VARIATION IN ABUNDANCE AND HATCH DATE OF PRAIRIE CHUB MACHRYBOPSIS AUSTRALIS IN THE UPPER RED RIVER BASIN

By

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Abstract: Understanding multi-scale population and life history relationships is key to informing management decisions. Abundance and life history relationships can provide insight on a species' status, population dynamics, recruitment requirements and guide fine scale conservation efforts. Life history strategies are often associated with a specialized habitat, connectivity and predictable flow patterns. These associations may vary across space and time. The Prairie Chub *Machrybopsis australis* is endemic to the upper Red River basin of Oklahoma and Texas. The Prairie Chub is of conservation interest due to uncertainty about its life history and status. Prairie Chub distributions are related to coarse scale flow metrics and are truncated by fragmentation. The goal of my thesis was to examine fine scale relationships to Prairie chub life history and abundance. For my first objective, I modeled the relationship between Prairie Chub hatch success and environmental variation. For my second objective, I estimated abundance and modelled the relationship between adult and juvenile Prairie Chub abundance and environmental variation. My findings help build upon known occurrence relationships and provide management agencies with a more complete picture of factors and potential threats influencing Prairie Chub populations and persistence.

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CHAPTER I INTRODUCTION

INTRODUCTION

Global freshwater fish biodiversity is declining rapidly due to compounding threats (Richter et al. 1997) and human modifications across the landscape (Miller et al. 1989; Hoagstrom et al. 2011). Freshwater fishes comprise the most threatened vertebrate group worldwide with 20% of species already extinct or in rapid decline (Moyle and Leidy 1992; Duncan and Lockwood 2001). There are many threats related to freshwater fish declines, the majority of which work concurrently (Richter et al. 1997) including habitat destruction and fragmentation, pollution, exotic species, and climate change (Miller et al. 1989; Stanford et al. 1996; Richter et al. 1997). Humans exacerbate threats to global fish biodiversity by altering biological and ecological processes that influence species abundance and distribution (Dudgeon et al. 2006; Vorosmarty et al. 2010). For example, extensive irrigation pumping throughout the US High Plains has severely depleted discharge and reduced stream connectivity (Kustu et al. 2010), altering live-history features of stream fishes, including movement and reproduction (Bestgen et al. 2016). Understanding the life history, abundance and distribution of species of concern is critical to developing effective conservation and management strategies.

Abundance and occurrence are often used to assess population status. Estimates of abundance (number of individuals in a population) is important for understanding population status and dynamics as it may be used to assess and monitor population variability over time (Pope et al. 2010). For example, abundance monitoring is often a key component of endangered species recovery plans as recovery criteria may necessitate positive trends in species abundance and adequate population size (e.g., Shortnose Sturgeon *Acipenser brevirostrum*, NOAA National Marine Fisheries Service 1998). Occurrence, the proportion of an area occupied can provide a useful surrogate measure of population status when accurate abundance information is scarce (MacKenzie and Nichols 2004). Understanding the status and fluctuation in species abundance (Hayes et al. 2007) and occurrence (MacKenzie and Nichols 2004) is essential to management aimed at mitigating the threats to a species.

Developing effective conservation strategies relies on understanding the drivers of species declines (Dudgeon et al. 2006), which, for freshwater ecosystems, often involves anthropogenically altered flow regimes (Miller et al. 1989; Poff et al 1997). The flow regime refers to the long-term hydrological variability of a flowing water system and comprises five elements: magnitude, frequency, duration, timing and rate of change (Poff et al 1997). The flow regime is considered a "master variable" governing the abundance and distribution of freshwater fauna in lotic ecosystems (Power et. al. 1995; Poff et al. 1997). It is a dynamic process that establishes a long-term pattern of natural variability and disturbance, which creates and maintains a mosaic of habitat complexity necessary for freshwater fishes to complete their life cycles (Poff et al 1997; Lytle and Poff 2004). Many native freshwater species have evolved behavioral, morphological, and synchronized life history adaptations to natural flow regimes.

In the United States, over 85% of inland waterways have flow patterns that are artificially controlled, and 1 million km of rivers are affected by dams (Echeverria et al. 1989; Poff et al. 1997). Hydrological consequences of current water-development practices include disrupted flow patterns, groundwater depletion, reduced water availability, and more frequent and intense flooding (Abramovitz 1996; Poff et al. 1997). Although the importance of natural flow patterns for freshwater biodiversity is well established, human alterations are widespread and predicted to increase (Matthews and Zimmerman 1990).

Rivers of arid and semi-arid lands often are shallow, slow-flowing streams with alluvial, sand-bed substrate and banks. Such rivers (hereafter alluvial rivers) are characterized as highly

variable, extreme environments. The world's landmass comprises over 40% semi-arid and 25% arid to hyper-arid regions (Davies et al. 1994; Middleton and Thomas 1997; Bunn et al. 2006b) with alluvial rivers (Bunn et al. 2006a). Alluvial rivers occur globally including Australia (Bunn et al. 2006a), China (Feng et al. 2001) and the Great Plains of the United States (Costigan et al. 2012). Alluvial rivers are characterized as "live" sand-bed rivers (Henderson 1963) that continually transport highly erodible sediments governing channel morphology. Alluvial rivers may be classified by varying degrees of sinuosity, braiding, anabranching and sediment load (Schumm 1985). Patterns in alluvial channel morphology and position are highly mercurial where channel stability is governed by variations in sediment load and river discharge (Schumm 1985). For example, the alluvial rivers of Australia are characterized by the most extreme flow patterns in the world (Puckridge et al. 1998) due to variable rainfall, extended droughts (Bunn et al. 2006a) and monsoon-generated episodic floods (Magor 2000). Although alluvial rivers are considered highly variable, human alteration to these ecosystems has exacerbated extreme conditions leading to degradation worldwide (Schumm 1985; Bunn et al. 2006a).

Alluvial rivers provide critical refugia to aquatic organisms and wildlife during prolonged periods of no flow (Bunn et al. 2006a; Arthington et al. 2010). Additionally, alluvial rivers experience major flood pulses that facilitate habitat connectivity (Taylor et al. 1993; Bunn et al. 2006a; Perkin and Gido 2012), provide adequate discharge, and inundate floodplains, which may be critical to life history of native fishes (Bestgen et al. 2016).

The natural morphology and flow patterns of alluvial rivers are threatened by human and climactic factors affecting stream flow and sediment loads (Hickin 1983). Threats to alluvial rivers are predicted to intensify as competition for water drives continued anthropogenic disturbances (Bunn et al. 2006b). Global water resource development (e.g., Colorado and Utah,

USA, Grams and Schmidt 2002; e.g., Australia, Keene et al. 2007; Chessman et al. 2010) and sedimentation (e.g., Australia, Atkinson et al. 2008; Downes et al. 2006; Great Plains, USA, Shields et al. 2013) are jeopardizing alluvial stream biodiversity (Bunn et al. 2006b). Despite their global prevalence, vulnerability to alteration by humans, and significance to aquatic organisms as "ecological arteries", alluvial rivers are poorly studied (Bunn et al. 2006b).

Ecological data are needed to better understand system processes and facilitate effective water-resource management and biodiversity conservation of stream ecosystems in arid and semi-arid lands. Correspondingly, the goal of my thesis is to provide useful data to help agencies improve river conditions to facilitate successful spawning and recruitment of Prairie Chub, Macrhybopsis australis, a small cyprinid endemic to the upper Red River basin in the Southern Great Plains, Oklahoma and Texas, USA. I had two major objectives. First, to determined relationships between environmental variables and timing of Prairie Chub spawning. Knowledge of both life history and reproduction is important for developing more effective species conservation and management plans (Falke et al. 2010). Quantifying relationships between environmental conditions and reproduction are key to understanding recruitment dynamics. However, successful reproduction does not necessarily equate to recruitment by stream fishes. Therefore, my second thesis objective was to examine how physicochemical factors related to variation in both juvenile and adult Priarie Chub abundance at the end of the first summer or early autumn of life when survivival typically stabilizes. My juvenile abundance estimates will contribute toward understanding the relationship between successful spawning and actual recruitment. Determining adult abundances in different stream reaches will help conservation and management agencies determine the relationship between reach-scale dynamics and adult

abundances. These data will be helpful in determining management locations and actions that might be most beneficial to improving conditions for adult fishes.

STUDY AREA

I sampled Prairie Chub within their endemic range of the upper Red River basin of the Great Plains (EPA level I ecoregion, Omernik 1987; Eisenhour 2004). 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 the Ogallala or High Plains Aquifer, one of the largest and fastest depleting aquifers. 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 from higher elevations and rugged canyons west of Amarillo to decreasing elevations and rolling plains as the river flows eastward. (Baldys et al. 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 which often produce localized flooding. The Red River basin is characterized by turbid, sandy-bottomed alluvial rivers with relatively high salinity, heavy mineral loads, and high turbidity. The mineral load comprises varying levels of sodium, chloride, calcium, sulfate, and dissolved solids, and are 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 year 2060 if the rate of extraction greater than the recharge rate goes unabated (Steward et al. 2013).

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CHAPTER II

RELATIONSHIPS BETWEEN PRAIRIE CHUB *MACHRYBOPSIS AUSTRALIS* HATCH TIMING AND ENVIRONMENTAL VARIABLES OF THE UPPER RED RIVER BASIN

INTRODUCTION

Quantifying relationships between environmental conditions and reproduction is key to understanding population dynamics (Falke et al. 2010). The number of larval fish surviving to the adult population (i.e., recruitment) each year drives adult abundance for many species (Roughgarden et al. 1988; Haworth and Bestgen 2017) and is fundamental to the long-term stability of fish populations (Chambers and Trippel 1997). Understanding processes that govern recruitment variability can help predict population fluctuations. Therefore, life-history investigations are often prompted by truncated distributions and perceived abundance decline (e.g., Great Plains cyprinids; Platania and Altenbach 1998). For example, studies focused on identifying discharge and connectivity requirements are needed to maintain populations (Durham and Wilde 2006; Durham and Wilde 2008a; Perkin and Gido 2011). However, knowledge of the life-history requirements needed to develop flow regulations and other management strategies is lacking. This is especially true for a unique freshwater reproductive guild of cyprinids called pelagophils.

A freshwater pelagophil is 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 minnows (family *Cyprinidae*) (*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, semi-buoyant 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 a. 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 have rapidly declined over the past 50 years (Dudley and Platania, 2007; Gido et al., 2010; Perkin and Gido 2015b). Pelagic broadcast spawning 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 there are viable hypotheses (Worthington et al. 2018).

Several hypothesized mechanisms have been proposed to explain the decline of pelagic broadcast spawning minnows. These 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 2016). 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, are projected to further the declines of endemic and threatened prairie stream fishes (Matthews and Zimmerman 1990; Covich et al. 1997; Perkin and Gido 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 pelagic broadcast spawning 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). Therefore, my first objective is to identify the timing and environmmeental conditions related to Prairie Chub spawning.

METHODS

Site Selection

I selected one site on each of 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 1). I selected my sites based on access, the known Prairie Chub distribution (Eisenhour 2004), and proximity to USGS stream gages. It is difficult to estimate the origin of spawning events because the rate of propagule drift or retention varies by species, discharge, and habitat complexity (Dudley and Platania 2007; Medley et al. 2007; Widmer et al. 2012; Worthington et al. 2014). Therefore, I conducted a preliminary survey to ensure that flow variability at and surrounding (i.e., approximately 25 rkm upstream and downstream) each sample location were represented by the nearest respective USGS gage. The results of my survey suggested I could reasonably assume the

hydrologic patterns at the stream gage reflected spawning conditions of propagules collected at each sample site.

