

## RELATIONSHIPS BETWEEN HYDROLOGY, SPATIAL HETEROGENEITY, AND FISH RECRUITMENT DYNAMICS IN A TEMPERATE FLOODPLAIN RIVER

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### ABSTRACT

Fish populations in the Brazos River, Texas, were surveyed monthly for 2 years to determine the relative influence of hydrology and habitat characteristics on the recruitment dynamics of seven species representing three divergent life history strategies. Surveys were conducted in two oxbow lakes with different flood recurrence intervals and the main river channel. The first year was relatively dry with few oxbow-river connections, whereas year 2 was relatively wet and connections between the main channel and floodplain habitats were common. Oxbow lakes supported greater juvenile abundances of most species relative to the main channel and were particularly important for nest building species with parental care. The river channel supported small species with extended reproductive periods and large, long-lived species that are able to store reproductive potential during sub-optimal periods. Hydrologic isolation was associated with greater rotifer densities in oxbows, and species with the greatest fecundity produced strong year classes during this period. Hydrologic connectivity did not increase juvenile production for most species, suggesting that recruitment dynamics in the Brazos River are similar to predictions of the low flow recruitment hypothesis (LFR). These results suggest that both hydrology and habitat heterogeneity interact with fish life history strategy to determine optimal conditions for recruitment and all three factors must be considered in restoration strategies for floodplain rivers. Copyright © 2007 John Wiley & Sons, Ltd.

KEY WORDS: Brazos River; flood pulse; life history; oxbow; Texas

*Received 19 March 2007; Accepted 25 July 2007*

### 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 fishes 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 water rise 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 follow the optimum described in the FPC, fishes 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

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*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), fish life history strategies provide a good framework for evaluating environmental influences on recruitment dynamics.

Our goals for this study were to evaluate the relative influence of hydrology and habitat characteristics for 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. We predicted that both conceptual models of recruitment would apply to fishes 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. 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. 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 typical low versus high connection frequencies. 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 was recorded to the nearest 1 cm. Days of isolation 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  $\mu\text{m}$  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  $\times$  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 travelled with the seine was recorded for calculation of 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  $16.5 \times 2$  m with 25.4-, 76-, and 51 mm bar mesh. The total hours of each set were 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 fishes 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 variations. 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 favourable 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 (in press) 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).

Specimens were classified as adults or juveniles based on minimum size-at-maturity estimates for each species (Zeug and Winemiller, in press). 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.

In order to provide a measure of recruitment independent of adult standing stock, species recruitment among habitats and years was also 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. GEE models were performed in SAS version 9.1 and log-likelihood tests were performed in NCSS 2000 version.

Principal components analysis (PCA) was performed on the sample  $\times$  environmental variable matrix of monthly data in order to associate variation in biotic and abiotic characteristics with variation in recruitment. Prior to PCA,

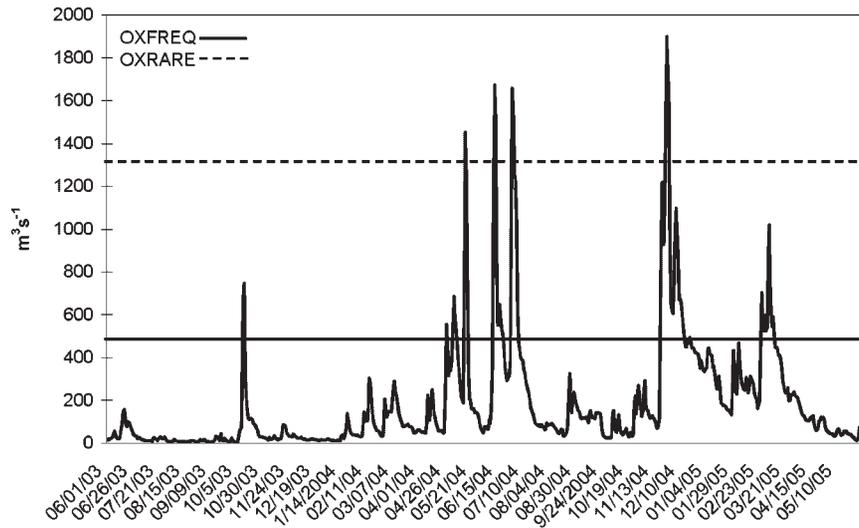


Figure 1. Daily stream flow hydrograph of the Brazos River during the two year study period. Horizontal lines indicate flows required to connect oxbow lakes with the Brazos River channel

