FINAL PERFORMANCE REPORT

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Movement and flow-recruitment relationships of Prairie Chub: An Endemic Great Plains cyprinid

Oklahoma Department of Wildlife Conservation

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Executive Summary

The Prairie Chub *Macrhybopsis australis* is a poorly studied endemic cyprinid of the upper Red River basin and is listed as threatened in Texas and of greatest conservation need in Oklahoma. Hypothesized mechanisms have been proposed to explain the decline of pelagic broadcast spawning minnows including disrupted spawning cues, reduced recruitment, degraded habitat complexity, and reduced water availability and connectivity. Our study objectives were to evaluate Prairie Chub movement, identify spawn timing, and estimate abundance of Prairie Chub at locations in the upper Red River basin. We assessed Prairie Chub movement using a mark-recapture experiment with multiple tag and recapture occasions during late spring through summer (i.e., May-August) of 2019 and 2020. We tagged 5,771 Prairie Chub during summers of 2019 and 2020 and recaptured 213 fish across both summers. We conducted recapture events at approximately 2-week intervals from late May to August of 2019 and 2020. Movement by Prairie Chub was consistently greater than expected under the restricted movement paradigm. The average expected movement distance of the stationary population component was 2 m in 2019 and 3 m in 2020, whereas the expected average movement distance for the mobile population component was 42 m in 2019 and 75 m in 2020. We found no evidence of upstream bias in adult Prairie Chub movement during our study. We processed otoliths for 2,017 age-0 Prairie Chub across 7 rivers and two spawning seasons (i.e., 2019 and 2020). The likelihood of spawning and frequency of observed hatches per spawning date were higher in 2019 compared to 2020. The probability of spawning increased with increasing scaled discharge and average temperature in both 2019 and 2020. Spawning was more likely to occur earlier in the sample season though substantial spatial and temporal variation in spawning success was evident among rivers. The number of successful hatches observed per spawning day was highest in the Pease and Red rivers and lowest in the Salt Fork and South Wichita rivers for both years. We conducted 104 abundance surveys in 2019 and 2020. Our abundance estimates were consistently lower in upstream reaches, higher in downstream reaches, and more variable in mid reaches. We found Prairie Chub abundance was related to several covariates, but abundance did not vary much between years. Overall, adult Prairie Chub abundance was higher in the eastern portion of their range and increased with increasing discharge and turbidity but decreased at higher water temperatures. Adult Prairie Chub abundance had a quadratic relationship with salinity where Prairie Chub density peaked at a salinity of 10 ppt and then declined by nearly 100% when salinities reached 20 ppt. Our juvenile Prairie Chub abundance model had similar but weaker relationships with covariates compared to the adults; however, juvenile abundance was higher in 2020 compared to 2019. Our results indicate conservation of Prairie Chub and ecologically similar species would benefit from maintaining broadly connected habitats (i.e., for movement and drift). We show substantial variation in spawning patterns among rivers that has important implications for developing conservation actions. If agencies are concerned about abundance of Prairie Chub, then management agencies may want to consider the strong relationship with salinity when desalinization projects are proposed. Considering how salinity may narrow the realized niche of Prairie Chub, agencies interested in Prairie Chub persistence may want to prevent large changes in salinity concentrations in the species' remaining habitat.

I. OBJECTIVES

The purpose of this project is to improve the conservation and management of Prairie Chub and other pelagic broadcast minnows including members of the *Macrhybopsis* complex. We will assess movement at several locations to determine the relationship with recruitment. We will also evaluate the importance of flow regime metrics and relationships between hydrology and recruitment. Our objectives are:

1. Assess movement of Prairie Chub at 6 to 9 locations in the upper Red River basin using VIE and/or a PIT tag combination

2. Determine the relationship between the presence or abundance of the species and components of the flow regime (duration, magnitude, frequency, etc)

3. Estimate abundance of Prairie Chub in three of the river systems (Red River, Pease River, and North Fork Wichita)

4. Identify the relationship between hatch date and hydrology of the upper Red River Basin

II. SUMMARY OF PROGRESS

Background

Freshwater pelagophils belong to a fish reproductive guild emblematic of the Great Plains. Although pelagic spawning is common in the marine environment, it is restricted to only a few families in freshwater (Hoagstrom and Turner 2015) including the pelagic broadcast spawning (PBS) minnows of the Great Plains (family Cyprinidae; hereafter pelagophils) (see Worthington et al. 2018 for an overview). Pelagophils employ a "bet-hedging" strategy where spawning occurs multiple times over a protracted reproductive season (Lambert and Ware 1984; Rinchard and Kestemont 1996). Pelagophils spawn by releasing non-adhesive eggs into the water column that are fertilized and become semi-buoyant as they absorb water. The resulting propagules are kept in suspension during development via minimal velocities (Mueller et al. 2017) and are either transported downstream by currents (Platania and Altenbach 1998; Hoagstrom and Turner 2015) or retained by instream or floodplain habitat features (Widmer et al. 2012; Chase et al. 2015). Propagules hatch, on average, after 24-48 h and develop rapidly for 3-5 days before becoming free-swimming (Moore 1944; Bottrell et al. 1964; Platania and Altenbach 1998). Spawning seasons vary both temporally and spatially and appear species-specific; however, detailed information on the reproductive ecology of many pelagophils is assumed or lacking despite their widespread declines across the Great Plains (Worthington et al. 2018).

Pelagophils of the Great Plains have rapidly declined over the past 50 years (Dudley and Platania, 2007; Gido et al., 2010; Perkin et al. 2015b). PBS cyprinids within the Arkansas River basin (e.g., Arkansas River Shiner *Notropis girardi*, Moore 1944; Peppered Chub *Machrybopsis tetranema*, Luttrell et al. 1999, Pennock et al. 2017; Plains Minnow *Hybognathus placitus*, Taylor and Miller 1990; Flathead Chub *Platygobio gracilis*, Rahel and Thel 2004, Bestgen et al. 2016) were once widespread but their distributions have become truncated and their abundance reduced after reservoir construction (Luttrell et al. 1999; Bonner and Wilde 2000; Durham and Wilde 2006) and other human landscape modifications (see Worthington et al. 2018 for an overview). For example, the federally threatened Arkansas River Shiner and the Peppered Chub have been extirpated from 80% (Cross et al. 1983) and 90% of their historical ranges, respectively (Luttrell et al. 1999). The reasons for the overall declines of these fishes are not well established, although several hypotheses have been proposed (Worthington et al. 2018).

Hypothesized mechanisms explaining the decline of PBS minnows include disrupted spawning cues, reduced recruitment, degraded habitat complexity, and reduced water availability and connectivity (Hoagstrom et al. 2011; Perkin et al. 2015a; Perkin et al. 2016). These drivers are typically linked to flow alteration and stream fragmentation (Perkin and Gido 2011), but other changes to the physicochemical environment may also play a role (Worthington et al. 2018). Perkin et al. (2015a) hypothesized that an ecological ratchet mechanism (i.e., an irreversible degradation resulting in a truncated distribution, Birkeland 2004) caused by fragmentation and stream drying may explain long-term declines in the distributions of Great Plains fishes. The survival and reproduction of Great Plains fishes (Hoagstrom et al. 2011) including the Peppered Chub (Pennock et al. 2017) are thought related to discharge patterns (Wilde and Durham 2008) and linear connectivity (Perkin and Gido 2011). Synchronous spawning of prairie stream fishes has been related to increasing discharge (e.g., Arkansas River Shiner, Moore 1944; Plains Minnow, Taylor and Miller 1990; Flathead Chub, Hawthorn and Bestgen 2017). Durham and Wilde (2006) suggest the presence of a minimum discharge is more important than variation in discharge magnitude, but examination of long-term population trends is lacking. In the absence of adequate flow, drifting propagules may fall out of suspension and become buried by sediment (Platania and Altenbach 1998). Although spawning does occur during times of low to no flow, recruitment success may be reduced during such periods (Durham and Wilde 2006). Flow regime alteration, combined with climate change, is projected to further the declines of endemic and threatened prairie stream fishes (Matthews and Zimmerman 1990; Covich et al. 1997; Perkin et al. 2015b) including the Prairie Chub *Machrybopsis australis* (Eisenhour 2004; Jelks et al. 2008).

The Prairie Chub is a poorly studied endemic cyprinid of the upper Red River basin and is listed as threatened in Texas (Birdsong et al. 2020) and of greatest conservation need in Oklahoma (Oklahoma Department of Wildlife Conservation 2016). Although Prairie Chub life history is largely unknown, it is assumed to belong to the PBS reproductive guild of its sister taxon, the Peppered Chub (Bottrell et al. 1964; Platania and Altenbach 1998; Wilde and Durham 2008). Consequently, the Prairie Chub may be susceptible to similar threats affecting other freshwater pelagophils (e.g., Sturgeon Chub *Macrhybopsis gelida*, Kelsh 1994; Burrhead Chub

Macrhybopsis marconis, Perkin et al. 2013; Peppered Chub, Pennock et al. 2017). Knowledge of both life history and reproduction is critical for developing more effective species conservation and management plans (Falke et al. 2010).

Study area

We sampled Prairie Chub within its endemic range of the upper Red River basin of the Great Plains (EPA level I ecoregion). The upper Red River basin extends from eastern New Mexico across the Texas Panhandle, and terminates at Lake Texoma, OK-TX. The basin drains east over one of the largest and fastest depleting aquifers, the Ogallala or High Plains aquifer. The major Red River tributaries are the North, Salt, and Prairie Dog Town Forks of Texas and Oklahoma, and the Pease, Wichita, and Little Wichita rivers in north-central Texas. The topography varies with higher elevations and rugged canyons west of Amarillo, and with decreasing elevation and rolling plains as the river flows eastward (Baldys and Phillips, 1998). The climate ranges from semi-arid in the west to sub-humid in the east. Average rainfall follows the climate gradient with an average of 406 mm at the New Mexico-Texas border to 990 mm at Denison Dam (USDA Field Advisory Committee 1977). Annual rainfall is mercurial with extended drought periods and intermittent heavy rainstorms that often produce localized flooding. The Red River basin is characterized by turbid, sandy-bottomed alluvial streams with relatively high salinity, heavy mineral load, and visible suspended sediments. The mineral load comprises varying levels of sodium, chloride, calcium, sulfate, and dissolved solids, and is attributed to natural salt springs, seeps, and oil and gas brines (Wurbs 2002). Regional industries include agriculture, oil and gas production, copper and gypsum harvesting, ranching, and tourism. (USDA Field Advisory Committee 1977). The agriculture irrigation within this region relies on unsustainable groundwater pumping from the Ogallala Aquifer, which is projected to decline 69% by 2060 if the rate of extraction greater than the recharge rate is unabated (Steward et al. 2013). Prevalent water development, pollution, and groundwater pumping throughout the basin have altered the flow regime, channel dimensions (i.e., habitat), and water quality and may confound the effects of prolonged drought conditions on fishes.

A. APPROACH

Objective 1. Assess movement of Prairie Chub at 6 to 9 locations in the upper Red River basin using VIE and/or a PIT tag combination.

The purpose of this objective was to test the applicability of the restricted movement paradigm (RMP; Gowan et al. 1994) versus the colonization cycle hypothesis (CCH; Müller 1954) in describing the movement ecology of Prairie Chub. The RMP describes fish populations as composed of two components: a larger stationary component that does not move far and a smaller mobile component that disperses greater distances (Gowan et al. 1994, Skalski and Gilliam 2000, Rodriguez 2002, Radinger and Wolter 2014). The CCH posits that stream organisms with obligatory drift phases must move upstream to compensate for downstream displacement (Müller 1954). The CCH later became the more general "drift paradox" (DP), which highlights the apparently contradictory pattern in which drifting stream organisms that are displaced sometimes great distances downstream can maintain upstream populations without evidence of mass upstream dispersal (Hershey et al. 1993). We hypothesized that adult Prairie Chub movement would be greater than expected under the RMP (H1) because of anecdotal evidence of long-range movements by Prairie Chub (Ruppel et al. 2020) and empirical evidence of such movements by other Great Plains PBS fishes (Chase et al. 2015; Platania et al. 2020). We also hypothesized that adult movement would be upstream biased (H2) as adult fish move upstream to compensate for downstream drift of eggs and larvae (Bottrell et al. 1964; Platania and Altenbach 1998; Albers and Wildhaber 2017). Support for the RMP might exist if H1 and H2 are rejected (Figure 1a), while support for the CCH might exist if both H1 and H2 are supported (Figure 1d). Support for one hypothesis but not the other is consistent with a paradoxical pattern in which upstream movement to compensate for downstream drift is not evident, and thus evokes a drift paradox (DP) (Figure 1b, 1c).

Study Area

We studied the movement ecology of Prairie Chub in the upper Red River basin located in the Central Lowlands physiographic province of Oklahoma and Texas, USA. Land use in this area is primarily agricultural, with 80-90% being used for rangeland and cropland (Benke and Cushing 2005). We focused on six sites: two on the Red River (6th order, Strahler 1957), two on the Salt

Fork Red River (5th order), and two on the Pease River (5th order; Figure 2). We selected these streams because they are inhabited by Prairie Chub but occur upstream of a zone of hybridization with closely related Shoal Chub *M. hyostoma* (Sotola et al. 2019).

Daily discharge was monitored throughout our study period. We obtained data from the U.S. Geological Survey (USGS) stream gages on the Pease River at Vernon, Texas (USGS gage 07308200), the Salt Fork Red River at Elmer, Oklahoma (USGS gage 07301110), and the Red River proper at Burkburnett, Texas (USGS gage 07308500) (Figure 2).

Study Design

We assessed Prairie Chub movement using a mark-recapture experiment with multiple tag and recapture occasions during late spring through summer (i.e., May-August) of 2019 and 2020. At each of the six study sites, we established a 1-km tagging reach buffered upstream and downstream by 1-km search reaches. In the Red River and Salt Fork Red River, the two tagging reaches were distributed so that they were 1 km apart resulting in a shared search reach in the middle (Figure 3). Each 1-km tagging reach was divided into five 0.2-km sub-reaches where fish were batch tagged using VIE. We collected fish for tagging from each sub-reach using four 50-m seine hauls (9.1 m by 1.8 m, 1 m shallow-bag, tapering to 0.5 m) repeated three times (i.e., triple pass).

Fish captured during each pass were held together in a 68-L perforated tub to allow oxygenated stream water to flow through, for batch tagging with VIE. During tagging, fish were individually netted and tagged by injecting VIE into the muscle tissue just under the scales with a single 2-mm fluorescent elastomer mark (Northwest Marine Technology) using a 0.3-ml syringe and a 27-gauge, 12-mm-long needle. We used 140 unique combinations of VIE colors and body locations to ensure fish could be traced back to the sub-reach and date in which they were tagged (Figure 3). Colored elastomer was injected as the needle was withdrawn, creating a streak until the bevel of the needle reached the injection point (Olsen and Vøllestad 2001). We recorded the date, VIE color, body location of the tag, and total length (1 mm) for each tagged fish and placed them in a second aerated 68-L recovery tub for 2 h prior to release (Wells et al. 2017). We recorded global positioning system (GPS) coordinates at the release site (i.e., center of sub-reach) for all fish using a handheld Oregon 700 series GPS (Garmin, Olathe, KS, USA).

We conducted recapture events at approximately 2-week intervals from late May to August of 2019 and 2020. We occasionally deviated from this 2-week time interval when water levels were too high, or restrictions associated with the COVID-19 global pandemic prohibited travel (Table 1). During each site visit, we spent two consecutive days tagging fish and then conducted recapture searches across all search and tagging reaches on the third day. We made recaptures by conducting 50-m seine hauls across the entire search and tagging reaches (Figure 3). On August 8-9, 2020, we searched three long-distance sites using 50-m seine hauls across a 2-km extent surrounding the mainstem Red River site (Figure 2). On this trip, we completed 40, 50-m seine hauls on each day. On August 10-12, 2020, we completed a 20-km long search for recaptures from the Salt Fork Red River to the Red River mainstem across 4 of our 6 study sites (i.e., excluding the Pease River tributary sites) (Figure 2). In total, we completed 400, 50-m seine hauls across the 3-day period. All fish captured during long-distance searches were visually scanned for VIE tags by two observers. Recapture efforts targeted habitats most likely to be inhabited by chub (Luttrell et al. 2002), including habitats near the stream thalweg where the water is deepest and fastest. We recorded date, total length (mm), GPS coordinates, VIE color, and body tagging location for each recapture.

Daily discharge was monitored throughout our study period by the United States Geological Survey (USGS) on the Pease River at Vernon, Texas (USGS gage 07308200), the Salt Fork Red River at Elmer, Oklahoma (USGS gage 07301110), and the Red River proper at Burkburnett, Texas (USGS gage 07308500).

Statistical Analyses

We first assessed tag retention and survival to determine the minimum total length of Prairie Chub that could be tagged in the movement experiment. We conducted two 24-hour tagging trials using a 68-L perforated tub (i.e., to allow flow through) placed in the Red River at the state highway 283 access point. The first trial took place on July 23, 2019 and included one treatment group (n=24; single VIE tag) and one control group (n=24; untagged). The second trial took place on August 5, 2019, and included two treatment groups (n=23, single tag; n=24, double tag) and one control group (n=23, untagged). For each of these trials, we collected Prairie Chub from the mainstem Red River and pooled all collected fish in a single tub. We then randomly netted fish one at a time from the tub and alternated assignment to control and treatment groups that were housed in separate tubs (Musselman et al. 2017). Control group fish were handled but not tagged or measured, single tag fish received one dorsal VIE tag at the posterior end of the caudal peduncle and were measured for total length, and double tag fish received two dorsal VIE tags at the posterior end of the caudal peduncle and were measured for total length. At the completion of the 24-hour trials, fish were classified as retaining (tag still present on fish's body) or shedding (tag not evident) their tag and as alive or dead (Pennock et al. 2016). Although we did not address longer-term tag retention, we had to balance the need to evaluate retention while not holding the fish long enough to affect survival.

We analyzed survival using generalized linear regression in the form of a multiple logistic regression model, where survival was a binomial dependent variable (0 = dead, 1 = alive), length was a continuous independent variable, and treatment was a categorical factor (control, single tag, double tag). We did not model tag retention because all fish retained their tags during the trials. We used the 'glm' function from the 'stats' package in R (version 4.0.4) to fit the model and used the length at which survival equaled 0.50 probability as the minimum size fish to tag in the movement experiment.

We tested the hypothesis that Prairie Chub would move greater distances than expected under the RMP (H1) using the R package 'fishmove' (Radinger and Wolter 2014). We first estimated expected movements using the function 'fishmove', which generates a double-normal distribution of movement distances at the population level using stream size (stream order; Strahler 1957), fish length (total length, mm), fish morphology (aspect ratio of caudal fin; Sambilay 1990), and time since tagging (days, d) based on the meta-analysis conducted by Radinger and Wolter (2014). We parameterized the expected movement model with the largest stream order we studied (6th order), the median length (mm, total length [TL]) of adult individuals we captured during this study (54 mm in 2019; 58 mm in 2020), a caudal fin aspect ratio ($A = \text{height}^2/\text{surface area}$) we estimated from images of Prairie Chub (1.09), and the median number of days between mark and recapture for all recaptured fish in our study (8 d in 2019; 18 d in 2020). This function provides an estimate and 95% confidence interval for distances moved by the stationary (sigma-stat) and mobile (sigma-mob) components of the population. Next, we estimated observed movement from our mark-recapture field data using the function 'fishmove.estimate', which fits a double normal distribution to a vector of movement distances observed in the field to generate estimates of distances moved by mobile and stationary components of the population. We then assessed whether the fitted estimate for observed movement fell within the 95% confidence intervals of the expected movement and accepted H1 if the observed movement distance was greater than the upper 95% confidence interval for expected movement. We repeated this test for 2019 and 2020 separately for net movement and daily movement rate. Net movement was defined as the linear distance (m) between tagging and recapture locations along the stream thalweg. Daily movement rate (m/d) was defined as net distance moved divided by the number of days between tagging and recapture. We estimated the expected movement rate by changing the time interval in the function 'fishmove' from 8 d (2019) or 18 d (2020) to 1 d.

We tested the hypothesis that Prairie Chub exhibited biased upstream movement (H2) using frequency histograms and distances/rates moved upstream versus downstream. We tested for skewness, kurtosis, and upstream bias based on 2019 and 2020 recapture data. We tested normality and kurtosis of net movement (m) and daily movement rate (m/d) distributions using D'Agostino's test for normality (1970) and Anscombe and Glynn's test of kurtosis (1983) following previous methodologies (Petty and Grossman 2004; Hudy and Shiflet 2009; Wells et al. 2017). We tested our hypothesis that Prairie Chub net movement (m) and daily movement rate (m/d) was biased in an upstream direction (H2) using a Mann Whitney U-test implemented with the 'wilcox.test' function in R (Bauer 1972). We converted the distances moved upstream versus downstream to absolute values and then tested for differences between the ranks of distances in either direction. All functions were executed in R version 4.0.4 (R Core Team 2021).

Other comparisons

We investigated the implications of the results from our hypothesis testing with respect to Prairie Chub conservation and management. The mobile component of populations is important for connecting meta-populations and recolonization of habitat (Rodriguez 2002; Cooke et al. 2016), including Prairie Chub (Ruppel et al. 2020). Consequently, we compared the movement rate (m/d) for the mobile component of the Prairie Chub population with species examined by Radinger and Wolter (2014). The list of species comprised multiple fish families included in the R package 'fishmove' and is available within the package ('fishmove:::speciesfishmove'). We estimated the daily (i.e., time = 1 d) movement of the mobile component for each of these species. We then plotted the daily movement rate for the mobile component of the Prairie Chub population from our study for 2019 and 2020 separately to illustrate the contrast between Prairie Chub movement and movement by other river fishes analyzed by Radinger and Wolter (2014). Next, we estimated the range (i.e., maximum distance that Prairie Chub might move) for the mobile component by multiplying the estimated movement rate (m/d) by 123 days, which encompassed the summer season for which we collected movement data (May through August 31). This period also corresponds with females having mature ovaries (Ruppel et al. 2020). Greater movement might be possible if time periods outside of this season are included, but we did not measure movement for other seasons and therefore did not extrapolate beyond the summer season. We calculated potential ranges for 2019 and 2020 separately and then used the locations of our tagging as source locations to estimate the upstream and downstream ranges of Prairie Chub. The spatial extent of the estimated ranges of Prairie Chub indicates a spatial extent for management and conservation decisions, with movement range estimated as originating from the tagging sites.

Objective 2. Determine the relationship between the presence or abundance of the species and components of the flow regime (duration, magnitude, frequency, etc).

The methods and results associated with this objective were published. The citation is provided in the results section (and the manuscript sent to the funding agency). See Attachment A.

Objective 3. Estimate abundance of Prairie Chub in three of the river systems (Red River, Pease River, and North Fork Wichita).

Study Area

We sampled stream reaches within the Southern Tablelands and Central Great Plains level III ecoregions (Omernik and Griffith 2014) to estimate Prairie Chub abundance. We did not sample within the Cross Timbers level III ecoregion to avoid regions of Shoal Chub *Macrhybopsis hyostoma* sympatry (Eisenhour 2004) and introgression (Sotola et al. 2019). The topography across the basin varies from higher elevations and rugged canyons west of Amarillo to decreasing elevations and rolling plains as the Red River flows eastward (Baldys and Phillips 1998). The climate ranges from semi-arid in the west to sub-humid in the east following a precipitation gradient.

Stream reaches were selected for sampling using multiple criteria. First, we categorized stream segments (i.e., tributary confluence to tributary confluence) within the upper Red River basin by stream order (Strahler 1952) using ArcMap Version 10.5.1 (ESRI 2017). We accounted for spatial variation (e.g., precipitation gradient) by selecting stream segments from throughout the upper Red River basin. We chose a group of possible segments based on 1) the known Prairie Chub distribution (Eisenhour 2004), 2) stream size (> 3 Strahler Order because Prairie Chub are typically found in permanent streamflow, Eisenhour 2004), and 3) permission to access private lands. Next, we used a stratified, random sampling design to choose a reach after meeting the first two criteria (above) using ArcMap Version 10.5.1 (ESRI 2017). Lastly, we selected stream reaches (i.e., length of stream designated as a sampling unit), within each randomly selected segment based on permission to access privately owned lands.

Our reach length was based on both stream wetted width and additional criteria for minimum and maximum length. We used a rangefinder to measure the wetted width (0.1 m) of the stream at 5 evenly spaced transects. We calculated reach length by multiplying 20 by the average stream wetted width to characterize stream morphology. We incorporated a minimum and maximum reach length of 100 m and 500 m, respectively, to ensure available habitat were represented in each reach and abundance estimates could be completed in 1-3 days (i.e., to meet design assumptions). A minimum reach length of ~60 m is adequate to encompass representative mesohabitat in sand bed systems in New Mexico and Texas (Widmer et al. 2012). The maximum reach length of 500 m provided adequate representation of stream morphology and could be sampled in < 2 days, thereby allowing us to meet the reach-closure assumption (See Sample Design).

Sample Design

We used a multi-pass removal (i.e., depletion or sampling without replacement; Lockwood and Schneider 2000; MacKenzie and Royle 2005) sampling protocol and multinomial N-mixture model design to estimate Prairie Chub abundance. The removal method is commonly used to estimate site-specific fish abundances (Zippin 1958). Briefly, this method involves removal of fish from a closed population using sequential passes. We defined our survey as the collection of multi-pass removal seine hauls required to reasonably deplete our sample gear at a reach within a maximum 3-day period (See Fish Sampling). A pass was defined as multiple seine hauls required to systematically seine all available habitat within a reach. Removal techniques may be superior to catch-per unit effort methods (Widmer et al. 2010) and are appropriate for monitoring small-bodied minnows (Angermeier and Smogor 1995) including those in prairie streams (Bertrand et al. 2006). The observed fish counts obtained from our removal sampling can be translated into an unbiased abundance index using a variety of models including multinomial N-mixture models (Dorazio et al. 2005). Multinomial N-mixture models use a flexible hierarchical framework to model variation in abundance and capture probability simultaneously (Royle 2004; Dorazio et al. 2005). However, removal models depend on adequate sampling to produce accurate estimates. To ensure adequate sampling, we used a metapopulation approach.

We used a metapopulation design to improve the accuracy and precision of our removal estimates. Using a traditional population (i.e., non-metapopulation) approach, it is difficult to capture an appropriate portion of a population within a large region. Inadequate sampling can reduce both the accuracy and precision of removal estimates (Williams et al. 2002). Therefore, it is advantageous to consider the population as a collection of spatially distinct subpopulations (i.e., a metapopulation; Hanski 1999) where removal samples are conducted for selected subpopulations. Although the overall population is assumed constant during each survey, a metapopulation approach allows fish to move freely otherwise (Dorazio et al. 2005).

Removal models require adherence to three basic assumptions to ensure accuracy (Zippin 1958). These assumptions are (1) closed study system during sampling, (2) equal capture probability among individuals, and (3) constant capture probability within and among surveys. To address assumptions 2 and 3, we grouped surveys by year (2019 and 2020; Figure 5) and began surveys at the end of the summer reproductive season. Because fish exhibit a type-3 survivorship curve, juvenile abundances should be relatively stable by the end of the first summer. To address the closed-system assumption, we limited each survey to < 3 days. Following Peterson and Cederholm (1984), we allowed 1 h between the start time of successive passes to allow for system recovery and to ensure relatively constant capture probability among passes. We standardized seine hauls based on area to ensure effort was consistent between survey passes and across segments (See Fish Sampling). Because capture probability is likely to vary among surveys, we measured environmental covariates to account for variable capture probability due to sampling conditions. Prairie Chub are short lived (~2 years) with little sexual size dimorphism (Eisenhour 2004), enabling the assumption that capture probability was equivalent for males and females. However, capture probability likely varies due to size and life stage (Hayes et al. 2007) so we modeled size classes separately.

We modeled the abundance of two size classes of Prairie Chub to account for differences between presumptive juveniles and adults. As expected, we observed overlap between the TL of age-0 and age-1 Prairie Chub that were not yet reproducing. We used a cut-off of 42-mm TL to separate fish that were thought to be large enough to reproduce (≥ 43 mm; hereafter adults) from juveniles (≤ 42-mm TL). Juveniles included age-0 Prairie Chub and slower-growth age-1 fish that were likely hatched later in the previous reproductive year. Modelling life stages separately will provide insight into which rivers or what conditions facilitate recruitment success. Because factors including fish size, life stage, behavior, and body morphology can affect capture probability (Hayes et al. 2007; Crane and Kapuscinski 2018), modelling size classes separately may improve abundance estimates.

We used spatially replicated surveys within a hierarchical framework (i.e., multiple spatial scales) to account for among-basin heterogeneity. Hydraulic response units (i.e., approximated sub-basin; HRUs) are cataloged using hydraulic unit codes (i.e., HUCs). HUC delineation was derived from the National Hydrography Dataset (NHD; U.S Geological Survey, 2020). We conducted 1-3 spatially replicated surveys on segments nested within level 10 HUCs, hereafter sites. Surveys were grouped by stream segments, and segments were nested within sites because finer-scale patterns driving habitat complexity and species distributions are often constrained by coarser-scale features (Frissell et al., 1986). The highly dynamic nature of sand bed streams precludes the use of temporal replication due to violation of the closed system assumptions. Spatially replicated surveys may also violate the closed-system assumption because a species' availability at a site may not remain constant between surveys (Kendall and White 2009). However, the closed-system assumption of the N-mixture removal model relates to each survey (i.e., no emigration/immigration during survey), where individuals are treated as members of a meta-population of the study area (Dorazio et al. 2005). This allowed mixing of individuals among sites and between surveys while the meta-population abundance for the study area (upper Red River basin) remained constant (Royle 2004; Dorazio et al. 2005). Consequently, this framework allowed spatially replicated observations despite the highly dynamic nature of sand-bed streams.

Fish Sampling

The depletion method requires that an adequate number of fish be removed on each sampling pass so that measurably fewer fish are available for subsequent removal (Lockwood and Schneider 2000). We considered depletion to be adequate when the number of Prairie Chub captured declined by ~50% for two subsequent passes (i.e., typically 2-7 passes). We calculated depletion rates between passes and added additional passes as needed to deplete the gear. If < 3 Prairie Chub were encountered for at least two sequential passes, then we ended the survey and assumed zero fish for subsequent passes. After sampling was completed at each reach, we released the sampled Prairie Chub back to the stream.

We used a standardized seining method across multiple surveys to sample Prairie Chub at each sampled reach. We sampled with one or two seines (3.5 m x 1.5 m, 1.5-mm mesh), following standardized seining protocols for warmwater, wadeable streams (Rabeni et al. 2009). Seine efficiency may decrease as seine haul duration increases (Lombardi et al. 2014). Also, it is difficult to execute seine hauls > 20 m long when mesh size is small. Therefore, we covered a maximum area of 3 m (seine width) x 20 m (maximum haul length) per seine haul. We divided our reaches into regularly spaced transects ≤ 20 m long to evenly distribute effort. We seined each transect systematically, from bank to bank prior to proceeding to the next downstream transect. Captured Prairie Chub were transferred into live wells and incidental catches of other species were released back to the stream after each seine haul. Sampled Prairie Chub were separated by size class and enumerated. Prairie Chub were transferred to instream live wells and held until sampling was completed at each reach.

Abundance and Capture Probability Covariates

We measured environmental covariates that we hypothesized would influence the abundance of Prairie Chub. The survival and reproduction of Great Plains fishes including the Peppered Chub *Machrybopsis tetranema* are hypothesized related to discharge (Wilde and Durham 2008), flood plain inundation (King et al. 2003), water temperature (Mueller et al. 2017), timing within a season (Durham and Wilde 2005), and turbidity (Bonner and Wilde 2002; Mueller et al. 2017). These environmental variables may influence the successful completion of the life history of prairie stream fishes through direct (e.g., survival) or indirect (e.g., stream morphology) pathways (Perkin and Gido 2011). Therefore, we measured discharge (m^3/s), bankfull discharge, water temperature (0.1 °C), salinity (0.01 ppt), and turbidity (5 NTU) at each reach. We measured discharge, salinity, bankfull discharge and thalweg depth once per survey as these variables were not likely to vary among surveys. We recorded the date of each survey to calculate calendar day and account for variation in the timing of each survey. We quantified discharge (0.1 m^3/sec) using a flow meter (Flo-Mate; Marsh-McBirney Incorporated, Frederick, Maryland, USA) and the velocity-area method (Gordon et al. 2004). We measured salinity using a waterproof infrared pen (Myron PT1 Ultrapen, Carlsbad, California) at the approximate center of each reach at a mid-depth, well-mixed location. We measured thalweg water depth (Simonson 1993) every 10-20 m (depending on reach length) to calculate an average reach depth. We measured bankfull discharge following Gordon et al. (2004). We measured water temperature (°C) and turbidity (NTU) at each transect but averaged measurements for each survey. We measured water temperature (0.1 °C) and turbidity (5 NTU) at mid-depth at the center of the main channel at each reach (Brungs et al. 1977). We used a waterproof infrared pen (Myron PT1 Ultrapen, Carlsbad, California) to measure water temperature (0.1 °C), and we used a turbidity tube (i.e., combination of Jackson candle and Secchi disk methods) to measure turbidity (5 NTU) following Myre and Shaw (2006).

We quantified drainage area, ecoregion, and fragmentation metrics to account for unexplained variation in Prairie Chub abundance at coarse spatial scales. We used ArcMap Version 10.5.1 (ESRI 2017) to determine drainage area (Strahler 1952) and ecoregion (Omernik and Griffith 2014) of segments. We included fragmentation metrics that represented upstream, downstream, and total (i.e., both upstream and downstream) fragmentation due to dams for each stream segment (Cooper et al. 2017; Table 6). The upstream metrics we calculated were upstream network dam density (UNDR) along the stream network (number of dams per 100 rkm), and upstream network dam density (UNDC) within the network catchment (number of dams per 100 km^2 of catchment). We calculated percentage of downstream mainstem length free of dams (DMO), density of downstream mainstem dams (DMD), and distance (rkm) to the nearest downstream mainstem dam (DM2D) to characterize downstream metrics. The metrics that we calculated to represent total fragmentation were percentage of total mainstem length free of dams (TMO), total density of mainstem dams (TMD), and total mainstem distance (rkm) between nearest upstream and nearest downstream dams (TM2D).

We measured survey-level environmental covariates to account for variable capture probability due to sampling conditions. Environmental variables such as water temperature (Danzmann et al. 1991; Mollenhauer et al. 2018), clarity (Lyon et al. 2014), water body size (Rosenberger and Dunham 2005), water depth (Rabeni et al. 2009), and discharge (Mollenhauer et al. 2018) may influence capture probability. Therefore, we measured average wetted width (m), thalweg depth (m), discharge (m^3/sec), water temperature (°C) and turbidity (NTU) to capture variation in sampling conditions among surveys.

