

Ecological correlates of fish reproductive activity in floodplain rivers: a life-history-based approach

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Abstract: Reproductive activity of seven species representing three divergent life history strategies was monitored monthly for 2 years in channel and floodplain habitats of the Brazos River, Texas, USA, to evaluate associations between reproductive activity and biotic and abiotic factors predicted by conceptual models to influence reproduction. An information-theoretic approach was used to select best approximating models for each species, and model-averaged estimates of regression coefficients were calculated. Model selection indicated that monthly flow based on the 30-year hydrograph and temperature was strongly supported as factors associated with reproductive activity of all three life history strategies. The timing of reproduction in relation to the long-term hydrograph was related to life history traits. Reproductive activity of species with large adult size and high fecundity was greatest in spring just prior to increasing flows, whereas species with small adult size and extended breeding seasons exhibited greater activity in late spring and summer when mean flow was greatest. Nest-building species with parental care were more abundant in off-channel habitats where floods were less common. Instream flow management would benefit from consideration of flow and habitat requirements needed to support the diverse life history strategies displayed by fishes in river–floodplain systems.

Résumé : Nous avons suivi à chaque mois pendant 2 ans l'activité reproductive de sept espèces représentant trois stratégies de cycle biologique distinctes dans les habitats du chenal et de la plaine d'inondation de la Brazos, Texas, É.U., afin d'évaluer les associations entre l'activité reproductive et les facteurs biotiques et abiotiques qui, d'après certains modèles conceptuels, l'influencent. Nous utilisons une approche basée sur la théorie de l'information pour sélectionner les modèles qui s'ajustent le mieux à chaque espèce et nous calculons à l'aide des modèles les estimations moyennes des coefficients de régression. La sélection des modèles indique que le débit mensuel basé sur la courbe de 30 ans et la température sont les facteurs le plus fortement retenus pour expliquer l'activité reproductive dans les trois stratégies de cycle biologique. La détermination du moment de la reproduction en fonction de la courbe de débit à long terme dépend des caractéristiques du cycle biologique. Les espèces avec adultes de grande taille et à forte fécondité ont une activité reproductive maximale au printemps juste avant l'accroissement des débits, alors que les espèces avec des adultes de petite taille et une saison de fraye étendue montrent plus d'activité reproductive à la fin du printemps et en été quand le débit moyen est maximal. Les espèces qui construisent des nids et qui prennent soin de leurs petits sont plus abondantes dans les habitats hors du chenal où les crues sont moins fréquentes. La gestion des débits dans les cours d'eau pourrait être améliorée si on tenait compte des exigences de débit et d'habitat requises pour le maintien des diverses stratégies de cycle biologique possédées par les poissons des systèmes de rivières et de leurs plaines d'inondation.

[Traduit par la Rédaction]

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 regimes have been developed to

restore the ecological integrity of modified systems (Jowett 1997; Richter et al. 1997). Most of these strategies focus on minimum 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

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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. 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 fishes time reproduction to coincide 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 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 life history 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.

Our 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. We predicted that combinations of biotic and abiotic factors related to reproductive activity would be strongly associated with life history strategy. We also predicted that the value of habitats for reproduction by fishes with different life history strategies would be associated with hydrologic connections among aquatic habitats.

Materials and methods

Study system

The mainstem Brazos River flows 1485 km from its origin near the Texas – New Mexico border to the Gulf of Mexico near Freeport, Texas, USA. The current study was conducted on the Middle Brazos between 30°25'N and 30°37'N. 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 predam flows.

