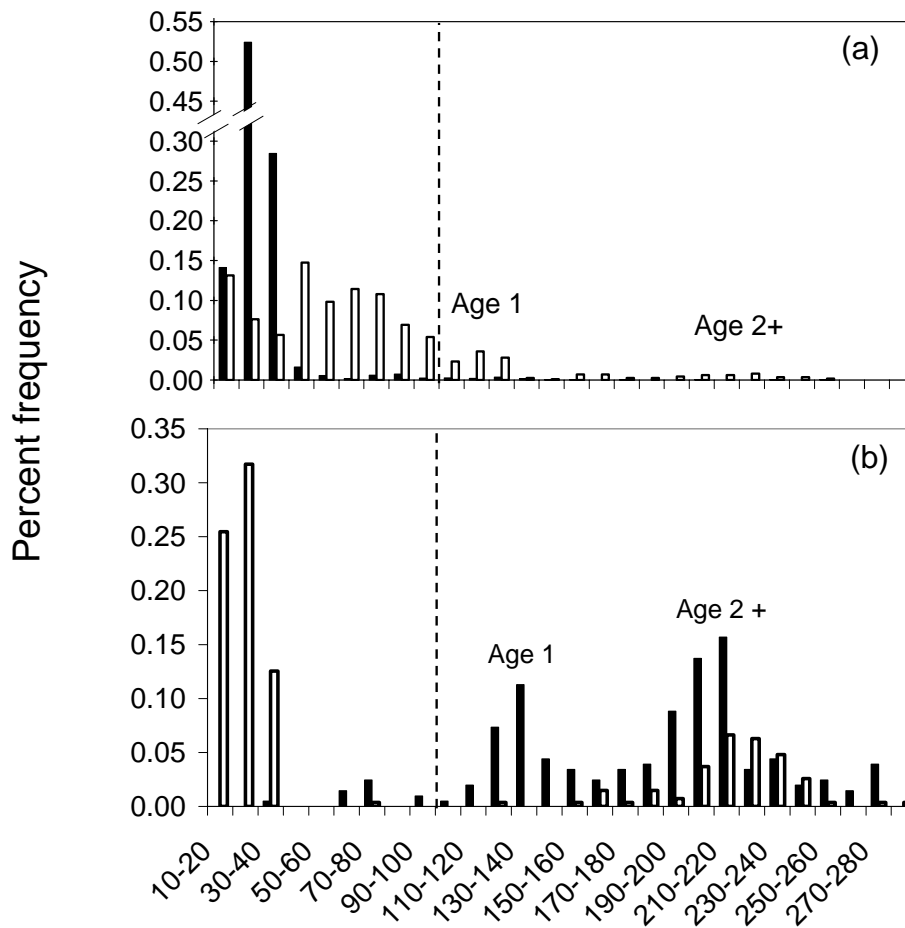


Figure 9. Size frequency distributions white crappie in OXFREQ (a) and OXRARE (b). Dashed lines indicate minimum size at maturity. Closed bars = dry year, open bars = wet year.

Table 5. Results of generalized estimating equations comparing juvenile abundance between habitats and years.

Species	Habitat		Year		Habitat x Year	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
mosquitofish	8.43	0.015	4.51	0.034	1.21	0.547
red shiner	10.29	0.006	6.50	0.011	4.15	0.125
shad	9.85	0.007	10.45	0.001	9.47	0.009
spotted gar	7.05	0.030	2.26	0.133	3.85	0.146
longnose gar	3.82	0.148	4.63	0.031	2.26	0.323
white crappie	7.74	0.021	0.46	0.497	2.60	0.273
bluegill	9.17	0.010	3.19	0.074	3.33	0.189

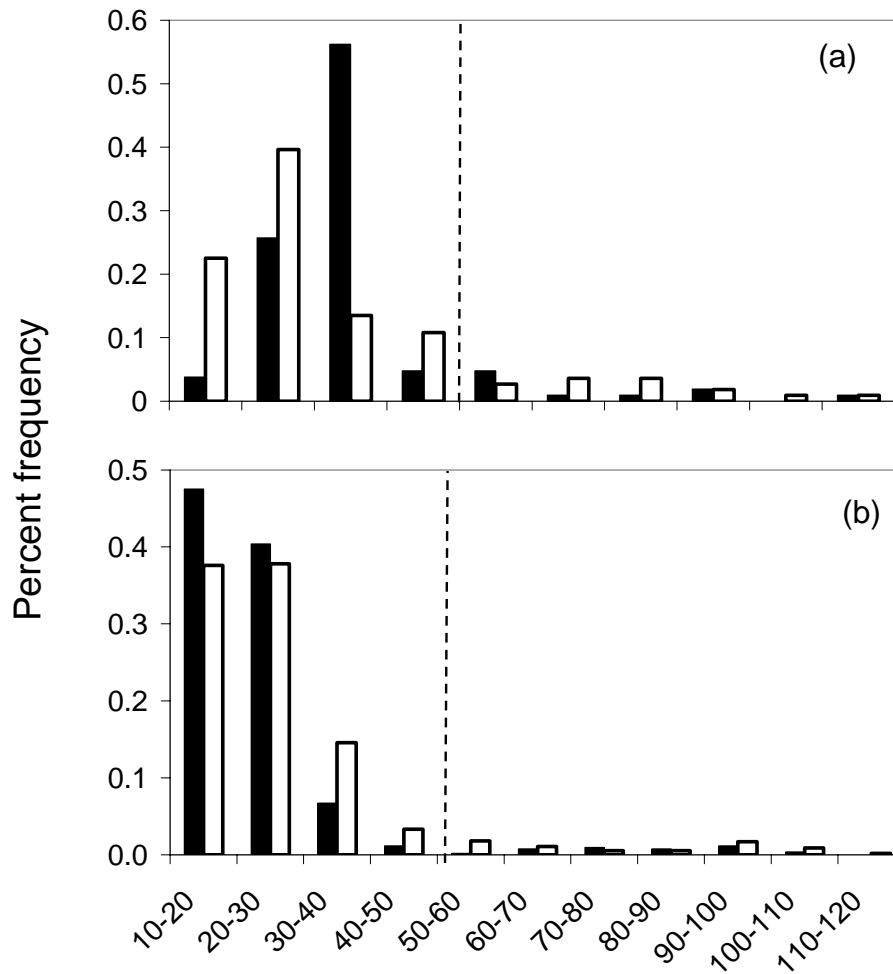


Figure 10. Size frequency distributions bluegill in OXFREQ (a) and OXRARE (b). Dashed lines indicate minimum size at maturity estimates. Closed bars = dry year, open bars = wet year.

Table 6. Results of multiple comparisons of juvenile abundance between habitats using generalized estimating equations. *P*-values were adjusted using the Bonferroni correction $\alpha_{\text{adjusted}} = 0.025$

Species	BR x OXFREQ		BR x OXRARE		OXFREQ x OXRARE	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
mosquitofish	8.01	0.005	7.34	0.007	1.21	0.270
red shiner	10.70	0.001	10.79	0.001	3.03	0.082
shad	4.27	0.039	9.57	0.002	5.32	0.021
spotted gar	5.38	0.020	6.49	0.011	1.87	0.172
longnose gar	-	-	-	-	-	-
white crappie	6.88	0.009	2.08	0.149	7.66	0.006
bluegill	5.06	0.024	8.56	0.003	8.46	0.004

Table 7. Results of log likelihood tests comparing the ratio of juvenile to adult individuals of each species among habitats and years. Spotted gar ratios in oxbows were compared with longnose gar ratios in the river channel.

Species	OXFREQ x OXRARE		OXFREQ x BR		OXRARE x BR		Wet x Dry	
	G	P	G	P	G	P	G	P
white crappie	252.78	< 0.001	-	-	-	-	38.47	< 0.001
bluegill	3.71	0.054	-	-	-	-	0.29	0.593
gizzard shad	192.08	< 0.001	19.39	< 0.001	1.29	0.257	200.46	< 0.001
gar	4.78	0.029	11.02	0.001	54.22	< 0.001	1.28	0.258
mosquitofish	66.16	< 0.001	10.9	0.001	0.15	0.696	0.08	0.772
red shiner	0.46	0.500	84.83	< 0.001	114.75	< 0.001	71.33	< 0.001

Periodic strategist recruitment

Variation in shad abundance was significant between habitats and years however a significant interaction between factors complicated interpretation of results (Table 5). Shad juvenile-to-adult ratios were greater in OXRARE and the river channel relative to OXFREQ, and the year-1 (dry year) ratio was significantly greater than the year-2 ratio (Table 7). Shad populations in all habitats were primarily composed of juveniles and age-2+ individuals in year-1 (Figure 11). Year-2 size distributions in both oxbow lakes had greater proportions of age-1 individuals suggesting good recruitment of juveniles produced in year 1 (Figure 11). This trend was not apparent in the river channel where size frequency distributions were similar for both years (Figure 11).

Spotted gar abundance was greater in the two oxbows relative to the river channel and no difference was detected between years (Tables 5 and 6). Longnose gar abundance in the river channel was similar to the two oxbow lakes, and abundance was greater in the wet year (Table 5). Juvenile-to-adult ratios for the two gar species were greater in both oxbow lakes than the river channel, and no difference was detected between years (Table 7). Size-frequency distributions in all habitats did not reveal any obvious adult cohorts. The spotted gar population in OXRARE was dominated by juveniles during both years (Figure 12) whereas the OXFREQ population had similar proportions of juveniles and adults during both years (Figure 12). The Brazos River longnose gar population was dominated by adults during both years with few juveniles collected (Figure 13).

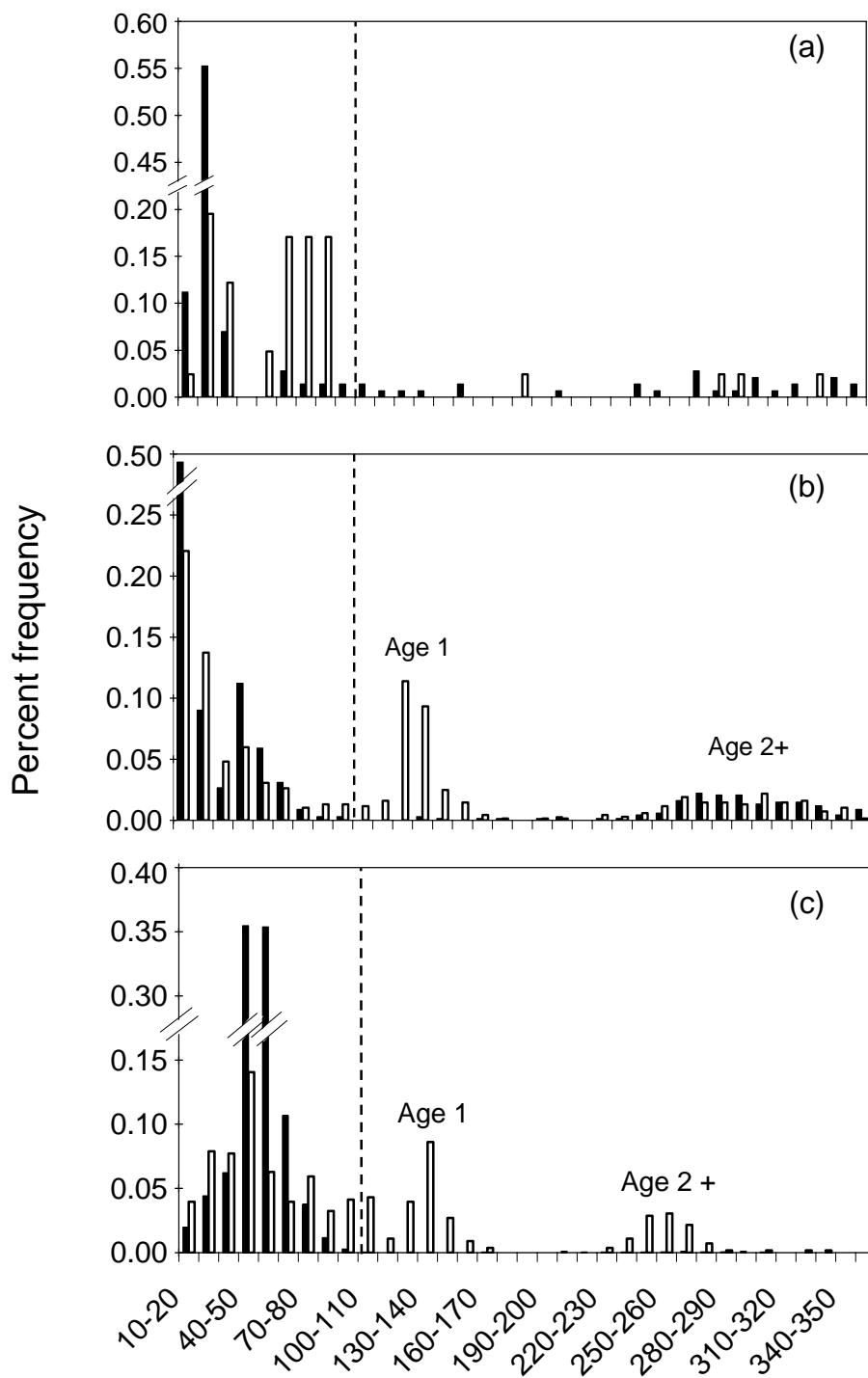


Figure 11. Size frequency distributions of gizzard shad in the main channel (a), OXFREQ (b) and OXRARE (c). Dashed lines indicate minimum size at maturity estimates. Closed bars = dry year, open bars = wet year.

