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SPECIAL SECTION

Avoiding a Macabre Future for *Macrhybopsis*—Improving Management and Conservation of Chubs

Flow–recruitment relationships for Shoal Chub and implications for managing environmental flows

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Abstract

Objective: Regulation of river flow regimes by dams and diversions impacts aquatic biota and ecosystems globally. However, our understanding of the ecological consequences of flow alteration and ecological benefits of flow restoration lags behind our ability to manipulate flows, and there is a need for broader development of flow–ecology relationships. Approaches for establishing flow–ecology relationships have recently shifted away from state-based methods that analyze snapshots of ecological conditions and towards rate-based methods focused on mechanisms that link hydrology with dynamics of important ecological components and processes.

Methods: We used a rate-based approach to validate environmental flow standards developed for the lower Brazos River, Texas, by analyzing the relationship between flow regime components and recruitment strength of imperiled Shoal Chub *Macrhybopsis hyostoma*, a fluvial specialist and pelagic-broadcast-spawning fish. We collected 254 age-0 Shoal Chub (9–40 mm total length), extracted their otoliths to estimate age in days, and used a generalized additive model to regress the number of captured recruits that hatched on a calendar date against flow regime metrics, such as pulse magnitude, flow rate of change, and pulse timing in relation to environmental flow standards proposed by a science advisory committee (Brazos Basin and Bay Area Expert Science Team).

Result: The model revealed that flow magnitude, rate of change, and timing were all significant predictors that collectively explained 60% of variation in the recruitment strength index. Hindcasting for 1919–2020 showed a general reduction in recruitment strength following commencement of flow regulation in the lower Brazos River and revealed that high recruitment correlated with years in which most or all proposed flow tiers were attained, whereas low recruitment correlated with years when less than half of the targeted tiers were attained.

Conclusion: Our work represents an effective validation method for environmental flow recommendations and reveals specific flow regimes that benefit an imperiled fish species.

KEYWORDS

age and growth, early life history, ecology, in-stream flow, management, reproduction, riparian and stream, threatened and endangered species

INTRODUCTION

Flow regime alteration affects nearly all major river systems on Earth (Lehner et al. 2011), and although dams and water diversions provide benefits to humans, they come at a cost to biodiversity and ecosystem services (Anderson et al. 2019). Consequently, the science of environmental flows has emerged as a framework for managing regulated flows to sustain freshwater and estuarine ecosystems while supporting human needs for freshwater and energy (Arthington et al. 2018a). Historically, environmental flow science focused on states of ecosystems derived from single snapshots of ecological conditions that were not necessarily repeated through time (Wheeler et al. 2018). Recent advances are moving the field towards a more predictive science capable of developing trajectories for a future beset by climate change, an accelerated water cycle, and amplified water demands (Arthington et al. 2018b; Poff 2018). Critical to improving understanding of flow–ecology relationships is the development of rate-based approaches that link ecological processes to streamflow through mechanistic pathways, especially with regards to population dynamics of aquatic and riparian species (Wheeler et al. 2018). Rate-based research, therefore, has great potential to reveal how flow regime alteration will affect biota and ecosystems (Palmer and Ruhi 2019).

In recent decades, approaches for the management and protection of rivers have relied heavily on the natural flow regime paradigm (NFP) as proposed by Poff et al. (1997). The NFP addresses the dynamic nature of fluvial systems by quantifying five characteristics of hydrology, including magnitude (i.e., how much water is present), frequency (i.e., how often flows of a given magnitude occur), duration (i.e., how long flows of a given magnitude persist), timing (i.e., when flows of a given magnitude occur), and rate of change (i.e., how quickly flows transition among magnitudes) (Poff et al. 1997). These flow regime components can be used to assess deviations from natural flow regimes caused by river modifications (e.g., reservoir construction) using a suite of metrics collectively known as indicators of hydrologic alteration (Richter et al. 1996; Mathews and Richter 2007). The NFP posits that the key to the conservation and restoration of river biota and ecosystem services is maintenance of flow magnitude, frequency, duration, timing, and rate of change sufficient to capture essential functions of the natural flow regime (Bunn and Arthington 2002). Despite widespread recognition of the NFP, many efforts to estimate environmental flows have focused heavily on flow magnitude without formal integration of other flow regime characteristics (Poff and Zimmerman 2010; Nguyen et al. 2021). In some regulated rivers, existing water infrastructure, water withdrawals, and climate change prevent the complete restoration of natural flow regimes (Poff 2018), yet even partial restoration of some aspects of the NFP in these rivers provides ecological benefits (Propst and Gido 2004; Kiernan et al. 2012).

Impact statement

Environmental flows science guides reservoir releases to promote river water security for humans and nature, but natural water needs are challenging to estimate. We derive flow–recruitment relationships for Shoal Chub and validate environmental flow standards in a regulated river.

Recruitment dynamics are a highly relevant and practical rate-based indicator of flow–ecology relationships. Recruitment, the production and subsequent survival of new individuals in a population, has been linked to flow patterns in freshwater fishes with diverse life history strategies (e.g., Rodger et al. 2016; Buckmeier et al. 2017). Age estimation of fish from samples collected over time intervals sufficient to encompass variation in river discharge and associated environmental conditions is necessary to determine flow–ecology relationships based on recruitment dynamics. Estimation of age based on growth rings in otoliths or other hard structures is effective for temperate fishes (Maceina et al. 2007; Quist and Isermann 2017). Otoliths are calcium carbonate structures that occur in three pairs (asteriscus, lapillus, sagittal) in the heads of most fishes (excluding cartilaginous and jawless fishes) and expand as fish grow by accumulating new material around the edges of a core through a process known as accretion (Campana 1999). Accretion results in daily growth increments that can be used to age fishes at daily (visible only in young or short-lived fish) or annual time scales (visible as bands where increments are densely packed during intervals of slow growth). Daily growth increments in otoliths were analyzed to estimate recruitment strength of Great Plains cyprinids, including Shoal Chub *Macrhybopsis hyostoma* (Rodger et al. 2016; Starks et al. 2016), Peppered Chub *M. tetranema* (Durham and Wilde 2006), and Flathead Chub *Platygobio gracilis* (Haworth and Bestgen 2016, 2017). Recruitment strength of Shoal Chub in the Brazos River, Texas, was shown to be higher during flow pulses (Rodger et al. 2016), whereas recruitment strength of Peppered Chub and Flathead Chub in the Canadian River, Texas (Durham and Wilde 2006), and Flathead Chub in Fountain Creek, Colorado (Haworth and Bestgen 2017), tended to be highest immediately following flow pulses. Among these example fishes, Shoal Chub is widely distributed throughout the Mississippi River basin and could provide an effective indicator species for flow–ecology relationships (Starrett 1951; Rodger et al. 2016).

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As these examples demonstrate, analysis of recruitment dynamics based on age estimates is a promising avenue for developing rate-based flow–ecology relationships to inform flow management in regulated rivers.

In 2001, the Texas Legislature established the Texas Instream Flow Program with Senate Bill 2 (TWC 2019a) out of recognition of the need to ensure sustainable water security for nature and people (Wurbs 2017). In 2007, Senate Bill 3 (TWC 2019b) mandated a stakeholder-driven, science-based process for establishing environmental flow standards for the state's rivers and bays for use by the Texas Commission on Environmental Quality (TCEQ) in evaluating applications for new water rights. In response to Senate Bill 3, the Brazos Basin and Bay Area Stakeholder Committee and the Brazos Basin and Bay Expert Science Team (BBEST) were formed to develop flow recommendations for locations throughout the basin, and these recommendations were then submitted to the TCEQ for review (Brazos BBEST 2012). Senate Bill 3 mandated periodic review of environmental flow standards with potential for revision. Consequently, efforts to validate or otherwise assess the ecological relevance of flow standards adopted by the TCEQ are necessary. To evaluate flow standards for the lower Brazos River, Rodger et al. (2016) analyzed the relationship between Shoal Chub recruitment strength and discharge magnitude on the day of hatching. Findings were preliminary and the authors emphasized that additional research over a longer time period and broader range of flows was "urgently needed" to evaluate the ecological relevance of the adopted environmental flow standards for the Brazos River.

The goal of this study was to quantify the relationship between streamflow in the lower Brazos River and recruitment strength of Shoal Chub. To accomplish this goal, we established three objectives. The first objective was to collect age-0 Shoal Chub from the Brazos River and quantify an estimated recruitment strength index using fish ages assigned based on otolith daily growth increments. The second objective was to relate multiple streamflow regime characteristics to temporal variability in recruitment strength. The third and final objective was to use the modeled relationships developed from efforts addressing the second objective to hindcast recruitment strength over a longer time period and assess the relationship between interannual variation in streamflow in the context of adopted TCEQ standards and projected Shoal Chub recruitment strength.

