Abiotic drivers of spawning and early life stage assemblage dynamics of Great Plains fishes

by

Elle McKenna Krellwitz

B.S., University of Wisconsin - Madison, 2023

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2025

Approved by:

Major Professor
Dr. Keith Gido

Copyright

Abstract

The hydrologic regime is a primary driver of environmental conditions in rivers and plays a key role in structuring fish assemblages. Fish have adapted life history strategies in response to natural flow and temperature regimes that provide spawning cues and influence recruitment success. However, the extent to which abiotic factors shape early life stage assemblage structure, particularly hatching and recruitment, remains understudied in Great Plains rivers where fish are adapted to stochastic hydrologic regimes. We used multivariate models to assess the influence of discharge, temperature, and season on early life stage fish assemblage structure in the Kansas and Marais des Cygnes rivers. We also developed length-at-age models to estimate hatch dates and evaluate how hatch timing aligns with environmental conditions. Early life stage assemblages exhibited chronological patterns in abundance, with large-bodied species such as common carp *Cyprinus carpio* and longnose gar *Lepisosteus osseus* peaking in late spring, while small-bodied species such as red shiner *Cyprinella lutrensis* and western mosquitofish *Gambusia affinis* remained abundant throughout the summer. Hatch frequency exhibited predictable patterns based on life history strategy, with opportunistic species hatching continuously over extended periods, while periodic species hatched intermittently, often coinciding with flow pulses. These findings highlight the need for a nuanced approach to environmental flow management that accounts for species-specific responses to variable hydrologic conditions. Future research in the Kansas and Marais des Cygnes rivers should focus on identifying hatch timing and recruitment patterns for species of conservation concern to capture effects of hydrological variation and better inform conservation efforts.

Table of Contents

List of Figures v
List of Tables vii
Acknowledgements viii
Chapter 1 - Abiotic drivers of spawning and early life stage assemblage dynamics of Great Plains fishes 1
Introduction 1
Methods 4
Study Site 4
Data collection 5
Data analysis – Early life stage fish assemblage 6
Estimated hatch dates 7
Results 7
Annual discharge 7
Assemblage dynamics 8
Environmental predictors of abundance 9
Kansas River 9
Marais des Cygnes River 10
Emergence of larval fish 10
Environmental predictors of hatching 11
Discussion 12
Hatching and assemblage dynamics 12
Environmental flow management 15
Figures 18
..... 24
..... 26
Tables 27
References 28
Appendix 38

List of Figures

Figure 1. Study map of the Kansas and Marais des Cygnes rivers with impounded tributaries and sampling locations. 18

Figure 2. Discharge (blue) and temperature (red) for the Kansas (at Wamego, KS) and Marais des Cygnes (at La Cygne, KS) rivers between January 2022 and October 2024. Grey boxes indicate sampling periods. 19

Figure 3. Non-metric multidimensional scaling of Bray-Curtis distances among sampling events (stress 0.18) of early life sage assemblage in the Kansas and Marais des Cygnes rivers over the summers of 2022-2024 (panel A). Panel B shows weighted species scores and colored points indicate centroids for each month across rivers. 20

Figure 4. Date of peak abundance of early life stage fish sampled at frequent intervals from the Kansas and Marias des Cygnes rivers across three years. Red dot indicates mean date of maximum abundance. Letters indicate groups that are significantly different based on ANOVA post hoc tests..... 21

Figure 5. Significant relationships from regression models of early life stage fish from the Kansas River throughout the summers of 2022-2024. Abundance patterns varied across species by seasonal (panel A), annual (panel B), and discharge (panel C) variability. 22

Figure 6. Significant relationships from regression models of early life stage fish from the Marais des Cygnes River throughout the summers of 2022-2024. Panel A shows increase in red shiner *Cyprinella lutrensis* abundance throughout the summer. Panel B shows interannual variability for bluntnose minnow *Pimephales notatus* and red shiner. Red shiner abundance decreased in 2022 and 2024 with discharge but was more constant in 2023 (panel C). *Note different x-axis scales in panel C. 23

Figure 7. Density plots showing smoothed trends of back calculated hatch dates of common Great Plains fishes collected from the Kansas and Maris des Cygnes rivers throughout the summers of 2022-2024. Annual densities are relative to each species. 24

Figure 8. Hatch probability as a function of temperature for each taxa grouped by life-history modes (panel A). Taxa labels are as follows: river carpsucker (RCS), gizzard shad (GZS), longnose gar (LNG), sunfishes (LEP), common carp (CCA), red shiner (RSH), sand shiner (SSH), western mosquitofish (WMF), bullhead minnow (BHM), bluntnose minnow (BNM).

Violin plot shows the range of temperatures under which hatching occurred, where the height of the bars corresponds to the relative number of individuals (panel B). 25
Figure 9. Cumulative hatch probability of taxa grouped by life history modes across different discharge scenarios: low (75-100% exceedance), medium (25-75% exceedance), and high (0-25% exceedance) (panel A). Violin plot shows the range of discharge conditions under which hatching occurred, where the height of the bars corresponds to the relative number of individuals (panel B). 26

List of Tables

Table 1. Summary of minimum, maximum, and mean ($\bar{x}$) water temperature (°C) and discharge (m^3/s) during the hatching period of each species. 27

Acknowledgements

I would like to thank my advisor, Dr. Keith Gido, for all his guidance throughout my research and insights into graduate school. I would also like to thank my committee members, Dr. Zak Ratajczak and Dr. Joe Gerken. I am grateful for your feedback and the opportunity to learn from you both throughout my time at K-State. Thank you to Saiph Sorell, Macey Willard, Jack Yates, and Johannes Glymore for their assistance with lab and field work. I would not have been able to complete this project without all your help.

Above all, I am beyond thankful for those closest to me for supporting my dream as if it were their own. To my parents, Peggy, Andy, Dave, and siblings, thank you for all your love and encouragement.

Chapter 1 - Abiotic drivers of spawning and early life stage assemblage dynamics of Great Plains fishes

Introduction

Abiotic and biotic factors interact at multiple spatial and temporal scales to shape community structure in lotic systems. Organisms must navigate a series of environmental filters, including biological, chemical, and physical factors that influence their survival and reproductive success (Smith and Powell 1971; Jackson et al. 2001). At any given locality, environmental variability, habitat availability, and predator-prey dynamics serve as mechanisms structuring fish assemblages (Menge and Sutherland 1987; Grossman et al. 1982; Grossman et al. 1998), but the relative strength of these factors is context-dependent (Matthews 2012; Grossman et al., 1998). Flow variability in rivers can alter habitats, provide spawning cues, influence recruitment success and disrupt critical life stages throughout the lifetimes of fish (Poff and Ward 1989). Consequently, the flow regime is often considered the most dominant factor shaping fish assemblages in lotic ecosystems (Poff et al. 1997; Grossman et al. 1998), although biotic interactions such as competition and predation may intensify during periods of high stress (i.e., drought conditions; Matthews 2012).

Patterns of river discharge define the disturbance regime (Resh et al. 1988), structure physical habitats, and control lateral and longitudinal connectivity (Poff et al. 1997; Bunn and Arthington 2002) in lotic systems. Such environmental variability influences the distribution and abundance of fish by creating conditions favoring specific adaptations, behaviors, and life history traits (Poff et al. 1997; Winemiller and Rose 1992). Fish rely on various environmental cues, acting over multiple temporal scales to time their reproduction (Krabbenhoft et al. 2014; Munro et al. 1990). Months or weeks prior to spawning, cyclical patterns, such as photoperiod and temperature, act as the primary drivers of 'reproductive readiness' by influencing gonadal development, while discharge is an important proximate cue triggering spawning activity (Krabbenhoft et al. 2014). Both low (Humphries et al. 1999) and high (Junk et al. 1989) flows influence fish recruitment but population responses depend on species specific life history strategies. For example, Cheshire et al. (2016) found that flow-dependent specialists like golden perch *Macquaria ambigua* and silver perch *Bidyanus bidyanus*, which are large and long-lived,

rely on high discharge events for successful spawning and recruitment. In contrast, small-bodied, low-flow specialists such as flathead gudgeon *Philypnodon grandiceps* and Australian smelt *Retropinna semoni* exhibit increased abundance during drought conditions. In temperate river systems, where seasonal discharge is highly variable, fish assemblages consist of species with diverse life history strategies (Zeug & Winemiller 2008; Cheshire et al. 2016), suggesting that a range of hydrologic conditions is necessary to sustain this diversity.

River impoundments have altered the natural flow regime of lotic systems by reducing flow variability and altering the timing, magnitude, and duration of discharge. Alterations to natural flow patterns can modify downstream temperature (Olden & Naiman 2010) and reduce lateral and longitudinal connectivity (Tockner & Stanford 2002). These changes can disrupt critical environmental cues for spawning, such as gonadal development (Mackay 1973) and migration (Pelicice, Pompeu, & Agostinho 2015; Tornabene et al. 2020), ultimately affecting recruitment success (Bunn & Arthington 2002; Poff & Zimmerman 2010). Streams in the Great Plains region USA are highly altered with at least 19,000 impoundments that exceed a height of 1.8 m (Cooper 2013). Extensive flow alteration and fragmentation has led to the decline of Great Plains fishes (Fisher and Pauckert 2008; Perkin and Gido 2011; Perkin et al. 2015). Declines in these species have led to a greater emphasis on understanding flow-ecology relationships (Franssen et al. 2006; Perkin et al. 2015; Perkin et al. 2019) to direct water management efforts. Flow manipulation provides an important conservation tool to minimize or restore negative impacts on stream fishes by mimicking elements of a natural hydrologic regime (Poff et al. 2010).

Early life stage fish provide critical insights into flow-ecology relationships because they are direct indicators of spawning and recruitment. During these early life stages, fish exhibit unique physiological and ecological characteristics making them sensitive to environmental conditions, thus early-stage recruitment is a main contributor to adult population dynamics (Fuiman and Werner 2009). Understanding how early life stage fishes respond to environmental conditions is important for predicting species persistence. However, environmental flow strategies are often developed based on conceptual frameworks of species' life histories and lack empirical data to test flow-ecology predictions (Freeman et al. 2022). Moreover, there is limited understanding of spawning and recruitment dynamics in prairie rivers, where fish are adapted to stochastic conditions. To address these gaps in knowledge, we evaluated early life stage

assemblage dynamics and spawning chronologies of fishes in Great Plains rivers. Our objectives were to (1) quantify the timing of peak abundance for early life stage fishes, (2) develop length at age models to estimate hatch timing, and (3) evaluate interspecific hatch timing relative to environmental conditions.

Humphries and colleagues (1999) proposed a refined classification of life histories for fishes in the Murray-Darling Basin, Australia. Their classification groups fish into three life history modes based on traits such as body size, spawning strategy, timing and duration of spawning, and larval characteristics at first feeding. These modes are also relevant to fishes in Great Plains rivers, which experience similar environmental stochasticity. Mode 1 species are large-bodied fish that spawn once per season over a short breeding period and have well-developed larvae with large gapes at first feeding. While their spawning may coincide with flooding, their populations are not necessarily reliant on high-flow events for persistence. Mode 2 species are also large-bodied and typically spawn once per season, but their spawning timing is flexible, allowing them to extend or delay reproduction based on environmental conditions. Spawning in these species is thought to be triggered by flow increases and may forgo reproduction if conditions are unfavorable. Larvae are poorly developed at hatch and require small prey, making early survival dependent on the availability of suitable resources. This strategy is hypothesized to be advantageous in unpredictable environments where resource availability varies in space and time. Mode 3 species are small-bodied, have extended spawning periods, and produce larvae with small gapes, restricting their feeding ability. Thus, they do well in environments with high prey densities. This mode aligns with the opportunistic strategy described by Winemiller and Rose (1992), which are predicted to do well in environments with frequent disturbances. These life history classifications can be useful predictors of fish recruitment. Therefore, we hypothesized that body size and spawning strategy will influence timing and extent of larval emergence. We predict that assemblage structure will shift throughout the summer, reflecting species-specific environmental spawning cues (Turner et al. 1994). Species that are small-bodied and exhibit prolonged spawning (opportunistic; Mode 3) and large-bodied with flexible spawning (Mode 2) are expected to exhibit the highest interannual variability in relative abundance. Mode 3 species are likely to be the most common in Great Plains rivers due to the region's highly variable flow conditions. In contrast, we predict that species with well-developed larvae (Mode 1) are likely to maintain more stable abundances

across years due to their longer yolk-sac feeding period, reducing dependence on prey availability. Additionally, we predict that opportunistic species will have prolonged spawning periods across a wide range of environmental conditions, while large-bodied species will experience increased recruitment during high-flow events (Humphries et al. 2020).