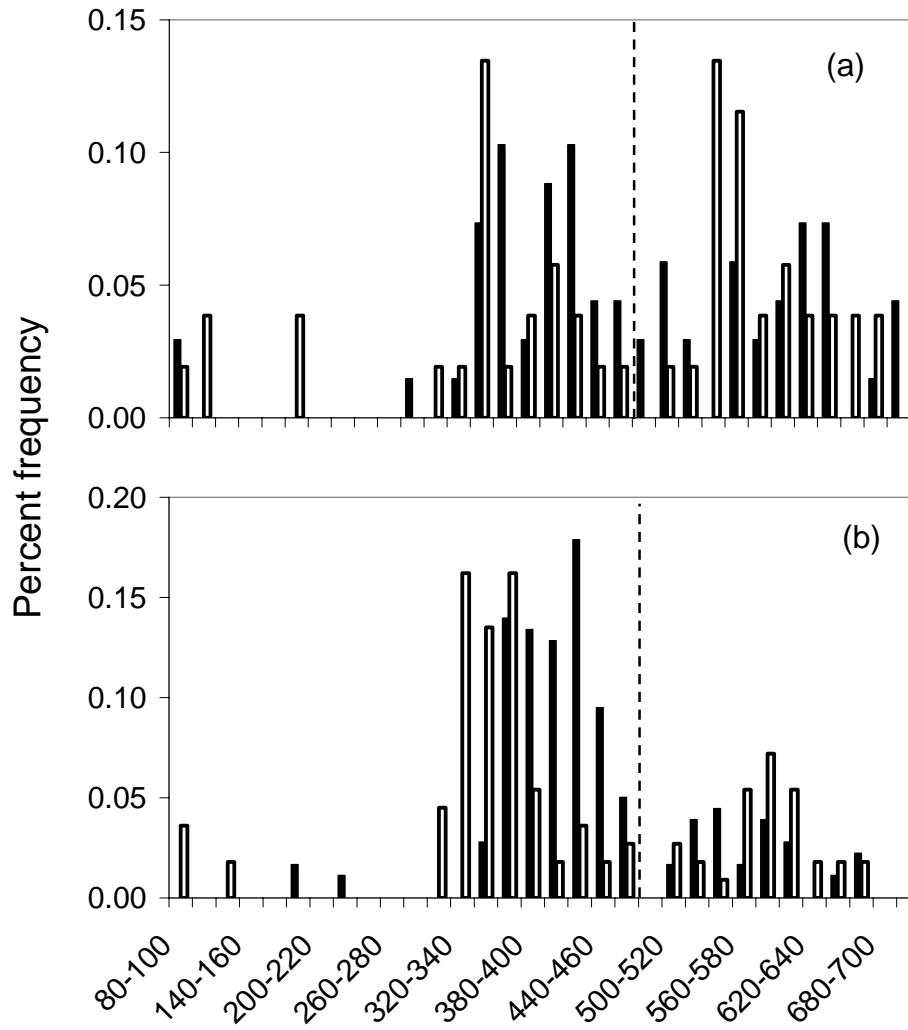


Figure 12. Size frequency distributions of spotted gar in OXFREQ (a) and OXRARE (b). Dashed lines indicate minimum size at maturity estimates. Closed bars = dry year, open bars = wet year.

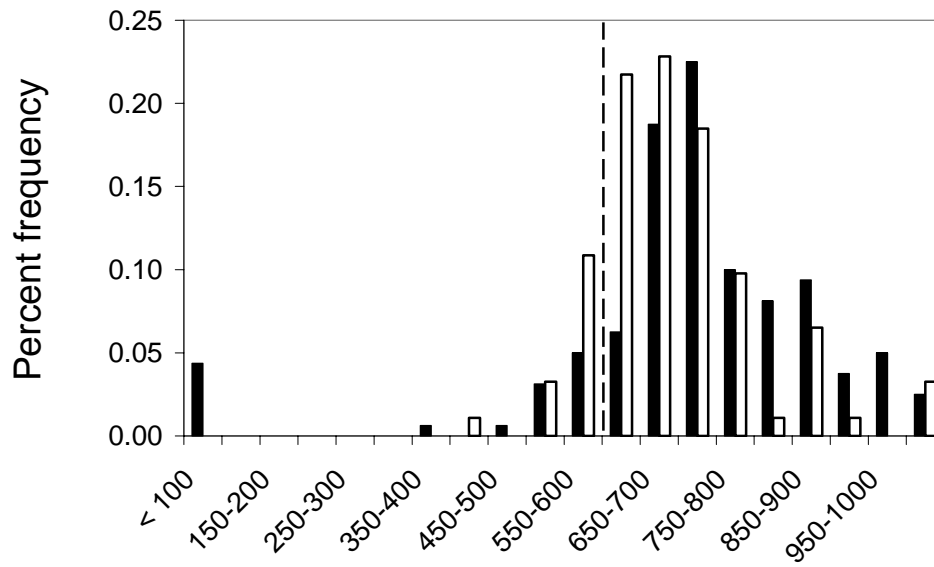


Figure 13. Size frequency distributions of longnose gar in the main river channel. Dashed lines indicate minimum size at maturity estimates. Closed bars = dry year, open bars = wet year.

Opportunistic strategist recruitment

Oxbow lakes had significantly greater mosquitofish abundance relative to the river, and abundance was greater in the dry year (Tables 5 and 6). Mosquitofish juvenile-to-adult ratios were greater in the river and the rarely connected oxbow than the frequently connected oxbow. There was no difference in ratios between years (Table 7). Populations in all habitats were dominated by juveniles; however, OXRARE and the river channel had greater proportions of adults (Figure 14). Size distributions in all habitats were consistent among years.

Red shiner abundance and juvenile-to-adult ratios were significantly greater in the river channel than oxbows (Tables 6 and 7). Between years, both abundance and the juvenile-to-adult ratio were greater during the dry year. Populations in OXRARE and the river channel were dominated by juveniles, and distributions were similar among years, whereas the OXFREQ population had a greater proportion of adults during year 2 (Figure 15).

DISCUSSION

Patterns of juvenile abundance indicated that both habitat characteristics and variation in hydrologic connectivity contributed to recruitment variability. Oxbow lakes supported successful recruitment of species that spanned all three life history strategies, but were particularly important for equilibrium strategists (white crappie and bluegill) that were rarely collected in the river channel. The reproductive ecology of both equilibrium species includes nest building, and high flows may reduce recruitment of these species in the river channel where flow is relatively unpredictable within and

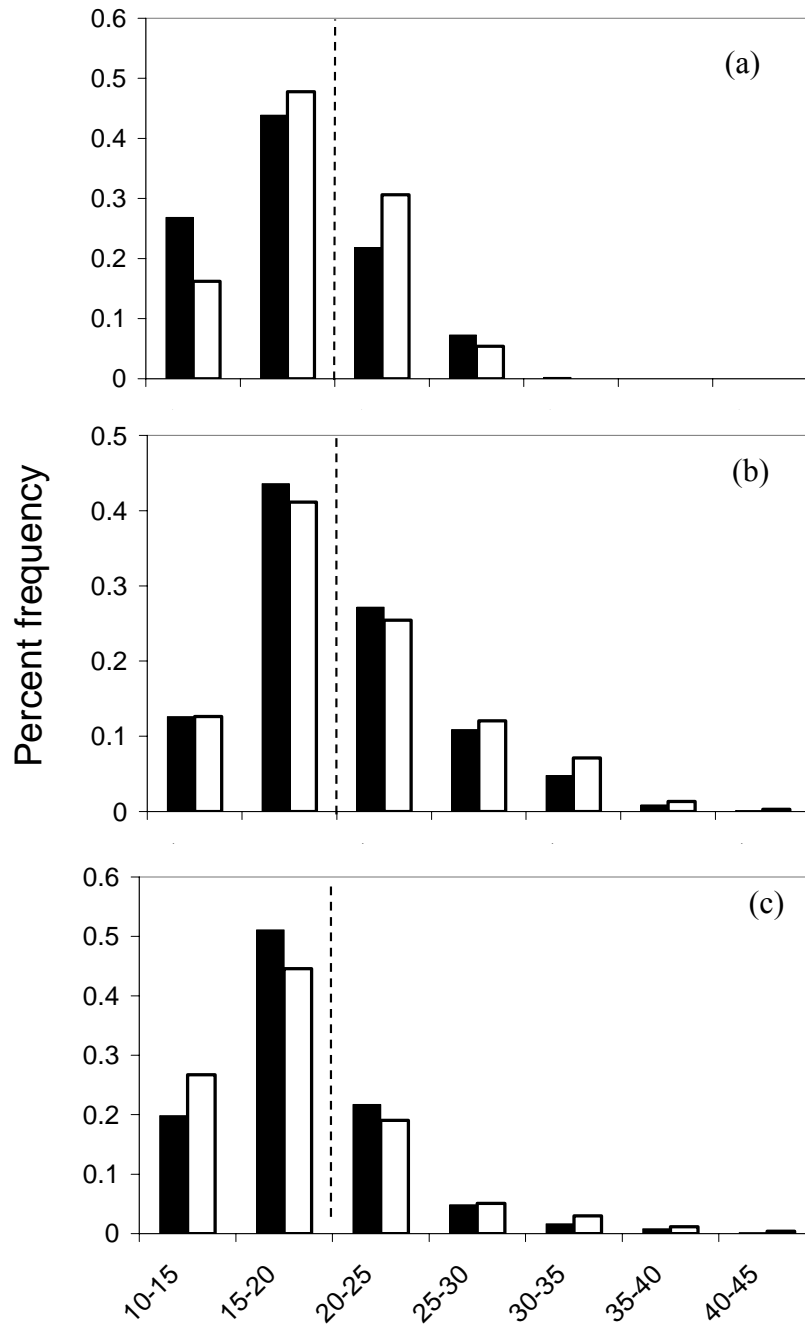


Figure 14. Size frequency distributions of mosquitofish in the main river channel (a), OXFREQ (b) and OXRARE (c). Dashed lines indicate minimum size at maturity estimates.