Statistical Analyses

We built a multinomial N-mixture abundance model to examine variation in Prairie Chub abundance and capture probability among sites**.** Multinomial N-mixture models use a flexible hierarchical framework to independently model ecological and detection processes as a function of covariates and allow detection to vary across surveys and sites (Royle 2004; Dorazio et al. 2005; Royle and Dorazio 2006). The hierarchical framework allows for an empirical Bayesian approach (Carlin and Louis 2000) which enables information to be “shared” across all sites (Dorazio et al. 2005; Royle and Dorazio 2006) and provides survey or site-specific abundance estimates. Consequently, this Bayesian approach improves abundance estimates for surveys and sites with few or missing data and improves the precision of the credibility intervals.

A multinomial N-mixture model comprises three components to model abundance (N), variation in abundance (λ), and capture probability (p). The three-part conditional model components described by Kery and Royle (2015) are expressed as:

$$y_i | n_i \sim Multinom\ (n_i\ , p^c{}_i) \qquad \text{(Component 1)}$$

$$n_i \sim Binomial\ (N_i\ , 1\text{-}\ p_0\ ) \qquad \text{(Component 2)}$$

$$N_i \sim Poisson\ (\lambda_i) \qquad \text{(Component 3)}$$

where n is the number of individuals captured (i.e., observed counts), p is the multinomial cell probability (i.e., encounter histories), $1\text{-}\ p_0$ is total capture probability, and N is abundance. The observation process comprises components 1 and 2 where component 1 is a multinomial conditioned on observed counts (*n*), and component 2 where is a binomial where N_i represents the unknown counts (i.e., the unknown number of animals that are available to be captured during a survey). The ecological process is represented by component 3 where λ is the expected number of individuals at a site *i*, and y_i is a vector of the number of individuals at a site, each with their own unique encounter history. Within this framework, site-specific abundance *N* is treated as a latent variable with a discrete distribution (usually Poisson; Chandler et al. 2015). The Poisson prior distribution is a natural choice for abundance models because it assumes random spatial distribution of fishes while allowing departures from this assumption to be explained explicitly using covariates or by modifying the prior to accommodate extra variation (Royle 2004).

Zero inflation and overdispersion are modeled using generalizations of the Poisson model. Ecological datasets are often considered zero-inflated, where the number of zeros prevent the data from fitting standard distributions. Overdispersion occurs when the variance exceeds the mean, potentially violating assumptions of standard Poisson models, especially when data are zero inflated (Cox 1983; Cameron and Trivedi 2013). Poisson alternatives used to account for zero-inflation and overdispersion include zero-inflated Poisson and Poisson log-normal models (Kery and Royle 2015). The zero-inflated Poisson model (ZIP) adds a two-part layer to our hierarchical model and describes the suitability of a site, where $w_i = 1$ represents a “suitable” site and $w_i = 0$ represents a “non-suitable” site (Kery and Royle 2015). A suitable site may have an abundance greater than or equal to zero, whereas an unsuitable site must have an abundance of zero. Unsuitable sites that do not fit the Poisson distribution are omitted from the abundance model to better meet distributional assumptions. The ZIP model as described by Kery and Royle (2015) is expressed as:

$w_i \sim Bernoulli\ (1-\theta)$ “Suitability” component
$N_i \sim Poisson\ (w_i\ \lambda_i)$ “Abundance” component

where the zero-inflation parameter θ is the expected proportion of unsuitable sites that cannot be occupied by a species (i.e., abundance is zero). The abundance component includes suitable sites, including sites with zero abundance that adhere to the Poisson distribution. The suitability component of the model does not include the use of covariates (Kery and Royle 2015). The ZIP model may also accommodate overdispersion by adding random effects. For example, a binomial mixture model with a zero-inflated Poisson-log normal (PLN) mixture for abundance may accommodate both zero-inflation and overdispersion (Kery and Royle 2015). The PLN simply entails adding an "extra residual" term to the abundance component to model overdispersion. Incorporating ZIP and PLN alternatives to a Poisson model may reduce bias and improve abundance estimates by accommodating zero inflation and overdispersion.

We prepared our data for analyses by setting an equal number of passes across surveys and averaging pass-varying covariates. Our model required that the number of passes be equal across surveys because equal capture probabilities are totaled across passes to calculate cell probabilities for the detection process of the model. The actual number of passes was variable among surveys (usually 2-7). If we did not detect any Prairie Chub while sampling, then we completed 2 passes (n = 80). Surveys that detected Prairie Chub generally required 3-5 passes (n = 22). Only two surveys required more than 5 passes. Therefore, we chose 5 passes as the cut-off to limit the number of count extrapolations. When more than five passes were required, we omitted counts for passes beyond the fifth. Surveys with 5 passes (n=9) required no extrapolation. If > 3 Prairie Chub were detected in a survey requiring less than 5 passes, we extrapolated count data to 5 passes. We extrapolated Prairie Chub counts for 8 surveys based on the average percentage rate of change between passes for those surveys. For example, if we captured 100, 50, and 25 Prairie Chub during passes 1, 2, and 3, respectively, then we used the average rate of decline (50%) to obtain counts of 12 and 6 Prairie Chub for passes 4 and 5, respectively. If < 3 Prairie Chub were observed at a site for two subsequent passes, we assumed 0 Prairie Chub observations for all subsequent passes (n = 85). For example, if we captured 1 and 0 Prairie Chub during passes 1 and 2, respectively, then we assumed 0 Prairie Chub for passes 3, 4, and 5.

We checked our data to ensure they met linear, orthogonality, and error assumptions prior to fitting models. We made histograms of all continuous predictor variables to check for linear relationships. We added a constant of 0.001 to UNDR, UNDC, and DMO to eliminate zeros (Warton and Hui 2011). We natural-log transformed all covariates except calendar day and water temperature due to right-skewed distributions. Next, we standardized all covariates to a mean of zero and a standard deviation of one to improve model interpretation and promote parameter convergence (Gelman and Hill 2007). After transformations and standardizations were completed, we checked the orthogonality of the predictor variables using Pearson's pair-wise correlation coefficient cut off $r = |0.50|$. We removed calendar day, thalweg depth, bankfull width-to-depth ratio, UNDC, TMO, TMD, TM2D, DMO, DMD, and DM2D due to multicollinearity. Retained covariates were discharge, water temperature, turbidity, salinity, longitude, UNDR, and drainage area. We plotted raw counts against our variables and salinity appeared to be a quadratic polynomial. Therefore, we included a quadratic term for salinity to account for the apparent non-linear relationship.

We included both fixed and random effects in our abundance and capture probability models for adult and juvenile Prairie Chub. Covariates for our abundance model were discharge, water temperature, turbidity, salinity (linear and quadratic effect), and longitude, and covariates for the capture-probability model were discharge, water temperature, and turbidity. We included a categorical factor for year (2019 and 2020) in both models. To prevent over-parameterization of the models, we did not include drainage area or UNDR due to the small effect sizes. We included random effects for HUC (i.e., sites) and segments nested in HUCs to account for coarse scale spatial correlation (i.e., grouping factors; Wagner et al. 2006). Lastly, we included an offset for wetted area (m^2) to account for abundance variation due to the size of each reach sampled (i.e., modeled as density, fish per m^2).

We built a ZIP regression model with a log-normal distribution to examine variation in Prairie Chub abundance among surveys and sites as a function of covariates. Our abundance model formula was expressed as:

Zero-inflation (i.e., suitability) model:

$$w_i \sim Bernoulli\ (1-\theta_i)$$

$$logit(\theta_i) = \beta_0$$

Where w_i denotes whether a survey i is suitable ($w_i = 1$) or unsuitable ($w_i = 0$; zero-inflation part).

Abundance model (given suitability):

$$N_i | w_i \sim \text{Poisson}\ (w_i * \lambda_i)$$

$$\log(\lambda_i) = \beta_0 + \alpha_1 Year + \sum_{z=1}^{5} (\beta_z X_i) + \beta_6 X_i^2 + \omega_h + o_k + \eta_i$$

$$\omega_h \sim t\ (0, \sigma_h^2, \upsilon), \text{ for } h = 1, 2, \ldots.. H \text{ (HUC grouping factor)}$$

$$o_k \sim t\ (0, \sigma_k^2, \upsilon), \text{ for } k = 1, 2, \ldots.. K \text{ (segment grouping factor)}$$

$\eta_i \sim t(0, \sigma_i^2, \upsilon)$, for $i = 1, 2, \ldots I$ (overdispersion parameter)

where λ_i was the estimated mean density of Prairie Chub (where abundance was offset for wetted area, expressed as fish per m^2) within the *i* th survey, β_0 is the grand intercept, α_1 was the factor for year (i.e., 2019, 2020). β_1 to β_5 were slopes for associated environmental predictor variables at the survey scale including discharge, water temperature, turbidity, salinity (i.e., linear) and longitude. β_6 represented the higher order term for salinity (i.e., quadratic effect). Random intercepts for site (i.e., HUC) and segment were ω_h and o_k , respectively. The overdispersion parameter is η_i.

We modeled variation in Prairie Chub capture probability (p) among surveys and sites using covariates and a logit link function. The general equation for our Prairie Chub capture probability model was expressed as:

Capture probability model (given abundance):

$C_i | N_i \sim \text{Binomial}(N_i, p_i)$

$logit(p_{ij}) = \beta_0 + \alpha_1 \text{Year} + \sum_{z=1}^{3} (\beta_z X_i) + \omega_h + o_k$

for $i = 1, 2, \ldots n$

$\omega_h \sim t(0, \sigma_h^2, \upsilon)$, for $h = 1, 2, \ldots H$ (HUC grouping factor)

$o_k \sim t(0, \sigma_k^2, \upsilon)$, for $k = 1, 2, \ldots K$ (segment grouping factor)

where $C_i | N_i$ denoted the observed counts given local abundance, p_i was the estimated capture probability of Prairie Chub within the *i*th survey, β_0 was the grand intercept, α_1 was a factor for year (i.e., 2019, 2020), β_1 to β_3 were slopes for associated environmental predictor variables at the site scale including discharge, water temperature, and turbidity. Random intercepts for site (i.e., HUC) and segment were ω_h and o_k, respectively.

We fit the adult and juvenile models using program JAGS (Plummer 2003) called from the statistical software R (version 4.0.0, R Core Team 2021) with the packages jagsUI (Kellner 2018), and rjags (Plummer et al. 2016). We used broad uniform priors for model coefficients, and vague gamma priors for standard deviations (Kéry and Royle 2015). We estimated the posterior distribution estimates for retained coefficients with Markov chain Monte Carlo methods using four chains of 30,000 iterations each after a 10,000-iteration burn-in phase and a thin rate of 10. We assessed convergence using the Brooks-Gelman-Rubin statistic ($\hat{R}$, Gelman and Rubin 1992), where values <1.1 for all coefficients indicated adequate mixing of chains (Kruschke and Vanpaemel 2015; Kellner 2018).

After fitting our adult and juvenile models, we checked the posterior distributions of our parameter values to examine uncertainty, direction, and the strength of the relationships. Histograms of posterior distributions provide a measure of uncertainty of estimated slopes because they show the relative credibility of values across the continuum (Kruschke 2014). Uncertainty was summarized using 90% highest density intervals (HDIs) which represent an interval of the most credible values that cover 90% of the distribution. The width of the interval also indicates uncertainty where narrower intervals indicate less uncertainty compared to wider intervals (Kruschke and Vanpaemel 2015).

Objective 4. Identify the relationship between hatch date and hydrology of the upper Red River Basin.

Study Area

We selected one site on 7 rivers within the upper Red River basin: Red River, Pease River, Prairie Dog Town Fork, North Wichita, South Wichita, North Fork, and Salt Fork (Figure 4). Our sites were chosen based on access, the known Prairie Chub distribution (Eisenhour 2004), and proximity to USGS stream gages.

Environmental Measurements

We measured environmental variables pertinent to stream-fish reproduction to examine relationships associated with Prairie Chub spawning events. We obtained mean daily discharge (1.00 m^3/sec) measurements from the USGS stream gage nearest to our sites: North Fork Red River, 07307028, Tipton, OK; Salt Fork Red River, 07301110, Elmer, OK; Red River, 07308500, Burkburnett, TX; Pease River, 07308200, Vernon, TX; North Wichita River, 07311700, Truscott, TX; South Wichita River, 07311800, Benjamin, TX; and Prairie Dog Town Fork, 07299540, Childress, TX. We scaled discharge by dividing each measurement by the respective drainage area to allow more direct comparison of discharge values across sites with variable orders of magnitude. Because discharge variability patterns are linked to spawning by pelagophils (Durham and Wilde 2006; Moore 1944; Taylor and Miller 1990), we calculated the coefficient of variation (CV) in scaled discharge for 10 days prior to each estimated spawning date to represent flow variation that would be unaccounted for by including only discharge on the spawning date. Timing of the first daily increment formation may vary by species and otolith type (Buckmeier et al. 2017). Therefore, including a 10-day buffer also helped account for spawning-date uncertainty caused by a potential delay of first band formation. We collected average daily air temperature (0.1 °C) and total daily rainfall (0.01 mm) from the weather station nearest to each stream sample location (Table 2; Oklahoma Mesonet; Texas Automated Surface Observing System (ASOS), NOAA 1998; McPherson et al. 2007; Brock et al. 1995). We attempted to measure continuous water temperature data at each site using temperature loggers (HOBO, Onset Computer Corporation, Bourne, Massachusetts, USA) but we had constant issues with logger theft, tampering, stream channel shifts, and unpredictable sand accumulation that buried our loggers. Therefore, we used air temperature data as a surrogate for water temperature data. We also collected precipitation data because weather patterns including drought may influence fish recruitment (Perkin et al. 2019). We recorded precipitation by 5-day totals prior to spawning date to account for variation in weather patterns and possible error in our spawning estimates. Lastly, we recorded calendar day because spawning timing can affect both survival and growth rates (Durham and Wilde 2005). We converted sample season dates each year (April 1through September 30) into calendar days within each reproductive season.

Fish Collection and Preservation

We sampled age-0 Prairie Chub < 40-mm TL to improve precision of our otolith age estimates. The approximate maximum age that can be accurately estimated from daily annuli on otoliths is 90 days for cyprinids but varies by species and climate (Sakaris et al. 2011; Buckmeier et al. 2017). Bonner (2000) estimated an average age-0 Peppered Chub growth rate of 0.426 mm per day over a 91-day period based on a single-year sample. If Prairie Chub share a similar growth rate to Peppered Chub (Bottrell et al. 1964; Bonner 2000), then young of year measuring < 40-mm TL will be within the 90-day maximum age limit used for daily age estimation.

We used a fine-mesh seine (1.8 m x 3.4 m seine with 1.5-mm mesh) to sample age-0 Prairie Chub at each sample location. Seining is the most common method of sampling wadeable sand-bed rivers because abiotic factors including high conductivity and turbidity reduce the effectiveness of more-common methods such as electrofishing (Rabeni et al. 2009, Widmer et al. 2010; Archdeacon et al. 2015; Hoagstrom and Turner 2015). Seining is also considered effective for collecting larval stages in similar species (e.g., Peppered Chub, Durham and Wilde 2005; Flathead Chub, Haworth and Bestgen 2017). We sampled each site approximately every other week beginning in mid-May until age-0 Prairie Chub measuring < 40-mm TL were no longer captured. We seined each sample location for approximately 2 h or until we captured 50 age-0 Prairie Chub. We enumerated and measured TL of all Prairie Chub and released incidental catch and Prairie Chub ≥ 40 mm TL back into the stream. Prairie Chub meeting our length criteria were euthanized via immersion in a 10 g/L solution of tricaine methanesulfonate (MS-222), buffered with sodium bicarbonate, for at least 10 minutes after cessation of opercular movement prior to preservation in 1-L bottles of 95% ethanol until later laboratory processing.

Otolith Extraction, Processing, and Ageing

We extracted, mounted, and polished otoliths from the age-0 Prairie Chub. Enumerating daily growth increments of lapilli otoliths from young-of-year cyprinids (e.g., Sharpnose Shiner *Notropis oxyrhynchus*, Smalleye Shiner *Notropis buccula*, and Plains Minnow) has been validated as a reliable method to estimate spawning date (Durham and Wilde 2008b). The sagittal otolith is the smallest otolith in cyprinids and catostomids, and it is brittle and asymmetrical so not a good choice for ageing. The asteriscus, alternatively, does not develop until 14 days post hatch and is therefore, unreliable as an ageing structure. Therefore, we used the lapilli otoliths from age-0 Prairie Chubs to estimate spawning date (also verified for ageing in other cyprinids). We mounted the whole otoliths to a glass slide using thermoplastic quartz cement (70 C Lakeside Brand). We polished the mounted otoliths by hand using a combination of 0.1-, 1.0- and 3.0-micrometer diamond lapping films (Diamond Lapping Film 8", plain backing, Electron Microscopy Sciences, Thermo Fisher Scientific) to increase clarity and smooth scratches. Polishing duration varied from 20 sec to 5 min per otolith depending on the amount of cement used. An otolith was considered adequately polished when a complete transect of daily bands was visible from the nucleus through the margin of the otolith.

We quantified daily otolith bands to estimate Prairie Chub spawning date. Otolith daily growth bands were counted using a Motic BA400 trinocular compound microscope at 40x magnification. A “blind reading” is recommended to reduce bias of age estimates (Buckmeier et al. 2017). Therefore, readers did not have information on sample date, total length, or previous band counts prior to reading. For verification, two readers conducted two independent otolith readings. Age estimates from both readers within 10% agreement were averaged and recorded. Consensus age estimates among experienced readers can improve accuracy and resolve discrepancies (Buckmeier 2002; Buckmeier et al. 2017). Therefore, ageing discrepancies that did not meet the 10% agreement criteria required readers to reach a consensus. If a consensus could not be reached, the otolith was eliminated from the dataset. Because *Machrybopsis spp.* hatch ≤ 28 h after fertilization (Bottrell et al. 1964; Rodger et al. 2016), we added 1 day to our final counts to estimate spawning date.

Statistical Analyses

We modeled our data using a hurdle modeling framework because of zero inflation, overdispersion, and the ability to model spawning, no spawning, and the number of successful Prairie Chub hatches observed per spawning date. Both zero-inflated and hurdle models accommodate excessive zeros while accounting for overdispersion (Lambert 1992; Hofstetter et al. 2016). A computational advantage of using a hurdle model framework is the ability to fit zeros and non-zeros as separate processes (Welsh et al. 1996). We used both a logistic regression and negative binomial count model in a hurdle model framework (i.e., modeling the two processes separately). The first model consisted of a binary outcome logistic regression model (i.e., Bernoulli), hereafter referenced as our zero model. The second model was a zero-truncated count model (i.e., negative binomial), hereafter count model. We used a negative binomial distribution for the count model to address overdispersion (Hofstetter et al. 20162016). The two-step hurdle framework that we used allowed us to incorporate both fixed and random effects to account for dependent data (Cantoni et al. 2017).

We built our zero (i.e., logistic regression) and count (i.e., negative binomial) models using both fixed and random effects to explain variation in Prairie Chub spawning events (i.e., spawn versus the number of successful hatches observed per spawning date). Prior to developing candidate model sets for both the zero and count models, we made the necessary data transformations, examined plots to determine the need for higher order terms, and standardized our continuous covariates. Both models needed to meet the basic assumptions of linear regression. The 5-day precipitation data were highly skewed and were not improved through natural log transformation. Therefore, we made 5-day precipitation categorical with two levels where one category represented 0 mm of rain, and the other represented > 0 mm of rain. We natural log transformed scaled discharge to reduce skewness after adding a constant of 0.001 to eliminate zeros. We included higher order quadratic terms for scaled discharge, average temperature, calendar date, and CV to the count model only. We standardized all continuous variables to a mean of zero and standard deviation of one to improve model interpretation and promote model convergence (Gelman and Hill 2007). Next, we tested for correlation among our continuous predictor variables using Pearson's correlation coefficient and retained all variables with $r < |0.6|$. Retained variables used in our zero model included scaled discharge, average daily air temperature, calendar date, and CV. Retained variables used in our count model included scaled discharge, average daily air temperature, CV, and a quadratic term for calendar day. We used the retained variables to develop candidate model sets comprised of all subset combinations for both models.

Our final two-part model comprised a binary logistic regression and a zero truncated negative binomial count model. Our binomial logistic regression was expressed as:

$$\text{logit}(p_{it}) = \ln\left(\frac{p_{it}}{1-p_{it}}\right) = \beta_0 + \alpha_1 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + v_t + \varepsilon_{it}$$

for $i = 1\text{-}2196$ observations where $y_i = (0,1)$

$v_t \sim N(0, \sigma^2)$, for $t = 1,2,\ldots..T$ (stream)

$\varepsilon_{it} \sim N(0, \sigma^2)$, for observation i, stream t

where p was the probability of a spawning event occurring for observation i (where $y_i = (0,1)$ and stream t). The grand intercept was β_0. The fixed categorical effect for year was α_1. The environmental predictor variables for the zero model were scaled discharge, calendar day, average temperature, and CV and were represented by β_1 to β_4. The random intercept for stream was v_t, and ε_{it} represented the residual error term for observation i stream t. The zero model was built in the statistical software R (version 4.0.0; R Core Team 2021) using package "lme4" (Bates et al. 2015).

Our zero truncated negative binomial count model equation was expressed as:

$$\log(\,Y_{it}\,) = \beta_0 + \alpha_1 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_3^2 + v_t + \varepsilon_{it}$$

for $i = 1 – 509$ observations where $y_i > 0$

$v_t \sim N(0, \sigma^2)$, for $t = 1,2,\ldots..T$ (stream)

$\varepsilon_{it} \sim N(0, \sigma^2)$, for observation i, stream t

where Y was the estimated mean number of successful hatches observed per spawning date for observation i (when $y_i > 0$) and stream t. The grand intercept was β_0. The fixed categorical effect for year was α_1. The environmental predictor variables for the count model were scaled discharge, calendar day, and CV and represented by β_1 to β_3, and the quadratic term for calendar Day was β_3^2. The random intercept for stream was v_t , and ε_{it} represented the residual error term for observation i stream t. The count model was built in the statistical software R (version 4.0.0; R Core Team 2021) using the package "glmmTMB" (Brooks et al. 2017).

We ranked both candidate model sets to determine which to include in our final models. We used Akaike's information criterion adjusted for small sample size (AIC_c; Hurvich and Tsai 1989; Bedrick and Tsai. 1994) to select our top models based on the lowest AICc score (Burnham and Anderson 2002). We included a categorical fixed effect for year (2019, 2020) in all our models to account for variation due to season. All candidate models also included a random effect for stream to account for spatial correlations and unequal sample sizes across sites (i.e., grouping factors; Wagner et al. 2006). We used Akaike weights (w_i) to determine the relative model support (Burnham and Anderson 2002). We ranked all subsets (n = 63) of the zero model and the count model (n = 323). To avoid including uninformative parameters, we determined the top zero and count models as the most parsimonious models within 2 AIC_c of the top model with the highest weight (Arnold 2010; Table 3).

We calculated R^2 values for the top-ranked zero models (Table 4) and count models (Table 5). The zero and count model R^2 calculations were performed in the statistical software R (version 4.0.0; R Core Team 2021) using package "performance" (Lüdecke et al. 2021). We examined model fit using a binned residual plot for the zero model where 95% of the residuals falling within the error bounds suggests adequate fit (Gelman et al. 2000). We plotted the observed versus predicted residuals associated with our count model using the R package “DHARMa” (Hartig 2021). The DHARMa residual diagnostic plots include a QQ plot and a scatterplot of the residuals against fitted values. A uniform distribution on the QQ plot and a lack of patterns in the scatterplot indicate adequate fit (Hartig 2021, Rizopoulos 2021).

B. RESULTS

Objective 1. Assess movement of Prairie Chub at 6 to 9 locations in the upper Red River basin using VIE and/or a PIT tag combination.

Survival and Tag Retention

Prairie Chub tag retention and survival were generally high. Both trials had a tag retention rate of 100% after 24 h. The control group experienced 100% survival. Survival of the single tag treatment group was 98% (46 of 47), and survival of the double tag treatment group was 75% (18 of 24). Results from the glm indicated a significant treatment effect (Z = 2.36, P = 0.02) and a significant effect of length on survival (Z = 2.66, P = 0.01). The only mortality in the single tag treatment group was a fish that was 35-mm TL, the smallest fish in the treatment group. The six mortalities in the double tag treatment group included the five smallest fish (range = 38-40 mm TL) and one fish that was 58-mm TL. The probability of survival exceeded 0.50 for double-tagged fish at 45-mm TL (Figure 6), and we did not double-tag fish in the movement experiment if they were less than this length.

Movement

Prairie Chub movement was determined using mark-recapture methods during four visits to each site during 2019 and three visits to each site during 2020 (Figure 2). We tagged 5,771 Prairie Chub during summers of 2019 (n = 2,499) and 2020 (n = 3,272) and recaptured 213 fish across both summer 2019 (n = 94, 3.7%) and summer 2020 (n = 119, 3.6%). The average length of fish recaptured was 54-mm TL (range 42-70) during 2019 and 58-mm TL (range 48-67) during 2020. Fish spent, on average, 11 d (range 1-64 d) at large during 2019 and 17 d (range 1-57 d) at large during 2020. A single fish that was tagged in summer 2019 was recaptured during summer 2020. This fish was tagged at the downstream site in the Red River on July 21, 2019 and was recaptured at the downstream site on the Salt Fork River on July 17, 2020. The Prairie Chub moved at least 11,745 m over 362 d (movement rate = 32.4 m/d). We removed these data from our analysis because it represented the only recapture between the two summers. We recaptured very few tagged fish outside of our usual survey extents. The long-distance searches at state highway 6, state highway 183, and below the confluence of Bitters Creek yielded no recaptured Prairie Chub. The 20-km long-distance search yielded recaptures that were all within the normal tagging and search reaches except for one fish that moved 69 m below the Salt Fork lower search site.

Restricted Movement Paradigm

Movement by Prairie Chub was consistently greater than expected under the RMP. The expected movement distances of the stationary and mobile components differed slightly between 2019 and 2020. Tagged chub, on average, spent more time at large during 2020 (1-68 days; median = 18) compared to 2019 (range = 1-57; median = 8). Based on these data, the expected movement distance of the stationary component was 2 m (95% CI = 1-6) in 2019 and 3 m (95% CI = 1-9) in 2020, whereas the expected movement distance for the mobile component was 42 m (95% CI = 19-94) in 2019 and 75 m (95% CI = 35-158) in 2020. Observed movements were greater than the upper confidence interval of expected movement for the stationary (159 m in 2019; 243 m in 2020) and mobile (2,169 m in 2019; 1,392 m in 2020) components (Figure 8). Similarly, movement rates were consistently faster than expected under the RMP. The expected movement rate of the stationary component was 1 m/d (95% CI = 0-3) in 2019 and 1 m/d (95% CI = 0-3) in 2020, whereas the expected movement rate for the mobile component was 14 m/d (95% CI = 6-33) in 2019 and 15 m/d (95% CI = 6-37) in 2020. Observed movement rates were significantly higher than the upper 95% confidence interval of expected movement rate for the stationary (9 m/d in 2019; 21 m/d in 2020) and mobile (740 m/d in 2019; 258 m/d in 2020) components (Figure 8). The expected share of the stationary component (p) within the population was 0.67, and the observed values for p were close to this value during 2019 (0.79) and 2020 (0.69). The share of the stationary component (p) for movement rates was also consistent with the expected value during 2019 (0.60) and 2020 (0.63). Based on these data, we accepted H1 and concluded that Prairie Chub moved greater distances and at faster rates than expected under the RMP.

Colonization Cycle Hypothesis

There was no evidence of upstream bias in Prairie Chub movement during the summer of 2019 and 2020. All movement distributions were leptokurtic, including net distance moved in 2019 (kurt = 15.3, z = 5.70, p-value < 0.01) and 2020 (kurt = 5.57, z = 3.39, p-value < 0.01) and daily movement rate for 2019 (kurt = 12.7, z = 5.34, p-value < 0.01) and 2020 (kurt = 21.9, z = 6.76, p-value < 0.01). We found no difference in the distances moved upstream versus downstream for 2019 (W = 1035, p-value = 0.78) when 51 fish moved upstream and 42 fish moved downstream, nor 2020 (W = 1601, p-value = 0.50) when 64 fish moved upstream, and 54 fish moved downstream (Figure 9a). Similarly, there was no difference in upstream versus downstream movement rate in 2019 (W = 1063, p-value = 0.95) nor 2020 (W = 1428, p-value = 0.10; Figure 9b). Data were positively skewed (i.e., in an upstream direction) for net distance moved in 2019 (Figure 10a; skew = 0.97477, z = 3.58, p-value < 0.01) and 2020 (Figure 10b; skew = 1.1962, z= 4.61, p-value < 0.01), while movement rate data were negatively skewed in 2019 (Figure 10c; skew = -1.00, z = -3.67, p-value < 0.01) and positively skewed (Figure 10d; skew = 1.88, z = 6.22, p-value < 0.01) in 2020. Based on these data, there was no support for H2, and we concluded that Prairie Chub did not exhibit biased upstream movement during summer months of their adult life stage as predicted by the CCH.

Comparisons with Other Species

Comparison of Prairie Chub with the 40 species included in the package ‘fishmove’ illustrated that the mobile component of the Prairie Chub population moved at a much higher rate (m/d) compared with other fishes, including other cyprinids (Radinger and Wolter 2014). Given their size (i.e., median length of adults we captured), Prairie Chub movement rate was 28 times (2020) to 82 times (2019) faster than expected based on data from 40 other river fishes (Figure 11a). Consequently, conservation and management options for Prairie Chub would likely differ from the typical riverine fish of similar size. When extrapolated across the 123 days of the summer season including the months of May (31 days), June (30 days), July (31 days), and August (31 days), the potential range of Prairie Chub was 31.7 km during 2020 and 91.0 km during 2019. Using only the three tagging locations as sources of movement, the mobile component range during 2020 connected the Red River mainstem, Salt Fork Red River, North Fork Red River, and

Pease River, and an even larger range during 2019 included a greater extent of all these streams (Figure 11b).

Objective 2. Determine the relationship between the presence or abundance of the species and components of the flow regime (duration, magnitude, frequency, etc).

The results from this objective have been published (see Attachment A):

> Mollenhauer, R., S. K. Brewer, J. S. Perkin, D. Swedberg, M. Wedgeworth, and Z. Steffensmeier. 2021. Connectivity and flow regime direct conservation priorities for pelagophil fishes. Aquatic Conservation: Marine and Freshwater Ecosystems 2021:1-13. DOI: 10.1002/aqc.3631

Objective 3. Estimate abundance of Prairie Chub in three of the river systems (Red River, Pease River, and North Fork Wichita).

Fish Sampling

We surveyed in 2019 and 2020 across stream segments and HUCS (Figure 5). We sampled 57 stream segments where we averaged 5 spatially replicated surveys per HUC (i.e., site). We surveyed 34 HUCs in 2019 and 24 HUCs in 2020. Adult Prairie Chub had a broader distribution than juveniles, particularly in 2019 (Figures 17 and 18). We detected adult Prairie Chub in 12 HUCs in 2019 and 10 HUCs in 2020, whereas juvenile Prairie Chub were detected in 8 HUCs in 2019 and 9 HUCs in 2020.

The number of abundance surveys, the study duration, and number of Prairie Chub detections (i.e., at least one Prairie Chub captured) varied by year. We conducted 104 surveys in 2019 (n=44) and 2020 (n=60). In 2019, we began sampling in late September to avoid high initial juvenile mortality (i.e., type III mortality curve) due to evidence of recent spawning and ended in early November. In 2020, we began sampling in mid-August due to evidence of an earlier decline in spawning activity (i.e., no gravid females) and completed our sampling in late October. Our final adult dataset comprised 104 surveys with 24 Prairie Chub detections (i.e., 12 surveys each year) and 80 non-detections (i.e., n=32 in 2019, n=48 in 2020; Figure 17). The final juvenile dataset comprised 104 surveys with 22 Prairie Chub detections (i.e., n=8 in 2019, n=14 in 2020) and 82 non-detections (i.e., n=36 in 2019, n=46 in 2020; Figure 18).

Abundance and Capture Probability Covariates

Mean, standard deviation, and range of modeled covariates (i.e., discharge, water temperature, turbidity, salinity, and longitude) varied among surveys and year (Table 12 and Table 13). Average and maximum discharge were higher in 2019 compared to 2020 (Appendix A). Average water temperature values were higher in 2020, whereas the maximum water temperature recorded (35°C) occurred in 2019 (Figure 12). Salinity was the most variable covariate with much lower average and maximum values in 2019 compared to 2020. In general, juvenile Prairie Chub were observed farther downstream (i.e., eastern regions) than adults during both seasons (Figure 18). Some western stream reaches dried completely in 2020 preventing surveys, therefore Prairie Chub were observed farther west in 2019 when streamflow was available.

Prairie Chub Abundance

Our abundance estimates for surveys were consistently lower in upstream reaches, higher in downstream reaches, and more variable in central (i.e., transitional) reaches (Appendix B, Table B1). Estimated Prairie Chub abundance was zero for 6 streams regardless of sample date, sample location or size class. Estimated Prairie Chub abundance was > 0 for at least one survey in the remaining 9 streams. Adult and juvenile abundance estimates were generally higher in 2019 compared to 2020.

Adult Prairie Chub Abundance

We found abundance of Prairie Chub was related to several covariates, but there were little differences in abundance between years. Adult Prairie Chub abundance (λ) was related to longitude, discharge, water temperature, turbidity, and salinity (Table 11). Interestingly, adult Prairie Chub abundance had a quadratic relationship with salinity where Prairie Chub density peaked at a salinity of 10 ppt and then declined by nearly 100% when salinities reached 20 ppt indicating a tolerance threshold relationship with salinity (Figure 19). Overall, adult Prairie Chub abundance was higher in the eastern portion of their range (Figure 20) and increased with increasing discharge and turbidity but decreased as water temperatures warmed (Figure 21). Abundance relationships varied little between 2019 and 2020.

We examined the direction and uncertainty of our adult Prairie Chub abundance model parameter relationships using 90% highest density intervals (HDIs; Figure 22). Although there was a clear negative relationship between adult abundance and salinity over 10 ppt (Figure 19), several other parameters overlapped with zero indicating more uncertainty. Although a slope of 0 is possible within the 90% HDIs for turbidity, the most likely value (i.e., the mode) was positive (Figure 22). Similarly, the 90% HDI for water temperature suggests a negative relationship is more plausible than a slope of zero.

Adult Prairie Chub capture probability (*p)* was related to discharge, water temperature, and turbidity (Table 21) and varied each year. Adult Prairie Chub capture probability decreased with increasing discharge. Adult Prairie Chub capture probability increased with increasing water temperature. Lastly, adult Prairie Chub capture probability was lower in 2019 compared to 2020.

