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

The duality of drought: Pelagic- and benthic-spawning stream fishes show opposing responses to drought in the southern great plains

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Abstract
Objective: Streamflow is a primary determinant of fish assemblage structure in riverine systems, but alteration of natural flow regimes can result in fish assemblage shifts through the process of environmental filtering. Because natural drought conditions reduce and homogenize streamflow in a manner comparable to projections for climate change in some regions, drought could serve as a proxy for expected future flow conditions.

Methods: We investigated the effects of drought as a temporally dynamic environmental filter of the occurrence of two guilds of fishes, benthic spawners that deposit adhesive ova along the benthic zone of rivers and pelagic spawners that release semibuoyant, nonadhesive ova into the pelagic zone of rivers. We developed species-specific random forest models to estimate annual probability of occurrence for three benthic-spawning and four pelagic-spawning minnow species at three sites in the upper Brazos River, Texas, for the period 1950–2018. We then used a generalized additive mixed-effects model to assess the relationship between drought intensity and likelihood of occurrence to test whether reproductive modes differed in response to drought (hypothesis 1) and whether response to drought was spatially (hypothesis 2) or temporally (hypothesis 3) variable.

Result: We found support for hypothesis 1 as two of four pelagic-spawning species (Shoal Chub Macrhybopsis hyostoma, Smalleye Shiner Notropis buccula) declined and two of three benthic-spawning species increased as drought intensified, support for hypothesis 2 as responses to drought varied by gauge location, and no support for hypothesis 3 as drought response was consistent for periods 1950–1979 and 1980–2018.

Conclusion: These findings offer insight into the future of riverine fish assemblages as climate change is expected to exacerbate regional drought conditions. Management of pelagic-spawning fishes during extreme drought in the southern Great Plains may require strategies such as (1) rescues of fish from drying reaches, (2) captive holding and propagation, and (3) assisted recolonization following subsidence of drought conditions.
INTRODUCTION

Understanding the mechanisms that regulate species occurrence is necessary for conservation and management of fishes (Jackson et al. 2001; Guisan et al. 2013). Among the theoretical frameworks employed to synthesize and predict species occurrences (see synthesis by Vellend 2010), environmental filtering is among the most widely documented (Kraft et al. 2015). Environmental filtering is defined as the process through which abiotic conditions regulate the occurrence (establishment or persistence) or dominance (abundance) of species with suitable traits (Keddy 1992). Though debate exists as to whether the process should be viewed in isolation of biotic interactions for most organisms (e.g., Aguilar-Trigueros et al. 2017; Cadotte and Tucker 2017), environmental filtering is known to play a larger role compared with biotic interactions for stream fishes (Giam and Olden 2016). This is because environmental gradients in streams are strongly linked to fish life history traits, including traits that describe demographic trade-offs along axes of growth, reproduction, and survival (Winemiller and Rose 1992), as well as spawning strategies such as benthic (stream bottom), pelagic (open water), or placental-care reproduction (Balon 1975). Examples of abiotic filters governing dominance of life history strategies include riverine flow regimes and elevational gradients (Mims and Olden 2012; Kirk et al. 2022), while filters governing dominance of reproductive strategy guilds include riverine flow regimes and channel geomorphology (Welcomme et al. 2006; McManamay and Frimpong 2015). Given that most global rivers have flow regimes that are altered by humans (Grill et al. 2019), integrating the concept of environmental filtering into water and lotic fisheries management is necessary within contemporary, human-modified riverscapes (Sedell et al. 1990; Erős et al. 2012).

The process of environmental filtering of stream fish occurrences can be dynamic, can operate over relatively short time periods, and is susceptible to disruptions by human actions. For example, alterations to flow regimes caused by dams can change the dominance of fishes with different life history strategies (Mims and Olden 2013; Perkin et al. 2017a). Throughout the Great Plains of North America, construction of dams, groundwater depletion, and the resulting stream dewatering have filtered stream fish reproductive guilds to exclude pelagic-broadcast-spawning strategists and favor benthic-spawning strategists when streams are highly fragmented and devoid of water (Perkin et al. 2015a, 2017b). Pelagic-broadcast-spawning fishes represent a guild that release gametes externally in the water column, after which fertilized ova develop as they passively drift downstream over the course of multiple days (Platania and Altenbach 1998; Hoagstrom and Turner 2014; Worthington et al. 2018). Conversely, benthic-spawning fishes deposit gametes on substrates or within crevices, after which adhesive ova develop without obligatory drift phases (reviewed by Simon 1999). Potential mechanisms underpinning the pattern of replacement of pelagic-spawning fishes by benthic-spawning fishes in the Great Plains (reviewed by Perkin et al. 2015a) include the need for pelagic-spawning fish ova to drift within currents that do not exist under fragmented or dewatered conditions (Dudley and Platania 2007), a lack of minimum water volume or pulses required to synchronize spawning within pelagic-spawning fish populations under dewatered conditions (Wilde and Durham 2008), or removal of pulses that scour the benthos where benthic-spawning ova are deposited under dewatered conditions (Keirnan et al. 2012). Altered environmental filters that benefit benthic-spawning fishes but cause the decline of pelagic-spawning fishes have increased the need for management and conservation of pelagic-spawning strategists (Hoagstrom et al. 2011; Perkin and Gido 2011). One promising management practice is the rehabilitation of altered flow regimes to more closely match natural patterns that occurred prior to alteration (Propst et al. 2008; Keirnan et al. 2012). This management framework is based on the natural flow regime (NFR) paradigm, which posits that maintaining or restoring naturally occurring streamflow magnitude (i.e., volume of water), frequency (i.e., recurrence of flows of specific magnitudes), duration (i.e., length of time magnitudes persist), rate of change (i.e., rate at which magnitudes change), and timing (i.e., time of year that flows of a given magnitude occur) promotes the preservation or reestablishment of natural ecosystem processes and properties (Poff et al. 1997). The NFR paradigm was recently linked
to the occurrence of pelagic-spawning fishes in the southern Great Plains, effectively setting the stage for developing flow management targets that underpin environmental filtering of pelagic-spawning traits (Nguyen et al. 2021). However, Nguyen et al. (2021) also identified drought as a mechanism that could contribute to the filtering out of pelagic-spawning traits because flows were substantially altered during drought. Consequently, the extent to which extreme drought can cause temporal fluctuations in environmental filtering of stream fish life history traits requires additional research (Lennox et al. 2019).