Environmental measurements

I measured environmental variables pertinent to stream-fish reproduction to examine relationships associated with Prairie Chub spawning events (Table 1). Discharge may cue spawning initiation and is known to influence recruitment success (Durham and Wilde 2006). I obtained mean daily discharge (1.00 m³/sec) measurements from the USGS stream gage nearest to each of my 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. I 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. Discharge variability patterns are linked to spawning by pelagophils (Durham and Wilde 2006; Moore 1944; Taylor and Miller 1990). Therefore, I calculated the coefficient of variation (CV) in scaled discharge for 10 days prior to each estimated hatch date to represent flow variation that would be unaccounted for by including only discharge on the hatch date. To compute CV, I divided the 10-day SD by the 10-day mean. Timing of the first daily increment formation may vary by species and otolith type (Buckmeier et al. 2017). Therefore using 10 days helps account for hatch-date uncertainty caused by a potential delay of first band formation. I collected average daily air temperature (1.0 °C) and total daily rainfall (1.00 mm) from the weather station nearest to each stream sample location (Table 2; Oklahoma Mesonet; Texas Automated Surface Observing System (ASOS); McPherson et al.

2007; Brock et al. 1995). I attempted to measure continuous water temperature data at each site using temperature loggers (HOBO, Onset Computer Corporation, Bourne, Massachusetts, USA) but my measurements were unreliable due to logger theft, tampering, stream channel shifts, and unpredictable sand accumulation that buried loggers. Therefore, I collected air temperature data because temperature is a primary mechanism that governs spawning initiation and developmental growth rates among 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, Mueller 2013; Flathead Chub, Hawthorn and Bestgen 2016). I collected precipitation data because weather patterns including drought may influence fish recruitment (Perkin et al. 2019). I recorded precipitation by 5-day totals prior to hatch date to account for variation in weather patterns and possible error in our hatch estimates. Lastly, I recorded Julian day because spawning timing can affect both survival and growth rate (Durham and Wilde 2005a). I converted sample season dates each year (April 1st through September 30th) into Julian days within each reproductive season.

Fish Collection and Preservation

I sampled age-0 Prairie Chub measuring < 40-mm total length to improve precision of my 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; Hill and Bestgen 2014; 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. Therefore, I collected Prairie Chub young-of-year measuring < 40-mm TL to minimize aging discrepancies among readers.

We used a fine-mesh seine (1.8 m X 3.4 m seine with 1.5-mm mesh) to sample for age-0 Prairie Chub at each sample location. Seining is the most common method of sampling wadeable sandbed 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, 2020; Hoagstrom et al. 2015). Seining is also considered effective for collecting larval stages in similar species (e.g., Peppered Chub, Durham and Wilde 2005; FlatheadChub, Haworth and Bestgen 2016). I sampled each site approximately every other week beginningin mid-May until age 0 Prairie Chub measuring < 40-mm total length (TL) were no longer captured. I seined each sample location for approximately 2 hrs or until I captured 50 age-0 PrairieChub measuring < 40-mm TL. I counted and measured TL of all Prairie Chub and released incidental catch and Prairie Chub \geq 40 mm TL back into the stream. Prairie Chub measuring < 40mm TL were euthanized via immersion in a 10g/L solution of Tricaine Methanesulfonate (MS-222; Matthews and Varga 2012), buffered with sodium bicarbonate, for at least 10 minutes after cessation of opercular movement (Matthews and Varga 2012) prior to preservation in 1-L bottles of 95% ethanol (Campana 1992) until later laboratory processing. Chemical preservation with ethanol is recommended for larval fish as other methods such as freezing (Long and Grabowski. 2017) and formalin-based preservatives (McMahon and Tash. 1979) can damage small specimens and degrade otoliths.

Laboratory Methods

Otolith Extraction, Mounting and Polishing

I extracted, mounted, and polished otoliths from the age-0 Prairie Chubs to prepare for daily age estimation. 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 hatch date (Durham and Wilde 2008b). Therefore, I used the lapilli otolith to estimate Prairie Chub hatch date. I used the guillotine method (Long and Grabowski 2017) to extract the lapilli otoliths using a dissecting scope (Secor et al. 1992). Briefly, I used a razor blade to make a vertical cut through the skull, posterior to the otic capsules (Long and Grabowski 2017) and used fine tip forceps to extract the otoliths. Next I mounted the whole otoliths to a glass slide using thermoplastic quartz cement (Secor et al. 1992; Long and Grabowski 2017). I melted the cement on a microscope slide using a hot plate set to 40-60 °C to reduce bubbles. I placed the whole otolith onto the cement and allowed it to cool and harden at room temperature (Secor et al. 1992). I 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 (Long and Grabowski 2017). Briefly, I applied light pressure and polished in small circular motions using my index finger and frequently checked progress under the microscope. I used the diamond lapping film in order from coarse to fine as clarity increased to prevent over polishing. Polishing duration varied between 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 were visible from the nucleus through the margin of the otolith.

Otolith Aging and Verification

I quantified daily otolith bands to estimate Prairie Chub hatch 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. Readers identified a counting path based on the shortest radius length with a complete increment sequence and the highest increment clarity (Campana 1992). For verification, two readers conducted two independent otolith readings. Age estimates from both readers within 10% agreement were averaged and recorded (Miller & Storck 1982). Consensus age estimates among experienced readers can improve accuracy and resolve discrepancies (Buckmeier 2002; Buckmeier et al. 2017). Therefore, aging 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 data set. Because *Machrybopsis spp.* hatch \leq 28 h after fertilization (Bottrell et. al. 1964; Rodger et. al. 2016), I added 1 day to my final counts to estimate hatch date.

Analysis

I modeled my data using a hurdle modeling framework because of zero inflation (Figure 2), overdispersion, and the ability to model hatch, no hatch, and the number of hatch events. Ecological data are often considered zero-inflated (i.e., number of zeros prevent the data from fitting standard distributions, Heilbron 1994; Tu 2002). Both zero-inflated and hurdle models accommodate excessive zeros while accounting for overdispersion (Lambert 1992; Hofstetter and Dusseldorp et al. 2016). Hurdle models consider all zero values to be "true", whereas zero-inflated models allow for false zeros (Martin et al. 2005). The sources of zeros are often

unknown (i.e., detection versus no hatch); thus, one solution is to model the non-zero counts separately (Baum and Myers 2004) as is done with hurdle models (Potts and Elith 2006). A computational advantage of using a hurdle model framework is the ability to fit zeros and nonzeros as separate processes (Welsh et al. 1996). I 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 zero model. The second model was a zero-truncated count model (i.e., negative binomial), hereafter count model. I used a negative binomial distribution for the count model to address overdispersion (Hofstetter and Dusseldorf et al. 2016). The two-step hurdle framework that I used allowed me to incorporate both fixed and random effects to account for dependent data (Cantoni et al. 2017).

I built my zero (i.e., logistic regression) and count (i.e., negative binomial) models using both fixed and random effects to explain variation in Prairie Chub hatch events. Prior to developing candidate model sets for both the zero and count models, I made necessary data transformations, examined plots to determine the need for higher order terms, and standardized my continuous covariates. Both models needed to meet the basic assumptions of linear regression. The 5-day precipitation data were highly skewed and was not improved through natural log transformation. Therefore, I made 5-day precipitation categorical with two levels where one category represented 0-mm of rain, and the other represented > 0-mm of rain. I natural log transformed scaled discharge to reduce skewness after adding a constant of 0.001 to eliminate zeros (Warton and Hui 2011). I plotted my continuous covariates against counts to determine if quadratic terms needed to be considered in the count model. I included higher order quadratic terms for scaled discharge, average temperature, Julian date, and CV to the count model only. I 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, I tested for correlation among my continuous predictor variables using Pearson's correlation coefficient and retained all variables with r < |0.6| (Table 3; Kruschke 2015). Retained variables used in my zero model included scaled discharge, average daily air temperature, Julian date, and CV. Retained variables used in my count model included scaled discharge, average daily air temperature, CV, and a quadratic term for Julian day. I used the retained variables to develop candidate model sets comprised of all subset combinations for both models.

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

logit(
$$p_{it}$$
) = ln $\left(\frac{pp_{iii}}{1-pp_{iiii}}\right)$ = $\beta_0 + \alpha_1 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + v_t + \varepsilon_{it}$
for i = 1-2196 observations where y_i = (0,1)
 $v_t \sim N(0, \sigma^2)$, for t = 1,2,....T (stream)
 $\varepsilon_{it} \sim N(0, \sigma^2)$, for observation i, stream t

Where *p* is the probability of a hatch event occurring for observation *i* (where $y_i = (0,1)$ and stream *t*. The grand intercept is β_0 . The fixed categorical effect for year is α_1 . The environmental predictor variables for the zero model are scaled discharge, Julian day, average temperature, and CV are represented by β_1 to β_4 . The random intercept for stream is v_t , and ε_{it} represents 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 2020) using package "Ime4" (Bates et al. 2015).

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

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

for i = 1 – 509 observations where $y_i > 0$ $v_t \sim N(0, \sigma^2)$, for $t = 1, 2, \dots, T$ (stream) $\varepsilon_{it} \sim N(0, \sigma^2)$, for observation *i*, stream *t*

Where *Y* is the estimated mean number of hatches for observation *i* (when $y_i > 0$) and stream *t*. The grand intercept is β_0 . The fixed categorical effect for year is α_1 . The environmental predictor variables for the count model are scaled discharge, Julian day, and CV and represented by β_1 to β_3 , and the quadratic term for Julian Day is β_3^2 . The random intercept for stream is v_t , and ε_{it} represents 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 2020) using package "glmmTMB" (Brooks et al. 2017).

I ranked both candidate model sets to determine which to include in my final models. I used Akaike's information criterion adjusted for small sample size (AIC_c; Hurvich and Tsai 1989; Bedrick and Tsai. 1994) to select my top models based on the lowest AICc value (Burnham and Anderson 2002). I included a categorical fixed effect for year (2019, 2020) in all 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). I used Akaike weights (w_i) to determine the relative model support (Burnham and Anderson 2002). I ranked all subsets (n = 63) of the zero model and the count model (n = 323). To avoid including uninformative parameters, I 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 4).

I calculated R^2 values for the top ranked zero models (Table 5) and count models (Table 6). The zero and count model R^2 calculations were performed in the statistical software R (version 4.0.0; R Core Team 2020) using package "performance" (Lüdecke et al. 2021). I used a binned residual plot for my zero model to examine model fit where 95% of the residuals falling within the error bounds suggests adequate fit (Gelman et al. 2000; Figure 3). I plotted the observed versus predicted residuals associated with my count model using the R package "DHARMa" (Hartig 2019a; Figure 4). 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 2019b, Rizopoulos 2021).

RESULTS

Environmental conditions

Trends in environmental conditions including discharge and air temperature varied by season. Average annual discharge statistics of six 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 10). For example, the average annual discharge of the Red River in 2019 was 71 m³/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*). Contrastingly, in 2020 annual average discharge was 12 m³/s and ranked less than the 20th percentile. Accordingly, I 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. I matched up my air temperature and water temperature data to determine whether air temperature reasonably corresponded to water temperature during my sample seasons (Figure 5). Average air temperature was higher in 2020 but more variable in 2019 (Figure 5). The earliest observed hatches coincided with temperatures of 10 °C in 2019 and 14 °C in 2020. Temperature ranges during peak spawning periods indicated by highest frequency of hatches in late-June through early-July (Figure 15) were relatively consistent between 2019 (22-28 °C) and 2020 (24-28 °C). The highest observed air temperature for Prairie Chub hatch dates were 33 °C in 2019 and 32 °C in 2020.

Fish Collections

I collected and processed otoliths for 2,017 young of year Prairie Chub across 7 rivers and two spawning seasons (i.e., 2019 and 2020; Table 6). I sampled every 2 weeks beginning late May through September in 2019 as discharge and weather permitted. In 2020, I sampled every two weeks beginning the first week of May through mid-August. I collected 1,378 and 639 Prairie Chub in 2019 and 2020, respectively. I collected the most Prairie Chub from the North Wichita River and the fewest from the Salt Fork (Table 6). Prairie Chub collected measured between 11 and 41-mm TL (Table 7). Despite equal sampling efforts across sites, I did not observe any Prairie Chub young of year in the Prairie Dog Town Fork in either year. Due to zero observations I did not include data collected from the Prairie Dog Town Fork in my models.