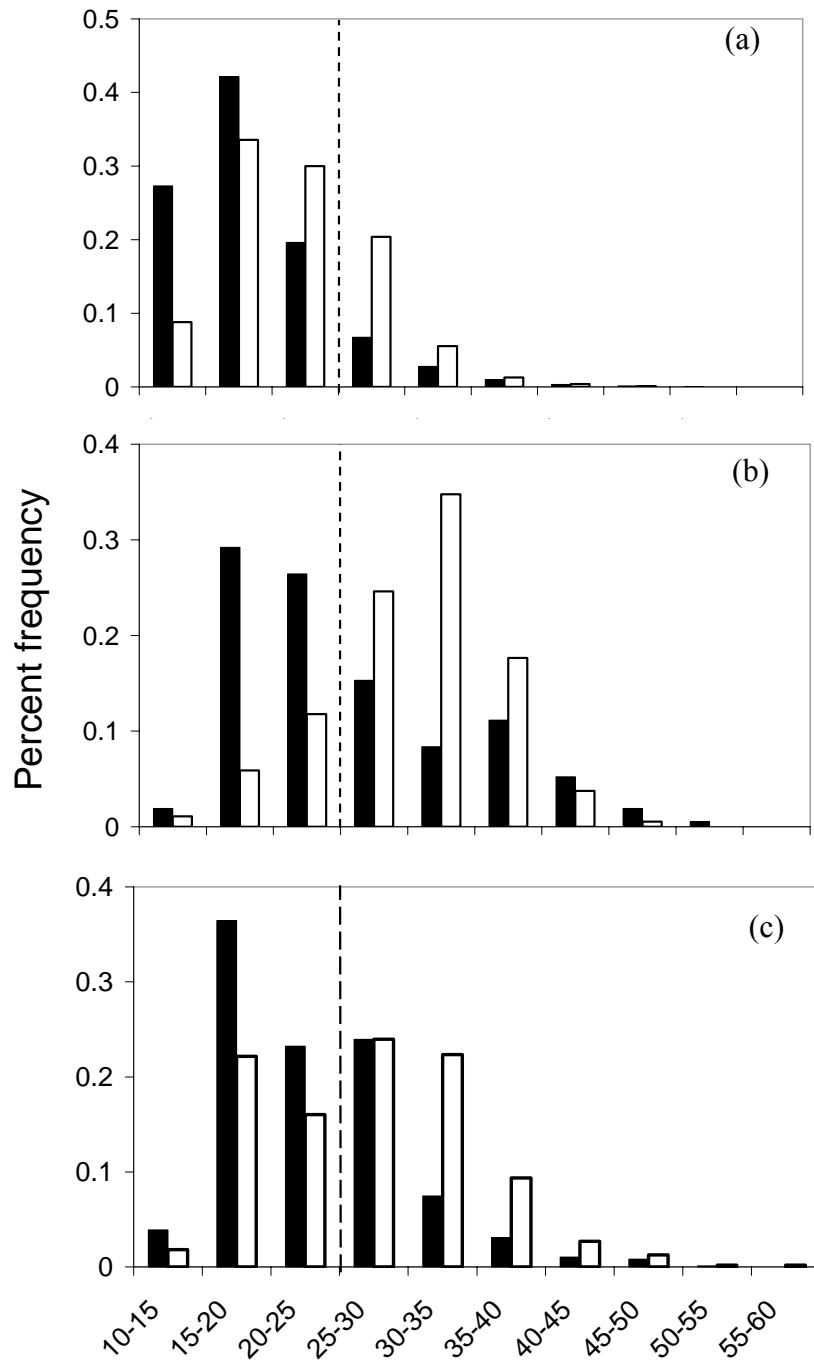


Figure 15. Size frequency distributions of red shiner in the main river channel (a), OXFREQ (b) and OXRARE (c). Dashed lines indicate minimum size at maturity estimates.

between years (Winemiller, 1996; Bonvechio and Allen 2005). The two species that were abundant in the river channel represented the periodic (longnose gar) and opportunistic (red shiner) life history strategies. The storage effect allows periodic-type species, such as longnose gar, to produce strong year classes during optimal periods that may occur rarely in habitats such as the Brazos River channel where food resources for larvae appear to be less predictable compared to oxbow lakes. Opportunistic species have extended breeding seasons that increase the probability that at least some offspring will encounter favorable conditions for recruitment despite relatively unpredictable environmental conditions (Winemiller, 1989; Humphries et al. 2002). These species were common in all habitats although mosquitofish appeared to prefer oxbows, whereas red shiner preferred the main channel.

Overall, oxbow lakes supported greater abundances of most species (white crappie, bluegill, shad, mosquitofish and spotted gar). Off-channel floodplain habitats such as oxbow lakes, have been shown to be sources of production for certain fish populations (Crook and Gillanders 2006) and probably are sources of biological production in most river-floodplain systems (Junk et al. 1989; Winemiller, 2005). Oxbow lakes had greater rotifer and microcrustacean densities than the river channel and food resources may have influenced differences in juvenile abundance. Among oxbows, abundance patterns were similar for mosquitofish, red shiner and spotted gar however, bluegill and shad were more abundant in the rarely connected oxbow, whereas white crappie were more abundant in the frequently connected oxbow. Habitat-specific factors such as hydrology, depth, turbidity and geomorphology significantly influence species

composition and abundance in river-floodplain systems and likely contributed to observed patterns between oxbows in the current study (Halyk and Balon 1983; Rodriguez and Lewis 1997; Feyrer et al. 2004). Only two oxbows were surveyed in the current study and population dynamics may vary among oxbows with similar connection frequencies however, a previous study of 10 Brazos oxbows by Winemiller et al. (2000) found that oxbows with similar geomorphology (yielding similar connection frequencies) supported similar fish assemblages. Thus, my results probably represent a robust pattern of recruitment variation in response to abiotic factors in this system.

Analysis of juvenile-to-adult ratios yielded additional recruitment patterns that could not be elucidated with abundance estimates alone. Shad and crappie ratios were greatest in habitats that had the lowest adult abundance, a finding that suggests density dependent recruitment in these species (Vandenbos et al. 2006). Spotted gar ratios in oxbow lakes were greater than longnose gar ratios in the river channel, and juveniles comprised a small proportion of the longnose gar population. This implies that oxbow lakes provided better conditions for recruitment, however this may be an artifact of comparing ratios of different species. Bluegill ratios were similar in the two oxbows, although abundance was significantly different. Recruitment of this species appeared to be strongly associated with adult abundance. The pattern of red shiner ratios was similar to that of abundance patterns with a greater ratio in the river channel relative to the two oxbow lakes.

Annual floodplain inundation has been inferred to be the primary factor driving fish recruitment in large rivers (Junk et al. 1989; Bayley, 1991; Winemiller, 2005);

however, only one of seven species (longnose gar) was significantly more abundant in the wet year and no species had greater juvenile-to-adult ratios. Red shiners, mosquitofish and gizzard shad were more abundant during the dry year, and three species (white crappie, gizzard shad and red shiner) had greater juvenile-to-adult ratios. Additionally, greater proportions of age-1 shad and crappie during the wet year suggested good recruitment of juveniles spawned during the previous dry year. These findings suggest that recruitment dynamics in the Brazos River conform more closely to the low-flow recruitment hypothesis (LFR; Humphries et al. 1999) than the flood pulse concept (FPC; Junk et al. 1989).

The low-flow recruitment hypothesis describes fish recruitment dynamics in rivers in where over-bank flooding is relatively unpredictable or aseasonal (Humphries et al. 1999). Flood dynamics in the Brazos River during our two-year study period did not display a seasonal pattern. King et al. (2003) found that most species in the Ovens River, Australia, were able to recruit in river channel and perennial floodplain habitats during hydrologic isolation, and similar patterns were apparent in the Brazos River. Periods of isolation (low flow) in oxbows, and to a lesser extent in the river channel, were associated with greater rotifer densities and planktonic invertebrates tend to be important food items consumed by fish larvae at the onset of exogenous feeding (Gehrke, 1992; Bremigan and Stein 1994; King, 2005). The transition to exogenous feeding is a critical period that may determine species year-class strength, especially for periodic strategists that produce large numbers of small offspring (Miller et al. 1988; Winemiller and Rose 1993). White crappie and gizzard shad had the greatest mean

fecundity and the smallest eggs of the seven species examined (Zeug and Winemiller unpublished manuscript) and both species produced a strong year class during the dry year. Red shiners deposit their eggs in crevices and may require periods of low flow to reproduce successfully (Gale, 1986).

Flooding can have large effects on fish recruitment both positive and negative and the limited duration of our study may have under-emphasized the importance of habitat connectivity. Periods of hydrologic isolation were important for recruitment, yet extended isolation can result in oxbow desiccation and large-scale fish mortality (Winemiller et al 2000). Periodic flooding is likely to be important for maintaining oxbow water levels and providing opportunities for faunal exchange with the river channel. Zeug and Winemiller (Unpublished manuscript) found that reproductive activity of periodic species coincided with high flow periods in the 30-year hydrograph, and greater recruitment should be observed in years when flood dynamics are optimal (Bayley, 1991). Periods of hydrologic connectivity were associated with lower predator abundance; however, floods during the study occurred outside of periodic species' annual reproductive periods.

Observed patterns of species recruitment conformed well to tenets of the riverine ecosystem synthesis (RES) regarding community regulation (Thorp et al. 2006). The middle Brazos River can be classified as a floodplain functional process zone (FPZ) with individual oxbows and the river channel included as ecological nodes within the FPZ. Recruitment success was dependent on interactions between geomorphic habitat features (oxbows with different connection frequencies and the river channel) and flood

dynamics. These characteristics also were associated with recruitment of fish with particular life history strategies. This differential recruitment success among habitats and hydrologic periods may be the primary factor driving differences in assemblage structure described previously in aquatic habitats of the Brazos River (Winemiller et al. 2000; Zeug et al. 2005).

The RES also emphasizes the importance of scale for investigations of ecological dynamics in lotic systems. The spatial scale of the current study was sufficient for fishes that are able to move between habitat units during periods of hydrologic connectivity (Zeug et al. 2005). Two years seemed to be sufficient to characterize recruitment of most species, with the possible exception of gars that have greater life spans relative to other species examined. Flood dynamics were significantly different between years however, periods of severe drought can result in extensive drying of off-channel habitats and the current study did not cover the entire range of hydrologic dynamics that occur in the middle Brazos. Populations of crappie and bluegill in the river channel, though small, are likely to be important for recolonization of floodplain habitats following extended droughts. Future studies would benefit by increasing the temporal scale of analysis, especially in relation to long-lived periodic species that may have strong recruitment only during occasional years when flood dynamics are optimal. Although individual oxbows were important habitats for recruitment during our two-year study, a given oxbow lake is a temporary floodplain feature when viewed over longer geological time scales. Fluvial process such as erosion and deposition create these habitats and drive their succession. Thus, fluvial geomorphologic dynamics over the long term are as

important for the maintenance of fish populations in the Brazos River as the dynamics of lateral connectivity and basal food web production that occur over shorter time scales.

CHAPTER IV

CAN ALLOCHTHONOUS CARBON SOURCES SUPPORT LARGE RIVER FOOD

WEBS?

INTRODUCTION

Several conceptual models have been proposed to describe sources of organic carbon supporting aquatic consumers in large river-floodplain systems. The river continuum concept (RCC; Vannote et al. 1980) proposes that organic material transported from upstream reaches and tributaries supports consumer biomass in lowland reaches. This model was developed primarily from observations in small headwater streams and a few studies have implied weak longitudinal food web linkages in large rivers (Thorp et al. 1998; Huryh et al. 2002). The flood pulse concept (FPC: Junk et al. 1989) puts greater emphasis on lateral connectivity between the channel and floodplain habitats and predicts that terrestrial material originating on floodplains provides the majority of organic carbon supporting aquatic fauna in the main river channel. Thorp and DeLong (1994) proposed the riverine productivity model (RPM) that states carbon transported from upstream reaches and the floodplain is difficult for consumers to assimilate directly. Autochthonous carbon sources (e.g. benthic algae, phytoplankton and direct inputs from riparian zones) are more labile and may be assimilated by consumer taxa in greater proportions despite the lower abundance of these carbon sources in the environment (Thorp et al. 1998).