METHODS

Study area

The Brazos River basin drains an area of 115,566 km^2 across portions of New Mexico and Texas as it flows to the Gulf of Mexico. The river flows through the Great Plains, Central Lowland, and Coastal Plain physiographic provinces, where the mean annual precipitation is 81 cm, mean annual air temperature is 19°C, and mean annual discharge is 249 m^3/s (Dahm et al. 2005). Land cover and land use in the upper basin are dominated by rangeland with limited forest, and sites in the lower basin are dominated by cultivated crops, pasture, and woodlands, with some wetlands (Becker et al. 2014). There are 132 large dams (>3 m in height; Dahm et al. 2005) in the basin, including main-stem flood-control reservoirs (upstream to downstream) Possum Kingdom (completed in 1940), Granbury (completed in 1969), and Whitney (completed in 1951; Figure 1). These reservoirs have contributed to altered and highly regulated streamflow in the lower Brazos River (Vogl and Lopes 2009; Lehner et al. 2011; Dawson et al. 2015). The largest water-right holder in the basin is the Brazos River Authority, and all permits to divert water are subject to regulation by the TCEQ (Brazos BBEST 2012; Roach 2013). We collected fish from the Farm to Market 485 crossing west of Hearne, Texas (−96.695, 30.865), and obtained flow regime data from the U.S. Geological Survey gauge (ID = 08108700) located at the State Highway 21 crossing near Bryan, Texas (−96.545, 30.629). We also obtained data collected by Rodger et al. (2016) from the State Highway 105 road crossing (−96.155, 30.362) on the Brazos River just upstream from its confluence with the Navasota River (Figure 1).

Fish collections

We collected Shoal Chub from the Farm to Market 485 crossing using a larval seine (3.6 m long, 1.8 m deep, 0.8-mm mesh) pulled over fine gravel substrate in a downstream direction. Seine hauls were typically 5–10 m in length depending on available habitat, and we typically conducted 10–12 seine hauls. Seining effort was standardized as 1 h on each survey date, passing over the same areas during repeat visits. Surveys were conducted on August 30, September 2, September 8, September 21, September 26, and October 1 of 2019, and on June 19, August 18, August 23, and August 30 of 2020 (Table 1). These survey dates were designed to encompass the season over which Shoal Chub fractionally spawns multiple cohorts (May–August; Williams 2011) and periods when flows were low enough to access the river. During each survey, all Shoal Chub ≤40 mm total length (TL) were euthanized by submersion in a lethal dose of MS-222 (tricaine methanesulfonate; 80 mg/L) and then stored in 95% ethanol and labeled according to date. The threshold of 40 mm TL was selected because this is likely the upper limit of age-0 individuals that can be aged at the daily scale (Starks et al. 2016). The identity of Shoal Chub

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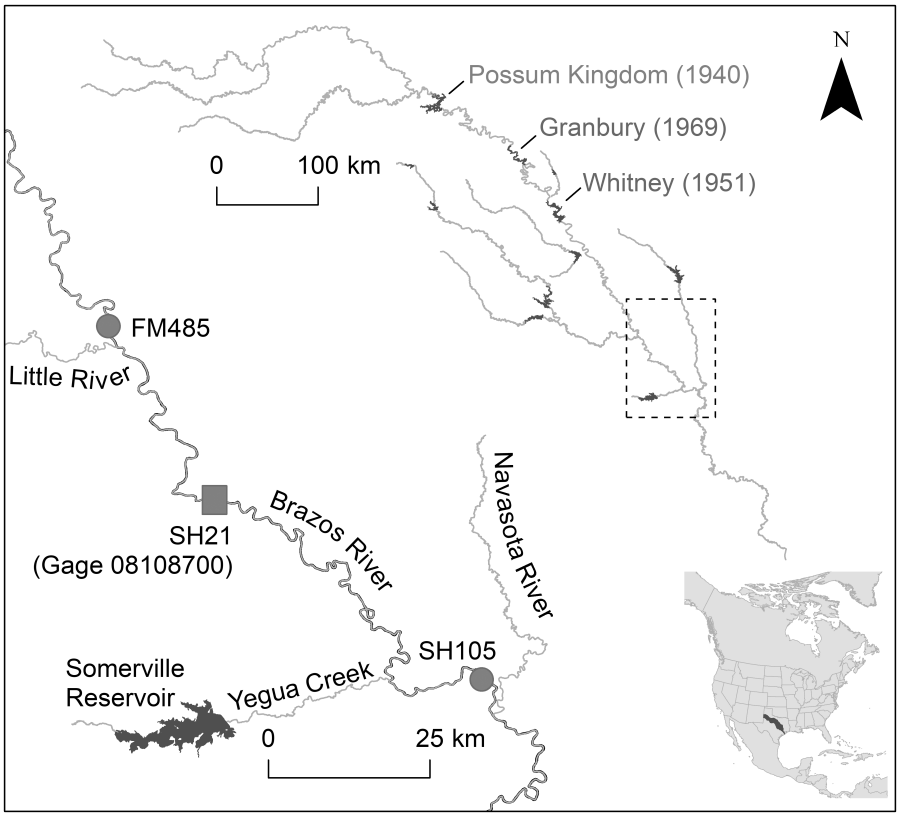

FIGURE 1 Study area showing the locations of fish collection sites (circles) at the Farm to Market (FM) 485 crossing (this study) and State Highway (SH) 105 crossing (Rodger et al. 2016) and the U.S. Geological Survey streamflow gauge at the SH 21 crossing (square). Fish and flow data were collected from the lower Brazos River downstream of multiple main-stem reservoirs, including Possum Kingdom Reservoir, Granbury Reservoir, and Whitney Reservoir. The Brazos River flows from New Mexico across Texas and eventually into the Gulf of Mexico as shown in the lower right inset.

TABLE 1 Number of Shoal Chub collected, range of total lengths, and range of ages during visits to the Farm to Market Road 485 crossing on the lower Brazos River during 2019 and 2020.

Date	Number collected	Length range (mm)	Age range (day)
Aug 30, 2019	1	28	42
Sep 2, 2019	1	27	40
Sep 8, 2019	1	21	28
Sep 21, 2019	7	32–39	49–63
Sep 26, 2019	27	30–39	45–63
Oct 1, 2019	1	33	51
Jun 19, 2020	36	13–36	12–57
Aug 18, 2020	68	21–39	28–63
Aug 23, 2020	83	24–40	34–65
Aug 30, 2020	29	28–39	42–63

retained for analysis was confirmed using distinct characteristics, including canonical snout, small eyes relative to snout length, and presence of maxillary barbels (Hubbs et al. 2008).

Laboratory procedures

In the laboratory, we extracted, mounted, and aged otoliths. We first assigned each individual a unique accession number linked to the date of capture and recorded total length (mm). We then removed lapillus otoliths following the methods of Starks et al. (2016). Validation methods in which fish of known age were used to assess the reliability of otoliths for aging exist for lapillus otoliths (Durham and Wilde 2008) and sagittal otoliths (Haworth and Bestgen 2016), confirming that daily growth increments of cyprinid otoliths represent a reliable method for aging young fish and ultimately estimating recruitment strength. We elected to use lapillus otoliths based on previous multispecies assessment of *Macrhybopsis* spp. (Starks et al. 2016) and because lapillus otoliths were validated for fishes in the Brazos River (Durham and Wilde 2008). Once otoliths were mounted, we sequentially sanded with 6-, 3-, and 1-μm-grit sandpaper until the macular hump was sanded down completely and an evenly polished surface was created. If the sanding and polishing process proceeded without incident, then the second otolith from the same fish was not aged. We added a drop of immersion oil to the

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polished surface and placed the slide underneath a compound microscope with 20× magnification. We counted rings beginning at the edge of the nucleus and moved outward to the edge of the otolith along the longest plane of the polished surface (Figure S1 in the Supplement provided in the online version of this article). Each otolith was aged by two readers independently using a double-blind process in which the reader did not know the size of the fish or the age assigned by the other reader. Once two readers had aged each otolith, we compared ages to assess consensus using widely implemented methods for estimating daily age among minnows. For otoliths with assigned ages that were not identical, we used the mean value of the two ages if the difference between the ages was <10% of the maximum age (Durham and Wilde 2006, 2009; Rodger et al. 2016) or used a third independent reading to determine age if consensus could be reached (Starks et al. 2016). Otoliths for which we could not reach a consensus age were removed from the analysis.