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*

Principal components' analysis produced two axes that explained 82.5% of the variation in environmental characteristics (Figure 2). Axis 1 modelled 59.5% of the total variation and described a gradient between the most

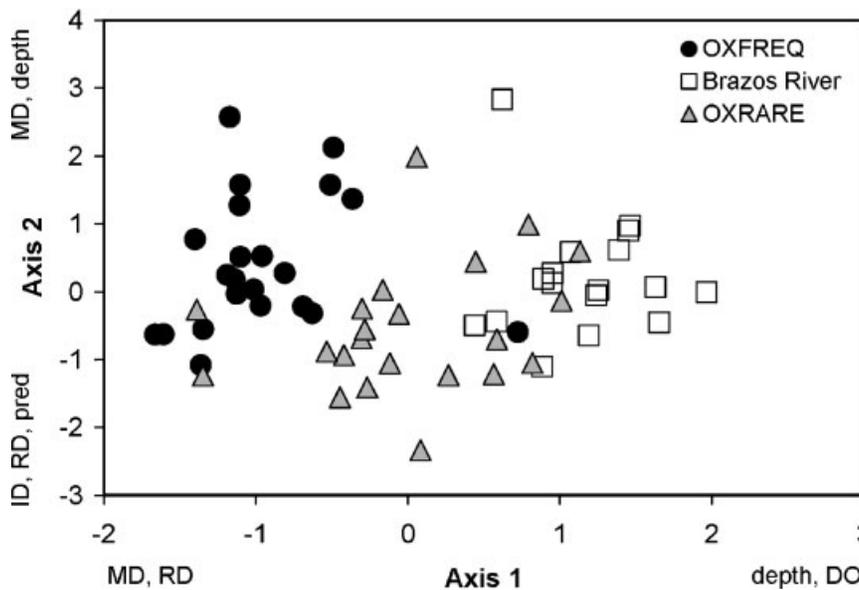


Figure 2. Sample scores of environmental variables from principal components' analysis. Abbreviations are as follows: ID = isolation days, MD = microcrustacean density; RD = rotifer density; DO = dissolved oxygen; pred = predator abundance. Variable loadings are listed in Table I

Table I. 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 <sup>-1</sup> )	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 <sup>-1</sup> )	-0.796	-0.314	537 (642)	388 (606)	28 (35)
Microcrustacean density (# l <sup>-1</sup> )	-0.939	0.215	181 (179)	26 (56)	2 (3)
Isolation days	-0.077	-0.921	75 (65)	161 (128)	—
Predator abundance (# h <sup>-1</sup> )	-0.110	-0.291	0.52 (0.40)	0.82 (0.46)	0.44 (0.28)

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 I). Sample scores for the rarely connected oxbow (OXRARE) had intermediate values on axis 1. Axis 2 modelled 23.0% of the total variation and described differences between periods of hydrologic connectivity and isolation in oxbow lakes. Low scores on axis 2 were associated with greater isolation days, rotifer density and predator abundance. High scores on axis 2 were associated with greater depth and microcrustacean density (Table I).

#### *Equilibrium strategist recruitment*

Surveys in the Brazos River produced 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 II and III). The ratio of juvenile-to-adult crappie was also greatest in this habitat (Table IV). Crappie abundance was similar among years; however, juvenile-to-adult ratios were significantly different with a greater ratio in the dry year (Tables II and IV). 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 3). 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 4). 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 (Table II). The bluegill juvenile-to-adult ratio was not

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

Species	Habitat		Year		Habitat × Year	
	$\chi^2$	$p$	$\chi^2$	$p$	$\chi^2$	$p$
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

Table III. Results of multiple comparisons of juvenile abundance between habitats using generalized estimating equations

Species	BR × OXFREQ		BR × OXRARE		OXFREQ × OXRARE	
	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>	$\chi^2$	<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

*p*-values were adjusted using the Bonferroni correction  $\alpha_{\text{adjusted}} = 0.025$ .

significantly different among habitats or years (Table III). Size-frequency distributions suggested that bluegill populations in both oxbow lakes were dominated by juveniles with little between-year variation in size structure (Figures 3 and 4).