Methods

Study Site

The Kansas River is a principal tributary of the Missouri River and at our study sites is a 7th-order stream originating at the confluence of the Republican and Smoky Hill rivers in northeastern Kansas. The Kansas River watershed spans approximately 156,000 km² and includes portions of northern Kansas, southern Nebraska, and eastern Colorado. Several tributaries within the watershed are impounded, and many dams serve as flood control structures. Consequently, the natural flow regime of the Kansas River has been modified since dam construction. Duration of high flows have decreased by 88% and rise rate and fall rate have decreased by > 30% (Costigan & Daniels 2012), such that rate of change in flows has become more gradual, likely a consequence of less flash flooding. The mainstem of the Kansas River is highly braided and mainly composed of sandy substrate. The channel has an average width of 164 m and an average depth of 1.5 m (Makinster 2006), with the lower reach being deeper and more channelized (Pauckert et al. 2008).

The Marais des Cygnes joins the Little Osage River in western Missouri to form the Osage River which is another main tributary of the Missouri River. The river at our study sites is a 6th-order stream originating in east-central Kansas. Its basin drains an area of approximately 8,400 km², spanning eastern Kansas and western Missouri. Flow alteration is associated with impoundments on three of its tributaries, which regulate 34% of the basin (Heimann et al. 2007). The river channel is narrow (24-30 m), highly channelized with tall banks (12-15 m), and composed mainly of mud, gravel, and rock substrates.

Temperature and discharge data were obtained from U.S. Geological Survey (USGS) gauges to contextualize assemblage responses to environmental conditions. For the Kansas River, discharge and temperature data were sourced from the USGS gauge (06887500) at Wamego, Kansas. For the Marais des Cygnes River, discharge data were obtained from the

gauge (06915800) at La Cygne, Kansas, while temperature data were sourced from the Osage River gauge (06918250), the nearest available station providing temperature measurements.

Data collection

To evaluate temporal shifts in species composition and abundances of early life stage fish assemblages, bi-weekly samples were taken from each site on the Kansas and Marais des Cygnes rivers from June to September in 2022-2023 and May to September in 2024. Sites were selected based on public accessibility and proximity to USGS gauges (Figure 1). At each site, we sampled six microhabitats with an area of 10 m^2. We targeted shallow, low velocity habitats that are widely recognized as important for larval fishes (Schiemer et al. 1991; Scheidegger & Bain 1995; Farrington et al. 2015). When catch per unit effort (individuals/m^2) was low, additional replicates were conducted to reduce potential sampling bias associated with suboptimal habitat selection and to determine whether low catches reflected true population densities. All fish collected at a given location were compiled into a composite sample. Specimens were preserved in 95% ethanol solution and were identified to species in the laboratory and measured for total length. If specimens were too small to identify to species they were placed into a higher taxonomic classification. On three sampling occasions in each river, particularly high catch rates occurred across sites. For these instances, we subsampled half of the original catch and multiplied the resulting counts by two to estimate total abundance. A subsample of three individuals per 1 mm bin per species were measured and sagittal otoliths (Brothers et al 1976) were extracted to develop length-at-age models to estimate hatch dates. To account for potential differences in growth rates throughout the summer, we ensured that the subsample of individuals included specimens collected across a range of sampling dates and years, giving an approximation of growth during the early life stage period; however, otoliths were only available from individuals sampled in 2023 and 2024. If fewer than three individuals were available for a given 1 mm length bin, we extracted otoliths from all available specimens. Lapping film was used to polish the otoliths and expose the annuli. Ages were determined by counting these increments under a compound microscope at 20–40x magnification. The first prominent ring at the otolith's core, corresponding to the hatch check, was identified as the starting point for aging (Campana 2001). Each daily increment was counted from the hatch check outward along the longest axis to estimate age in days. Multiple passes were made across each otolith to confirm the accuracy of age estimates, and unclear or damaged otoliths were excluded from analysis.

Data analysis – Early life stage fish assemblage

Length thresholds were chosen to ensure that individuals represented age-0 fish from the current year, rather than late-spawned fish from the previous year. Length-frequency histograms were used to identify cutoffs between age-0 and age-1 fish. Otolith analyses confirmed that only age-0 individuals were included. Species CPUE data were square root transformed to reduce the influence of highly abundant species and species sampled on fewer than two occasions were excluded. Cumulative abundance was calculated across the three locations in each river for each species to provide one data point for a given sampling event. Bray-Curtis coefficients were used to compute the dissimilarity across samples and non-metric multidimensional scaling (NMDS) was used to visualize the variation in assemblage structure in ordination space.

To quantify temporal changes in early life stage fish assemblages, a two-way ANOVA was used with species and river as fixed factors to test for interspecific differences in the timing of seasonal abundance and intraspecific differences between rivers. Cumulative species abundances were calculated for a given sampling occasion in each river to determine the timing of peak abundance. Post-hoc pairwise comparisons were conducted using Tukey's Honest Significant Difference (HSD) test to determine which species differed in their timing of maximum abundance.

To assess how environmental factors influenced early life stage assemblage structure, we used a multivariate generalized linear model framework, using the function manyglm() from the 'mvabund' package in R (Wang et al. 2012). For this analysis, we excluded rare species that contributed less than 1% of the cumulative abundance in each river. This approach is well-suited for analyzing assemblage data as it allows for the simultaneous modeling of multiple species' abundances, while accounting for potential correlations in species responses. Additionally, the 'mvabund' package uses permutation testing to resample data and controls for Type I errors when conducting multiple univariate tests. Separate models were run for each river, with the abundance response of each species modeled as a function of several predictor variables including date, lagged (7d) temperature, lagged (7d) discharge and year. To meet assumptions, a multivariate regression model was fit using a negative binomial distribution. The "p.uni" function within anova.manyglm was applied to identify species that exhibited significant correlations with variables in the manyglm.

Estimated hatch dates

We developed linear models for each species to estimate the average age for each 1 mm length bin. Estimates for length-age relationships were rounded to the nearest whole number and hatch date was calculated by subtracting the predicted age from the sample date after accounting for species specific length at hatch (Table A.1). These models were used to generate a distribution of hatching dates for early life stage fishes during each sampling year (Humphries et al. 2008). Length frequency histograms were used to identify hatching cohorts. Individuals that exceeded a given threshold (species specific) in length were excluded from analysis because they were assumed to have hatched in the previous season.

To assess how environmental conditions influenced hatch probability, we used a similar approach as described for multivariate abundance; however, we used a binomial distribution, where the response variable was binary (1 = hatch, 0 = no hatch). Separate models were run for each river to evaluate how hatch probability varied in response to changing environmental conditions. Predictor variables included year, lagged (7d) temperature, and lagged (7d) discharge. Hatching was analyzed at weekly intervals and was highly correlated with temperature, thus, we omitted date from the logistic regression models. All analyses were conducted in the R statistical programming language (R Core Team 2024).

Results

Annual discharge

Discharge (m^3/s) varied across rivers and among years. The Marais des Cygnes River had more variable discharge with higher maximum and lower minimum seasonal (May – September) flows across all years compared to the Kansas River (Figure 2). Discharge during our study period ranged from 563 – 2 m^3/s in 2022, 413 – 1 m^3/s in 2023 and 597 - 64 m^3/s in 2024 for the Marais des Cygnes River. The Kansas River had seasonal variation of 419 – 23 m^3/s in 2022, 90 – 20 m^3/s in 2023, and 291 – 22 m^3/s in 2024. The highest average seasonal discharges were recorded in 2022, with the Kansas River at 117 m^3/s and the Marais des Cygnes River at 74 m^3/s. A severe drought in 2023 resulted in extreme low flow conditions for both rivers. The Kansas River had an average discharge of 30 m^3/s and the Marais des Cygnes River had an average discharge of 15 m^3/s in the summers of 2023. These were historic low flow events with the mean summer discharge for the Kansas River in 2023 being the lowest seasonal flow event on record,

since 1919. In comparison, the Marais des Cygnes River's mean summer discharge for 2023 fell in the 10th percentile.

Assemblage dynamics

In total, 8,541 early life stage fish from 23 species and 10 families were sampled throughout the study period. The NMDS ordination of early life stage fish assemblages resulted in a two-dimensional solution with a stress value of 0.18, indicating an acceptable fit of community dissimilarity (Figure 3A). Assemblage structure showed interannual (Kansas: $p < 0.01$; Marais des Cygnes: $p < 0.01$) and seasonal variation (Kansas: $p < 0.001$; Marais des Cygnes: $p < 0.01$) across river basins. Assemblage structure changed throughout the summer with common carp *Cyprinus carpio*, suckermouth minnow *Phenacobius mirabilus*, percids, central stoneroller *Campostoma anomalum*, longnose gar *Lepososteus osseus*, and largemouth bass *Micropterus salmoides* occurring more frequently in early summer, whereas assemblage composition was dominated by small-bodied species mid-late summer (Figure 3B). Richness peaked in mid-summer in the Marais des Cygnes River consistently across all years, and was highest in 2024 with 11 species. In the Kansas River average richness decreased from 10 species to 3 species throughout the summer, with highest richness (13 species) in 2022.

Four species accounted for nearly 90% of all individuals sampled in the Kansas River with red shiner *Cyprinella lutrensis* (40%), western mosquitofish *Gambusia affinis* (22%), sand shiner *Notropis stramineus* (22%) and bullhead minnow *Pimephales vigilax* (6%) being the most abundant. In the Marais des Cygnes River, red shiner (64%), western mosquitofish (20%), and sunfishes (*Lepomis* spp., 5%) were the most abundant taxa (Figure A.1). Blue catfish *Ictalurus furcatus* and brook silverside *Labidesthes sicculus* were only sampled in the Marais des Cygnes River, while river carpsucker *Carpiodes carpio* and freshwater drum *Aplodinotus grunniens* were unique to the Kansas River. However, routine surveys of adult fish assemblages indicate that all these species are present in both rivers.

A two-way ANOVA indicated that the timing of peak abundance varied across species ($F = 4.47$, $p < 0.05$), albeit there was substantial overlap and timing in abundance did not differ across rivers ($F = 2.16$, $p > 0.05$). We found that timing of peak abundance exhibited interannual variability, with three general groupings: early summer, mid-summer, and prolonged summer (spanning mid to late summer) (Figure 4). In general, large-bodied species peaked in abundance earlier than small-bodied fishes. Common carp and longnose gar exhibited the earliest peak

abundance, occurring in late May and early June, respectively. These species peaked in abundance earlier than red shiner and bluntnose minnow *P.* notatus ($p < 0.05$). Sand shiner, bluntnose minnow and red shiner appeared to peak in abundance later in 2024 compared to 2022 and 2023, whereas longnose gar and river carpsucker appeared to peak in abundance earlier. Western mosquitofish, red shiner, bullhead minnow, and sand shiner were present in high abundances throughout the summer, whereas river carpsucker, longnose gar, gizzard shad, common carp, bluntnose minnow, and sunfishes exhibited more sporadic abundances throughout the summer. Longnose gar, gizzard shad, sunfishes, and common carp were sampled more frequently in 2022 and 2024, which corresponded with higher discharge. River carpsucker was the only large-bodied species that had the highest relative abundance in 2023.

