Trends in River Discharge and Water Temperature Cue Spawning Movements of Blue Sucker, Cycleptus elongatus, in an Impounded Great Plains River

Authors: Tornabene, Brian J., Smith, Troy W., Tews, Anne E., Beattie, Robert P., Gardner, William M., et al.

Trends in River Discharge and Water Temperature Cue Spawning Movements of Blue Sucker, *Cycleptus elongatus,* in an Impounded Great Plains River

Brian J. Tornabene[1], Troy W. Smith[1], Anne E. Tews[2], Robert P. Beattie[2], William M. Gardner[2], and Lisa A. Eby[1]

Riverine fishes are sensitive to human-induced changes to their ecosystems and have experienced substantial declines in the past century. The presence and operation of dams modifies natural flow regimes thereby disrupting cues that signal migration and negatively influencing habitats critical to riverine fishes. Blue Suckers (*Cycleptus elongatus*) make large annual movements, require large and unfragmented reaches of river, and may be sensitive to modifications of cues that initiate migration. We assessed the influence of individual and abiotic factors on home ranges and movements of 62 transmittered Blue Suckers from 2006–2014 in the Missouri River upstream of Fort Peck Reservoir in Montana. Populations in this area are disjunct from those downstream and are influenced by upstream dam regulation. Blue Suckers used large expanses of river with overall home ranges ~88 river kilometers, but these home ranges were about two times smaller than reported elsewhere. Increasing discharge and water temperature were associated with movement rate and movement probability and cued spawning movements of Blue Suckers. Movement rates increased with discharge to peak and decreased thereafter. Surprisingly, movement rate and probability were highest at the lowest water temperatures we observed (~1–5°C) unlike previous studies in other systems when peak movement occurred at ≥10°C. Blue Suckers aggregated and showed interannual fidelity to several locations during spawning. Aggregation and fidelity suggest that optimal spawning areas, which exist in tributaries, may be limited within our study area. Our results support evidence that riverine fishes require natural trends in discharge and water temperature, including occasional flood pulses and connectivity among seasonal habitats. The Upper Missouri River retains pseudo-natural discharge and temperature regimes that elicit responses of Blue Sucker to environmental cues, but other rivers may not. Preserving or restoring these features, and entire riverscapes, would maintain natural environmental cues and habitats required by riverine fishes to complete their life histories.

RIVERS are among the most threatened ecosystems because of the pervasive influence of dams (Tockner and Stanford, 2002). More than half of large rivers throughout the world are affected by dams (Nilsson et al., 2005). Dams convert rivers from lotic to lentic ecosystems, alter river discharge and temperature regimes, and influence nutrient and sediment transportation thereby influencing river geomorphology (Junk et al., 1989; Ligon et al., 1995; Ward and Stanford, 1995; Graf, 2006). By altering temperature and discharge regimes, the operation of dams can also negatively influence cues that initiate migrations of many riverine fishes.

The operation of dams can disrupt or eliminate cues that initiate spawning of riverine fishes (Graf, 1999; Helfrich et al., 1999; Poff and Hart, 2002) by reducing flows, modifying temperature regimes, and altering the timing of flood events and rising flows (reviewed in Bunn and Arthington, 2002). Spring runoff in many mountain-snowmelt rivers has been altered by dam operations, which also reduces or eliminates available breeding habitat for many organisms. In particular, spring-spawning fishes that use ephemeral floodplains, side channels, and tributaries are influenced by these changes (Pegg et al., 2003). Fishes with periodic life history characteristics are adapted to variation in streamflow (Winemiller and Rose, 1992). Modifications to, and dampening of, these natural oscillations can select against fishes with periodic life-history characteristics in favor of fishes with equilibrium life

history characteristics such as many nonnative species (Mims and Olden, 2012, 2013). One such fluvial specialist, which has periodic life history characteristics and may be vulnerable to these anthropogenic changes, is the Blue Sucker (*Cycleptus elongatus*).

Blue Suckers are a large-bodied species of sucker (family Catostomidae) native to the Mississippi and Missouri river drainages that make long-distance migrations to spawning sites (Coker, 1930; Neely et al., 2009) and can have fidelity to spawning and summer habitats (Adams et al., 2017; AET and WMG, unpubl. data). Blue Suckers spawn from April–June and migrations are ostensibly cued by photoperiod, discharge, and water temperature (Coker, 1930; Moss et al., 1983; Neely et al., 2009). Spawning sites of Blue Suckers are often shallow, swift riffles over gravel and cobble substrates (Coker, 1930; Moss et al., 1983; Neely et al., 2010). Summer habitats may also be critical for population persistence because they provide abundant prey resources for post-spawn recovery of adults (Adams et al., 2006; Neely et al., 2010). Additionally, site fidelity to seasonal habitats may be related to habitat homogenization resulting from river alterations (Switzer, 1993), which can also increase susceptibility to subsequent natural and anthropogenic disturbances (Switzer, 1993; Buzby and Deegan, 2000).