Age estimates

I retained daily age estimates that met my agreement or consensus standards to analyze hatch date relationships. I retained, on average, 72% of daily age estimates across all rivers (Table 7). I 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 retentions rates were caused by an inability to reach a consensus due to highly irregular ring formation or processing error (e.g., too much heat when melting cement burnt cement or over polishing). For example, age-0 Prairie Chub 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 (Table 7). In 2019, the estimated hatch dates occurred between April 24th through September 20th. In 2020, estimated hatch dates occurred between May 11th and August 7th. Daily age estimates ranged 10 – 87 days. My age estimates suggest the North Wichita and Red River had the highest number of hatch days. The lowest number of hatch days occurred in the North Fork and Salt Fork rivers.

Zero model/ spawning probability

My final logistic regression model predicting the probability of hatch (*P*) contained scaled discharge, average air temperature, Julian day, and year as fixed effects and a random effect for stream (Table 8). The probability of hatch increased with increasing scaled discharge (Figure 9) and average temperature (Figure 10) for both sample seasons. Hatch probability decreased with increasing Julian day indicating hatch was more likely earlier in the sample season (Figure 11). The probability of hatch was higher in 2019 compared to 2020 (Figure 12). The probability of hatch was higher in the North Wichita and South Wichita Rivers and lowest in the North and Salt Fork Rivers during both sample seasons (Figure 12).

I assessed fit to my zero model and calculated the amount of variance explained by fixed and random effects. Fixed effects in my zero model explained 45% of the variance in the probability

of hatch (marginal $R^2 = 0.45$). The total explained variance indicated the random effect for stream increased the amount of variance explained by my model (conditional $R^2 = 0.61$). Adequate model fit was indicated by 95% of residuals falling within the error bounds of my binned residual plot for my zero model (Gelman et al. 2000; Figure 3).

Count model / estimated number of hatches

My final count model contained scaled discharge, Julian day, a quadratic term for Julian day, 10-day CV of discharge, and year as fixed effects and a random effect for stream. The number of Prairie Chub hatches per day increased with increasing scaled discharge (Figure 13) and CV of discharge (Figure 14). The estimated number of hatches were higher in 2019 than in 2020 (Table 8). There was a statistically significant non-linear relationship with Julian day which suggests a threshold relationship existed where the highest frequency of hatches per day peaked in late June through early July in both years (Figure 15). The number of hatches per day were highest in the Pease and Red Rivers and lowest in the Salt Fork and South Wichita Rivers for both years (Figure 16).

I assessed my count model fit and calculated the amount of variance explained by fixed effects. Fixed effects accounted for 57% of the variation in my 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 (Hartig 2019b; Rizopoulous 2021; Figure 4)

DISCUSSION

Prairie Chub spawning peaked in early June for both seasons while 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; Hoagstrom and Turner 2013; Durham and Wilde 2006). Hatches began in April, peaked in early June, and tapered off through September (i.e., nonlinear) in both seasons. 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 \leq 20mm TL were found in the Wichita River mainstem after a high discharge period in early November 2020 which indicated that spawning occurred as late as October. Although Prairie Chub reproduced through October, later hatch dates provide a narrow window for growth prior to winter and may contribute to over-winter mortality. Therefore, timing of hatch may be a strong determinant of recruitment (see Chapter 3). Although I show general patterns of long-term reproduction by Prairie Chub, it is more important to focus on the patterns of hatch I observed across environmental conditions and the river systems.

The timing of peak reproductive effort often corresponds to spring floods and rising air temperatures (i.e., both important in my models). Higher discharge conditions and flow variability (CV) increased Prairie Chub hatch frequency but hatches still occurred at stable and low discharge conditions. Several prairie stream fishes are thought to synchronize spawning with
high flow pulses (e.g., Smalleye Shiner, Durham and Wilde 2008a; Shoal Chub *Macrhybopsis hyostoma*, Rodgers et al. 2016; Flathead Chub, Haworth and Bestgen 2017); though evidence of spawning outside of these higher-flow events is not uncommon (e.g., Arkansas River Shiner, Peppered Chub, Plains Minnow, Flathead Chub, Red Shiner, Durham and Wilde 2006).

The positive linear relationship I found between Prairie Chub hatch probability and discharge corroborates an association between higher flows and spawning. The relationship with increasing discharge is not simply related to stream size because I standardized by drainage area. Higher flows, relative to the drainage area, related to increased hatch 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 hatch success related to discharge would 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 hatch 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 prairie stream fishes (e.g., Shoal Chub, Rodgers 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 increased with discharge variability (i.e., CV), it would be wise to determine optimal and potential threshold conditions

for both spawning and recruitment especially if future discharge regulation such as prescribed dam releases are 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; though, I found no threshold relationship. Temperature is considered a primary mechanism governing spawning and growth of prairie stream fishes (e.g., Central Stoneroller, Orangethroat Darter, Brassy Minnow, Fathead Minnow and Creek Chub, 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. 2016). The non-linear term for temperature did not improve explanatory power of my count model suggesting a threshold was not observed. However, 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. Thermal relationships have important implications for managers as temperature extremes are expected to increase due to climate change (Covich et al. 1997).

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 my study, photoperiod and date were correlated so I did

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not include photoperiod in my analysis. Although a relationship between spawning initiation and photoperiod may exist, a laboratory study would be needed to separate date and photoperiod due to correlation between these variables.

The probability of hatch and frequency of Prairie Chub hatches per day were higher in 2019 than in 2020 and correspond to changes in coarse scale patterns. In particular, 2019 was considered a wet year, whereas 2020 was relatively dry (Table 10, Figure 6, Figure 7, Figure 8). In 2020, lower stream flows also corresponded to higher salinity (Chapter 3, Table 6), a predominant factor governing Prairie Chub abundance (Chapter 3, Figure 9, Figure 13). 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 et al. 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 are suggested if population predictions are of management interest.

The probability of hatches and frequency of Prairie Chub hatches per day varied by stream suggesting coarse scale spatial variation may influence Prairie Chub spawning. Prairie Chub abundance is predominantly governed by a threshold relationship with salinity (Chapter 3) while occurrence is related to mainstream connectivity and artificial fragmentation (Mollenhauer et al. 2021). The South Wichita river dried completely upstream of the sample site and periodically dried to isolated pools at the sampling location during both seasons which may have contributed to lower frequency of hatches per day. The North Wichita river had more persistent connectivity and higher discharge during both seasons compared to the South Wichita (Figure 7). This suggests that among-stream variation in climate and connectivity affect recruitment success.

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 (Figure 1). Surprisingly, the North and South Wichita rivers had the highest hatch 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 identify recruitment requirements such as fragmentation thresholds (Perkin and Gido 2011). Anthropogenic disturbance including dams and nutrient input may explain variation in spawning within the North Fork and Pease Rivers, respectively. The 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. 2007) and reduced habitat availability are often attributed to losses in native fishes biodiversity (Meador and Carlisle 2012). Therefore, Lake Altus may contribute to the lower hatch probability of the North Fork and why relatively few age-0 Prairie Chub were collected in the North Fork during both sample seasons (Table 6).

Water quality degradation due to municipal effluents may contribute to variable recruitment success within the Pease River. Interestingly, the Pease River had the highest estimated number of hatches per day (Figure 16) while very few age-0 Prairie Chub were collected in the 2020 sample season (Table 6). I observed excessive algal growth in the Pease River during both sample seasons 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

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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 my Pease River sample location until late July (Figure 8). 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 phenomenon may explain why age-0 Prairie Chub were more readily abundant (i.e., maximum sample size was achieved for every sample) in 2019 compared to 2020 (Table 6). I suspect that the algae growth degraded water quality and negatively affected Prairie Chub spawning and recruitment. Therefore, I recommend further investigation into the source and impacts of the algal blooms in the Pease River, especially during periods of lower discharge.

Physicochemical conditions of the Prairie Dog Town Fork may inhibit Prairie Chub reproduction resulting in a population sink. Despite equal sampling efforts across streams I 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 my sample location during both seasons (Figure 8). I observed emaciated adult Prairie Chub (n=8) at this location once during a period of higher discharge in early June 2019. Additionally, I observed one adult in the Prairie Dog Town Fork upstream of my sample site in November 2019 that was further upstream than previously recorded (Mollenhauer et al. 2021; Chapter 3). My 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 (Chapter 3). Therefore, the lack of spawning maybe attributed to high salinities that are characteristic of the Prairie Dog Town Fork (Chapter 1 Study Area). Although predominant sources of salinity are natural (e.g., geology and salt springs, Chapter 1 Study Area), artificial input (e.g., oil and gas brine pollution) has increased salinity concentrations (Wurbs 2002). Concentrations in excess of salinity tolerance thresholds could functionally extirpate Prairie Chub from the Prairie Dog Town Fork (Ostrand and Wilde 2001; Higgins and Wilde 2005; Chapter 3). Therefore, an investigation on salinity trends in the Prairie Dog Town Fork may help management agencies determine whether saltmitigation efforts should be implemented.

Although reproductive adults (i.e., gravid females and mature males) were commonly observed, the Salt Fork had the lowest hatch probability and lowest frequency of hatches per day. Interestingly, this suggests that recruitment success varies by stream despite evidence of spawning. The Salt Fork dried completely upstream of my sample site in 2020 which may explain why age-0 Prairie Chub were only collected on one sampling occasion late in the season (Table 7). However my findings suggest that the Salt Fork may have low recruitment regardless of wet or dry conditions.

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, my findings show that successful reproduction does not guarantee successful recruitment. This implies that management agencies focused on population persistence should not focus solely on spawning facilitation. Temporal variation both within and among spawning seasons should be considered if spawning facilitation or predicting trends in populations are of interest. Spatial variability including climate, connectivity, and

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anthropogenic disturbances also pose 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. As climatic and anthropogenic disturbances are expected to increase, future research is needed to identify 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). Lastly, despite cooperative efforts to captive spawn Prairie Chub and personal attempts to mark otoliths via immersion in oxytetracycline hydrochloride (Fielder 2002) I was unable to confirm first band formation or band periodicity. Further studies to improve daily age estimation for Prairie Chub may refine my hatch date estimates. Overall my studies showed that Prairie Chub hatch relationships vary both temporally and spatially and further research is recommended to better understand long term trends in Prairie Chub populations.

Tables and figures

Table 1. The resolution and justification of environmental covariate data collected to explain variation in spawning dates. I collected average daily discharge $(1.00 \text{ m}^3/\text{s})$ at the U.S. Geological Survey stream gauge nearest to each sample site. I converted the date range of April 1 – September 30 to Julian day for each sample year (2019 and 2020). I collected average daily air temperature (1.0 °C) and total daily rainfall amount (1.00 mm) from weather recording stations nearest to each sample site (Table 2).

| Resolution | Justification and citation |
|-------------------------------|--|
| 24 h (1.00 m ³ /s) | Pelagophil spawning is linked to discharge ¹ and |
| | high flow pulses ^{2,3} |
| 24 h | Timing of prairie stream fishes spawning events are |
| | linked to photoperiod ⁴ and timing within a |
| | spawning season may affect survival and growth |
| | rate ⁵ |
| 24 h (1.0 °C) | Temperature is a primary mechanism governing |
| | spawning initiation and growth rate in prairie |
| | stream fishes ^{4,6,7} |
| 24 h (1.00 mm) | Rainfall may represent coarse-scale climate factors |
| | including drought, that may influence recruitment |
| | of stream fishes in the Great Plains ⁸ |
| | Resolution 24 h (1.00 m³/s) 24 h 24 h 24 h (1.0 °C) 24 h (1.00 mm) |

1. (Durham and Wilde 2006) 2. (Moore 1944) 3. (Taylor and Miller 1990) 4. (e.g., Central Stoneroller, Orangethroat darter, Brassy minnow, Fathead minnow and Creek Chub, Falke et al. 2010) 5. (Durham and Wilde 2005a) 6. (e.g., Flathead Chub, Hawthorn and Bestgen 2016) 7. (e.g., Arkansas River Shiner, Mueller 2013) 8. (Perkin et al. 2019). **Table 2.** Data sources and location of each station collecting air temperature and precipitation data for 7 rivers of the southern Great Plains. I 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. Pearson's pairwise correlation coefficients for continuous predictor variables associated with Prairie Chub spawning and recruitment in the Great Plains. Discharge (m³/s) scaled to each rivers' respective drainage area is represented by Q. Day represents Julian day. Tavg represents average 24-h air temperature (°C). CV represents coefficient of variation of scaled discharge for 10 days prior to hatch. All variables were standardized to a mean of zero and a standard deviation of 1 prior to checking correlations.

