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Connectivity and flow regime direct conservation priorities for pelagophil fishes

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Abstract

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

KEYWORDS

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

1 | INTRODUCTION

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

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

Stream fragmentation and flow alterations are expected to increase because of climate change and growing human demands for water. Both the magnitude and duration of wet and dry climatic periods are projected to increase (Dore, 2005), thus altering ecosystem functioning in rivers (Meyer et al., 1999). The combination of extended periods of drought and increased water demands threaten the long-term persistence of many stream fishes (Magalhaes et al., 2007; Bond, Lake & Arthington, 2008; Falke et al., 2011). Arid and semi-arid ecoregions are particularly vulnerable because they are often extensively dammed (Palmer et al., 2008; Costigan & Daniels, 2012) and have naturally harsh environmental conditions (Puckridge et al., 1998; Bunn et al., 2006). Native stream fishes have evolved to tolerate drought and other dynamics of arid and semi-arid systems. For example, flood pulses can offset pressures of extended dry periods and facilitate stream fish recolonization by increasing connectivity and inundating floodplains (Taylor, Winston &

Matthews, 1993; Bunn et al., 2006; Haworth & Bestgen, 2017). However, interactions of dams, loss of baseflows caused by water withdrawals, and climate change have reduced flood magnitude and durations and intensified naturally harsh drought conditions (Palmer et al., 2008). Given the multifaceted challenges, identifying stream fish relationships with fragmentation and flow regimes at multiple spatial scales is essential to developing successful conservation strategies. Understanding coarse-scale constraints on distributions is particularly important to guiding finer-scale conservation and recovery efforts. For example, the stream reach is a natural scale for fish conservation and management activities, but effective strategies are dependent on coarser-scale species relationships (Frissell et al., 1986; Fausch et al., 2002).

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

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

Prairie chub (*Macrhybopsis australis*) is a suspected pelagophil endemic to the upper portion of the Red River catchment in the Great Plains (Figure 1). Prairie chub has historically occupied the Red River mainstem and its higher-order tributaries (Worthington et al., 2018); however, the historical and present distribution of prairie chub is unknown, and associated multiscale ecological relationships, including coarse-scale constraints, are not well understood (Hoagstrom, Brooks & Davenport, 2011; Worthington et al., 2018). The uncertainty in ecology and suspected population declines and range reductions have resulted in conservation interest for prairie chub in

multiple states (Texas Parks & Wildlife Department, 2012; Oklahoma Department of Wildlife Conservation, 2016). At the federal level, prairie chub is included at present on the 2021–2025 National Domestic Listing Workplan (U.S. Fish & Wildlife Service, 2021). The decision to list prairie chub and propose a critical habitat designation will be based on a 12-month finding in 2025. Prairie chub is also listed as Vulnerable on the Red List of Threatened Species of the International Union for Conservation of Nature (NatureServe, 2013), with improved information about its current distribution and ecology cited as primary research needs. Although prairie chub spawning behaviour has not been examined directly, egg characteristics, habitat use, and body form resemble other pelagophils (e.g. speckled chub *Macrhybopsis aestivalis*, Worthington et al., 2018). Prairie chub also hybridizes with shoal chub (*Macrhybopsis hystoma*), a known pelagophil (Sotola et al., 2019). Prairie chub has received less research attention than other endemic Great Plains fishes (Worthington et al., 2018), and the lack of information inhibits the development of effective conservation strategies.