A previous survey of 10 Brazos oxbow lakes by Wine-miller 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 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 TWDB; mean daily flow was provided 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 handheld 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 µm mesh in the cod end. Individuals were identified as rotifers, cladocerans, or copepods, and densities were determined from two 1 mL subsamples 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 standard length, SL) were collected with two experimental gill nets that consisted of three panels measuring 16.5 × 2 m, with 25.4, 76, and 51 mm bar mesh. Gill nets were set between approximately 1700 and 0700 the next day. The duration in hours of each set was recorded for calculation of species catch per unit effort (CPUE). Small-bodied fish (<100 mm SL) were collected using a 10 m × 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 number of metres traveled per survey was estimated, and CPUE was calculated as species number·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 gill nets. Collections were not made in the Brazos River during certain months because of high flows, and oxbows were not sampled during November 2004 because of extensive flooding. All fishes were euthanized by immersion in tricaine methanesulfonate (MS-222). 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 represent the equilibrium strategy; and gizzard shad (*Dorosoma cepedianum*), spotted gar, and longnose gar 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 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 (Fig. 1). Characteristics included in CA were minimum length at maturity (L_{\min}), maximum length (L_{\max}), mean fe-

cundity, 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 (GSI) and presence of mature oocytes in ovaries. Mature oocytes were those as big as or bigger than 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 GSI for females ((gonad mass/body mass) × 100) (Figs. 2, 3). Individuals were measured to the nearest millimetre 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 shiner were collected in monthly surveys (>100 individuals); for these species, individuals were placed into 5 mm size classes, and three individuals from each size class were processed.

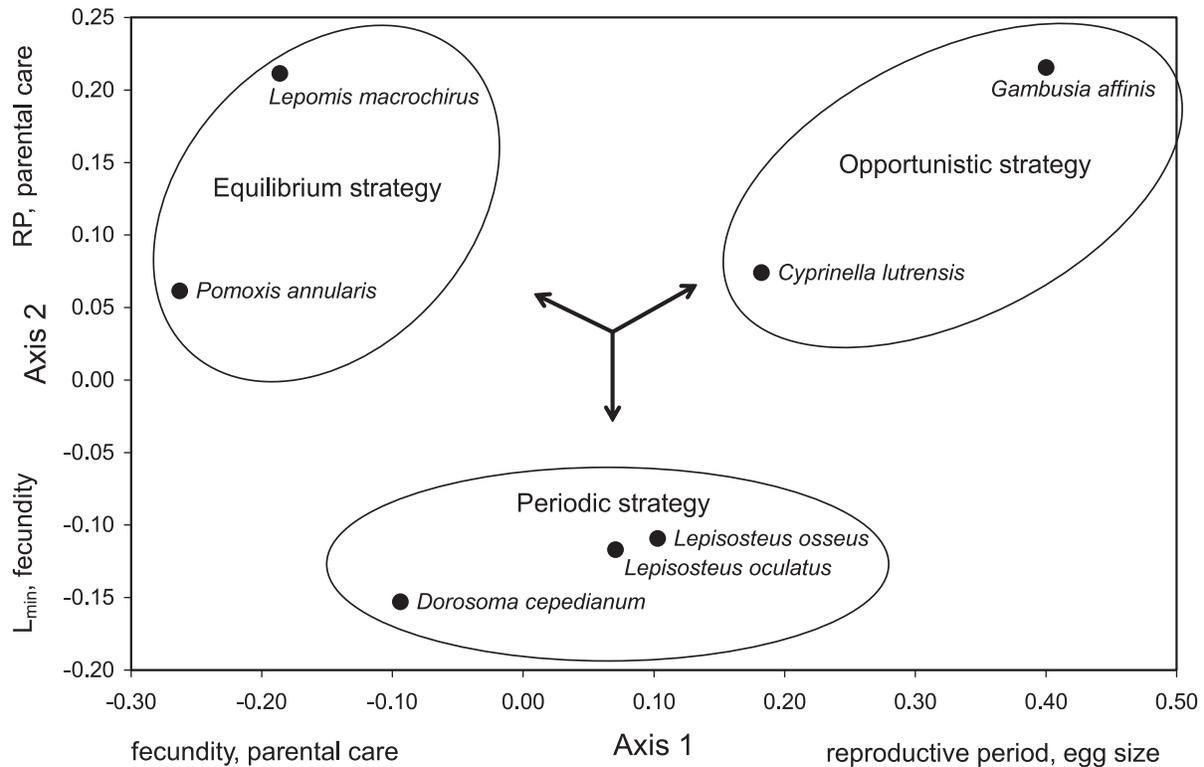
Red shiner and mosquitofish fecundity was estimated by direct count. Red shiner ovaries contained multiple batches of eggs based on size frequency distributions, and only the largest size class was used for fecundity estimation (batch fecundity). For all other species, a subsample of the anterior portion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