Juvenile Prairie Chub Abundance

Our juvenile Prairie Chub abundance model had similar but weaker relationships with covariates compared to the adults; however, annual differences in abundance were detected. Juvenile Prairie Chub abundance (λ) was related to salinity and longitude (Table 11). Like the adults, juvenile abundance was higher in eastern portions of the upper basin compared to farther west (Figure 23) and had a quadratic relationship with salinity (Figure 24). The 90% highest density intervals (HDIs) of our juvenile abundance parameters for discharge, water temperature, and turbidity indicated high uncertainty and that a slope of zero was likely (Figure 25); these relationships represent weak effects (Figure 26). Interestingly, juvenile abundance was higher in 2020 compared to 2019 (Table 11).

Juvenile Prairie Chub capture probability (*p)* was related to discharge, water temperature, and turbidity (Table 14). Similar to adults, juvenile capture probability increased with increasing turbidity and decreased with increasing discharge (Figure 25). In contrast to adults, juvenile capture probability decreased as water temperature increased. Juvenile capture probability was lower in 2019 compared to 2020 (Table 14).

Abundance Model Diagnostics

Model diagnostics for both the adult and juvenile models indicated adequate model convergence. In both cases, the $\hat{R}$ was < 1.1 for slope, intercept, and grouping factor coefficients indicating adequate model convergence (Gelman and Hill 2007). Although $\hat{R}$ was > 1.2 for some abundance estimates (n = 2 for adult model and n = 11 for the juvenile model), $\hat{R}$ values did not exceed 1.3 and high associated effective sample sizes (i.e., > 1000) suggested good model convergence.

Objective 4. Identify the relationship between hatch date and hydrology of the upper Red River Basin.

Environmental Measurements

Trends in environmental conditions including discharge and air temperature varied by season. Average annual discharge statistics of 7 rivers of the upper Red River basin over thirty years (1990-2020) showed higher than average stream discharges in 2019 (61st to 95th percentile depending on stream) compared to low discharges in 2020 (8th to 31st percentile depending on stream; Table 7). For example, the average annual discharge of the Red River in 2019 was 71 m^3/s ranking above the 90th percentile for average annual discharge over the past 60 years (USGS annual water summary, *https://nwis.waterdata.usgs.gov/tx/nwis/annual).* However, in 2020 annual average discharge was 12 m^3/s and was below the 20th percentile (over a 30-yr period). We found that western (i.e., upstream) reaches of several rivers including the North Fork, Salt Fork, Prairie Dog Town Fork, North Pease River, and South Wichita River either dried completely or formed isolated pools in 2020. Average air temperature was higher in 2020 but more variable in 2019 (Figure 12). The earliest observed spawning events coincided with air temperatures of 10 °C in 2019 and 14 °C in 2020. Air temperature ranges during late-June through early-July were relatively consistent between 2019 (22-28 °C) and 2020 (24-28 °C). The highest observed air temperatures for Prairie Chub spawning dates were 33 ℃ in 2019 and 32 ℃ in 2020.

Otolith Extraction, Processing, and Ageing

We processed otoliths for 2,017 age-0 Prairie Chub across 7 rivers and two spawning seasons (i.e., 2019 and 2020; Table 5). We collected 1,378 and 639 Prairie Chub (11-41-mm TL, Table 8) in 2019 and 2020, respectively. We collected the most Prairie Chub from the North Wichita River and the fewest from the Salt Fork (Table 5). Despite equal sampling efforts across sites, we did not observe any age-0 Prairie Chub in the Prairie Dog Town Fork in either year.

We retained daily age estimates that met our agreement or consensus standards to analyze spawning date relationships. We retained, on average, 72% of daily age estimates across all rivers (Table 8). We retained the highest percentage of age estimates from Prairie Chub collected in the Pease River and Salt Fork, whereas the lowest percent of estimates retained were from the North and South Wichita rivers. Lower retention rates were caused by an inability to reach a consensus due to highly irregular ring formation or processing error (i.e., too much heat when melting cement or overpolishing). For example, the age-0 Prairie Chub we collected from isolated pools in the South Wichita River had irregular ring formation (i.e., rings crossed or split) which prevented reader aging and agreement. In 2019, the estimated spawning dates were between April 24 and September 20. In 2020, estimated spawning dates were between May 11 and August 7. Daily age estimates ranged from 10 to 87 days. Our age estimates suggest the North Wichita and Red rivers had the highest number of spawning days whereas the lowest number of spawning days occurred in the North Fork and Salt Fork rivers.

Statistical Analyses

Our final logistic regression model predicting the probability of spawning (P) contained scaled discharge, average air temperature, calendar day, and year as fixed effects and a random effect for stream (Table 9). The probability of spawning increased with increasing scaled discharge (Figure 13) and average temperature (Figure 14) for both sample seasons. Spawning probability decreased with increasing calendar day indicating spawning was more likely earlier in the sample season (Figure 15). The probability of spawning was higher in 2019 compared to 2020. The probability of spawning was highest in the North Wichita and South Wichita rivers and lowest in the North and Salt Fork rivers during both sample seasons.

We assessed fit of our zero model and calculated the amount of variance explained by both our fixed and random effects. Fixed effects in our zero-model explained 45% of the variance in the probability of spawning (marginal $R^2 = 0.45$). Including a random effect for stream increased the amount of variance explained by our model (conditional $R^2 = 0.61$). Adequate model fit was indicated by 95% of residuals falling within the error bounds of our binned residual plot for the zero model.

Our final count model contained scaled discharge, calendar day, a quadratic term for calendar day, 10-day CV of discharge, and year as fixed effects and a random effect for stream (Table 10). The number of observed Prairie Chub hatches per spawning day increased with increasing scaled discharge and CV of discharge. The estimated number of hatches per spawning day were higher in 2019 than in 2020. There was a statistically significant non-linear relationship with calendar day suggesting a threshold relationship existed where the highest frequency of hatches per day peaked in late June through early July in both years (Figure 16). The number of hatches per day was highest in the Pease and Red rivers and lowest in the Salt Fork and South Wichita rivers for both years (see also Figures A1-A3).

We assessed model fit of our count model and calculated the amount of variance explained by the fixed effects. Our fixed effects accounted for 57% of the variation in our data. Adequate model fit was indicated by a uniform distribution on the QQ plot and lack of patterns in the scatterplot of the DHARMa diagnostic plots.

III. DISCUSSION & RECOMMENDATIONS

Prairie Chub Movement

This study provides direct measurements of Prairie Chub movement distances and rates. Ruppel et al. (2020) recently inferred seasonal movement of Prairie Chub based on occurrence of age groups along upstream to downstream gradients in the Pease and North Fork Wichita rivers in Texas. Though the authors concluded that Prairie Chub are capable of long-distance upstream movements, no quantitative assessment of movement was provided. Wilde (2016) used VIE tagging and mark-recapture to track movement of closely related Peppered Chub *Macrhybopsis tetranema* in the Canadian River of Texas, the presumed last remaining population for that species (Pennock et al. 2017). However, because of limited recaptures, movement rate could only be estimated when combined with Plains Minnow *Hybognathus placitus* and Arkansas River Shiner *Notropis girardi* to yield a rate of 370 m/d (Wilde 2016). Compared with this estimate, our empirical measures of Prairie Chub movement rate for the mobile component were twice as fast for 2019 (i.e., 740 m/d) and largely consistent for 2020 (i.e., 258 m/d). These results collectively point to Prairie Chub and closely related Peppered Chub moving farther than expected under the RMP. However, we did not find bias in summer upstream movement as would be expected under the CCH. Instead, we found that summer movements were strongly leptokurtic and nearly symmetrical in terms of upstream versus downstream distances. This finding is consistent with results from a movement study of Flathead Chub *Platygobio gracilis* in a Colorado stream (Walters et al. 2014). Flathead Chub showed upstream bias in reproductive readiness but not movement (April-October), although an artificial barrier placed on the stream blocked upstream movement. Later evidence suggesting that Flathead Chub produce non-adhesive eggs that are displaced potentially long distances downstream alluded to upstream movement as a requirement as described in the CCH (Bestgen et al. 2016). Thus, for at least Flathead Chub in Colorado and Prairie Chub in our study system, neither the RMP nor the CCH fully describes summer movement dynamics by adult fish. We suggest these findings point to an existing drift paradox for Great Plains fishes (Archdeacon et al. 2018; Platania et al. 2020; Ruppel et al. 2020).

Resolving the drift paradox for Prairie Chub and similar Great Plains fishes will be helped with a deeper understanding of their reproductive biology. The obligatory nature of downstream drift for ova during the early development period for PBS fishes was first proposed by Moore (1944) for Arkansas River Shiner and similar characteristics were later noted for Peppered Chub (Bottrell et al. 1964). Observations of spawning by PBS fishes held in captivity, including Speckled Chub *M. aestivalis* and Sickelfin Chub *M. meeki*, remain some of the most detailed accounts of Great Plains PBS reproductive ecology and support the notion that ova remain in suspension during development and are therefore transported downstream (Platania and Altenbach 1998; Albers and Wildhaber 2017). Properties of eggs documented during captive spawning led to the use of egg surrogates termed passive drifting particles (PDPs) in experiments testing characteristics of drift, displacement, and retention of passive drifting particles (Worthington et al. 2014; Medley et al. 2007; Widmer et al. 2012; Dudley and Platania 2007).

More information on movement by Great Plains fishes could help resolve the considerably debate about these species' reproductive ecology. For example, Medley et al. (2007) modeled drift and retention of PDPs that simulated PBS Pecos Bluntnose Shiner *Notropis simus pecosensis* eggs in the middle Pecos River and concluded that retention was high enough in the upstream section of river that drift into the lower, degraded reach posed little threat to the species. Zymonas and Propst (2009) reanalyzed the PDP data presented by Medley et al. (2007) and suggested that drift into the lower, degraded reach was in fact likely. Chase et al. (2015) used otolith microchemistry of adult Pecos Bluntnose Shiner to show that 82% of ova drifted and hatched in the lower reach and the fished then moved to the upper reach, whereas the remaining 18% of individuals hatched in the upper reach and remained resident. This example highlights that retention of at least some ova at upstream locations is possible, but the retained portion is small relative to the portion of the population that might be transported downstream. In the context of Prairie Chub, collection of a limited number of age-0 individuals at upstream sites by Ruppel et al. (2020) suggests that at least a portion of the population is retained upstream, but dominance of age-0 fish downstream is consistent with either downstream displacement during drift or greater recruitment at downstream locations. As a second example, drift rates for PDPs in the North Canadian and Canadian rivers in Oklahoma, two systems comparable to the Red River, ranged from 0.07 to 0.55 m/s depending on discharge and channel geomorphology (Worthington et al. 2014). These rates equate to 6-47 km/d and over a 3-day period (i.e., presumed larval development timing; Albers and Wildhaber 2017) that could result in downstream distances ranging from 18 to143 km. If consistent drift distances occur in the Red River system, our data suggest the mobile component of the Prairie Chub population could move comparable distances (i.e., 32-91 km) within in a single summer. Based on data collected during this study, high rates of dispersal in either upstream or downstream directions, rather than upstream alone, could present a solution to the apparent drift paradox.

Although we provide insight to movements by Prairie Chub across two summers, additional information on movements in other seasons would be beneficial to our understanding of their movement ecology. We tagged Prairie Chub fish during the known spawning period and our study was limited to tracking movements of individuals between 45 and 70-mm TL. It is possible that there is an upstream bias in movement during other times of the year or by smaller fish (e.g., Chase et al. 2015; Archdeacon et al. 2018). Future studies gathering individual information across a broader range of fish sizes and seasons would provide greater insight. Use of p-chips to collect individual movement data for diminutive fishes is one possible strategy (Moore and Brewer 2021). Alternatively, the application of otolith microchemistry in a manner consistent with Chase et al. (2015) could be used to test for movements by individuals that are too small to tag with VIE or p-chips.

Another unknown from our study was the ultimate fate of the large number of tagged fish that were never recaptured. Our recapture rate (i.e., 3.7%) was similar to other studies that used VIE on freshwater PBS fishes. Platania et al. (2020) tagged 11,500 Rio Grande Silvery Minnow *Hybognathus amarus* and had a 0.6% recapture rate, whereas Wilde (2016) tagged three PBS species with recapture rates varying from 1.4% for Arkansas River Shiner, 0.8% for Plains Minnow, and 8.7% for Peppered Chub. However, we suggest that recapture number is more important than percentage (e.g., 50% recapture of 6 individuals would not give enough statistical power to analyze an entire population) and our numbers of recaptured fishes matched or exceeded previous movement studies of fishes (Wells et al. 2017; Platania et al. 2020). However, the fate of uncaptured individuals could be related to movement outside our search areas, predation or other mortality, tag loss, or our not detecting tagged fish using our sampling gear. Rodríguez (2002) suggested high turnover in Salmonidae fishes could not be used to conclude larger displacement distances because tagged fish could move only short distances outside of search areas. Our search area (i.e., 5 km) was two orders of magnitude greater than the typical 50-m search reach Rodriquez used, which suggests our search reach was relatively large and turnover caused by short movements (about 50 m) was unlikely to be the major reason tagged fish were not recaptured. Our mark-recapture study used an unprecedented search area relative to fish body size and documented relatively long distances moved compared to similarly sized fishes in the ‘fishmove’ dataset. This ultimately supports the notion that fishes are capable of greater movements that might be expected under traditional thinking.

Conservation of Prairie Chub and ecologically similar species is likely to benefit from preservation and management of broadly connected habitats. Dudley and Platania (2007) demonstrated the combined threats that flow alteration and habitat fragmentation pose to PBS fishes, particularly downstream transport of ova into reservoirs where survival and recruitment are presumed limited. Results from several studies in the Great Plains show local extirpations of PBS fishes in truncated stream fragments (Worthington et al. 2014; Wilde and Urbanczyk 2013; Perkin and Gido 2011; Dudley and Platania 2007), though the mechanisms are debatable. Hoagstrom (2014) suggested there was a lack of evidence that fragmentation alone had contributed to PBS fish extirpations, but Wilde and Urbanczyk (2014) provided examples of extirpations that occurred upstream of large barriers where interrupted dispersal was a likely explanation. As an example, Prairie Chub extirpation from the North Fork Red River upstream of Altus Reservoir was attributed to habitat fragmentation (Winston et al. 1991). More recently, the loss of PBS fishes, including *Macrhybopsis* spp., was documented from fragmented streams that either suffer the effects of extreme drought (e.g., Perkin et al. 2013, 2015a) or the long-term effects of water depletion, extraction, or diversion (Perkin et al. 2015b). Extreme drought events are known to suppress or thwart recruitment of PBS fishes (Perkin et al. 2019; Archdeacon et al. 2020), and under scenarios of local extirpation, populations can only persist when recolonization is possible. Mollenhauer et al. (2021) recently assessed broad-scale occurrence and detection patterns for Prairie Chub and found detection was lower during extended dry periods compared to wet periods. We found evidence of greater dispersal in 2019 when flows were higher compared to 2020 when flows were generally lower, which may relate to increased average detection across multiple sites (i.e., more sites with fish). Further hypothesis testing is needed to completely understand the linkage between flow and dispersal, but positive correlation between flow and dispersal are apparent in many mobile populations (Wells et al. 2017). Prior to our study, the distances PBS fishes such as Prairie Chub were able to move to (re)colonize river segments was largely unknown outside of qualitative descriptions of “long distances” (Ruppel et al. 2020). Our work provides empirical evidence for high dispersal and potential movement ranges that far exceed those expected for the average river fish. The validity of this finding is further supported by movement of Plains Killifish *Fundulus zebrinus* studied in the same system and using the methods, which ultimately found agreement between the RMP and movement by a non-PBS species (Santee et al., 2021).

Prairie Chub Spawning

Prairie Chub spawning peaked in early June in both seasons whereas some spawning generally occurred over a 6-month protracted season. This bet-hedging reproductive strategy is common among fishes in prairie rivers including pelagophils (Platania and Altenbach 1998; Durham and Wilde 2006; Hoagstrom and Turner 2015). Spawning began in April, peaked in early June, and tapered off through September (i.e., non-linear) in both sample seasons (i.e., 2019 and 2020). Similar timing of peak reproductive effort has been documented in other prairie stream fishes (e.g., Arkansas River Shiner, Plains Minnow, Flathead Chub, Red Shiner *Cyprinella lutrensis,* Durham and Wilde 2006) including Peppered Chub (Durham and Wilde 2006). Spawning earlier provides a longer growing period, faster growth, and subsequently increases recruitment success in prairie stream cyprinids (e.g., Arkansas River Shiner, Plains Minnow, Flathead Chub, Red Shiner, Durham and Wilde 2005). However, as part of another sampling effort, age-0 Prairie Chub measuring < 20-mm TL were found in the Wichita River mainstem after a high discharge event in early November 2020 which indicated that spawning occurred as late as October. Although Prairie Chub reproduced through October, later spawning dates provide a narrow window for growth prior to winter and may contribute to over-winter mortality. Therefore, timing of spawning may be a strong determinant of recruitment (see also abundance estimates). Although we show general patterns of long-term reproduction by Prairie Chub, it is more important to focus on the spatial and temporal patterns of spawning we observed (i.e., differences among rivers and years).

The positive linear relationship we found between Prairie Chub spawning probability and discharge corroborates an association between higher flows and spawning. The relationship with increasing discharge is not simply related to stream size because we standardized by drainage area. Higher flows, relative to the drainage area, related to increased spawning frequency and could be related to a variety of factors including facilitated propagule suspension, dispersal, and increased habitat availability (Platania and Altenbach 1998). Future efforts that examine spawning success related to discharge could help elucidate the relative importance of adult habitat selection or offspring success. This is especially important given Prairie Chub and other prairie stream fishes appear to spawn over a broad range of discharge conditions that include lower flows (e.g., Arkansas River Shiner, Peppered Chub, Plains Minnow, Flathead Chub, Red Shiner, Durham and Wilde 2006; Prairie Chub, this study). Interestingly, increased variation in discharge was related to increased spawning frequency, suggesting future flow management, if desired, would benefit from consideration of variability and not just higher discharge during the spawning season. A threshold relationship between discharge variability and recruitment has been observed in some prairie stream fishes (e.g., Shoal Chub, Rodger et al. 2016; Flathead Chub, Haworth and Bestgen 2017) suggesting too much variability may reduce recruitment by damaging or displacing propagules downstream. Although the frequency of Prairie Chub hatches per spawning date increased with discharge variability (i.e., CV), it would be useful to determine optimal and potential threshold conditions for both spawning and recruitment especially if future discharge regulation such as prescribed dam releases is of interest (Freeman et al. 2001; Poff et al. 2003).

Increased Prairie Chub hatches at higher temperatures support the importance of temperature for spawning and recruitment of prairie stream fishes. Temperature is considered a primary mechanism governing spawning and growth of prairie stream fishes (e.g., Central Stoneroller *Campostoma anomalum*, Orangethroat Darter *Etheostoma spectabile*, Brassy Minnow *Hybognathus hankinsoni*, Fathead Minnow *Pimephales promelas*, and Creek Chub *Semotilus atromaculatus*, Falke et al. 2010; Arkansas River Shiner, Plains Minnow, Flathead Chub, Red Shiner, and Peppered Chub, Durham and Wilde 2005a; Flathead Chub, Hawthorn and Bestgen 2017). Temperature may also affect recruitment by influencing larval incubation periods (Gillooly et al. 2002) and dissolved oxygen (Mueller et al. 2017). The highest observed air temperatures in 2019 (34.7 °C) and 2020 (34.6 °C) did not reach known hyperthermia tolerances (37-41 °C) of Great Plains fishes (e.g., Red River Pupfish *Cyprinodon rubrofluviatilis*, Plains Killifish *Fundulus zebrinus,* Plains Minnow, Smalleye Shiner, Ostrand and Wilde 2001). This does not imply an absence of a threshold response but that it is higher than the air temperatures we observed in 2019 and 2020.

The general timing of peak reproductive effort may also correspond to photoperiod. Consistent spawning initiation for fishes across variable conditions suggests photoperiod may be an important spawning cue (e.g., temperate fishes, De Vlaming 1972; Flathead Chub, Haworth and Bestgen 2017). Photoperiod is a recurring and predictable indicator of seasonal variation. Due to the spatial and temporal scale of our study, photoperiod and date were correlated so we could not include both variables in our analysis. Although a relationship between spawning initiation and photoperiod may exist, a laboratory study would be needed to separate date and photoperiod if deemed of interest.

The probability of spawning and frequency of Prairie Chub hatches per spawning date were higher in 2019 than in 2020 and correspond to changes in coarse scale patterns. In particular, 2019 was a wet year, whereas 2020 was relatively dry. In 2020, lower stream flows also corresponded to higher salinity, a predominant factor governing Prairie Chub. This suggests that temporal variation in Prairie Chub spawning and recruitment may be related to coarser scale discharge and other physicochemical patterns. However, different patterns emerge at different scales (Wiens 1989) and long-term data on Prairie Chub spawning are lacking. Understanding how spawning relationships vary over time could inform management decisions and potentially aid in predicting trends in population size. Therefore, long-term monitoring efforts would be beneficial if population predictions are of management interest.

The probability of spawning and frequency of Prairie Chub hatches per spawning date varied by stream suggesting coarse-scale spatial variation likely influences Prairie Chub spawning. Prairie Chub abundance is predominantly governed by a strong threshold relationship with salinity (see abundance results) whereas occurrence is related to mainstream connectivity and artificial fragmentation (Mollenhauer et al. 2021). The South Wichita river dried completely upstream of our sample site and periodically dried to isolated pools during both years which may have contributed to lower frequency of hatches per day. The North Wichita river tend to have higher connectivity and discharge during both seasons compared to the South Wichita River. Our results indicate strong spatial-temporal variation in recruitment success due primarily to connectivity and salinity conditions.

A large reservoir, Lake Kemp, located on the Wichita River mainstem (below the confluence of the North and South Wichita rivers) isolates Prairie Chub in the Wichita system from the Red River mainstem populations. Surprisingly, the North and South Wichita rivers had the highest spawning probabilities despite both natural (i.e., drying) and artificial (i.e., Lake Kemp reservoir) fragmentation. Therefore, the Wichita River population poses a unique research opportunity if managers seek to isolate finer-scale factors driving this success. Human disturbance including dams and nutrient inputs may also be related to variation in spawning within the North Fork and Pease rivers, respectively. Altus Dam is located on the North Fork of the Red River and is thought to have contributed to the extirpation of Prairie Chub upstream of the dam (Eisenhour 2004). Downstream degradation from dams including altered flow regime (Poff et al. 1997) and reduced habitat availability are often attributed to losses in native fish biodiversity (Meador and Carlisle 2012). Therefore, Lake Altus may contribute to the lower spawning probability of the North Fork and explain why relatively few age-0 Prairie Chub were collected in the North Fork during both sample years.

Water quality degradation due to municipal effluents may also contribute to variable recruitment success within the Pease River. Interestingly, the Pease River had the highest estimated number of hatches per spawning day whereas very few age-0 Prairie Chub were collected in the 2020 sample season. We observed excessive algal growth in the Pease River during both sample years presumably due to nutrient input from a waste treatment facility located on an upstream tributary. Nutrient input from wastewater treatment facilities can cause eutrophication, lower dissolved oxygen content, and may contain toxic contaminants including ammonia and chloride that negatively influence stream fish assemblages in prairie streams (Chambers et al. 1997; Cooke 2006). For example, sewage discharge in the Rio Grande River, New Mexico, threatens Rio Grande Silvery Minnow populations by increasing ammonia to toxic levels (Passell et al., 2007). In 2019, flows were higher and more variable which may have prevented the buildup of algae at our Pease River sample location until late July. In 2020, algal build up was present as early as late May and persisted throughout the reproductive season. Impaired water quality (e.g., high ammonia and low dissolved oxygen) combined with high temperatures during the reproductive season can cause fish kills in prairie stream fishes (e.g., Sharpnose Shiner, Plains Minnow, and Smalleye Shiner, Ostrand and Wilde 2001), which may negatively affect recruitment success. This may explain why age-0 Prairie Chub were more abundant (i.e., maximum sample size was achieved for every sample) in 2019 compared to 2020. If agencies are concerned about the possible implications of water quality on recruitment, then further investigation into the source and effects of the algal blooms in the Pease River, especially during periods of lower discharge, may be warranted.

Physicochemical conditions of the Prairie Dog Town Fork may inhibit Prairie Chub reproduction resulting in a population sink. Despite equal sampling efforts across streams, we did not observe age-0 Prairie Chub within the Prairie Dog Town Fork. Although discharge was higher in 2019 compared to 2020, the Prairie Dog Town Fork dried completely upstream of our sample location during both seasons. We observed emaciated adult Prairie Chub (n=8) at this site during a period of higher discharge in early June 2019 suggesting they may move into these areas when discharge is high. Additionally, we observed one adult in the Prairie Dog Town Fork upstream of our sample site in November 2019 that was farther upstream than previously recorded (Mollenhauer et al. 2021). Our observations of adult use when discharge was present, and the apparent lack of spawning evidence indicate that the Prairie Dog Town Fork may be a population sink for Prairie Chub. Salinity is a dominant factor governing Prairie Chub abundance; therefore, the lack of spawning maybe attributed to high salinities that are characteristic of the Prairie Dog Town Fork. Although predominant sources of salinity are natural (e.g., geology and salt springs), artificial input (e.g., oil and gas brine pollution) has increased salinity concentrations (Wurbs 2002). Concentrations exceeding salinity tolerance thresholds could functionally extirpate Prairie Chub from the Prairie Dog Town Fork (see also Ostrand and Wilde 2001; Higgins and Wilde 2005) even if they are able to reproduce during some years (i.e., under conditions we did not observe). If maintaining or repopulating this area is of interest, investigating salinity trends over time may be useful to assess both the sources of salinity and determine if concentrations have changed over time.

Although reproductive adults (i.e., gravid females and mature males) were commonly observed, the Salt Fork had the lowest spawning probability and lowest frequency of hatches per spawning date. Interestingly, our results suggest that recruitment success varies by stream despite evidence of spawning (i.e., spawning does not equate to successful recruitment).

Future research and management efforts would benefit by considering how recruitment relationships vary both temporally and spatially when allocating resources and efforts. Despite general support of a protracted spawning season, we show that successful reproduction does not guarantee successful recruitment and factors related to recruitment success may create a population bottleneck. Spatial variability including climate, connectivity, and human disturbances also poses a variety of considerations for future research and management efforts. Unique research opportunities exist to better understand how anthropogenic disturbances including dams in the North Fork and Wichita River systems, nutrient loading in the Pease River, and brines in the Prairie Dog Town Fork may affect Prairie Chub persistence. Because climatic and human disturbances are expected to increase, future research identifying the role of refugia (e.g., thermal and drought refuge) in the persistence of Prairie Chub and other prairie stream fishes within the Great Plains (Magoulick and Kobza 2003) might be beneficial. Lastly, despite cooperative efforts to captively spawn Prairie Chub and multiple attempts to mark otoliths via immersion in oxytetracycline hydrochloride, we were unable to spawn chub in the laboratory or confirm first band formation or band periodicity (i.e., we observed no bands on marked fish).

Unfortunately, Covid-related complications prevented the successful spawn of Prairie Chub in captivity during our study. Further studies to improve daily age estimation for Prairie Chub may be useful for refining spawning date estimates if finer-scale resolution is needed.

Prairie Chub Abundance

Adult and juvenile Prairie Chub densities both had strong quadratic relationships with salinity. Our findings showed Prairie Chub density peaked at a salinity of 10 ppt and then declined by nearly 100% when salinities reached 20 ppt indicating a tolerance threshold relationship with salinity (i.e., realized niche). Although Prairie Chub have been collected from isolated salt-encrusted pools at salinities up to 19.6 ppt (Echelle et al. 1972), our data suggest that lower salinities are preferable, and they may attempt to move away from these high-salinity areas. The regulatory relationship between salinity tolerance and distribution are apparent among stream-fish assemblages within the Great Plains (e.g., Plains Minnow *Hybognathus placitus*, Green Sunfish *Lepomis cyanellus*, and Western Mosquitofish *Gambusia affinis,* Echelle et al. 1972; Ostrand and Wilde 2001, Worthington et al. 2018) including sympatric *Machrybopsis spp*. (Eisenhour 2004; Ruppel et al. 2020). For example, Sotola et al (2019) found that Prairie Chub, Shoal Chub, and their hybrid distribution partitioning followed a gradient of specific conductance levels across sympatric regions of the upper Red River basin. Future efforts to examine movement in the streams with higher salinity levels may provide insight into the species ability to navigate changing salinity levels. Though the mechanism is unknown, the apparent absence of Prairie Chub in lower salinities may also be related to other extrinsic factors (e.g., competition, reduced predation, Echelle et al. 1972, Gido and Propst 1999). It is possible that moderate salinities may result in a competitive advantage for Prairie Chub; conversely, salinity may be an important factor related to physiology or their life history (e.g., egg development).

We found Prairie Chub abundance was also strongly influenced by coarse-scale longitudinal variation across the upper Red River basin. Prairie Chub adults and juvenile abundance increased downstream. Western reaches of the upper Red River basin have lower rainfall, greater fragmentation by dams, and higher salinities compared to eastern (i.e., downstream) reaches. Additionally, pools critical for refuge during droughts are less likely to form in the headwaters of prairie streams (Taylor et al. 1996). However, longitude was not highly correlated with climatic variables including ecoregion (i.e., Southwestern Tablelands and

Central Great Plains level III ecoregions) or fragmentation metrics. Therefore, factors not captured by our metrics such as long-term streamflow patterns may explain the relationship between Prairie Chub abundance and longitude (see below).

Coarse-scale flow regime patterns may account for some variability in Prairie Chub abundance and distribution. Coarse-scale Prairie Chub occurrence was related to long-term flow regime metrics including flow magnitude, downstream open mainstem, and flood duration (Mollenhauer et al. 2021). Flow regime patterns may vary depending on the scale of observations. It is not possible to capture long-term streamflow variability in a two-year study, though variability may relate to long-term abundance patterns. However, our study did coincide with greatly contrasting streamflows in 2019 and 2020 which provides insight on relationships to discharge at finer scales.

Relationships between discharge and Prairie Chub abundance varied in 2019 and 2020. During 2019, discharge was higher and more persistent providing connectivity to western stream reaches. Contrastingly, in 2020, western reaches of the North Fork, Salt Fork, Prairie Dog Town Fork, Pease River, and South Wichita rivers had little to no streamflow or dried completely. Although seasonal fragmentation due to drying is characteristic of the basin, current water development practices and climate change are thought to exacerbate fragmentation and contribute to declines in the distributions of prairie stream fishes (Perkin et al. 2015a). Therefore, it is important to understand how Prairie Chub discharge relationships vary at both fine and coarse temporal scales (Wiens 1989). For example, in 2019 when flows and connectivity were higher, we observed a single adult Prairie Chub farther west than historically indicated by naïve occurrence surveys (Mollenhauer et al. 2021; Figure 2). Although flow patterns relate to distributions, it is unclear how this might regulate abundance.

We anticipated the positive relationship observed between turbidity and adult Prairie Chub abundance. Decreased turbidity is associated with decreased abundances of prairie stream fishes (e.g., Plains Minnow, Smalleye Shiner, and Sharpnose Shiner, Ostrand and Wilde 2001; Worthington et al. 2018). High turbidity caused by suspended sediments is characteristic of the upper Red River basin. Physiological adaptations including barbels, sensory papillae, and cutaneous taste buds allow Prairie Chub to feed efficiently in high turbidities (Davis and Miller 1967) and provide a competitive advantage over less tolerant fishes. Higher turbidity may also increase recruitment by increasing the duration that drifting eggs remain suspended (e.g., Rio

Grande Silvery Minnow *Hybognathus amarus,* Medley and Shirey 2013). Although tolerant of variable turbidities, a combination of environmental stressors may influence Prairie Chub abundance.

Thermal tolerance and other associated factors (e.g., dissolved oxygen) are known to influence the distributions of prairie stream fishes in the Red River. We observed Prairie Chub at temperatures of 9.2 – 31.6 °C indicating a broad thermal tolerance similar to that of other prairie stream cyprinids (Ostrand and Wilde 2001, Worthington et al. 2018). Despite their tolerance, the negative relationship observed between Prairie Chub density and water temperature suggests high temperatures may limit abundance. This relationship is likely exacerbated when combined with additional stressors. For example, high temperatures combined with low dissolved oxygen and high salinities can exacerbate stress and cause mortality in prairie stream fishes, especially in isolated pools (Matthews and Zimmerman 1990; Ostrand and Wilde 2001).

The relationships between Prairie Chub abundance and discharge, temperature, and turbidity varied between size classes. Relationships to biotic and abiotic factors may vary among ages and size classes within stream fish populations (Schlosser 1985). Juvenile fishes can often tolerate a broader range of environmental conditions than adults including lower dissolved oxygen (Everett and Crawford 2010) and higher temperatures during the first summer growth period (Turko et al. 2020). In contrast to adults, we found few relationships between juvenile Prairie Chub abundance and environmental parameters. As assumed pelagophils, Prairie Chub propagules are broadcasted into the water column and require adequate streamflow to remain suspended and increase recruitment success (Durham and Wilde 2009). Whether propagules are retained or drift downstream is dependent on factors including adult spawning location, streamflow variability, and habitat complexity (Widmer et al. 2012; Worthington et al. 2014). Moreover, juveniles may not yet have the swimming ability to migrate long distances to locate preferred habitat. Consequently, juvenile abundance relationships during their first summer may be contingent upon a combination of deterministic and stochastic processes.

Variation in adult and juvenile Prairie Chub abundance estimates across streams and seasons may provide insight on population source-sink dynamics. The Prairie Dog Town Fork and Elm Fork had the lowest adult abundance with few adults estimated in 2019, zero adults in 2020, and zero juveniles for both years. Although these two streams may be used by adults in wet years, it seems unlikely that they contribute to recruitment. Future efforts to model changing salinities over time (i.e., have they increased?) could provide important information relevant to developing criteria for re-establishing populations in these streams.

Juvenile Prairie Chub abundance estimates may help elucidate variation in recruitment success across streams. Pelagophil recruitment success is known to vary across environmental conditions (Durham and Wilde 2005, 2006). Similar to other pelagophils, Prairie Chub spawning does not guarantee successful recruitment. For example, asynchronous spawning of pelagophils has been observed in isolated pools with little to no recruitment success (Durham and Wilde 2008a). Accordingly, despite evidence of spawning in the Pease River, estimated adult and juvenile abundance was low in both years, indicating low recruitment. However, in the North Wichita and Wichita River mainstem, abundance estimates for both years were consistently higher for juveniles compared to adults which may indicate a higher rate of recruitment success in these streams regardless of relatively wet or dry year conditions.