#### Periodic strategist recruitment

Variation in shad abundance was significant between habitats and years; however a significant interaction between factors complicated interpretation of results (Table II). 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 III). Shad populations in all habitats were primarily composed of juveniles and age-2 + individuals in year 1 (Figures 3–5). Year 2 size distributions in both oxbow lakes had greater proportions of age 1 individuals suggesting good recruitment of juveniles produced in year 1 (Figures 3 and 4). This trend was not apparent in the river channel where size-frequency distributions were similar for both years (Figure 5).

Spotted gar abundance was greater in the two oxbows relative to the river channel and no difference was detected between years (Tables II and III). Longnose gar abundance was greater in the river channel than the two oxbow lakes, and abundance was greater in the wet year (Table II). Juvenile-to-adult ratios for gar species were greater in both oxbow lakes than the river channel, and no difference was detected between years (Table III). Size frequency distributions in all habitats did not reveal any obvious adult cohorts. The Brazos River longnose gar population was dominated by adults during both years with few juveniles collected (Figure 5). The spotted gar population in OXRARE was dominated by juveniles during both years (Figure 4) whereas the OXFREQ population had similar proportions of juveniles and adults during both years (Figure 3).

Table IV. Results of log-likelihood tests comparing the ratio of juvenile to adult individuals of each species among habitats and years

Species	OXFREQ × OXRARE		OXFREQ × BR		OXRARE × BR		Wet × Dry	
	G	<i>p</i>	G	<i>p</i>	G	<i>p</i>	G	<i>p</i>
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

Spotted gar ratios in oxbows were compared with longnose gar ratios in the river channel.