Recently, studies using stable isotopes have identified autochthonous algal carbon as the primary source of organic carbon supporting aquatic consumers in large

ivers (Thorp and Delong 2002 and references therein). These studies have primarily focused on aquatic fauna in lotic main-channel habitats during low-flow periods. Off-channel aquatic habitats, such as oxbow lakes, are recognized as areas of high biological productivity in large river systems, yet they have received comparatively little attention with regards to the sources of carbon supporting consumers in these habitats. Food webs are dynamic in space and time, and their structure can change in response to environmental drivers, species interactions, or a combination of these factors (Winemiller 1996; Woodward and Hildrew 2002; de Ruiter et al. 2005). Variation in water level facilitates connectivity between different habitat units (main-channel and floodplain) and has the potential to significantly influence food web structure through the movement of potential source materials and consumer taxa (Winemiller 2005).

In North America, the fluvial dynamics of most large river-floodplain systems have been significantly altered, which complicates attempts to examine ecological dynamics under natural conditions (Sparks 1995; Michener and Haeuber 1998). Here we use stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) to examine proportional contributions of aquatic and terrestrial primary production sources to aquatic consumer taxa in the main channel and floodplain habitats of the Brazos River, Texas, USA over five months. The hydrology of the Lower Brazos River is less modified than most other North American floodplain systems, and provides a unique opportunity to examine food web structure in a lowland river with frequent floodplain-river channel connections. Research goals were to identify the principal terrestrial and aquatic carbon sources supporting consumer taxa representing three trophic guilds in the main channel of the

Brazos River and two oxbow lakes with different flood-recurrence intervals in order to test predictions of the flood pulse concept and the riverine productivity model.

Additionally, we use $\delta^{15}\text{N}$ values to compare vertical trophic structure among the three habitats surveyed to reveal direct versus indirect assimilation of carbon from primary producers.

We predicted that hydrologic connectivity and flow history would significantly influence carbon sources supporting consumer taxa. Several studies that support the importance of autochthonous algal carbon were conducted during low-flow periods (Thorp et al. 1998; Bunn et al. 2003; Delong and Thorp 2005), whereas studies conducted during different hydrologic periods (both high and low-flow) or within habitats with different flow regimes have inferred that terrestrial carbon sources may significantly contribute to consumer biomass (Huryn et al. 2001; Wantzen et al. 2002; Herwig et al. 2004; Hoeinghaus et al. *In press*). We predicted that autochthonous carbon sources in the Brazos main-channel would be important during low-flow periods (RPM), and allochthonous terrestrial sources would increase in importance following high flows that import terrestrial carbon from the floodplain (FPC), and reduce the availability of autochthonous sources via scouring and sedimentation (Huryn et al. 2001). Hydrologic disruptions in oxbow lakes are much less frequent and tend to be more gradual compared to those affecting the main channel (Winemiller et al. 2000; Zeug et al. 2005), and we predicted that autochthonous carbon sources would support a larger fraction of consumer biomass than the main channel. Greater fractions of

allochthonous material were predicted to be assimilated by for consumers in oxbows with shorter flood-recurrence intervals.

METHODS

Study site

The Brazos River is the 11th longest river in the United States draining an 116,000 km² catchment from its headwaters near the Texas-New Mexico border to its mouth near Freeport, Texas. Agriculture and cattle grazing are prevalent land uses on the Brazos floodplain and large areas of native post oak (*Quercus stellata*) savanna are common. The river is partially regulated by dams above the city of Waco, Texas, however, the middle and lower regions of the Brazos lack dams and levees. Consequently, the actively meandering channel continues to form aquatic floodplain features such as oxbow lakes. Flood dynamics are primarily driven by regional precipitation patterns that are relatively unpredictable within and between years. This high-flow variation yields aseasonal patterns of connectivity between the river channel and oxbow lakes that are similar to historical flow patterns (Winemiller 1996; Zeug et al. 2005).

Samples of basal sources and consumer taxa for analysis of stable isotope ratios were collected from two oxbow lakes with different flood recurrence intervals and the main channel of the middle Brazos River between 30° 37' and 30° 27' N (Figure 1). One of the oxbows connects to the river frequently (recurrence interval < 1 year) at moderate levels of river discharge and is hereafter referred to as OXFREQ. The other oxbow connects to the river channel at high levels of discharge with a recurrence interval of

approximately 2 years and is hereafter referred to as OXRARE. Samples from the main river channel were collected from a 7-km reach located near OXRARE. Both oxbow lakes were located on cattle ranches but retained relatively unaltered riparian buffers surrounded by pasture. Willow trees (*Salix nigra*) were the dominant riparian tree at both sites, and sycamores (*Platanus occidentalis*) also were common at OXRARE. Willows dominated the riparian zone of the river channel, and the floodplain contains row crops (primarily corn and cotton) and pasture with areas of native post oak savanna. Aquatic macrophytes were rare in the channel and sparse in oxbow lakes.

Sample collection

A previous survey of one Brazos oxbow found significant seasonal variation in isotopic ratios of primary producers (Jepsen 1999). In order to capture this temporal variability for modeling contributions of production sources to consumer species that integrate variability in source materials over time, production sources were collected monthly at each site from September 2003 to August 2004. Samples of dominant riparian vegetation (*S. nigra*, *P. occidentalis*) were collected when live leaves were available (early fall, spring and summer). Leaves were clipped, placed in plastic bags, and frozen for later processing. Samples of grasses from adjacent pastures were collected during flood periods (May and June) when water inundated these areas. Benthic algae were scraped directly off the mud substrate using a metal spatula. Samples were rinsed with distilled water to remove sediment and large particles of detritus and then examined under a microscope to remove small particles and microorganisms. Because this collection and processing technique was unlikely to

produce pure samples, we hereafter refer to this source as phytomicrobenthos (benthic algae with associated microorganisms). Samples of phytomicrobenthos were not collected in the river channel during certain months due to scouring and sediment deposition. Water samples were collected in two 1-l opaque bottles and transported to the laboratory on ice. Samples were passed through a 64-mm sieve to remove zooplankton and then examined under a microscope to insure the sample primarily contained phytoplankton. Sieved samples were filtered onto pre-combusted (450°C for 24 hr) Whatman GF/F filters and frozen for later analysis. Samples contained both phytoplankton and suspended organic matter and are hereafter referred to as “seston”. Seston samples could not be collected in the river channel during high flow periods due to heavy sediment loads.

Fish and invertebrates were collected monthly from April 2004 to August 2004. Small-bodied species (< 100 mm) were collected with a 10 x 2 m bag seine and large-bodied species (> 100 mm) were collected with experimental gillnets. Abundance estimates of consumer taxa were standardized by the total number of meters traveled for seine hauls and the total hours for each gillnet set. For a more detailed description of the collection methodology see Zeug et al. (2005). Species collected for isotopic analysis were selected based on previous surveys that identified them as dominant consumers (Winemiller et al. 2000; Zeug et al. 2005) and their representation of different trophic guilds. In oxbow lakes, gizzard shad (*Dorosoma cepedianum*), smallmouth buffalo (*Ictiobus bubalus*), grass shrimp (*Palaemonetes kadiakensis*), and crayfish (cambaridae) represented the detritivore/omnivore guild. Western mosquitofish (*Gambusia affinis*),

red shiner (*Cyprinella lutrensis*), and bluegill (*Lepomis macrochirus*) represented the insectivore guild. White crappie (*Pomoxis annularis*) and spotted gar (*Lepisosteus oculatus*) represented the piscivore guild. Species assemblage structure of the river channel is significantly different than oxbow lakes (Zeug et al. 2005), and several lotic-associated species were dominant guild members in the main channel. In the river channel, gizzard shad, river carpsucker (*Carpionodes carpio*), and Ohio River shrimp (*Macrobrachium ohione*) represented the detritivore/omnivore guild. Red shiner, bullhead minnow (*Pimephales vigilax*), and longear sunfish (*Lepomis megalotis*) represented the insectivore guild. Longnose gar (*Lepisosteus osseus*) represented the piscivore guild. During each month we attempted to collect three individuals of each species, however, in certain months three replicates were not available. When more than 3 specimens were collected, individuals were selected to represent the minimum, maximum, and approximate mean size in the sample. All samples were placed in plastic bags and frozen for later processing.

In the laboratory, fish and invertebrate samples were defrosted, measured to the nearest 0.1 mm (standard length for fishes and total length for decapods) and weighed to the nearest gram. Samples of dorsal muscle were used for fishes, and abdominal muscle was used for decapods. For some small species (mosquitofish and grass shrimp), composite samples of up to three similar sized individuals were used to ensure adequate sample mass. Muscle tissue was removed using a scalpel, rinsed with distilled water, and inspected to ensure samples were free of bone, scales, or exoskeleton fragments. Samples of muscle and processed basal source materials were placed in individually

labeled, acid-washed Petri dishes and dried for 48 h at 60°C. Dried samples were ground to a fine powder and sub-samples were weighed to the nearest 0.01 mg on an analytical balance. Sub-samples were sealed within Ultra-Pure tin capsules (Costech Analytical Technologies, Inc) and then sent to the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, for analysis of carbon and nitrogen isotope ratios. Isotopic results for carbon and nitrogen were quantified as deviations relative to isotopic standards (delta notation):

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}} / R_{\text{standard}}) - 1] * 1000,$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. For carbon isotopes, the standard was Pee Dee Belemnite limestone, and atmospheric nitrogen was the nitrogen standard.

Some samples were destroyed due to equipment malfunctions during isotopic analysis. Destroyed consumer samples were re-analyzed when additional processed material was available however, samples of phytomicrobenthos and seston usually did not contain enough additional material to be re-analyzed.

Data analysis

The IsoSource procedure described by Phillips and Greg (2003) was performed to model the contribution of source materials to consumer taxa. Plots of carbon and nitrogen ratios of source materials indicated that baseline nitrogen values (average $\delta^{15}\text{N}$ of all production sources) may have been different between the three habitats surveyed. A one-way ANOVA indicated that differences among habitats were significant ($F_{2,86} = 32.19$, $P < 0.001$), and Tukey's multiple comparisons test indicated that differences were significant between each habitat (Figure 16). Because of these differences, models were

run for each habitat separately using source and consumer taxa collected only in that habitat. Plots revealed that some sources could be combined. In OXRARE,

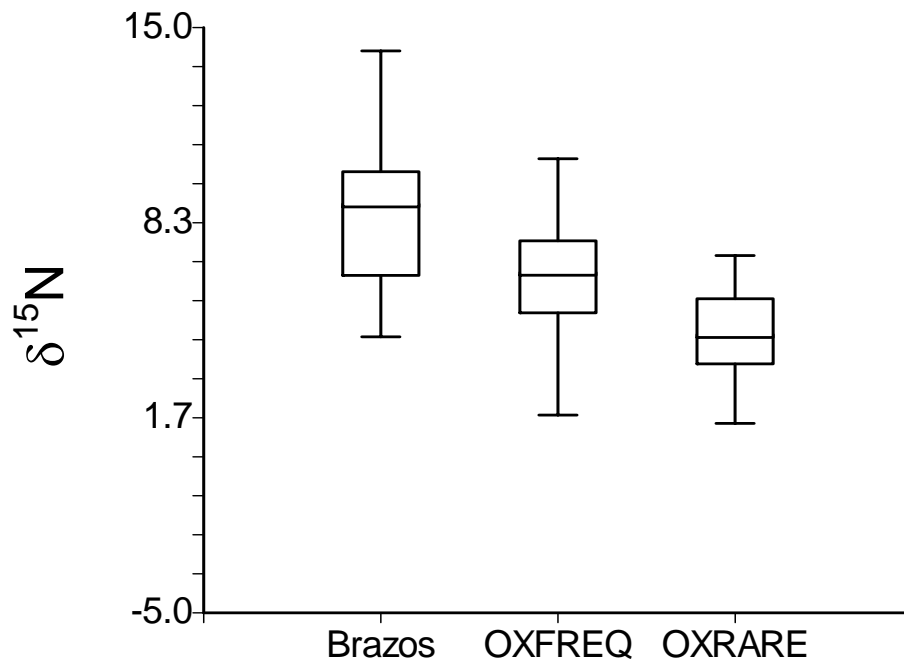


Figure 16. Box and whisker plots of average $\delta^{15}\text{N}$ values of production sources in each habitat. One-way ANOVA and Tukey's multiple comparisons test indicated values were significantly different between each habitat.

willow and sycamore had similar isotopic ratios and were combined into the variable C_3 terrestrial plants. Grasses collected along the river channel and OXFREQ were C_3 . In the river channel, C_3 grasses had signatures similar to willow and were combined into

the variable C₃. Grasses in OXFREQ did not overlap with willow isotope ratios and these sources were not combined. Although C₃ grasses appeared to be dominant in the section of the Brazos channel that was surveyed, C₄ plants also occur on the broader landscape therefore, isotopic values for Brazos River C₄ grasses collected previously by K.O. Winemiller (unpublished data) were included in the Brazos River model.