| Variable | Q | Day | Tavg | CV |
|----------|-------|------|-------|------|
| Q | 1.00 | | | |
| Day | -0.41 | 1.00 | | |
| Tavg | -0.34 | 0.57 | 1.00 | |
| CV10 | 0.05 | 0.00 | -0.07 | 1.00 |

Table 4. Results from the 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 hatch on the logit scale, β_0 is the grand intercept, β_1 to β_x are slopes associated with the predictor variables scaled discharge, temperature, CV, and Julian day. I 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. Models were ranked using Akaike's information criterion adjusted for small sample size (AICc) and Δ AICc 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 |
|--|---|---------|----------------|------------|-------|---------|---------|
| logit(p_{it}) = $\beta_0 + \alpha_1 + \beta_1$ ScaledDischarge ₁ + β_2 Temperature ₂ + β_3 Day ₃ + v_t + | 7 | 1674.19 | 0.00 | -831.078 | 0.40 | 0.45 | 0.61 |
| \mathcal{E}_{it} | | | | | | | |
| logit(p_{it}) = $\beta_0 + \alpha_1 + \beta_1$ ScaledDischarge ₁ + β_2 Temperature ₂ + β_3 Day ₃ + β_4 CV ₄ + $v_t + \varepsilon_{it}$ | 8 | 1674.62 | 0.43 | -830.285 | 0.33 | 0.45 | 0.60 |
| logit(p_{it}) = $\beta_0 + \alpha_1 + \alpha_2 + \beta_1$ ScaledDischarge ₁ + β_2 Temperature ₂ + β_3 Day ₃ + β_4 CV ₄ + $v_t + \varepsilon_{it}$ | 9 | 1676.21 | 2.01 | -831.078 | 0.15 | 0.45 | 0.60 |
| logit(p_{it}) = $\beta_0 + \alpha_1 + \alpha_2 + \beta_1$ ScaledDischarge ₁ + β_2 Temperature ₂ + β_3 Day ₃ + $v_t + \varepsilon_{it}$ | 8 | 1676.59 | 2.39 | -830.262 | 0.12 | 0.45 | 0.61 |
| $logit(p_{it}) = \beta_0 + v_t + \varepsilon_{it}$ | 3 | 2255.82 | 581.62 | -1125.91 | 0.00 | Na | Na |

Table 5. Results from the 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 where Y_{it} is the estimated number of Prairie Chub hatches per day on the log scale, β_0 is the grand intercept, β_1 to β_x are slopes associated with the predictor variables scaled discharge, temperature, CV, and Julian day. I included a random effect for stream v_t , and a 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) and Δ AICc 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 |
|--|---|------------------|----------------|------------|-------|---------|
| $\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1 \text{Discharge}_1 + \beta_2 \text{Day}_2 + \beta_3 \text{Day}_3^2 + \beta_4 \text{CV}_4 + \nu_t + \varepsilon_{it}$ | 8 | 1657.028 | 0 | -820.37 | 0.12 | 0.57 |
| $\log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1 \text{Discharge}_1 + \beta_2 \text{Day}_2 + \beta_3 \text{Day}_3^2 + \beta_4 \text{CV}_4 + \nu_t + \varepsilon_{it}$ | 9 | 1657.85 | 0.82 | -819.74 | 0.07 | 0.55 |
| $\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1 \text{Discharge}_1 + \beta_2 \text{Day}_2 + \beta_3 \text{Day}_3^2 + \beta_4 \text{CV}_4 + \beta_5 \text{Temperature}_5$ | 9 | 1658.22 | 1.19 | -819.93 | 0.06 | 0.56 |
| $+ v_t + \varepsilon_{it}$ | | | | | | |
| $\log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1 \text{Day}_1 + \beta_2 \text{Day}_2^2 + \beta_4 \text{CV}_4 + v_t + \varepsilon_{it}$ | 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 + \beta_5 \text{Day}_4^2 + \beta_5 \text{Day}_4^2 + \beta_5 \text{CV}_5 + \beta_5 \text{Day}_5^2 + $ | 9 | 1659.06 | 2.03 | -820.35 | 0.04 | 0.58 |
| $v_t + \varepsilon_{it}$ | | | | | | |
| $\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1 \text{Temperature}_1 + \beta_2 \text{Day}_2 + \beta_3 \text{Day}_3^2 + \beta_4 \text{CV}_4 + v_t + \varepsilon_{it}$ | 8 | 1659.28 | 2.25 | -821.49 | 0.04 | 0.55 |

| $\log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1 \text{Discharge}_1 + \beta_2 \text{Temperature}_2 + \beta_3 \text{Day}_3 + \beta_4 \text{Day}_4^2 + \beta_5 \text{CV}_5 + \nu_t + \varepsilon_{it}$ | 10 | 1659.38 | 2.35 | -819.47 | 0.03 | 0.55 |
|---|----|---------|-------|---------|------|------|
| $log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1 Discharge_1 + \beta_2 Temperature_2 + \beta_3 Temperature_3^2 + \beta_4 Day_4 + \beta_5 Day_5^2 + \beta_6 CV_6 + \nu_t + \varepsilon_{it}$ | 10 | 1659.51 | 2.48 | -819.53 | 0.03 | 0.55 |
| $\log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1 \text{Temperature}_1 + \beta_2 \text{Day}_2 + \beta_3 \text{Day}_3^2 + \beta_4 \text{CV}_4 + \nu_t + \varepsilon_{it}$ | 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 |
| $log(Y_{it}) = \beta_0 + \alpha_1 + \alpha_2 + \beta_1 Discharge_1 + \beta_2 Discharge_2^2 + \beta_3 Day_3 + \beta_4 Day_4^2 + \beta_5 CV_5 + v_t + \varepsilon_{it}$ | 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 |

| Stream name | No. collected 2019 | No. collected in 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. 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.

Table 7. Summary of age estimates and hatch 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, the number and percent of age estimates retained (i.e., met double reader agreement or conference standards) per season, the number of days where at least 1 hatch occurred (No. hatch dates) per season, the range of total lengths and estimated ages of Prairie Chub collected, and the range of successful hatch dates observed in the 2019 and 2020 sample seasons. No Prairie Chub were collected in the Prairie Dog Town Fork in either year.

| River | No. aged | No. retained | No. aged | No. retained | No. hatch dates | No. hatch dates | TL | Age | Hatch dates | Hatch dates |
|-----------------------|----------|--------------|----------|--------------|-----------------|-----------------|-------|-------|-------------|-------------|
| | 2019 | 2019 | 2020 | 2020 | 2019 | 2020 | | | 2019 | 2020 |
| North Wichita | 344 | 277 | 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 8. Coefficient estimates (logit scale), standard error (SE), and 95% confidence intervals (CI) for my mixed-effects logistic regression model relating the probability of Prairie Chub hatch to environmental parameters and year. The intercept represents the probability of hatch (logit scale) in 2019 at mean values for all other predictor variables. Discharge was scaled by drainage area. Year was a fixed effect.

| Estimate | SE | 95% CI | p value |
|----------|---|---|---|
| -1.73 | 0.48 | -2.68, -0.79 | 0.0003 |
| 1.49 | 0.48 | 1.25, 1.73 | < 2e-16 |
| 1.38 | 0.12 | 1.16, 1.60 | < 2e-16 |
| -1.06 | 0.11 | -1.28, -0.84 | < 2e-16 |
| -0.58 | 0.14 | -0.87, -0.29 | 8.38e-05 |
| | Estimate -1.73 1.49 1.38 -1.06 -0.58 | EstimateSE-1.730.481.490.481.380.12-1.060.11-0.580.14 | EstimateSE95% CI-1.730.48-2.68, -0.791.490.481.25, 1.731.380.121.16, 1.60-1.060.11-1.28, -0.84-0.580.14-0.87, -0.29 |

Table 9. Coefficient estimates (log scale), standard error (SE), and 95% confidence intervals (CI) for the mixed-effects negative-binomial regression model relating the number of Prairie Chub hatch events in 2019 and 2020 to physicochemical parameters and year. The intercept represents the estimated number of daily hatch events (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 hatch. Year 2020 represents the shift in the intercept for sample season 2020. All continuous predictor variables (i.e., Scaled discharge, Julian 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 |
| Julian day (linear) | -0.67 | 0.08 | -0.22, 0.09 | 0.401 |
| Julian 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 10. Annual discharge (m ³ /sec) mean, range, and 30 yr (1990-2020) percentile ranks of seven upper |
|---|
| Red River basin rivers (i.e., 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). |

| | 2019 discharge | | 2020 discharge | | | | |
|-----------------------|-----------------------|-----------------|----------------------|-----------------|--|--|--|
| Stream | mean (range) | 2019 percentile | mean (range) | 2020 percentile | | | |
| 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 | | | |



Figure 1. Map of stream sample locations and respective USGS stream gauges used to collect discharge data. I sampled one site on seven rivers including the North Fork, Salt Fork, Red River, Pease River, North Wichita River, South Wichita River, and Prairie Dog Town Fork and collected discharge data from the USGS stream gauge nearest to each sample site. The seven USGS gauges 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.



Figure 2. Bar plots representing frequency of observations for Prairie Chub hatches per day in 2019 (left panel) and 2020 (right panel). The high frequency of zeros for both years indicate that my data was zero-inflated.



Figure 3. Binned residual plot for my zero (i.e., logistic regression) model representing adequate fit. Gray lines represent theoretical error bounds. If ~95% of binned residuals fall within error bound, then the model is considered to have adequate fit (Gelman et al. 2000).

DHARMa residual diagnostics



Figure 4. DHARMa residual diagnostic plots for my count model indicating adequate model fit. The left panel shows the QQ-plot of the observed versus expected residuals where a uniform distribution in the interval (0, 1) indicates a well-specified model. The p-value reported in the plot is obtained from the Kolmogorov-Smirnov test for uniformity. The right panel is a scatterplot of the residuals against fitted values where a lack of strong patterns indicates adequate fit. A quantile regression is also performed to provide 0.25, 0.5, and 0.75 quantile lines as visual aids which should be straight, horizontal, and at y-values of 0.25, 0.5, and 0.75. (Rizopoulus 2021).



Figure 5. 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 was collected using a temperature logger set at the sample site (HOBO, Onset Computer Corporation, Bourne, Massachusetts, USA). Gaps in the water temperature data set reflect periods when temperature data was unreliable due to the logger being buried in sediment or dried on a sandbar.



Figure 6. 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 hatches per day. Black circles represent hatch events.



Figure 7. Summary of average daily discharge (m^3/sec) values 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 hatches per day. Black circles represent hatch events.



Figure 8. Summary of average daily discharge (m^3/sec) values 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 hatches per day. Black circles represent hatch events. There were no hatches observed in the Prairie Dog Town Fork in either year.



Figure 9. Plots representing the positive linear relationship between Prairie Chub hatch probability scaled between 0 and 1 on the y-axis and scaled discharge (m³/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 10. Plots representing the positive linear relationship between Prairie Chub hatch 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 11. Plots representing the negative linear relationship between Prairie Chub hatch 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 12. Plots representing the shifts in linear relationship between hatch probability (0-1) and scaled discharge by sample stream in 2019 (left panel) and 2020 (right panel). Sample rivers are Pease River, Red River, Salt Fork, North Fork, North Wichita River, and South Wichita River of the upper Red River basin.



Figure 13. Plot representing the positive linear relationship between the number of Prairie Chub hatches per day and scaled discharge with all other variables held constant at mean values for both 2019 (left panel) and 2020 (right panel) sample seasons. The black dotted lines represent 95% confidence intervals.



Figure 14. Plot representing the positive linear relationship between the number of Prairie Chub hatches per day and CV of discharge with all other variables held constant at mean values for both 2019 and 2020 sample seasons. The black dotted lines represent 95% confidence intervals.



Figure 15. Plots representing the quadratic relationship between the number of Prairie Chub hatches per day and date in both the 2019 (left panel) and 2020 (right panel) sample seasons. The black dotted lines represent 95% confidence intervals.