Age analysis

We used direct aging and regression-based methods to estimate age of all Shoal Chub specimens collected from the lower Brazos River as part of this study and the study by Rodger et al. (2016). We processed a subset of randomly selected individuals across a stratified range of sizes (28–40 mm TL) using the laboratory process described above and then used linear regression analysis to estimate the age of the remaining specimens. We built the linear regression model using the measured total lengths and consensus ages for 40 fish collected in this study plus total length and consensus ages for 68 specimens analyzed by Rodger et al. (2016). It should be noted that Rodger et al. (2016) used drift nets to collect fish from a different location (see Figure 1) and pulled asteriscus, rather than lapillus, otoliths. Consequently, fish aged by Rodger et al. (2016) tended to be smaller than fish collected during 2019–2020. We used an analysis of covariance to test for differences in the intercept and slope of linear regression models fit to each data set using age (day) as the dependent variable, total length (mm) as the independent variable, and study identity (this study versus Rodger et al. 2016) as a categorical covariate. Based on the results of this analysis (see below), we combined individuals from this study and Rodger et al. (2016) to develop a single regression model useful for predicting age based on total length of age-0 (i.e., 8–40 mm TL) Shoal Chub from the lower Brazos River. We applied this regression equation to estimate the ages of remaining fish collected as a part of this study and plotted length-frequency and age-frequency histograms for all fish collected during 2019 and 2020. Finally, we calculated recruitment strength or cohort size as the total number of fish that were estimated to be hatched on the same calendar date. We emphasize that our index of recruitment strength is meant to be interpreted as an index rather than the absolute magnitude of total recruitment within the population. While some previous studies have elected to add a single day to the end of the age estimate when assigning a calendar day to each fish (e.g., Rodger et al. 2016), we elected not to do this for simplicity and because doing so produced similar results.

Streamflow analysis

Our primary goal was to assess the extent to which Shoal Chub might be used as an indicator species for flow–ecology relationships. We addressed this goal by using streamflow data from the lower Brazos River collected by the U.S. Geological Survey gauge at the State Highway 21 crossing near Bryan, Texas (Figure 1). Streamflow from this location represents historical records from two slightly differing locations. The initial gauge location was the Brazos River near Bryan, Texas (ID 08109000), and this gauge was in service from August 1, 1899, until September 29, 1993, when the gauge was moved to the State Highway 21 crossing (ID 08108700), which has been in service since July 15, 1993. We combined these data sets because the Brazos BBEST (2012) had previously combined these data sets owing to the short distance and negligible difference in drainage area between these locations. We downloaded daily mean streamflow data for the historical periods starting January 1, 1919 (following a large gap in data), and extending until December 31, 2020. We obtained threshold values for relevant flow targets recommended by the Brazos BBEST (2012). These summer season (i.e., July–October) streamflow targets included thresholds for base flow during an average (non-drought) year (base flow; 26 m^3/s), four pulses per season (4P/S; 58 m^3/s), three pulses per season (3P/S; 85 m^3/s), and two pulses per season (2P/S; 142 m^3/s). Additional flow thresholds developed by the Brazos BBEST (2012) included high flow pulses occurring once every 2 years (1,894 m^3/s), once per year (1,399 m^3/s), and once per season (343 m^3/s); however, these thresholds were not used for analyses in this study because of the short-term nature of our fish collections (i.e., over two summers). We calculated six daily flow regime characteristics using these thresholds, including mean streamflow for each calendar day, the rate of change (i.e., m^3/s/day) in discharge between each day and the previous day, and the number of days since flows declined past seasonal pulse thresholds (Table 2). We used the time since the day streamflow declined below threshold values rather than the day

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TABLE 2 Daily streamflow regime characteristics, the associated natural flow regime paradigm (NFP) category, and definitions used to link streamflow with Shoal Chub recruitment strength. Thresholds used in the timing/frequency category are based on the Brazos Basin and Bay Area Expert Science Team (Brazos BBEST 2012). Abbreviations are as follows: 4P/S = four pulses per season, 3P/S = three pulses per season, and 2P/S = two pulses per season.

Characteristic	NFP category	Definition
Magnitude	Magnitude	Mean streamflow magnitude (m^3/s) across all measurements made on the same calendar day.
Rate of change	Rate of change	Difference in mean discharge magnitude for each calendar day and the previous day.
Time since base flow	Timing/frequency	Number of days since mean daily discharge magnitude decreased below the Brazos BBEST (2012) threshold for base flow (i.e., 26 m^3/s).
Time since 4P/S	Timing/frequency	Number of days since mean daily discharge magnitude decreased below the Brazos BBEST (2012) threshold for four pulses per summer season (i.e., 58 m^3/s).
Time since 3P/S	Timing/frequency	Number of days since mean daily discharge magnitude decreased below the Brazos BBEST (2012) threshold for three pulses per summer season (i.e., 85 m^3/s).
Time since 2P/S	Timing/frequency	Number of days since mean daily discharge magnitude decreased below the Brazos BBEST (2012) threshold for two pulses per summer season (i.e., 142 m^3/s).

streamflow increased above threshold values because of previous research demonstrating fish spawning activity following flow pulses (Durham and Wilde 2006, 2009; Haworth and Bestgen 2017).

Streamflow–recruitment analysis

We analyzed Shoal Chub flow–recruitment relationships using the number of recruits estimated to have hatched on a calendar day and streamflow regime statistics for that same day. We defined the recruitment strength index as the number of recruits from a given calendar day, otherwise known as the number of fish that hatched on a given day and survived until the day of collection. This requires the assumption that our sampling was random and that the size distribution of fish collected was representative of the larger population. This assumption is likely satisfied because we employed a small-mesh seine that is known to capture age-0 individuals at a rate consistent with fish collected via drift net (Haworth and Bestgen 2017). Furthermore, this index does not capture all spawning events or individuals spawned and instead represents a proxy for the broader spawning and recruitment dynamics within the population (Quist 2007). The number of recruits was then used as the response variable in a multiple regression model with streamflow regime variables as independent variables. We elected to use a generalized additive modeling approach because of the nonlinear relationships among the dependent variable and multiple independent variables (for this and subsequent analyses). In addition, a Poisson error distribution was more appropriate than a Gaussian error distribution given that the response variable represents count data that are near to and bounded by zero. We fit a generalized additive model (GAM) using the "gam" function from the "mgcv" package in R (Wood 2017). This function allows for automatic term selection by conducting a chi-square test of all smoothing parameters ($\alpha = 0.05$) and reporting parameter-level test statistics. We also used the "gam.check" function to ensure that the selected smoothing parameters were not overly smoothed, "get_gam_predictions" function from the "tidymv" package to create partial-dependence plots (Coretta 2021), and the "predict.gam" function from the "mgcv" package to develop daily cohort predictions using streamflow data from 1919–2020. We limited these predictions to flow observations that were within our model domain (i.e., rare and extreme daily flow values not observed during 2019–2020 were excluded) and then summed the daily number of recruits for the entirety of May–August, which collectively represent the core reproductive season for Shoal Chub (Williams 2011). This produced an estimate for recruitment strength (i.e., the total number of recruits) for each summer season for an entire century.

We used the hindcasting results to assess the historical relationship between Shoal Chub recruitment strength and interannual variation in streamflow. We fit a GAM to the relationship between estimated number of annual summer recruits (dependent variable) and time (independent variable with a smoothing function) to test for a significant change in the predicted number of recruits through time. This analysis was used to gauge whether, and to what extent, the central

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tendency of recruitment projections changed over time. We did not expect time alone to be a strong predictor of recruitment strength index, though we expected recruitment to change through time as the flow regime changed (Rodger et al. 2016). Next, we developed a scoring index to quantify the proportion of annual summer flow targets suggested by the Brazos BBEST (2012) that were achieved during each summer. This summer flow target index ranged from 0 to 10, with 0 indicating that no suggested targets were achieved and 10 indicating that all suggested summer targets were achieved. The selected scale (i.e., from 0 to 10) was based on the recommendation that four small pulses (>58 m^3/s), three slightly larger pulses (>85 m^3/s), two slightly larger pulses (>142 m^3/s), and one larger pulse (>343 m^3/s) be achieved each summer (i.e., 10 pulses total). When calculating this index, flow pulses that surpassed the threshold for smaller flow thresholds were counted as achieving the lower threshold value, meaning that a large magnitude pulse might count as achieving multiple thresholds. For example, a summer flow regime characterized by four independent pulses of ~100 m^3/s followed by another pulse of 150 m^3/s would receive an index score of 6. This score would be assigned because the minimum of four recommended pulses >58 m^3/s was achieved (score = 4), a single pulse >85 m^3/s was achieved (score = 4 + 1), and a single pulse >142 m^3/s was achieved (score = 4 + 1 + 1 = 6). We then regressed the estimated number of summer recruits for each year after completion of the final main-stem reservoir (Granbury Reservoir) on the Brazos River (i.e., 1970–2020) with the flow target index for the same year to assess the relationship between flow target achievement and recruitment strength. We quantified this relationship using a GAM to test for significant changes in the number of recruits across the gradient of flow targets achieved. For this GAM, we used a quasi-Poisson error distribution to account for the zero-bounded count data (i.e., Poisson necessary) and overdispersion in the data (i.e., quasi-distribution necessary) caused by large variation in recruitment strength index.