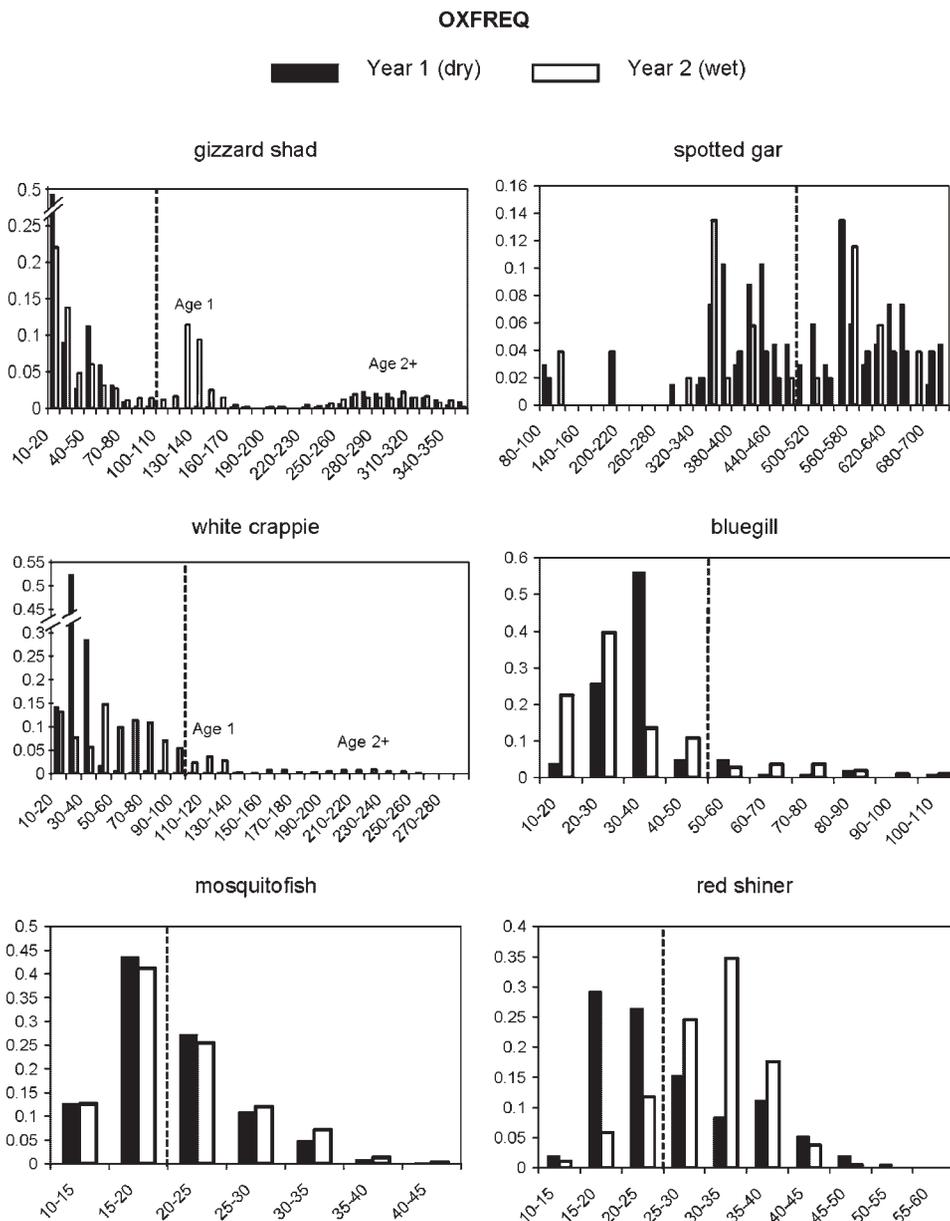


Figure 3. Size-frequency distributions of the six species examined in the most frequently connected oxbow lake. Dashed lines indicate minimum size at maturity estimates

*Opportunistic strategist recruitment*

Oxbow lakes had significantly greater mosquitofish abundance relative to the river, and abundance was greater in the dry year (Tables II and III). 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 IV). Populations in all habitats were dominated by juveniles; however, OXRARE and the river channel had greater proportions of adults (Figures 3–5). 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 II and III). 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