Drought disturbance within contemporary, fragmented riverscapes might represent a temporarily dynamic form of environmental filtering. Malone et al. (2022) showed that drought disturbance affecting a largely protected riverscape within a U.S. national park filtered life history strategies over decadal time periods in the direction predicted by life history theory (Winemiller and Rose 1992). That is, equilibrium strategists characterized by longer life spans and higher parental care declined during extreme drought periods when opportunistic strategists characterized by shorter life spans and absence of parental care increased in richness and dominance (Malone et al. 2022). Even within the opportunistic life history strategist group, drought can alter species persistence. Perkin et al. (2015b) demonstrated the decline and extirpation of opportunistic fishes belonging to the pelagic-spawning reproductive guild during extreme drought when benthic-spawning fishes persisted or increased their distributions. Although ultimate mechanisms for this pattern are unknown, a proximal mechanism related to failed recruitment among pelagic-spawning fishes is known. For example, Perkin et al. (2019) studied recruitment of pelagic-spawning and benthic-spawning fishes from the family Leuciscidae during extreme drought and found a general pattern of no recruitment by pelagic-spawning fishes but clear recruitment by benthic-spawning fishes. Similar filtering of pelagic-spawning fishes caused by drought-related recruitment failure caused by reduced streamflow is known from the southwestern United States (Archdeacon et al. 2020a). Consequently, management intervention has emerged as a mechanism for conserving the abundance and distribution of pelagic-spawning fishes. These management actions include rescuing fish from drying stream reaches and either holding them in captivity (Mayes et al. 2019) or moving them to continually flowing reaches (Archdeacon and Reale 2020). However, moving fish during drought might not be sufficient for maintaining long-term persistence and additional research is necessary (Archdeacon et al. 2020b). It is possible that extreme drought could act as a counter to the NFR and three-dimensional (longitudinal, lateral, vertical; Ward 1989) connectivity of riverscapes when viewed through the lens of environmental filtering (Figure 1A). This process would result in a dynamic or loose equilibrium in stream fish community structure (sensu Matthews and Marsh-Mathews 2016) that maintains a balance among benthic-spawning and pelagic-spawning fishes in the assemblage as conditions fluctuate between wet and dry over the long term. Under drought conditions, the balance might tip in favor of benthic-spawning fishes because components of the NFR associated with high-flow pulses and the associated connectivity along the longitudinal, lateral, and vertical dimension are fragmented by a lack of water (Figure 1B). These dry conditions most closely approximate the conditions that Perkin et al. (2015a) documented as being dominated by benthic-spawning fishes. Under wetter conditions, the balance might tip in favor of pelagic-spawning fishes because ample surface and groundwater maintain pulses in the NFR and multidimensional hydrologic connectivity (Figure 1C). These wet conditions most closely approximate the conditions that Perkin et al. (2015a) documented as being dominated by pelagic-spawning fishes. Ultimately, improving the conservation outlook for pelagic-spawning fishes through enhanced management will require a better understanding and treatment of linkages among extreme drought, environmental filtering, and the distribution and abundance of stream fishes.

The goal of this paper was to test for relationships between the occurrence of pelagic-spawning and benthic-spawning fishes across a gradient of drought magnitudes using retrospective modeling of flow–ecology relationships. Nguyen et al. (2021) recently developed random forest models grounded in the NFR paradigm that are useful for predicting the occurrence of pelagic-spawning fishes. We extended this modeling framework to include benthic-spawning fishes and laid the foundation for three hypotheses regarding the expected response of each reproductive guild to differing drought conditions while accounting for potential influences from study site and time the time period prior to (i.e., 1950–1979) and following (i.e., 1980–2018) alteration of the riverscape by humans. The first hypothesis (H1) was that fishes with different reproductive modes would differ in their response to drought based on previous research demonstrating transformation of Great Plains fish communities caused by fragmentation and dewatering (Perkin et al. 2015a). We predicted that the occurrence of pelagic-spawning fishes would positively correlate with the Palmer drought severity index such that their occurrence was greater during relatively wet periods, and benthic-spawning fishes would show an opposing pattern. The second hypothesis (H2) was that fish occurrences would be spatially variable such that the strength of response to drought would vary by gauge location. This hypothesis is based on the notion that flow–ecology relationships are spatially variable (Bruckerhoff et al. 2019),
particularly for pelagic-spawning fishes (Nguyen et al. 2021). The third and final hypothesis (H3) was that fish occurrence might be lower during the contemporary time period (1980–2018), when rivers are more highly fragmented and groundwater depletion has removed some buffering capacity against drought compared with a historical (1950–1979) period (Perkin et al. 2017b). This hypothesis is based on the idea of fish occurrences being ratcheted down by drought in fragmented landscapes, resulting in loss of pelagic-spawning fishes but persistence or expansion of benthic-spawning fishes (Perkin et al. 2015b). By addressing these three hypotheses, this study aims to inform future conservation management actions by revealing the extent to which reproductive traits coupled with flow–ecology models might inform how fishes will react to an increasingly drought-stricken world (Lennox et al. 2019).

**METHODS**

**Study area**

Our study area consisted of three reaches of the Brazos River, including two tributaries and the main-stem river.
Tributaries included the Double Mountain Fork Brazos River and the Salt Fork Brazos River as well as the main-stem river downstream of these tributaries (Figure 2). The Brazos River is one of the longest rivers in Texas, with a length of roughly 2,000 km from its headwaters in New Mexico to its end in the Gulf of Mexico. Along its course, the Brazos River drains seven ecoregions, including the High-, Central-, East Central-, and Coastal Plains as well as the Southwestern Tablelands, Cross Timbers, and Blackland Prairies. These ecoregions range from temperate to subtropical conditions from north to south and exhibit a strong east–west precipitation gradient wherein eastern regions are rainier than their western counterparts. The basin supports 85 native fish species, some of which are federally imperiled, including Smalleye Shiner *Notropis buccula* and Sharpnose Shiner *Notropis oxyrhynchus* (Dahm et al. 2005; Mayes et al. 2019). The Brazos River main stem is fragmented by large reservoirs that alter downstream flow regimes (Lehner et al. 2011; Dawson et al. 2015). Land cover and land use within the basin are also highly modified, consisting primarily of grassland and rangeland to the north and pasture and cropland to the south (Dahm et al. 2005). All three study sites were situated in the upper Brazos River, including the Double

**FIGURE 2** Map of the study area, depicting the three USGS stream gauges of interest: Double Mountain Fork of the Brazos River (BR) near Aspermont, Texas (USGS gauge 08080500, orange circle), the Salt Fork of the BR near Aspermont (USGS gauge 08082000, blue square), and the main-stem BR at Seymour, Texas (USGS gauge 08082500, green triangle). The hydrographs on the right panel show the full available period of record for mean daily flows (cubic meters per second [cms]) for each respective gauge. Breaks along the x-axis in the hydrograph denote missing data. The dotted vertical line at 1980 shows the approximate time of completion of major reservoirs and installation of groundwater extraction infrastructure in the region.
Mountain Fork of the Brazos River near Aspermont, Texas (U.S. Geological Survey [USGS] gauge 08080500), the Salt Fork of the Brazos River also near Aspermont, Texas (USGS gauge 08082000), and the main-stem Brazos River at Seymour, Texas (USGS gauge 08082500).