Environmental predictors of abundance

Kansas River

In the Kansas River, total fish abundance was highest in 2023 (58.08 fish/m²), and lowest in 2024 (33.41 fish/m²). The multivariate generalized linear model identified significant relationships between environmental predictors and abundances across species. However, post hoc univariate analyses indicated idiosyncratic responses of species abundances to environmental conditions. Bullhead minnow and western mosquitofish showed no discernible patterns over time or in relation to environmental variables. Red shiner increased throughout the summer ($p < 0.05$; Figure 5A) with densities ranging from 0.11 fish/m^2 in late spring/early summer to 31.19 fish/m^2 in late summer. Sand shiner exhibited interannual variability and decreased with discharge ($p < 0.01$; Figure 5B), with highest and most variable densities in 2023 (15.05 fish/m^2 $\pm$ 11.51 SD). Bluntnose minnow, longnose gar, and river carpsucker were also included in the analysis but appeared more sporadically and in lower densities throughout our sampling period. Bluntnose minnow density was low in 2022 (0.06 fish/m^2) and exhibited a decreasing relationship ($p < 0.05$; Figure 5C) with discharge, peaking in 2024 (1.83 individuals/m^2; $p < 0.005$). Longnose gar and river carpsucker, appeared more periodically and exhibited responses to seasonal and hydrologic changes that contrasted with those of the small-bodied cyprinids. Longnose gar decreased exponentially with day of year, with densities in late spring at 2.26 fish/m^2 ($\pm$ 0.04 SD), and by early mid-summer dropping to 0.11 fish/m^2 ($\pm$ 0.09 SD). River carpsucker increased with discharge in 2023 ($p < 0.05$) but were sampled on only two occasions in 2022 and 2024.

Marais des Cygnes River

Overall density was lower in the Marais des Cygnes compared to the Kansas River, but assemblage structure showed similar trends in relative abundance. The highest densities in 2023 were 15.48 fish/m^2 and the lowest density was 7.64 fish/m^2 in 2024. Assemblage structure significantly changed with year ($p < 0.01$), date ($p < 0.005$), and temperature ($p < 0.01$), which was driven mostly by abundance of red shiner. Univariate analyses indicated that western mosquitofish, bluntnose minnow, and sunfishes were consistent across a range of environmental conditions and across years. Red shiner increased throughout the summer ($p < 0.005$; Figure 6A) from 0.28 fish/m^2 in late spring to 33.64 fish/m^2 by the end of August with the highest annual density and variation in 2023 ($p < 0.001$) and showed a decreasing relationship with discharge in 2022 and 2024 (Figure 6C). Bluntnose minnow were not sampled in 2022 but were at higher densities in 2024 compared to 2023 (0.32 fish/m^2 and 0.22 fish/m^2, respectively; $p < 0.05$; Figure 6B). Sunfishes were consistently sampled in low densities across all years, generally in mid-summer.

Emergence of larval fish

All species exhibited strong relationships between estimated age and total length ($p < 0.001$; Table A.2), indicating that total length can be used as reliable predictors of hatch dates. Red shiner, sand shiner, western mosquitofish, bullhead minnow, and bluntnose minnow had extended periods of emergence, with hatching estimated to span from late April to mid-September (Figure 7). Bullhead minnow and red shiner hatched under the widest range of temperatures (14.3 – 33.3 °C) (Table 1). Sand shiner had an emergence period of about 3 months lasting from mid-May to early August, which was 43 days shorter compared to the other small-bodied fishes. We only detected hatching of common carp in 2024. All individuals were sampled on the same occasion in late-May and were estimated to have hatched from April 30th – May 8th. The relative hatch frequency for common carp was at the highest range of discharge (83.3 – 603 m^3/s) with temperatures ranging from 17.8 – 20.0 °C. Longnose gar had the second shortest period of emergence from June 9th – June 25th in 2022 and from May 9th – May 25th in 2024. In 2022, there were three hatching cohorts, and in 2024 most individuals hatched in early May, with few individuals emerging later in May. Longnose gar hatched between 21.2 – 27.2 °C and the greatest proportion of individuals hatched shortly following flow pulses in 2022 and 2024 and

ranged from 27.2 – 303.0 m^3/s. Gizzard shad had a cohort in 2022 in the Kansas River in early May hatching within a 3-week window spanning early-mid May. The hatching window was longer for gizzard shad in the Marais des Cygnes River in 2024 spanning from early May to mid-July, peaking in late June. Gizzard shad hatching occurred over a wide range of temperature (13.4 - 31.5 °C) and discharge conditions (15.9 – 563.5 m^3/s). River carpsucker hatched from late July – early July in 2022, appeared earlier in 2024 in mid-May, and had a small cohort appear in late July 2024. River carpsucker hatched for a longer duration and more continuously throughout 2023 from mid-May to mid-June and in higher numbers compared to the other years. River carpsucker hatching occurred at the lowest temperatures among all species analyzed (12.5–27.8 °C) and under discharge conditions of 21.2–399.3 m^3/s, with the greatest hatching frequency in 2023 at discharges below 100 m^3/s. Sunfishes hatch date range was highest in 2022 ranging from late May-late June and few individuals estimated to have hatched in late July. The shortest hatching period (late June-early July) occurred in 2023. In 2024 sunfishes had the lowest hatch frequency but the longest period of hatching, occurring from May to September. The highest hatch frequency for Sunfishes occurred at temperatures between 22–29 °C and discharges of 2.01–158.9 m^3/s, though hatching was observed over a broad range of conditions (14.8–32.9 °C; 2.01–562.5 m^3/s).

Environmental predictors of hatching

The multivariate logistic regression showed significant effects of year ($p < 0.05$), week ($p < 0.05$), temperature ($p < 0.001$), and discharge ($p < 0.05$) for the Kansas River. Post-hoc univariate tests revealed that temperature was a significant predictor of hatching for most Mode 3 species (bluntnose minnow, bullhead minnow, sand shiner, western mosquitofish; $p < 0.05$) with increasing probability with temperature (Figure 8). River carpsucker was the only species in which hatch probability exhibited seasonal change decreasing throughout the summer ($p < 0.005$), however, hatch probability for most Mode 1 and 2 species decreased with temperature. Longnose gar hatch probability increased with discharge ($p < 0.005$) where hatching shortly followed (~7-10 d) flow pulse events. The multivariate logistic regression model for the Marais des Cygnes River only revealed that hatch probability for sunfishes increased with discharge ($p = 0.05$). Generally, hatch probability for Mode 1 and Mode 2 species increased with discharge (Figure 9A), while Mode 3 species had highest hatch frequency under low discharge conditions (Figure 9B).

Discussion

Hatching and assemblage dynamics

Our study quantified the response of early life stage fishes to temperature, discharge, and season in the Kansas and Marais des Cygnes rivers, revealing interspecific responses to environmental conditions across years and river basins. As predicted, the most abundant species in our study were small-bodied generalists, including red shiner, sand shiner, western mosquitofish, bullhead minnow, and bluntnose minnow. These species align with Mode 3 opportunistic strategists, as described by Humphries et al. (1999), given their broad tolerance to varying temperature and discharge conditions in Great Plains rivers. Common carp exhibit traits of Mode 2, as they occurred sporadically and coincided with flow pulses. Early life stages of longnose gar and gizzard shad occurred in low densities across years and corresponded to Mode 1. River carpsucker was the most abundant large-bodied species and exhibited serial spawning, and sunfishes were consistently in low densities across all years and larvae hatched throughout the summer. These two species exhibit traits spanning multiple modes, highlighting the challenges of making hard classifications within the proposed reproductive strategies. Early life stage assemblages changed throughout the summer, showing chronological patterns in abundance. We found that large-bodied species (Modes 1 and 2) were most abundant early in the season, except for gizzard shad, which appeared in late July. Opportunistic species (Mode 3) were abundant throughout the summer, but the timing of peak abundance varied by 4–5 weeks across years. Our findings generally align with predicted responses based on life history traits.

Both the Kansas and Marais des Cygnes river basins experienced a severe drought in 2023. These drought conditions were characterized by assemblage homogenization with increased densities of red shiner, sand shiner, bullhead minnow, and western mosquitofish. These are common Great Plains fishes that exhibit resilience to drought conditions (Summerfelt & Minkley 1969; Matthews 2000, Perkin et al. 2019). Fish can be resilient to drought by resisting the environmental effects or by rapid recolonization following channel drying (Van Looy et al. 2019). However, when monitoring red shiner movement during experimental channel drying, Archdeacon and colleagues (2022) concluded that movement to local refuges was not likely. This suggests that the resilience of these small-bodied fish is dependent on their ability to persist or recolonize from regional refuges. Their ability to persist in low flow conditions is linked to

their short generation times and ability to spawn multiple clutches. Our findings provide evidence supporting a mechanism for the resilience of some small-bodied opportunists during drought conditions through prolonged spawning and heightened recruitment.

We estimated that opportunistic strategists in our study spawn from late April to early September. Although our sampling periods increased from 2022 to 2024, length-at-age models (i.e., back-calculating hatch dates) allowed us to predict hatch dates before our sampling began. This approach ensured that even with variability in the sampling periods, we could still make predictions for individuals within the established length cutoffs. Nonetheless, this general timeframe aligns with other studies of Great Plains fishes (Farringer, Echelle, & Lehtinen 1979; Tiemann 2007) demonstrating that opportunistic spawning is a common strategy in environments subject to frequent and intense disturbance. For example, Stocks et al. (2021) found that un-speckled hardyhead *Craterocephalus stercusmuscarum* and Australian smelt spawned over a prolonged period which included a broad range of temperature (9 – 27 °C) and discharge (0 – 45 GL/day) conditions in a dryland river in Australia, which is characterized by climactic variability.

The window-of-opportunity hypothesis posits that, in systems with environmental variability, species with extended spawning seasons will have a greater chance of producing offspring that coincide with favorable conditions (Humphries et al. 2013). Prolonged spawning is advantageous in Great Plains streams, where highly variable and unpredictable discharge regimes are common. Gale (1986) and Gale (1983) found that red shiner and bluntnose minnow can reproduce at continuous intervals of 1-4 days. Apparent indeterminate fecundity of females in many opportunistic species suggests that reproduction is controlled by length of spawning season and temperature, rather than egg supply (Fausch & Bestgen 1997). Through prolonged spawning, larval cohorts appear frequently, increasing the likelihood that at least some offspring will hatch under favorable environmental conditions including temperature, discharge, and prey availability. Prolonged spawning can confer an advantage over species with brief spawning periods, where resources could potentially be missed if hatching does not coincide with favorable environmental conditions (Cushing 1990). We found that recruitment for opportunistic species was highly variable within and across years, where apparent peaks in abundance due to increased reproduction or early survival aligned with seemingly optimal conditions. For example, predicted hatch dates of sand shiner, red shiner, and bluntnose minnow peaked in late summer 2024 and

mid-summer 2023, coinciding with the lowest discharge levels observed during the study period. Sand shiner exhibited the strongest negative relationship with discharge, showing a 14-fold increase in abundance during low-flow conditions. Our findings are consistent with Summerfelt and Minckley (1969) who found that sand shiners have high recruitment during periods of low discharge. Their preference for sandy substrates aligns with low-flow conditions, as reduced discharge limits sediment movement, creating a more stable habitat. During periods of low flow, water temperature increases and habitats constrict, concentrating nutrients and prey into the remaining wetted area. These conditions enhance growth rates and turnover of zooplankton which increasing prey density for larval fish. Thus, species that can benefit most from low flows may be small-bodied, spawn demersal eggs, and have small gape at first feeding. Collectively, these results support the window-of-opportunity hypothesis because heightened recruitment is likely due to a combination of optimal temperature, discharge, and feeding conditions (Humphries et al. 2013).