RESULTS

Age analysis

A total of 254 age-0 Shoal Chub was collected from the lower Brazos River between 2019 ($n = 38$) and 2020 ($n = 216$). We collected Shoal Chub during six sampling trips between August and October of 2019 and four sampling trips between June and August of 2020 (Table 1). Once aged, agreement between the two readers of each otolith regarding the assigned age of fish was high for both asteriscus and lapillus otoliths combined ($r = 0.99$), and inclusion of both data sets lengthened the gradient of fish sizes in the analysis (9–64 mm TL). Only a single fish (TL = 39 mm) from 2019–2020 was removed because of disagreement among readers; otherwise, consensus was reached for all specimens. The analysis of covariance test showed no difference in the relationship between age and total length when age was estimated with asteriscus (Rodger et al. 2016) versus lapillus (this study) otoliths ($F_{1, 105} < 0.01$, $p = 0.97$). The linear regression model based on combined data showed that age significantly increased as total length increased (slope = 1.74, intercept = −11.15, $R^2 = 0.967$, $p < 0.001$). Based on this regression model and the lengths of 254 Shoal Chub ≤40 mm TL (Figure 2A), the mean age of fish collected during 2019–2020 was 46 day, mode age was 50 days, range was 11–59 days, and most fish were 30–59 days old (Figure 2B). Temporal variation in recruitment strength showed peaks in recruitment that occurred in the days following flow pulses during 2019 and 2020 (Figure 3).

Streamflow–age analysis

Streamflow and recruitment strength revealed a strong flow–ecology relationship. Tests for collinearity among flow regime attributes revealed high correlation between days since flows declined below the threshold for 4P/S

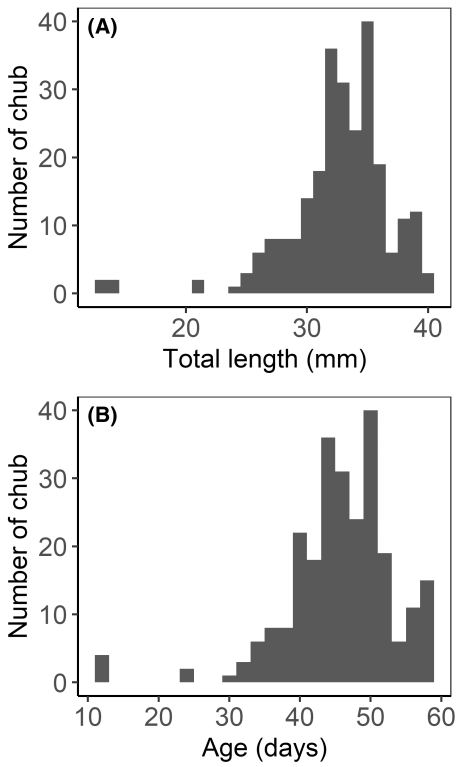

FIGURE 2 Histograms illustrating (A) length frequency and (B) age frequency for 254 Shoal Chub collected from the lower Brazos River during 2019 and 2020.

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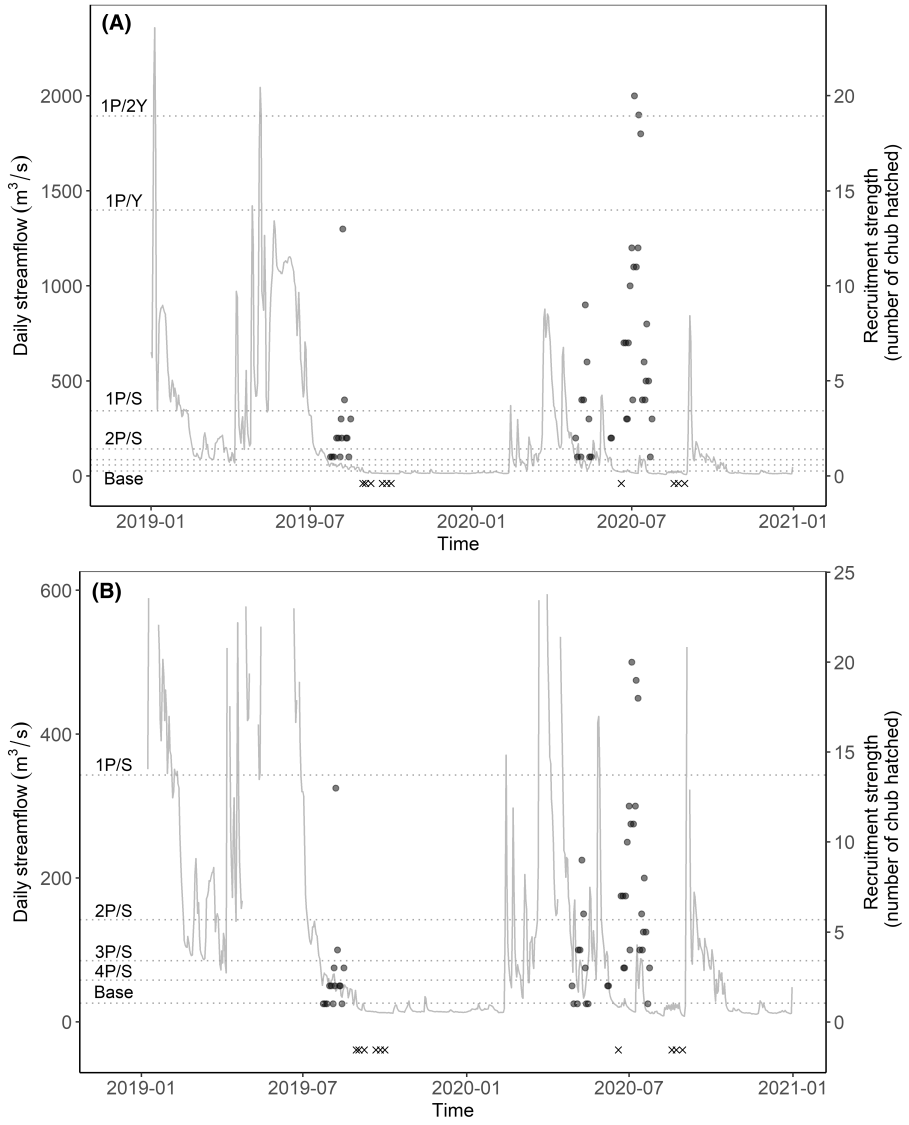

FIGURE 3 Panel (A) shows a hydrograph for the Brazos River at State Highway 21 near Bryan, Texas (U.S. Geological Survey gauge 08108700; gray line, left axis) illustrating flow tiers (dashed horizontal gray lines) developed by the Brazos Basin and Bays Expert Science Team (Brazos BBEST 2012), including one overbank pulse per 2 years (1P/2Y; 1,894 m^3/s), one overbank pulse per year (1P/Y; 1,399 m^3/s), one high flow pulse per season (1P/S; 343 m^3/s), two high flow pulses per season (2P/S; 142 m^3/s), three high flow pulses per season (not labeled; 85 m^3/s), four high flow pulses per season (not labeled; 58 m^3/s), and base flow (Base; 26 m^3/s). Dotted lines for seasonal thresholds (1P/S, 2P/S, 3P/S, and 4P/S) are shown across the entire timeline but apply only to Brazos BBEST recommendations for July–October (i.e., summer season). The recruitment strength of Shoal Chub (gray points; right axis) is shown on the same timeline but on a different axis (i.e., note that left and right *y*-axes scales differ). The dates of sampling are shown as x-shaped symbols at the base of the graph. Panel (B) shows a zoomed in view of the data showing the relationship between recruitment strength index and small pulses that followed larger pulses.

and 3P/S as well as time since base flow and 4P/S, but all other pairwise comparisons had correlation coefficients with absolute values <0.70 (Table 3). Consequently, the parameter for 4P/S threshold was not included in modeling to avoid overfitting. The GAM fit to the relationship between Shoal Chub recruits and multiple flow regime parameters explained most of the variation in recruitment strength (adjusted $R^2 = 0.60$, deviance explained = 70.2%). Smoothing parameters were significant for rate of change, days since 2P/S, and days since base flow, whereas the smoothing parameter for discharge on the day of collection was nearly significant, and days since flow declined below the 3P/S threshold was not significant (Table 4). Partial dependence plots provided insight into the relationships between recruitment strength and individual flow parameters (Figure 4). The number of recruits generally declined as discharge on the day of hatch increased above base flow (Figure 4A). Recruitment strength peaked 8, 30, and 45 days following flows declining past the threshold for 2P/S (Figure 4B). Recruitment strength

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TABLE 3 Pairwise correlation coefficients for streamflow regime metrics included in the generalized additive model used to predict the number of Shoal Chub hatched and surviving (i.e., recruited) during 2019 and 2020. Parameters were removed when the absolute value of the correlation coefficient was >0.70 to avoid multicollinearity, which included only time since four pulses per season (4P/S).

Streamflow metrics	Time since base	Time since 4P/S	Time since 3P/S	Time since 2P/S	Magnitude	Rate of change
Time since base	1	0.79	0.62	0.22	−0.52	0.00
Time since 4P/S		1	0.82	0.25	−0.62	0.00
Time since 3P/S			1	0.36	−0.61	0.13
Time since 2P/S				1	−0.49	0.08
Magnitude					1	0.14
Rate of change						1

TABLE 4 Results of parameter selection for the generalized additive model fit to the relationship between flow and number of Shoal Chub hatched and surviving (i.e., recruitment) in the lower Brazos River during 2019 and 2020. Flow parameters include discharge measured on the day of hatch (m^3/s), rate of change in flow between the previous day and the day of hatch ($m^3/s/d$), and time in days since flow fell below the threshold for three pulses per season (3P/S; 85 m^3/s), two pulses per season (2P/S; 142 m^3/s), and base flow (i.e., 26 m^3/s) for an average summer season. The effective and reference degrees of freedom, chi-square test statistic, and *p*-value are given for each smoothing parameter in the model.