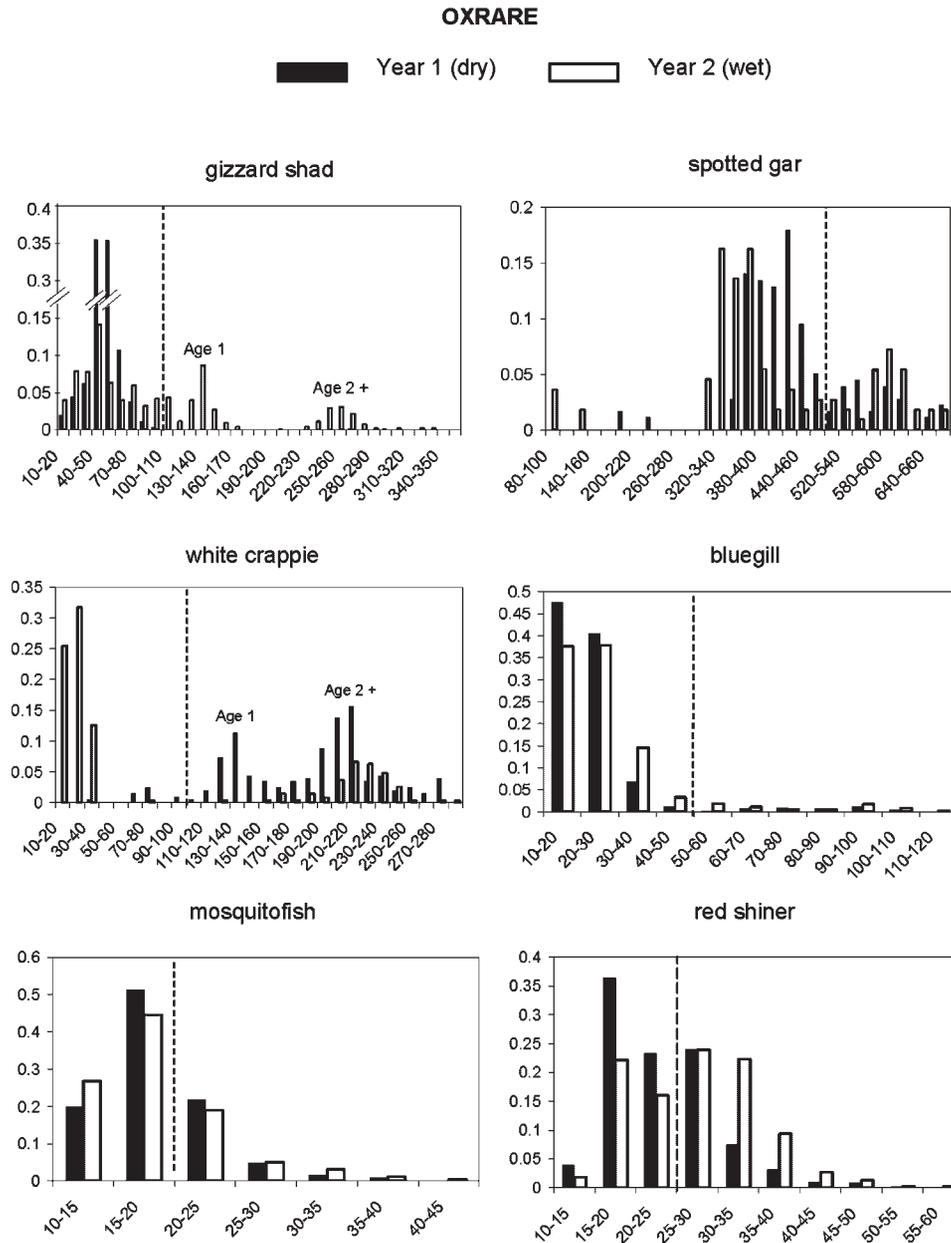


Figure 4. Size-frequency distributions of the six species examined in the rarely connected oxbow lake. Dashed lines indicate minimum size at maturity estimates

years (Figures 4 and 5), whereas the OXFREQ population had a greater proportion of adults during year 2 (Figure 3).

### 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

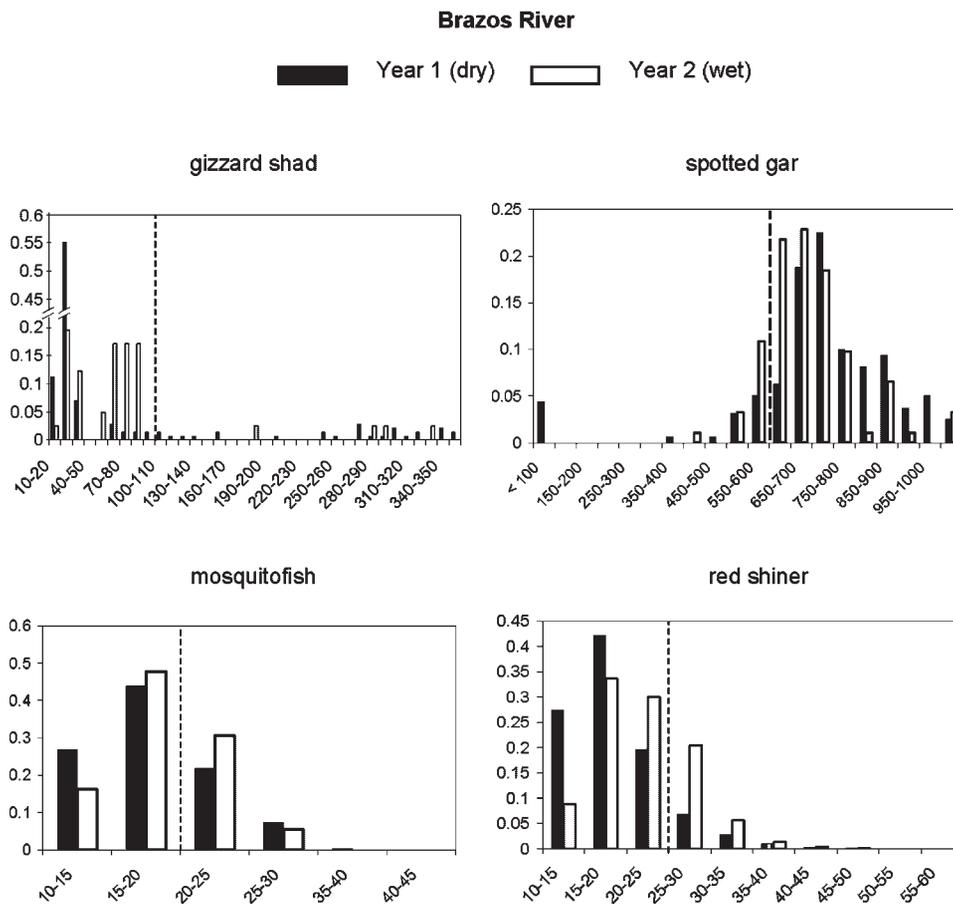


Figure 5. Size-frequency distributions of the four species examined in the Brazos River channel. Few crappie or bluegill were collected in this habitat and size distributions were not constructed. Dashed lines indicate minimum size at maturity estimates

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 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 favourable 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.

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 artefact 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 LFR (Humphries *et al.*, 1999) than the FPC (Junk *et al.*, 1989).