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

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

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 (SL) 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 (S.C. Zeug, unpublished data). The relationship between SL 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.

Fig. 1. 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: minimum length at maturity (L_{\min}) = 0.45, maximum length (L_{\max}) = 0.36, reproductive period (RP) = 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 , RP = 2.40, fecundity = -0.48 , parental care = 7.07, egg size = 0.29.



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 among 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 flow for the previous 30 years, days of floodplain isolation, temperature, photoperiod, rotifer density, copepod density, cladoceran density, and predator abundance.

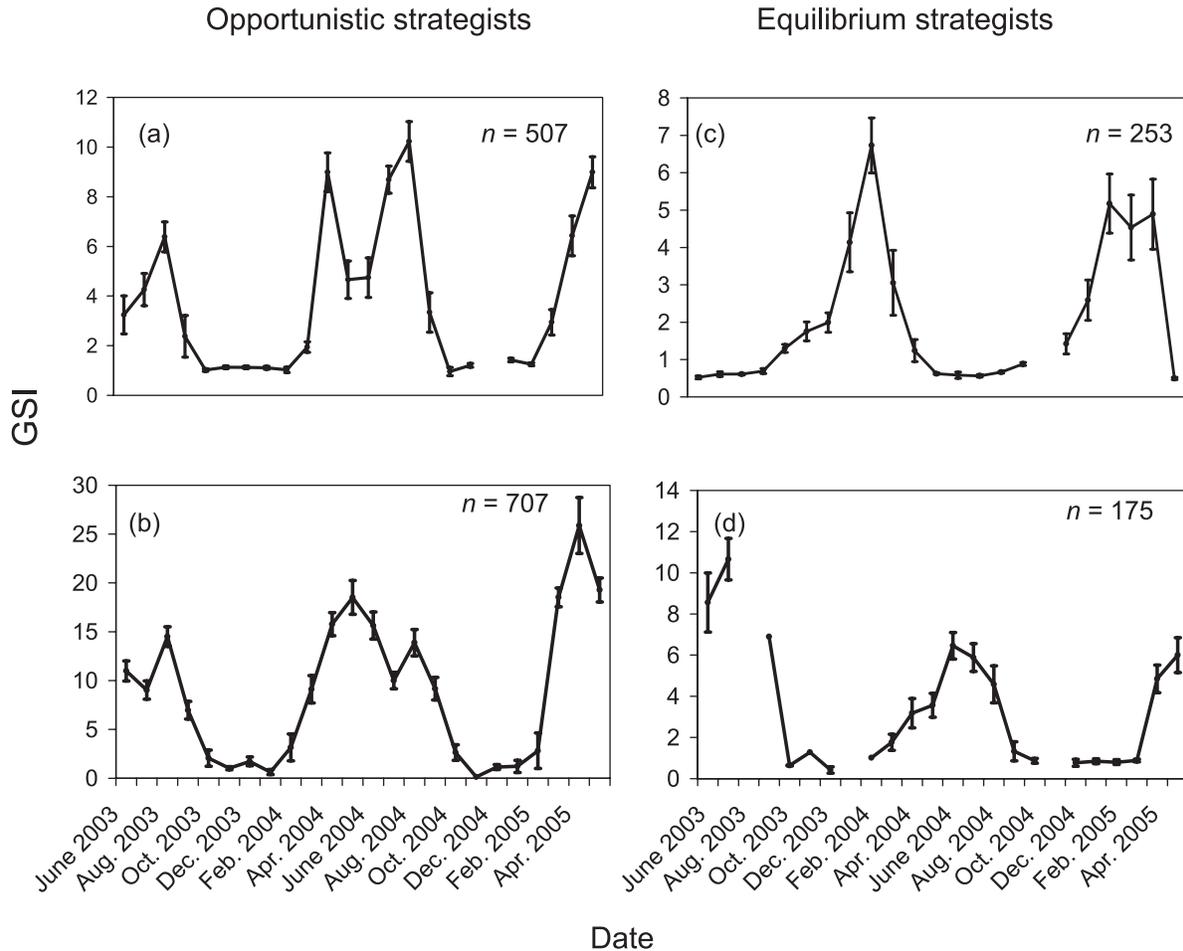
Correlation analysis was performed on independent variables to identify potential sources of multicollinearity. Temperature was significantly and positively correlated with rotifer density and photoperiod. Temperature was retained, and rotifer density and photoperiod were excluded from the analysis. 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 because of 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, SAS Institute Inc., Cary, North Carolina).