Prairie Chub capture probability relationships with discharge, temperature, and turbidity had little influence on our abundance estimates (i.e., weak effects). Capture probabilities of prairie stream fishes may vary due to environmental conditions (Peterson and Rabeni 2001; Lyon et al. 2014; Mollenhauer et al. 2018). However, we found little evidence that Prairie Chub capture probability relationships were important during our study, though environmental conditions in other years could change these relationships. Interestingly, as temperatures increased, we often captured Prairie Chub in deeper channels that were contiguous with a sand bar or stream bank (i.e., edge or trough, Cant 1978, O'Neill 2010). Stream banks or sand bars associated with edge habitats may increase capture probability by blocking escape (Bayley and Herendeen 2000). If adult Prairie Chub aggregate in edge habitats seeking thermal refuge, the resulting higher densities may also explain the increased capture probability (Ries et al. 2004). Overall, our findings suggest that under similar sampling conditions, capture probability would have little influence on Prairie Chub abundance estimates, though this is not the case for other species in Great Plains streams (Mollenhauer et al. 2018).

Our findings on Prairie Chub abundance relationships are intended to benefit management agencies interested in population monitoring and conservation of Prairie Chub and other prairie stream fishes. We produced the first abundance estimates (i.e., not catch per effort or counts) for Prairie Chub in the upper Red River basin. In doing so, our findings provide an important baseline that managers may use to assess the status and variation in Prairie Chub populations over time. Our findings on relationships with Prairie Chub abundance build upon known occurrence relationships and provide management agencies with a more complete picture of the factors and potential threats influencing Prairie Chub populations and persistence. Future monitoring, if under similar conditions, may be adequate (i.e., we found little to no detection relationships) without estimating capture probability. Threats attributed to the declines in Prairie Chub abundance and distributions are likely shared by other prairie stream fishes across the Great Plains (Worthington et al. 2018). Therefore, management decisions aimed to mitigate threats to Prairie Chub may also benefit fishes in the same reproductive guild.

Understanding the relationships between abundance and persistence of Prairie Chub and salinity, discharge, and fragmentation is helpful for agencies making management decisions. Managers face a difficult and growing challenge as threats to prairie stream fishes including water development (e.g., dams and water withdrawal), salinity alteration (e.g., desalination projects, oil field salt brine contamination) and climate change are expected to increase as competition for water drives further human disturbance (Covich et al. 1997; Williams 2001; Bunn et al. 2006). The strong relationship between Prairie Chub abundance and salinity may be useful to consider when desalinization projects are proposed. Because salinity may narrow the realized niche of Prairie Chub, it might be worth agency consideration when actions are proposed that result in large changes in salinity concentrations in the species remaining habitat. However, there may be some opportunities to desalinize areas that have greater salinity concentrations than historical baselines and to revert conditions back to historical levels. Lastly, because discharge patterns are important to Prairie Chub abundance and life history, managers might consider the effects of discharge variability and connectivity when considering additional water permit requests.

IV. SIGNIFICANT DEVIATIONS

There have been no significant deviations.

V. EQUIPMENT

No equipment was purchased.

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Table 1. Sampling dates during summers of 2019 and 2020 for each river showing the number of fish tagged (T) and recaptured (R) and discharge (Q, cms). The final sampling dates for the Red River and Salt Fork Red River in August 2020 were long-distance searches and no fish were tagged.

2019	River	T(R)	Q (cms)	2020	River	T(R)	Q (cms)
Jun. 5-11	Pease	86(4)	15.12	Jun. 19-22	Pease	332(2)	0.44
Jul. 16-17	Pease	88(0)	1.08	Jul. 7-9	Pease	27(1)	1.16
Jul. 31 – Aug. 2	Pease	110(1)	0.24	Jul. 24-26	Pease	11(1)	0.37
Aug. 9-12	Pease	95(2)	0.02	-	-	-	-
Total	Pease	379(7)		Total	Pease	370(4)	
May 15-18	Red	576(3)	302.99	Jun. 16-18	Red	955(13)	5.52
Jun. 25-27	Red	113(6)	61.45	Jul. 4-6	Red	404(19)	5.10
Jul. 19-22	Red	95(2)	27.92	Jul. 21-23	Red	677(12)	2.97
Aug. 3-5	Red	96(1)	14.53	Aug. 12	Red	NA(18)	2.18
Total	Red	880(12)		Total	Red	2,036(62)	
Jun. 28- Jul. 1	Salt Fork	59(1)	4.87	Jun. 24-26	Salt Fork	284(4)	1.10
Jul. 23-25	Salt Fork	191(3)	3.23	Jul. 17-19	Salt Fork	404(26)	0.76
Aug. 6-8	Salt Fork	436(20)	2.75	Aug. 4-6	Salt Fork	178(18)	0.31
Aug. 13-15	Salt Fork	541(51)	3.14	Aug. 10-11	Salt Fork	NA(5)	0.27
Total	Salt Fork	1,227(75)		Total	Salt Fork	866(53)	
Grand total	All	2,486(94)		Grand Total	All	3,272(119)	

Table 2. Data sources and location of each station collecting air temperature and precipitation data for 7 rivers of the southern Great Plains. We collected data from both Oklahoma Mesonet and Texas Automated Surface Observing System (ASOS). Station ID is a unique station identifier relevant to these data sources. The North and South Wichita River sites were located within 4.8 km of one another and therefore shared data between sites.

River	Station name, location	Station ID	Data Source
Red River	Grandfield, OK	GRA2	Oklahoma Mesonet
Salt Fork	Altus, OK	ALTU	Oklahoma Mesonet
North Fork	Tipton, OK	TIPT	Oklahoma Mesonet
Pease River	Wilbarger county airport, Vernon, TX	KF05	Texas ASOS
North Wichita	Wichita Falls, TX	KSPS	Texas ASOS
South Wichita	Wichita Falls, TX	KSPS	Texas ASOS
Prairie Dog Town Fork	Childress municipal airport, Childress, TX	KCDS	Texas ASOS

Table 3. Results from our top ranked zero models within 2 AIC_c of the top model with the highest weight (n=4) and the intercept only (i.e., null) model where p_{it} is the probability of spawning on the logit scale, β_0 is the grand intercept, and β_1 to β_x are slopes associated with the predictor variables scaled discharge, temperature, CV, and calendar day. We included a random effect for stream v_t and a fixed effect for year α_1. The number of parameters (K) are reported for each model. We ranked our models using Akaike's information criterion adjusted for small sample size (AICc). ΔAICc represents the difference between the given model and the top model in terms of AICc. Likelihood and Akaike weight (wi) indicate the relative support for each model. The marginal (R^2m; variance explained by fixed effects) and conditional (R^2c; variance explained by fixed and random effects) R^2 are reported.

Zero model	K	AIC_c	ΔAIC_c	Likelihood	W_i	R^2_m	R^2_c
$\text{logit}(p_{it}) = \beta_0 + \alpha_1 + \beta_1\text{ScaledDischarge}_1 + \beta_2\text{Temperature}_2 + \beta_3\text{Day}_3 + v_t + \varepsilon_{it}$	7	1674.19	0.00	-831.078	0.40	0.45	0.61
$\text{logit}(p_{it}) = \beta_0 + \alpha_1 + \beta_1\text{ScaledDischarge}_1 + \beta_2\text{Temperature}_2 + \beta_3\text{Day}_3 + \beta_4\text{CV}_4 + v_t + \varepsilon_{it}$	8	1674.62	0.43	-830.285	0.33	0.45	0.60
$\text{logit}(p_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1\text{ScaledDischarge}_1 + \beta_2\text{Temperature}_2 + \beta_3\text{Day}_3 + \beta_4\text{CV}_4 + v_t + \varepsilon_{it}$	9	1676.21	2.01	-831.078	0.15	0.45	0.60
$\text{logit}(p_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1\text{ScaledDischarge}_1 + \beta_2\text{Temperature}_2 + \beta_3\text{Day}_3 + v_t + \varepsilon_{it}$	8	1676.59	2.39	-830.262	0.12	0.45	0.61
$\text{logit}(p_{it}) = \beta_0 + v_t + \varepsilon_{it}$	3	2255.82	581.62	-1125.91	0.00	NA	NA

Table 4. Results from our top ranked count models within 2 AIC$_c$ of the top model with the highest weight (n=14) and the intercept only (i.e., null) model. Y_{it} is the estimated number of Prairie Chub hatches per spawning day on the log scale, β_0 is the grand intercept, and β_1 to β_x are slopes associated with the predictor variables of scaled discharge, temperature, CV, and calendar day. We included a random effect for stream v_t and fixed effects for year α_1 and precipitation α_2. The number of parameters (*K*) is reported for each model. Models were ranked using Akaike's information criterion adjusted for small sample size (AICc). ΔAICc represents the difference between the given model and the top model in terms of AICc. Likelihood and Akaike weight (wi) indicate the relative support for each model. The marginal (R^2m; variance explained by fixed effects) are reported.

Count Model	*K*	AIC$_c$	ΔAIC$_c$	Likelihood	W_i	R^2_m
$\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1\text{Discharge}_1 + \beta_2\text{Day}_2 + \beta_3\text{Day}_3^2 + \beta_4\text{CV}_4 + v_t + \varepsilon_{it}$	8	1657.028	0	-820.37	0.12	0.57
$\log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1\text{Discharge}_1 + \beta_2\text{Day}_2 + \beta_3\text{Day}_3^2 + \beta_4\text{CV}_4 + v_t + \varepsilon_{it}$	9	1657.85	0.82	-819.74	0.07	0.55
$\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1\text{Discharge}_1 + \beta_2\text{Day}_2 + \beta_3\text{Day}_3^2 + \beta_4\text{CV}_4 + \beta_5\text{Temperature}_5 + v_t + \varepsilon_{it}$	9	1658.22	1.19	-819.93	0.06	0.56
$\log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1\text{Day}_1 + \beta_2\text{Day}_2^2 + \beta_4\text{CV}_4 + v_t + \varepsilon_{it}$	8	1658.63	1.60	-821.17	0.05	0.54
$\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1\text{Day}_1 + \beta_2\text{Day}_2^2 + \beta_4\text{CV}_4 + v_t + \varepsilon_{it}$	7	1658.87	1.85	-822.33	0.04	0.56
$\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1\text{Discharge}_1 + \beta_2\text{Day}_2 + \beta_3\text{Day}_3^2 + \beta_4\text{CV}_4 + \beta_5\text{Day}_5^2 + v_t + \varepsilon_{it}$	9	1658.96	1.93	-820.30	0.04	0.57
$\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1\text{Discharge}_1 + \beta_2\text{Discharge}_2^2 + \beta_3\text{Day}_3 + \beta_4\text{Day}_4^2 + \beta_5\text{CV}_5 + v_t + \varepsilon_{it}$	9	1659.06	2.03	-820.35	0.04	0.58
$\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1\text{Temperature}_1 + \beta_2\text{Day}_2 + \beta_3\text{Day}_3^2 + \beta_4\text{CV}_4 + v_t + \varepsilon_{it}$	8	1659.28	2.25	-821.49	0.04	0.55
$\log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1\text{Discharge}_1 + \beta_2\text{Temperature}_2 + \beta_3\text{Day}_3 + \beta_4\text{Day}_4^2 + \beta_5\text{CV}_5 + v_t + \varepsilon_{it}$	10	1659.38	2.35	-819.47	0.03	0.55
$\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1\text{Discharge}_1 + \beta_2\text{Temperature}_2 + \beta_3\text{Temperature}_3^2 + \beta_4\text{Day}_4 + \beta_5\text{Day}_5^2 + \beta_6\text{CV}_6 + v_t + \varepsilon_{it}$	10	1659.51	2.48	-819.53	0.03	0.55
$\log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1\text{Temperature}_1 + \beta_2\text{Day}_2 + \beta_3\text{Day}_3^2 + \beta_4\text{CV}_4 + v_t + \varepsilon_{it}$	9	1659.75	2.72	-820.70	0.03	0.53
$\log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1\text{Discharge}_1 + \beta_2\text{Day}_2 + \beta_3\text{Day}_3^2 + \beta_4\text{CV}_4 + \beta_5\text{CV}_5^2 + v_t + \varepsilon_{it}$	10	1659.86	2.83	-819.71	0.03	0.56
$\log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1\text{Discharge}_1 + \beta_2\text{Discharge}_2^2 + \beta_3\text{Day}_3 + \beta_4\text{Day}_4^2 + \beta_5\text{CV}_5 + v_t + \varepsilon_{it}$	10	1659.89	2.86	-819.72	0.03	0.56
$\log(Y_{it}) = \beta_0 + v_t + \varepsilon_{it}$	3	1739.02	81.99	-866.49	0.00	NA

Table 5. The number of age-0 Prairie Chub collected by river (n=7) in the 2019 and 2020 sample seasons. The total represents the combined number of Prairie Chub captured in both seasons.

Stream	2019	2020	Total
North Wichita	344	266	610
Red River	351	181	532
South Wichita	210	173	383
Pease River	311	7	318
North Fork	123	3	126
Salt Fork	39	9	48
Prairie Dog Town Fork	0	0	0

Table 6. Description of USGS fragmentation metrics used to measure aspects of dam proximity, dam density, and connectivity relative to each site (Cooper et al. 2017). Upstream metrics include UNDR and UNDC. Downstream metrics include DMO, DMD, and DM2D. Total metrics (i.e., combined upstream and downstream) include TMO, TMD, and TM2D.

Metric	Description
UNDR	Upstream network dam density along the stream network (units are in number of dams per 100 rkm)
UNDC	Upstream network dam density within the network catchment (units are in number of dams per 100 km^2 of catchment)
TMO	Percentage of total mainstem length free of dams.
TMD	Total density of mainstem dams.
TM2D	Total mainstem distance (rkm) between nearest upstream and nearest downstream dams.
DMO	Percentage of downstream mainstem length free of dams
DMD	Density of downstream mainstem dams
DM2D	Distance (rkm) to nearest downstream mainstem dam (DM2D)

Table 7. Mean annual discharge (m^3/sec), range (in parentheses), and percentile (relative to 30 years of record, 1990-2020) for the Red River, Pease River, North Wichita River, South Wichita River, North Fork of the Red River, Salt Fork of the Red River, and Prairie Dog Town Fork for both sample seasons (i.e., 2019, 2020). Gage numbers are provided in the methods (U.S. Geological Survey, 2020).

Stream	2019 discharge mean (range)	2019 (%)	2020 discharge mean (range)	2020 (%)
Red River	71.19 (6.14 – 730.57)	90	11.94 (1.53-184.63)	22
Pease River	3.91 (0.00 – 91.18)	76	0.82 (0.00 – 8.50)	20
North Wichita	1.50 (0.05 – 25.97)	61	0.54 (0.00 - 8.33)	8
South Wichita	1.18 (0.00 – 37.94)	69	0.54 (0.00 – 36.53)	31
North Fork	38.00 (0.65- 705.09)	95	3.92 (0.65 – 127.72)	22
Salt Fork	9.57 (1.11 – 231.35)	96	1.83 (0.16 – 39.36)	19
Prairie Dog Town Fork	1.45 (0.00 – 79.57)	24	0.50 (0.03 – 15.6)	5

Table 8. Summary of age estimates and spawning dates for age-0 Prairie Chub collected by river (n=7) and season (2019, 2020). From left to right this table summarizes the number of Prairie Chub aged successfully in each year (Aged), the number of age estimates retained each year (i.e., met double reader agreement or conference standards, in parentheses), the number of days where at least 1 hatch occurred (No.) each year, the range of total lengths (TL), the estimated daily ages of Prairie Chub (Ages), and the range of successful spawning dates observed in 2019 and 2020 (Spawn).

River	Aged 2019	Aged 2020	No. 2019	No. 2020	TL	Ages	2019 Spawn	2020 Spawn
North Wichita	344 (299)	266 (136)	93	57	13-41	24-87	4/17-8/12	5/11-7/28
Red River	351 (300)	181 (153)	69	46	11-39	14-64	5/13-8/6	5/14-7/13
South Wichita	210 (160)	173 (101)	62	36	14-41	10-84	4/15-9/20	5/13-7/8
Pease River	311 (302)	7 (7)	53	6	17-40	18-74	4/24-7/12	6/2-8/1
North Fork	123 (103)	3 (2)	53	2	17-40	27-73	5/6-8/11	6/6-6/12
Salt Fork	39 (34)	9 (9)	24	8	18-40	22-79	5/19-6/23	8/3-8/7
Prairie Dog Town Fork	0 (0)	0 (0)	0	0	NA	NA	NA	NA

Table 9. Coefficient estimates (logit scale), standard error (SE), and 95% confidence intervals (CI) associated with our mixed effects logistic regression model relating the probability of Prairie Chub spawning to environmental parameters. The intercept represents the probability of spawning (logit scale) in 2019 at mean values for all other predictor variables. Discharge was scaled by drainage area. Year was a fixed effect.

Predictor variable	Estimate	SE	95% CI	p value
Intercept	-1.73	0.48	-2.68, -0.79	0.0003
Scaled discharge	1.49	0.48	1.25, 1.73	< 2e-16
Air temperature	1.38	0.12	1.16, 1.60	< 2e-16
Calendar day	-1.06	0.11	-1.28, -0.84	< 2e-16
Year 2020 (fixed effect)	-0.58	0.14	-0.87, -0.29	8.38e-05

Table 10. Coefficient estimates (log scale), standard error (SE), and 95% confidence intervals (CI) for our mixed effects negative-binomial regression model relating the number of Prairie Chub hatches per spawning date to physicochemical parameters. The intercept represents the estimated number of daily hatches (log scale) in 2019 at mean values of all predictor variables. Discharge was scaled by drainage area. CV is the coefficient of variation for discharge over 10 days prior to spawning. Year 2020 represents the shift in the intercept for the 2020 sample season. All continuous predictor variables (i.e., scaled discharge, calendar day, and CV) were standardized to a mean of zero and a standard deviation of one.

Predictor variable	Estimate	SE	95% CI	p value
Intercept	0.75	0.35	0.06, 1.43	0.032
Scaled discharge	0.19	0.09	0.00, 0.37	0.047
Calendar day (linear)	-0.67	0.08	-0.22, 0.09	0.401
Calendar day (quadratic)	-0.41	0.07	-0.55, -0.27	4.18e-19
CV	0.20	0.08	0.07, 0.37	0.016
Year 2020	-0.34	0.14	-0.62, -0.07	0.003

Table 11. Prairie Chub abundance model coefficients for both adult and juvenile models reported on the natural log scale from posterior distributions reported as the mode with associated 90% highest density intervals (HDIs). Coefficients include discharge, average water temperature, average water turbidity, linear and quadratic term for water salinity, and longitude. Segment and HUC are random error terms. SD is the standard deviation and ν is the normality parameters for the t-distribution of random error terms and overdispersion parameter η. The intercept is interpreted as the estimated number of Prairie Chub per meter squared at mean levels of covariates. All coefficients are interpreted with other variables held constant at mean levels.

Abundance coefficient	Adult mode (90% HDI)	Juvenile mode (90% HDI)
Intercept	-1.38 (-3.63, 0.77)	-6.69 (-10.88, -2.68)
Year 2020	0.12(-1.42, 1.57)	0.81 (-0.94, 2.71)
Discharge	1.10 (-0.10, 2.17)	0.41(-1.27, 1.83)
Water temperature	-0.47 (-1.33, 0.40)	0.24 (-0.96, 1.35)
Turbidity	0.58 (-0.56, 1.89)	-0.38 (-1.81,1.02)
Salt	6.17 (3.43, 9.15)	5.36 (2.05,9.89)
Salt^2	-6.18 (-9.61, -3.20)	-5.41 (-9.24, -1.69)
Longitude	-2.12(-3.84, -0.35)	-6.75 (-10.00, -3.80)
Segment SD	1.08 (0.00, 2.09)	1.55 (0.00, 3.20)
Segment ν	31.78(1.00, 69.91)	32.50 (1.01, 71.23)
HUC SD	0.86 (0.00,1.65)	2.37 (0.64, 4.06)
HUC ν	32.48 (1.02,71.07)	33.69 (1.07, 72.31)
η SD	1.39 (0.60, 2.14)	2.00 (1.03, 3.05)
η ν	27.68 (1.00, 64.78)	29.44 (1.00, 66.58)

Table 12. Covariate summary statistics for surveys completed in 2019: at all survey locations (Total survey mean), at locations where adult Prairie Chub were detected (n = 12, Adult PC), and where juvenile Prairie Chub were detected (n = 8, Juvenile PC). Covariates include discharge (m^3/sec), water temperature (°C), average survey turbidity (NTU), water salinity (ppt), and longitudinal coordinate of the surveyed reach. Summary statistics include the mean plus or minus the standard deviation, and range of covariate values.

Covariate	Total survey mean ± SD (range)	Adult PC mean ± SD (range)	Juvenile PC mean ± SD (range)
Discharge	0.55 ± 0.95 (0.00 - 5.00)	1.06 ± 1.46 (0.00 - 5.00)	1.34 ± 1.74 (0.00 - 5.00)
Water temperature	21.58 ± 7.12 (7.60 - 35.40)	18.27 ± 7.26 (9.20 - 29.20)	18.19 ± 7.84 (9.20 - 29.20)
Turbidity	1129.90 ± 1353.12 (124.80 - 4045.00)	962.40 ± 687.88 (124.80 - 2644.20)	1229.00 ± 1215.54 (160.60 - 3388.30)
Salinity	5.43 ± 5.57 (0.28 - 24.33)	7.01 ± 3.64 (2.81 - 14.33)	5.10 ± 2.02 (2.81 - 9.04)
Longitude	99.85 ± 0.61 (98.99 - 101.09)	99.52 ± 0.43 (99.10 - 100.75)	99.33 ± 0.16 (99.10 - 99.58)

Table 13. Covariate summary statistics for surveys completed in 2020: at all survey locations (Total survey mean, n =60), at locations where adult Prairie Chub were detected (n = 12, Adult PC), and where juvenile Prairie Chub were detected (n = 14, Juvenile PC). Covariates include discharge (m^3/sec), water temperature (°C), average survey turbidity (NTU), water salinity (ppt), and longitudinal coordinate of the surveyed reach. Summary statistics include the mean plus or minus the standard deviation, and range of covariate values.

Covariate	Total survey mean ± SD (range)	Adult PC mean ± SD (range)	Juvenile PC mean ± SD (range)
Discharge	0.17 ± 0.43 (0.00 - 2.68)	0.55 ± 0.79 (0.00 - 2.68)	0.59 ± 0.76 (0.00 - 2.68)
Water temperature	22.61 ± 7.47 (3.70 - 34.00)	24.90 ± 5.88 (13.60 - 31.60)	25.53 ± 4.56 (13.60 - 31.60)
Turbidity	783.10 ± 926.876 (124.80 - 4045.00)	1126.80 ± 751.84 (124.8 - 2731.70)	1198.40 ± 740.08 (124.80 - 2731.70)
Salinity	17.58 ± 30.85 (0.27 - 134.00)	7.90 ± 4.37 (2.62 - 16.00)	7.43 ± 3.90 (2.62 - 16.00)
Longitude	99.60 ± 0.34 (98.98 - 100.29)	99.46 ± 0.23 (98.98 - 99.79	99.44 ± 0.24 (98.98 - 99.79)

Table 14. Capture probability model coefficients for both adult and juvenile models (reported on the logit scale from posterior distributions) reported as the mode with associated 90% highest density intervals (HDIs). Coefficients include discharge, average water temperature, and average water turbidity. Year 2020 represents the deflection for the second season. The intercept is interpreted as the estimated Prairie Chub capture probability in 2019 at mean levels of covariates. All other coefficients are interpreted with other variables held constant at mean levels.

Capture probability coefficient	Adult mode (90% HDI)	Juvenile mode (90% HDI)
Intercept	-0.23 (-0.47, 0.02)	-0.58 (-0.72, -0.44)
Year 2020	0.45 (0.15, 0.75)	-0.28 (-0.45, -0.10)
Discharge	-0.18 (-0.30, -0.05)	-0.09 (-0.21, 0.03)
Turbidity	0.40 (0.30, 0.48)	0.21(0.03,0.40)
Water temperature	0.32 (0.17, 0.47)	-0.09 (-0.20, 0.02)

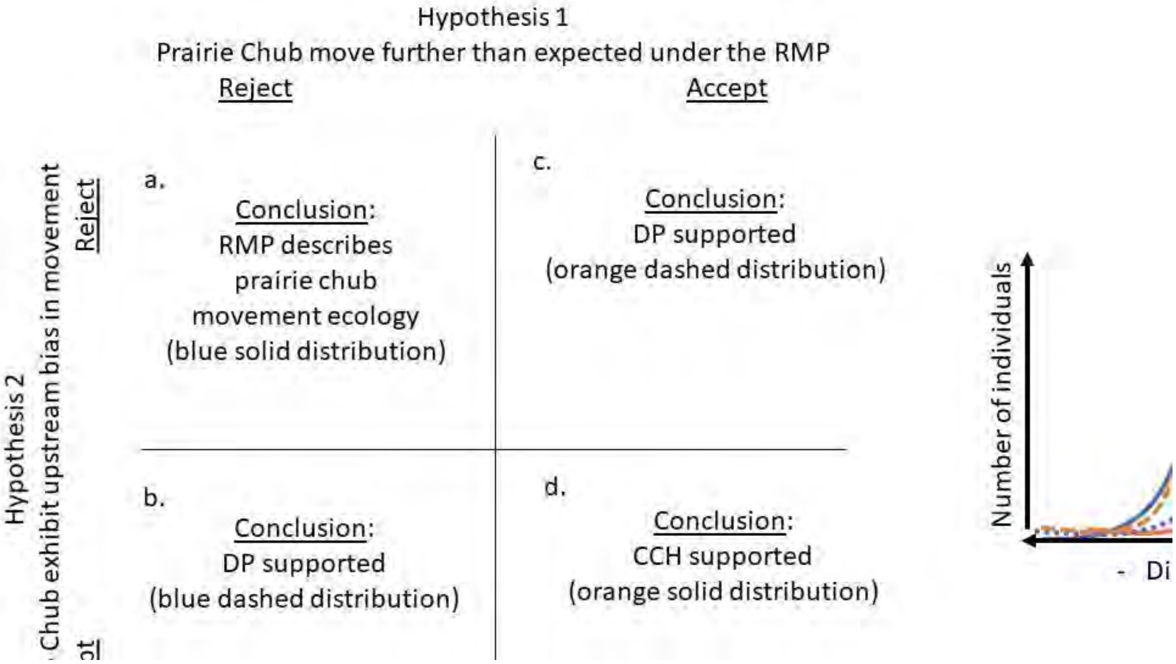

Figure 1. Conceptual diagram showing a decision matrix of two hypotheses regarding competing theories for Prairie Chub movement. The restricted movement paradigm (RMP) posits that stream fish are largely sedentary and do not move far from their tagging location, whereas the colonization cycle hypothesis (CCH) posits that if downstream drift occurs during early life stages, then upstream bias in movement must occur at adult life stages. The drift paradox (DP) describes the situation in which upstream populations persist despite little evidence of upstream movement bias. Our first hypothesis (H1) was that Prairie Chub would move more than the RMP predicts, whereas our second hypothesis (H2) was that Prairie Chub movement was biased in an upstream direction. Acceptance of both hypotheses would be consistent with the CCH (panel d), whereas rejection of both hypotheses would be consistent with the RMP (panel a). Acceptance of one hypothesis but not the other results in a paradoxical situation in which upstream movement does not complete the colonization cycle (panel c) or upstream bias in movement does not occur over far distances (panel b).

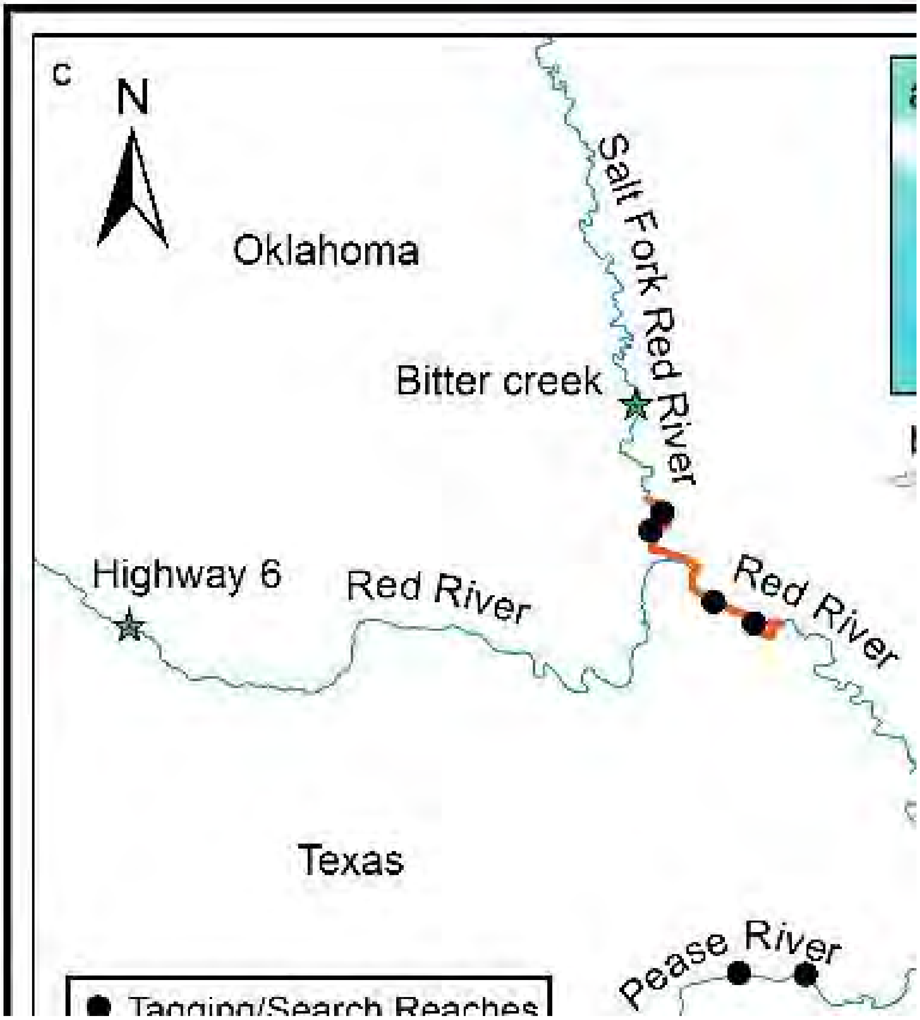

Figure 2. Sample sites located within North America (panel a) in the Red River basin (panel b) that were used in our mark-recapture analyses of Prairie Chub movement. Tagging and searching sites were located on the Salt Fork Red River, the Red River, and the Pease River (panel c). The long searches were completed August 8-9, 2020, to look for relatively long-distance movers outside of our tagging and regular search sites. The 20-km search was completed August 10-12, 2020, to systematically look for tagged Prairie Chub above and below 4 of 6 sites along the Salt Fork Red River and the Red River (August 10-12, 2020). NHDplus flowlines were used for the rivers (https://www.epa.gov/waterdata/nhdplus).

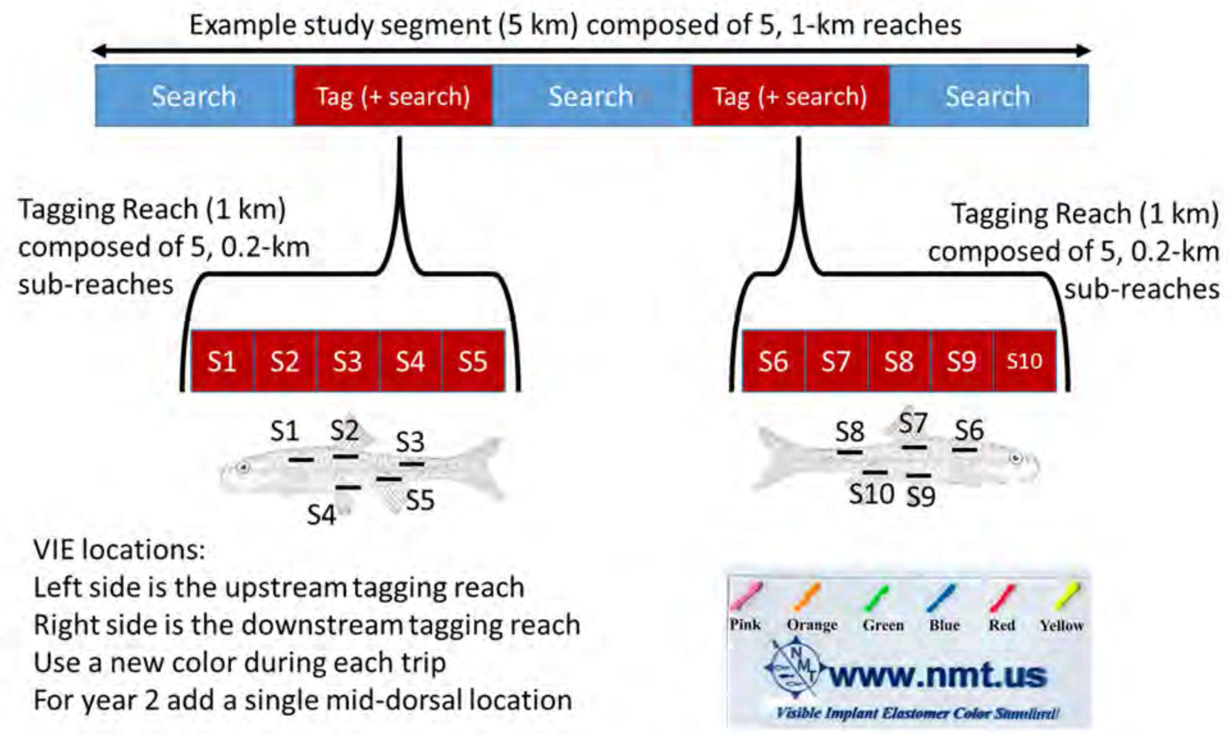

Figure 3. Conceptual diagram for a visible implant elastomer (VIE) mark-recapture study to assess movement of Prairie Chub. On each of three tributaries, we established a study segment that was 5-km long. The study segments comprised 5, 1-km reaches. Every other reach was a search or tagging reach, in which fishes were either only searched for (i.e., search reach) or tagged and searched for (i.e., tag reach). Each tag reach comprised 5, 0.2-km sub-reaches, and within these sub-reaches fish were batch marked with sub-reach-specific body locations. This allowed greater resolution of fish movement during recaptures. During each tagging trip, a new color of VIE was used so that the time recaptured individuals were at large could be calculated.