A four-source dual-isotope $\delta^{13}\text{C}/\delta^{15}\text{N}$ model was run for consumer species in each habitat. Sources in the river channel and OXRARE models included C₃ macrophytes, C₄ macrophytes, phytomicrobenthos and seston. Because C₄ macrophytes used in the river channel model were not collected during the study period and $\delta^{15}\text{N}$ values were higher than other production sources, an additional model was run for the Brazos using only $\delta^{13}\text{C}$ values. The OXFREQ model included C₃ trees, C₃ grasses, phytomicrobenthos and seston. Nitrogen values were corrected for trophic fractionation using the value of 2.54 ‰ calculated from a meta-analysis of fractionation studies (Vanderklift and Ponsard 2003). Each model examined source contributions in 1% intervals with a tolerance of 0.1‰.

Trophic position (TP) of each species was estimated based on fractionation of $\delta^{15}\text{N}$ between consumers and basal production sources (Vander Zanden & Rasmussen 1999; Post 2002). Calculations were performed using the methodology described in Jepsen and Winemiller (2002), and the trophic position of each consumer was calculated as:

$$\text{TP} = ((\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{reference}})/2.54) + 1,$$

where $\delta^{15}\text{N}_{\text{reference}}$ was the mean $\delta^{15}\text{N}$ of basal sources (C_3 macrophytes, C_4 macrophytes, phytomicrobenthos, and seston), and 2.54 ‰ was the mean trophic fractionation value from a meta-analysis of trophic fractionation studies (Vanderklift and Ponsard 2003). Reference nitrogen values were calculated separately for each habitat due to the significant spatial difference in nitrogen ratios of basal sources discussed above. Because reference values were calculated separately, estimates of consumer trophic positions were directly comparable among the three habitats surveyed.

RESULTS

A total of 378 consumer and basal source samples was analyzed for carbon and nitrogen isotopic ratios with 85, 151, and 142 samples analyzed in the Brazos River, OXFREQ and OXRARE, respectively. The months during which consumer taxa were sampled (April – August 2004) represented a period of greater than normal hydrologic connectivity in the Brazos River-floodplain and there was not a prolonged low-flow period in the main channel. Five separate flood connections occurred between the river channel and OXFREQ, and OXRARE was connected to the river channel on three occasions. In total, the river channel was hydrologically connected with at least one of the study oxbows for a total of 24 days.

Mean $\delta^{13}\text{C}$ values of basal sources were relatively well differentiated within each habitat, however some sources had different isotopic ratios between habitats. Terrestrial C_3 macrophytes had relatively light carbon ratios and had similar mean $\delta^{13}\text{C}$ values among habitats (Brazos = -29.40 ‰, OXFREQ = -29.13 ‰, and OXRARE = -28.86 ‰). Terrestrial C_4 macrophytes were relatively enriched in ^{13}C and had similar values in the

two habitats where they were collected (Brazos = -13.32 ‰, OXRARE = -12.78 ‰). Seston samples had similar values in the two oxbow lakes, and these ratios were intermediate between those of the two terrestrial sources (OXFREQ = -25.00 ‰, OXRARE = -26.37 ‰), whereas seston in the river channel was more ^{13}C enriched (-15.36 ‰) relative to oxbow samples. Values in the river channel may have resulted from contamination of by sediment carbonates, or organic particles may have been primarily of C_4 origin. Samples of phytomicrobenthos had mean values of -20.15, -25.50, and -17.63 ‰ in the river channel, OXFREQ and OXRARE, respectively. Factors such as current velocity, CO_2 concentration and temperature can influence the $\delta^{13}\text{C}$ values of benthic algae (Finlay et al. 1999), and may have contributed to the spatial variation observed in our study. Coefficients of variation for $\delta^{13}\text{C}$ of sources sampled over one year (September 2003 –August 2004) were generally greater for aquatic production sources (0.07 – 0.36) relative to terrestrial sources (0.04 – 0.11) (Figure 3), a result similar to that found by Jepsen (1999).

$\delta^{15}\text{N}$ values of sources were significantly different between habitats as discussed above. Within habitats, the range of mean $\delta^{15}\text{N}$ values between sources was greater in the Brazos River (7.21 – 12.12 ‰) relative to OXFREQ (5.91 – 6.94 ‰), and OXRARE (3.78 – 4.90 ‰). Coefficients of variation for source $\delta^{15}\text{N}$ were generally greater than $\delta^{13}\text{C}$ (Figure 17) which supported results reported by Jepsen (1999) that there is considerable seasonal variation in nitrogen ratios of production sources in Brazos oxbows.

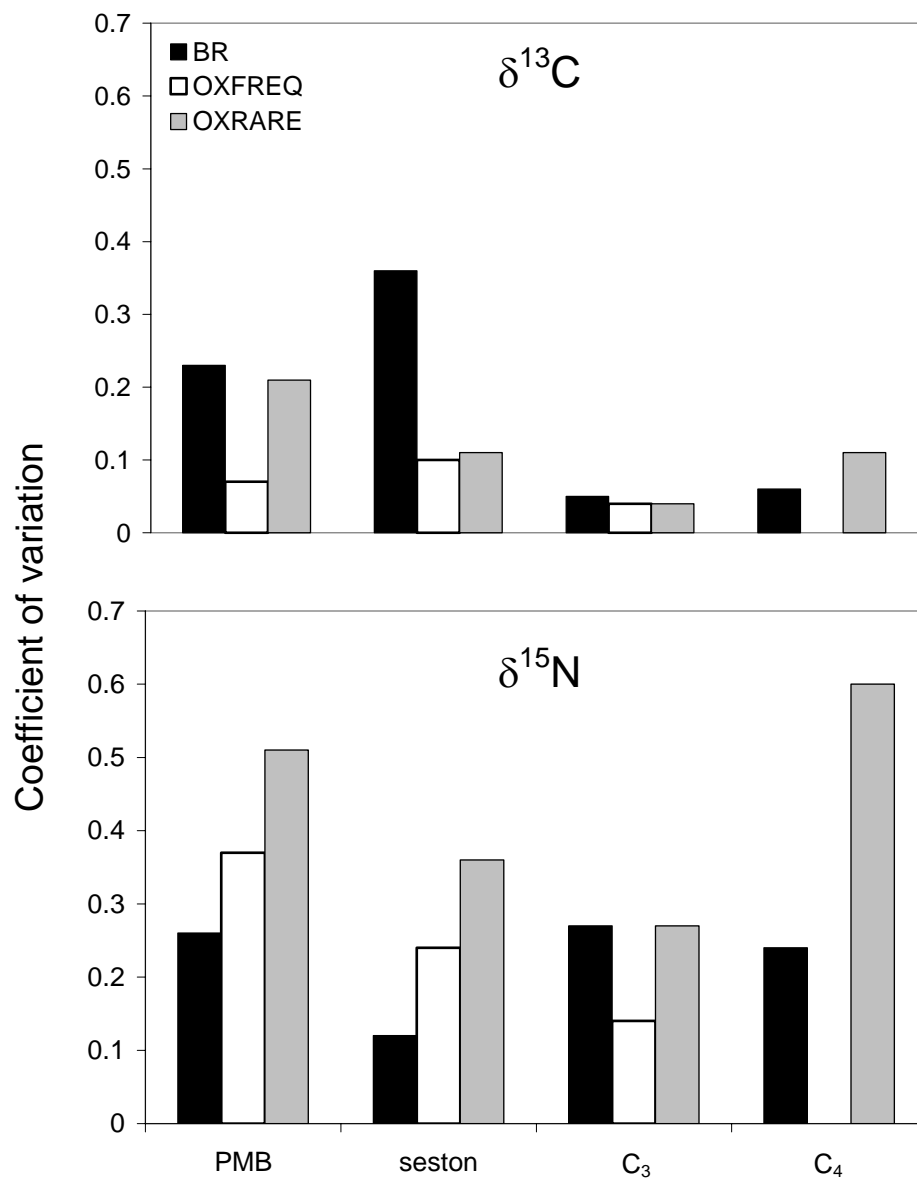


Figure 17. Coefficients of variation for $\delta^{13}\text{C}$ (top panel) and $\delta^{15}\text{N}$ (bottom panel) values of production sources sampled over a one-year period in each habitat. PMB = phytomicrobenthos.

Carbon sources supporting aquatic consumers

Consumer taxa in the Brazos River channel had a narrow range of $\delta^{13}\text{C}$ values that were intermediate relative to the range of mean values of production sources (Figure 18). Ohio River shrimp were the most ^{13}C enriched (-23.39 ‰) and bullhead minnow were the most depleted (-24.67 ‰) species. IsoSource model solutions (1 – 99th percentile ranges) indicated that C_3 macrophytes were the most important production source supporting biomass of all seven taxa examined, and C_4 macrophytes also accounted for a significant fraction of assimilated carbon (Table 8). Model results suggested that the two aquatic production sources (phytomicrobenthos and seston) probably made minor contributions, although 99th percentile values were greater for phytomicrobenthos relative to seston (Table 8). Solutions from the carbon-only model supported the importance of C_3 macrophytes to consumer biomass, however ranges for other sources had 1 percentile values of zero.

Species in OXFREQ had a greater range of $\delta^{13}\text{C}$ values relative to the river channel, and they were, on average, more ^{13}C depleted (Figure 18). IsoSource solutions indicated assimilation of material from a mixture of production sources. Phytomicrobenthos accounted for a large fraction of crayfish and mosquitofish biomass, with seston also being an important contributor (Table 9). Terrestrial production sources appeared to contribute little to crayfish, whereas greater, although relatively minor, contributions were possible for mosquitofish. Terrestrial C_3 trees accounted for a large fraction of grass shrimp, white crappie, bluegill, and smallmouth buffalo biomass (Table 9). Seston contributions for these species also were important (1 percentile values > 0),

although 99th percentile values were relatively low for white crappie and smallmouth buffalo, suggesting that seston was a minor yet consistent contributor to biomass of these species (Table 9). For bluegill and grass shrimp, large contributions from terrestrial C₃ grasses were also possible, although ranges of potential contributions were broad (Table 9). Red shiner and gizzard shad seemed to assimilate material from all four sources, although only the two aquatic sources had 1-percentile values > 0, indicating they likely were consistent contributors (Table 9). Model results did not suggest a dominant production source for spotted gar. As apex predators with broad diets, spotted gar likely feed on a prey assemblage that assimilate material from multiple aquatic and terrestrial sources.

Carbon ratios of consumers in OXRARE had similar means and ranges as those in OXFREQ (Figure 18). A large fraction of all consumer biomass was accounted for by terrestrial C₃ macrophytes, with 1 percentile values ranging from 47 - 84%, and 99th percentile values ranging from 67 - 98% (Table 10). Terrestrial C₄ macrophytes likely contributed little to most consumers. Similar to patterns in OXFREQ, phytomicrobenthos accounted for significant fractions of mosquitofish and crayfish biomass, and this also was an important source for red shiner. Phytomicrobenthos also accounted for a smaller, yet similar fraction of spotted gar, bluegill, white crappie, and grass shrimp biomass. Seston seemed to be a minor contributor for most consumers, although a relatively large fraction was possible for spotted gar (Table 10).