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

Fig. 2. Plot of mean gonadosomatic index (GSI) values over the 2-year study period for the two equilibrium and opportunistic strategists. Species in each panel are as follows: (a) red shiner (*Cyprinella lutrensis*), (b) mosquitofish (*Gambusia affinis*), (c) white crappie (*Pomoxis annularis*), and (d) bluegill (*Lepomis macrochirus*).



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, and w_j is the model weight of the model being considered. 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

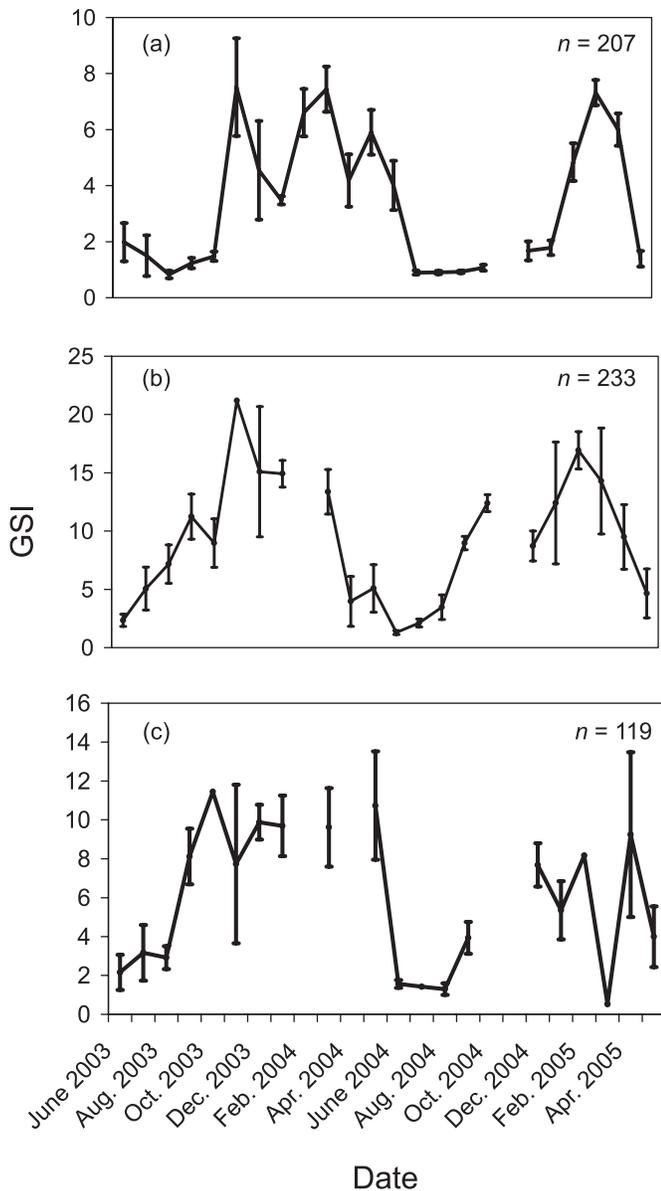
CPUE of adults of each species was compared among habitats using generalized estimating equations. Abundance estimates were log-transformed ($\log_{10}(x+1)$) to meet assumptions of the generalized estimating equation procedure. The variable "month" was included as the repeated variable in the model, 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