Figure 16. Plots representing the relationship between the number of Prairie Chub hatches per day and scaled discharge (m³/sec), with all other variables held constant, separated by stream and season. The left and right panels represent the 2019 and 2020 seasons, respectively. Sampled rivers are the Pease River, Red River, North Wichita River, North Fork, Salt Fork, and South Wichita River of the upper Red River basin.

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CHAPTER III

RELATIONSHIPS BETWEEN ENVIRONMENTAL VARIABLES AND VARIATION INJUVENILE AND ADULT PRAIRIE CHUB MACHRYBOPSIS AUSTRALIS ABUNDANCEACROSS THE UPPER RED RIVER BASIN

INTRODUCTION

Abundance (number of individuals in a population) is an important indicator of population status and a useful indicator of population decline and recovery. The IUCN red list requires documentation of a species decline prior to being considered threatened (IUCN 2001). A common recovery goal for listed species is to increase either abundance or distribution. Species listed under the U.S. Endangered Species Act (1973) require a recovery plan, "a roadmap to species recovery", that necessitates monitoring to document population status over time (https://www.fws.gov/endangered/laws-policies/RPG-NMFS%20only-062410-no%20dates%20-%20but%20FWS%20on%20title%20page.pdf). Likewise, the European Union Habitats Directive (Directive 92/43/EEC, 1992) requires population trends be evaluated every 6 years (http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index en.html). Rarely is abundance estimated directly; rather, surrogates are often used because they are easier to obtain. For example, relative abundance (proportion relative to other species) has been used to quantify the response of salmonids to instream habitat restoration (e.g., Brook Trout Salvelinus fontinalis, Brown Trout Salmo trutta, Rainbow and Steelhead Trout Onchorhynchus mykiss, Cutthroat Trout Onchorhynchus kisutch, and Atlantic Salmon Salmo salar, Whiteway et al. 2010). Moreover, abundance surrogates such as occupancy (proportion of an area occupied; Mackenzie and Nichols 2004) and relative abundance (Angermeier and Smogor 1995) are useful for understanding population changes over time. In many instances, population estimates are specific to different life stages.

Life-stage-specific abundance is fundamental to management through documenting population trends and understanding recruitment. The relationships to biotic and abiotic factors may vary among ages and size classes within a population (Schlosser 1985). In some cases,

juvenile abundance may be more sensitive to physicochemical factors such as water temperature and discharge, whereas adult abundance may be predominantly governed by biotic factors such as competition and predation (Rahel et al. 1984; Schlosser 1985). Knowledge of factors influencing separate size classes, such as sources of recruitment failure (e.g., White Sturgeon *Acipenser transmontanus*, Coutant 2004) or adult persistence are important for directing management decisions. For example, relationships between stream fish recruitment and discharge variability in flow-regulated systems may inform experimental flow modification procedures (Freeman et al. 2001). Therefore, conservation of stream fishes relies, in part, on understanding relationships between seasonal environmental variability and abundance estimates of different size classes. Regardless of the life stage of focus, accurate abundance estimates facilitate more effective management strategies and inform conservation decisions.

Analytical approaches to assessing changes in abundance must account for variable detection (i.e., the probability of detecting an individual, if present; Peterson and Paukert 2009) and capture probability (i.e., proportion of individuals sampled relative to abundance; Peterson and Paukert 2009). Species detection probability (p) depends on both capture probability (q) and true fish abundance (N). As a result, species detection is influenced by many of the same factors affecting capture probability. Fish detection probability may vary in response to many environmental conditions and instream characteristics such as water clarity, water depth, water temperature, conductivity and streamflow (Peterson and Paukert 2009; Rabeni et al. 2009; Gwinn et al. 2016). Capture probability is influenced by factors such as physicochemical characteristics, sampling methods, fish species, body size and behavior (Peterson and Paukert 2009). If unaccounted for, variable detection can result in spurious and sometimes contradictory findings, thereby confounding conservation and management programs (Gwinn et al. 2016).

Consequently, sampling protocols paired with appropriate statistical models that account for detection heterogeneity have been developed to simultaneously estimate animal abundance and detection probability (Royle and Dorazio 2006). For example, a removal sampling protocol (Zippin 1958) and multinomial N-mixture model design may be used to explicitly model variation in abundance and detection (Royle 2004; Dorazio et al. 2005). A flexible study design and model framework can facilitate accurate and unbiased estimates of population abundance.

The Prairie Chub *Machrybopsis australis* is a poorly studied endemic fish species of the upper Red River Basin (Eisenhour 2004) and is of conservation interest in multiple states (e.g., Texas, Birdsong et al. 2020; Oklahoma Department of Wildlife Conservation, 2016). Prairie chub is listed as state threatened in Texas (Birdsong et al. 2020) and is a Tier 1 species of greatest conservation need in Oklahoma (Oklahoma Department of Wildlife and Conservation 2016). Despite its conservation concern, information on Prairie Chub abundance, distribution and recruitment is insufficient for developing monitoring and conservation strategies. Therefore, my objective was to estimate size-class- specific abundance of Prairie Chub using a removal sampling protocol and multinomial N- mixture models. I designed my study using a removal model while accounting for detection heterogeneity via use of covariates to facilitate accurate abundance estimates. I modelled the abundance and capture probability to determine factors related to both juvenile and adult Prairie Chub abundance across the upper Red River basin.

METHODS

Study area and site selection

I sampled wadeable stream reaches (Rabeni et al. 2009) within the Southern Tablelands and Central Great Plains level III ecoregions (Omernik and Griffith 2014) to estimate Prairie Chub abundance. I did not sample within the Cross Timbers level III ecoregion (Omernik and Griffith 2014) 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 river flows eastward. (Baldys et al. 1998). The climate ranges from semi-arid in the west to subhumid in the east following a precipitation gradient. The Red River basin is characterized by turbid, sandy-bottomed alluvial rivers with relatively high salinity, heavy mineral loads, and high turbidity. Spatial and temporal variation in dissolved solids across the study area contribute to high salinities regularly exceeding that of seawater (Echelle et al. 1972, Keller et al. 1988). High concentrations of dissolved solids (e.g., chlorides and sulfates) originate from salt springs in the western part of the basin (i.e., headwaters) and generally decrease in a downstream direction (Keller et al. 1988).

Stream reaches were selected for sampling using multiple criteria. First, I 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). I accounted for spatial variation (e.g., precipitation gradient) by selecting stream segments from throughout the upper Red River basin. I 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, I used a stratified, random sampling design (Gordon et al., 2004) to choose a reach among meeting the first two criteria (above) using ArcMap (Version 10.5.1; ESRI 2017). Lastly,

I 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.

My reach length was based on both stream wetted width and additional criteria for minimum and maximum length. I used a rangefinder to measure the wetted width (1.0 m) of the stream at 5 evenly spaced transects (Simonson et al. 1993). I calculated reach length by multiplying 20 by the average stream wetted width (e.g., Montgomery and Buffington 1997) to characterize stream morphology. I 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 1-2 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. 2010). The maximum reach length of 500 m provided adequate representation of stream morphology and could be sampled in < 2 days, thereby allowing me to meet the reach-closure assumption (*See Sample Design*).

Sample Design

I 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. I defined my survey as the collection of multi-pass removal seine hauls required to reasonably deplete my 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 smallbodied minnows (Angermeier and Smoger 1995) including those in prairie streams (Bertrand et al. 2006). The observed fish counts obtained from my removal sampling can be translated into an unbiased abundance index using a variety of models (Williams et al. 2002) including multinomial N-mixture models (Dorazio et al. 2005). Multinomial N-mixture models provide inference on species abundance (Royle and Dorazio 2006) and use a flexible hierarchical framework to model variation in abundance and capture probability simultaneously (Royle 2004; Dorazio et al. 2005). The hierarchical framework may help identify any multiscale factorsrelated to abundance fluctuations and can be used to predict variations in abundance outside of sample locations if appropriate covariates are measured (Dorazio et al. 2005). However, removal models depend on adequate sampling to produce accurate estimates (Williams et al. 2002). To ensure adequate sampling, I used a metapopulation approach.

I incorporated a meta-population design to improve the accuracy and precision of my 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 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, I grouped surveys by year (2019 and 2020; Figure 1) 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 (e.g., Smallmouth Bass Micropterus dolomieu, DeAngelis et al. 1993, Knotek and Orth 1998; Brown Trout Salmo trutta, Elliot 1989). To address the closed-system assumption, I followed MacKenzie et al. (2006) and limited each survey to < 3 days. Following Peterson and Cederholm 1984), I allowed 1h between the start time of successive passes to allow for system recovery and to ensure relatively constant capture probability among passes. I 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 (Mollenhauer et al 2018), I measured environmental covariates at the survey level to account for variable capture probability due to sampling conditions (Table 2). 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. 2012) so I modeled size classes separately.

I modeled the abundance of two size classes of Prairie Chub to account for differences between presumptive juveniles and adults. As expected, I observed overlap between the total lengths of age 0 and age-1 Prairie Chub that were not yet reproducing (see Chapter II). I used a cut-off of > 42-mm TL to separate fish that were thought to be large enough to reproduce (hereafter adults) from juveniles (\leq 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 (Crane and Kapuscinski 2018; Hayes et al. 2012), modelling size classes separately may improve abundance estimates.

I used spatially replicated surveys within a hierarchical framework (i.e., multiple spatial scales) to account for among-basin heterogeneity (Wiens 1989; Frissell et al., 1986). 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). I 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 (Kendal 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 et al. 2004a; Dorazio et al. 2005). Consequently, this framework allowed spatially replicated observations despite the highly dynamic nature of sand-bed streams.

Fish Sampling

A survey comprised all sampling passes (i.e., seine hauls required to systematically seine the reach) needed to reasonably deplete the gear at a reach. A pass was a set of seine hauls required to systematically sample a reach. 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). I 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). I 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 I ended the survey and assumed zero fish for subsequent passes. After sampling was completed at each reach, I released the sampled Prairie Chub back to the stream.

I used a standardized seining method across multiple surveys to sample Prairie Chub at each sampled reach. I 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, I covered a maximum area of 3 m (seine width) x 20 m (maximum haul length) per seine haul. I divided my reach into regularly spaced transects \leq 20-m long to evenly distribute effort. For example, if a reach was 160-m long, I divided the reach into eight 20-m transects and seined each transect in a downstream direction beginning at the upstream end of each reach. I 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, as previously described, and enumerated. Prairie Chub were transferred to instream live wells and held until all sampling was completed at each reach.

Environmental Measurements

Abundance Covariates

I measured environmental covariates that I hypothesized would influence the abundance of Prairie Chub (Table 1). The survival and reproduction of Great Plains fishes (Hoagstrom et al. 2011), including the Peppered Chub Machrybopsis tetranema (Pennock et al. 2017), the sister species to Prairie Chub (Eisenhour 2004), are hypothesized related to discharge (Wilde and Durham 2008), flood plain inundation (King et al. 2003), water temperature (Mueller 2013), timing within a season (Durham and Wilde 2005a), and turbidity (Bonner and Wilde 2002; Mueller 2013). 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, I measured discharge (m³/s; Gordon et al. 2004), bankfull discharge (Williams 1978), water temperature (1.0 °C), salinity (1.00 ppt), and turbidity (5 NTU) at each reach. I measured discharge, salinity, bankfull discharge and thalweg depth once per survey as these variables were not likely to vary among surveys. I recorded the date of each survey to calculate Julian day and account for variation in the timing of each survey. I quantified discharge (1.0 m³/sec) using a flow meter (Flo-Mate; Marsh-McBirney Incorporated, Frederick, Maryland, USA) and the velocity-area method (Gordon et al. 2004). I 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. I measured thalweg water depth (Simonson 1993) every 10-20 m (depending on reach length) to

calculate an average reach depth. I measured bankfull discharge following Gordon et al. (2004). I measured water temperature (°C) and turbidity (NTU) between each pass to capture variation within a survey. My analysis method was not capable of accommodating pass varying covariates. Therefore, I averaged water temperature and turbidity measurements across passes for each survey. I measured water temperature (1.0 °C) and turbidity (5 NTU) at mid-depth at the center of the main channel at each reach (Brungs et al. 1977). I used a waterproof infrared pen (Myron PT1 Ultrapen, Carlsbad, California) to measure water temperature (1.0 °C), and I used a turbidity tube (i.e., combination of Jackson candle and Secchi disk methods) to measure turbidity (5 NTU) following Myre and Shaw (2006).