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

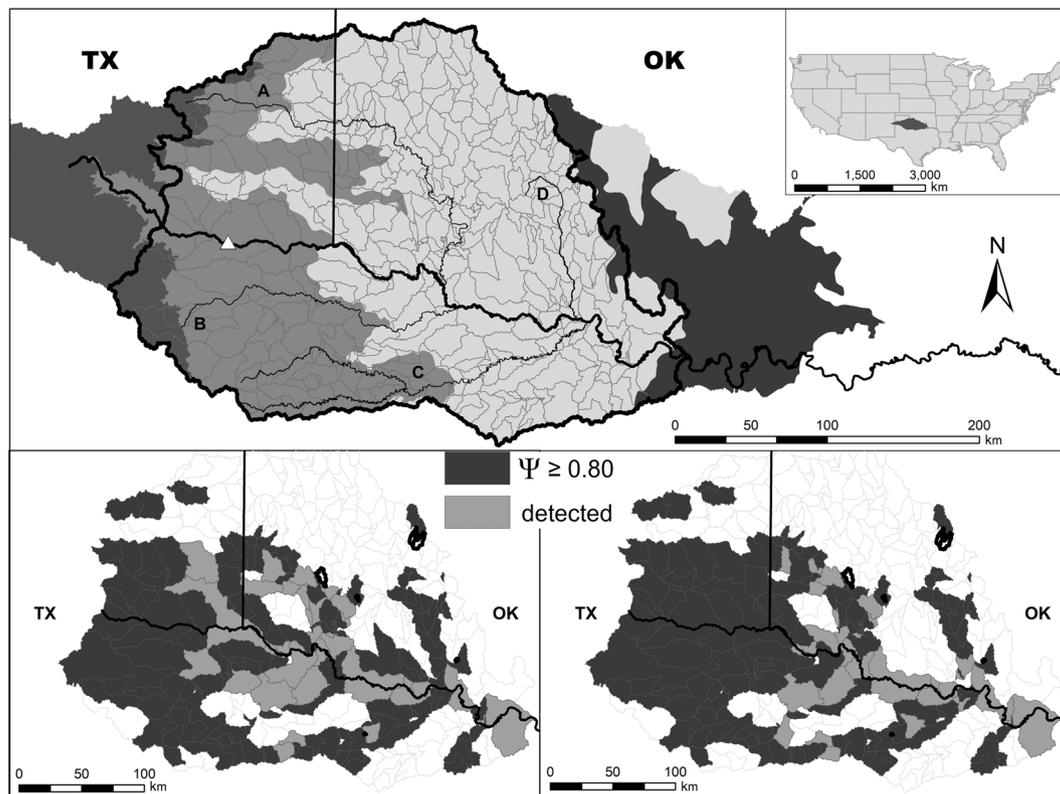


FIGURE 1 Study area (dark outer border of top panel) in the upper Red River catchment and projected prairie chub distribution based on the wet period (1982–2001, bottom left panel) and dry period (2002–2014, bottom right panel). Ψ is estimated prairie chub occurrence probability. The shading in the upper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

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

2 | MATERIALS AND METHODS

2.1 | Study area and sites

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

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

2.2 | Climatic periods and surveys

The study period was divided into a relatively wet climatic period (hereafter 'wet period', 1982–2001) and a relatively dry climatic period (hereafter 'dry period', 2002–2014) based on annual precipitation in the upper Red River catchment (see Figure 3 of Smith

et al., 2017). The periods provided an ecologically meaningful division of time (as opposed to a cut-off based on an arbitrary length of time). The beginning of the wet period also coincided with the start of the 'post impoundment' era in the Great Plains (i.e. additional dam construction had largely ceased, Costigan & Daniels, 2012).

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

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

2.3 | Fragmentation and flow regime metrics

Sites were characterized using fragmentation metrics hypothesized to be associated with prairie chub occurrence at a coarser spatial scale. The metrics were compiled from an online database of spatially verified large dams primarily from the National Anthropogenic Barrier Dataset (Cooper & Infante, 2017). Values associated with the most downstream NHD stream segment were used to represent each site. Temporal variation in fragmentation was not available, and the same values were used for both periods. This assumption of a constant

level of fragmentation owing to damming is consistent with the timing of major dam construction in the study area (see Section 2.1). A preliminary analysis indicated a very strong negative relationship between prairie chub occurrence and both upstream network dam density per catchment area (UNDC, no./km²) and upstream network dam density per stream length (UNDR, no./100 km), which were near perfectly correlated (Pearson's pairwise correlation coefficient ($r = 0.96$, $n = 358$). The extreme nature of this relationship resulted in an analytical challenge when trying to examine additional variables. Thus, this upstream dam 'effect' was mitigated by removing sites with ≥ 5 UNDC and UNDR (i.e. prairie chub were assumed not to occur at sites with five or more upstream network dams, $n = 60$). This cut-off was chosen based on a natural data break (i.e. low-high) and is consistent with survey records (i.e. prairie chub was never detected at a site with five or more upstream network dams). Prairie chub were also assumed not to occur at eight sites that were completely below reservoirs (Figure 1). The remaining fragmentation metrics were also highly correlated. Thus, only percentage open (i.e. free of dams) downstream mainstem (DMO), total mainstem dam density per stream length (TMD, no./100 km), and UNDR were retained to achieve a variable set for prairie chub occurrence modelling with $|r| < 0.50$.

The flow regime metrics (Olden & Poff, 2003) median daily discharge (MA2), flood duration (DH14), high-flow duration (DH20), and variability in the date of annual minimum flow (TL2) were also used to examine prairie chub occurrence relationships (Table S2). These flow regime metrics were chosen because pelagophil reproduction and persistence is likely to depend on increased flow magnitude and predictable and extended periods of elevated flows (see Section 1). Daily discharge estimates associated with the main segment of each HRU were used to calculate the streamflow metrics. Streamflow estimates for tributaries of the main segment were not available. The discharge estimates were derived from a precipitation-runoff modelling system adapted from the national model for the Red River catchment (see Regan et al., 2018, for a complete description). All daily discharge estimates had a Nash-Sutcliffe Efficiency coefficient ≥ 0.50 suggesting satisfactory prediction of streamflow (Moriyas et al., 2007). The flow regime metrics were calculated in EflowStats (version 5.0.1, median option, Kennen, Henriksen & Nieswand, 2007; USGS, 2019) based on daily discharge for the associated period. High-flow duration was removed from the occurrence variable set to maintain $|r| < 0.50$ (Table S3). A relative flow magnitude was calculated as median monthly discharge (m³ s⁻¹)/site drainage area (km²) for each survey to account for variation in the detection probability of prairie chub associated with sampling conditions. The values of drainage area for each site corresponded to the most downstream NHD stream segment.