Flooding can play a large role in fish spawning and recruitment. While periods of low flow were important for recruitment in some species, prolonged drought conditions can negatively affect fish through habitat isolation, poor water quality, and enhanced predation and/or competition (Crook et al. 2010; Cheshire et al. 2016). Although the Kansas and Marais des Cygnes rivers do not completely dry, species that are most vulnerable to drought are those that depend on flows for a part of their life cycle or those who are more periodic in spawning. Flow pulses can sustain spawning and recruitment by providing an influx of nutrients, increasing floodplain connectivity, and initiating reproductive cues (Junk et al. 1989; Bunn et al. 2006). We found that large-bodied species were sampled in higher densities during 2022 and early summer of 2024, which were periods of relatively high discharge. The Kansas and Marais des Cygnes river basins differ morphologically, with the Kansas River characterized by a shallower channel and broader floodplain, whereas the Marais des Cygnes requires a significantly higher water level rise for floodplain inundation. Despite these differences, periodic species responses to flow pulse events were similar. Longnose gar were most frequently sampled in the Kansas River near inundated shoreline vegetation and hatched under high flow conditions in 2022 and in late spring of 2024. Similarly, Zeug and Winemiller (2007) found that gonadal development of longnose gar in the Brazos River, Texas, coincided with increasing spring discharge. Common carp were present on the Marais des Cygnes floodplain in 2024, with hatching commencing shortly after

overbank flow. Common carp are known to exhibit similar recruitment patterns in floodplain habitats across their non-native range, with hatching and recruitment often enhanced through floodplain inundation (Turner 1994; King et al. 2003; Pease et al. 2006; Stuart and Jones 2006). Floodplains can provide optimal conditions for larval fish through enhanced feeding abundant nursery habitat and recruitment for some species is maximized when high flow events coincide with elevated temperatures (Turner et al. 1994; Balcombe et al. 2007). To summarize, high flows and floodplain inundation were associated with the appearance of the above-mentioned species, but the absence of early life stages of other species, such as suckers, that are known to occupy these systems was unexpected.

Numerous sucker species are prevalent in Great Plains rivers, notably blue sucker *Cycleptus elongatus* and different species of redhorse *Mosostoma* spp. (Metcalf 1964; Quist et al. 2005). Whereas, adults of other sucker species are relatively common in these rivers (personal observation), river carpsucker was the only member of this group observed at an early life stage during our study and was exclusively sampled in the Kansas River, suggesting potential differences in life history compared to other suckers. While many suckers are periodic spawners that use discharge as a cue for migration to spawn in tributaries (Turner et al. 2010; Tornabene et al. 2020; Bonjour et al. 2023), river carpsucker exhibits an intermediate life history strategy. Although it is large-bodied, it matures relatively quickly (3–4 years; Morris 1965) and is capable of spawning intermittently throughout the summer (Behmer 1964). In our study, river carpsucker hatching was highest during drought conditions in 2023. Because this species typically spawns in shallow, low-velocity habitats (Jenkins and Burkhead 1997), it is possible that high-flow events may negatively impact spawning success by reducing the availability of these habitats. The absence of early life stage river carpsucker in our Marais des Cygnes River samples could be due to the limited availability of low-velocity habitats in this system, which could restrict suitable spawning and larval rearing conditions. We attribute the general absence of sucker species in our study to the rarity of occurrence of early life stages, low capture probabilities, and infrequent successful spawning events, specifically related to discharge conditions (Dyer & Brewer 2020).

Environmental flow management

The Kansas and Marais des Cygnes rivers are enrolled in the Sustainable Rivers Program, a joint venture between the U.S. Army Corps of Engineers and The Nature Conservancy, which aims to manage flows in a way that mimics elements of a natural flow regime. Our findings

provide insight into species responses to varying environmental conditions during early life stages in these two Great Plains rivers, offering a foundation for developing testable flow-ecology predictions (Freeman et al. 2022). When designing environmental flow plans, it is important to consider how discharge influences key ecological factors such as habitat complexity, temperature, dispersal, and predation pressure (Humphries et al. 2020). Additionally, life history traits should be accounted for at multiple life stages, including adult spawning behaviors and larval characteristics (e.g., size at hatch, gape size, and swimming ability), as these traits shape species-specific responses to flow variability.

Life history strategies provide a useful framework for predicting species responses to hydrologic variation; however, many species do not fall into a single life history category and instead may exhibit intermediate traits. This complexity highlights the need for a nuanced approach to flow-ecology relationships, considering how alternative mechanisms may drive opposing outcomes. For example, while low flows may enhance recruitment success for some species by providing low-velocity nursery habitats, they may simultaneously lead to recruitment failure in species that rely on flow pulses as reproductive cues. Conversely, high flows can promote spawning and dispersal in certain species, yet may also reduce water temperature, resulting in failed recruitment. Notably, high-flow pulses can facilitate the spawning of non-native species such as common carp, potentially altering community composition and competitive dynamics. Nonetheless, our research provides general guidance on predicting flow responses based on life history traits, primarily body size, but further research across a range of flow scenarios is necessary to capture responses of less common species.

A notable limitation of our study lies in its emphasis on common species that are not considered conservation priorities in Kansas. While the species we sampled provide valuable insights into general flow-ecology relationships, they may not fully represent the needs of flow-sensitive or imperiled species, such as blue sucker and shoal chub *Macrohybopsis hyostoma*. These species may have more specialized ecological requirements and distinct responses to hydrologic variability that were not captured in our study. Their absence from our samples may be attributed to periodic spawning occurring outside our sampling window or beyond the spatial extent of our sampling (e.g., in tributaries or other reaches) as well as recruitment failure caused by unfavorable environmental conditions during our study period. Future research should aim to address these gaps by explicitly incorporating species of conservation concern into flow-ecology

studies. Expanding the temporal and spatial scope of sampling efforts, particularly during key spawning windows for rare or sensitive species, will improve our ability to assess their responses to discharge variability. Additionally, integrating long-term datasets and experimental flow manipulations could further enhance our understanding of how hydrologic alterations impact fish recruitment and assemblage dynamics in Great Plains rivers.

Figures

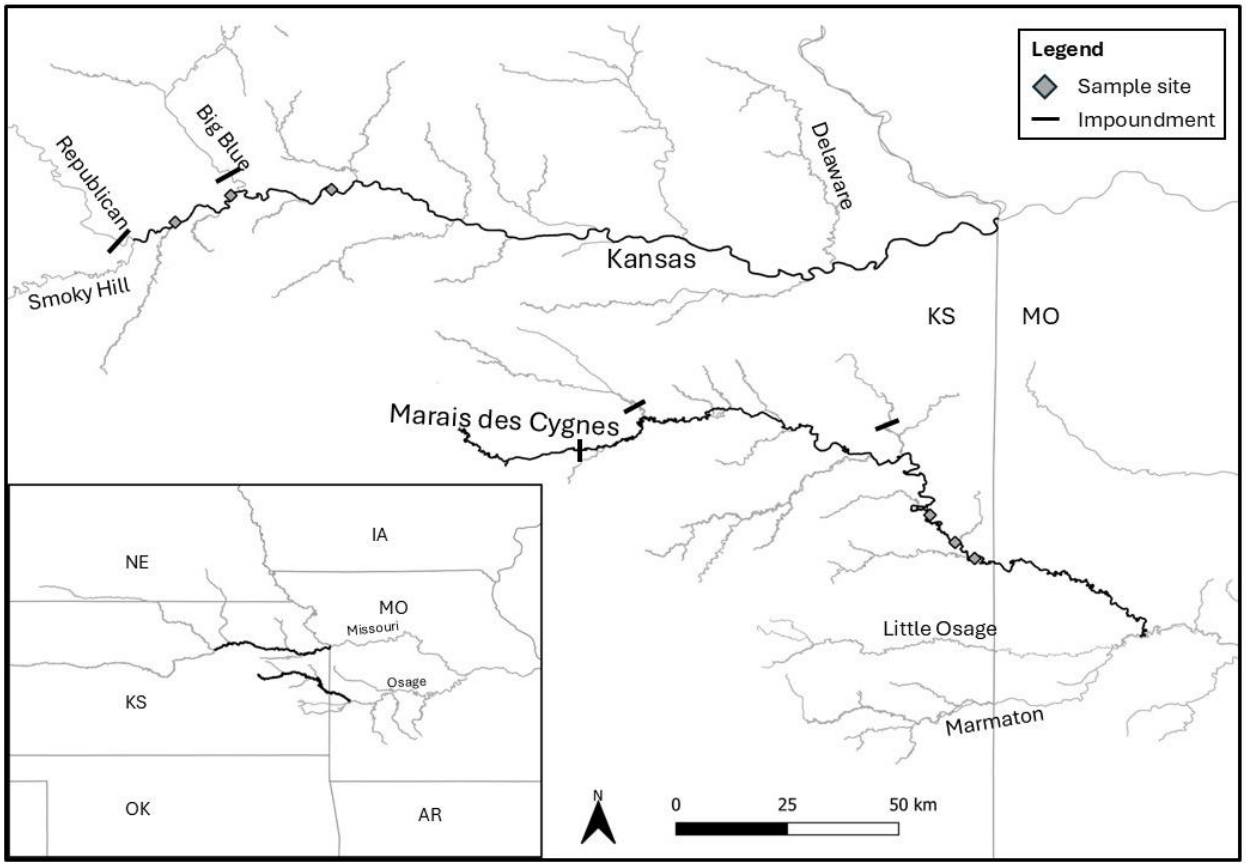


Figure 1. Study map of the Kansas and Marais des Cygnes rivers with impounded tributaries and sampling locations.

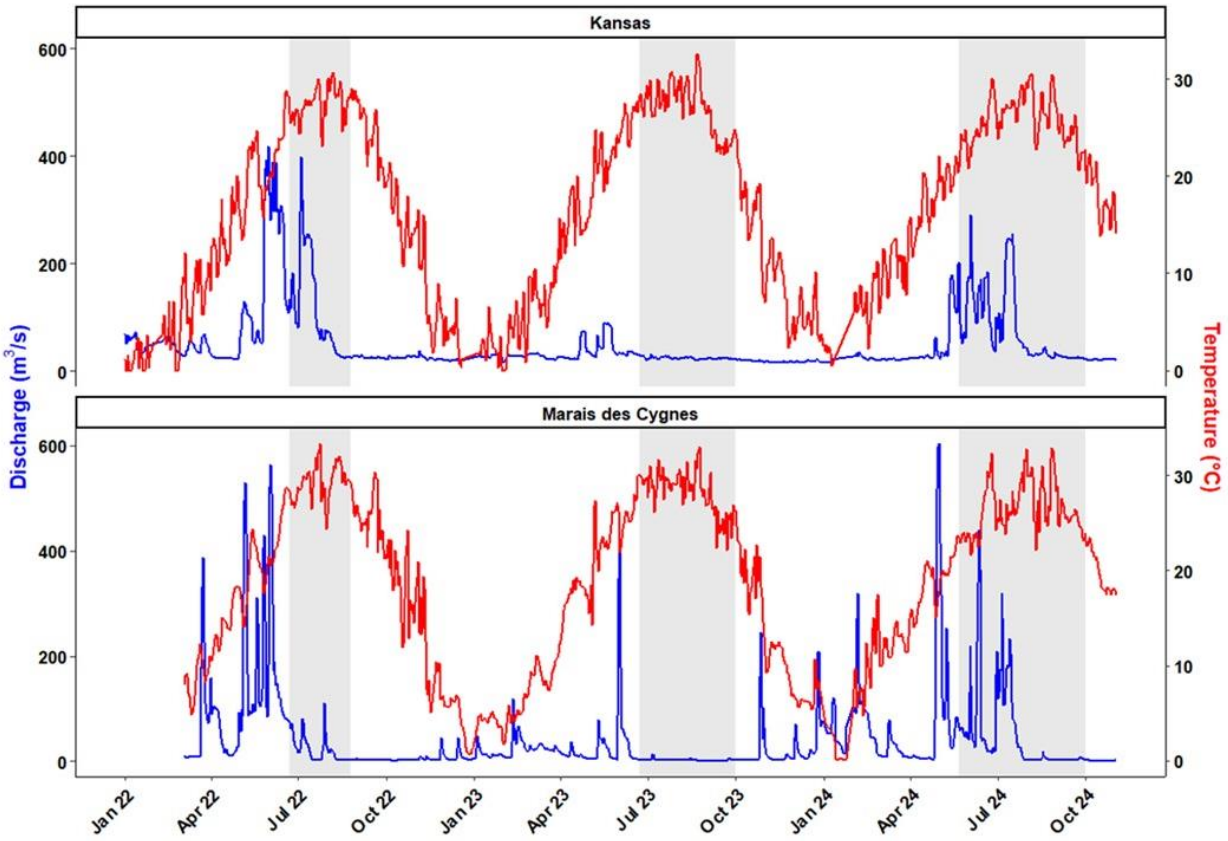


Figure 2. Discharge (blue) and temperature (red) for the Kansas (at Wamego, KS) and Marais des Cygnes (at La Cygne, KS) rivers between January 2022 and October 2024. Grey boxes indicate sampling periods.