CA produced two axes that explained 85.1% of the variation in species life history characteristics (Fig. 1). 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

Fig. 3. Plot of mean gonadosomatic index (GSI) values over the 2-year study period for the three periodic strategists. Species in each panel are as follows: (a) gizzard shad (*Dorosoma cepedianum*), (b) spotted gar (*Lepisosteus oculatus*), and (c) longnose gar (*Lepisosteus osseus*).



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 (Fig. 4). 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.

Opportunistic strategists

The best approximating model for mosquitofish indicated positive associations among GSI, the 30-year hydrograph, and temperature (Table 1). 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 among GSI, the 30-year hydrograph, and temperature (Table 1). 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 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 among GSI, the 30-year hydrograph, and microcrustacean density and negative associations among 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.

Adult abundance

Significant differences among habitats were detected for all species, with the exception of mosquitofish (Table 3).

Fig. 4. Daily stream flow hydrograph of the Brazos River during the 2-year study period. The solid horizontal line represents flows required to connect OXFREQ (an oxbow lake that connects to the active channel relatively frequently) with the river channel; the broken line represents flows required to connect OXRARE (an oxbow lake that connects relatively rarely).

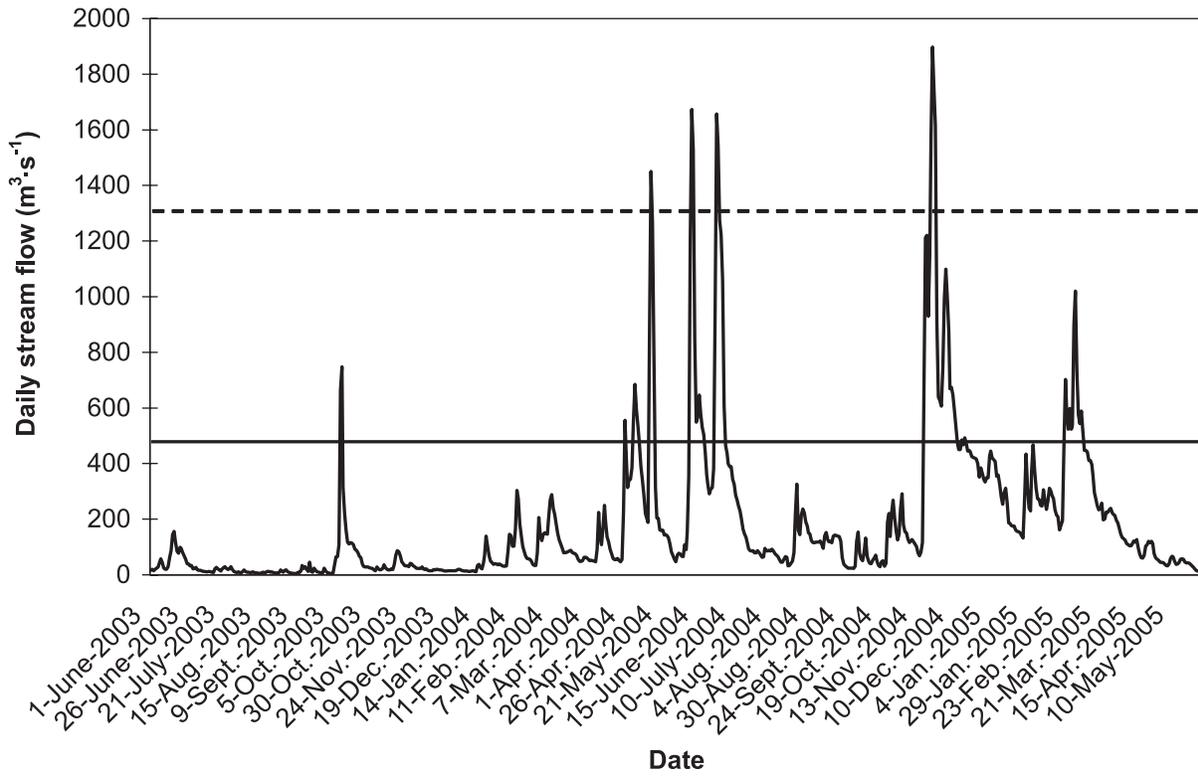


Table 1. Best approximating models for each species based on ΔAIC_c values, model weights, and evidence ratios.

Species	Models	ΔAIC_c	AIC_c weight	Evidence ratio	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
	β_1, β_2	0.00	0.37	1.00	4
Red shiner (<i>Cyprinella lutrensis</i>)	$\beta_1, \beta_2, \beta_4$	1.60	0.17	2.24	5
	$\beta_1, \beta_2, \beta_3$	1.64	0.16	2.29	5