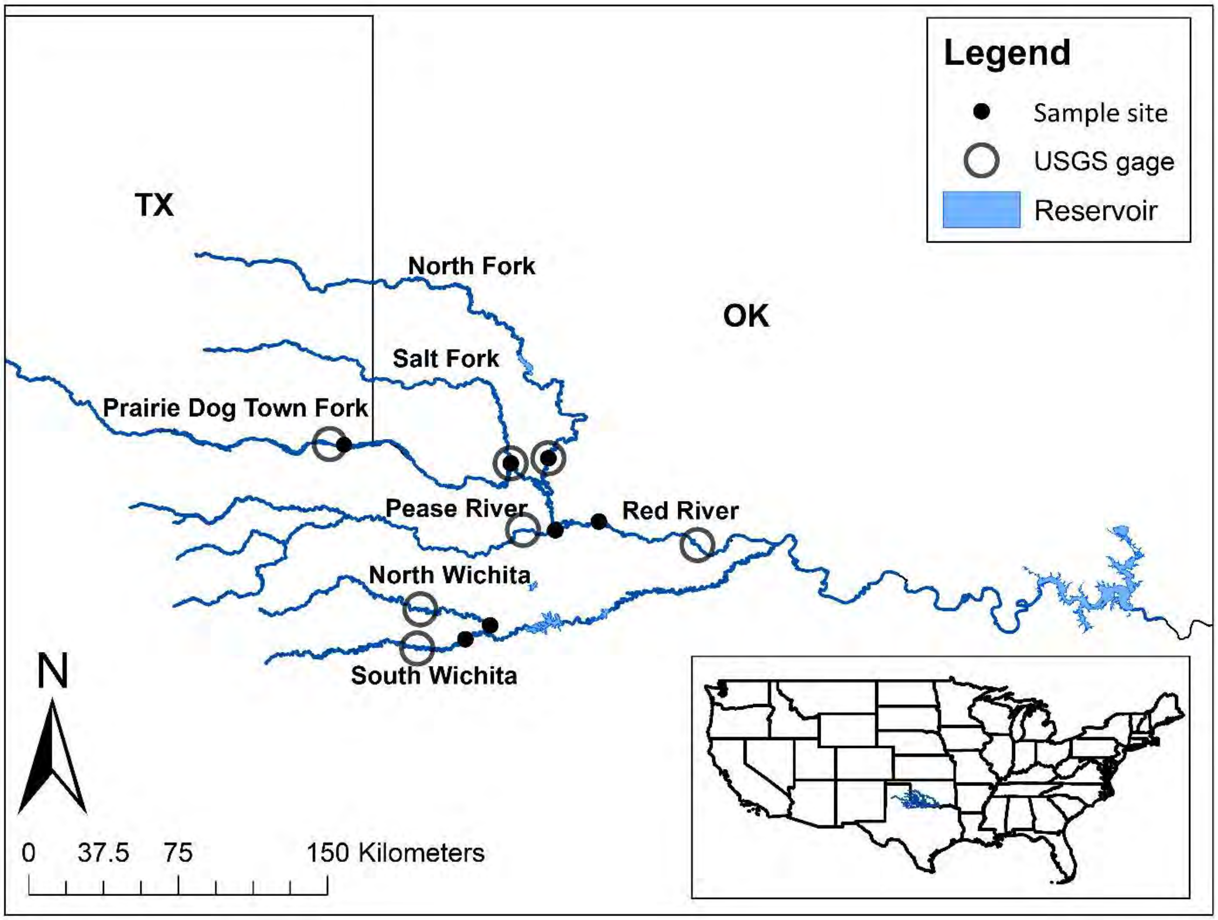

Figure 4. We sampled age-0 Prairie Chub from seven rivers: North Fork, Salt Fork, Red River, Pease River, North Wichita River, South Wichita River, and Prairie Dog Town Fork. We collected discharge data from the USGS stream gauge nearest to each sample site. The seven USGS gages are identified by name, identification number, city, and state: North Fork Red River, 07307028, Tipton, OK; Salt Fork Red River, 07301110, Elmer, OK; Red River, 07308500, Burkburnett, TX; Pease River, 07308200, Vernon, TX; North Wichita River, 07311700, Truscott, TX; South Wichita River, 07311800, Benjamin, TX; and Prairie Dog Town Fork, 07299540, Childress, TX (U.S. Geological Survey, 2021). NHDplus flowline was used to depict the rivers (https://www.epa.gov/waterdata/nhdplus).

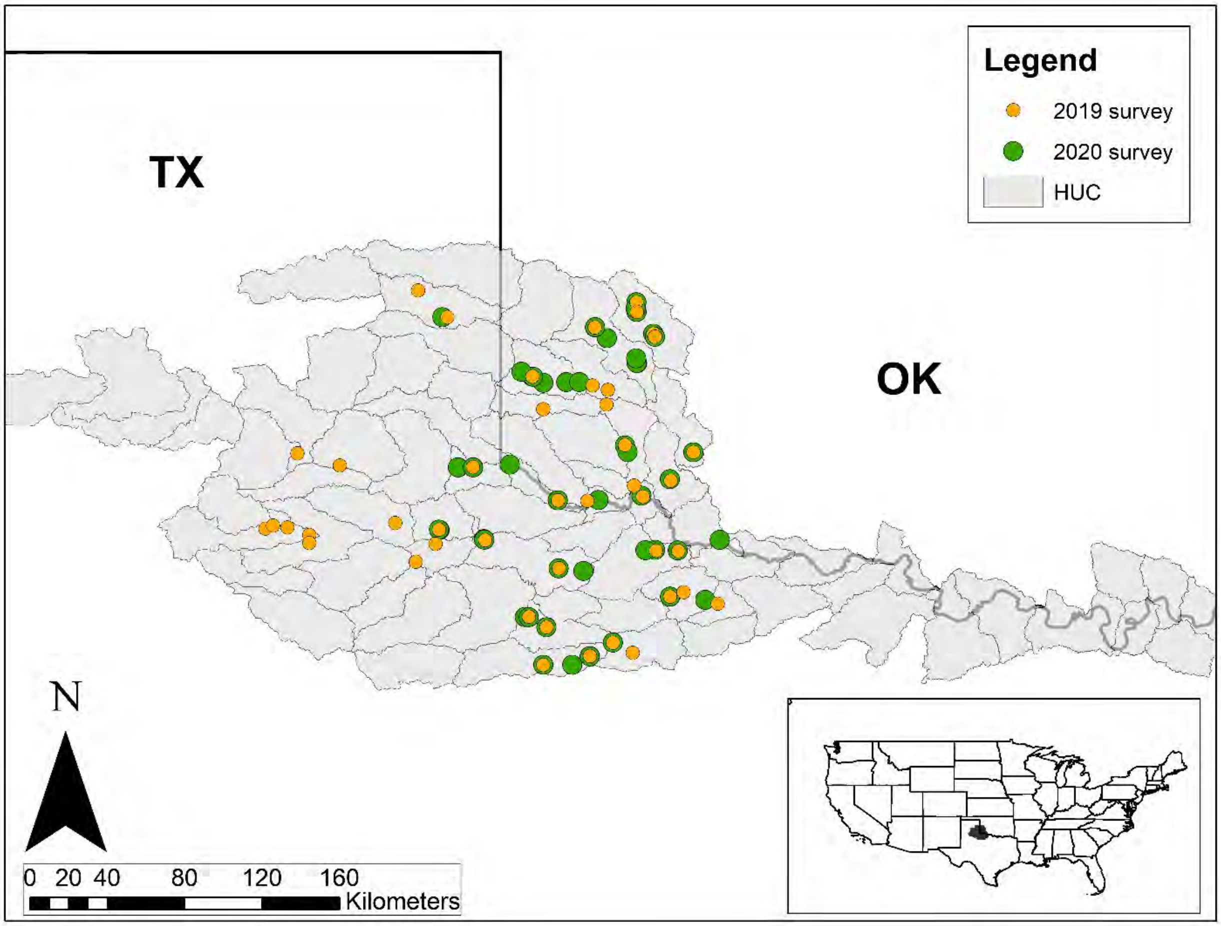

Figure 5. Map of upper Red River basin study area in Texas and Oklahoma representing spatially replicated surveys (n=104) nested within HUCs (n=34) in 2019 and 2020. We completed 44 surveys in 2019 and 60 surveys in 2020 to estimate Prairie Chub abundance. NHDplus flowline was used to depict the rivers (https://www.epa.gov/waterdata/nhdplus).

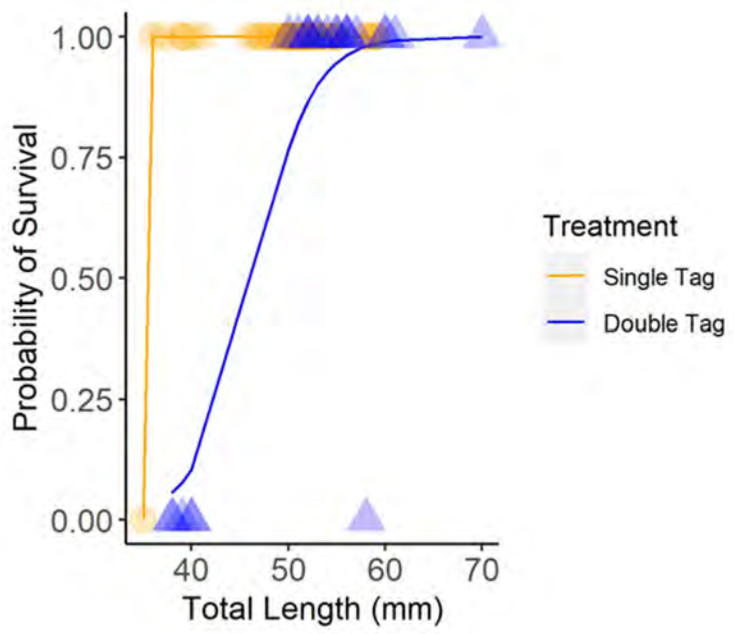

Figure 6. Probability of survival over a 24-hour period for Prairie Chub tagged with a single visible implant elastomer (VIE) tag (blue circles) and double VIE tag (orange triangles) as a function of fish total length (1 mm). Lines of corresponding colors show logistic regression model fits for each treatment level and points with darker colors illustrate higher densities of observations.

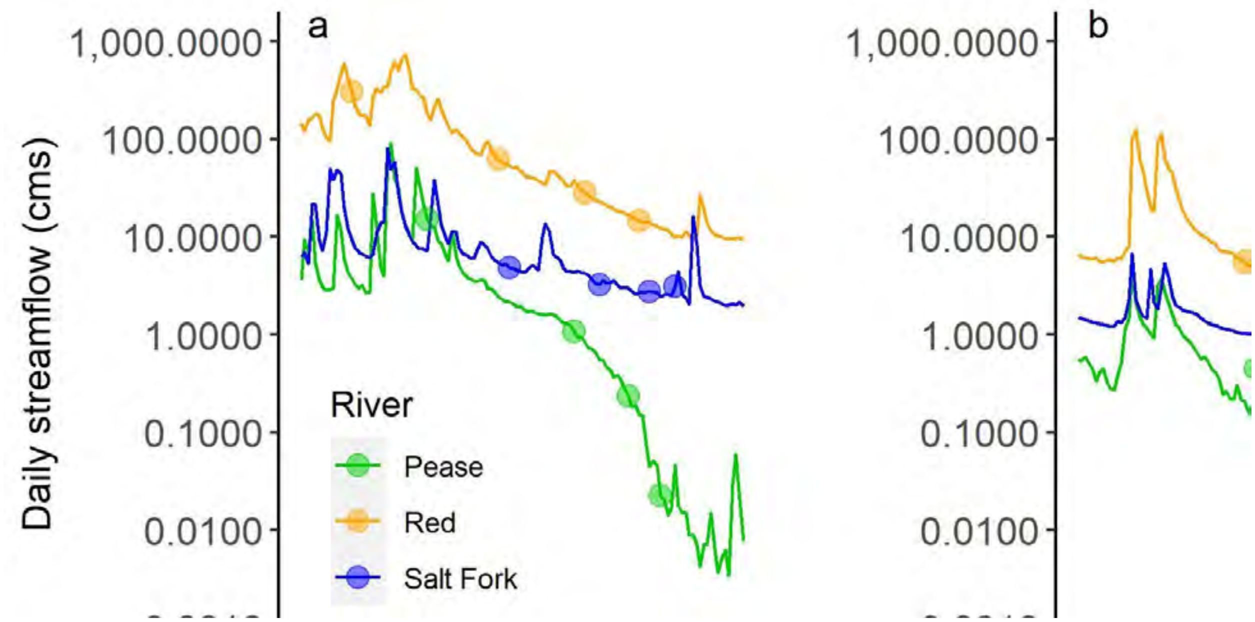

Figure 7. Hydrographs for the Red River (U.S. Geological Survey gage # 07308500), Salt Fork Red River (USGS gage # 07301110), and Pease River (USGS gage # 07308200) indicating daily discharge from May through September of (a) 2019 and (b) 2020 (U.S. Geological Survey, 2020). Lines are colored by river and similarly colored points on lines represent sampling dates. Note the y-axis is shown on a $\log_{10}$ scale.

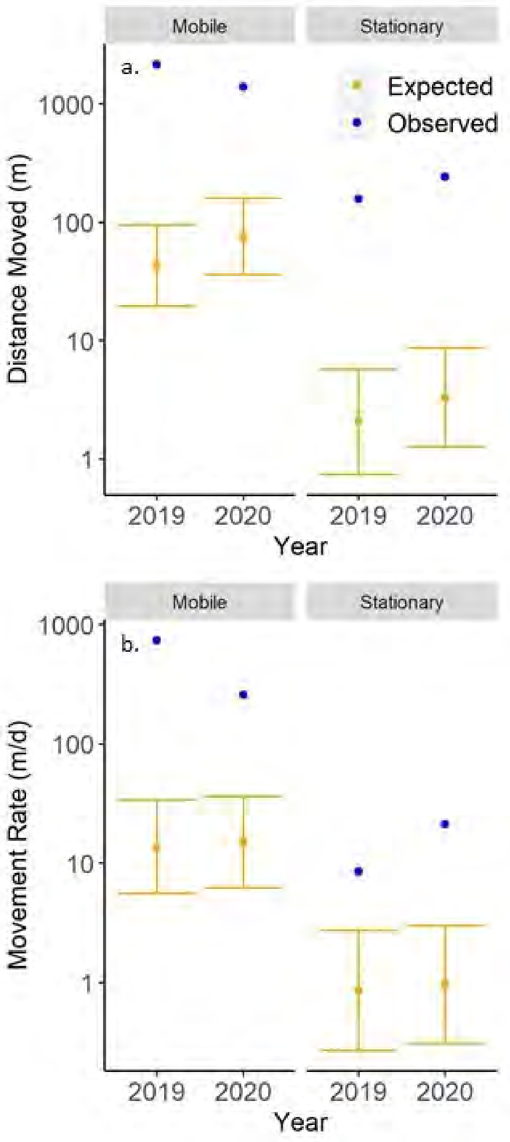

Figure 8. Plot of expected (orange) versus observed (blue) Prairie Chub (a) movement distances and (b) movement rates for mobile (left) and stationary (right) components of the population measured during the summers of 2019 and 2020. The bars around expected movements are upper and lower 95% confidence intervals generated using the ‘fishmove’ package in R.

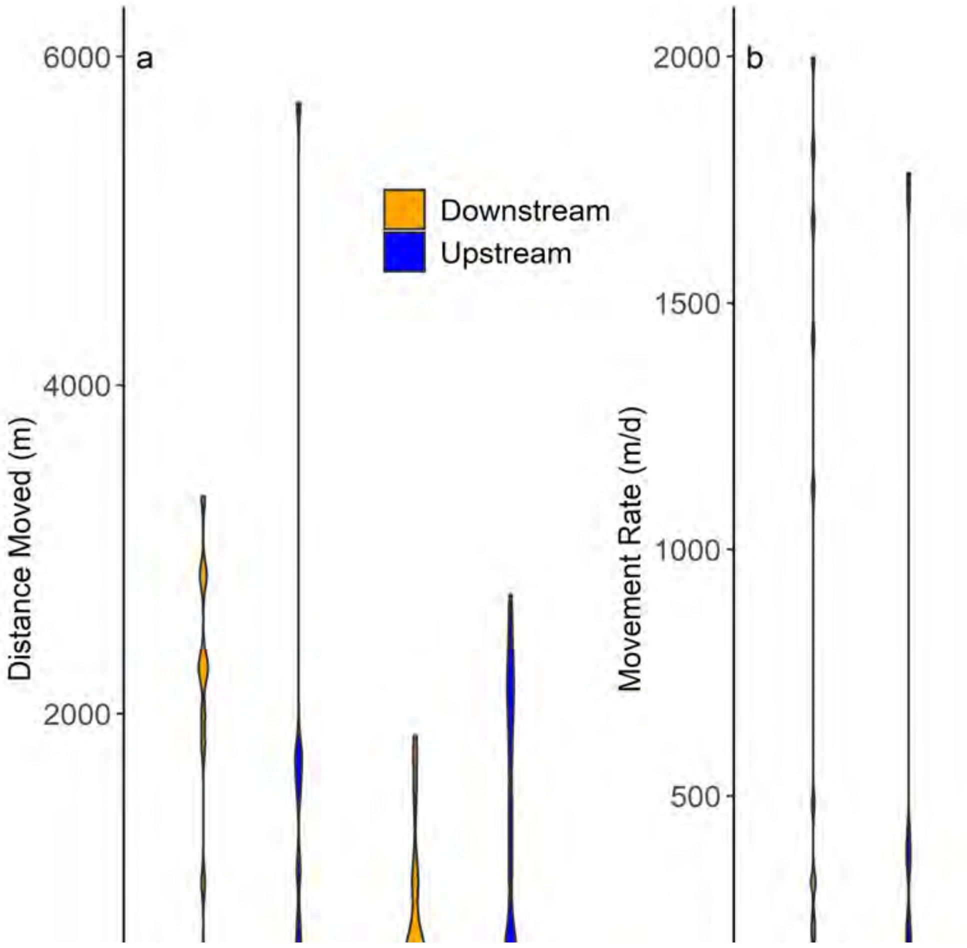

Figure 9. Violin plots comparing (a) absolute distance moved (m) and (b) movement rate (m/d) in downstream (orange) and upstream (blue) directions for Prairie Chub recaptured across all sites during the summers of 2019 and 2020. The width of each violin plot denotes data density.

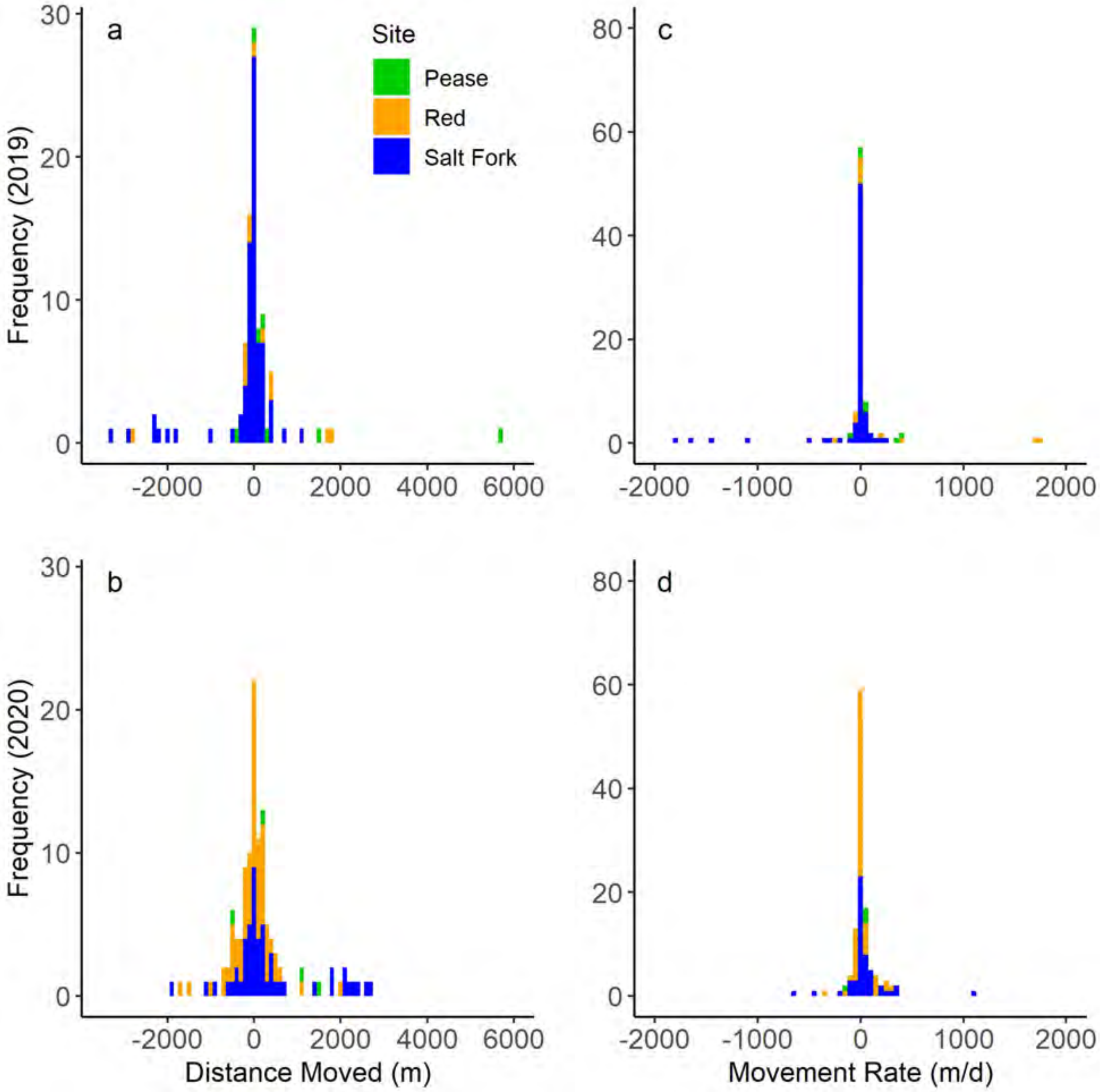

Figure 10. Frequency histograms of Prairie Chub movement distance (m) and rate (m/d) for 2019 (a, c) and 2020 (b, d). Colors correspond with fish recaptured in the Pease River (green), Red River (orange), and Salt Fork Red River (blue) and are shown as stacked bars. Negative values represent downstream movement and positive values represent upstream movement. Distance moved is shown using 100-m bins and movement rate is shown using 50-m bins.

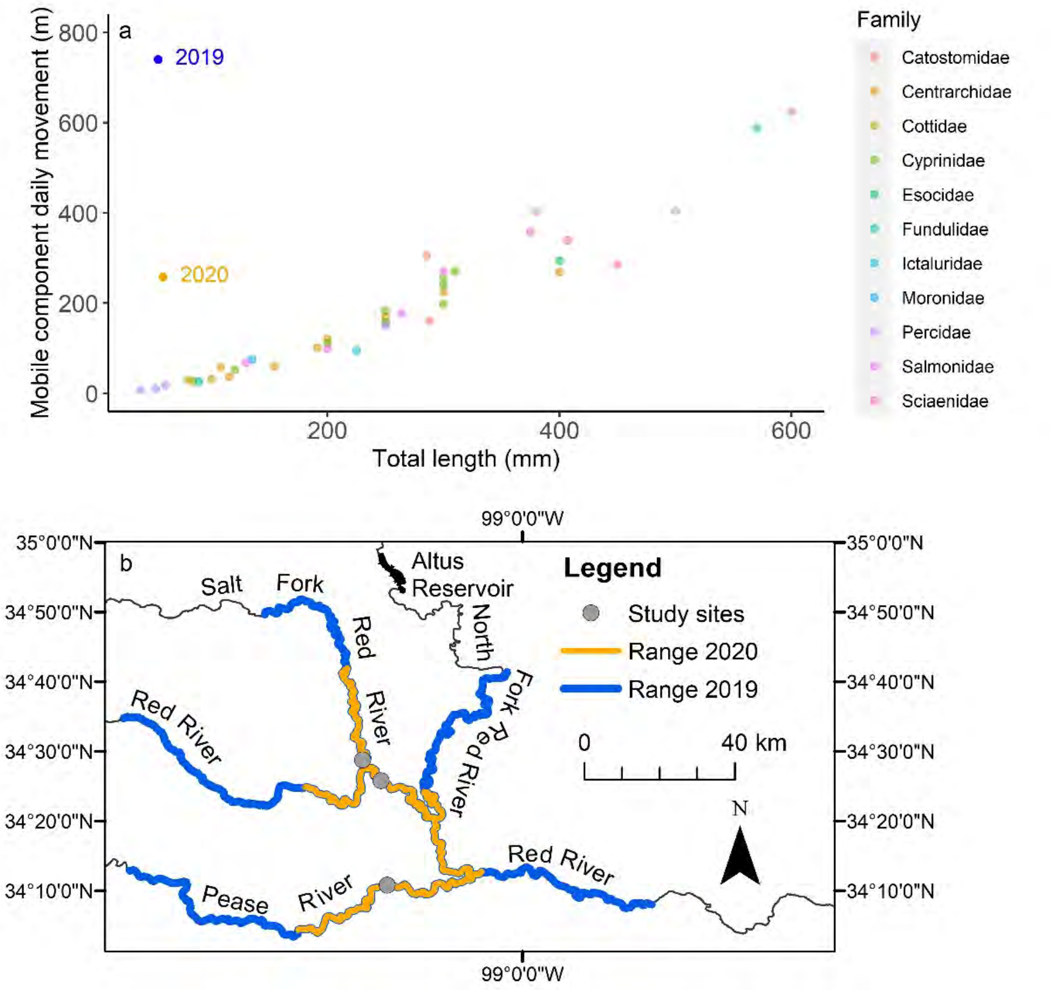

Figure 11. (panel a) Prairie Chub mobile component movement for one day (i.e., daily movement rate) for 2019 (blue) and 2020 (orange) compared with 40 other species included in the ‘fishmove’ package in R. The x-axis shows mean fish total length (mm) and the y-axis is the distance moved by the mobile component of populations; symbols for fishes from ‘fishmove’ are shown by taxonomic family with Prairie Chub being part of the family Cyprinidae. (b) Movement range (i.e., maximum distance possible during a single summer) for the mobile component of the Prairie Chub population for 2019 (blue) compared to 2020 (orange). Movement range is measured from the locations where fish were tagged (gray points) and does not include other locations where the species is known to occur.

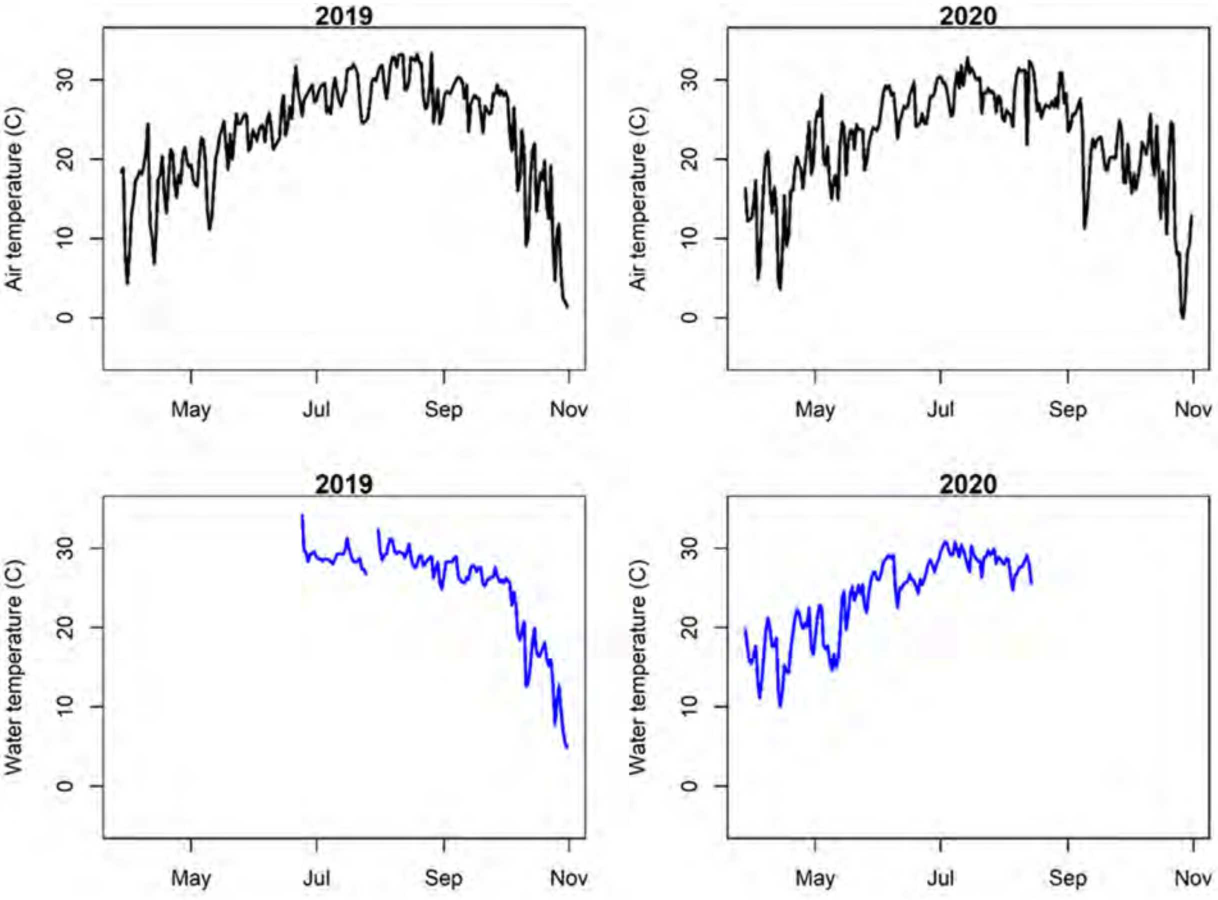

Figure 12. Summary of daily average values representing correspondence between air temperature (°C) and water temperature (°C) of the Red River mainstem throughout two survey seasons (i.e., summer-autumn) in 2019 and 2020. Air temperature was collected from the Oklahoma Mesonet station nearest to the USGS stream gauge (Oklahoma Mesonet station GRA2, Grandfield, OK). Water temperature data were collected using a temperature logger set at the sample site (HOBO, Onset Computer Corporation, Bourne, Massachusetts, USA). Gaps in the water temperature dataset reflect periods when temperature data were unreliable due to the logger being buried in sediment or dried on a sandbar.

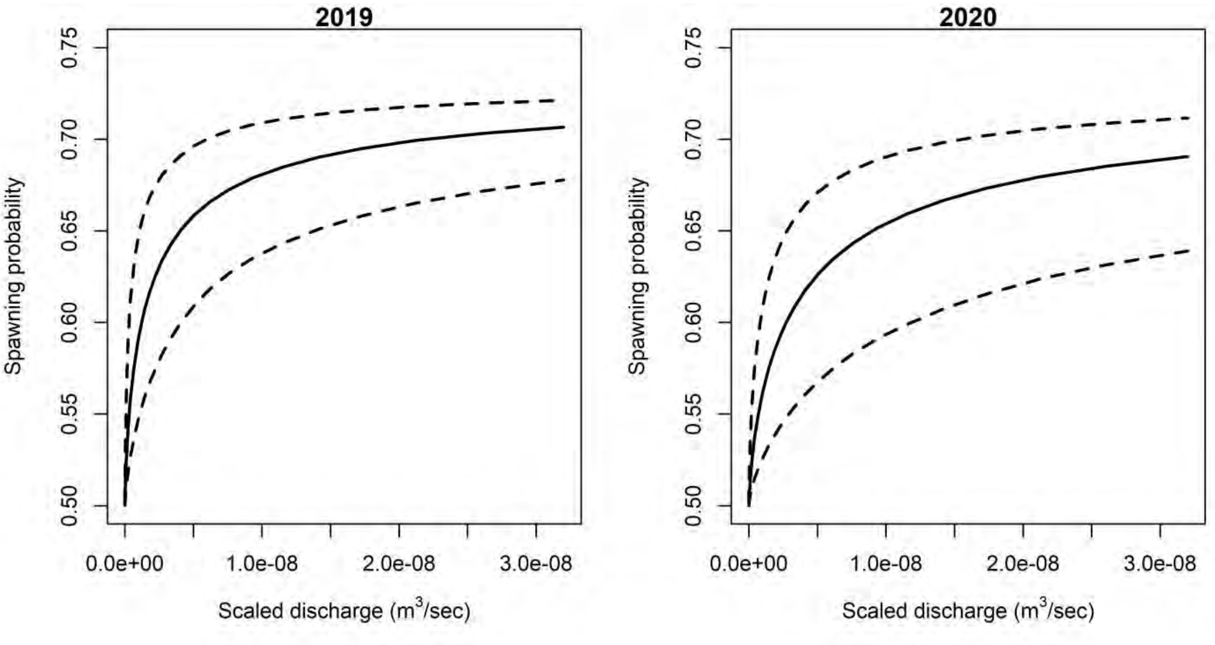

Figure 13. Plots representing the positive linear relationship between Prairie Chub spawning probability scaled between 0 and 1 on the y-axis and scaled discharge (m^3/sec) on the x-axis with all other variables held constant at mean values for both the 2019 (left panel) and 2020 (right panel) sample seasons. All other variables were held constant at mean values. The black dotted lines represent 95% confidence intervals.

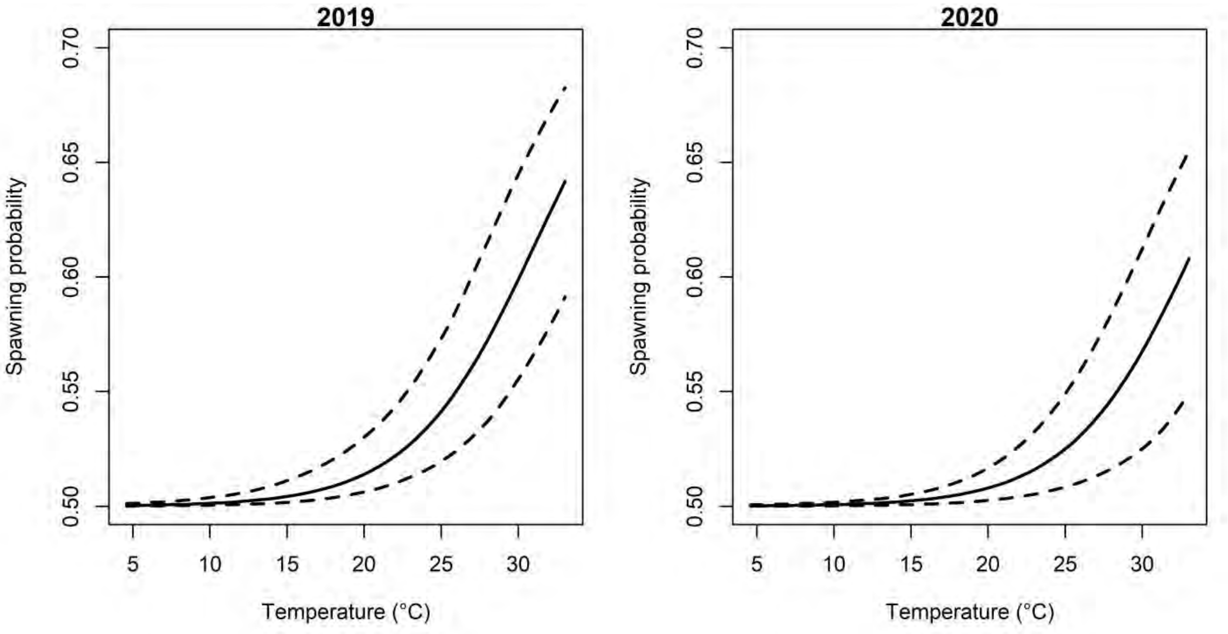

Figure 14. Plots representing the positive linear relationship between Prairie Chub spawning probability scaled between 0 and 1 on the y-axis and temperature (°C) on the x-axis for both the 2019 (left panel) and 2020 (right panel) sample seasons. All other variables were held constant at mean values. The black dotted lines represent 95% confidence intervals.