Flow data

We downloaded daily stream flow data for each of the three study sites at their associated USGS stream gauges for years 1950–2018. These flow data were then divided into two time periods, pre-1980 (i.e., 1950–1979) and post-1980 (i.e., 1980–2018), based on previous literature describing 1980 as the point at which most large reservoirs and groundwater infrastructure were in place within the Great Plains (Perkin et al. 2015a, 2017a). We retained only flow data from the year 1980 and beyond as input for model construction, while pre-1980 data were retained solely for the purpose of hindcasted predictions. This allowed us to model fish occurrence solely in a postalteration context, expanding upon the existing four models for pelagic-spawning fishes at the Salt Fork site near Aspermont, Texas, first constructed by Nguyen et al. (2021). The modeled flow data were compiled into 18 indices of hydrologic alteration representing magnitude, duration, frequency, timing, and rate of change (Table 1). Input flow variables, or indices, were selected based on the correlations calculated in Nguyen et al. (2021) to avoid multicollinearity. In addition to these eighteen indices, we included two geographical indices to account for other spatial indices not directly included in this analysis: USGS stream gauge ID and drainage area.

Fish data

We used the occurrence (i.e., presence/absence) data set comprised of 116 fish collections from the Brazos River described by Nguyen et al. (2021). These data were collected

<table>
<thead>
<tr>
<th>Index abbreviation</th>
<th>Index description</th>
<th>Units</th>
<th>Total contribution to MDG</th>
</tr>
</thead>
<tbody>
<tr>
<td>DrainAreaSKM</td>
<td>Drainage area</td>
<td>km²</td>
<td>70.97</td>
</tr>
<tr>
<td>Gauge</td>
<td>USGS stream gauge identification number</td>
<td></td>
<td>68.19</td>
</tr>
<tr>
<td>Fall.rate</td>
<td>Median of all negative changes in flow for consecutive days</td>
<td>m³·s⁻¹·d⁻¹</td>
<td>38.64</td>
</tr>
<tr>
<td>Spr</td>
<td>Median flows for the months of March–May</td>
<td>m³/s</td>
<td>37.13</td>
</tr>
<tr>
<td>Base</td>
<td>7-d minimum flows divided by the mean annual flow</td>
<td>m³/s</td>
<td>33.39</td>
</tr>
<tr>
<td>Xlowfreq</td>
<td>Frequency of low-flow (&lt;25th percentile) pulses</td>
<td>Count</td>
<td>31.32</td>
</tr>
<tr>
<td>Hifreq</td>
<td>Frequency of high-flow (&gt;75th percentile) pulses</td>
<td>Count</td>
<td>30.55</td>
</tr>
<tr>
<td>Dtmax</td>
<td>Julian calendar date of maximum flow</td>
<td>Date</td>
<td>28.45</td>
</tr>
<tr>
<td>Dtmin</td>
<td>Julian calendar date of minimum flow</td>
<td>Date</td>
<td>27.13</td>
</tr>
<tr>
<td>30dmax</td>
<td>Maximum 30-d mean discharge</td>
<td></td>
<td>24.51</td>
</tr>
<tr>
<td>SprZeroTot</td>
<td>Total duration of zero flow days between March and May</td>
<td>Count</td>
<td>19.36</td>
</tr>
<tr>
<td>1ps_Win</td>
<td>Frequency of the HEFR 1 pulse between December and February</td>
<td>Count</td>
<td>18.01</td>
</tr>
<tr>
<td>SumZeroTot</td>
<td>Total duration of zero flow days between June and August</td>
<td>Count</td>
<td>16.89</td>
</tr>
<tr>
<td>FallZeroTot</td>
<td>Total duration of zero flow days between September and November</td>
<td>Count</td>
<td>11.59</td>
</tr>
<tr>
<td>S0dfreq</td>
<td>Frequency of small (&gt;2-year return period) floods</td>
<td>Count</td>
<td>6.92</td>
</tr>
<tr>
<td>1ps_Fall</td>
<td>Frequency of the HEFR 1 pulse between September and November</td>
<td>Count</td>
<td>6.78</td>
</tr>
<tr>
<td>1ps_Spr</td>
<td>Frequency of the HEFR 1 pulse between March and May</td>
<td>Count</td>
<td>4.62</td>
</tr>
<tr>
<td>1ps_Sum</td>
<td>Frequency of the HEFR 1 pulse between June and August</td>
<td>Count</td>
<td>4.23</td>
</tr>
<tr>
<td>WinZeroTot</td>
<td>Total duration of zero flow days between December and February</td>
<td>Count</td>
<td>2.25</td>
</tr>
<tr>
<td>L1dfreq</td>
<td>Frequency of large (&gt;10-year return period) floods</td>
<td>Count</td>
<td>0.66</td>
</tr>
</tbody>
</table>
using seines between the years 1980 and 2018, though samples were not present for every year, and linked to the nearest USGS stream gauge within 25 km upstream or downstream (Nguyen et al. 2021). Collections were linked to three sites on the upper Brazos River (Table 2). One site with limited collections (i.e., 14 collections) that was analyzed in Nguyen et al. (2021) was not analyzed here because the previous study combined gauge locations, while the current study analyzed gauges independently and thus required greater sample size. We focused on pelagic- and benthic-spawning fishes in the family Leuciscidae as defined by earlier works (Balon 1975; Frimpong and Angermeier 2010; Worthington et al. 2018). This resulted in a focus on four pelagic-spawning species (Plains Minnow Hybognathus placitus, Sharpnose Shiner, Shoal Chub Macrhybopsis hyostoma, and Smalleye Shiner) as well as three benthic-spawning species (Bullhead Minnow Pimephales vigilax, Fathead Minnow P. promelas, and Red Shiner Cyprinella lutrensis). These two guilds of fishes linked by their reproductive mode were selected for their shared family and antithetical reproduction strategies for an assemblage-level approach to assessing the impacts of flow alteration and drought on fish occurrence.