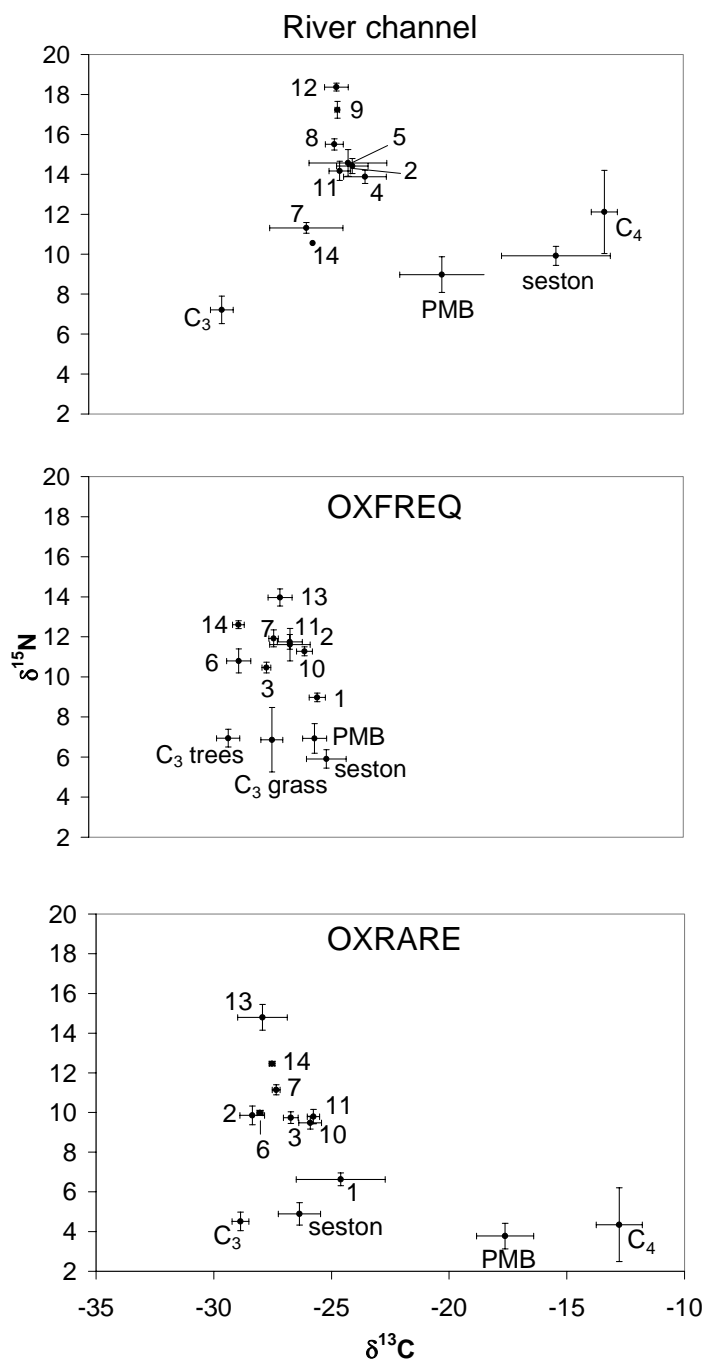


Figure 18. Carbon and nitrogen isotope ratio biplots of production sources and consumer taxa in each habitat. Species codes are as follows: PMB = phytomicrobenthos, 1 = crayfish, 2 = gizzard shad, 3 = grass shrimp, 4 = Ohio River shrimp, 5 = river carpsucker, 6 = smallmouth buffalo, 7 = bluegill, 8 = bullhead minnow, 9 = longear sunfish, 10 = mosquitofish, 11 = red shiner, 12 = longnose gar, 13 = spotted gar, 14 = white crappie.

Table 8. Means and 1 - 99th percentile ranges (in parentheses) of sources contributions to Brazos River consumer biomass from IsoSource models. Sample sizes for consumers are in parentheses next to species names.

Species	C₄	C₃	Phytoplankton	Seston
Fish				
red shiner (15)	0.28 (0.27-0.31)	0.68 (0.66-0.69)	0.02 (0.00-0.07)	0.01 (0.00-0.05)
river carpsucker (3)	0.27 (0.23-0.33)	0.64 (0.59-0.67)	0.06 (0.00-0.16)	0.04 (0.00-0.11)
gizzard shad (9)	0.25 (0.21-0.32)	0.62 (0.56-0.66)	0.08 (0.00-0.21)	0.05 (0.00-0.14)
longnose gar (11)	0.29 (0.28-0.30)	0.69 (0.68-0.70)	0.01 (0.00-0.04)	0.01 (0.00-0.02)
longear sunfish (2)	0.29 (0.27-0.30)	0.69 (0.67-0.70)	0.02 (0.00-0.05)	0.01 (0.00-0.03)
bullhead minnow (12)	0.29 (0.29-0.30)	0.70 (0.70-0.70)	<0.01 (0.00-0.01)	<0.01 (0.00-0.01)
Invertebrates				
Ohio River shrimp (2)	0.21 (0.15-0.27)	0.55 (0.47-0.61)	0.15 (0.00-0.35)	0.10 (0.00-0.22)

Table 9. Means and 1 - 99th percentile ranges (in parentheses) of sources contributions to OXFREQ consumer biomass from IsoSource models. Sample sizes for consumers are in parentheses next to species names.

Species	C₃ grasses	C₃ trees	Phytoplankton	Seston
Fish				
red shiner (8)	0.33 (0.00 - 0.67)	0.16 (0.00 - 0.34)	0.28 (0.04 - 0.50)	0.24 (0.13 - 0.34)
gizzard shad (17)	0.32 (0.00 - 0.66)	0.16 (0.00 - 0.34)	0.27 (0.03 - 0.49)	0.25 (0.14 - 0.35)
mosquitofish (12)	0.15 (0.00 - 0.34)	0.08 (0.00 - 0.17)	0.53 (0.36 - 0.70)	0.24 (0.14 - 0.34)
smallmouth buffalo (10)	0.07 (0.00 - 0.24)	0.83 (0.71 - 0.93)	0.03 (0.00 - 0.10)	0.07 (0.03 - 0.14)
spotted gar (14)	0.35 (0.00 - 0.81)	0.26 (0.01 - 0.45)	0.15 (0.00 - 0.37)	0.24 (0.13 - 0.36)
bluegill (11)	0.29 (0.00 - 0.73)	0.36 (0.12 - 0.52)	0.12 (0.00 - 0.31)	0.23 (0.13 - 0.36)
white crappie (25)	0.05 (0.00 - 0.16)	0.84 (0.76 - 0.91)	0.02 (0.00 - 0.07)	0.09 (0.07 - 0.14)
Invertebrates				
crayfish (13)	0.02 (0.00 - 0.08)	0.01 (0.00 - 0.04)	0.68 (0.57 - 0.82)	0.28 (0.17 - 0.36)
grass shrimp (14)	0.20 (0.00 - 0.54)	0.49 (0.29 - 0.61)	0.08 (0.00 - 0.23)	0.23 (0.14 - 0.36)

Table 10. Means and 1 - 99th percentile ranges (in parentheses) of sources contributions to OXRARE consumer biomass from IsoSource models. Sample sizes for consumers are in parentheses next to species names.

Species	C₄	C₃	Phytoplankton	Seston
Fish				
red shiner (11)	0.01 (0.00 - 0.03)	0.71 (0.67 - 0.74)	0.26 (0.23 - 0.28)	0.02 (0.00 - 0.06)
gizzard shad (15)	0.01 (0.00 - 0.04)	0.92 (0.84 - 0.98)	0.02 (0.00 - 0.06)	0.04 (0.00 - 0.11)
mosquitofish (9)	0.01 (0.00 - 0.04)	0.73 (0.69 - 0.75)	0.24 (0.21 - 0.27)	0.02 (0.00 - 0.06)
smallmouth buffalo (15)	0.02 (0.00 - 0.06)	0.89 (0.79 - 0.95)	0.04 (0.00 - 0.09)	0.05 (0.00 - 0.15)
spotted gar (12)	0.07 (0.00 - 0.21)	0.57 (0.36 - 0.72)	0.23 (0.07 - 0.26)	0.12 (0.00 - 0.34)
bluegill (15)	0.02 (0.00 - 0.06)	0.84 (0.77 - 0.89)	0.11 (0.06 - 0.15)	0.03 (0.00 - 0.10)
white crappie (17)	0.01 (0.00 - 0.03)	0.87 (0.81 - 0.90)	0.11 (0.08 - 0.13)	0.02 (0.00 - 0.07)
Invertebrates				
crayfish (2)	0.04 (0.00 - 0.11)	0.59 (0.47 - 0.67)	0.31 (0.21 - 0.38)	0.07 (0.00 - 0.19)
grass shrimp (15)	0.03 (0.00 - 0.08)	0.79 (0.70 - 0.84)	0.15 (0.08 - 0.20)	0.04 (0.00 - 0.13)

Trophic position of consumers

¹⁵N data indicated approximately 5 trophic levels in the river channel and OXRARE, and 4 trophic levels in OXFREQ (Figure 19). In the river channel, no consumers had a trophic level below 3, suggesting that trophic level 2 may be dominated by aquatic insects that were not well sampled in our survey. The third trophic level contained species in the detritivore/omnivore guild (gizzard shad, Ohio River shrimp and river carpsucker) and two species in the insectivore guild (red shiner and bullhead minnow), although the TP of bullhead minnow approached level 4 (3.7). Longear sunfish and longnose gar comprised the fourth trophic level, and the longnose gar value approached trophic level 5 (TP = 4.8).

Trophic level 2 in OXFREQ included crayfish, grass shrimp and smallmouth buffalo. Crayfish had a trophic position slightly less than 2.0 (TP = 1.9) which may have resulted from error in the estimation of reference nitrogen values. Five species approximated trophic level 3 (gizzard shad, bluegill, mosquitofish, red shiner and white crappie) and spotted gar approached trophic level 4 (TP = 3.8). In OXRARE, crayfish were the only species in trophic level 2, and similar to crayfish in OXFREQ, crayfish trophic position was slightly less than 2.0 (1.9). Gizzard shad, grass shrimp, smallmouth buffalo, mosquitofish, red shiner, and bluegill comprised trophic level 3. White crappie was the only species in trophic level 4, and spotted gar approximated trophic level 5 (Figure 19).

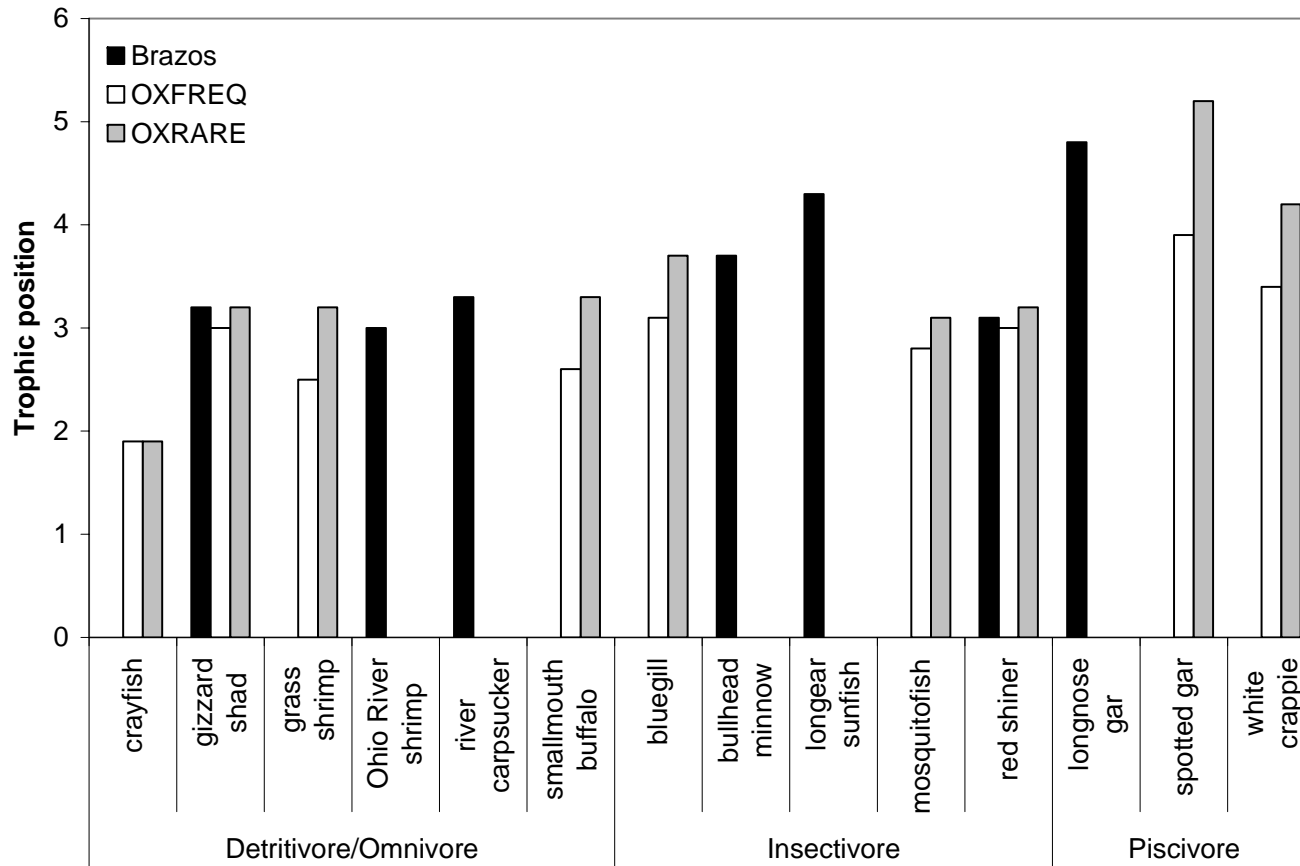


Figure 19. Trophic positions of main channel and oxbow consumers based on $\delta^{15}\text{N}$ values.