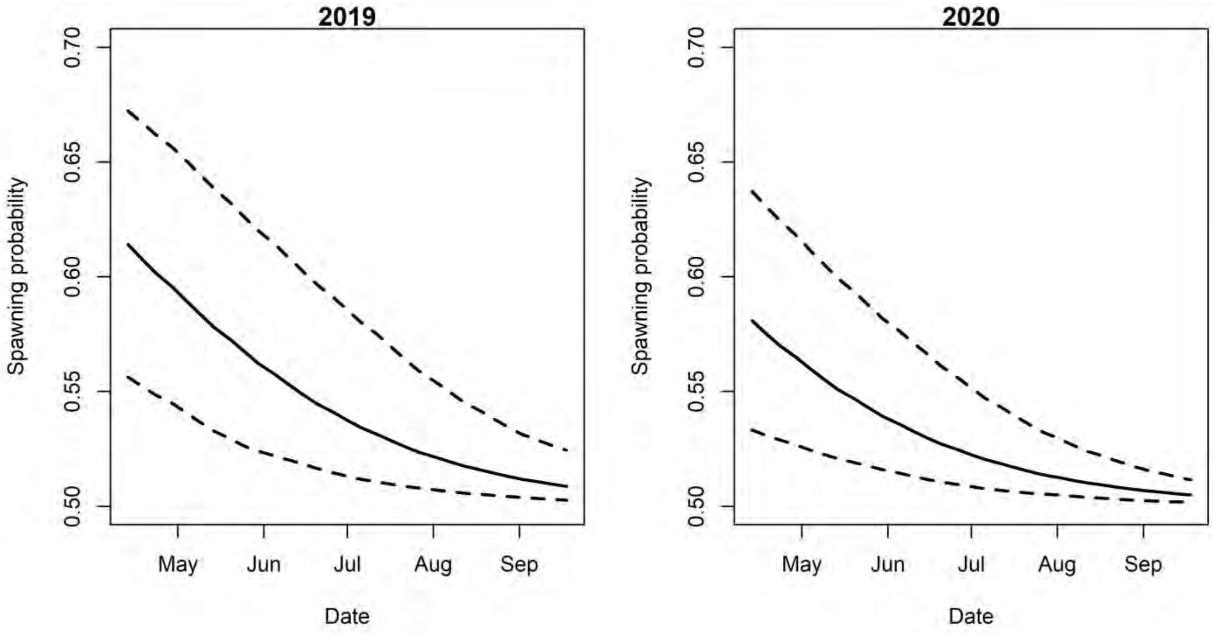

Figure 15. Plots representing the negative linear relationship between Prairie Chub spawning probability (scaled between 0 and 1) on the y-axis and date on the x-axis for both the 2019 (left panel) and 2020 (right panel) sample seasons. All other variables were held constant at mean values. The black dotted lines represent 95% confidence intervals.

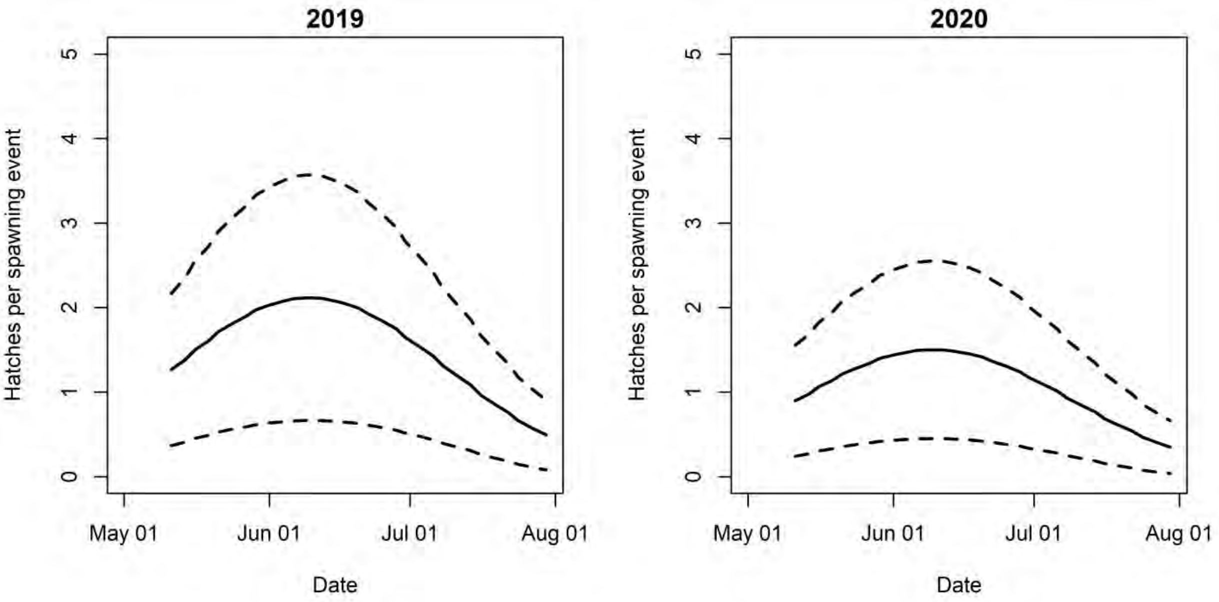

Figure 16. Plots representing the quadratic relationship between the number of Prairie Chub hatches observed per spawning event and date in both the 2019 (left panel) and 2020 (right panel) sample seasons. The black dotted lines represent 95% confidence intervals.

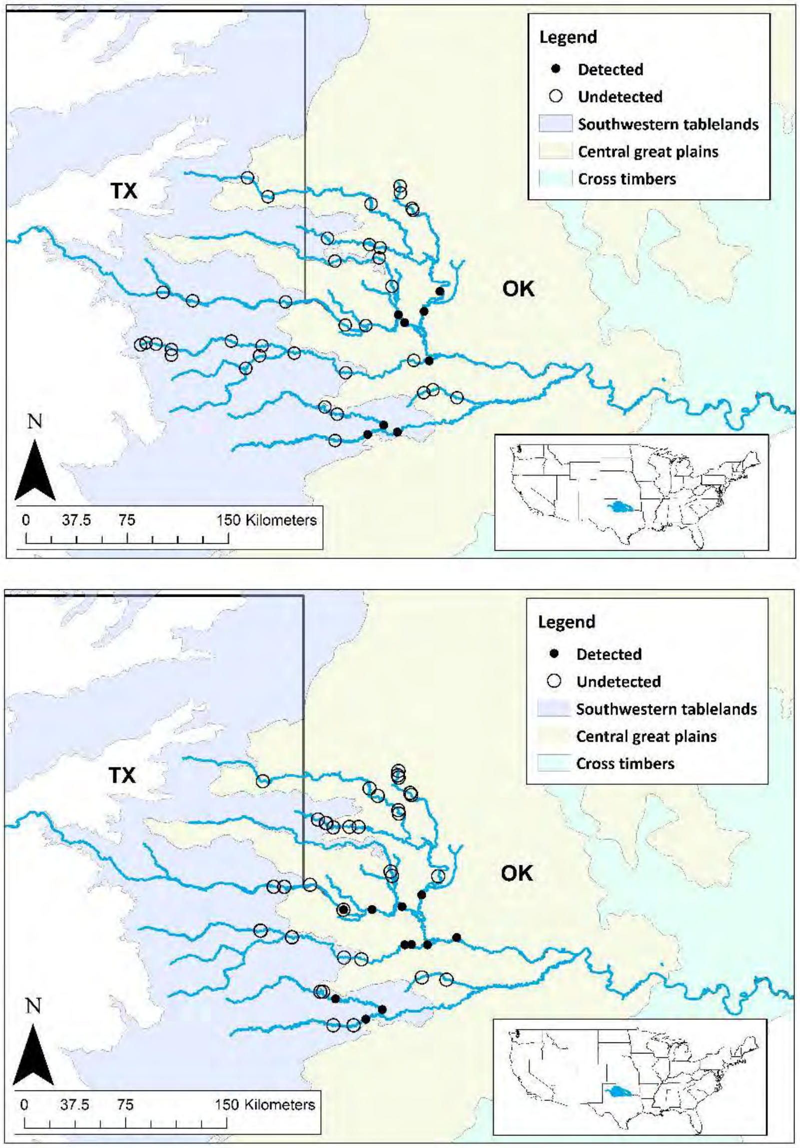

Figure 17. Location of adult Prairie Chub abundance surveys (n=104) where adult Prairie Chub were detected in 2019 (top panel) and 2020 (bottom panel) and non-detected in both seasons. Surveys were distributed across the Southwestern Tablelands and Central Great Plains (level III ecoregions) of the upper Red River basin in Texas and Oklahoma.

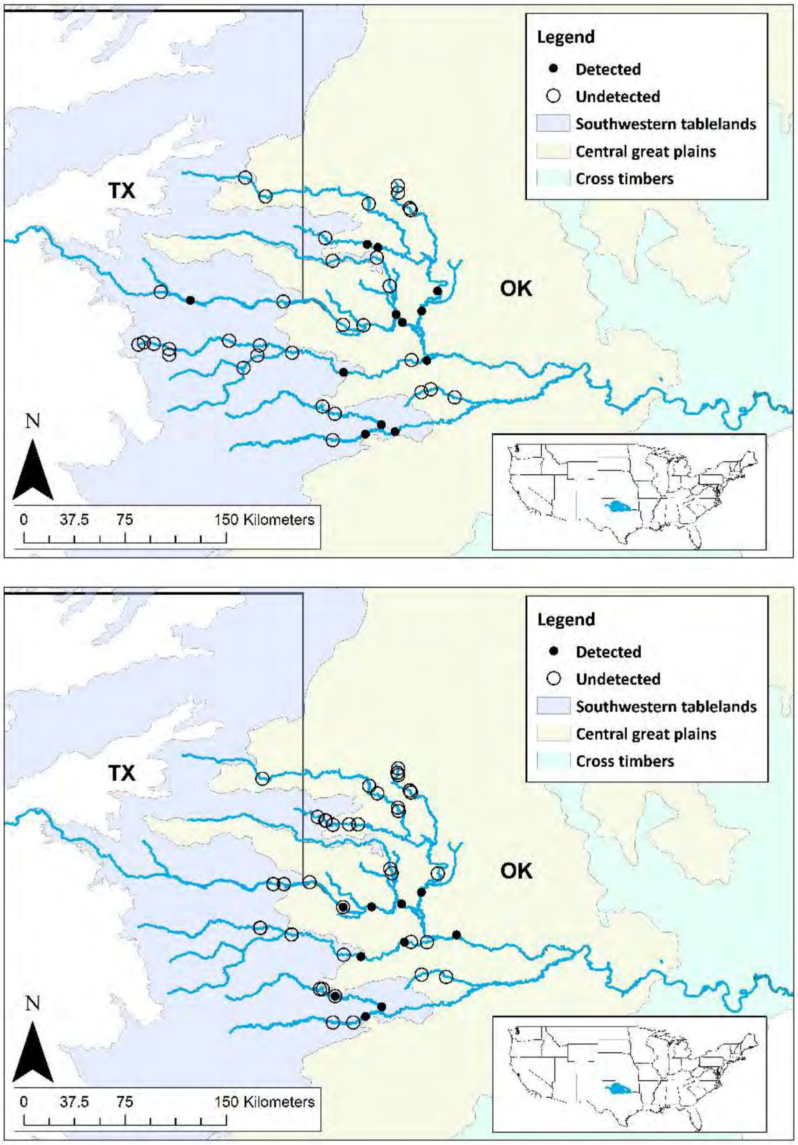

Figure 18. Location of juvenile Prairie Chub abundance surveys (n=104) where juvenile Prairie Chub were detected in 2019 (top panel) and 2020 (bottom panel) and non-detected (n=82) in both seasons. Surveys were distributed across the Southwestern Tablelands and Central Great Plains (level III ecoregions) of the upper Red River basin in Texas and Oklahoma.

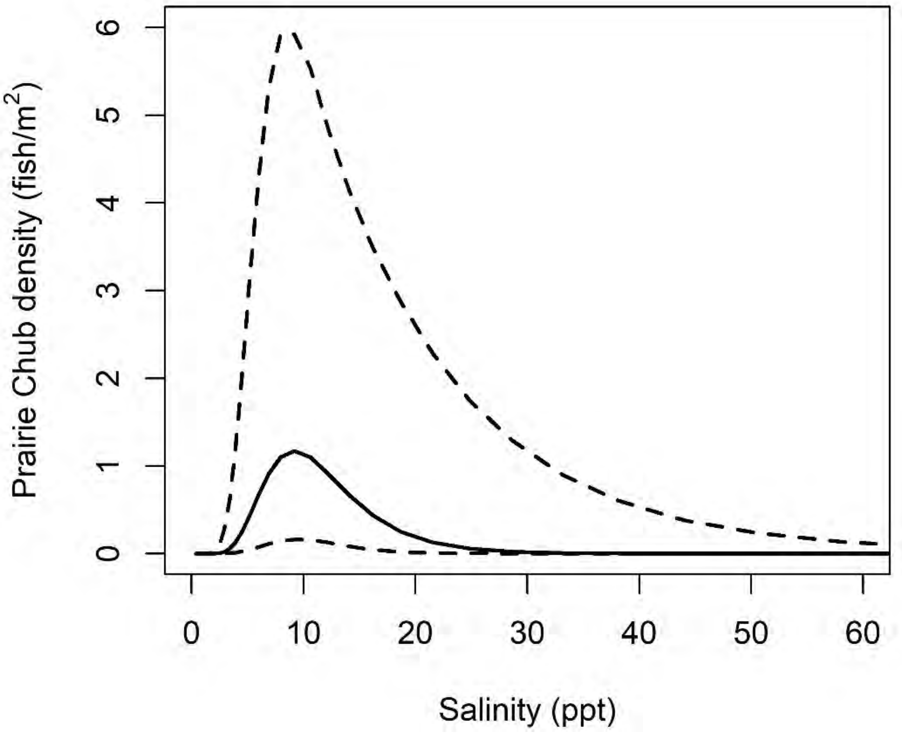

Figure 19. Plot representing the quadratic relationship between adult Prairie Chub density (fish/m^2) and salinity (ppt). The solid line black line represents estimated y values, and the dotted lines represent 90% confidence limits.

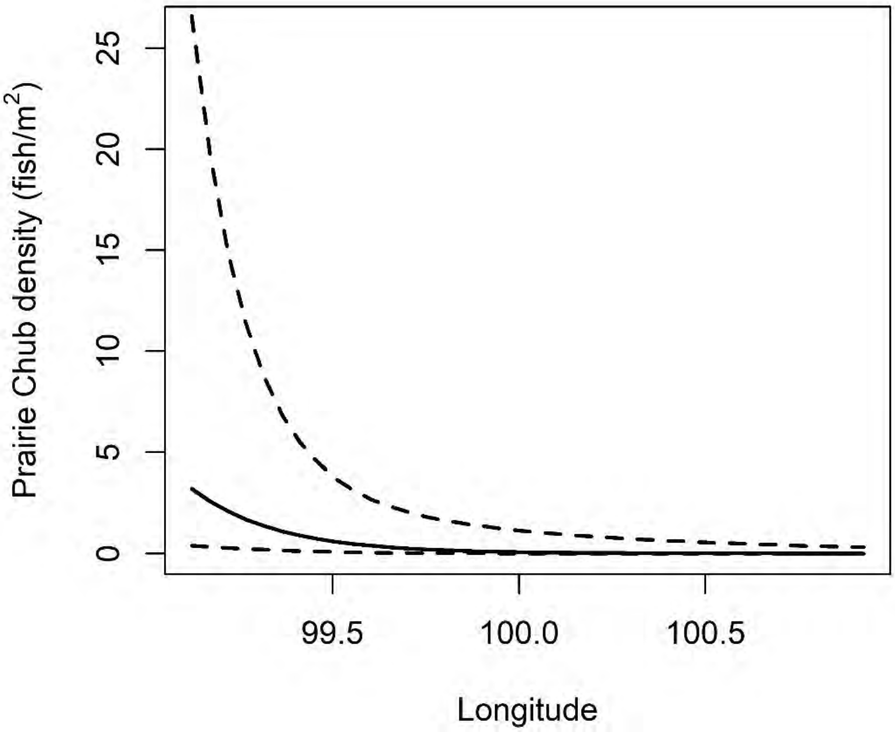

Figure 20. Plot representing the negative linear relationship between adult Prairie Chub density (fish/m^2) and longitude. The solid line black line represents estimated y values, and the dotted lines represent 90% confidence limits.

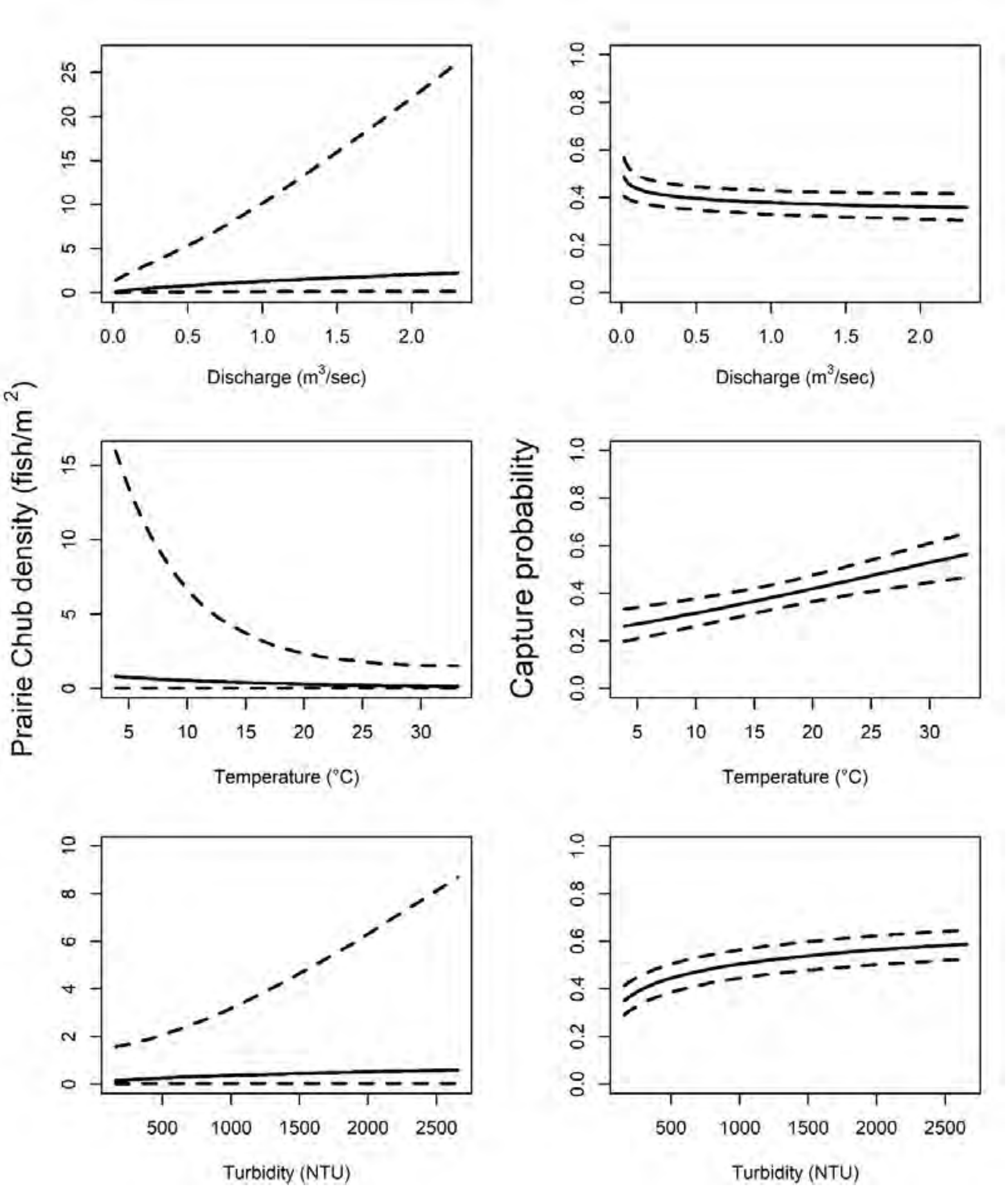

Figure 21. Plots depicting the linear relationships between adult Prairie Chub density (fish/m^2) and environmental parameters (left column) and capture probability and environmental parameters (right column). Environmental parameters are discharge, water temperature, and turbidity. The solid line black line represents estimated y values, and the dotted lines represent 90% confidence limits.

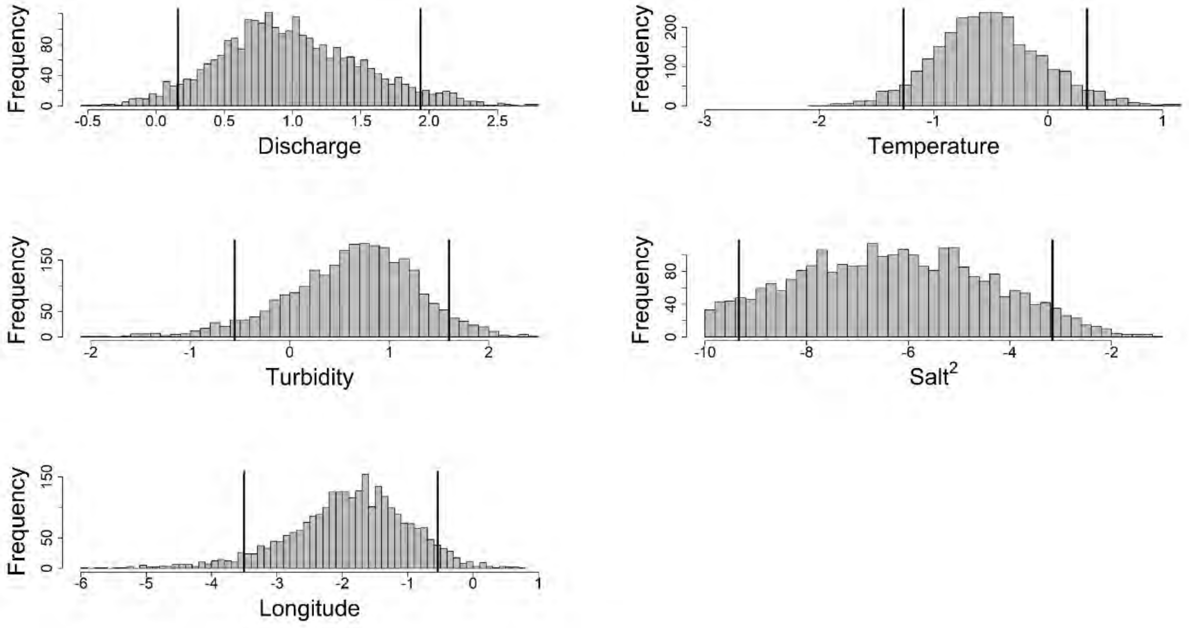

Figure 22. Histograms of posterior distributions (log scale) representing uncertainty and the direction of relationships for five parameters included in the adult Prairie Chub abundance model. Black bars reflect 90% highest density intervals (HDIs). Environmental parameters are discharge, water temperature, water turbidity, salinity (non-linear), and longitude.

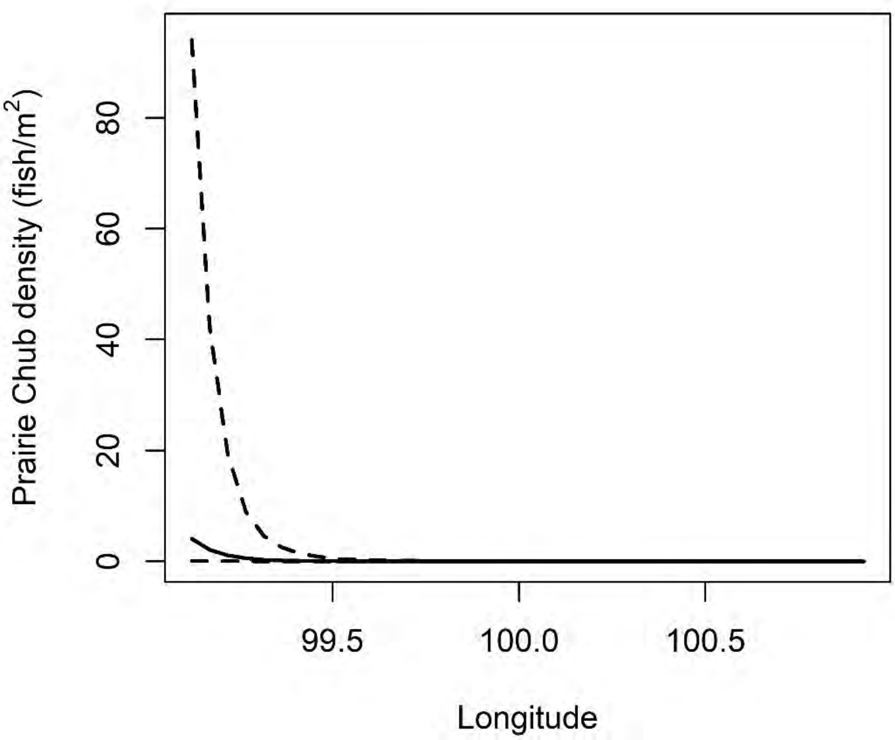

Figure 23. Plot showing the negative linear relationship between juvenile Prairie Chub density (fish/m^2) and longitude. The solid line black line represents estimated y values, and the dotted lines represent 90% confidence limits.

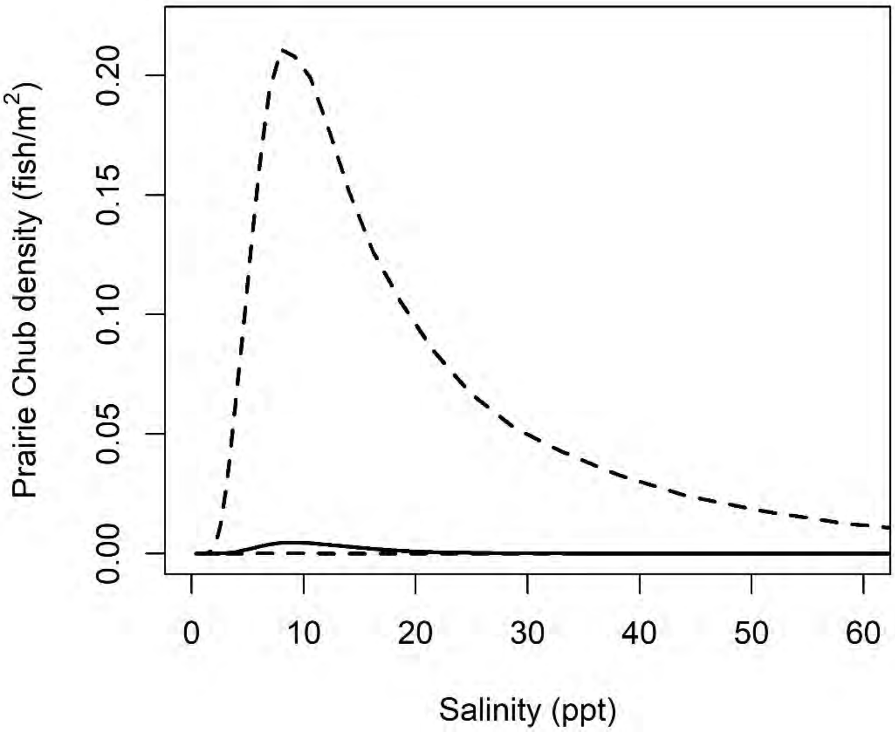

Figure 24. Plot representing the quadratic relationship between juvenile Prairie Chub density (fish/m^2) and salinity (ppt). The solid line black line represents estimated y values, and the dotted lines represented 90% confidence limits.

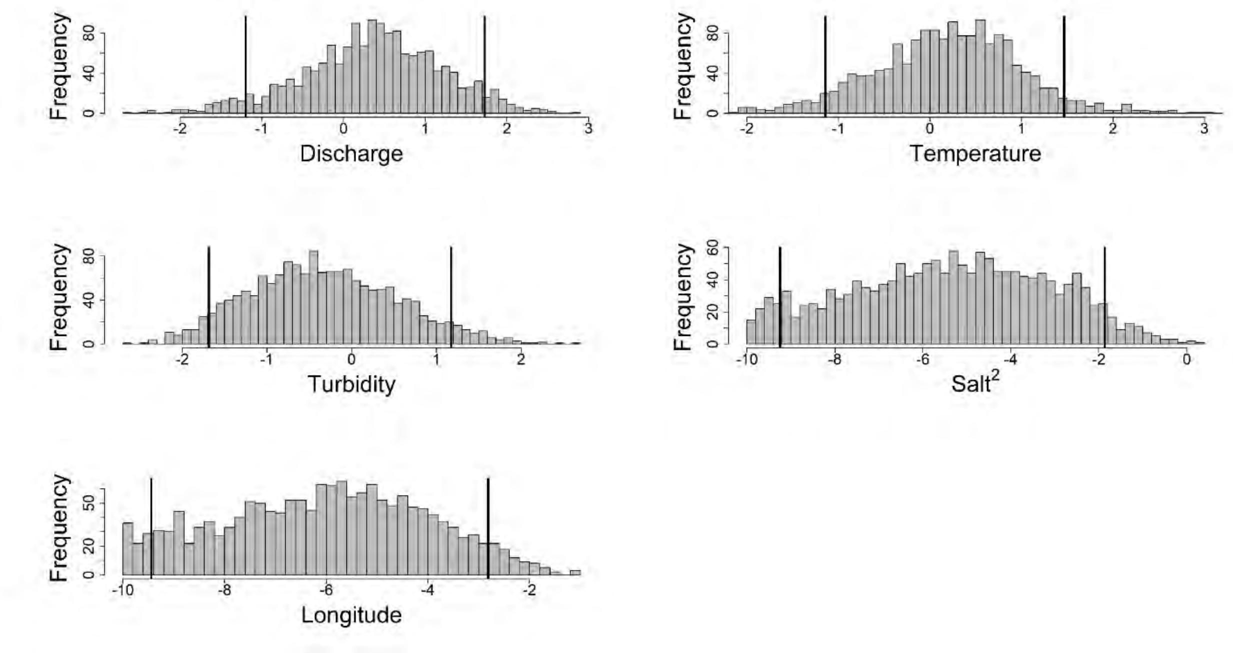

Figure 25. Histograms of posterior distributions (log scale) for the five juvenile Prairie Chub abundance model parameters: discharge, water temperature, water turbidity, salinity (non-linear), and longitude. Histograms of posterior distributions represent uncertainty and the direction of relationships. Black bars indicate 90% highest density intervals (HDIs).

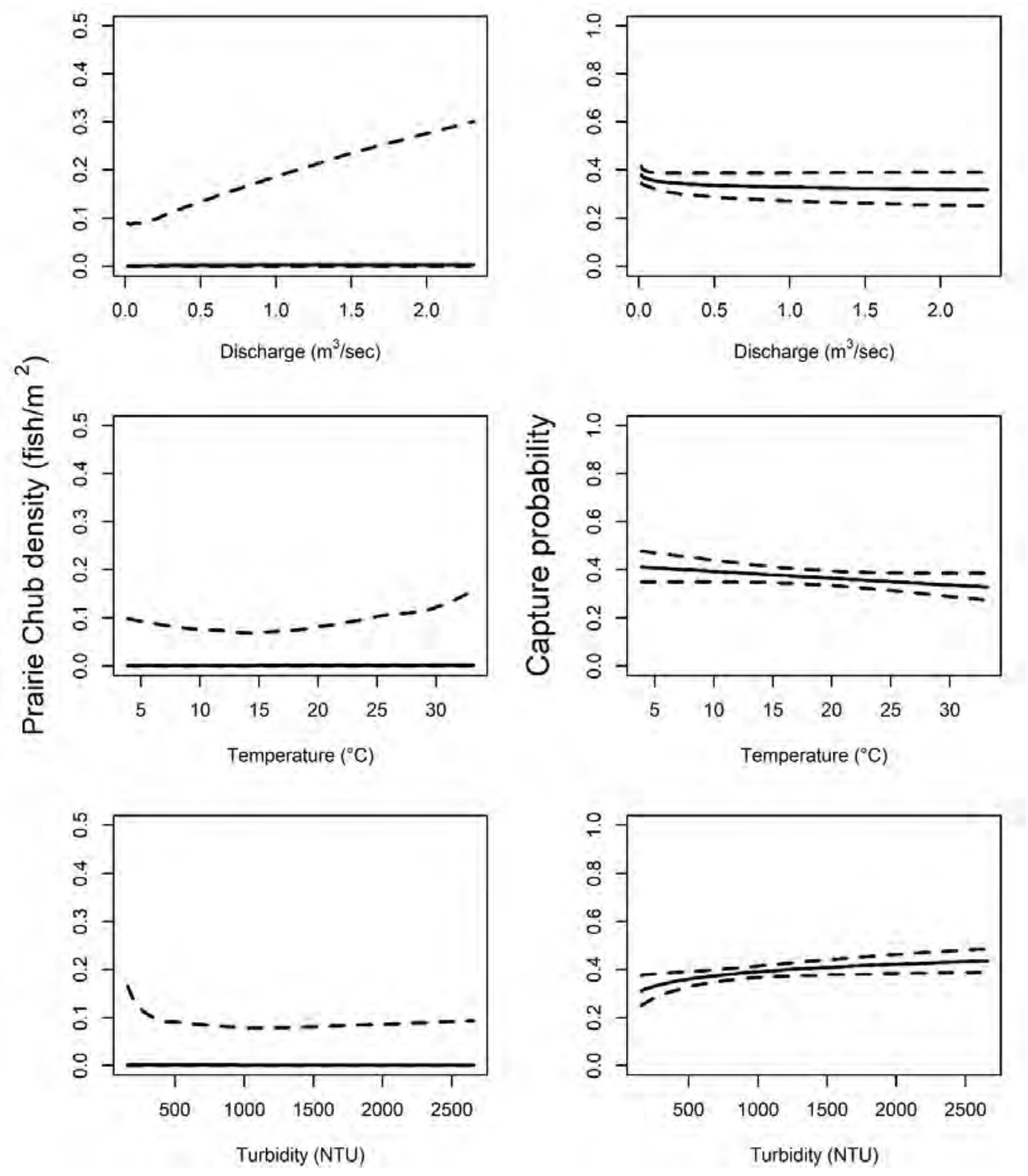

Figure 26. Plots representing linear relationships between juvenile Prairie Chub density (fish/m^2) (left column) and capture probability (right column) and discharge, water temperature, and turbidity. The solid line black line represents estimated y values, and the dotted lines represent 90% confidence limits.