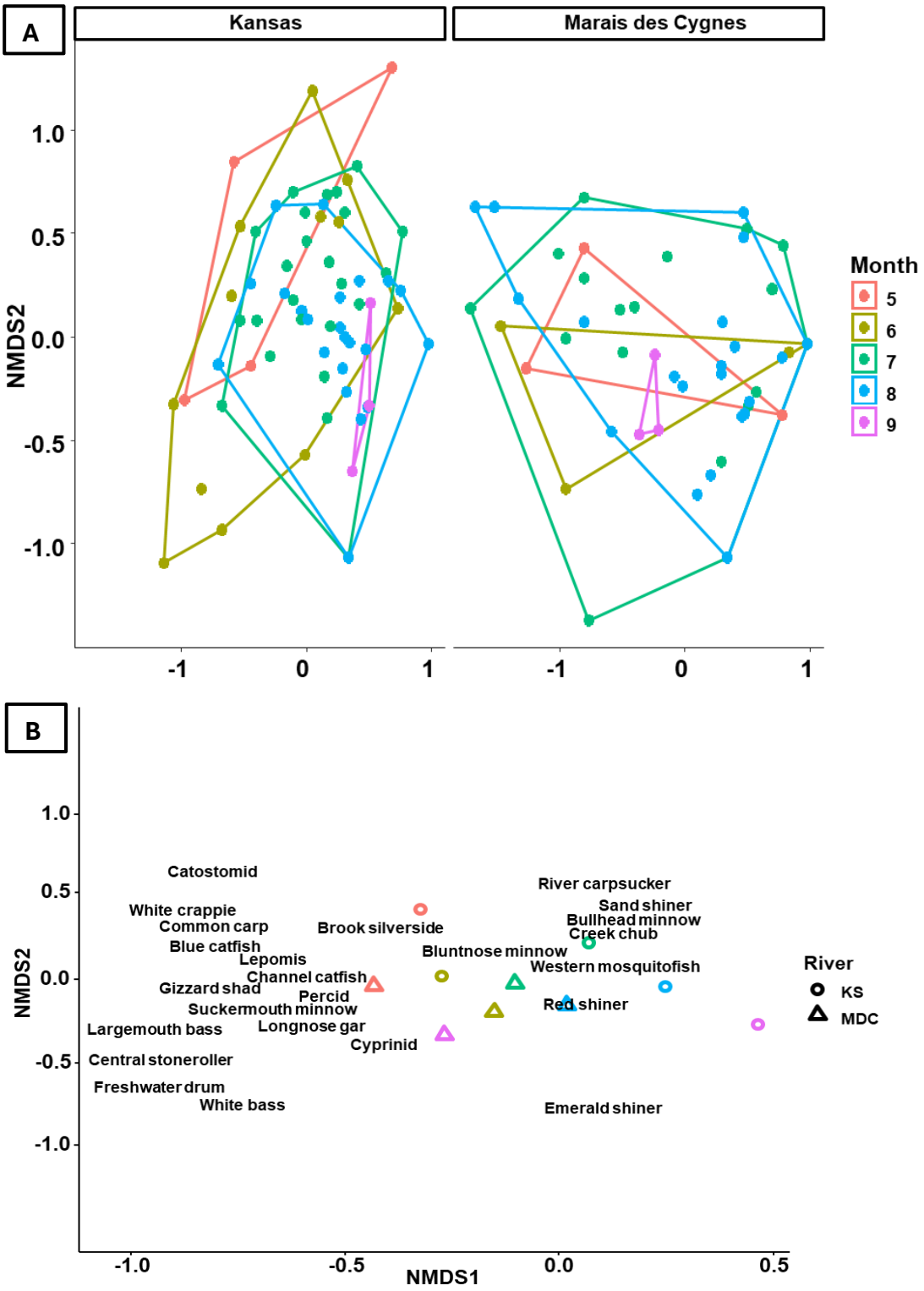


Figure 3. Non-metric multidimensional scaling of Bray-Curtis distances among sampling events (stress 0.18) of early life sage assemblage in the Kansas and Marais des Cygnes rivers over the summers of 2022-2024 (panel A). Panel B shows weighted species scores and colored points indicate centroids for each month across rivers.

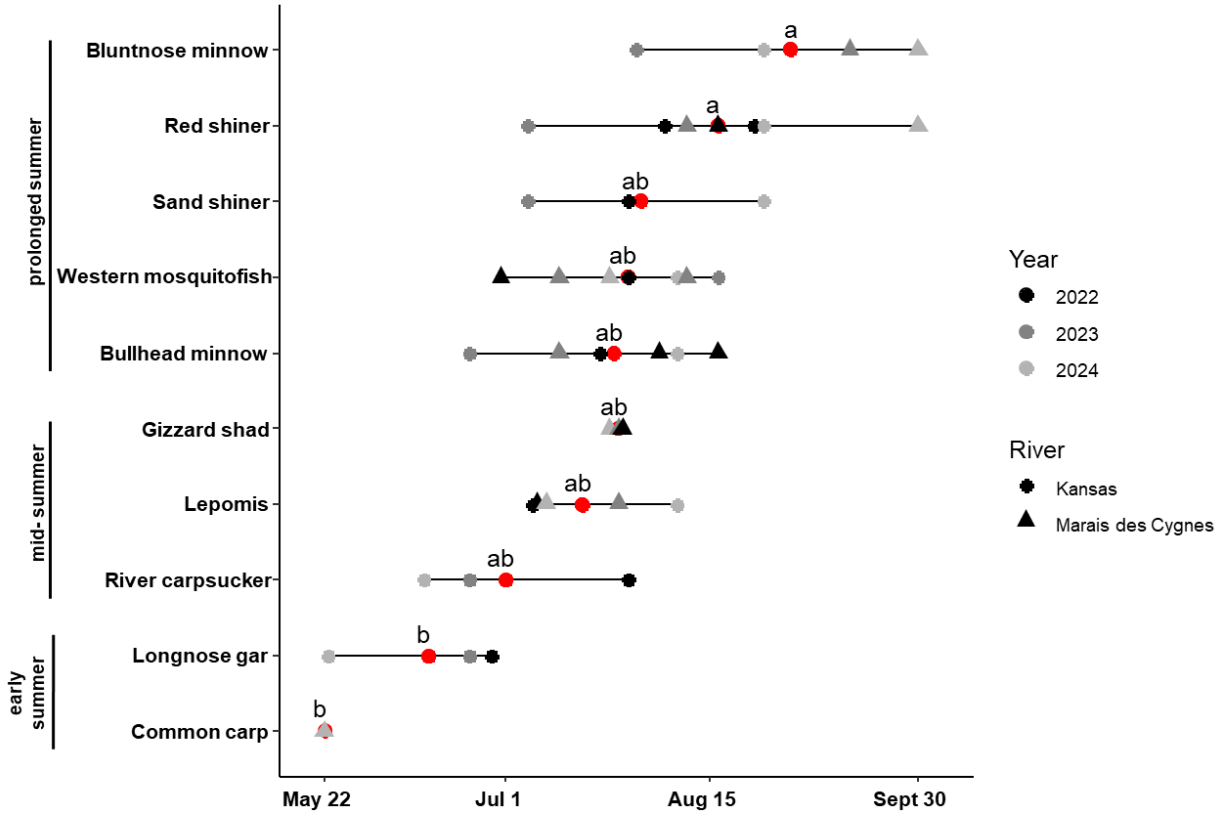


Figure 4. Date of peak abundance of early life stage fish sampled at frequent intervals from the Kansas and Marias des Cygnes rivers across three years. Red dot indicates mean date of maximum abundance. Letters indicate groups that are significantly different based on ANOVA post hoc tests.

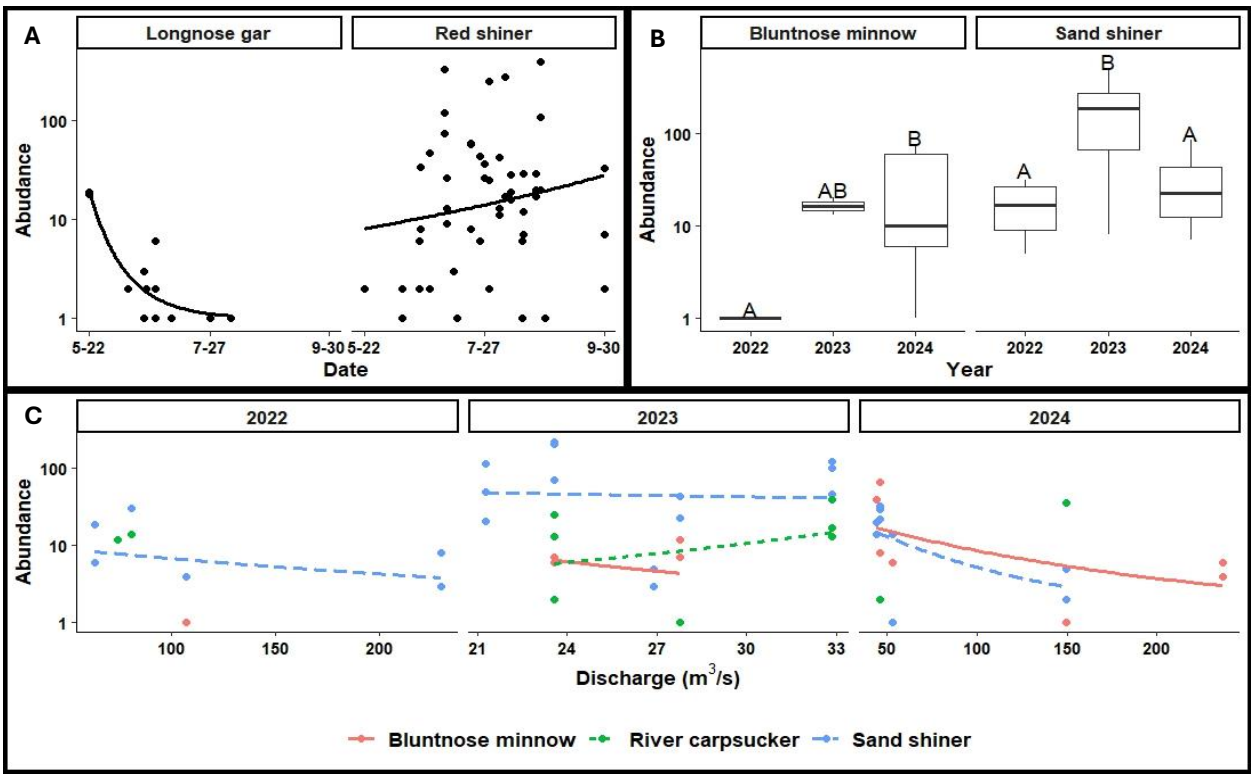


Figure 5. Significant relationships from regression models of early life stage fish from the Kansas River throughout the summers of 2022-2024. Abundance patterns varied across species by seasonal (panel A), annual (panel B), and discharge (panel C) variability.