Parameter	df	Chi-square	*p*-value
Discharge (m^3/s)	1, 9	2.34	0.06
Time since 3P/S (d)	1, 9	0.00	0.53
Time since 2P/S (d)	7, 9	28.02	<0.001
Time since base (d)	2, 9	10.74	<0.001
Rate of change ($m^3/s/d$)	7, 9	38.91	<0.001

increased steadily during the 9 days after streamflow dropped below the threshold for base flow (Figure 4C). The highest level of recruitment strength occurred when rate of change increased >40 m^3/s from the day prior to hatch (Figure 4D).

Recruitment projection analysis

Hindcasting recruitment strength estimates revealed long-term fluctuations during 1919–2020. The GAM used to summarize long-term patterns in predicted recruitment had a significant smoothing parameter for time ($F_{1,1}=8.47$, $p=0.005$), explained a small amount of variation (adjusted $R^2=0.07$; deviance explained = 8.35%), and indicated that the central tendency of recruitment strength index changed over time. Following construction of the final main-stem reservoir on the Brazos River (i.e., Granbury Reservoir in 1969), recruitment strength was highly variable, revealing an initial decline in recruitment during 1970–1980, an increase during 1981–2000, and then another decline during 2001–2020 (Figure 5A). Flow target index scores ranged from 1 to 10 during the postimpoundment period (1970–2020). Example summer season hydrographs for index scores 1, 4, 7, and 10 illustrated the relationship between observed flows and flow pulse targets (Figure 6). Regression of the relationship between postimpoundment recruitment strength (1970–2020) and the flow pulse target index revealed a decline in recruitment strength as the number of seasonal flow pulse targets that were achieved declined below 6 (Figure 5B). The GAM fit to summarize the relationship between recruitment strength and the seasonal flow pulse target index had a significant smoothing function ($F_{3,4}=10.05$, $p<0.001$), which explained most of the variation in the data (adjusted $R^2=0.58$, deviance explained = 58.3%) and showed a nearly linear decline in recruitment strength as the number of seasonal flow pulse targets declined from 6 to 1.

DISCUSSION

Our study provides empirical evidence for a link between streamflow and recruitment of Shoal Chub in the lower Brazos River. The GAM we fit to the nonlinear relationship between streamflow and Shoal Chub recruitment strength explained 60% of the variation in the number of recruits and revealed that most hatched within a 50-day window following seasonal pulses >142 m^3/s (i.e., 2 P/S) and 9 days after flows declined to base flow levels. We also found that the largest number of recruits were spawned during positive rates of change as flows were rising again at a rate of >40 m^3/s per day. These results collectively highlight how pulsed increases and decreases in flow are beneficial for Shoal Chub recruitment and presumably population growth (Rodger et al. 2016). When we projected these relationships across Shoal Chub spawning season (May–August; Williams 2011) during the century between 1919 and 2020, we found that projected recruitment strength was temporally dynamic, as might be expected for a fish species classified as an opportunistic life history strategist (Winemiller and

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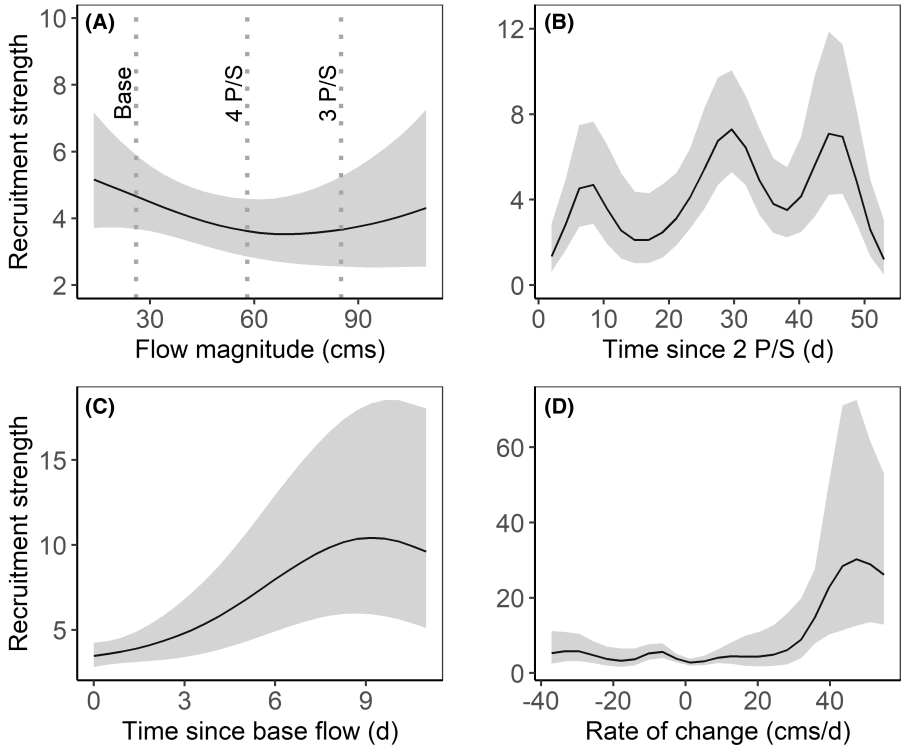

FIGURE 4 Partial dependence plots from a generalized additive model fit to the relationship between Shoal Chub recruitment strength (number of fish hatched) and (A) flow magnitude on the day of hatch, (B) time since magnitude dropped below the Brazos Basin and Bays Expert Science Team (Brazos BBEST 2012) threshold for two pulses per season (2P/S), (C) time since magnitude declined below the Brazos BBEST threshold for base flow, and (D) the rate of change in discharge magnitude from the day before the estimated hatch date and the hatch date (where negative values denote declining flow and positive values denote increasing flow) for fish collected during 2019–2020. Solid black lines represent partial dependence (i.e., all other variables held at their mean) of Shoal Chub recruitment strength on each variable, and gray shaded areas represent 95% confidence intervals. Reference points for Brazos BBEST thresholds for base flow, four pulses per season (4P/S), and three pulses per season (3P/S) are given in panel (A).

Rose 1992). The weakest recruitment years estimated from the hindcasted model all occurred after completion of a series of main-stem reservoirs that regulated flows in the lower Brazos River (Vogl and Lopes 2009). When we compared the recruitment strength index to an index for the number of summer flow pulses recommended by the Brazos BBEST (2012) that were achieved, we found that recruitment was highest when most (i.e., ≥60%) of the recommended pulses had occurred. Even among the two summers that we surveyed fish, 2019 had experienced fewer Brazos BBEST (2012) target flows (8) and had a lower recruitment strength index (219) compared to 2020 (targeted flows achieved = 10, recruitment strength index = 263). Among summers in which <60% of recommended flow pulses were achieved, recruitment strength declined precipitously towards zero. In fact, zero recruitment was projected for years of extreme drought when only a single pulse occurred, including 1996, 2011, and 2013. Drought-induced recruitment failure was recently reported for closely related Peppered Chub in the Arkansas River basin during the 2011–2013 extreme drought (Perkin et al. 2015, 2019), which supports our finding of low projected recruitment for summers with limited flow pulses. More broadly, our study provides empirical support for the hypothesis proposed by Starrett (1951) more than 70 years ago that flow regime changes in the Des Moines River, Iowa, could strongly influence Shoal Chub recruitment. Our findings suggest that summer season flow pulse recommendations set by the Brazos BBEST (2012), if adopted by the TCEQ, maintain a "sound ecological environment" for at least one broadly distributed, flow-sensitive fish.