Appendix A. Summary of discharge conditions by river in 2019 and 2020

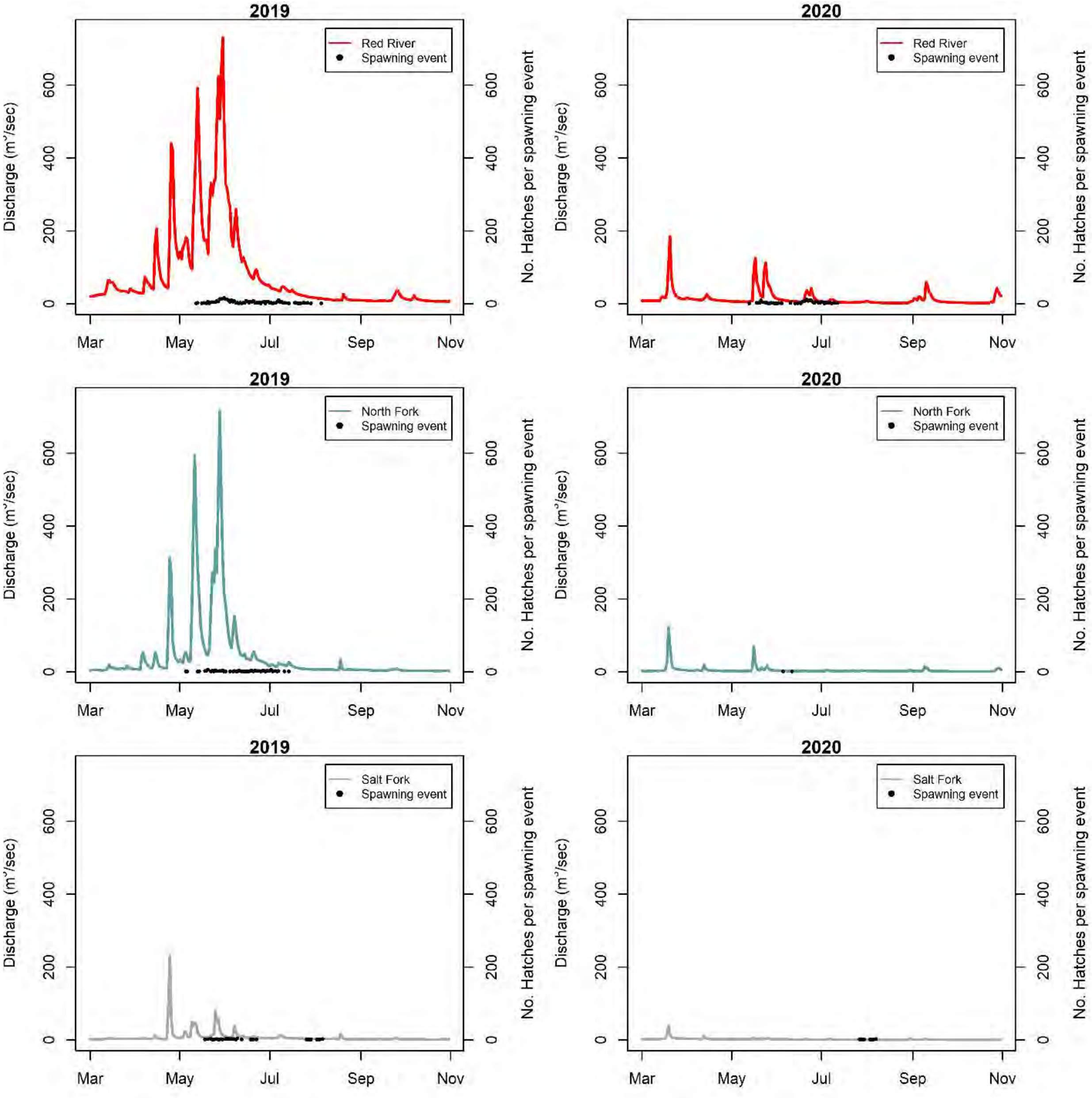

Figure A1. Summary of average daily discharge (m^3/sec) values in the Red River, North Fork, and Salt Fork in 2019 (left panel) and 2020 (right panel). The left y axis represents discharge (m^3/sec), and the right y axis represents number of observed hatches per spawning date. Black circles indicate spawning events. Gage numbers are provided in the methods for reference.

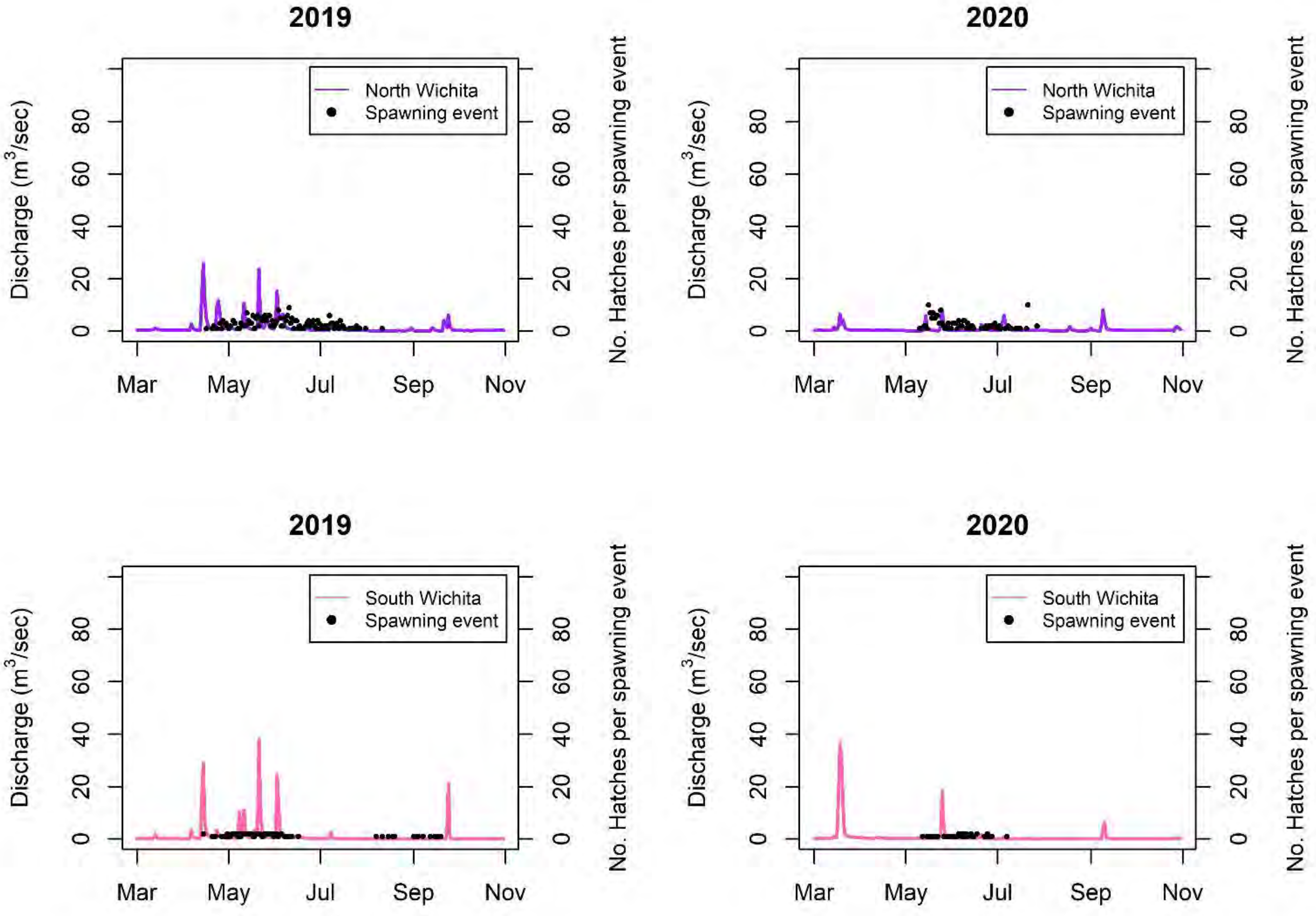

Figure A2. Summary of average daily discharge (m^3/sec) in the North Wichita and South Wichita rivers in 2019 (left panel) and 2020 (right panel). The left y axis represents discharge (m^3/sec), and the right y axis represents number of observed hatches per spawning date. Black circles indicate spawning events. Gage numbers are provided in the methods for reference.

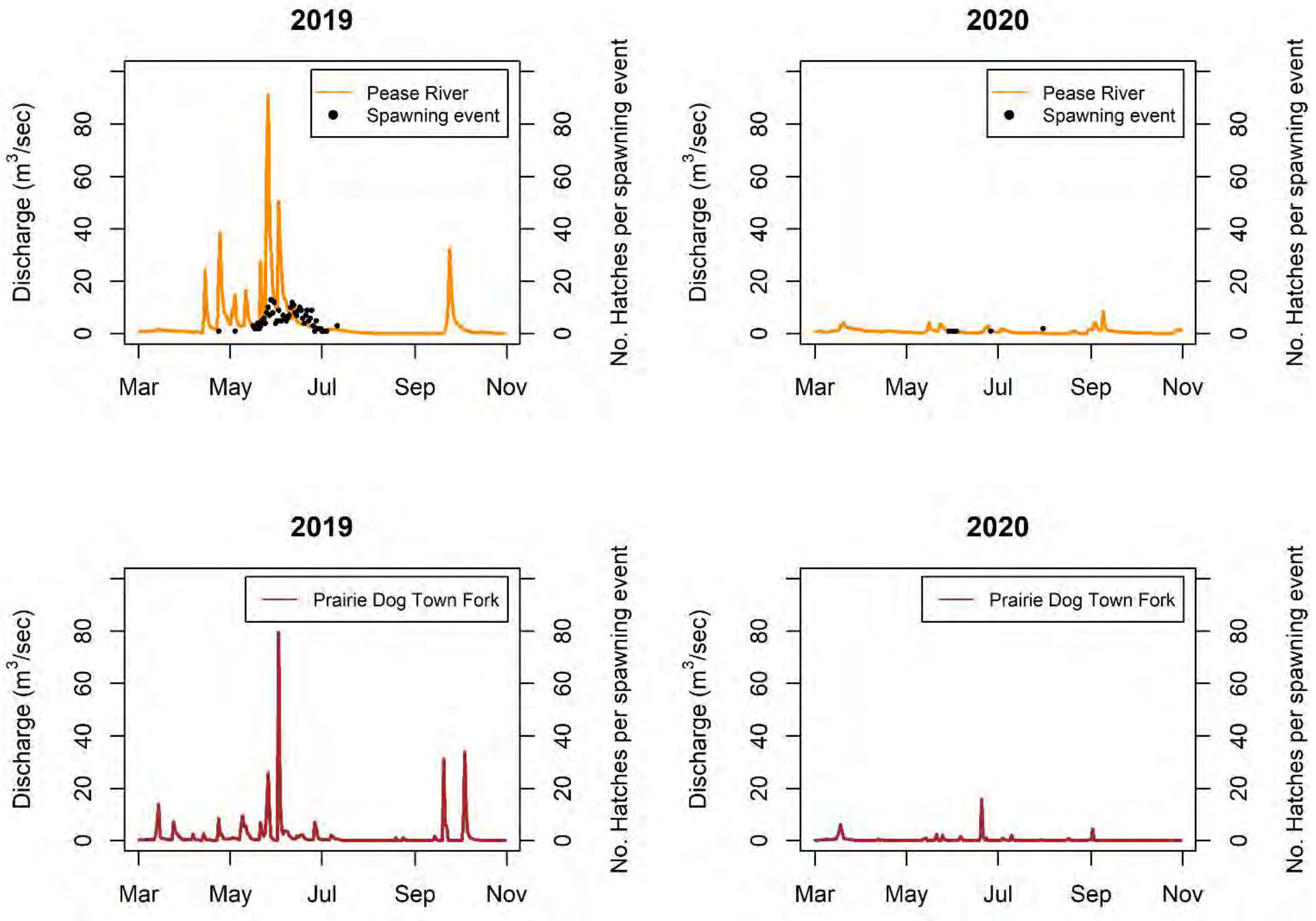

Figure A3. Summary of average daily discharge (m^3/sec) in the Pease River (top row) and Prairie Dog Town Fork (bottom row) in 2019 (left panel) and 2020 (right panel). The left y axis represents discharge (m^3/sec), and the right y axis represents number of observed hatches per spawning date. Black circles indicate spawning events. No spawning events were observed in the Prairie Dog Town Fork in either year. Gage numbers are provided in the methods for reference.

Appendix B. Adult and juvenile Prairie Chub abundance estimates by survey and stream.

Table B1. Adult and juvenile abundance estimates for each survey (n=105) grouped by stream name. Date sampled represents the date the survey was conducted. Spatial coordinates are shown in latitude and longitude. The mode and 90% highest density intervals (HDI) for adult and juvenile Prairie Chub indicate abundance estimates (N) and associated uncertainty.

Stream	Date sampled	Latitude	Longitude	Adult *N* mode (90% HDI)	Juvenile *N* mode (90% HDI)
Beaver Creek	9/19/2019	33.92927	-98.98891	0 (0,0)	0 (0,0)
Beaver Creek	9/19/2019	33.96317	-99.21094	0 (0,0)	0 (0,0)
Beaver Creek	10/6/2019	33.98338	-99.14868	0 (0,0)	0 (0,0)
Beaver Creek	8/23/2020	34.94777	-99.04758	0 (0,0)	0 (0,0)
Beaver Creek	8/23/2020	33.96302	-99.21119	0 (0,0)	0 (0,0)
Beaver Creek	10/12/2020	33.96305	-99.2111	0 (0,0)	0 (0,0)
Elk Creek	10/4/2019	35.33564	-99.36754	0 (0,0)	0 (0,0)
Elk Creek	10/4/2019	35.28976	-99.36566	0 (0,0)	0 (0,0)
Elk Creek	10/4/2019	35.18829	-99.28834	0 (0,0)	0 (0,0)
Elk Creek	10/5/2019	35.17472	-99.28153	0 (0,0)	0 (0,0)
Elk Creek	8/26/2020	35.17474	-99.2811	0 (0,0)	0 (0,0)
Elk Creek	9/1/2020	35.18839	-99.28843	0 (0,0)	0 (0,0)
Elk Creek	9/1/2020	35.29054	-99.36628	0 (0,0)	0 (0,0)
Elk Creek	9/1/2020	35.30519	-99.37063	0 (0,0)	0 (0,0)
Elk Creek	9/1/2020	35.33546	-99.36752	0 (0,0)	0 (0,0)
Elk Creek	10/22/2020	35.18865	-99.2892	0 (0,0)	0 (0,0)

Stream	Date sampled	Latitude	Longitude	Adult *N* mode (90% HDI)	Juvenile *N* mode (90% HDI)
Elk Creek	10/24/2020	35.3355	-99.36755	0 (0,0)	0 (0,0)
Elk Creek	10/24/2020	35.29048	-99.36626	0 (0,0)	0 (0,0)
Elk Creek	10/24/2020	35.30641	-99.37145	0 (0,0)	0 (0,0)
Elm Fork	9/28/2019	34.92627	-99.50027	16 (15,19)	0 (0,1)
Elm Fork	10/6/2019	34.98853	-99.85097	0 (0,0)	0 (0,0)
Elm Fork	11/3/2019	34.94611	-99.57139	20 (16,26)	0 (0,0)
Elm Fork	8/31/2020	34.96286	-99.69395	0 (0,0)	0 (0,0)
Elm Fork	8/31/2020	34.98853	-99.8513	0 (0,0)	0 (0,0)
Elm Fork	10/23/2020	35.01158	-99.90198	0 (0,0)	0 (0,0)
Elm Fork	10/23/2020	34.95923	-99.80051	0 (0,0)	0 (0,0)
Elm Fork	10/23/2020	34.98802	-99.84756	0 (0,0)	0 (0,0)
Middle Pease River	9/27/2019	34.12479	-100.39436	0 (0,0)	0 (0,0)
Middle Pease River	9/27/2019	34.20825	-100.30231	0 (0,0)	0 (0,0)
North Fork	10/20/2019	35.39016	-100.38333	0 (0,0)	0 (0,0)
North Fork	10/27/2019	34.50306	-99.20833	110 (99,125)	9 (8,12)
North Fork	11/1/2019	34.63583	-99.10277	616 (540,728)	48 (42,60)
North Fork	11/3/2019	35.21701	-99.56086	0 (0,0)	0 (0,0)
North Fork	11/4/2019	35.26487	-100.24707	0 (0,0)	0 (0,0)
North Fork	8/7/2020	35.2183	-99.56004	0 (0,0)	0 (0,0)
North Fork	8/26/2020	35.07393	-99.36818	0 (0,0)	0 (0,0)
North Fork	8/26/2020	35.0517	-99.36541	0 (0,0)	0 (0,0)

Stream	Date sampled	Latitude	Longitude	Adult *N* mode (90% HDI)	Juvenile *N* mode (90% HDI)
North Fork	9/21/2020	34.63578	-99.10311	0 (0,0)	0 (0,1)
North Fork	9/30/2020	34.51106	-99.21207	94 (92,99)	73 (67,82)
North Fork	10/2/2020	35.0738	-99.36823	0 (0,0)	0 (0,0)
North Fork	10/22/2020	35.21913	-99.55897	0 (0,0)	0 (0,0)
North Fork	10/22/2020	35.16832	-99.50481	0 (0,0)	0 (0,0)
North Fork	10/22/2020	35.05132	-99.36374	0 (0,0)	0 (0,0)
North Fork	10/23/2020	34.96297	-99.6328	0 (0,0)	0 (0,0)
North Fork	10/24/2020	35.26607	-100.27031	0 (0,0)	0 (0,0)
North Pease River	10/11/2019	34.27485	-100.28625	0 (0,0)	0 (0,0)
North Pease River	10/11/2019	34.30618	-100.49034	0 (0,0)	0 (0,0)
North Pease River	10/13/2019	34.21292	-100.88902	0 (0,0)	0 (0,0)
North Pease River	8/24/2020	34.27489	-100.28614	0 (0,0)	0 (0,0)
North Pease River	10/13/2020	34.27328	-100.2832	0 (0,0)	0 (0,0)
North Wichita River	9/8/2019	33.74773	-99.47684	14 (14,15)	696 (672,731)
North Wichita River	9/9/2019	33.86848	-99.86847	0 (0,0)	0 (0,0)
North Wichita River	10/11/2019	33.82008	-99.78589	0 (0,0)	0 (0,1)
North Wichita River	8/6/2020	33.82027	-99.78604	1 (1,1)	9 (7,13)
North Wichita River	8/25/2020	33.74914	-99.4763	54 (54,55)	2184 (2114,2265.025)
North Wichita River	10/1/2020	33.86712	-99.86852	0 (0,0)	1 (1,2)
North Wichita River	10/1/2020	33.82024	-99.78611	0 (0,0)	0 (0,0)
North Wichita River	10/12/2020	33.86767	-99.88702	0 (0,0)	0 (0,0)

Stream	Date sampled	Latitude	Longitude	Adult *N* mode (90% HDI)	Juvenile *N* mode (90% HDI)
Pease River	9/15/2019	34.17709	-99.27665	0 (0,0)	0 (0,1)
Pease River	9/15/2019	34.17513	-99.17356	1 (1,2)	4 (4,7)
Pease River	9/18/2019	34.22571	-100.07159	0 (0,0)	0 (0,0)
Pease River	11/5/2019	34.09523	-99.72862	38 (32,49)	0 (0,0)
Pease River	8/6/2020	34.22878	-100.07471	0 (0,0)	0 (0,0)
Pease River	8/6/2020	34.09513	-99.72924	0 (0,0)	1 (1,3)
Pease River	9/14/2020	34.1808	-99.28033	0 (0,0)	3 (3,6)
Pease River	9/17/2020	34.17889	-99.17459	0 (0,0)	0 (0,0)
Pease River	9/22/2020	34.09511	-99.72882	0 (0,0)	0 (0,0)
Pease River	10/13/2020	34.23098	-100.07662	0 (0,0)	0 (0,0)
Pease River	10/14/2020	34.17948	-99.32533	3 (3,4)	0 (0,0)
Pease River	10/14/2020	34.08279	-99.613921	2 (2,3)	8 (6,13)
Prairie Dog Town Fork	9/7/2019	34.56639	-100.12891	0 (0,0)	0 (0,0)
Prairie Dog Town Fork	10/20/2019	34.57378	-100.74819	1 (1,1)	0 (0,0)
Prairie Dog Town Fork	10/20/2019	34.63027	-100.94482	0 (0,0)	0 (0,0)
Prairie Dog Town Fork	8/24/2020	34.56546	-100.12685	0 (0,0)	0 (0,0)
Prairie Dog Town Fork	8/24/2020	34.56539	-100.19667	0 (0,0)	0 (0,0)
Prairie Dog Town Fork	10/13/2020	34.56553	-100.19827	0 (0,0)	0 (0,0)
Prairie Dog Town Fork	10/25/2020	34.56584	-100.12779	0 (0,0)	0 (0,0)
Quiteque Creek	9/29/2019	34.27966	-101.09388	0 (0,0)	0 (0,0)
Quiteque Creek	9/29/2019	34.29368	-101.05791	0 (0,0)	0 (0,0)

Stream	Date sampled	Latitude	Longitude	Adult *N* mode (90% HDI)	Juvenile *N* mode (90% HDI)
Quiteque Creek	9/29/2019	34.28518	-100.99126	0 (0,0)	0 (0,0)
Quiteque Creek	9/29/2019	34.25008	-100.88916	0 (0,0)	0 (0,0)
Red River	9/13/2019	34.4118	-99.73267	0 (0,0)	0 (0,0)
Red River	10/25/2019	34.4282	-99.33771	1541 (1508,1582)	431 (418,449)
Red River	8/4/2020	34.41222	-99.73338	0 (0,0)	0 (0,1)
Red River	8/5/2020	34.4136	-99.54319	180 (179,183)	49 (43,57)
Red River	8/10/2020	34.43325	-99.34361	32 (32,33)	54 (47,63)
Red River	8/12/2020	34.2278	-98.97926	51 (51,52)	349 (326,383)
Red River	9/22/2020	34.41214	-99.73282	5 (5,6)	15 (13,19)
Red River	10/25/2020	34.57875	-99.95582	0 (0,0)	0 (0,0)
Salt Fork	9/30/2019	34.83679	-99.80144	0 (0,0)	0 (0,0)
Salt Fork	10/14/2019	34.66953	-99.42142	0 (0,0)	0 (0,0)
Salt Fork	10/18/2019	34.48014	-99.37859	337 (323,356)	88 (81,97)
Salt Fork	10/21/2019	34.85794	-99.50758	0 (0,0)	0 (0,0)
Salt Fork	8/4/2020	34.6674	-99.41996	0 (0,0)	0 (0,0)
Salt Fork	9/14/2020	34.63712	-99.40907	0 (0,0)	0 (0,0)
Salt Fork	9/15/2020	34.4799	-99.3784	66 (66,68)	47 (41,54)
Sandy Creek	9/16/2019	34.40866	-99.596	0 (0,0)	0 (0,0)
South Wichita River	9/14/2019	33.68581	-99.58376	13 (13,14)	0 (0,0)
South Wichita River	9/14/2019	33.64484	-99.80087	0 (0,0)	6 (6,8)
South Wichita River	8/23/2020	33.68571	-99.58403	49 (49,51)	81 (74,91)

Stream	Date sampled	Latitude	Longitude	Adult *N* mode (90% HDI)	Juvenile *N* mode (90% HDI)
South Wichita River	10/12/2020	33.64495	-99.80076	0 (0,0)	0 (0,0)
South Wichita River	10/12/2020	33.64519	-99.66555	0 (0,0)	0 (0,0)
South Wichita River	10/25/2020	33.68531	-99.58462	1 (1,2)	1 (1,2)
Wichita River	10/13/2019	33.7008	-99.38555	44 (40,50)	493 (477,515)

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Attachment A

RESEARCH ARTICLE

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Connectivity and flow regime direct conservation priorities for pelagophil fishes

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Abstract

1. Dam construction threatens global aquatic biodiversity by fragmenting stream networks and altering flow regimes. The negative effects of dams are exacerbated by increased drought periods and associated water withdrawals, especially in semi-arid regions. Stream fishes are particularly threatened owing to their mobile nature and requirement for multiple habitats to complete their life cycles. An understanding of relationships with fragmentation and flow regimes, particularly as coarse-scale (e.g. catchment) constraints on species distributions, is essential for stream fish conservation strategies.
2. Prairie chub (*Macrhybopsis australis*) is a small-bodied minnow (Cyprinidae) with poorly understood ecology endemic to the North American Great Plains. Suspected declines in abundance and extirpations have resulted in conservation interest for prairie chub at state and federal levels. Prairie chub is thought to share its reproductive strategy with pelagic-broadcast spawning minnows (pelagophils). Freshwater pelagic-broadcast spawning fishes have been disproportionately affected by fragmentation and streamflow alteration globally.
3. Relationships of prairie chub occurrence with coarse-scale fragmentation and streamflow metrics were examined in the upper Red River catchment. Occurrence probability was modelled using existing survey data, while accounting for variable detection. The modelled relationships were used to project the distribution of prairie chub in both a wet and dry climatic period.
4. The probability of prairie chub occurrence was essentially zero at sites with higher densities of upstream dams, but increased sharply with increases in flow magnitude, downstream open mainstem, and flood duration. The projected distribution of prairie chub was broader than indicated by naïve occurrence, but similar in both climatic periods. The occurrence relationships are consistent with the hypotheses of pelagic broadcast spawning and represent coarse-scale constraints that are useful for identifying areas of the stream network with higher potential for finer-scale prairie chub conservation and recovery efforts. In addition to informing pelagophil conservation, the relationships are also applicable to pelagic-broadcast spawning fishes in marine environments.

KEYWORDS
Bayesian, catchment management, damming, occupancy modelling, pelagic broadcast spawning, prairie chub

1 | INTRODUCTION

Dam construction threatens global aquatic biodiversity by altering flow regimes and instream habitats and fragmenting stream networks. In 2011 there were more than 16 million reservoirs worldwide (Lehner et al., 2011), with increased damming expected throughout the current decade and beyond (Zarfl et al., 2015; Winemiller et al., 2016). Major changes in assemblages and detrimental effects on lotic species following dam construction are well documented for a range of aquatic taxa (Vinson, 2001; Martínez et al., 2013; Fitzgerald et al., 2018; Liu et al., 2018; Wegscheider et al., 2019). Stream fishes are particularly affected as a result of their mobility and requirement for multiple habitat types to complete their life cycles (Fausch et al., 2002).

North American freshwater fishes are experiencing the highest extinction rates among vertebrates (Burkhead, 2012), with flow alteration and fragmentation often cited as primary causes (Poff & Zimmerman, 2010; Carlisle, Wolock & Meador, 2011; Cooper et al., 2017). Dams can alter fish assemblages in areas of close proximity to reservoirs by creating habitats more favourable for lentic species (Anderson, Freeman & Pringle, 2006; Guenther & Spacie, 2006; Freedman et al., 2014). Farther reaching changes to flow regimes and fragmented stream networks caused by dams are also detrimental to species persistence. Dams can disrupt spawning cues and block migration routes, prevent access to spawning and nursery habitats, and alter nutrient cycles (Anderson, Freeman & Pringle, 2006; Freedman et al., 2014; Hoagstrom & Turner, 2015). The direct, wide-ranging effects of dams alone result in numerous stream fish conservation challenges (Liermann et al., 2012); however, fragmentation and flow alterations are exacerbated by drought and associated increases in water withdrawals.

Stream fragmentation and flow alterations are expected to increase because of climate change and growing human demands for water. Both the magnitude and duration of wet and dry climatic periods are projected to increase (Dore, 2005), thus altering ecosystem functioning in rivers (Meyer et al., 1999). The combination of extended periods of drought and increased water demands threaten the long-term persistence of many stream fishes (Magalhaes et al., 2007; Bond, Lake & Arthington, 2008; Falke et al., 2011). Arid and semi-arid ecoregions are particularly vulnerable because they are often extensively dammed (Palmer et al., 2008; Costigan & Daniels, 2012) and have naturally harsh environmental conditions (Puckridge et al., 1998; Bunn et al., 2006). Native stream fishes have evolved to tolerate drought and other dynamics of arid and semi-arid systems. For example, flood pulses can offset pressures of extended dry periods and facilitate stream fish recolonization by increasing connectivity and inundating floodplains (Taylor, Winston & Matthews, 1993; Bunn et al., 2006; Haworth & Bestgen, 2017). However, interactions of dams, loss of baseflows caused by water withdrawals, and climate change have reduced flood magnitude and durations and intensified naturally harsh drought conditions (Palmer et al., 2008). Given the multifaceted challenges, identifying stream fish relationships with fragmentation and flow regimes at multiple spatial scales is essential to developing successful conservation strategies. Understanding coarse-scale constraints on distributions is particularly important to guiding finer-scale conservation and recovery efforts. For example, the stream reach is a natural scale for fish conservation and management activities, but effective strategies are dependent on coarser-scale species relationships (Frissell et al., 1986; Fausch et al., 2002).

Pelagic-broadcast spawning (Balon, 1975) is a common reproductive strategy globally in fresh water (e.g. golden perch *Macquaria ambigua* and silver perch *Bidyanus bidyanus*, Reynolds, 1983), anadromous (shads *Alosa* spp., Maitland & Lyle, 2005), and marine teleosts (anchovies [Engraulidae], Bertrand et al., 2004, and pollacks *Pollachius* spp., Bakun, 2010), but rare in inland systems of North America. Freshwater pelagic-broadcast spawning is restricted in inland systems of North America to mooneyes (Hiodontidae) and three genera of small-bodied minnows (Cyprinidae, hereafter ‘pelagophils’) that occur in the semi-arid North American Great Plains ecoregion (hereafter ‘Great Plains’, Hoagstrom & Turner, 2015). Pelagophils typically spawn in higher-order streams and release transparent, non-adhesive ova that are semi-buoyant (Worthington et al., 2018). The downstream displacement of eggs and larvae is hypothesized to rely on drift (Platania & Altenbach, 1998). Thus, both minimal fragmentation and higher flow magnitude are likely to be essential for successful recruitment (Durham & Wilde, 2009). Perkin & Gido (2011) found a positive relationship between pelagophil population stability and increasing unimpeded lengths of stream, which supports the downstream displacement hypothesis. Juvenile survival is dependent on high-flow events. High flows increase nutrient concentrations, create temporary slackwater habitats that serve as nurseries, and ensure dispersal of individuals among nursery habitats (Hoagstrom & Turner, 2015). The pelagophil life cycle is thought to be completed through extensive upstream movement by juveniles and adults (Platania & Altenbach, 1998; Albers & Wildhaber, 2017; Archdeacon et al., 2018). Despite the inherent differences between riverine and marine environments, there are similarities in physicochemical and habitat characteristics associated with the success of pelagic-broadcast spawning (Hoagstrom & Turner, 2015). Thus, identifying fragmentation and flow regime relationships with Great Plains pelagophils can broaden the general understanding of pelagic-broadcast spawning ecology globally (see Section 4).

The Great Plains is one of the most extensively impounded areas of the world (Palmer et al., 2008; Lehner et al., 2011; Costigan & Daniels, 2012), and pelagophils have been strongly negatively affected by disrupted stream networks, altered flow patterns and reduced flow magnitude, and loss of lotic and floodplain habitats. For example, large declines in pelagophil abundance have been observed after dam construction (Winston, Taylor & Pigg, 1991; Luttrell et al., 1999; Bonner & Wilde, 2000). Pelagophil population declines and local extirpation are thought to be exacerbated by interactions between damming and both drought and increased groundwater pumping (Falke et al., 2011; Perkin et al., 2015b).

Prairie chub (*Macrhybopsis australis*) is a suspected pelagophil endemic to the upper portion of the Red River catchment in the Great Plains (Figure 1). Prairie chub has historically occupied the Red River mainstem and its higher-order tributaries (Worthington et al., 2018); however, the historical and present distribution of prairie chub is unknown, and associated multiscale ecological relationships, including coarse-scale constraints, are not well understood (Hoagstrom, Brooks & Davenport, 2011; Worthington et al., 2018). The uncertainty in ecology and suspected population declines and range reductions have resulted in conservation interest for prairie chub in multiple states (Texas Parks & Wildlife Department, 2012; Oklahoma Department of Wildlife Conservation, 2016). At the federal level, prairie chub is included at present on the 2021–2025 National Domestic Listing Workplan (U.S. Fish & Wildlife Service, 2021). The decision to list prairie chub and propose a critical habitat designation will be based on a 12-month finding in 2025. Prairie chub is also listed as Vulnerable on the Red List of Threatened Species of the International Union for Conservation of Nature (NatureServe, 2013), with improved information about its current distribution and ecology cited as primary research needs. Although prairie chub spawning behaviour has not been examined directly, egg characteristics, habitat use, and body form resemble other pelagophils (e.g. speckled chub *Macrhybopsis aestivalis*, Worthington et al., 2018). Prairie chub also hybridizes with shoal chub (*Macrhybopsis hyostoma*), a known pelagophil (Sotola et al., 2019). Prairie chub has received less research attention than other endemic Great Plains fishes (Worthington et al., 2018), and the lack of information inhibits the development of effective conservation strategies.