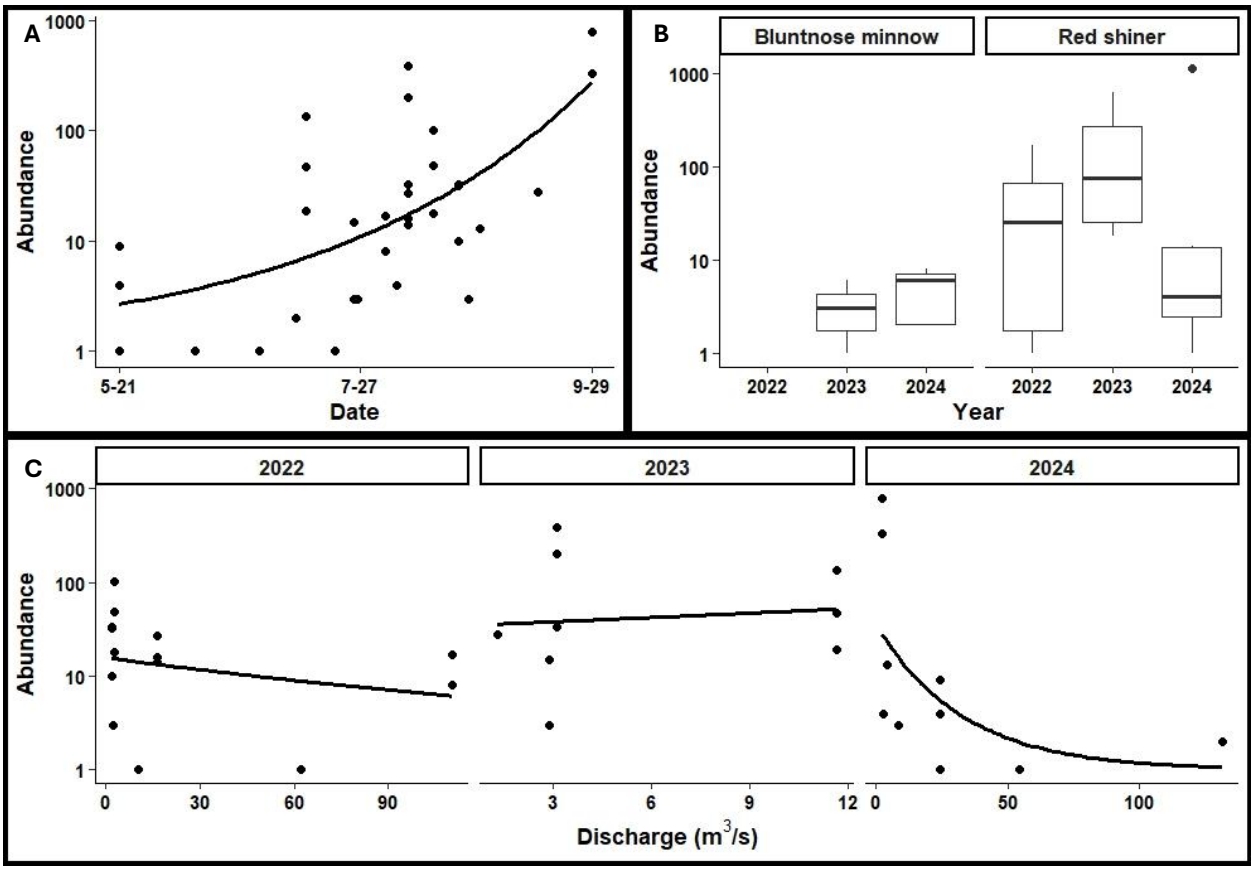


Figure 6. Significant relationships from regression models of early life stage fish from the Marais des Cygnes River throughout the summers of 2022-2024. Panel A shows increase in red shiner *Cyprinella lutrensis* abundance throughout the summer. Panel B shows interannual variability for bluntnose minnow *Pimephales notatus* and red shiner. Red shiner abundance decreased in 2022 and 2024 with discharge but was more constant in 2023 (panel C). *Note different x-axis scales in panel C.

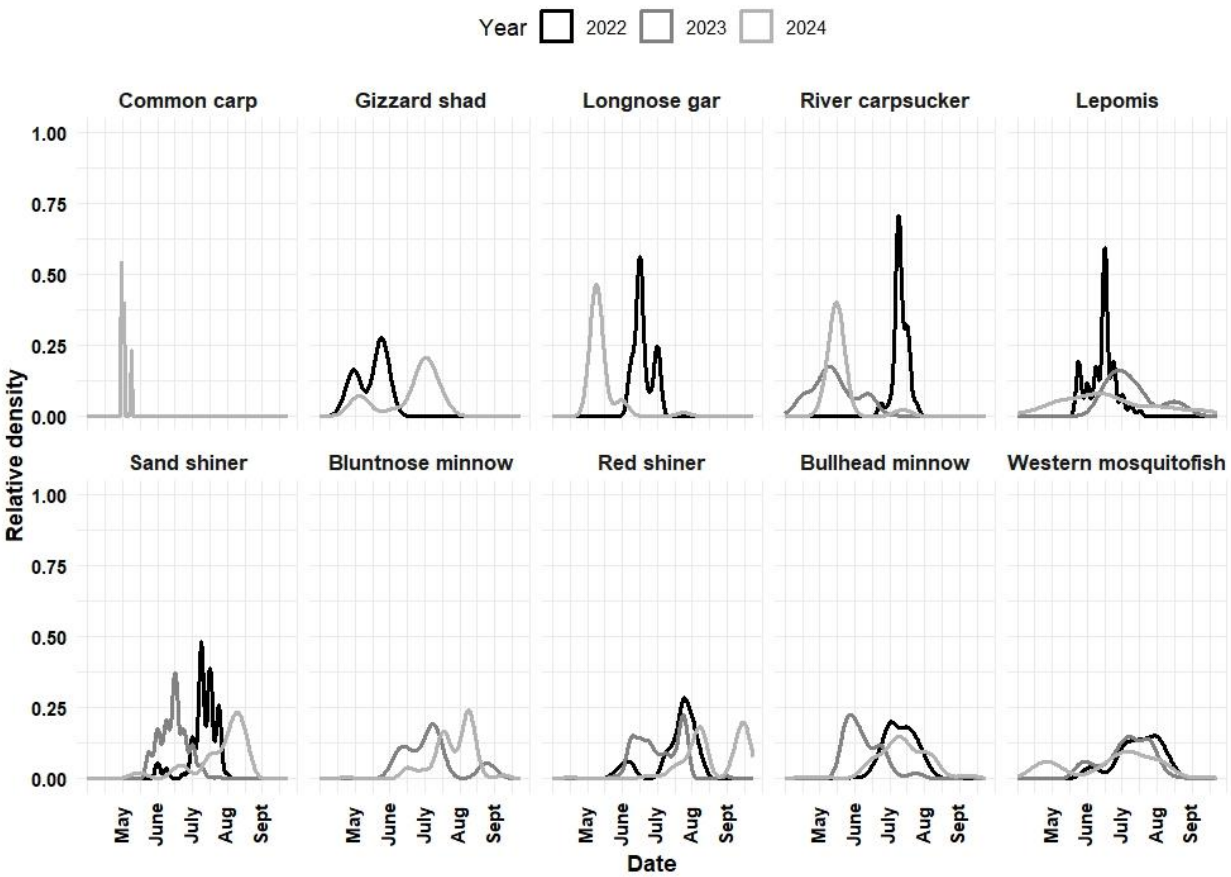


Figure 7. Density plots showing smoothed trends of back calculated hatch dates of common Great Plains fishes collected from the Kansas and Maris des Cygnes rivers throughout the summers of 2022-2024. Annual densities are relative to each species.

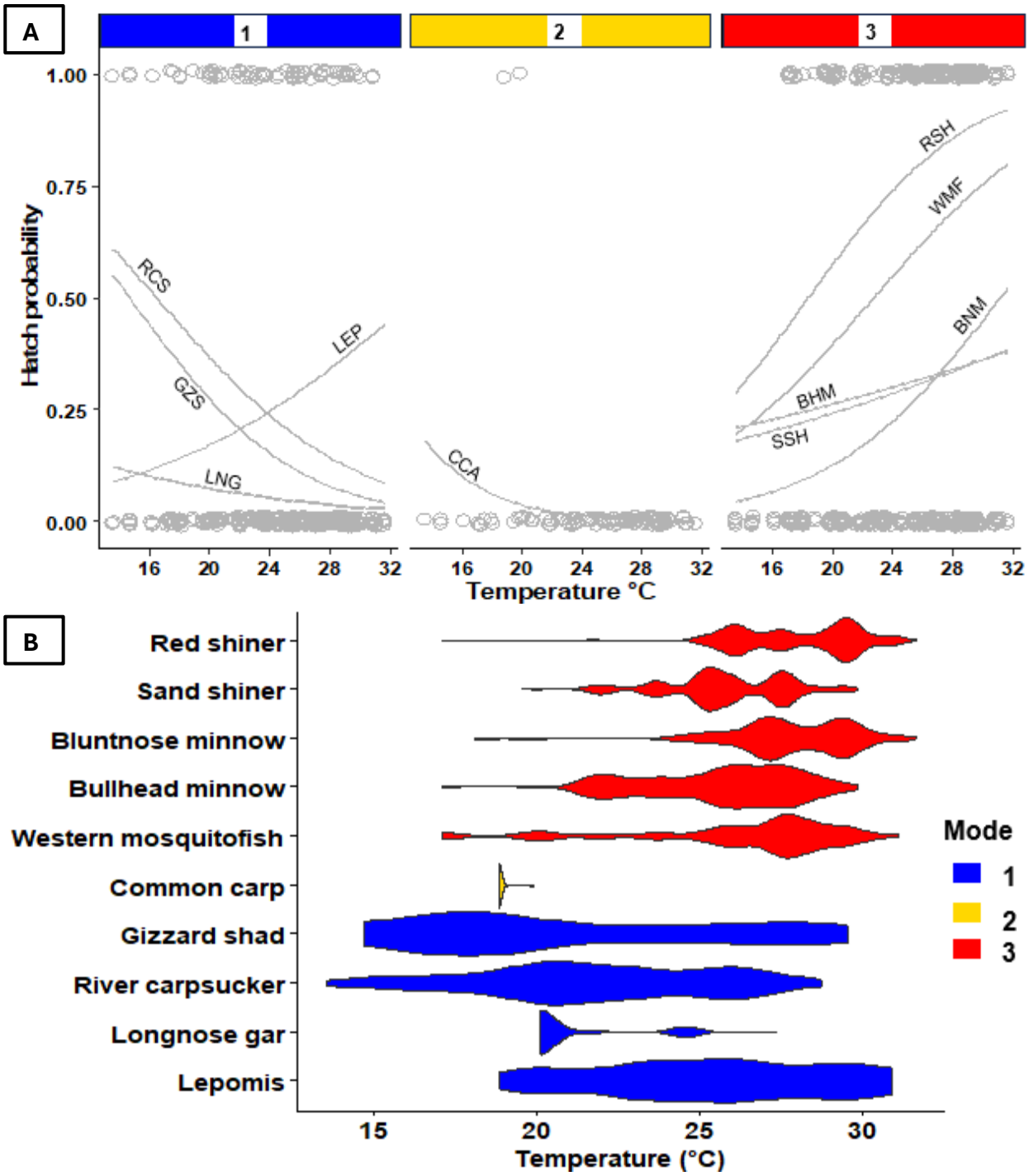


Figure 8. Hatch probability as a function of temperature for each taxa grouped by life-history modes (panel A). Taxa labels are as follows: river carpsucker (RCS), gizzard shad (GZS), longnose gar (LNG), sunfishes (LEP), common carp (CCA), red shiner (RSH), sand shiner (SSH), western mosquitofish (WMF), bullhead minnow (BHM), bluntnose minnow (BNM). Violin plot shows the range of temperatures under which hatching occurred, where the height of the bars corresponds to the relative number of individuals (panel B).