Drought data

Monthly Palmer drought severity index (PDSI) values for the time period 1950–2018 were obtained from National Oceanic and Atmospheric Administration Climate Division data sets (nClimDiv) for the low-rolling plains region of Texas (region code 4102), in which all three study sites were contained. We used the median PDSI value for the spawning period of these fishes (i.e., March through September) of the same year as when a fish collection took place. Given that the species in this study are typically short-lived species (<2 years), drought values from the year of the data of collection would be most influential upon successful recruitment and likelihood of occurrence (Malone et al. 2022). The PDSI values for the time period of interest ranged between −5.86 and 6, where negative numbers represent drier-than-average years (values exceeding −4 indicate an extreme drought; Wells et al. 2004) and positive numbers represent wetter-than-average years.

Table 2: Identifying information for each study site, the number of fish collections obtained, and identity of benthic-spawning and pelagic-spawning species encountered at each site. Species codes are Bullhead Minnow (BHM), Fathead Minnow (FHM), Red Shiner (RS), Plains Minnow (PM), Sharpnose Shiner (SNS), Shoal Chub (SC), and Smalleye Shiner (SES). See Figure 2 for the locations of each stream gauge.

<table>
<thead>
<tr>
<th>Gauge ID</th>
<th>Site description</th>
<th>Number of fish collections</th>
<th>Benthic-spawning species present</th>
<th>Pelagic-spawning species present</th>
</tr>
</thead>
<tbody>
<tr>
<td>08080500</td>
<td>Double Mountain Fork of the Brazos River near Aspermont, Texas</td>
<td>32</td>
<td>BHM, FHM, RS</td>
<td>PM, SNS, SC, SES</td>
</tr>
<tr>
<td>08082000</td>
<td>Salt Fork of the Brazos River near Aspermont, Texas</td>
<td>28</td>
<td>BHM, FHM, RS</td>
<td>PM, SNS, SC, SES</td>
</tr>
<tr>
<td>08082500</td>
<td>Main-stem Brazos River at Seymour, Texas</td>
<td>56</td>
<td>BHM, FHM, RS</td>
<td>PM, SNS, SC, SES</td>
</tr>
</tbody>
</table>

Statistical analyses: indicators of hydrologic alteration evaluation

We used the indicators of hydrologic alteration (IHA) tool (version 7.1; Richter et al. 1996) to assess whether flows differed through time at each gauge by running a nonparametric least-squares fit regression on the entire period of flow record at each site. These regressions allowed us to determine the slope and significance for the following flow indices: base flows, frequency of high- and low-flow pulses, frequency of large and small floods, maximum 30-d discharge, Julian date of maximum and minimum discharge, and fall rate. This analysis was useful for understanding the extent to which the study gauges were consistent with the broader changes occurring throughout the Great Plains (Hoagstrom et al. 2011; Perkin et al. 2015a).

Random forest models

We fit seven species-specific random forest models using flow metrics (Table 1) and fish data and applied the models to the three Brazos River sites of interest to predict occurrence. Random forest classification models are most appropriate when the number of predictor variables is large (e.g., 20 in this case), when independent variables might interact in complex ways, and when threshold responses to predictor variables are possible (Cutler et al. 2007). First, flow data for the year prior to a fish collection were linked to occurrence data that had
been adjusting using the synthetic minority oversampling technique (SMOTE; Chawla et al. 2002). The “SMOTE” function from the “DMwR” R package (version 0.4.1 available for download at Comprehensive R Archive Network; Chawla et al. 2002) corrects class imbalances (e.g., caused by rare occurrences relative to frequent absences) by oversampling the minority class and undersampling the majority class to generate equal numbers of both presences and absences. This is accomplished by randomly subsampling the majority class and doubling the number of minority class observations with synthetic data generated through prediction of independent variables within the multivariate space of existing observations (Chawla et al. 2002). These corrected data served as the response variable for random forest models constructed using the “randomForest” function from the R package of the same name. Each random forest model consisted of 500 trees with four variables tried at each split. We elected to use 500 trees because increasing the number of trees did not reduce error rates, and we selected four variables at each split based on the “tuneRF” function from the “rfUtilities” to avoid overfitting caused by too many viable being considered at splits (Nguyen et al. 2021). To assess model performance and significance, we used the “rf.crossValidation” as well as the “rf.significance” functions from the “rfUtilities” R package to generate measures of model specificity (proportion of correctly predicted absences), sensitivity (proportion of correctly predicted presences), accuracy (average of specificity and sensitivity), kappas (difference between observed and expected accuracy), and significance (p-value <0.05) based on splitting the data sets into five subsets and conducting fivefold cross validation for each subset, in which 90% of the data were used for training and 10% of the data were used for testing (Cutler et al. 2007; Nguyen et al. 2021). Kappa values ranging from 0.41 to 0.60, 0.61 to 0.8, and 0.81 to 1.0 denote moderate, good, and excellent classification performance, respectively (Landis and Koch 1977). Assessments of random forest models based on these criteria can show high classification accuracy (e.g., accuracy = 1) without concern for overfitting because the assessments are based on cross validation of the models (Cutler et al. 2007). Tests of model significance are used to determine if predictions of species occurrence based on the model are greater than random chance alone.

We generated variable importance plots to graphically rank the input flow indices based on their contribution to successfully predicting occurrence of fishes. Model performance was assessed by considering node purity, or the proportion of correct classifications within terminal nodes on trees, where high node purity equates to greater predictive accuracy. The mean decrease in Gini metric is a measure of node purity and is calculated by considering the difference in node purity among trees that include each variable versus trees that exclude variables. Because Gini impurity is the likelihood that an observation is incorrectly classified based on the distribution of possible response classes, indices that lead to larger decreases in this measure are considered important to model performance. These same models were then used in the “predict.randomforest” function from the R package “randomForest” to hindcast likelihood of occurrence for each species for every year from 1950 to 2018 at each stream gauge.