The LFR hypothesis describes fish recruitment dynamics in rivers in which 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, in press) 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. 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 (in press) 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 were also 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 flowing 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 processes such as erosion and deposition create these habitats and drive their succession. Thus, fluvial geomorphometric 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.

#### ACKNOWLEDGEMENTS

We would like to thank D. Lightsey and J.T. Lyons for allowing us access to their land during the study. Ray Matthews and Tim Osting (Texas Water Development Board) provided oxbow connectivity estimates. We are grateful to C. Robertson, V. Shervette, J. Putegnat, J. Muir, D. Perretti, D. Hoeinghaus and J. Birnbaum for their assistance in the field. Funding for this study was provided by the Texas Water Development Board. During the study SCZ was supported by the Texas A&M Merit Fellowship, Texas Water Resources Institute Mills Scholarship and the Tom Slick Senior Graduate Fellowship. Collections were made under Texas Parks and Wildlife Department permit number SPR-0193-580.

#### REFERENCES

- Aarts BG, Van Den Brink FWB, Nienhuis PH. 2004. Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. *River Research and Applications* **20**: 3–23.
- Agostinho AA, Gomes LC, Verissimo S, Okada EK. 2004. Flood regime, dam regulation and fish in the Upper Parana River: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries* **14**: 11–19.
- Amoros C, Bornette G. 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology* **47**: 761–776.
- Bayley PB. 1991. The flood pulse advantage and the restoration of river-floodplain systems. *Regulated Rivers Research and Management* **6**: 75–86.
- Bonvechio TF, Allen MS. 2005. Relations between hydrological variables and year-class strength of sport fish in eight Florida water bodies. *Hydrobiologia* **532**: 193–207.
- Bremigan MT, Stein RA. 1994. Gape-dependent larval foraging and zooplankton size: implications for recruitment across systems. *Canadian Journal of Fisheries and Aquatic Sciences* **51**: 913–922.
- Crook DA, Gillanders BM. 2006. Use of otolith chemical signatures to estimate carp recruitment sources in the Mid-Murray River, Australia. *River Research and Applications* **22**: 871–879.
- Feyrer F, Sommer TR, Zeug SC, O'Leary G. 2004. Fish assemblages of perennial floodplain ponds of the Sacramento River, California (USA) with implications for the conservation of native fishes. *Fisheries Management and Ecology* **11**: 335–344.
- Feyrer F, Sommer T, Harrell W. 2006. Importance of flood dynamics versus intrinsic physical habitat in structuring fish communities; evidence from two adjacent engineered floodplains on the Sacramento River, California. *North American Journal of Fisheries Management* **26**: 408–417.
- Gale WF. 1986. Indeterminate fecundity and spawning behavior of captive red shiners-fractional crevice spawners. *Transactions of the American Fisheries Society* **115**: 429–437.