	$\beta_1, \beta_2, \beta_4, \beta_5$	1.90	0.14	2.60	6
Gizzard shad (<i>Dorosoma cepedianum</i>)	$\beta_1, \beta_3, \beta_4, \beta_5, \beta_6$	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

Note: K , the number of parameters estimated for each model; β_1 , 30-year hydrograph; β_2 , temperature; β_3 , microcrustacean density; β_4 , isolation days; β_5 , predator abundance; β_6 , autocorrelation correction parameter.

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 in oxbows (Fig. 5). Spotted gars were more abundant in oxbows, and longnose gars were more abundant in the river (Fig. 5). Bluegills were more abundant in OXRARE than in

the river channel, and white crappies were more abundant in oxbows relative to the river channel (Fig. 5).

Discussion

Model selection indicated that temperature and the 30-year hydrograph had strong support as factors associated

Table 2. Model-averaged estimates of regression coefficients (unconditional 95% confidence intervals in parentheses).

Species	β_1	β_2	β_3	β_4	β_5	β_6
Mosquitofish	0.55 (0.37–0.74)	1.74 (1.45–2.02)	–0.03* (–0.01–0.07)	–0.02* (–0.08–0.04)	0.53 (0.18–0.89)	—
Red shiner	0.49 (0.33–0.64)	1.56 (1.32–1.79)	–0.03* (–0.06–0.00)	0.05* (0.00–0.10)	–0.40 (–0.68 – –0.13)	—
Gizzard shad	0.41 (0.28–0.54)	–0.03* (–0.30–0.24)	0.12 (0.09–0.16)	–0.03* (–0.08–0.03)	–0.69 (–0.94 – –0.43)	–0.32 (–0.48 – –0.16)
Spotted gar	–0.31 (–0.52 – –0.10)	–1.04 (–1.37 – –0.71)	–0.01* (–0.07–0.04)	–0.01* (–0.08–0.07)	–0.20* (–0.63–0.23)	—
Longnose gar	0.24* (0.00–0.49)	–0.94 (–1.28 – –0.60)	–0.04* (–0.12–0.40)	0.08* (–0.05–0.21)	–0.51* (–1.13–0.11)	—
Bluegill	0.40 (0.24 –0.55)	1.36 (1.12–1.60)	–0.05* (–0.09–0.00)	0.03* (–0.03–0.08)	–0.15* (–0.50–0.19)	—
White crappie	0.10* (–0.14–0.34)	–0.69 (–0.99 – –0.40)	0.15 (0.09–0.21)	–0.04* (–0.02–0.10)	–0.30* (–0.66–0.06)	–0.48 (–0.65 – –0.32)

Note: β_1 , 30-year hydrograph; β_2 , temperature; β_3 , microcrustacean density; β_4 , isolation days; β_5 , predator abundance; β_6 , autocorrelation correction parameter.