Generalized additive mixed-effects model

We developed a generalized additive mixed-effects model (GAMM) using the “gamm” function from the “mgcv” package in R to test hypotheses related to the relationship between drought and fish occurrence. The first hypothesis (H1) was that response to drought would differ by reproductive guild, while the second hypothesis (H2) was that species occurrences were spatially variable and the third hypothesis (H3) was that species occurrences were temporally variable. Because these hypotheses suggest that response to drought may be contingent upon reproductive guild, gauge location, or time period, we constructed a multivariate GAMM that modeled fish likelihood of occurrence as a function of the interaction between drought (PDSI) and reproductive mode (benthic or pelagic) and the additive effects of gauge location (main-stem Brazos River, Double Mountain Fork, or Salt Fork), species identity (Red Shiner, Fathead Minnow, Bullhead Minnow, Plains Minnow, Shoal Chub, Smalleye Shiner, or Sharpnose Shiner), and time period (pre- or postalteration). We also included gauge location and time period as random effects to address repeated collections made at gauge locations and within time periods:

\[
Y_{ij} = \beta_0 + s(\beta_1 X_{1ij}) \times \beta_2 X_{2ij} + \beta_3 X_{3ij} + \beta_4 X_{4ij} + \beta_5 X_{5ij} + \mu_j + \epsilon_{ij},
\]

(1)

where \(Y_{ij}\) is probability of occurrence indexed by the \(i\)th gauge during the \(j\)th time period, \(\beta_0\) is the intercept; \(s(\beta_1 X_{1ij})\) is a smoothing term for PDSI; \(\beta_2 X_{2ij}\) is reproductive mode, for which the smoothing term shapes were allowed to vary; \(\beta_3 X_{3ij}\) is the gauge location identifier; \(\beta_4 X_{4ij}\) is species; \(\beta_5 X_{5ij}\) is time period; \(\mu_j\) is the random intercept for gauge; \(\epsilon_{ij}\) is the random intercept for time period; and \(\epsilon_{ij}\) is the error term. The model notation for implementation in R was as follows:

Fish occurrence \(\sim s(PDSI \times \text{reproductive mode}) + \text{gauge} + \text{species} + \text{time, random = list} (\text{gauge} = \sim 1, \text{time} = \sim 1)\) (2)
We fit the model using a quasibinomial error distribution because the response variable was the probability of occurrence from the random forest models and represented continuous proportional data bound by 0 and 1. We then used the results of the GAMM to determine whether there was support for each of the three hypotheses. We concluded support for H1 (the two reproductive modes differed in their response to drought) if the interaction terms between reproductive mode and drought were significant for each reproductive mode. We concluded support for H2 (species occurrences differed by gauge locations) if the gauge location parameter was significant. Lastly, we concluded support for H3 (species occurrences differed between the pre- and postalteration time periods) if the time period parameter was significant. We illustrated relationships between predicted occurrence likelihoods from the random forest models (dependent variable) as a function of the corresponding PDSI values (independent variable) for each species at each gauge location. We interpreted positive slopes for smoothed GAMM lines as evidence that occurrence was positively correlated with wetter conditions and negative slopes for smoothed GAMM lines as evidence that occurrence was positively correlated with drier conditions. Random forest and GAMM were fitted using R version 4.2.0 (R Core Team 2022).

RESULTS

Indicators of hydrologic alteration evaluation

The IHA analysis revealed that flows changed through time at each gauge location. Nonparametric least-squares regression showed that 19 out of 27 slopes for nine IHA flow indices across three study sites were significant (Table 3). Of these, the following flow indices had significant slopes across all gauge locations: maximum 30-d discharge, base flows, fall rate, and small-flood frequency. The slopes associated with Julian date of maximum and minimum flows were not significant, with one notable exception for date of minimum flows at the Salt Fork of the Brazos. The slopes of regression lines fit to the relationship between time and parameters representing low- and high-flow frequency were significantly negative at the Double Mountain Fork and the Brazos River main-stem gauge locations. Small-flood frequency significantly declined at all three gauge locations, while large-flood frequency significantly declined at the Salt Fork and Brazos River main-stem gauge locations.

Random forest models

We fit seven species-specific random forest models to a total of 116 fish collections across the three sites. All models were significant, with accuracy ranging from 0.82 to 1.0 and kappa ranging from 0.67 to 0.82 (Table 4). The most important flow indices in predicting fish occurrence varied among species, but overall, stream gauge ID, drainage area, base flow, and spring flow were consistently important for the majority of the models, as evidenced by higher mean decrease in Gini values (Figure 3). Among the four pelagic-spawning fishes, fall rate and low-flow pulse frequency were moderately important predictors. However, among the three benthic-spawning fishes we found that duration of zero flow days in the spring and base flow were consistently of greater relative importance.

Generalized additive mixed-effects model

The GAMM explained 43% (adjusted $R^2 = 0.43$) of variation in likelihood of occurrence among the seven species.

<table>
<thead>
<tr>
<th>IHA index</th>
<th>Double Mountain Fork</th>
<th>Salt Fork</th>
<th>Brazos River main stem</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Slope</td>
<td>p-value</td>
<td>Slope</td>
</tr>
<tr>
<td>30-d maximum</td>
<td>−8.202</td>
<td>0.005</td>
<td>−9.402</td>
</tr>
<tr>
<td>Base flows</td>
<td>0.0005</td>
<td>0.001</td>
<td>0.00006</td>
</tr>
<tr>
<td>Date of minimum</td>
<td>0.476</td>
<td>0.25</td>
<td>0.543</td>
</tr>
<tr>
<td>Date of maximum</td>
<td>−0.252</td>
<td>0.5</td>
<td>−0.223</td>
</tr>
<tr>
<td>Fall rate</td>
<td>0.0468</td>
<td>0.005</td>
<td>0.0213</td>
</tr>
<tr>
<td>Low-flow frequency</td>
<td>−0.0850</td>
<td>0.001</td>
<td>−0.0001</td>
</tr>
<tr>
<td>High-flow frequency</td>
<td>−0.0308</td>
<td>0.025</td>
<td>0.0279</td>
</tr>
<tr>
<td>Small-flood frequency</td>
<td>−0.00816</td>
<td>0.005</td>
<td>−0.0136</td>
</tr>
<tr>
<td>Large-flood frequency</td>
<td>−0.00177</td>
<td>0.25</td>
<td>−0.00351</td>
</tr>
</tbody>
</table>
studied. The smoothing parameters fit to the interaction between PDSI and reproductive mode were significant for both benthic and pelagic spawning modes (Table 5), indicating that the likelihood of occurrence varied across drought intensity levels differently according to reproductive mode. The parameter estimates for gauge location and species were also significant, indicating that fish species had varying likelihoods of occurrence across the three gauge locations. The parameter estimate for time period was not significant, indicating that probability of occurrence did not change between pre- and postalteration periods. The GAMM model ultimately illustrated differing responses to drought intensity among guilds, species, and gauge locations; as drought conditions became drier, benthic fishes generally increased in likelihood of occurrence and pelagic species generally decreased (Figure 4). These results supported H1 and H2 by revealing reproductive-mode-specific responses to drought among locations, but

**TABLE 4** Random forest model results for each species-specific model, including the number of raw records and the number of records after a synthetic minority oversampling technique (SMOTE) was used to address class imbalance. The results of fivefold cross validation performance metrics are also shown, including specificity (i.e., the proportion of correctly predicted absences), sensitivity (i.e., the proportion of correctly predicted presences), accuracy (i.e., the average of specificity and sensitivity), and kappa (i.e., the difference between observed and expected accuracy). Model significance measures whether or not the model predictions differed from random chance alone, with significant values denoting that predictions were improved from random chance.