Isotopic evidence of faunal exchange

Isotopic ratios of gizzard shad in the oxbow lakes had a wider range of values relative to shad in the river channel. When isotope ratios were plotted by standard length, two distinct groupings were evident (Figure 20). Shad < 150 mm in oxbow lakes had nitrogen and carbon ratios that were depleted relative to shad > 150 mm, whereas this trend was not apparent in the river channel where shad of all sizes had similar isotopic ratios. Large shad in oxbow lakes had isotopic signatures more similar to shad in the river channel, which suggests that large shad immigrated into oxbow lakes from the river channel during flood periods. Stomach contents analysis of shad in oxbow lakes indicated that large and small individuals consumed similar proportions of food items (Zeug, unpublished data), which supports the idea that differences in diet composition were not the source of isotopic variation. Some of the large shad in oxbows had signatures similar to juveniles or intermediate between river and oxbow signatures, and these individuals may have been produced *in situ* or resided in oxbows for a period sufficient for muscle tissue to reach isotopic equilibrium (Figure 20). The rarely flooded oxbow had a greater proportion of large shad with oxbow-like signatures (57%) relative to the frequently connected oxbow (20%) where opportunities for faunal exchange are more common.

Two bluegill sunfish and 1 crappie captured in the river channel were relatively enriched in $\delta^{13}\text{C}$ and had $\delta^{15}\text{N}$ values less than some source materials (Figure 18). These isotopic ratios were similar to values for these same species in oxbow lakes, which may

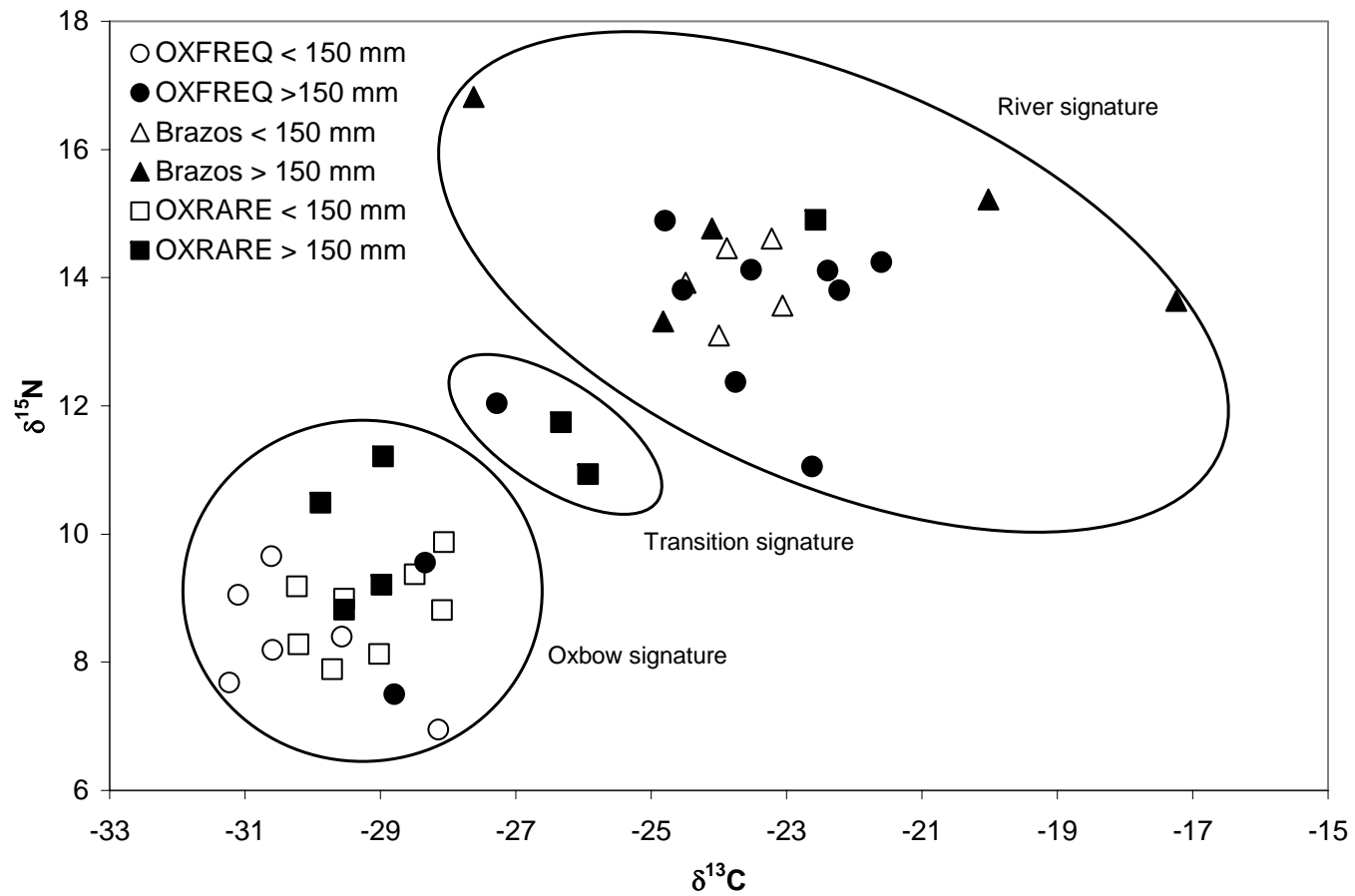


Figure 20. Biplot of carbon and nitrogen isotope ratios of gizzard shad collected in the Brazos River channel and two oxbow lakes.

suggest these individuals migrated to the river channel during flood connections and had retained their “oxbow” isotopic signature. Both of these species are abundant in oxbow lakes and relatively rare in river channel (Winemiller et al. 2000; Zeug et al. 2005).

DISCUSSION

Isotopic mixing model estimates indicated that terrestrial carbon (C_3 macrophytes) was the primary source supporting consumer biomass in the main channel and the rarely flooded oxbow, and accounted for a large fraction of biomass of certain consumers in the frequently flooded oxbow. In the river channel, terrestrial C_4 macrophytes made a consistent, yet smaller contribution relative to C_3 macrophytes, whereas this source only had the potential for minor contributions to oxbow consumers. Isotopic studies of other temperate and subtropical rivers have found that C_4 macrophytes are relatively unimportant as an energy and nutrient source contributing to consumer biomass (Thorp et al. 1998; Clapcott and Bunn 2003; Herwig et al. 2004), and the inclusion of isotopic values for C_4 macrophyte samples that were not collected during the study interval could have overestimated their importance. Surveys of tropical river food webs indicate relatively minor contributions from C_4 macrophytes (Leite et al. 2002; Watzen et al. 2002; Hoeninghaus et al. *In press*). The large estimated contribution of terrestrial carbon to consumers within the Brazos River ecosystem contradicts recent studies reporting the importance of autochthonous algal carbon to large river food webs (Lewis et al. 2001; Thorp and Delong 2002; Douglas et al. 2005).

Hydrologic characteristics of the Brazos River could influence the importance of terrestrial relative to aquatic (algal) primary production sources. The current study

was conducted during a period of greater than average flows in the middle Brazos River. High flows in the main channel resulted in scouring of benthic algae from shallow areas and/or deposition of large volumes of sediment that prevented collection of algal samples during certain periods. IsoSource model results for certain consumer taxa in oxbow lakes, where flow disruptions were less frequent, indicated significant contributions from autochthonous algal carbon (phytomicrobenthos and seston). Mosquitofish, red shiner and crayfish in oxbows potentially had assimilated large amounts of carbon derived from benthic algae (phytomicrobenthos). These species are small-bodied (< 100 mm) and exploit shallow littoral habitats where benthic algae are most abundant. Thus, benthic algae may be a more ephemeral resource than terrestrial material during high flow periods in the channel, and greater contributions of algal carbon to certain consumers may be observed during stable low-flows. Delong et al. (2001) reported little change in carbon sources supporting consumers in response to a flood in the Upper Mississippi River, however, the flow regime of the Brazos is much less predictable among years relative to other floodplain systems (Winemiller 1996). Shifts in the contribution of terrestrial and aquatic carbon sources to consumers based on resource availability, as mediated by river hydrology, were reported for a New Zealand river by Huryn et al. (2001). Bunn et al. (2003) found that benthic algae were the primary carbon source supporting consumers in isolated water holes during a low-flow period in Cooper Creek, Australia.

Conspecifics collected from different habitats in the Brazos system had similar trophic positions in most cases, despite the significant spatial difference in reference

$\delta^{15}\text{N}$ values. This pattern suggests that materials assimilated by most of the consumers in the main channel and oxbow lakes were produced locally. Finlay et al. (2002) reported that locally produced carbon sources supported consumer taxa in the Eel River, California. The flood pulse concept predicts that production sources supporting consumers in the main channel are primarily terrestrial materials originating on the floodplain (Junk et al. 1989). Our results support the importance of terrestrial materials to consumer biomass, and similar results have been inferred for other large rivers (Leite et al. 2002; Wantzen et al. 2002; Hoeninghaus *In press*), however, these materials did not appear to originate on the floodplain. The riverine productivity model (Thorp and Delong 1994) emphasizes the importance of autochthonous production to consumer biomass in large rivers. Direct terrestrial inputs from the riparian zone are included as one of the potential autochthonous production sources supporting consumers. Although revisions of the RPM model have increasingly recognized the importance of algal carbon (Thorp et al. 1998; Thorp and Delong 2002; Delong and Thorp 2006), trophic dynamics in the main channel of the Brazos River appear to support the RPM model as originally proposed. Consumers in oxbow lakes assimilated greater proportions of algal carbon in addition to smaller fractions of C_3 terrestrial material, thus trophic dynamics in these habitats also supported the RPM model.

Differences in $\delta^{15}\text{N}$ values in the Brazos River and associated oxbows indicated a gradient of distance with the most enriched values in the river channel and the least enriched values in the most distant oxbow (≈ 1200 m from the main channel). Enriched $\delta^{15}\text{N}$ values in the river channel may result from agricultural nitrogen inputs and/or

sewage treatment plants located on tributaries of the main channel. Allochthonous inputs of nitrogen have been shown to influence consumer $\delta^{15}\text{N}$ values in other aquatic systems (Cabana and Rasmussen 1996; Steffy and Kilham 2004; Schlacher et al. 2005). Oxbow lakes have small catchments and receive river water during flood pulses when potential sources of enriched $\delta^{15}\text{N}$ should be diluted. Despite the pattern of less enrichment with increasing distance, samples were only collected from three habitats, and future studies would benefit by collecting samples from more habitats encompassing a greater range of distances from the main channel.