I quantified drainage area, ecoregion, and fragmentation metrics to account for unexplained variation in Prairie Chub abundance at coarser spatial scales. I used ArcMap *Version 10.5.1* (ESRI 2017) to determine drainage area (Strahler, 1952) and ecoregion (Omernik and Griffith 2014) of segments. I hypothesized that dams may influence Prairie Chub abundance and recruitment by limiting downstream distance available for drifting propagules, impeding upstream dispersal, and disrupting natural flow and sediment regimes. Therefore, I included fragmentation metrics that represented upstream, downstream and total (i.e., both upstream and downstream) fragmentation due to dams for each stream segment (Cooper and Infante 2017; Table 3). The upstream metrics I 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 km² of catchment). I 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 I 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).

Capture Probability Covariates

I measured survey-level environmental covariates to account for variable capture probability due to sampling conditions (Table 2). 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; Wagner et al. 2014), water depth (Rabeni et al. 2009), and discharge (Mollenhauer and Brewer, 2018) may influence capture probability. Therefore, I measured average wetted width (m), thalweg depth (m), discharge (m³/sec), water temperature (°C) and turbidity (NTU) to capture variation in sampling conditions among surveys.

Analysis

I 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:

 $y_i | n_i \sim Multinom (n_i, p^c_i)$ (Component 1) $n_i \sim Binomial (N_i, 1 - p_0)$ (Component 2) $N_i \sim Poisson (\lambda_i)$ (Component 3)

Where *n* is the number of individuals captured (i.e., observed counts), *p* is the multinomial cell probability (i.e., encounter histories), $I - p_0$ 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 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 et al. 2004a).

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, Heilbron 1994; Tu 2002). 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.

I prepared my data for analyses by setting an equal number of passes across surveys and averaging pass-varying covariates. My 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 my model. The actual number of passes was variable among surveys (usually 2-7; see Fish sampling). If I did not detect any Prairie Chub while sampling, then I 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, I chose 5 passes as the cut-off to limit the number of count extrapolations. When more than five passes were required, I 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, I extrapolated count data to 5 passes. I extrapolated Prairie Chub counts for 8 surveys based on the average percentage rate of change between passes for those surveys. For example, if I captured 100, 50, and 25 Prairie Chub during passes 1, 2 and 3, respectively, I used the average rate of decline (50%) to obtain counts of 12 and 6 Prairie Chub for passes 4 and 5, respectively. If < 3Prairie Chub were observed at a site for two subsequent passes, I assumed 0 Prairie Chub observations for all subsequent passes (n = 85). For example, if I captured 1 and 0 Prairie Chub during passes 1 and 2, respectively I assumed 0 Prairie Chub for passes 3, 4 and 5.

I checked my data to ensure it met linear, orthogonality, and error assumptions prior to fitting models. I made histograms of all continuous predictor variables to check for linear relationships. I added a constant of 0.001 to UNDR, UNDC, and DMO to eliminate zeros (Warton and Hui 2011). I natural-log transformed all covariates except Julian day and water temperature due to right-skewed distributions. Next I 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, I checked the orthogonality of the predictor variables using Pearson's pair-wise

correlation coefficient cut off r = |0.50| (Table 4). I removed Julian day, thalweg depth, bankful 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. I plotted raw counts against my variables and salinity appeared to be a quadratic polynomial. Therefore, I included a quadratic term for salinity to account for the apparent non-linear relationship.

I included both fixed and random effects in my abundance and capture probability models for adult and juvenile Prairie chub. The covariates were the same for both models. Covariates for my abundance model were discharge, water temperature, turbidity, salinity (linear and quadratic effect), and longitude (Table 5). Those for the capture-probability model were discharge, water temperature, and turbidity (Table 5). I included a categorical factor for year (2019 and 2020) in both models. To prevent over-parameterization of the models, I did not include drainage area or UNDR due to the small effect sizes. I 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, I included an offset for wetted area (m²) to account for abundance variation due to the size of each reach (i.e., modeled as density, fish per m²).

I built a zero-inflated Poisson-regression model with a log-normal distribution to examine variation in Prairie Chub abundance among surveys and sites as a function of covariates. My abundance model formula was expressed as:

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

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

 $logit(heta_i) = eta_0$

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):

$$\begin{aligned} N_{i}| w_{i} \sim \text{Poisson} (w_{i} * \lambda_{i}) \\ \log(\lambda_{i}) &= \beta_{0} + \alpha_{1} Year + \sum_{zz=1}^{5} (\beta_{z} X_{i}) + \beta_{6} X_{i}^{2} + \omega_{h} + o_{k} + \eta_{i} \\ \omega_{h} \sim t (0, \varpi_{h}^{2}, \upsilon), \text{ for } h = 1, 2, \dots, H (\text{HUC grouping factor}) \\ o_{k} \sim t (0, \varpi_{k}^{2}, \upsilon), \text{ for } k = 1, 2, \dots, K \text{ (segment grouping factor)} \\ \eta_{i} \sim t (0, \varpi_{i}^{2}, \upsilon), \text{ for } i = 1, 2, \dots, I \text{ (overdispersion parameter)} \end{aligned}$$

Where λ_i is the estimated mean density of Prairie Chub (where abundance was offset for wetted area, expressed as fish per m²) within the *i* th survey, β_0 is the grand intercept, α_1 is the factor for year (i.e., 2019, 2020). β_1 to β_5 are 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 are ω_h and o_k , respectively. The overdispersion parameter is η_i .

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

Capture probability model (given abundance):

 $C_i | N_i \sim Binomial (N_i, p_i)$

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

for *i* = 1, 2,....*n*

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

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

Where $C_i | N_i$ denoted the observed counts given local abundance, p_i is the estimated capture probability of Prairie Chub within the *i*th survey, β_0 is the grand intercept, α_1 is a factor for year (i.e., 2019, 2020), β_1 to β_3 are 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 are ω_h and o_k , respectively.

I fit the adult and juvenile models using program JAGS (Plummer 2003) called from the statistical software R (version 4.0.0, R Core Team 2020) with the packages jagsUI (Kellner 2018), and rjags (Plummer 2016). I used broad uniform priors for model coefficients, and vague gamma priors for standard deviations (Kéry and Royle 2016). I 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. I assessed convergence using the Brooks-Gelman-Rubin statistic (*R*C Gelman and Rubin 1992), where values <1.1 for all coefficients indicated adequate mixing of chains (Kruschke 2015; Kellner 2018).

After fitting my adult and juvenile models, I checked the posterior distributions of my 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 may be summarized using 90% highest density intervals (HDIs) which represent an interval of the most credible values that cover 90% of the distribution. The HDIs are not interpreted as a probability of containing the true value as is traditional in Frequentist statistics. Instead, the most plausible value is the coefficient mode whereas the HDI contains credible values from the posterior distribution with a total probability of 90% (Kruschke and Liddell 2018). Values within the 90% HDI have a higher probability than values outside the HDI, and the values inside the HDI have a total probability of 90% (Kruschke 2014; Kruschke and Liddell 2018). The width of the interval may also indicate uncertainty where narrower intervals indicate less uncertainty compared to wider intervals (Kruschke 2015).

RESULTS

Fish sampling/ removal surveys

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. I conducted 104 surveys in 2019 (n=44) and 2020 (n=60). In 2019, I 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, I began sampling in mid-August due to evidence of an earlier decline in spawning activity (i.e., no gravid females) and completed my sampling in late October. The 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 2018, n=48 in 2020; Figure 2). 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 3).

Hierarchical design

I surveyed in 2019 and 2020 across stream segments and HUCS (Figure 4). I sampled across 57 stream segments where I averaged 5 spatially replicated surveys per HUC (i.e., site). I surveyed 34 HUCs in 2019 and 24 HUCs in 2020. Adult Prairie Chub had a broader distribution than juveniles, particularly in 2019 (see Figure 1 for discharge conditions). Adult prairie Chub were detected 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.

Covariates

Mean, standard deviation, and range of modelled covariates (i.e., discharge, water temperature, turbidity, salinity, and longitude) varied among surveys and year (Table 6, Table 7). Average and maximum discharge were higher in 2019 compared to 2020 (see Chapter 2, Figure 6, Figure 7, and Figure 8). Average water temperature values were higher in 2020, whereas the maximum water temperature recorded (35°C) occurred in 2019 (see Chapter 2, Figure 5). 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 further downstream (i.e., eastern regions) than adults during both seasons. Some western stream reaches dried completely in 2020 preventing surveys, therefore Prairie Chub were observed further west in 2019 when streamflow was available.

Covariates and Prairie Chub detections

I detected adult and juvenile Prairie Chub across a range of discharge, water temperature, turbidity, and locations across the catchment (Table 6, Table 7). In both seasons, I detected adult and juvenile Prairie Chub in reaches with above average discharge compared to other surveyed reaches, indicating an association with higher discharge when available. In 2019, I observed both size classes in below average water temperatures compared to the average water temperature of surveys for this season. Inversely, I observed both size classes in above average water temperatures compared to the average water temperature of surveys in 2020. Juvenile Prairie Chub were detected at higher turbidities than adults in both 2019 and 2020. Prairie Chub were detected across a broader range of salinities in 2020 compared to 2019. On average, juvenile Prairie Chub were detected at lower salinities than adults in both years. Lastly, I detected adult Prairie Chub further west in the catchment in 2019 when compared to juveniles but found them in similar parts of the catchment in 2020.

Adult Prairie Chub abundance

Adult Prairie Chub abundance (λ) was related to longitude, discharge, water temperature, turbidity, and salinity (Table 8). 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 5). Adult Prairie Chub abundance was higher in the eastern portion of their range (Figure 6). Adult Prairie Chub abundance also increased with increasing discharge and turbidity but decreased as water temperatures warmed (Figure 7). Abundance relationships varied little between 2019 and 2020.

I examined direction and uncertainty of my adult Prairie Chub abundance model parameter relationships using 90% highest density intervals (HDIs; Figure 8). Although there was a clear negative relationship between adult abundance and salinity (Figure 8), 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 indicating a positive relationship is more likely than a slope of zero (Figure 8). 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 9) and varied each year. Unsurprisingly, adult Prairie Chub capture probability decreased with increasing discharge (Figure 7) Adult Prairie Chub capture probability increased with increasing water temperature (Figure 7). Lastly, adult Prairie Chub capture probability was lower in 2019 compared to 2020.

Model diagnostics indicated adequate model convergence. The RR was < 1.1 for slope, intercept, and grouping factor coefficients indicating adequate model convergence (Gelman and Hill 2007). Although RR was > 1.2 for some abundance estimates (n=2), RR values did not exceed 1.3 and high associated effective sample sizes (i.e., > 1000) suggested good model convergence.

Juvenile Prairie Chub analysis

Juvenile Prairie Chub abundance (λ) was related to salinity and longitude (Table 8, Figure 12). Like the adults, juvenile abundance was greater downstream (Figure 9) and had a quadratic relationship with salinity (Figure 10). The 90% highest density intervals (HDIs) of my juvenile abundance parameters for discharge, water temperature and turbidity indicated high uncertainty and that a slope of zero was likely (Figure 11). There were no apparent relationships between juvenile abundance and discharge, water temperature, and turbidity (Figure 12). Interestingly, juvenile abundance was higher in 2020 compared to 2019 (Table 8).

Juvenile Prairie Chub capture probability (*p*) was related to discharge, water temperature, and turbidity (Table 9). Similar to adults, juvenile capture probability increased with increasing

turbidity (Figure 12) and decreased with increasing discharge. In contrast to adults, juvenile capture probability decreased as water temperature increased (Figure 12). Like the adults, juvenile capture probability was lower in 2019 compared to 2020 (Table 9).

Model diagnostics for my juvenile model were similar to the adult model and indicated adequate model convergence. The RR was < 1.1 for slope, intercept, and grouping factor coefficients indicating adequate model convergence (Gelman and Hill 2007). Although RR was > 1.2 for some abundance estimates (n=11), RR values did not exceed 1.3 and high associated effective sample sizes (i.e., > 1000) suggested good model convergence.