<table>
<thead>
<tr>
<th>Mode</th>
<th>Species</th>
<th>Presence/absence</th>
<th>SMOTE presence/absence</th>
<th>Specificity</th>
<th>Sensitivity</th>
<th>Accuracy</th>
<th>Kappa</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Benthic</td>
<td>Bullhead Minnow</td>
<td>13/117</td>
<td>39/39</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>0.81</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Fathead Minnow</td>
<td>9/121</td>
<td>18/18</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>0.71</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Red Shiner</td>
<td>75/55</td>
<td>110/110</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>0.67</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Pelagic</td>
<td>Plains Minnow</td>
<td>83/47</td>
<td>94/94</td>
<td>0.8</td>
<td>0.8</td>
<td>0.8</td>
<td>0.75</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Sharpnose Shiner</td>
<td>73/57</td>
<td>114/114</td>
<td>0.83</td>
<td>0.86</td>
<td>0.85</td>
<td>0.82</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Shoal Chub</td>
<td>45/85</td>
<td>90/90</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>0.74</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Smalleye Shiner</td>
<td>79/51</td>
<td>102/102</td>
<td>0.8</td>
<td>0.83</td>
<td>0.82</td>
<td>0.73</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

**FIGURE 3** Variable importance plots for each species-specific random forest model. Modeled indices are listed by overall contribution across all models, where indices with a greater mean decrease in Gini are more important predictors of fish likelihood of occurrence. See Table 1 for a full description of indices.
these results provided no support for H3 because likelihood of occurrence for fishes did not vary over the long term (i.e., 1950–1979 versus 1980–2018).

**DISCUSSION**

Our findings suggest that fish occurrence is linked to drought through environmental filtering of reproductive-mode traits. We found support for the first hypothesis that fish with different reproductive guilds differed in response to drought conditions, but not all species within a guild responded similarly. Of the three benthic-spawning fishes, two species (Bullhead Minnow and Fathead Minnow), as well as one of four pelagic-spawning fishes (Plains Minnow), exhibited higher likelihoods of occurrence at negative (drier) PDSI values, and two of four pelagic-spawning fishes (Shoal Chub and Smalleye Shiner) exhibited higher likelihoods of occurrence at positive (wetter) PDSI values. One benthic-spawning fish (Red Shiner) and one pelagic-spawning fish (Sharpnose Shiner) were consistently nonresponsive to drought across all three sites. Matthews and Zimmerman (1990) suggested that fish exhibit species-specific thresholds in temperature regimes, and the same may extend to species-specific thresholds in drought tolerance. Therefore, although the direction and degree of responses are generally consistent within a reproductive guild, there exists variation due to species and site identity. This is the likely mechanism that led to support for the second hypothesis that response to drought was spatially variable. Because spatial processes influence fish occurrence through flow–ecology relationships (Bruckerhoff et al. 2019), we parsed out the data set to examine site-specific trends. These trends revealed that

**TABLE 5** Results from a generalized additive mixed-effects model used to predict the likelihood of occurrence for seven stream fishes based on the smoothed interaction between the Palmer drought severity index (PDSI) and reproductive mode (benthic versus pelagic) and additive effects of gauge location, species identity, and time period. Degrees of freedom (df), test statistics (F), and p-values (p) are given for each parameter. Parameters in bold italics are statistically significant.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>df</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Benthic s(PDSI)</td>
<td>1</td>
<td>93.84</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Pelagic s(PDSI)</td>
<td>2</td>
<td>9.59</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Gauge location</td>
<td>3</td>
<td>165.66</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Species</td>
<td>6</td>
<td>97.52</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Time period</td>
<td>1</td>
<td>0.82</td>
<td>0.37</td>
</tr>
</tbody>
</table>

**FIGURE 4** Plots summarizing a generalized additive mixed-effects model summarizing likelihood of occurrence for multiple fishes (point shapes and colors) belonging to benthic (left column) versus pelagic (right column) reproductive guilds as a function of drought measured as Palmer drought severity index (PDSI; negative values = abnormally dry conditions; positive values = abnormally wet conditions) at three gauge locations (Double Mountain Fork of the Brazos River, Salk Fork of the Brazos River, and the main-stem Brazos River). Positive slopes indicate that fish occurrence is positively correlated with wetter conditions (positive PDSI values), and negative slopes indicate that fish occurrence is positively correlated with drier conditions (negative PDSI values). Statistical significance (S) is denoted by solid lines, and nonsignificance (NS) is denoted by dotted lines. See Figure 2 for locations of gauges.
Bullhead Minnow, Fathead Minnow, and Shoal Chub showed consistent significant responses across all three sites, whereas Smalleye Shiner had a significantly positive slope at only the Salt Fork and main-stem sites. Plains Minnow correlation with PDSI was only significantly negative at the Double Mountain Fork, but we found no evidence of trends at the two remaining sites. Finally, we found no support for the third hypothesis that responses to drought differed between time periods, probably because this fragment of river has not experienced the loss of species that others have (Wilde and Urbanczyk 2013; Perkin et al. 2015a). These findings collectively demonstrate support for the concept that fish reproductive guilds can be used to infer sensitivity to drought, but responses to drought are not universal within guilds and species identity and spatial context should also be considered.

Results from this study advance our understanding of how environmental filtering impacts Great Plains fish ecology and conservation. Streamflow is considered the master variable that regulates nearly all aspects of riverine systems and the primary filter for determining community assemblage (Power et al. 1995; Boltz et al. 2019). Consequently, threats such as dewatering, fragmentation, and general flow alteration are particularly detrimental to pelagic-spawning fishes that require particular flow regime components for persistence (Hoagstrom et al. 2011; Perkin et al. 2015a). We found that although the fragment of the Brazos River that we studied has not experienced species loss as other stream fragments in the Great Plains have (Perkin et al. 2015a), the flow regime has changed. In particular, 30-d maximum values and small-flood frequencies declined through time at all three sites, while low-flow frequencies, high-flow frequencies, small-flood frequencies, and large-flood frequencies declined at two of three sites. Conversely, base flows and fall rate slightly increased at all sites. These changes in flow regime reflect changes further downstream in the basin, where pelagic-spawning fishes have been lost (Taylor and Mayes 2022).