2.4 | Analyses

Prairie chub detection and occurrence probability was modelled using the hierarchical framework described by MacKenzie

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

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

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

prairie chub relationships between climatic conditions. The occurrence model can be written as:

$$\text{logit}(\Psi_i) = \alpha_0 + \alpha_1 \text{PERIOD}_{[ij]} + \sum_{k=1}^6 \sum_{n=1}^6 \beta_k X_{n[ij]} + \sum_{k=7}^{12} \sum_{n=1}^6 \beta_k X_{n[ij]} * \text{PERIOD}_{[ij]}, \text{ for } i = 1, 2, \dots, N,$$

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

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

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

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

A leave-one-out presence-only cross validation (hereafter ‘cross validation’) was performed using sites with a prairie chub detection (i.e. known occurrences) to evaluate the predictive performance of the final model. For each cross-validation step, one site with a prairie chub detection was removed, and the model was refitted. Prairie chub occurrence probability (Ψ) was calculated for the site omitted using resulting model coefficients. Logit occurrence probabilities were scaled to a value between zero and one (Jørgensen &

Pedersen, 1998). The model was considered ‘correct’ if Ψ was ≥ 0.80 . The cross validation assessed the model's ability to predict a high occurrence probability at sites known to be occupied by prairie chub. Failing to identify an occupied site (i.e. a ‘type-two error’) is often more detrimental from a conservation perspective (MacKenzie et al., 2002; MacKenzie et al., 2003). However, the test does not evaluate the model's ability to predict absence because it can never be known, but only inferred.

2.5 | Prairie chub distribution map

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

3 | RESULTS

3.1 | Fish surveys and fragmentation and flow regime metrics

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

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

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

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

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

3.2 | Analysis

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

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

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

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

The projected distribution of prairie chub was broader than suggested by naïve occurrence and was similar in both the wet and dry period (Figure 1). The final model projection indicated that 48%

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

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

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

and 47% of the sites were occupied by prairie chub in the wet period and the dry period, respectively. As expected, the projected distribution largely followed the Red River mainstem and its major tributaries. The model projection also showed that prairie chub occurred west and south west of where they were detected in the survey dataset.

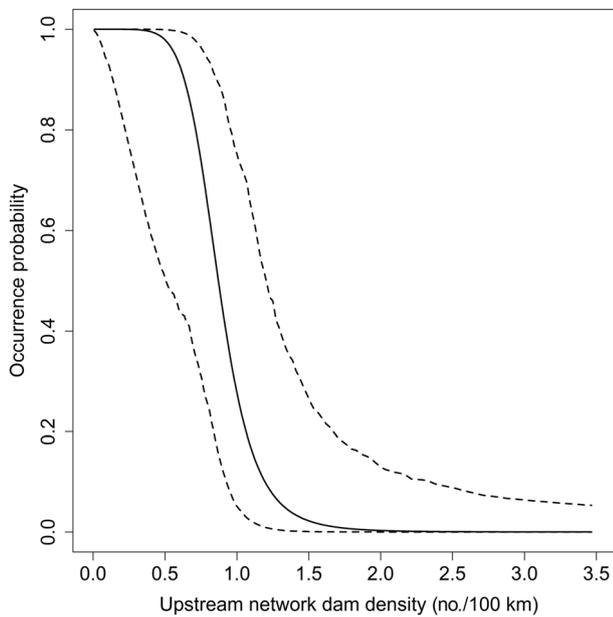


FIGURE 2 Relationship between prairie chub occurrence probability and upstream network dam density (UNDR). Occurrence probability estimates were calculated with percentage open downstream mainstem (DMO), flood duration (DH14), and median daily discharge (MA2) held at mean levels. Dashed lines are 95%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

4 | DISCUSSION

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

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

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

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

habits, MA2 was also highly correlated ($|r| > 0.90$) with numerous measures of flow magnitude suggested by Olden & Poff (2003). In particular, MA2 was highly positively correlated with the average discharge of each month. Thus, it is not possible to differentiate between the importance of higher flow magnitude at particular times of year and generally higher flow magnitude.

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

Any pelagophil conservation strategy is likely to have only limited success because of the extensive damming of the Great Plains stream network. Pelagophils are likely to be disproportionately affected by legacy effects of damming and expected future increases in water withdrawals (Garbrecht, Van Liew & Brown, 2004) and drought (Feng

et al., 2017). Dam removal is one option to support the persistence and potential expansion of pelagophils within their native range. Mass dam removal in the Great Plains is not feasible because of human water needs. However, the strategic removal of a small number of dams may be more effective at restoring stream network connectivity, while maintaining similar water-storage capacity, than random removal of larger dams (Kuby et al., 2005; Perkin et al., 2015a; Magilligan et al., 2016). Dam removal can also be supplemented with controlled water releases and finer-scale remediation of stream connectivity (e.g. fishways, Pennock et al., 2018) and instream habitat for a more comprehensive pelagophil approach.

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

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CONFLICT OF INTEREST

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

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