Our work supports the use of ages from otoliths for estimation of recruitment dynamics to establish flow–ecology relationships (e.g., Rodger et al. 2016; Buckmeier et al. 2017). Previous studies used otoliths from age-0 fish to assess age, growth, and recruitment for minnows in the Great Plains. Durham and Wilde (2005) reported strong linear relationships between age (independent variable) and size (dependent variable) for five minnow species from the Canadian River, Texas, and Starks et al. (2016) reported similar linear relationships for three species from the Missouri River, Missouri. The slopes of these regression models suggest that fishes in the Canadian River grew

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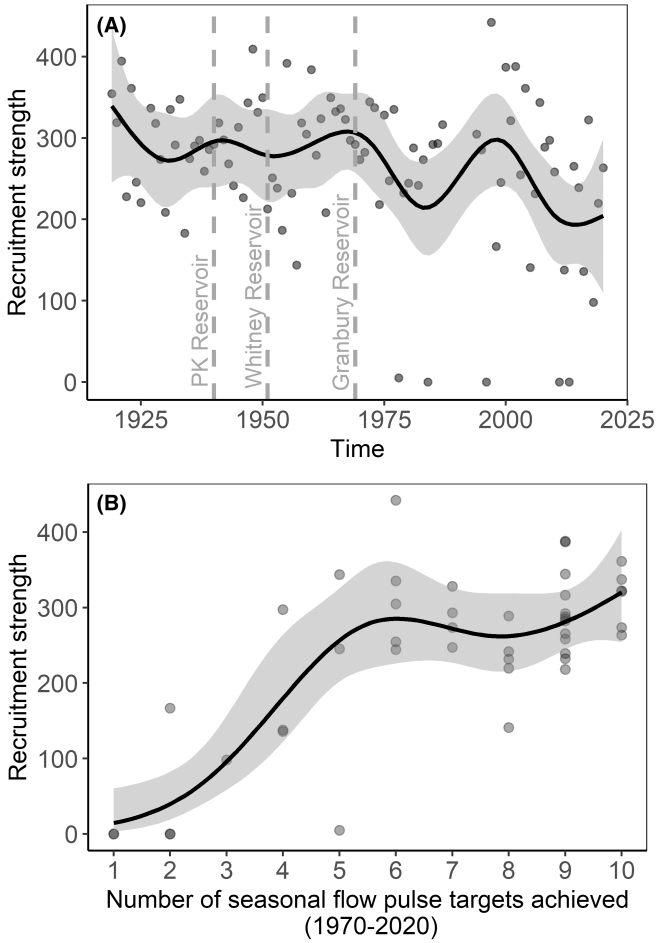

FIGURE 5 (A) Projected Shoal Chub recruitment strength based on the generalized additive model shown in Figure 4 fit to summertime flow regime data for the period 1919–2020. The number of recruits was estimated by summing daily predictions for recruitment strength during May–August (123 day) of each year because this corresponds with the Shoal Chub reproductive season. The projected annual values (points) are summarized with a second generalized additive model fit (black line) and 95% confidence interval (shaded area). The timing of upstream reservoir construction is shown as vertical dashed lines for Possum Kingdom (PK) Reservoir (1940), Whitney Reservoir (1951), and Granbury Reservoir (1969). Panel (B) shows the relationship between the projected number of recruits and the number of seasonal flow targets met for each year after completion of the final main-stem reservoir (i.e., 1970–2020). A score of 10 represents occurrence of all pulses that met Brazos BBEST criteria (i.e., at least one pulse >343 m^3/s, at least two pulses >142 m^3/s, at least three pulses >85 m^3/s, and at least four pulses >58 m^3/s; total pulse targets = 10). The relationship is summarized by a generalized additive model fit (black line) and 95% confidence interval (shaded area).

0.47–0.91 mm/day during their early life (Durham and Wilde 2005), and our findings place Shoal Chub from the lower Brazos River within this same range (i.e., 0.56 mm/day based on the slope from a regression of length as a function of age). Fishes from the Missouri River analyzed by Starks et al. (2016) grew faster (0.79–1.39 mm/day), including an estimate for Shoal Chub (i.e., 1.24 mm/day) that was roughly twice as fast as the lower Brazos River. Previous works have also linked spawning activity and recruitment of age-0 fish to streamflow pulses. Durham and Wilde (2008) hypothesize that flow pulses acted to synchronize spawning activity for fishes in the upper Brazos River, and results from a variety of systems suggest that spawning immediately after pulses reduces downstream transport of fertilized eggs and larvae (Dudley and Platania 2007; Hoagstrom and Turner 2015; Haworth and Bestgen 2017). Our finding that Shoal Chub likely spawned following pulses and after flows returned to below the threshold for base flow aligns with this narrative. However, the relationship between rise rate and increased recruitment strength that we observed for Shoal Chub points to spawning on the ascending limb of small pulses that followed larger pulses. This pattern is supported by observations by Rodger et al. (2016) that Shoal Chub captured in drift nets had the highest recruitment strength for discharge magnitudes that matched the thresholds for relatively small pulses, such as 3P/S and 2P/S. It is notable that these patterns are consistent across a variety of species even though studies used different methods to collect fishes and

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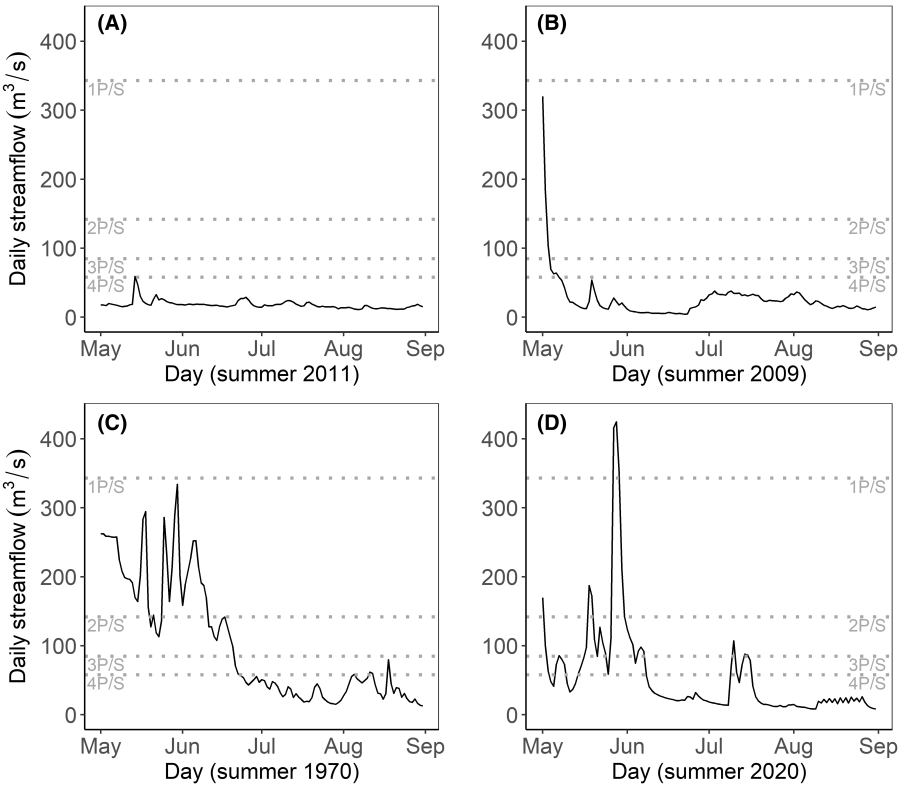

FIGURE 6 Example summer season hydrographs for years with varying scores for the flow pulse target index. (A) Summer 2011 received an index score of 1 because only a single pulse reached the threshold for 4P/S, (B) summer 2009 received an index score of 4 because a single pulse that began receding the last day of April satisfied all four thresholds, (C) summer 1970 received an index score of 7 because at least two pulses surpassed the threshold for 2P/S, one pulse surpassed the threshold for 3P/S, and four pulses surpassed the threshold for 4P/S, and (D) summer 2020 received an index score of 10 because the frequencies and magnitudes of observed pulses satisfied all targets set by the Brazos BBEST (2012). Threshold values for each target are given in Table 2 and were developed by the Brazos BBEST for July–October but are shown here for the duration of Shoal Chub spawning season (May–August).

estimate hatch dates. Durham and Wilde (2006) extracted sagittal otoliths from Peppered and Flathead chubs collected with seines, Rodger et al. (2016) extracted asteriscus otoliths from Shoal Chub collected with drift nets, and Haworth and Bestgen (2016, 2017) extracted sagittal otoliths from Flathead Chub collected with both drift nets and seines. Consequently, recruitment estimated from otoliths seems reliable even when there are differences in survey methods and the type of otolith used for aging. In our analysis of the relationship between fish age and length, we found no difference in the slopes of regression models from fish collected with different nets (seine versus drift net) from different locations (both in the lower Brazos River) and based on different otoliths (lapillus versus asteriscus).