The study objective was to identify relationships between prairie chub occurrence and coarser-scale (i.e. catchment) fragmentation and flow regime metrics using existing fish survey data. Occurrence

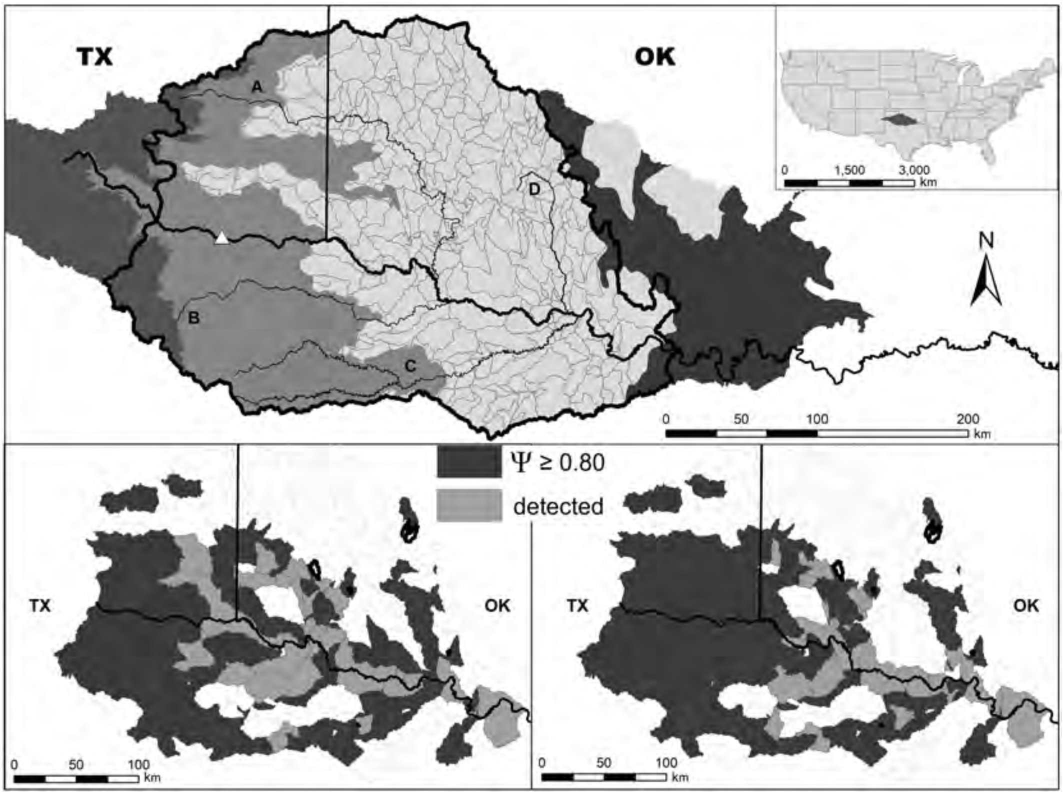

FIGURE 1 Study area (dark outer border of top panel) in the upper Red River catchment and projected prairie chub distribution based on the wet period (1982–2001, bottom left panel) and dry period (2002–2014, bottom right panel). Ψ is estimated prairie chub occurrence probability. The shading in the upper panel denotes level-three ecoregion boundaries (from west to east: High Plains, Southwestern Tablelands, Central Great Plains, and Cross Timbers). The polylines in the upper panel show the Red River mainstem (thicker line) and selected tributaries, where A is the North Fork Red River, B is the Pease River, C is the Wichita River, and D is Cache Creek. Inner borders on polygons show the delineation of hydraulic response units (HRUs). Thicker borders on hollow polygons in the lower panels indicate HRUs that are completely below reservoirs. Other hollow polygons are HRUs with Ψ < 0.80 that were either not surveyed or were surveyed without a prairie chub detection. The white triangle in the upper panel indicates a 2019 prairie chub detection (See Supporting Information S1)

probability was modelled among hydraulic response units (HRUs) of the upper Red River catchment in both a wet and dry climatic period. The modelled relationships were used to project the distribution of prairie chub in both periods. This study provides insight into coarse-scale constraints on prairie chub distribution and examines whether occurrence relationships are consistent with the pelagic-broadcast spawning hypothesis.

2 | MATERIALS AND METHODS

2.1 | Study area and sites

The study area in the Great Plains comprised portions of the Central Great Plains and Southwestern Tablelands level-three ecoregions (hereafter 'ecoregions') of Oklahoma and Texas (Figure 1). Level-three ecoregions further divide higher-level ecoregions based on characteristics such as climate, lithology, and landforms (Woods et al., 2005). The eastern boundary was constrained to the Central Great Plains owing to prairie chub sympatry (Eisenhour, 2004) and introgression (Sotola et al., 2019) with shoal chub in the western portion of the Cross Timbers and associated identification discrepancies in fish survey records. This ecotone also coincides with a reduction in salinity, which is thought to be a primary factor separating prairie chub and shoal chub ranges (Sotola et al., 2019). The western boundary was constrained to the higher-elevation, more arid High Plains ecoregion (Figure 1). The Central Great Plains is characterized by mixed-grass prairie vegetation, cropland, and landforms that include sand dunes, low mountains, and salt flats (Woods et al., 2005). The Southwestern Tablelands has a more rugged terrain, with dissected plain, hill, and canyon landforms, sparse short-grass prairie vegetation, and less cropland. Annual precipitation, although highly variable, increases eastwards (mean rainfall 56–97 cm from west to east). Streams in these ecoregions are primarily sand and silt bottom with minnows and plains killifish (*Fundulus zebrinus*) being the most common fishes.

The occurrence of prairie chub was examined among HRUs (hereafter 'sites') delineated within the study area ($n = 358$, mean cumulative stream length ± SD: 125 ± 123 km, Figure 1). HRUs are spatially similar to 10-digit hydrological units, but use local features to refine boundaries for hydrological modelling (Regan et al., 2018). The delineation of the HRUs in the Red River catchment was based on climate data, topography and land cover, and homogeneous surface water patterns derived from the national hydrography dataset (NHD; U.S. Geological Survey, 2020).

2.2 | Climatic periods and surveys

The study period was divided into a relatively wet climatic period (hereafter 'wet period', 1982–2001) and a relatively dry climatic period (hereafter 'dry period', 2002–2014) based on annual precipitation in the upper Red River catchment (see Figure 3 of Smith et al., 2017). The periods provided an ecologically meaningful division of time (as opposed to a cut-off based on an arbitrary length of time). The beginning of the wet period also coincided with the start of the 'post impoundment' era in the Great Plains (i.e. additional dam construction had largely ceased, Costigan & Daniels, 2012).

Stream fish assemblage surveys were compiled from a variety of government agencies and online databases (Table S1). The terms 'fish' and 'fishes' were used to search all Oklahoma and Texas counties within the study area from 1983–2015 for online databases. The time periods for the fish surveys differed to allow a 1-year time lag between the beginning of a period and the prairie chub occurrence state of the sites (i.e. wet period surveys: 1983–2002, dry period surveys: 2003–2015). Data were screened to remove duplicate surveys. Surveys were spatially referenced to a site using ArcMap (version 10.4.1, ESRI, Red Lands, California) based on the latitude and longitude. The surveys were assigned to the appropriate site when coordinates were not provided if an adequate description was provided. Repeat surveys at a site within a period were treated as spatial replicates with replacement (Kendall & White, 2009). In addition to the detection (1) or nondetection (0) of prairie chub, the date, collector identification (e.g. agency or scientist), and sampling gear type (if reported) were also compiled for each survey.

For prairie chub occurrence modelling, fish survey records were only used from one climatic period for sites sampled in both periods. This approach was chosen to avoid biases (i.e. spatial correlation) associated with fragmentation metrics that did not vary between the periods (see Section 2.3) and any inherent site fidelity (e.g. a site that was occupied by prairie chub in the wet period may be more likely to be occupied in the dry period). Two time periods with incomplete sampling did not provide adequate data to use a colonization–extinction approach (MacKenzie et al., 2003). The period to include was chosen using the following tiered process to balance the number of sites with at least one detection between the periods and retain as many surveys as possible: (i) if only one of the periods included a prairie chub detection in the encounter history, survey records were used from the corresponding period; (ii) for sites with a detection in both periods, a wet–dry ratio was used that first balanced the number of sites with at least one detection, and then retained the greatest number of surveys (see Section 3.1); and (iii) for remaining duplicated sites with all-zero encounter histories, the period with the greatest number of surveys was used.

2.3 | Fragmentation and flow regime metrics

Sites were characterized using fragmentation metrics hypothesized to be associated with prairie chub occurrence at a coarser spatial scale. The metrics were compiled from an online database of spatially verified large dams primarily from the National Anthropogenic Barrier Dataset (Cooper & Infante, 2017). Values associated with the most downstream NHD stream segment were used to represent each site. Temporal variation in fragmentation was not available, and the same values were used for both periods. This assumption of a constant level of fragmentation owing to damming is consistent with the timing of major dam construction in the study area (see Section 2.1). A preliminary analysis indicated a very strong negative relationship between prairie chub occurrence and both upstream network dam density per catchment area (UNDC, no./km^2) and upstream network dam density per stream length (UNDR, no./100 km), which were near perfectly correlated (Pearson's pairwise correlation coefficient (r) = 0.96, $n = 358$). The extreme nature of this relationship resulted in an analytical challenge when trying to examine additional variables. Thus, this upstream dam 'effect' was mitigated by removing sites with ≥5 UNDC and UNDR (i.e. prairie chub were assumed not to occur at sites with five or more upstream network dams, $n = 60$). This cut-off was chosen based on a natural data break (i.e. low-high) and is consistent with survey records (i.e. prairie chub was never detected at a site with five or more upstream network dams). Prairie chub were also assumed not to occur at eight sites that were completely below reservoirs (Figure 1). The remaining fragmentation metrics were also highly correlated. Thus, only percentage open (i.e. free of dams) downstream mainstem (DMO), total mainstem dam density per stream length (TMD, no./100 km), and UNDR were retained to achieve a variable set for prairie chub occurrence modelling with $|r| < 0.50$.

The flow regime metrics (Olden & Poff, 2003) median daily discharge (MA2), flood duration (DH14), high-flow duration (DH20), and variability in the date of annual minimum flow (TL2) were also used to examine prairie chub occurrence relationships (Table S2). These flow regime metrics were chosen because pelagophil reproduction and persistence is likely to depend on increased flow magnitude and predictable and extended periods of elevated flows (see Section 1). Daily discharge estimates associated with the main segment of each HRU were used to calculate the streamflow metrics. Streamflow estimates for tributaries of the main segment were not available. The discharge estimates were derived from a precipitation-runoff modelling system adapted from the national model for the Red River catchment (see Regan et al., 2018, for a complete description). All daily discharge estimates had a Nash–Sutcliffe Efficiency coefficient ≥0.50 suggesting satisfactory prediction of streamflow (Moriasi et al., 2007). The flow regime metrics were calculated in EflowStats (version 5.0.1, median option, Kennen, Henriksen & Nieswand, 2007; USGS, 2019) based on daily discharge for the associated period. High-flow duration was removed from the occurrence variable set to maintain $|r| < 0.50$ (Table S3). A relative flow magnitude was calculated as median monthly discharge (m^3 s^{-1})/ site drainage area (km^2) for each survey to account for variation in the detection probability of prairie chub associated with sampling conditions. The values of drainage area for each site corresponded to the most downstream NHD stream segment.

2.4 | Analyses

Prairie chub detection and occurrence probability was modelled using the hierarchical framework described by MacKenzie et al. (2002). The detection component of the model (hereafter 'detection model'), accounted for the size of the stream network, flow magnitude, time, and collector bias. Spatially replicated surveys can violate the closed-system assumption of the detection process because a species may not be locally present at the time of the survey (Kendall & White, 2009). Thus, the covariate (i.e. continuous predictor variable) cumulative site stream length (hereafter 'stream length', see Section 2.1) was included to account for variation in detection probability associated with proportional coverage of sites. In addition to relative flow magnitude (see Section 2.3), median daily discharge (MA2) was included as a covariate to account for increased detection probability associated with expected higher prairie chub abundance in higher-order streams. The detection probability relationship with relative flow magnitude varied by climatic period using an interaction term. The climatic period factor, using 'wet' as the reference level, also accounted for unexplained variation in detection probability. An interaction term was also used to account for changes in detection probability within a period. An ordered month of survey (wet period: 1–240, dry period: 1–156, hereafter 'time') covariate was included and also allowed it to vary by period. Stream length, MA2, and relative flow magnitude were natural-log transformed because of right-skewed distribution. The most correlated detection covariates were MA2 and relative flow magnitude ($r = 0.47$, $n = 697$ surveys). A collector grouping factor (Wagner, Hayes & Bremigan, 2006; Gelman & Hill, 2007) was used to account for unexplained variation in detection probability due to sampling effort, species and gear bias, etc. ($n = 12$ collectors, Table S4). A t distribution, rather than a normal distribution, was used for the grouping factor to account for heavy tails (Lee & Thompson, 2008; Kruschke, 2013). The gear type was reported for 79% of the surveys and was predominately seining (91% of the reported surveys). The only other reported gear type was electrofishing, which was associated with specific collectors (i.e. redundant with the collector factor). The detection model can be written as:

$$\begin{gathered}\operatorname{logit}(p_{ij}) = \alpha_0 + \alpha_1\,\mathit{PERIOD}_{[i,j]} + \beta_1 X_{1[i,j]} + \beta_2 X_{2[i,j]} + \beta_3 X_{3[i,j]} + \beta_4 X_{4[i,j]} \\ + \beta_5 X_{3[i,j]} * \mathit{PERIOD}_{[i,j]} + \beta_6 X_{4[i,j]} * \mathit{PERIOD}_{[i,j]} + \tau_{c[i,j]}, \\ \text{for}\, i = 1,2\ldots N, \text{for}\, j = 1,2\ldots J \tau_c \tilde{}\, t(0,\sigma^2, \upsilon), \text{for}\, c = 1,2\ldots 12,\end{gathered}$$

where p_{ij} is prairie chub detection probability for survey j at site i, α_0 is the detection model intercept, α_1 is the climatic period indicator variable, β_1–β_4 are slopes for associated covariates, β_5 is the relative flow magnitude–period interaction term, β_6 is the time–period interaction term, X_1 is area, X_2 is median daily flow, X_3 is relative flow magnitude, X_4 is time, τ_c is the grouping factor for collector c, and υ is the normality parameter. For the occurrence component of the model (hereafter occurrence model), the three fragmentation metrics and three flow regime metrics were included as covariates (see Section 2.3). In addition to MA2, UNDR was natural-log transformed (after adding a constant of 0.01 to account for values of zero) to improve linearity. A climatic period factor, with 'wet' as the reference, was also included. All covariates varied by period to examine differing prairie chub relationships between climatic conditions. The occurrence model can be written as:

$$\begin{aligned}\text{logit}\,(\Psi_i) = {} & \alpha_0 + \alpha_1 PERIOD_{[i]} + \Sigma_{k=1}^{6}\Sigma_{n=1}^{6}\beta_k X_{n[i]} \\ & + \Sigma_{k=7}^{12}\Sigma_{n=1}^{6}\beta_k X_{n[i]} * PERIOD_{[i]}, \quad \text{for}\, i = 1,2\ldots N,\end{aligned}$$

where Ψ_i is prairie chub occurrence probability for site *i*, α_0 is the occurrence model intercept, α_1 is the period factor, β_1–β_6 are slopes for associated covariates, β_7–β_{12} are period–covariate interaction terms, and X_1–X_6 are damming and streamflow metric covariates. All detection and occurrence covariates were standardized to a mean of zero and a variance of 1 to improve convergence and interpretation of model coefficients.

Models were fitted using the program JAGS (Plummer, 2003) from the statistical software R (version 3.5.3, R Core Team, 2019) with the package jagsUI (Kellner, 2018). Broad uniform priors were used for all model coefficients, and vague gamma priors were used for associated standard deviations (Kéry & Royle, 2016). Posterior distributions for coefficients were estimated with Markov chain Monte Carlo methods using four chains of 20,000 iterations each after a 5,000-iteration burn-in phase with no thinning. Convergence was assessed using the Brooks–Gelman–Rubin statistic ($\hat{R}$, Gelman & Rubin, 1992), where values <1.1 for all model coefficients indicated adequate mixing of chains (Kruschke, 2015; Kellner, 2018).

A two-step process was used to simplify the model and retain only significant relationships. Significance was defined as 95% highest density intervals (HDIs) that did not overlap zero. The HDIs are not interpreted in a traditional frequentist sense (i.e. a 95% probability of containing the true value). Rather, the mode for the coefficient is the most plausible value, and the HDI contains credible values from the posterior distribution with a total probability of 95% (Kruschke & Liddell, 2018). First, the most complex model was fitted, and the detection interaction terms were examined. These terms were removed if the HDI overlapped zero. If any terms were removed, the model was refitted, and the aforementioned criteria were used to remove main effects that were not significant. The same evaluation was used without refitting the model if both interaction terms were retained. The same process was used for the occurrence model.

Fit of the final model was assessed using posterior predictive checks. A goodness-of-fit test was used to examine dispersion (Kéry & Royle, 2016), where a Bayesian *P*-value near 0.5 indicates adequate fit and extreme values (e.g. <0.10 or >0.90) indicate a lack of fit. A histogram of the collector grouping factor was also examined to ensure the distributional assumption was reasonably met.

A leave-one-out presence-only cross validation (hereafter 'cross validation') was performed using sites with a prairie chub detection (i.e. known occurrences) to evaluate the predictive performance of the final model. For each cross-validation step, one site with a prairie chub detection was removed, and the model was refitted. Prairie chub occurrence probability (Ψ) was calculated for the site omitted using resulting model coefficients. Logit occurrence probabilities were scaled to a value between zero and one (Jørgensen & Pedersen, 1998). The model was considered 'correct' if Ψ was ≥0.80. The cross validation assessed the model's ability to predict a high occurrence probability at sites known to be occupied by prairie chub. Failing to identify an occupied site (i.e. a 'type-two error') is often more detrimental from a conservation perspective (MacKenzie et al., 2002; MacKenzie et al., 2003). However, the test does not evaluate the model's ability to predict absence because it can never be known, but only inferred.

2.5 | Prairie chub distribution map

The final model was used to project prairie chub distribution, adjusted for variable detection probability, across the entire study area for both the wet and dry period. All sites with known prairie chub occurrences were considered occupied, and prairie chub were assumed not to occur at sites that had values of UNDR ≥5 or were below reservoirs (see Section 2.3). Sites where prairie chub were either not surveyed, or surveyed but not detected, were considered occupied if Ψ was ≥0.80 using the calculations described for the cross validation.

3 | RESULTS

3.1 | Fish surveys and fragmentation and flow regime metrics

Fish assemblage surveys were compiled for 124 sites in the wet period and 119 sites in the dry period. UNDR was <5 for 109 and 96 sites for the wet period and dry period, respectively. Naïve prairie chub occurrence (i.e. the proportion of surveyed sites with a detection) was similar in both periods (0.27 and 0.25 in the wet period and dry period, respectively). After eliminating duplicated sites that did not have a prairie chub detection (step 1), eight sites with a detection in both periods were assigned to the wet period and 11 to the dry period to balance the number of sites with a detection (step 2, $n = 22$ sites for both periods). The eight sites assigned to the wet period had the greatest number of surveys. Assigning duplicated sites without a detection (step 3) resulted in 67 unique sites in the wet period and 68 unique sites in the dry period for occurrence modelling. Eliminating duplicated sites resulted in a 18% loss of surveys. The final dataset comprised 237 prairie chub detections and 460 non-detections, with 427 and 270 total surveys in the wet period and dry period, respectively.

The mean, standard deviation, and range of fragmentation and flow regime metrics were generally similar between climatic periods for both modelled sites and all sites in the study area (Table 1). Not surprisingly, MA2 was more variable in the wet period and DH14 was lower in the dry period. UNDR was the most variable fragmentation metric, and TMD was the least variable. The similar summary statistics between modelled sites and all sites ensured that extrapolation was minimal when projecting the distribution of prairie chub.

TABLE 1 Fragmentation and streamflow metric summary statistics for modelled sites only ($n = 67$ for period 1 and $n = 68$ for period 2) and all sites ($n = 358$ for both periods). DMO, the percentage of open downstream mainstem; TMD, total mainstem dam density per stream length; UNDR, upstream network dam density per stream length; MA2, median daily discharge; DH14, flood duration (see also Table A2)

Metric	Modelled sites mean ± SD (range)	All sites mean ± SD (range)
DMO – wet	21.09 ± 11.62 (0.33–35.01)	18.48 ± 13.08 (0.02–36.82)
DMO – dry	19.31 ± 12.05 (0.39–35.13)	18.48 ± 13.08 (0.02–36.82)
TMD – wet	0.40 ± 0.08 (0.29–0.54)	0.40 ± 0.08 (0.28–0.56)
TMD – dry	0.40 ± 0.08 (0.29–0.56)	0.40 ± 0.08 (0.28–0.56)
UNDR – wet	1.20 ± 1.14 (0.00–4.77)	2.49 ± 3.42 (0.00–19.76)
UNDR – dry	1.13 ± 0.96 (0.00–4.30)	2.49 ± 3.42 (0.00–19.76)
DH14 – wet	3.65 ± 0.87 (2.02–5.54)	3.67 ± 0.87 (1.42–6.14)
DH14 – dry	3.47 ± 0.96 (1.34–5.88)	3.46 ± 0.95 (1.34–7.34)
MA2 – wet	121.99 ± 323.70 (0.01–1578.00)	70.27 ± 204.56 (0.01–1578.00)
MA2 – dry	78.12 ± 181.74 (0.01–1093.00)	52.92 ± 158.28 (0.01–1197.00)
TL2 – wet	63.42 ± 9.42 (9.72–76.28)	61.39 ± 12.95 (1.39–80.32)
TL2 – dry	55.88 ± 12.84 (0.93–76.06)	54.88 ± 14.96 (0.36–80.91)

Note: Prairie chub were assumed not to occur at sites with UNDR >5 and not included the modelled dataset.

3.2 | Analysis

Model diagnostics indicated convergence and adequate fit. $\hat{R}$ was <1.1 for all coefficients. The Bayesian *P*-value was 0.36. The histogram indicated that the collector grouping factor reasonably followed a *t* distribution.

Prairie chub detection probability was significantly related to stream length, relative flow magnitude, MA2, and climatic period. (Table 2). At mean levels of covariates with no collector bias, detection probability was 0.34 in the wet period (HDI: 0.18–0.54) and decreased significantly in the dry period. Detection probability also decreased with increasing cumulative stream length and relative flow magnitude, but increased with increasing MA2. Detection relationships with relative flow magnitude and time did not vary significantly between the periods. The time main effect was also not significant.

Prairie chub occurrence probability (Ψ) was significantly related both to fragmentation and flow regime metrics, but there were no significant differences between the climatic periods (Table 2). There remained a strong negative relationship between Ψ and upstream dams among sites with UNDR <5. Ψ was high at mean levels of other covariates (0.96, HDI: 0.61–0.99), but decreased sharply with small increases in UNDR (Figure 2). Ψ increased with increasing MA2, DH14, and DMO. Ψ was not significantly related to TMD or TL2.

The cross validation indicated good model performance, although with some variation between the periods. Ψ was ≥0.80 at 91% (40 of 44) of modelled sites with a prairie chub detection. Predictive performance was higher in the wet period (correct at 22 of 22 sites) than in the dry period (correct at 18 of 22 sites). Thus, the model was more likely to predict that prairie chub did not occur at a site that was occupied in the dry period. Ψ at sites where the model did not pass the cross validation were 0.00, 0.13, 0.65, and 0.68.

The projected distribution of prairie chub was broader than suggested by naïve occurrence and was similar in both the wet and dry period (Figure 1). The final model projection indicated that 48% and 47% of the sites were occupied by prairie chub in the wet period and the dry period, respectively. As expected, the projected distribution largely followed the Red River mainstem and its major tributaries. The model projection also showed that prairie chub occurred west and south west of where they were detected in the survey dataset.

TABLE 2 Detection and occurrence model coefficients reported on the logit scale from posterior distributions reported as the mode with associated 95% highest density intervals (HDIs), where stream length is site cumulative stream length. SD, standard deviation; ν, normality parameter for the *t*-distribution; DMO, percentage of open downstream mainstem; DH14, is flood duration; UNDR, upstream network dam density per stream length

Coefficient	Mode (95% HDI)
Detection	
Intercept	−0.68 (−1.54, 0.14)
Stream length	−0.79 (−1.08, −0.51)
MA2	1.61 (1.23, 2.03)
Relative flow magnitude	−0.93 (−1.37, −0.55)
Dry period	−0.72 (−1.73, −0.34)
Collector SD	0.84 (0.33, 1.76)
Collector ν	23.48 (2.52, 111.88)
Occurrence	
Intercept	3.29 (0.44, 6.27)
DMO	3.93 (1.67, 7.32)
DH14	1.82 (0.17, 6.78)
MA2	4.69 (2.27, 8.00)
UNDR	−12.07 (−19.09, −2.80)

Note: The detection intercept is interpreted as estimated prairie chub detection probability at mean levels of covariates in the wet period. The occurrence intercept is interpreted as estimated prairie chub detection probability at mean levels of covariates. Other coefficients are interpreted with other variables held constant.

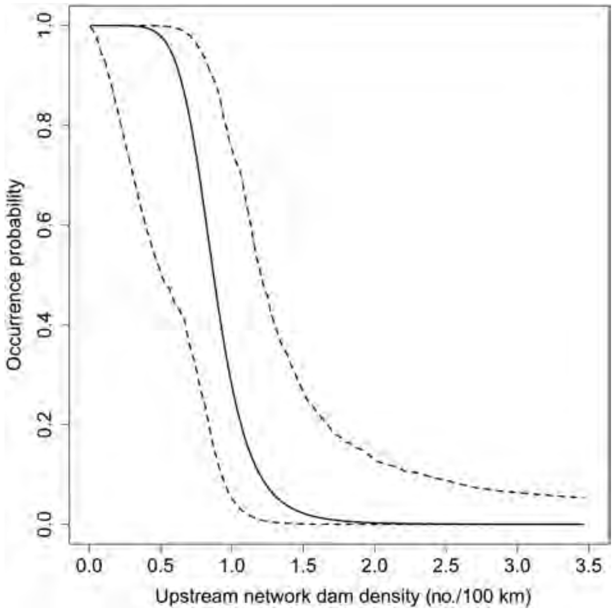

FIGURE 2 Relationship between prairie chub occurrence probability and upstream network dam density (UNDR). Occurrence probability estimates were calculated with percentage open downstream mainstem (DMO), flood duration (DH14), and median daily discharge (MA2) held at mean levels. Dashed lines are 95% credibility intervals. The intervals are asymmetric owing to the conversion of probability estimates from the logit scale (where they are symmetric) to values between zero and 1

4 | DISCUSSION

This study identified coarse-scale prairie chub occurrence relationships with fragmentation and streamflow that represent constraints on its distribution in the upper Red River catchment. Dam density in the upstream network was strongly associated with prairie chub distribution. The probability of prairie chub occurrence probability was essentially zero at sites with higher levels of UNDR, regardless of values for DMO and significant flow regime metrics. Luttrell et al. (1999) found a similar relationship with shoal chub, where upstream dams were associated with decreased population size. However, small increases in DMO, DH14, and, in particular, MA2 increased occurrence probability substantially at sites with lower levels of UNDR. The findings are consistent with previous studies that support pelagic-broadcast spawning as the reproductive strategy of prairie chub (Hoagstrom, Brooks & Davenport, 2011; Worthington et al., 2018). Thus, prairie chub is probably susceptible to factors threatening the persistence of other pelagophils not only in the Great Plains (see Section 1), but also other narrow-range freshwater pelagic-broadcast spawning fishes globally. For example, silver perch, a species of conservation concern endemic to the Murray–Darling River system in Australia, has declined rapidly because of the fragmented stream network (Rowland, 2009). Multiple pelagic-broadcast spawning fishes of commercial importance endemic to South America are of increasing conservation concern in heavily dammed riverine systems (Jiménez-Segura et al., 2016).

Understanding coarser-scale constraints on aquatic species distributions is essential to sound conservation strategies. Coarser-scale characteristics associated with species distributions should be considered before implementing finer-scale conservation actions. For example, reach-scale prairie chub conservation efforts would be likely to fail in HRUs with higher upstream dam densities, regardless of the suitability of finer-scale habitat. The distribution map identifies sites where prairie chub were not detected, but levels of fragmentation and flow regime metrics were associated with a high occurrence probability. The current prairie chub occurrence state at sites with a high probability may also not be of upmost importance for some conservation objectives. Sites with a high occurrence probability can provide target areas in the stream network for prairie chub recovery and translocation efforts.

Not surprisingly, the projected distribution of prairie chub was broader than indicated by naïve occurrence. Most species are more widely distributed than suggested by raw detection data (Gu & Swihart, 2004; Kéry, 2011; Lahoz-Monfort, Guillera-Arroita & Wintle, 2014). However, a high occurrence probability at sites where prairie chub were not detected does not, of course, guarantee occurrence. In addition to error inherent to any model prediction, additional coarse-scale factors may be constraining prairie chub distribution. In addition, biogeography is an often overlooked coarse-scale driver of species distributions (Stevenson, 1997), and prairie chub may simply not have exploited some areas of the catchment with favourable habitats. We suggest increased scrutiny for sites with a high occurrence probability in the extreme western, more arid, part of the study area. Also, sites west and south west of the Red River mainstem have patchy and periodic areas of very high salinity (Ruppel et al., 2017), which may be an additional constraint on prairie chub distributions at various spatial scales (Higgins & Wilde, 2005), although summer 2019 sampling did detect prairie chub south west of any sites with detections during the study period (Figure 1).

The modelled prairie chub occurrence relationships are, of course, correlative in nature, and the metrics are often surrogates for numerous processes. UNDR, for example, is not only a measure of dam density, but also represents loss of stream network connectivity and lotic habitats, alteration of flow and temperature regimes, and disruption of nutrient cycling. UNDR also only considers large dams (see Section 2.3), but low-head dams and other smaller barriers can also be detrimental to stream fishes (Cumming, 2004; Helms et al., 2011). Nevertheless, UNDR represents a strong constraint on the distribution of prairie chub in the upper Red River catchment, despite not elucidating actual mechanisms. Similarly, DH14 is a surrogate for the availability of nursery habitats known to be important to freshwater pelagic-broadcast spawning recruitment (Welcomme, Winemiller & Cowx, 2006; Hoagstrom & Turner, 2015; Jiménez-Segura et al., 2016). Correlations among covariates also make it difficult to speculate on the exact nature of prairie chub occurrence relationships. For example, DMO was highly positively correlated with TMO ($r = 0.93$), which makes it impossible to tease out differences in the importance of upstream or downstream mainstem connectivity. As well as providing a surrogate for increased availability of lotic habits, MA2 was also highly correlated ($|r| > 0.90$) with numerous measures of flow magnitude suggested by Olden & Poff (2003). In particular, MA2 was highly positively correlated with the average discharge of each month. Thus, it is not possible to differentiate between the importance of higher flow magnitude at particular times of year and generally higher flow magnitude.

The study findings support Great Plains pelagophil conservation and also inform the conservation of pelagic-broadcast spawning fishes globally. Generalizing species relationships in conservation planning can result in more efficient use of resources with broader implications (Becker et al., 2010; Van Noordwijk et al., 2012). Thus, understanding coarse-scale constraints of individual pelagophil species distributions informs effective catchment-level conservation strategies in the Great Plains. The findings can also be extended to other freshwater pelagic-broadcast spawning fishes, particularly in regions where dam construction is more recent. For example, the effects on pelagic-broadcast spawners following the construction of the Three Gorges Dam in 2003 in the upper Yangtze River in China are not well understood (Mu et al., 2014). Studies that establish coarse-scale constraints on distributions in systems where damming has stabilized, such as the Great Plains, can inform proactive conservation strategies in systems where species declines may not be fully realized. Despite inherent differences in environments, the findings are also applicable to the ecology of marine pelagic-broadcast spawning fishes (see Hoagstrom & Turner, 2015, for a detailed overview). A presumed advantage of pelagic-broadcast spawning is the delivery and dispersal of larvae to downstream nursery habitats. In marine fishes, the fundamental triad paradigm (Bakun, 1998; Bakun, 2010) identifies nutrient enrichment, nutrient concentration, and propagule retention as essential characteristics of pelagic-broadcast spawner nurseries. Adverse interspecific interactions associated with high densities are minimized by loophole strategies that disperse larvae among nursery habitats. For example, juvenile anchovies have been shown to avoid predation by exploiting microhabitats of generally unfavourable upwelling conditions (Bertrand et al., 2004). The fundamental triad paradigm is relevant to pelagophils with respect to the importance of hydrological complexity (including slackwaters). Fragmentation and flow alteration reduce the formation of these habitats, but also prevent the delivery of nutrients essential for rapid growth and survival. There is also evidence of loophole strategies in pelagophils through the dispersal and separation of individuals during flood recession (Hoagstrom & Turner, 2015). This exploitation of unfavourable floodplain microhabitats is analogous to upwelling in marine systems and emphasizes the importance of extended high-flow events for pelagophil recruitment. The fundamental triad paradigm and loophole strategies offer unifying theories for pelagic-broadcast spawning fishes in both freshwater and marine environments.

Any pelagophil conservation strategy is likely to have only limited success because of the extensive damming of the Great Plains stream network. Pelagophils are likely to be disproportionately affected by legacy effects of damming and expected future increases in water withdrawals (Garbrecht, Van Liew & Brown, 2004) and drought (Feng et al., 2017). Dam removal is one option to support the persistence and potential expansion of pelagophils within their native range. Mass dam removal in the Great Plains is not feasible because of human water needs. However, the strategic removal of a small number of dams may be more effective at restoring stream network connectivity, while maintaining similar water-storage capacity, than random removal of larger dams (Kuby et al., 2005; Perkin et al., 2015a; Magilligan et al., 2016). Dam removal can also be supplemented with controlled water releases and finer-scale remediation of stream connectivity (e.g. fishways, Pennock et al., 2018) and instream habitat for a more comprehensive pelagophil approach.

The nature of existing data results in caveats and challenges with study design and analysis; however, making use of historical surveys is important for successful conservation strategies. Amalgamated datasets provide important information to address contemporary challenges as they can provide insights into ecological relationships of past species distributions and expand the spatial and temporal extent of studies. Such datasets are particularly useful for identifying coarse-scale constraints on species distributions across a river catchment. However, existing data are inherently ‘messy’, with numerous sources of species detection error (e.g. gear and other collector biases and variable sampling conditions) and incomplete survey coverage across space and time (Hampton et al., 2013; Farley et al., 2018). Here, the nature of the data prevented an examination of prairie chub abundance relationships (e.g. counts, effort, and site size not reported); however, this did not entirely drive the decision to examine occurrence because this state variable better matched the coarser scale of HRUs. Despite the caveats associated with spatial replicates (see Section 2.4), repeat surveys helped account for variation in detection probably associated with relative flow conditions, the timing of the survey, and collector biases. We suggest that the importance of using existing data to inform aquatic conservation exceeds inherent limitations and encourage increased use of historical surveys to identify coarse-scale species relationships across broad spatial and temporal extents.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest, financial or otherwise, that influenced objectivity when conducting this study.

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