Spatial variation in stable isotope ratios has been used to examine consumer habitat use as well as movement of consumers between different habitat units (Hansson et al. 1997; Fry 2002; Cunjak et al. 2005). In the current study, variation in isotope ratios of several species suggested movement between the main channel and oxbow lakes during flood periods. Large gizzard shad were inferred to show net movement from the river channel into oxbow lakes during flood periods, whereas, based on limited sample sizes, bluegill and white crappie moved mostly from oxbows to the river channel. Floodplain habitats are favorable for fish reproduction and recruitment (Sabo and Kelso 1991; Killgore and Baker 1996), and adult gizzard shad frequently enter oxbow lakes to reproduce. Zeug et al. (2005) found that juvenile gizzard shad were much more abundant in Brazos oxbows relative to the main channel. Subsequent river-oxbow connections allow sub-adults to move back to the channel (oxbows are fine too). Crappie and bluegill seem to prefer lentic habitats and most individuals probably do not actively migrate to the main channel. Because sub-samples of each species were

analyzed and not all species collected were analyzed for stable isotope ratios, the magnitudes of fish movement during floods could not be estimated. Estimates of fish movement between habitats from isotopic data could be complemented with telemetry or mark-recapture studies (Cunjak et al. 2005). If, in fact, consumer taxa assimilate material produced locally, fish movement between oxbow lakes and the main channel may be a significant pathway for the transfer of floodplain organic matter to the main river channel (Winemiller and Jepsen 1998).

Estimates of consumer trophic positions indicated approximately 5 trophic levels in the main channel and OXRARE, and 4 levels in OXFREQ. The absence of a 5th trophic level in OXFREQ may have resulted from error in the estimation of reference nitrogen values, however, several species had similar trophic positions in OXFREQ and the other two habitats (crayfish, gizzard shad, mosquitofish and red shiner). Longnose and spotted gars were the only species that approximated the 5th trophic level. Differences in prey assemblages among habitats may have influenced gar trophic positions. Beaudoin et al. (1999) reported that trophic positions of northern pike (*Esox lucius*) could vary up to 1 trophic level in relation to consumption of invertebrate versus fish prey. Analysis of gar stomachs revealed that individuals in OXFREQ primarily consumed crayfish (TP = 1.9), whereas gar in OXRARE consumed more shad (TP = 3.2) and sunfish (TP = 3.7), and longnose gar consumed large volumes of catfish (Robertson et al. unpublished manuscript). Few consumers in the detritivore/omnivore guild had trophic positions below three, and trophic level two is likely composed of aquatic invertebrates that were not well sampled in this study. Species in this guild

consume large amounts of detritus but may assimilate large fractions of animal matter despite the lower abundance of the latter in consumer diets (Mantel et al. 2004; Winemiller et al. *In press*).

Stable isotopes are effective tracers of material assimilated by consumers because they integrate diet over relatively long time periods compared to stomach contents analysis. The current study examined the isotopic composition of consumers over 5 months, a period potentially insufficient to characterize the contribution of different production sources in relation to the hydrologic dynamics of the Brazos River. Seasonal variation in production sources supporting food webs can be significant, especially in floodplain systems that experience large fluctuations in water level and associated changes in species assemblage structure (Winemiller 1990; Huryn et al. 2001). The relative importance of terrestrial and aquatic production sources varied spatially as well as among consumer taxa within habitats. Identification of production sources supporting consumer biomass can be affected by the spatial and temporal scale of collections as well as the choice of species used in isotopic analysis, and these factors should be addressed in future studies of large-river food webs.

Identification of the trophic pathways supporting species in large river-floodplain systems is essential for their management and restoration (Winemiller 2005). Our results indicated that multiple terrestrial and aquatic production sources supported aquatic consumer taxa. Contributions from individual production sources varied among hydrologic periods, habitat units and species, which reinforces the need to examine the interaction between habitat heterogeneity and flow variability for the maintenance of

essential ecological functions in lotic systems (Poff et al. 1997; Bunn et al. 2002). Elimination of high flows due to dam and levee construction would impair the movement of floodplain carbon (in the form of mobile aquatic fauna) to the main channel and eliminate opportunities for some species to exploit off-channel areas for reproduction. Movement of fauna between different habitat units was inferred from isotopic data and river-floodplain connections may be essential to the persistence of populations that exploit multiple habitat types during some point in their life cycle, and predators that feed on prey populations as they move between habitats.

CHAPTER V

SUMMARY

The results presented in the preceding chapters suggest that conceptual models describing ecological function in large rivers (FPC, LFR, and RPM) are too vague to provide accurate predictions regarding fish reproduction, recruitment and trophic dynamics for the diversity of fish life history tactics and trophic guilds in the Brazos River, and perhaps in large rivers in general. These conceptual models are approximations of ecological structure and dynamics, yet they are often assumed to apply to large rivers with different hydrologic regimes despite a lack of empirical evaluation of these models (Humphreis et al. 1999; Thorp et al. 2006). Hydrologic variation between different habitats and time periods was a consistent factor influencing ecological dynamics in this investigation, and my results provide the basis for a model of fish reproduction, recruitment and trophic dynamics in relation to the spatial heterogeneity and flow variability of the Brazos River. Because these analyses were conducted at the level of life history strategy and trophic guilds, results provide a general approach for research on hydrologic influences on ecological dynamics as well as flow and habitat-related management prescriptions for impaired river systems.

FISH REPRODUCTION AND RECRUITMENT

Reproductive activity of fishes representing divergent life history strategies was positively associated with long-term flow dynamics similar to predictions of the flood pulse concept, however, fish with different life history strategies exploited different periods of the hydrograph and different habitat types. Floods in the Brazos River are

short (days to weeks) relative to many tropical floodplain systems where floods may last for almost half the year. This short period of floodplain connectivity reduces the probability of fish exploiting seasonally inundated areas for recruitment, because there is insufficient time for reproduction, larval rearing, and return to the main channel.

However, timing reproduction to coincide with high flow periods allows fish to exploit perennial oxbow lakes that contain greater standing stocks of larval and juvenile food resources and which appear to be profitable habitats for most of the species examined.

Reproductive activity of periodic strategists was greatest during spring as temperatures were rising and the probability of flooding was increasing. This strategy would allow larvae and juveniles of some species to be transported into oxbow lakes. Larvae and juveniles remain in oxbow lakes that are more favorable for recruitment relative to the main river channel, especially during periods of isolation when food resources are more abundant (Chapter II). Isotopic ratios of gizzard shad supported this interpretation. Adult shad populations in oxbow lakes contained individuals that immigrated from the river channel as well as individuals produced *in situ*. Juvenile shad were more abundant in oxbow lakes and had isotopic signatures that suggest their biomass was produced from materials originating in oxbows. Hydrologic connections between oxbows and the river channel following periods of isolation would allow juveniles produced in oxbows to return to the channel where conditions seem to be sufficient for adults. Longnose gar are largely restricted to the river channel and spotted gar are most common in oxbow lakes. These species can complete their entire life cycle in their preferred habitats, however there was no evidence to suggest a strong juvenile

year class of either species was produced during the study period. Both species have long life spans and may produce a strong year class only when optimal conditions occur in their preferred habitat, which may happen many years apart. Flood dynamics during the study did not conform to the long-term smoothed hydrograph, suggesting that flood connections did not occur during an optimal period for fishes generally. Robertson et al. (unpublished manuscript) found that gar species did benefit from oxbow-river connections during the period of my study by feeding on fishes as they moved between habitats.

Equilibrium strategists preferred lentic oxbow lakes and were rarely collected in the river channel where frequent changes in discharge may disrupt their reproductive activities, such as nest building and brood guarding. The white crappie population produced a strong year class during the dry year when flow disruptions were less common. For species with this strategy, oxbow lakes are particularly important for the persistence of their populations in the Brazos River-floodplain system however, periodic flooding is important for maintaining water levels in oxbows. Isotope data indicated that white crappie collected in the river channel originated in oxbow lakes. Although populations of the two equilibrium species in the river channel were small, these populations are likely to be essential for recolonization of oxbow lakes following extended periods of drought that result in desiccation of oxbow habitats (Winemiller et al. 2000).

Reproductive activity of opportunistic species was greatest during periods with the highest flood probability. This strategy would allow adults to colonize off-channel

habitats and exploit them for reproduction. Life history traits of these species are well suited for rapid colonization of frequently disturbed, ephemeral habitats. Opportunistic species had stronger recruitment during the dry year, suggesting that although high flow periods may facilitate colonization/reproduction, recruitment is greater during low flow periods.

These results support the growing contention of the importance of habitat heterogeneity and flow variability for fish populations in large rivers. The relative importance of each factor was associated with life history strategies as well as individual species traits. Fish populations in the Brazos River appear to be adapted to long-term hydrologic dynamics, and flow management strategies that focus on historical flows are more likely to support the persistence of fish populations with divergent life history traits than methods that seek to optimize one or a few flow elements (Richter et al. 1997). Off-channel habitats were critically important for the reproduction and recruitment of several species. In addition to flow regime, fluvial dynamics, such as erosion and sediment deposition that drive the creation and geomorphic succession of these habitats are important to maintain the ecological integrity of large rivers over long time intervals.

TROPHIC DYNAMICS

Terrestrial C₃ macrophytes generally supported the greatest fraction of consumer biomass in the Brazos River, even though some consumers in oxbow lakes probably assimilated large fractions of algal carbon (phytomicrobenthos and seston). This result contradicts an increasing recognition of the importance of autochthonous algal carbon to food webs in large rivers. Several factors related to improvement in isotopic mixing

models and bias in sampling strategies for isotopic studies may have influenced these results.

Estimation of proportional contributions of source materials to consumers using traditional two end-member mixing models is complicated by overlapping isotopic ratios of sources. This often results in the combination of sources that are not functionally related (Phillips et al. 2005). This is especially problematic because $\delta^{13}\text{C}$ values for terrestrial macrophytes and algal sources often overlap (Thorp et al 1998; Leite et al. 2002; Herwig et al. 2003). By simultaneously incorporating multiple elements, the IsoSource mixing model allows for the estimation of source contributions when the number of sources is too large to permit a unique solution. Future isotopic studies may reveal greater contributions of terrestrial materials to aquatic food webs as new isotopic mixing models are developed.

The temporal scale of isotopic investigations also may have a significant influence on the identification of production sources supporting consumer biomass. Most isotopic investigations involve sampling over short time scales (days to weeks) during low-flow periods that are easier for the collection of aquatic fauna. During high-flow periods, algae can be scoured from the benthos and terrestrial material can provide an alternative production source for consumers. Huryn et al. (2001) found that terrestrial carbon sources were important during high-flow periods, and algal sources increased in importance during low-flow periods. My isotopic study took place during a high-flow period, and terrestrial material was a significant source of consumer biomass in the channel. Oxbow lakes were exposed to fewer hydrologic disturbances, and algae made

greater contributions to consumers in these habitats. This bias toward low-flow periods in isotopic studies may represent a “hidden treatment” that should be addressed in future investigations of large river food webs.

In conclusion, conceptual models of ecological function in large rivers are too general to provide accurate predictions of fish reproduction, recruitment and trophic dynamics. The results presented in the preceding chapters suggest that fish with divergent live history strategies utilize flow periods and habitat units for reproduction and recruitment in different ways according to their life history traits and habitat affinities. Because a particular model may only apply to a sub-set of species with a certain suit of traits, or a certain stage of a species life cycle, conceptual models require evaluation with quantitative data before being applied to river restoration strategies. Production sources supporting aquatic fauna are influenced by hydrologic dynamics and predictions of conceptual models should be viewed as approximations, recognizing that large rivers are spatially heterogeneous and experience large scale changes in hydrology that have the potential to mediate sources of primary production supporting aquatic food webs.

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