Our application of a rate-based approach to identifying flow–ecology relationships revealed that multiple flow regime attributes, rather than discharge magnitude alone, correlated with recruitment strength. In their review of literature pertaining to flow regime alterations cast in the light of NFP flow characteristics, Poff and Zimmerman (2010) found that discharge magnitude was the most frequently assessed streamflow characteristic. This narrow focus on flow magnitude severely limits investigation of mechanisms by which flow regime alteration influences ecological processes (Poff and Zimmerman 2010). More recently, state-based approaches in which ecosystem state (i.e., species occurrence) variables were linked to flow revealed that multiple flow regime characteristics enhanced prediction of the occurrence of minnows in Great Plains streams, including Shoal Chub in the upper Brazos River (Nguyen et al. 2021). The most important flow characteristics for predicting occurrence of Shoal Chub in the upper Brazos River were seasonal magnitude (spring season magnitude, base flow magnitude), timing (date of maximum and minimum flows), rate of change (fall rate), and frequency (high flow and low flow frequency). Each of these flow characteristics were associated with intermediate optima for Shoal Chub occurrence, and temporal trajectories of occurrence showed that the probability of occurrence significantly declined during extreme drought (Nguyen et al. 2021). Our work extends the inclusion of multiple flow regime characteristics beyond state-based approaches and into the realm of rate-based approaches. Wheeler et al. (2018) suggested that rate-based approaches provide

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benefits over state-based approaches because they are based on demographic mechanisms and allow for predictive capacity, including hindcasting and forecasting. We provided an example of this predictive capability by demonstrating that the model we developed over a short time period could be used in conjunction with long-term daily flow data to assess historical changes in ecological dynamics that are not possible based on available historical ecological data. We found that historical variation in our recruitment strength index was not highly predictable based on time alone (i.e., $R^2 = 0.07$), but the central tendency of flow-based recruitment estimates changed significantly after streamflow regulation, and the years with lowest recruitment were those with few flow pulses. This ability to formulate projections is equally useful for making future projections based on modeled scenarios for streamflow regulation, climate change, or water use (Arthington et al. 2018b). Under conditions of nonstationarity, when future water availability differs greatly from historical water availability, such predictive capability will be critical for water resource management (Poff 2018). For example, the precipitation regime for the region drained by the Brazos River is nonstationary, and water resource management of the future will require new allocation strategies for a limited water supply (Lee and Singh 2020; Nielsen-Gammon et al. 2020). This phenomenon is reflective of water resource challenges on a global scale, and our research approach developed at a local scale will ultimately need to be applied more broadly.

Our research includes caveats and limitations that could be addressed in future research. First, age estimates suggest that *Macrhybopsis* spp. live up to 2.5 years (Wilde and Durham 2008; Perkin 2014), but our methodology is only applicable to age-0 fish ≤40 mm TL and cannot be used to produce daily ages for older fish. Still, demographic models linking age-structure survival and fecundity to streamflow suggest that many *Macrhybopsis* spp. and ecologically similar pelagic-broadcast-spawning fishes are essentially annual species and survival of age-0 fish is the most critical to population persistence (Wilde and Durham 2008). Our modeling framework is not applicable to longer-lived species that might employ equilibrium or periodic life history strategies and could presumably miss one or more years of recruitment without population-level consequences (Winemiller and Rose 1992). Still, these fishes are sensitive to the effects of flow regime alterations and extreme drought (Perkin et al. 2017; Malone et al. 2022) and future research could explore flow–ecology relationships involving recruitment over longer time intervals (Quist 2007). Another limitation to our work is that collection of specimens is most efficient, and sometimes only possible, at base flow conditions when large rivers can be seined. This limits inference on the range of flow conditions that can be modeled because fish can be aged up to ~60 days postrecruitment based on our results. Generating longer time intervals of inference will likely require alternative methods for collection during higher flows (e.g., benthic trawls; Herzog et al. 2009). We interpreted increments on otoliths as daily growth increments and assumed growth began at the edge of the nucleus based on validation of multiple Brazos River minnows (Wilde and Durham 2008), but validation of otoliths for Shoal Chub specifically has not been conducted. This is a potential area for research priority given the apparent utility of the species in flow–ecology studies (Rodger et al. 2016; Starks et al. 2016; Nguyen et al. 2021). It should be noted that our analysis of the summer reproductive season for Shoal Chub (May–August) differed slightly from the Brazos BBEST definition of summer (July–October) and that our validation of pulse recommendations pertains only to summer recommendations and not Brazos BBEST defined seasons for winter (November–February) or spring (March–June). Finally, given that Shoal Chub is a member of the pelagic-broadcast-spawning reproductive guild (Worthington et al. 2018), the precise spawning location associated with our sampled fish is unknown. Patterns of ichthyoplankton drift suggest that long-distance downstream displacement is possible (e.g., Dudley and Platania 2007), and future research in the lower Brazos River could investigate the distances Shoal Chub ichthyoplankton might drift given channel complexity and flow rates (e.g., Worthington et al. 2014). However, we suggest that analysis of fish samples from a limited river reach is appropriate for validating flow standards that are tied to specific gauge locations (Bruckerhoff et al. 2019; Nguyen et al. 2021).

The field of environmental flows emerged from the need to manage flows in regulated rivers to sustain natural ecosystem functioning, while securing freshwater supplies for human uses. Our understanding of the ecological consequences of flow alteration and ecological benefits of flow restoration lags behind our ability to manipulate flows, and there is a need for broader development of flow–ecology relationships to guide the science of environmental flows. The field of environmental flows is shifting from state-based methods that use snapshots of ecological condition towards rate-based methods with underlying demographic mechanisms linking flows and ecological processes (Arthington et al. 2018b; Wheeler et al. 2018). The historical focus on discharge magnitude could be expanded to include other characteristics, such as frequency, duration, timing, and rate of change (Poff and Zimmerman 2010). We addressed these challenges in the context of the Brazos River, Texas, using the Shoal Chub, a sensitive indicator species for flow–ecology relationships. We found that Shoal Chub recruitment strength correlated with multiple streamflow characteristics and that if the recommended flow standards suggested by the Brazos BBEST (2012) are achieved, then

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the Shoal Chub population is likely to successfully recruit. Though our work was focused on a single system, species, and site, the methods developed herein are transferable to any river system with historical flow data, suitable indicator species, and a need for science-based environmental flow standards for maintaining a sound ecological environment and water security for humans (Arthington et al. 2018a).

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared for this article.

ETHICS STATEMENT

This study followed the American Fisheries Society's *Ethical Guidelines for Publication of Fisheries Research* (Kočovský et al. 2019) and fish collection and handling protocols were approved by the Texas A&M University Institutional Animal Care and Use Committee (Animal Use Protocol 2018-0059).

DATA AVAILABILITY STATEMENT

Data is stored as an excel file at Texas A&M University. All data used in this manuscript are available from the corresponding author with reasonable request.

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REFERENCES

Anderson, E. P., S. Jackson, R. E. Tharme, M. Douglas, J. E. Flotemersch, M. Zwarteveen, C. Lokgariwar, M. Montoya, A. Wali, G. T. Tipa, T. D. Jardine, J. D. Olden, L. Cheng, J. Conallin, B. Cosens, C. Dickens, D. Garrick, D. Groenfeldt, J. Kabogo, D. J. Roux, A. Ruhi, and A. H. Arthington. 2019. Understanding rivers and their social relations: a critical step to advance environmental water management. Wiley Interdisciplinary Reviews: Water 6(6):e1381.

Arthington, A. H., A. Bhaduri, S. E. Bunn, S. E. Jackson, R. E. Tharme, D. Tickner, B. Young, M. Acreman, N. Baker, S. Capon, A. C. Horne, E. Kendy, M. E. McClain, N. L. Poff, B. D. Richter, and S. Ward. 2018a. The Brisbane declaration and global action agenda on environmental flows (2018). Frontiers in Environmental Science 6:45.

Arthington, A. H., J. G. Kennen, E. D. Stein, and J. A. Webb. 2018b. Recent advances in environmental flows science and water management—innovation in the Anthropocene. Freshwater Biology 63:1022–1034.

Becker, J. C., K. J. Rodibaugh, B. J. Labay, T. H. Bonner, Y. Zhang, and W. H. Nowlin. 2014. Physiographic gradients determine nutrient concentrations more than land use in a Gulf Slope (USA) river system. Freshwater Science 33:731–744.

Brazos BBEST (Basin and Bay Expert Science Team). 2012. Brazos River Basin and Bay Expert Science Team environmental flow regime recommendations report. Final submission to the Brazos River Basin and Bay Area Stakeholder Committee, Environmental Flows Advisory Group, and the Texas Commission on Environmental Quality, Austin. Available: https://texashistory.unt.edu/ark:/67531/metapth542291/m2/1/high_res_d/txca-0808.pdf. (October 2022).

Bruckerhoff, L. A., D. R. Leasure, and D. D. Magoulick. 2019. Flow–ecology relationships are spatially structured and differ among flow regimes. Journal of Applied Ecology 56:398–412.

Buckmeier, D. L., N. G. Smith, D. J. Daugherty, and D. L. Bennett. 2017. Reproductive ecology of Alligator Gar: identification of environmental drivers of recruitment success. Journal of the Southeastern Association of Fish and Wildlife Agencies 4:8–17.

Bunn, S. E., and A. H. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492–507.

Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188:263–297.

Coretta, S. 2021. tidymv: Tidy model visualisation for generalised additive models. R package version 3.2.1. Available: https://CRAN.R-project.org/package=tidymv. (January 2023).

Dahm, C. N., R. J. Edwards, and F. P. Gelwick. 2005. Gulf Coast rivers of the southwestern United States. Pages 180–228 *in* A. C. Benke and C. E. Cushing, editors. Rivers of North America. Academic Press, Burlington, Massachusetts.

Dawson, D., M. M. VanLandeghem, W. H. Asquith, and R. Patino. 2015. Long-term trends in reservoir water quality and quantity in two major river basins of the southern Great Plains. Lake and Reservoir Management 31:254–279.

Dudley, R. K., and S. P. Platania. 2007. Flow regulation and fragmentation imperil pelagic-spawning riverine fishes. Ecological Applications 17:2074–2086.