The increase in fall rate across all sites is also consistent with the broader Great Plains region, where flow regime alteration by dams has increased fall rates (Costigan and Daniels 2012). Though the ultimate mechanisms for pelagic-spawning fish loss are not clear, what is clear is that as flows become increasingly reduced and homogenized, pelagic-spawning fishes reach the upper extent of their physiological tolerances in temperature, dissolved oxygen, or flowing-habitat requirements (Matthews and Zimmerman 1990; Bunn and Arthington 2002; Dodds et al. 2004). Whereas extreme disruptions to the NFR such as complete stream desiccation are likely intolerable for all fish species, benthic-spawning fishes from this study demonstrated persistence of high likelihood of occurrence at moderate to high levels of drought intensity. Our findings thus support previous findings that drought might affect some fishes in opposing ways, and some species-specific responses could be linked to reproductive mode (Perkin et al. 2015a, 2015b). Another notable contribution of our work is that we modeled benthic-spawning fishes in addition to pelagic-spawning fishes. Previous works focused only on pelagic-spawning guild members because of the general need for conservation for these fishes (e.g., Perkin and Gido 2011; Nguyen et al. 2021), but simultaneous consideration of multiple guides is necessary to develop broader inference. We found that one benthic-spawning species was seemingly unresponsive to drought (Red Shiner), while two others (Bullhead Minnow and Fathead Minnow) showed greater likelihood of occurrence during drought. Although drought is an inherent and naturally occurring phenomenon for many riverine systems, it can be nonetheless detrimental to survival of some fish species when there is reduced or no flow (Lake 2003). Within the Great Plains region, Hopper et al. (2020) noted that extreme drought (PDSI values between −3 and −4) in Kansas resulted in flow decline to isolated pools and ultimately local extirpation of fluvial species until overall biodiversity declined. In addition to reducing the amount of riverine habitat, droughts also reduce the quality of the remaining habitat as temperature fluctuations increase and dissolved oxygen levels decrease, pushing many riverine species to their physiological limits (Matthews and Zimmerman 1990). For example, Durham et al. (2006) found that record-high air temperatures resulted in a fish kill within a flowing Great Plains riverscape, but this extreme event killed all fishes present rather than particular reproductive guilds. In addition to adult mortality, pelagic-spawning fishes such as Peppered Chub *Macrhybopsis tetranema*, Silver Chub *Macrhybopsis storeriana*, and Rio Grande Silvery Minnow *Hybognathus amarus* exhibit recruitment failure during periods of extreme drought (Perkin et al. 2019; Archdeacon et al. 2020a). These threats are not limited to only the Great Plains, however, as riverine systems worldwide are threatened by drought-driven declines, including those in California (Vander Vorste et al. 2020), Tennessee (Malone et al. 2022), Australia (Bond et al. 2008), Tasmania (Davies et al. 1988), and Bangladesh (Roy et al. 2019). Consequently, although drought is a natural disturbance that shaped the physiological tolerances of fishes in the Great Plains (Dodds et al. 2004), the effects of drought within modern, fragmented riverscapes can cause the ratcheting down of fish diversity, particularly among pelagic-spawning fishes (Perkin et al. 2013, 2015b; Schumann et al. 2019). Drought is a challenge for many ecosystems, organisms, and managers on a global scale (Crausby et al. 2020), and our work suggests that an increase in drought could create a need for more intensive management to preserve pelagic-spawning fishes.
Retrospective analysis of drought response can be informative of future responses. Droughts are projected to increase in frequency, intensity, and duration in the coming century (Mazdiyasni and AghaKouchak 2015), especially in the southern half of the United States and much of the Great Plains (Apurv and Cai 2021). Consequently, it is imperative to understand how these same systems historically responded to similar environmental stressors so that we might better confront future challenges (Kovach et al. 2019). To this end, advancements in ecological hindcasting allow for comparisons of ecological systems between the contemporary and past, ultimately allowing improved forecasting. Moreover, ecological hindcasting serves as a powerful conservation tool by identifying least disturbed areas to preserve as well as impacted but ecologically important areas to restore (Launois et al. 2011). We demonstrated how flow–ecology relationships can be used in predictive context by hindcasting the probability of occurrence across periods with historical flow records but only intermittent ecological data (see also Perkin et al. 2023, this special section). We found that probability of occurrence did not significantly change between 1950 to 1979 and 1980 to 2018, a finding that supports previous designation of the upper Brazos River as a refuge area for endemic Great Plains fishes (Hoagstrom et al. 2011).

Though historical data are required to validate such models, prioritizing sites that served as refugia or population strongholds historically is a useful approach for preservation of fish species and assemblages (Hoagstrom et al. 2011; Perkin et al. 2013), and similar forecasts can be conducted in the future as projected flow data become available. Ecological hindcasting has been applied to test theories about the linkages between drought as an environmental filter and fish biodiversity decline (Malone et al. 2022) as well as to develop models for restoration of river stretches and their fish biota (Maire et al. 2015). However, such applications to riverine systems are generally rare. This study expands on the approach of Nguyen et al. (2021), wherein flow–ecology modeling was used for four species of interest by expanding previous models to a broader, multiguild approach. As a result, multispecies responses to drought through time at specific stream gauges were estimated and can be used to inform both preservation and restoration actions. For example, we found that pelagic-spawning fish response to drought was strongest at the most downstream site (Brazos River main stem), while benthic-spawning response to drought was strongest at the upstream site (Double Mountain Fork Brazos River). This information can be used to direct management efforts related to fish rescues in the upper Brazos River (see description in Mayes et al. 2019) during extreme drought and where managers might first focus their efforts as drought conditions develop. During the extreme drought of 2022 when the upper Brazos River dried completely for the first time since the 2011–2012 extreme drought, managers required decision support tools for where fish should be obtained from the river for the creation of refuge populations, and our work provided such a decision support tool (i.e., fish collections for refuge populations were conducted at Seymour). Although our work focused on a single river fragment and should be replicated elsewhere in the Great Plains, the fragment we studied is the final fragment in which Sharpnose Shiner and Smalleye Shiner persist, and our work therefore provides critical information for these species (Wilde and Urbanczyk 2013).