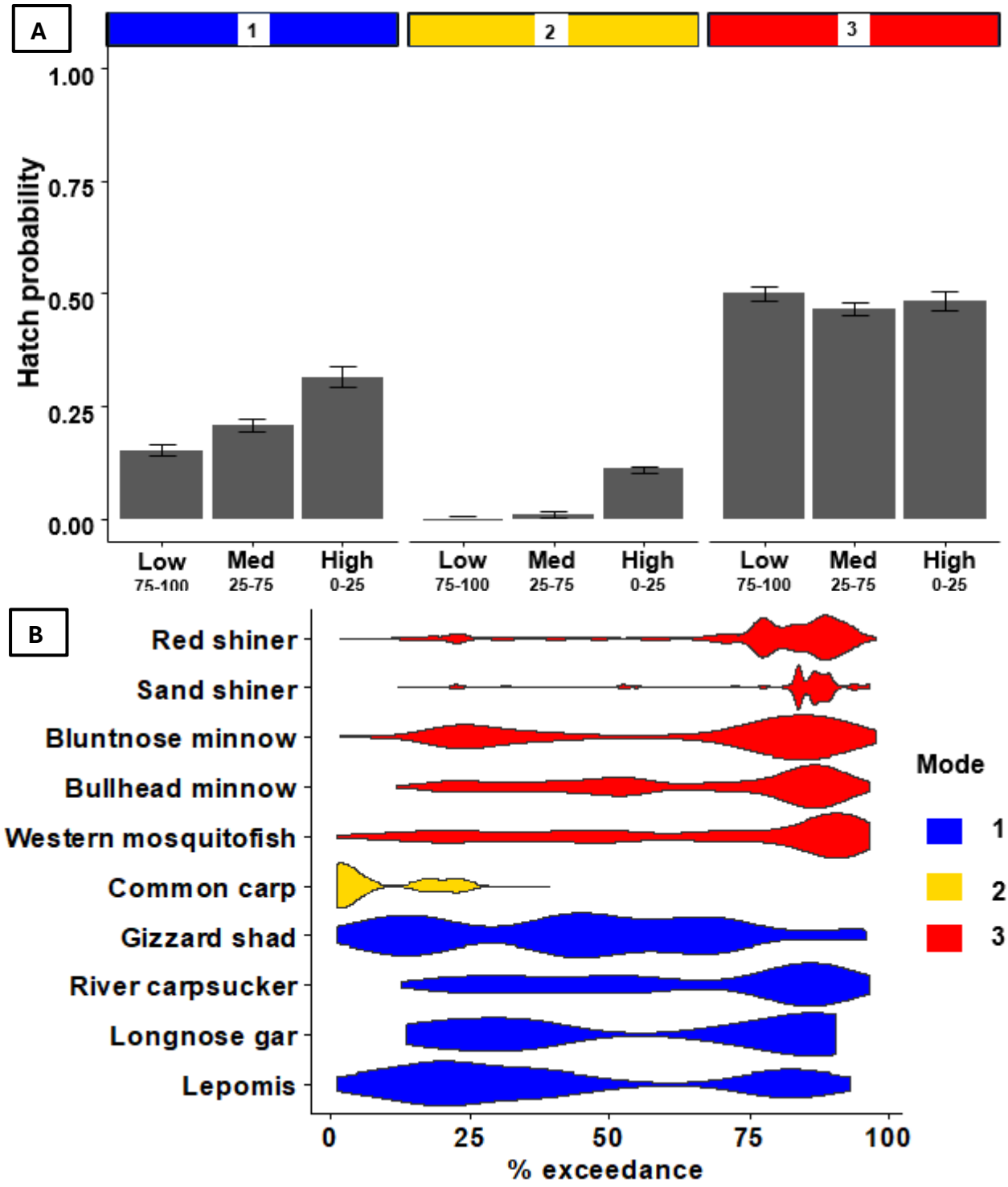


Figure 9. Cumulative hatch probability of taxa grouped by life history modes across different discharge scenarios: low (75-100% exceedance), medium (25-75% exceedance), and high (0-25% exceedance) (panel A). Violin plot shows the range of discharge conditions under which hatching occurred, where the height of the bars corresponds to the relative number of individuals (panel B).

Tables

Table 1. Summary of minimum, maximum, and mean ($\bar{x}$) water temperature (°C) and discharge (m^3/s) during the hatching period of each species.

Species	Min. temp	Max. temp	$\bar{x}$ temp	Min. discharge	Max. discharge	$\bar{x}$ discharge
Bluntnose minnow	16.4	31.5	27.8	1.6	438.9	96.2
Bullhead minnow	14.3	33.3	26.0	1.9	393.6	75.6
Common carp	17.8	22.7	19.6	83.8	603.1	252.6
Lepomis	15.7	32.9	24.9	2.01	521.0	119.6
Gizzard shad	14.9	31.5	22.4	16.0	393.6	151.1
Longnose gar	21.2	27.2	22.6	27.2	303.0	93.8
Red shiner	14.3	33.3	27.7	1.4	509.7	48.0
River carpsucker	18.3	27.9	22.4	27.2	399.3	105.7
Sand shiner	19.0	30.6	26.2	20.9	376.6	48.2
Western mosquitofish	15.0	33.3	26.1	1.8	597.5	77.4

References

Archdeacon, T. P., Gonzales, E. J., & Thomas, L. I. (2022). Movement of Red Shiner during a regulated, intentional surface-flow recession. Ecology of Freshwater Fish, 31(2), 358-368.

Auer, N. A. (Ed.). (1982). Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage (Vol. 82, No. 3). Great Lakes Fishery Commission.

Balcombe, S. R., Bunn, S. E., Arthington, A. H., Fawcett, J. H., McKenzie-Smith, F. J., & Wright, A. (2007). Fish larvae, growth and biomass relationships in an Australian arid zone river: links between floodplains and waterholes. Freshwater biology, 52(12), 2385-2398.

Behmer, D. J. (1964). Spawning periodicity of the river carpsucker, Carpiodes carpio. In Proceedings of the Iowa Academy of Science (Vol. 72, No. 1, pp. 253-262).

Bonjour, S. M., Gido, K. B., McKinstry, M. C., Cathcart, C. N., Bogaard, M. R., Dzul, M., ... & Yackulic, C. B. (2023). Migration timing and tributary use of spawning flannelmouth sucker (Catostomus latipinnis). Journal of Fish Biology, 103(5), 1144-1162.

Brothers, E. B., Mathews, C. P., & Lasker, R. E. U. B. E. N. (1976). Daily growth increments in otoliths from larval and adult fishes. Fish. Bull, 74(1), 1-8.

Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental management, 30, 492-507

Bunn, S. E., Thoms, M. C., Hamilton, S. K., & Capon, S. J. (2006). Flow variability in dryland rivers: boom, bust and the bits in between. River Research and Applications, 22(2), 179-186.

Chapman, Shannen S., Omernik, James M., Freeouf, Jerry A., Huggins, Donald G., McCauley,

James R., Freeman, Craig C., Steinauer, Gerry, Angelo, Robert T., and Schlepp, Richard L., 2001, Ecoregions of Nebraska and Kansas (color poster with map, descriptive text, summary tables, and photographs): Reston, Virginia, U.S. Geological Survey (map scale 1:1,950,000).

Campana, S. E., & Thorrold, S. R. (2001). Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations?. Canadian Journal of Fisheries and Aquatic Sciences, 58(1), 30-38.

Cheshire, K. J. M., Ye, Q., Gillanders, B. M., & King, A. (2016). Annual variation in larval fish assemblages in a heavily regulated river during differing hydrological conditions. River Research and Applications, 32(6), 1207-1219.

Cooper, A. R. (2013). Effects of dams on streams of the conterminous United States: characterizing patterns in habitat fragmentation nationally and fluvial fish response in the Midwest. Michigan State University.

Costigan, K. H., & Daniels, M. D. (2012). Damming the prairie: human alteration of Great Plains river regimes. Journal of Hydrology, 444, 90-99.Crook, D. A., Reich, P., Bond, N. R., McMaster, D., Koehn, J. D., & Lake, P. S. (2010). Using biological information to support proactive strategies for managing freshwater fish during drought. Marine and Freshwater Research, 61(3), 379-387.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In Advances in marine biology (Vol. 26, pp. 249-293). Academic Press.

Dyer, J. J., & Brewer, S. K. (2020). Seasonal movements and tributary-specific fidelity of blue

sucker Cycleptus elongatus in a Southern Plains riverscape. Journal of Fish Biology, 97(1), 279-292.

Farringer III, R. T., Echelle, A. A., & Lehtinen, S. F. (1979). Reproductive cycle of the red shiner, Notropis lutrensis, in central Texas and south central Oklahoma. Transactions of the American Fisheries Society, 108(3), 271-276.

Farrington, M. A., Dudley, R. K., Kennedy, J. L., Platania, S. P., & White, G. C. (2015). Colorado Pikeminnow and Razorback Sucker larval fish survey in the San Juan River during 2014. Final Report. US Bureau of Reclamation, Salt Lake City, UT, and the San Juan River Basin Recovery and Implementation Program, Albuquerque, NM.

Fausch, K. D., & Bestgen, K. R. (1997). Ecology of fishes indigenous to the central and southwestern Great Plains. In Ecology and conservation of Great Plains vertebrates (pp. 131-166). New York, NY: Springer New York.

Fischer, J. R., & Paukert, C. P. (2008). Historical and current environmental influences on an endemic Great Plains fish. The American Midland Naturalist, 159(2), 364-377.

Freeman, M. C., Bowen, Z. H., Bovee, K. D., & Irwin, E. R. (2001). Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. Ecological applications, 11(1), 179-190.

Freeman, M. C., Bestgen, K. R., Carlisle, D., Frimpong, E. A., Franssen, N. R., Gido, K. B., ... & Wenger, S. J. (2022). Toward improved understanding of streamflow effects on freshwater fishes. Fisheries, 47(7), 290-298.

Franssen, N. R., Gido, K. B., Guy, C. S., Tripe, J. A., Shrank, S. J., Strakosh, T. R., ... & Paukert, C. P. (2006). Effects of floods on fish assemblages in an intermittent prairie stream. Freshwater Biology, 51(11), 2072-2086.

Fuiman, L. A., & Werner, R. G. (Eds.). (2009). Fishery science: the unique contributions of early life stages. John Wiley & Sons.

Gale, W. F. (1983). Fecundity and spawning frequency of caged bluntnose minnows–fractional spawners. Transactions of the American Fisheries Society, 112(3), 398-402.

Gale, W. F. (1986). Indeterminate fecundity and spawning behavior of captive red shiners–fractional, crevice spawners. Transactions of the American Fisheries Society, 115(3), 429-437.

Grossman, G. D., Moyle, P. B., & Whitaker Jr, J. O. (1982). Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. The American Naturalist, 120(4), 423-454.

Grossman, G. D., Ratajczak Jr, R. E., Crawford, M., & Freeman, M. C. (1998). Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. Ecological Monographs, 68(3), 395-420.

Heimann, D. C., S. S. Licher, and G. K. Schalk. 2007. Effects of impoundments and land-cover changes on streamflows and selected fish habitat in the upper Osage River basin, Missouri and Kansas. U.S. Geological Survey, Scientific Investigations Report 2007-5175, Reston, Virginia.

Humphries, P., King, A. J., & Koehn, J. D. (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., King, A., McCasker, N., Kopf, R. K., Stoffels, R., Zampatti, B., & Price, A. (2020). Riverscape recruitment: a conceptual synthesis of drivers of fish recruitment in rivers. Canadian Journal of Fisheries and Aquatic Sciences, 77(2), 213-225.

Humphries, P., Richardson, A., Wilson, G., & Ellison, T. (2013). River regulation and recruitment in a protracted-spawning riverine fish. Ecological Applications, 23(1), 208-225.

Humphries, P., Wilson, G., Richardson, A. J., & Ellison, T. (2008). Impacts of managed flows on fish spawning and recruitment.

Jackson, D. A., Peres-Neto, P. R., & Olden, J. D. (2001). What controls who is where in freshwater fish communities the roles of biotic, abiotic, and spatial factors. Canadian journal of fisheries and aquatic sciences, 58(1), 157-170.

Jenkins, R. E., & Burkhead, N. M. (1993). Freshwater fishes of Virginia (p. 1079). American Fisheries Soc.

Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. Canadian special publication of fisheries and aquatic sciences, 106(1), 110-127.

Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. Canadian special publication of fisheries and aquatic sciences, 106(1), 110-127.

King, A. J., Humphries, P., & Lake, P. S. (2003). Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. Canadian Journal of Fisheries and Aquatic Sciences, 60(7), 773-786.

King, A. J., Tonkin, Z., & Mahoney, J. (2009). Environmental flow enhances native fish spawning and recruitment in the Murray River, Australia. River Research and Applications, 25(10), 1205-1218.

Krabbenhoft, T. J., Platania, S. P., & Turner, T. F. (2014). Interannual variation in reproductive phenology in a riverine fish assemblage: implications for predicting the effects of climate change and altered flow regimes. Freshwater Biology, 59(8), 1744-1754.

Liechti, P. (2007). Proposed Index of Biological Integrity and Sampling Strategy for Fish for the Lower Kansas River. Kansas Biological Survey, University of Kansas. Submitted to Kansas Water Office.

Mackay, N. J. (1973). Histological changes in the ovaries of the golden perch, Plectroplites ambiguus, associated with the reproductive cycle. Marine and Freshwater Research, 24(1), 95-102.

Makinster, A. S. (2006). Flathead catfish population dynamics in the Kansas River (Doctoral dissertation, Kansas State University).

Matthews, W. J. (2012). Patterns in freshwater fish ecology. Springer Science & Business Media.

Menge, B. A., & Sutherland, J. P. (1987). Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. The American Naturalist, 130(5), 737–761.

Mims, M. C., & Olden, J. D. (2012). Life history theory predicts fish assemblage response to hydrologic regimes. Ecology, 93(1), 35-45.

Morris, L. A. (1965). Age and growth of the river carpsucker, Carpiodes carpio, in the Missouri River. American Midland Naturalist, 423-429.

Olden, J. D., & Naiman, R. J. (2010). Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. Freshwater Biology, 55(1), 86-107.

Paukert, C., Schloesser, J., Fischer, J., Eitzmann, J., Pitts, K., & Thornbrugh, D. (2008). Effect of instream sand dredging on fish communities in the Kansas River USA: current and historical perspectives. Journal of Freshwater Ecology, 23(4), 623-633.

Pease, A. A., Justine Davis, J., Edwards, M. S., & Turner, T. F. (2006). Habitat and resource use by larval and juvenile fishes in an arid-land river (Rio Grande, New Mexico). Freshwater Biology, 51(3), 475-486.

Pelicice, F. M., Pompeu, P. S., & Agostinho, A. A. (2015). Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. Fish and Fisheries, 16(4), 697-715.

Perkin, J. S., Acre, M. R., Ellard, J. K., Rodger, A. W., Trungale, J. F., Winemiller, K. O., & Yancy, L. E. (2023). Flow–recruitment relationships for Shoal Chub and implications for managing environmental flows. North American Journal of Fisheries Management, 43(5), 1260-1275.

Perkin, J. S., & Gido, K. B. (2011). Stream fragmentation thresholds for a reproductive guild of Great Plains fishes. Fisheries, 36(8), 371-383.

Perkin, J. S., Gido, K. B., Cooper, A. R., Turner, T. F., Osborne, M. J., Johnson, E. R., & Mayes, K. B. (2015). Fragmentation and dewatering transform Great Plains stream fish communities. Ecological monographs, 85(1), 73-92.

Perkin, J. S., Starks, T. A., Pennock, C. A., Gido, K. B., Hopper, G. W., & Hedden, S. C. (2019). Extreme drought causes fish recruitment failure in a fragmented Great Plains riverscape. Ecohydrology, 12(6), e2120.

Poff, N. L., & Ward, J. V. (1989). Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences, 46(10), 1805–1818.

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., ... & Stromberg, J. C. (1997). The natural flow regime. BioScience, 47(11), 769–784.

Poff, N. L., Richter, B. D., Arthington, A. H., Bunn, S. E., Naiman, R. J., Kendy, E., ... & Warner, A. (2010). The ecological limits of hydrologic alteration (ELOHA): A new framework for developing regional environmental flow standards. Freshwater Biology, 55(1), 147–170.

Poff, N. L., & Zimmerman, J. K. (2010). Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshwater biology, 55(1), 194-205.

Quist, M. C., Hubert, W. A., & Rahel, F. J. (2005). Fish assemblage structure following impoundment of a Great Plains river. Western North American Naturalist, 53-63.

Resh, V. H., Brown, A. V., Covich, A. P., Gurtz, M. E., Li, H. W., Minshall, G. W., ... & Wissmar, R. C. (1988). The role of disturbance in stream ecology. Journal of the North American benthological society, 7(4), 433-455.

Rolls, R. J., Growns, I. O., Khan, T. A., Wilson, G. G., Ellison, T. L., Prior, A., & Waring, C. C. (2013). Fish recruitment in rivers with modified discharge depends on the interacting effects of flow and thermal regimes. Freshwater Biology, 58(9), 1804-1819.

Scheidegger, K. J., & Bain, M. B. (1995). Larval fish distribution and microhabitat use in free-flowing and regulated rivers. Copeia, 125-135.

Schiemer, F., Spindler, T., Wintersberger, H., Schneider, A., & Chovanec, A. (1991). Fish fry associations: important indicators for the ecological status of large rivers. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen, 24(4), 2497-2500.

Smith, C. L., & Powell, C. R. (1971). The summer fish communities of Brier creek, Marshall County, Oklahoma. American Museum Novitates, 2458(1), 30.

Stocks, J. R., Davis, S., Anderson, M. J., Asmus, M. W., Cheshire, K. J., van der Meulen, D. E., ... & Gilligan, D. M. (2021). Fish and flows: Abiotic drivers influence the recruitment response of a freshwater fish community throughout a regulated lotic system of the Murray-Darling Basin, Australia. Aquatic Conservation: Marine and Freshwater Ecosystems, 31(11), 3228-3247.

Stuart, I. G., & Jones, M. (2006). Large, regulated forest floodplain is an ideal recruitment zone for non-native common carp (Cyprinus carpio L.). Marine and Freshwater Research, 57(3), 333-347.

Tiemann, J. S. (2007). Reproductive traits in the Slim minnow (Pimephales tenellus) and the Bullhead minnow (Pimephales vigilax). Transactions of the Kansas Academy of Science, 110(3), 282-284.

Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: present state and future trends. Environmental conservation, 29(3), 308-330.

Tornabene, B. J., Smith, T. W., Tews, A. E., Beattie, R. P., Gardner, W. M., & Eby, L. A. (2020). Trends in river discharge and water temperature cue spawning movements of blue sucker, Cycleptus elongatus, in an impounded Great Plains river. Copeia, 108(1), 151-162.

Turner, T. F., Trexler, J. C., Miller, G. L., & Toyer, K. E. (1994). Temporal and spatial dynamics of larval and juvenile fish abundance in a temperate floodplain river. Copeia, 174-183.

Van Looy, K., Tonkin, J. D., Floury, M., Leigh, C., Soininen, J., Larsen, S., ... & Wolter, C. (2019). The three Rs of river ecosystem resilience: Resources, recruitment, and refugia. River Research and Applications, 35(2), 107-120.

Wang, Y. I., Naumann, U., Wright, S. T., & Warton, D. I. (2012). mvabund–an R package for

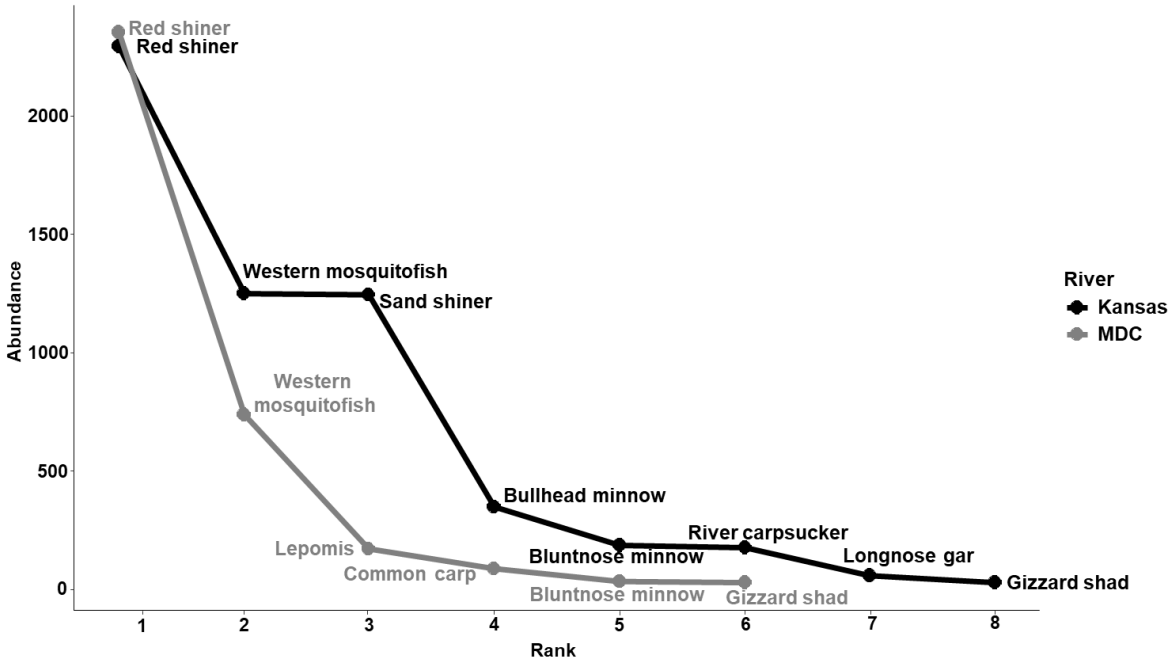
model-based analysis of multivariate abundance data. Methods in Ecology and Evolution, 3(3), 471-474.

Winemiller, K. O., & Rose, K. A. (1992). Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and aquatic sciences, 49(10), 2196-2218.

Zeug, S. C., & Winemiller, K. O. (2007). Ecological correlates of fish reproductive activity in floodplain rivers: a life-history-based approach. Canadian Journal of Fisheries and Aquatic Sciences, 64(10), 1291-1301.

Zeug, S. C., & Winemiller, K. O. (2008). Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. River Research and Applications, 24(1), 90-102.

Appendix



Appendix Figure A.1. Rank abundance plot for early life stage fishes in the Kansas and Marais des Cygnes rivers shows cumulative abundances for each species throughout the summers of 2022-2024. Only species that contributed $\geq$ 1% to total abundance in each river are shown.

Appendix Table A.1. Species length at hatch (TL) in mm used in length at age models with associated references.

Species	Length at hatch	Reference
Red shiner	5	Sakensa 1962
Sand shiner	4	Auer 1982
Bullhead minnow	5	Auer 1982
Bluntnose minnow	5	Auer 1982
Western mosquitofish	5	Meffe 1990
Gizzard shad	3	Bodola 1955
Common carp	3	Auer 1982
Longnose gar	9	Auer 1982
Lepomis	3	Auer 1982
River carpsucker	5	Yeager 1980

Appendix Table A.2. Linear equations for predicting age (A) from length (L), with estimates derived from otoliths with associated parameter t-statistic . The sample size represents the number of otoliths extracted from each species, r^2 values indicate the goodness of fit from linear models. *p-values for all species < .001.

Species	n	r^2	t-statistic	equation
Longnose gar	13	0.81	6.90	A = 0.14L + 10.54
Bluntnose minnow	22	0.82	9.68	A = 1.26L + 10.21
Bullhead minnow	13	0.75	5.69	A = 1.17L + 13.54
Sand shiner	25	0.79	9.40	A = 1.40L + 8.69
Red shiner	20	0.79	8.28	A = 0.99L + 16.97
River carpsucker	21	0.77	8.09	A = 1.75L + 0.38
Common carp	14	0.86	8.49	A = 1.13L + 2.05
Western mosquitofish	15	0.84	7.31	A = 3.18L + 2.49
Gizzard shad	14	0.84	7.91	A = 1.38L - 1.56
Sunfishes	14	0.76	6.16	A = 0.93L + 16.47