- Gehrke PC. 1992. Diel abundance, migration and feeding of fish larvae (Eleotridae) in a floodplain billabong. *Journal of Fish Biology* **40**: 695–707.
- Gutreuter S, Bartels AD, Irons K, Sandheinrich MB. 1999. Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the Upper Mississippi River system. *Canadian Journal of Fisheries and Aquatic Sciences* **56**: 2282–2291.
- Halls AS, Welcomme RL. 2004. Dynamics of river fish populations in response to hydrological conditions: a simulation study. *River Research and Applications* **20**: 985–1000.
- Halyk LC, Balon EK. 1983. Structure and ecological production of the fish taxocene of a small floodplain system. *Canadian Journal of Zoology* **61**: 2446–2464.
- Humphries P, King AJ, Koehn JD. 1999. Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray–Darling River system, Australia. *Environmental Biology of Fishes* **56**: 129–151.
- Humphries P, Serafini LG, King AJ. 2002. River regulation and fish larvae: variation through space and time. *Freshwater Biology* **47**: 1307–1331.
- Humphries P, Cook RA, Richardson AJ, Serafini LG. 2006. Creating a disturbance: manipulating slackwaters in a lowland river. *River Research and Applications* **22**: 525–542.
- Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. In *Proceedings of the International Large River Symposium*, Dodge DP (ed.): 110–127.
- King AJ. 2005. Ontogenetic dietary shifts of fishes in an Australian floodplain river. *Marine and Freshwater Research* **56**: 215–225.
- King AJ, Humphries P, Lake PS. 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **60**: 773–786.
- Magalhaes MF, Schlosser IJ, Collares-Pereira MJ. 2003. The role of life history in the relationship between population dynamics and environmental variability in two Mediterranean stream fishes. *Journal of Fish Biology* **63**: 300–317.
- Merigoux S, Doledec S, Statzner B. 2001. Species traits in relation to habitat variability and state: neotropical juvenile fish in floodplain creeks. *Freshwater Biology* **46**: 1251–1267.
- Miller TJ, Crowder LB, Rice JA, Marschall EA. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 1657–1670.
- Olden JD, Poff NL, Bestgen KR. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecological Monographs* **76**: 25–40.
- Pease AA, Davis JJ, Edwards MS, Turner TF. 2006. Habitat and resource use by larval and juvenile fishes in an arid-land river (Rio Grande, New Mexico). *Freshwater Biology* **51**: 475–486.
- Persat H, Olivier JM, Pont D. 1994. Theoretical habitat templates, species traits, and species richness: fish in the Upper Rhone River and its floodplain. *Freshwater Biology* **31**: 439–454.
- Rodriguez MA, Lewis WM. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecological Monographs* **67**: 109–128.
- Sabo MJ, Kelso WE. 1991. Relationships between morphometry of excavated floodplain ponds along the Mississippi River and their use as fish nurseries. *Transactions of the American Fisheries Society* **120**: 552–561.
- Scheerer PD. 2002. Implications of floodplain isolation and connectivity on the conservation of an endangered minnow, Oregon chub, in the Willamette River, Oregon. *Transactions of the American Fisheries Society* **131**: 1070–1080.
- Schramm HL, Eggleton MA. 2006. Applicability of the flood-pulse concept in a temperate floodplain river ecosystem: thermal and temporal components. *River Research and Applications* **22**: 543–553.
- Sommer TR, Nobriga ML, Harrell WC, Batham W, Kimmerer WJ. 2001. Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 325–333.
- Sparks RE. 1995. Need for ecosystem management of large rivers and their floodplains. *Bioscience* **45**: 168–182.
- Suarez YR, Junior MP, Catella AC. 2004. Factors regulating diversity and abundance of fish communities in Pantanal lagoons, Brazil. *Fisheries Management and Ecology* **11**: 45–50.
- Tejerina-Garro FL, Fortin R, Rodriguez MA. 1998. Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon Basin. *Environmental Biology of Fishes* **51**: 399–410.
- Thorp JH, Thoms MC, DeLong MD. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* **22**: 123–147.
- Townsend CR, Hildrew AG. 1994. Species traits in relation to a habitat template for river systems. *Freshwater Biology* **31**: 265–275.
- Vandenbos RE, Tonn WM, Boss SM. 2006. Cascading life-history interactions: alternative density-dependent pathways drive recruitment dynamics in a freshwater fish. *Oecologia* **148**: 573–582.
- Welcomme RL, Winemiller KO, Cowx IG. 2006. Fish environmental guilds as a tool for assessment of ecological condition of rivers. *River Research and Applications* **22**: 377–396.
- Winemiller KO. 1989. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* **81**: 225–241.
- Winemiller KO. 1996. Factors driving temporal and spatial variation in aquatic floodplain foodwebs. In *Food Webs: Integration of Patterns and Dynamics*, Polis GA, Winemiller KO (eds). Chapman and Hall: New York; 298–312.
- Winemiller KO. 2005. Floodplain river food webs: generalizations and implications for fisheries management. In *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries*, Vol. 2, Welcomme RL, Petr T (eds). Mekong River Commission: Phnom Penh, Cambodia; 285–312.
- Winemiller KO, Rose KA. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 2196–2218.

- Winemiller KO, Rose KA. 1993. Why do most fish produce so many tiny offspring? *American Naturalist* **142**: 585–603.
- Winemiller KO, Tarim S, Shormann D, Cotner JB. 2000. Fish assemblage structure in relation to environmental variation among Brazos River oxbow lakes. *Transactions of the American Fisheries Society* **129**: 451–468.
- Zeug SC, Winemiller KO, Tarim S. 2005. Response of Brazos River oxbow fish assemblages to patterns of hydrologic connectivity and environmental variability. *Transactions of the American Fisheries Society* **134**: 1389–1399.
- Zeug SC, Winemiller KO. 2007. Ecological correlates of fish reproductive activity in floodplain rivers: a life history-based approach. *Canadian Journal of Fisheries and Aquatic Sciences* **64**: 1291–1301.