Ecological hindcasting can parse apart the effects of environmental filtering, inform ecological forecasting, and shape conservation planning. Paukert et al. (2021) illustrated the interconnectedness of climate change upon nearly every facet of riverine systems, from the abiotic (e.g., temperature, dissolved oxygen, nutrient cycling) to the biotic (e.g., range shifts, extirpations and extinctions, community assemblage shifts). Such changes may have devastating consequences across biological and economic considerations (Ficke et al. 2007). Despite the severity of drought being intensified by climate change, there remains some natural counteracting forces within riverine systems that conservation efforts might emphasize. While natural drought serves as a homogenizing force or disturbance that reduces biodiversity at short-term scales (Perkin et al. 2015b), the natural connectivity of rivers and their NFR serve to buffer the effects of drought (Poff et al. 1997). Rivers exhibit three dimensions of physical connectivity: vertical through groundwater linkages, lateral through floodplains, and longitudinal through the upstream-to-downstream geomorphological structure of rivers (Ward 1989). These physical connections maintain some remaining riverine habitat during times of drought that can serve as refugia for riverine organisms. Under increasing drought projections, these areas of refugia will become increasingly important for fish persistence (Magoullick and Kobza 2003; Hoagstrom et al. 2011). However, refuge areas are expected to become increasingly rare, if not entirely absent, due to groundwater extraction (Falke et al. 2010; Perkin et al. 2017b). Where refugia are absent in times of intermittency or drought, loss of flow-sensitive species like pelagic-spawning Rio Grande Silvery Minnow is likely (Archeacon and Reale 2020). Our works provides insight into the levels of drought that managers might use to trigger action. For example, PDSI values of −3 might represent the tipping point at which fish assemblages change from higher likelihood of occurrence of pelagic-spawning fishes (e.g., Sharpnose Shiner, Smalleye Shiner) to relatively higher likelihood of benthic-spawning fishes (e.g., Fathead Minnow, Bullhead Minnow). Though the exact threshold used to trigger...
management action might vary by species or management goals, our work demonstrates how drought-related triggers might be incorporated into management actions (Cook et al. 2016).

Our work has clear implications for management of freshwater biodiversity, particularly pelagic-spawning fishes in the southern Great Plains. Two primary management strategies include protecting biotic (i.e., fishes) or abiotic (i.e., flow regimes and habitat connectivity) components of riverscapes. Methods for preserving fishes include conducting rescues, wherein conservation practitioners and managers collect fishes from drying streams and either move specimens to another stream segment (Archdeacon and Reale 2020) or hold specimens in captivity until drought conditions subside (Mayes et al. 2019).

Our work provides the first indications of PDSI values that might be used to guide when such rescues might be necessary in the basin. Replication of our framework elsewhere could be used to develop similar species-specific and system-specific thresholds. Another management method for preserving pelagic-spawning fish populations within fragmented, drought-prone riverinives is the process of reintroduction of captive-bred specimens or translocation of wild-caught specimens. Pennock et al. (2017) determined that Peppered Chub populations persist only within 5% of their original range in the Canadian River in the southern Great Plains and recommend that reintroductions be considered as a conservation strategy. The success of reintroduction programs hinges on understanding the initial cause of extirpations and requires consideration of habitat suitability and population genetics to ensure the long-term establishment of reintroduced fishes (Osborne et al. 2014; Malone et al. 2018). Our work provides evidence that extreme drought conditions could push pelagic-spawning fishes, such as Sharpnose Shiner and Smalleye Shiner, towards extinction (e.g., Perkin et al. 2019; Archdeacon et al. 2020a), but recovery of flows following drought could mean that future repatriation attempts within the historical range of these species might be successful barring replicated extreme drought. An alternative and contentious management strategy is “managed relocations,” in which fish are moved to refugia outside of their native range (Olden et al. 2011). Critics of the strategy express concerns over disrupting native ecosystems and the limited feasibility of successful establishment (Ricciardi and Simberloff 2009), but others suggest that when carefully implemented with ecological considerations, managed relocations will be increasingly successful and necessary to long-term conservation of many freshwater species (Shirey and Lamberti 2010; Olden et al. 2011). This strategy was done unintentionally for the pelagic-spawning Arkansas River Shiner Notropis girardi in the Pecos River of New Mexico, and that population maintains high levels of genetic diversity and could be used as a source for translocations into the native range of the species (Osborne et al. 2013). However, Cowley (2006) warned that managed relocations of the pelagic-spawning Silvery Minnow may be complicated by additional factors like dam fragmentation and the presence of congeners such as Plains Minnow, leaving a stark reminder that this strategy may require further research before it is widely adopted in management. Our work suggests that managed relocations for pelagic-spawning fishes from the upper Brazos River should, at a minimum, consider the drought regimes of any future target managed relocation regions.

An alternative management strategy that might be conducted in concert with those mentioned above is to focus on maintaining or restoring flow requirements for fishes. The extreme degree of flow regulation in the Great Plains region (Lehner et al. 2011) means that flow management is possible, albeit perhaps implausible given human demand for water during drought and the fact that full-flow restoration is likely not possible (Poff 2018). Still, flow rehabilitation, or the partial restoration of natural flow regimes, is known to elicit positive responses among native stream fishes even when entire flow regimes are not restored (e.g., Propst and Gido 2004; Kiernan et al. 2012). For example, Shoal Chub recruitment positively correlated with achievement of recommended flow pulses set by an expert science team in the lower Brazos River (Perkin et al. 2023), and Nguyen et al. (2021) provided similar flow targets for pelagic-spawning fishes in the upper Brazos River. Our study provides indication of the levels of drought during which flow releases would best benefit pelagic-spawning fishes in the Brazos River and similar southern Great Plains streams. For example, during the extreme drought of 2022, intentional release of water from Ute Reservoir in New Mexico was used to supplement flows to pelagic-spawning Peppercorn Chub in the Canadian River of New Mexico and Texas (Joanna Hatt, New Mexico Game and Fish, personal communication). This level of flow regime management necessitates integration of biological and social sciences to inform conservation and will only be possible when and where water availability is sufficient (McEvoy et al. 2018; Park et al. 2020). Despite our focus on a limited number of fishes and study sites, our results have widespread implications because they are built on trait data available for many fishes and emphasize how these traits are related to the widespread phenomenon of drought (Chessman 2013). Ultimately, this work should be repeated in other regions to advance our understanding of fisheries management in an increasingly drought-stricken world (Lennox et al. 2019).
**ACKNOWLEDGMENTS**

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**CONFLICT OF INTEREST STATEMENT**

There is no conflict of interest declared in this article.

**DATA AVAILABILITY STATEMENT**

The data that support the findings of this study are available from the corresponding author upon reasonable request.

**ETHICS STATEMENT**

This study followed the American Fisheries Society’s Ethical Guidelines for Publication of Fisheries Research (Kočovský et al. 2019) and no fishes were captured or handled during this meta-analysis of existing data.

**REFERENCES**


Erős, T., P. Sály, P. Takács, A. Specziár, and P. Bíró. 2012. Temporal variability in the spatial and environmental determinants...