Durham, B. W., and G. R. Wilde. 2005. Relationship between hatch date and first-summer growth of five species of prairie-stream cyprinids. Environmental Biology of Fishes 72:45–54.

Durham, B. W., and G. R. Wilde. 2006. Influence of stream discharge on reproductive success of a prairie stream fish

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assemblage. Transactions of the American Fisheries Society 135:1644–1653.

Durham, B. W., and G. R. Wilde. 2008. Validation of daily growth increment formation in the otoliths of juvenile cyprinid fishes from the Brazos River, Texas. North American Journal of Fisheries Management 28:442–446.

Durham, B. W., and G. R. Wilde. 2009. Effects of streamflow and intermittency on the reproductive success of two broadcast-spawning cyprinid fishes. Copeia 2009:21–28.

Haworth, M. R., and K. R. Bestgen. 2016. Daily increment validation and effects of streamflow variability and water temperature on growth of age-0 Flathead Chub. North American Journal of Fisheries Management 36:744–753.

Haworth, M. R., and K. R. Bestgen. 2017. Flow and water temperature affect reproduction and recruitment of a Great Plains cyprinid. Canadian Journal of Fisheries and Aquatic Sciences 74:853–863.

Herzog, D. P., D. E. Ostendorf, R. A. Hrabik, and V. A. Barko. 2009. The mini-Missouri trawl: a useful methodology for sampling small-bodied fishes in small and large river systems. Journal of Freshwater Ecology 24:103–108.

Hoagstrom, C. W., and T. F. Turner. 2015. Recruitment ecology of pelagic-broadcast spawning minnows: paradigms from the ocean advance science and conservation of an imperiled freshwater fauna. Fish and Fisheries 16:282–299.

Hubbs, C., R. J. Edwards, and G. P. Garrett. 2008. An annotated checklist of the freshwater fishes of Texas, with keys to identification of species, 2nd edition. Texas Journal of Science 53:2–87.

Kiernan, J. D., P. B. Moyle, and P. K. Crain. 2012. Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. Ecological Applications 22:1472–1482.

Kočovský, P. M., P. S. Gaunt, B. K. Peoples, and E. A. Frimpong. 2019. Ethical guidelines for the publication of fisheries research. Fisheries 44:445–448. https://doi.org/10.1002/fsh.10329

Lee, K., and V. P. Singh. 2020. Analysis of uncertainty and nonstationarity in probable maximum precipitation in Brazos River basin. Journal of Hydrology 590:125526.

Lehner, B., C. R. Liermann, C. Revenga, C. Vörösmarty, B. Fekete, P. Crouzet, P. Döll, M. Endejan, K. Frenken, J. Magome, C. Nilsson, J. C. Robertson, R. Rödel, N. Sindorf, and D. Wisser. 2011. High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. Frontiers in Ecology and the Environment 9:494–502.

Maceina, M. J., J. Boxrucker, D. L. Buckmeier, R. S. Gangl, D. O. Lucchesi, D. A. Isermann, J. R. Jackson, and P. J. Martinez. 2007. Current status and review of freshwater fish aging procedures used by state and provincial fisheries agencies with recommendations for future directions. Fisheries 32:329–340.

Malone, E. W., J. S. Perkin, W. K. Gibbs, M. Padgett, M. Kulp, and S. E. Moore. 2022. High and dry in days gone by: life-history theory predicts Appalachian Mountain stream fish assemblage transformation during historical drought. Ecology of Freshwater Fish 31:29–44.

Mathews, R., and B. D. Richter. 2007. Application of the indicators of hydrologic alteration software in environment flow setting. Journal of the American Water Resources Association 43:1400–1413.

Nielsen-Gammon, J. W., J. L. Banner, B. I. Cook, D. M. Tremaine, C. I. Wong, R. E. Mace, H. Gao, Z. L. Yang, M. F. Gonzalez, R. Hoffpauir, T. Gooch, and K. Kloesel. 2020. Unprecedented drought challenges for Texas water resources in a changing climate: what do researchers and stakeholders need to know? Earth's Futures 8(8):e2020EF001552.

Nguyen, E., J. S. Perkin, R. Smith, K. B. Mayes, and J. Trungale. 2021. Characteristics of the natural flow regime paradigm explain occurrence of Great Plains fishes. Ecosphere 12:e03669.

Palmer, M., and A. Ruhi. 2019. Linkages between flow regime, biota, and ecosystem processes: implications for river restoration. Science 365(6459):eaaw2087.

Perkin, J. S. 2014. Peppered Chub, *Macrhybopsis tetranema* Gilbert 1886. Pages 189–191 *in* Kansas Fish Committee, editor. *Kansas fishes*. University Press of Kansas, Lawrence.

Perkin, J. S., K. B. Gido, K. H. Costigan, M. D. Daniels, and E. R. Johnson. 2015. Fragmentation and drying ratchet down Great Plains streams fish diversity. Aquatic Conservation: Marine and Freshwater Ecosystems 25:639–655.

Perkin, J. S., N. E. Knorp, T. C. Boersig, A. E. Gebhard, L. A. Hix, and T. C. Johnson. 2017. Life history theory predicts long-term fish assemblage response to stream impoundment. Canadian Journal of Fisheries and Aquatic Sciences 74:228–239.

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

Poff, N. L. 2018. Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world. Freshwater Biology 63:1011–1021.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. Bioscience 47:767–784.

Poff, N. L., and J. K. Zimmerman. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshwater Biology 55:194–205.

Propst, D. L., and K. B. Gido. 2004. Responses of native and nonnative fishes to natural flow regime mimicry in the San Juan River. Transactions of the American Fisheries Society 133:922–931.

Quist, M. C. 2007. An evaluation of techniques used to index recruitment variation and year-class strength. North American Journal of Fisheries Management 27:30–42.

Quist, M. C., and D. A. Isermann, editors. 2017. Age and growth of fishes: principles and techniques. American Fisheries Society, Bethesda, Maryland.

Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. Conservation Biology 10:1163–1174.

Roach, K. A. 2013. Texas water wars: how politics and scientific uncertainty influence environmental flow decision-making in the lone star state. Biodiversity and Conservation 22:545–565.

Rodger, A. W., K. B. Mayes, and K. O. Winemiller. 2016. Preliminary findings for a relationship between instream flow and Shoal Chub recruitment in the lower Brazos River, Texas. Transactions of the American Fisheries Society 145:943–950.

Starks, T. A., M. L. Miller, and J. M. Long. 2016. Early life history of three pelagic-spawning minnows *Macrhybopsis* spp. in the lower Missouri River. Journal of Fish Biology 88:1335–1349.

Starrett, W. C. 1951. Some factors affecting the abundance of minnows in the Des Moines River, Iowa. Ecology 32:13–27.

15488675, 2023, 5, Downloaded from https://afspubs.onlinelibrary.wiley.com/doi/10.1002/nafm.10837 by Texas A&M University Libraries, Wiley Online Library on [02/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TWC (Texas Water Code). 2019a. Texas Water Code, section 16.001. Available: https://statutes.capitol.texas.gov/Docs/WA/htm/WA.16.htm. (January 2023).

TWC (Texas Water Code). 2019b. Texas Water Code, section 11.0237. Available: https://statutes.capitol.texas.gov/Docs/WA/htm/WA.11.htm. (January 2023).

Vogl, A. L., and V. L. Lopes. 2009. Impacts of water resources development on flow regimes in the Brazos River. Environmental Monitoring and Assessment 157:331–345.

Wheeler, K., S. J. Wenger, and M. C. Freeman. 2018. States and rates: complementary approaches to developing flow–ecology relationships. Freshwater Biology 63:906–916.

Wilde, G. R., and B. W. Durham. 2008. A life history model for Peppered Chub, a broadcast-spawning cyprinid. Transactions of the American Fisheries Society 137:1657–1666.

Williams, C. S. 2011. Life history characteristics of three obligate riverine species and drift patterns of lower Brazos River fishes. Doctoral dissertation. Texas State University, San Marcos. Available: https://digital.library.txstate.edu/handle/10877/2450. (October 2022).

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196–2218.

Wood, S. N. 2017. Generalized additive models: an introduction with R, 2nd edition. Chapman and Hall/CRC, Boca Raton, Florida.

Worthington, T. A., A. A. Echelle, J. S. Perkin, R. Mollenhauer, N. Farless, J. J. Dyer, D. Logue, and S. K. Brewer. 2018. The emblematic minnows of the North American Great Plains: a synthesis of threats and conservation opportunities. Fish and Fisheries 19:271–307.

Worthington, T. A., S. K. Brewer, N. Farless, T. B. Grabowski, and M. S. Gregory. 2014. Interacting effects of discharge and channel morphology on transport of semibuoyant fish eggs in large, altered river systems. PLoS ONE 9(5):e96599.

Wurbs, R. A. 2017. Incorporation of environmental flows in water allocation in Texas. Water International 42:18–33.

SUPPORTING INFORMATION

Additional supplemental information can be found online in the Supporting Information section at the end of this article.

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