Abundance estimates

My abundance estimates for surveys were consistently lower in upstream reaches, higher in downstream reaches, and more variable in central (i.e., transitional) reaches (Table 10). 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.

The abundance and ratio of adult to juvenile Prairie Chub estimates in the Red River varied at fine spatial and temporal scales. For example, in August 2020 adult Prairie Chub abundance estimates appear to decrease, whereas juvenile estimates appear to increase. Additionally, the highest adult and juvenile Prairie Chub abundance estimates in the Red River were generally further downstream compared to other survey locations.

DISCUSSION

Adult and juvenile Prairie Chub densities both had strong quadratic relationships with salinity. My 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. Although Prairie Chub have been collected from isolated saltencrusted pools at salinities up to 19.6 ppt (Echelle et al. 1972), my data suggest that lower salinities may be preferable. 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 Mosquitofish *Gambusia affinis*, Echelle et al. 1972; Ostrand and Wilde 2001, Worthington et al. 2017) including sympatric *Machrybopsis spp*. (Eisenhour et al. 2004; Ruppel et al. 2021). 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.

Though the mechanism is unknown, the apparent absence of Prairie Chub in lower salinities during my study may relate to extrinsic factors. Western reaches of the Red River basin with high salinities are often depauperate resulting in less competition for resources and reduced predation (Echelle et al. 1972, Gido et al 1999). For example, Echelle et al. (1972) suggested that the limited distribution of Red River Pupfish *Cyprinodon rubrofluviatilis*, a high salt-tolerant cyprinid found in the upper Red River basin (Higgins and Wilde 2005), may be due to competition and predation rather than just salinity. Likewise, low to moderate salinities may result in a competitive advantage for Prairie Chub. Conversely, salinity may be an important factor related to abundance and distribution independently of extrinsic pressures.
Prairie Chub abundance is 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 (*Chapter 1 Study Area*; USDA Field Advisory Committee 1977). Additionally, pools critical for refuge during droughts are less likely to form in the headwaters of prairie streams (Tayler et al. 1996). However, longitude was not highly correlated with climactic variables including ecoregion (i.e., Southwestern Tablelands and Central Great Plains level III ecoregions) or fragmentation metrics. Therefore, factors not captured by my 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 variability in Prairie Chub abundance and distribution. The flow regime is considered a master variable governing abundance and distribution relationships of stream fishes (Poff et al. 1997). For example, coarse scale Prairie Chub occurrence is 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, my study did coincide with years of greatly contrasting stream flows 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 (i.e., Ratchet-down mechanism; Perkin et al. 2015a). Therefore, it is important to understand how Prairie Chub discharge relationships vary at both fine and coarse temporal scales (Wiens 1981). For example, in 2019 when flows and connectivity were higher, I observed a single adult Prairie Chub further 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. Prairie Chub abundance patterns may also be influenced by other abiotic factors.

I anticipated the positive relationship between turbidity and adult Prairie Chub abundance. Decreased turbidity has been associated with decreased abundances of prairie stream fishes (e.g., Plains Minnow, Smalleye Shiner, and Sharpnose Shiner, Ostrand and Wilde 2004; Worthington et al. 2017). 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 Shiri 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 (Taylor et al. 1993). I

observed Prairie Chub within a temperature range 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. 2017). For example, Peppered Chub have been observed within a temperature range of 0.1 - 31.6 °C (Worthington et al. 2017). 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 observed relationships between Prairie Chub density and abiotic factors varied between adult and juvenile size classes.

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). Some juvenile fishes can 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, juvenile Prairie Chub abundance showed no relationship to environmental parameters (Table 8; Figure 12). The apparent lack of association between juvenile Prairie Chub abundance and environmental factors may be explained by early life history relationships. As assumed pelagophils, Prairie Chub propagules are broadcasted into the water column and require adequate streamflow for propagules to remain suspended and increase recruitment success (Durham and Wilde 2009). Whether propagules are retained or drift downstream are dependent on factors including adult spawning location, streamflow variability, and habitat complexity (Widmer et al. 2012). 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 (i.e., Prairie Dog Town Fork and Elm Fork) may be used by adults in wet years, it is likely that they serve as population sinks with little to no recruitment. It is possible that a similar relationship occurred in the North Fork which may have contributed to the likely extirpation of Prairie Chub after the construction of Altus Dam (Winston et al. 1991). Future efforts to model changing salinities over time (i.e., have they increased?) would be beneficial 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, 2008). 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 2008b). Accordingly, despite evidence of spawning in the Pease River (see Chapter 2), estimated adult and juvenile abundance was low in both years, indicating low recruitment and adult persistence. 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 wet or dry year conditions.

Prairie Chub abundance and occurrence relationships vary across coarse and fine scales. It is important to acknowledge the variation in scale when comparing different relationships to avoid making spurious conclusions (Wiens et al. 1989). Similar to other pelagophils, coarse scale fragmentation and flow regime metrics influenced Prairie Chub occurrence (Dudley and Platania 2007; Perkin et al. 2015; Mollenhauer et al. 2021), whereas fine scale physicochemical and coarse scale climactic factors are related to Prairie Chub abundance. The variation in abundance and occurrence relationships should not be compared directly due to mis-matched scales of observation. Rather, my findings help to build upon known occurrence relationships to provide a more complete understanding of factors governing Prairie Chub populations and persistence in the upper Red River basin.

Prairie Chub capture probability relationships with discharge, temperature, and turbidity had little influence on our abundance estimates. 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, Prairie Chub capture probability relationships were only weakly related to temperature and did not vary significantly with discharge or turbidity. The relationship between Prairie Chub capture probability and water temperature was positive for adults and negative for juveniles. The variation between adult and juvenile capture probability may be explained by differences in behavior or habitat use. 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 (Reis et al. 2004).

Overall, my findings indicate that under my sampling conditions, capture probability had limited influence on Prairie Chub abundance estimates.

My findings on Prairie Chub abundance relationships are beneficial to management agencies interested in population monitoring and conservation of Prairie Chub and other prairie stream fishes. I produced the first abundance estimates for Prairie Chub in the upper Red River basin. In doing so, my findings provide an important baseline that managers may use to assess the status and variation in Prairie Chub populations over time. My findings on relationships to 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. My findings on capture probability relationships show that future monitoring, if under similar conditions, would be adequate 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. 2017). Therefore, management decisions aimed to mitigate threats to Prairie Chub may also benefit similar prairie stream fishes.

It would be prudent for agencies to consider the salinity, discharge, and fragmentation relationships prior to making management decisions. Managers face a difficult and growing challenge as threats to prairie stream fishes including water development practices (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). Due to the regulatory relationship between Prairie Chub abundance and salinity, I would advise management agencies make careful considerations when desalination projects are proposed.

Considering how salinity may narrow the realized niche of Prairie Chub, it would be prudent to prevent large increases or decreases in salinity concentrations. 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. I would also emphasize that multi-scale discharge and connectivity relationships should be considered by management agencies. Although coarse scale fragmentation and flow metrics do not drive abundance, these metrics truncate distributions and continued alterations may contribute to further extirpations. Lastly, because discharge patterns are important to the Prairie Chub abundance and life history, it would be beneficial for managers to consider more natural discharge variability and connectivity when faced with additional water permits.

Table 1. Description, frequency, and justification for multiscale abundance parameters measured at the pass, survey, segment and huc scales. I nested spatially replicated surveys (n=1-4) into segments (n=57). Segments (i.e., tributary confluence to tributary confluence) are nested by HUC (i.e., hydraulic unit codes; n=39). I measured water temperature and turbidity once per pass. I measured Julien day, discharge, thalweg depth, bankfull depth, salinity, latitude, longitude and determined ecoregion (i.e., Southwestern Tablelands and Central Great Plains level III ecoregions) for each HUC once per study. I collected USGS fragmentation metrics (defined in Table 3) at the segment scale and measured drainage area at the HUC scale.

| Abundance parameter | Scale | Frequency | Justification |
|---------------------------------|--------|-----------|--|
| Water temperature (°C) | Pass | 1 x pass | Water temperature variability may influence developmental growth of pelagophil |
| | | | propagules ¹ . |
| Turbidity (NTU) | Pass | 1x pass | Turbidity may affect feeding and competition among prairie fishes ² . |
| Julien day | Survey | 1x survey | Continuous variable used to account for variation due to sampling date. Timing |
| | | | within a season may affect survival and growth rate ³ . |
| Discharge (m ³ /sec) | Survey | 1x survey | Streamflow is considered a master variable governing species abundance and |
| | | | distribution ^{4,5,6} . Variable discharge is known to influence stream fish capture |
| | | | probability ⁷ . |

| Thalweg depth (m) | Survey | 1x survey | Persistence of and distribution of prairie stream fishes are associated with stream |
|-----------------------|---------|------------|--|
| | | | connectivity ⁸ and depth ⁹ . |
| Bankfull width: depth | Survey | 1x survey | Referred to as "channel forming flow", bankfull can be used to measure channel size |
| | | | to compare among sites ¹⁰ . Bankfull may be used as a measure of floodplain |
| | | | inundation ¹⁰ that may influence stream fish recruitment ¹¹ . |
| Salinity (ppt) | Survey | 1x survey | Dissolved solids in Red River Basin are correlated with stream fishes |
| | | | distributions ^{12,13} . |
| Latitude, Longitude | Survey | 1x survey | Continuous variable used to account for coarse scale climate factors across the upper |
| | | | Red River basin ¹⁴ . Finer scale patterns are constrained by coarser scale patterns ¹⁵ . |
| TM2D, TMO, TMD | Segment | 1x segment | USGS fragmentation metrics representing total distance between upstream and |
| | | | downstream mainstem impoundments. The presence of surface water impoundments |
| | | | is strongly associated with Prairie Chub distribution ¹⁶ . |
| UNDR, UNDC | Segment | 1x segment | USGS fragmentation metrics representing distance to nearest upstream |
| | | | impoundment. The presence of surface water impoundments may compromise |
| | | | connectivity of freshwater ecosystems and limit habitat availability ¹⁷ . |

| DMO, DMD, DM2D | Segment | 1x segment | ent USGS fragmentation metrics representing distance to nearest downstream | |
|---------------------------------|---------|------------|--|--|
| | | | impoundment. The presence of surface water impoundments may compromise | |
| | | | connectivity of freshwater ecosystems and limit habitat availability ¹⁷ . | |
| Drainage Area (m ²) | Huc | 1x HUC | Continuous variable used as a surrogate measure of regional and local streamflow | |
| | | | variables. Densities of stream fishes may increase with increases in drainage area ¹⁸ . | |
| Ecoregion | Survey | 1x HUC | Factor used to account for coarse scale geological and climactic factors across the | |
| | | | upper Red River basin ¹⁴ . Finer scale patterns are constrained by coarser scale | |
| | | | patterns ¹⁵ . | |

1. (e.g., Arkansas River Shiner, Mueller 2013) 2.(Leopold, 1994) 3. (Durham and Wilde 2005a) 4.(Power et al. 1995) 5.(Resh et al. 1988) 6. (Poff et al. 1997) 7. (Peterson and Rabeni 2001) 8. (Perkin and Gido 2011) 9. (Angermeier and Schlosser 1989) 10. (Wolfman and Leopold 1957) 11. (King et al. 2003) 12. (e.g., Red River Pupfish *Cyprinodon rubrofluviatilis*, Echelle et al. 1972) 13. (e.g., 21 prairie stream fish species, Taylor et al 1993) 14. (e.g., precipitation gradient, USDA Field Advisory Committee 1977) 15. (Wiens 1989) 16. (Mollenhauer et al. 2021) 17. (Nilsson et al., 2005) 18. (Newall and Magnuson 1999

Table 2. Description, frequency of measurement and justification for detection parameters measured at the pass and survey scale to account for variation in capture probability. I measured temperature and turbidity once per pass and calculated an averaged between passes to obtain a single value per survey. I calculated a wetted area for each survey by multiplying average wetted width and site length. I measured discharge and thalweg depth once per survey.

| Detection parameter | Scale | Frequency | Justification |
|---------------------|--------|-----------|--|
| Water temperature | Pass | 1x pass | Capture efficiency may vary in response to changes in |
| | | | temperature ^{1,2} . |
| Turbidity | Pass | 1x pass | Turbidity is highly variable and may influence seine |
| | ä | | capture efficiency'. |
| Wetted area | Survey | Ix survey | Water body size can affect detection probability ^{4,3} . |
| Discharge | Survey | 1x survey | capture probability ⁶ . |
| Thalweg depth | Survey | 1x survey | Depth is correlated to variation in seine detection ^{7,8} . |

1.(Danzmann et al. 1991) 2. (Mollenhauer et al. 2018) 3. (Lyon et al. 2014) 4.(Rosenberger and Dunham, 2005) 5.