*Parameters were found to have little support following calculation of unconditional confidence intervals.

Table 3. Results of generalized estimating equations comparing abundance of adults between habitats.

Species	All habitats		BR × OF		BR × OR		OF × 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

Note: Significance was assessed at $\alpha = 0.013$ (Bonferroni-corrected). BR, Brazos River; OF, an oxbow lake that connects to the active channel relatively frequently at moderate levels of BR discharge (OXFREQ); OR, an oxbow lake that connects relatively rarely at high BR discharge (OXRARE).

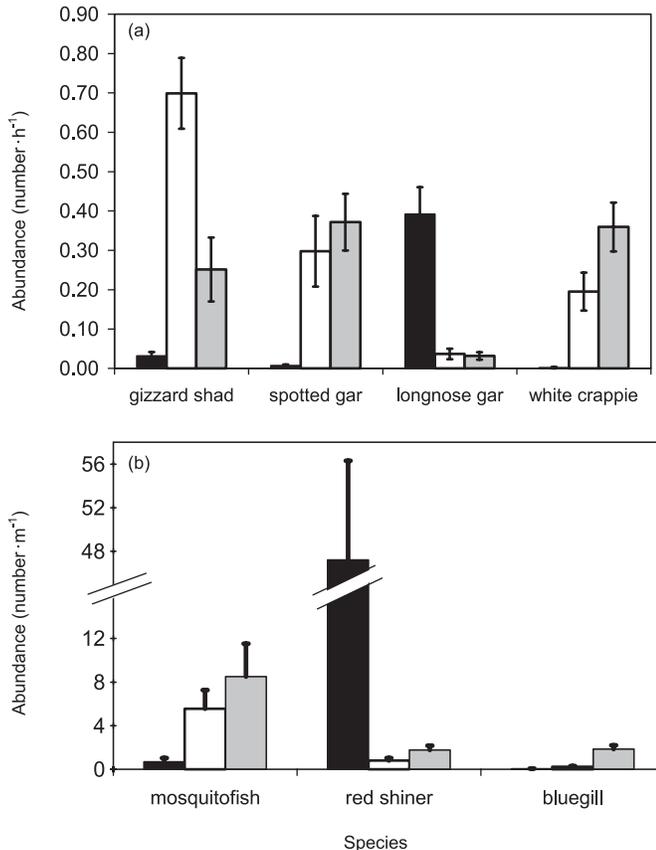
with reproductive activity of species with divergent life history strategies. Five of the seven species examined had competing models that included well-supported associations with the 30-year hydrograph, whereas isolation days during the study period had little support in data for any species. This suggests that a subset of Brazos River fishes have reproductive ecologies adapted to long-term hydrologic dynamics, which supports the 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' 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 might 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 iden-

Fig. 5. Mean abundances and standard errors for adults of the seven selected species in each habitat. (a) Abundances of large species captured in gill nets. (b) Abundances of small species captured with seines. Solid bars, Brazos River; open bars, OXFREQ (an oxbow lake that connects to the active channel relatively frequently at moderate levels of Brazos River discharge); shaded bars, OXRARE (an oxbow lake that connects relatively rarely at high Brazos River discharge).



tified. 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 (S.C. 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-bank-full 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 and Allen (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 suboptimal 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 are important for fish reproduction in rivers. Pease et al. (2006) found that both flood timing and the presence 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 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).

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 7 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 2-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 substantially 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.

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