(Wagner et al. 2014) 6. (Peterson and Rabeni 2001) 7. (Mollenhauer and Brewer 2018) 8. (Rabeni et al. 2009)

Table 3. Description of USGS fragmentation metrics used to measure aspects of dam proximity, dam density, and connectivity relative to each site (Cooper and Infante 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) |
| ТМО | 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 4. Pairwise Pearson's correlation coefficients (r) between abundance covariates. Q is discharge, BF is the bankfull width to

 depth ratio, Salt is salinity, Thal is average thalweg depth, Day is Julien day, Temp is average water temperature, Turb is turbidity,

 Long is longitude, Lat is latitude, and DA is drainage area. See Table 3 for description of three and four-character alphanumeric codes

for fragmentation metrics (i.e., TMO, TMD, TM2D, DMO, DM2D, DMD, UNDR, UNDC).

| | Q | BF | Salt | Thal | Day | Temp | Turb | Long | Lat | DA | ТМО | TMD | TM2D | DMO | DM2D | DMD | UNDR | UNDC |
|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|------|------|
| Q | 1 | | | | | | | | | | | | | | | | | |
| BF | 0.21 | 1 | | | | | | | | | | | | | | | | |
| Salt | -0.05 | 0.31 | 1 | | | | | | | | | | | | | | | |
| Thal | 0.64 | -0.19 | -0.22 | 1 | | | | | | | | | | | | | | |
| Day | 0.18 | -0.01 | -0.01 | 0.10 | 1 | | | | | | | | | | | | | |
| Temp | -0.12 | -0.02 | -0.02 | -0.01 | -0.71 | 1 | | | | | | | | | | | | |
| Turb | 0.09 | -0.10 | -0.22 | 0.22 | -0.22 | 0.30 | 1 | | | | | | | | | | | |
| Long | -0.18 | 0.42 | 0.20 | -0.45 | 0.16 | 0.00 | -0.17 | 1 | | | | | | | | | | |
| Lat | -0.02 | -0.13 | -0.24 | 0.01 | 0.19 | -0.31 | -0.38 | -0.10 | 1 | | | | | | | | | |
| DA | 0.27 | 0.67 | 0.45 | -0.04 | -0.11 | 0.07 | -0.05 | 0.04 | -0.26 | 1 | | | | | | | | |
| ТМО | 0.14 | 0.35 | 0.24 | -0.08 | 0.03 | -0.02 | -0.36 | 0.28 | 0.29 | 0.09 | 1 | | | | | | | |
| TMD | 0.17 | 0.20 | 0.09 | 0.09 | 0.04 | -0.19 | 0.12 | -0.14 | 0.23 | 0.45 | -0.34 | 1 | | | | | | |
| TM2D | 0.15 | 0.39 | 0.26 | -0.09 | 0.03 | -0.03 | -0.36 | 0.28 | 0.31 | 0.16 | 1.00 | -0.26 | 1 | | | | | |
| DMO | 0.23 | 0.31 | 0.12 | -0.01 | 0.07 | -0.05 | -0.29 | -0.29 | 0.31 | -0.01 | 0.91 | -0.33 | 0.89 | 1 | | | | |
| DM2D | 0.21 | 0.30 | 0.11 | -0.03 | 0.08 | -0.06 | -0.30 | 0.30 | 0.33 | -0.04 | 0.91 | -0.33 | 0.89 | 1.00 | 1 | | | |
| DMD | -0.08 | -0.22 | 0.06 | 0.09 | -0.14 | 0.13 | 0.35 | -0.30 | -0.67 | 0.13 | -0.75 | 0.15 | -0.74 | -0.83 | -0.84 | 1 | | |
| UNDR | 0.01 | -0.22 | -0.29 | 0.05 | 0.06 | -0.18 | -0.08 | -0.21 | 0.54 | -0.10 | 0.07 | 0.22 | 0.09 | 0.12 | 0.13 | -0.32 | 1 | |
| UNDC | 0.01 | -0.43 | -0.33 | 0.15 | 0.07 | -0.20 | -0.08 | -0.42 | 0.59 | -0.31 | 0.01 | 0.15 | 0.01 | 0.06 | 0.07 | -0.25 | 0.94 | 1 |

Table 5. Justification and hypothesized form of the relationship (i.e., linear, quadratic) in the abundance (λ) and capture probability (p) components of the multinomial N-mixture model used to estimate adult and juvenile Prairie Chub abundance. No interactions among variables were hypothesized.

| Predictor variable | Size class | Model(s) | Effect | Justification |
|---------------------------------|-----------------|----------|-----------|--|
| Discharge (m ³ /sec) | Adult, juvenile | λ, p | linear | Streamflow is considered a master variable governing species abundance and |
| | | | | distribution ^{1,2,3} . Variable discharge is known to influence stream fish capture |
| | | | | probability ⁴ . |
| Water temperature (°C) | Adult, juvenile | λ, p | linear | Water temperature variability may influence developmental growth of |
| | | | | pelagophil propagules ⁵ . Capture efficiency is known to vary by water |
| | | | | temperature in sand bed streams ^{6,7} . |
| Turbidity (NTU) | Adult, juvenile | λ, p | linear | Turbidity may affect feeding and competition among prairie fishes ⁸ . |
| | | | | Turbidity is highly variable and may influence seine capture efficiency ⁹ . |
| Salinity (ppt) | Adult, juvenile | λ | quadratic | Dissolved solids in Red River Basin are correlated with stream fishes |
| | | | | distributions ^{10,11} . |

1.(Power et al. 1995) 2.(Resh et al. 1988) 3. (Poff et al. 1997) 4. (Peterson and Rabeni 2001) 5.(e.g., Arkansas River Shiner, Mueller 2013) 6.(Danzmann et al. 1991) 7. (Mollenhauer et al. 2018) 8.(Leopold, 1994) 9. (Lyon et al. 2014) 10. (e.g., Red River Pupfish *Cyprinodon rubrofluviatilis*, Echelle et al. 1972) 11. (e.g., 21 prairie stream fish species, Taylor et al 1993) 12. (e.g., precipitation gradient, USDA Field Advisory Committee 1977) 13. (Wiens 1989)

Table 6. Covariate summary statistics for surveys in 2019 where adult Prairie Chub were detected (n = 12), juvenile Prairie Chub were detected (n = 8), and total surveys (i.e., Prairie chub detected and undetected; n = 44). 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 for each survey column.

| Covariate | Total survey mean ± SD (range) 2019 | Adult PC mean ± SD (range) 2019 | Juvenile PC mean ± SD (range) 2019 |
|-------------------|--------------------------------------|------------------------------------|--|
| Discharge | $0.55 \pm 0.95 \ (0.00 - 5.00)$ | 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) | $18.19 \pm 7.84 \ (9.20 - 29.20)$ |
| Turbidity | 1129.90 ± 1353.12 (124.80 - 4045.00) | 962.40 ± 687.88 (124.80 - 2644.20) | $1229.00 \pm 1215.54 \ (160.60 - 3388.30)$ |
| 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 7. Covariate summary statistics for surveys in 2020 where adult Prairie Chub were detected (n = 12), juvenile Prairie Chub were detected (n = 14), and total surveys (i.e., Prairie chub detected and undetected; n = 60). 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 for each survey column.

| Covariate | Total survey mean \pm SD (range) 2020 | Adult PC mean \pm SD (range) 2020 | Juvenile PC mean ± SD (range) 2020 |
|-------------------|--|-------------------------------------|-------------------------------------|
| Discharge | $0.17 \pm 0.43 \ (0.00 - 2.68)$ | $0.55 \pm 0.79 \ (0.00 - 2.68)$ | $0.59 \pm 0.76 \ (0.00 - 2.68)$ |
| 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 | $783.10 \pm 926.876 \ (124.80 - 4045.00)$ | 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 | $99.60 \pm 0.34 \ (98.98 \text{ - } 100.29)$ | $99.46 \pm 0.23 \; (98.98 - 99.79$ | $99.44 \pm 0.24 \ (98.98 - 99.79)$ |

Table 8. 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 v 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 v | 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 v | 32.48 (1.02,71.07) | 33.69 (1.07, 72.31) |
| ηSD | 1.39 (0.60, 2.14) | 2.00 (1.03, 3.05) |
| ην | 27.68 (1.00, 64.78) | 29.44 (1.00, 66.58) |

Table 9. 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) |

Table 10. 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) |
| 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) |
| 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) |
| 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) |
| 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) |
| 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) |
| | | | | | |



Figure 1. Summary of daily average values for discharge (m³/sec) and air temperature (°C) of the Red River mainstem throughout survey seasons (i.e., summer- autumn) in 2019 and 2020. Continuous discharge values were compiled from the USGS gage station on the Red River (USGS stream gauge 07308500, Burkburnett, TX). Air temperature was collected from the Oklahoma Mesonet station nearest to the USGS stream gauge (Oklahoma Mesonet station GRA2, Grandfield, OK).



Figure 2. Map representing the location of adult Prairie Chub abundance surveys (n=104) where adult Prairie Chub were detected (n=24) and non-detected (n=80) within the upper Red River basin of Texas and Oklahoma in both seasons (i.e., 2019, 2020). Surveys were distributed across two out of the three level III ecoregions (i.e., Southwestern tablelands, Central great plains, and Cross timbers) that overlap the upper Red River basin.



Figure 3. Map representing the location of juvenile Prairie Chub abundance surveys (n=104) where juvenile Prairie Chub were detected in 2019 (n=8) and 2020 (n=14) 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 4. 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. I completed 44 surveys in 2019 and 60 surveys in 2020.



Figure 5. Plot representing the quadratic relationship between adult Prairie Chub density (fish/m²) and salinity (ppt). The solid line black line represents estimated y values and the dotted lines represent 90% confidence limits.



Figure 6. Plot representing the linear relationship between adult Prairie Chub density (fish/m²) and longitude. The solid line black line represents estimated y values and the dotted lines represent 90% confidence limits.



Figure 7. Plots representing linear relationships between adult Prairie Chub density (fish/m²) on the left column and capture probability on the right column for parameters including discharge, water temperature, and turbidity. The solid line black line represents estimated y values and the dotted lines represent 90% confidence limits.



Figure 8. Histograms of posterior distributions on the log scale representing uncertainty and direction of relationships for five parameters included in the adult Prairie Chub abundance model. Black bars indicate 90% highest density intervals (HDIs). Parameters include discharge, water temperature, water turbidity, salinity (non-linear), and longitude.



Figure 9. Plot representing the negative linear relationship between juvenile Prairie Chub density (fish/m²) and longitude. The solid line black line represents estimated y values and the dotted lines represent 90% confidence limits.



Figure 10. Plot representing the quadratic relationship between juvenile Prairie Chub density (fish/m²) and salinity (ppt). The solid line black line represents estimated y values and the dotted lines represented 90% confidence limits.



Figure 11. Histograms of posterior distributions on the log scale for the five juvenile Prairie Chub abundance model parameters. Histograms of posterior distributions represent uncertainty and the direction of relationships. Black bars indicate 90% highest density intervals (HDIs). Parameters include discharge, water temperature, water turbidity, salinity (non-linear), and longitude.



Figure 12. Plots representing linear relationships between juvenile Prairie Chub density (fish/m²) on the left column and capture probability on the right column for parameters including discharge, water temperature, and turbidity. The solid line black line represents estimated y values and the dotted lines represent 90% confidence limits.

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