Although historical Blue Sucker population changes are not well defined (Coker, 1930; Pflieger, 1970; Burr and Mayden, 1999), they are considered to be declining through-
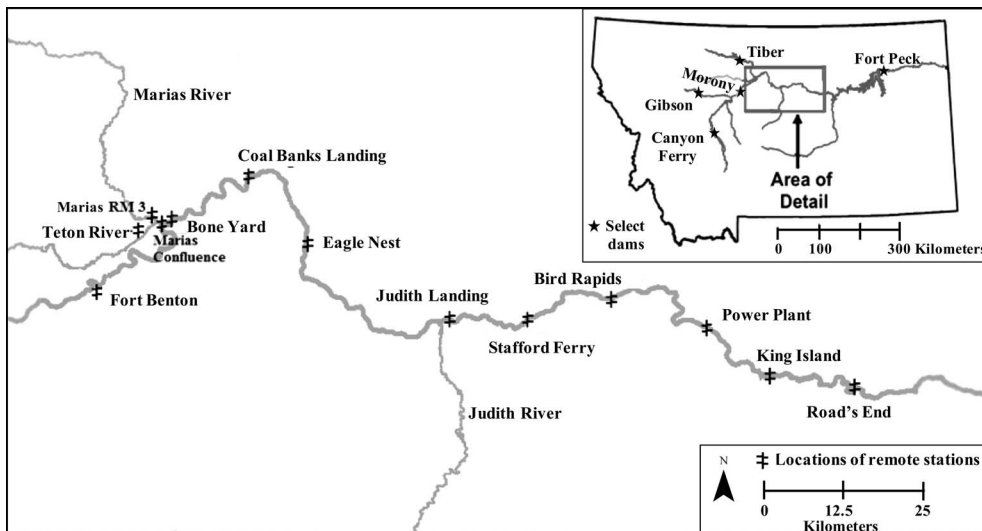

Fig. 1. Study area on the Missouri River in Montana ranging from upstream of the confluence with the Marias River to upstream of the headwaters of Fort Peck Reservoir. Locations of remote stations are denoted with a double-crossed vertical line and labeled with general location names. Locations of select dams are represented with stars on the inset map.

out their range and have even been extirpated in Pennsylvania. Anthropogenic disturbances such as dams, channelization, and dredging are associated with declines in Blue Sucker habitats and populations (Coker, 1930; Moss et al., 1983; Hand and Jackson, 2003). While dams are known to isolate populations, sparse information exists on the influence of fragmentation and dam operations on Blue Sucker movement and cues (Moss et al., 1983; Vokoun et al., 2003).

In Montana, at the northern extent of the range of the species, Blue Suckers are listed as a species of concern because of their declining abundance and limited habitats. For example, juvenile Blue Suckers are rarely captured in the Missouri River upstream of Fort Peck dam, and there are indications that the existing population primarily consists of old fish (AET, unpubl. data). These populations may also be vulnerable to extirpation because they are influenced by upstream dam regulation and are isolated from downstream populations by several dams and reservoirs. In addition, three of the largest dams on the Missouri River (Fort Peck, Garrison, and Oahe) have converted 874 km of the previous range of the species to lentic habitats thereby reducing available habitats and fragmenting populations. Because fisheries research on the Missouri River in Montana was not conducted prior to dam construction, the influence of these changes was undocumented. Environmental cues may be affected by flow regulation, which could result in suboptimal timing of spawning runs and juvenile emergence. In addition, Blue Suckers in altered and fragmented rivers may have limited habitats necessary to complete their life histories.

Our goal was to determine the spatiotemporal ecology of a disjunct population of Blue Suckers to enhance conservation and management efforts for the species throughout North American rivers. Our objectives were to (1) determine overall and seasonal home ranges; (2) determine seasonal movement patterns including distance, direction (upstream or downstream), rate, and movement probability; (3) determine the influences of abiotic variables (e.g., water temperature and discharge) on movement rate and probability; (4) evaluate how individual variables (e.g., tagging site, sex, and size) influence movements and home range; and (5) identify critical habitats by determining locations where aggregations and inter-annual seasonal fidelity occur.

MATERIALS AND METHODS

Study site.—Our study area was a 320-river-kilometer (rkm) reach of the Missouri River in Montana from Fort Benton to the confluence of the Musselshell River, upstream from Fort Peck reservoir (Fig. 1). Much of the area is designated as a Wild and Scenic River and is considered pseudo-natural because of semi-natural discharge and temperature regimes, compared to highly altered downstream reaches (Pegg et al., 2003; Galat et al., 2005; Sanford, 2007; Tornabene et al., 2017). Upstream operation of three major dams (Tiber Dam on the Marias River, Gibson Dam on the Sun River, and Canyon Ferry Dam on the Missouri River) influence downstream discharge patterns and habitat formation within our study site (Ramey et al., 1993; Scott et al., 1997). For example, discharge in spring can be reduced by up to 53% and discharge in summer and autumn (i.e., during baseflow) can be increased by up to 55% (Ramey et al., 1993; WMG, unpubl. data). Major tributaries include the Marias, Teton, Judith, and Musselshell rivers. Aquatic taxa within this study area are disjunct and fragmented from downstream populations by Fort Peck Dam and Reservoir. The Musselshell River now enters Fort Peck Reservoir, and the Yellowstone and Milk rivers enter the Missouri downstream of Fort Peck Dam. Upstream passage is blocked by Tiber Dam on the Marias River, but Morony Dam is located just downstream of the natural barrier of the Great Falls. Discharge patterns in our study area, particularly median daily discharge, differed among years, and we observed considerable variation within and among years (Kruskal-Wallis one-way analysis of variance test; $\chi^2 = 847.54$, df $= 8$, $P < 0.001$; Fig. 2). For example, in 2011 during a large flood event, peak discharge was nearly two times higher than all other years—and the 80-year average, 1934–2014—resulting from higher-than-average snowpack and near-record rainfall in eastern Montana.

Fish capture and radio telemetry.—We monitored spatial and temporal movements of Blue Suckers using radio telemetry. We captured Blue Suckers using trammel nets or electrofishing at six sites (two each upstream, mid-river, and downstream) throughout the study area from April–May of each year. Because technicians could also be handling endangered Pallid Sturgeon (*Scaphirhynchus albus*), all Blue Suckers were handled and surgeries were conducted accordingly with handling protocols developed for Pallid Sturgeon (USFWS,
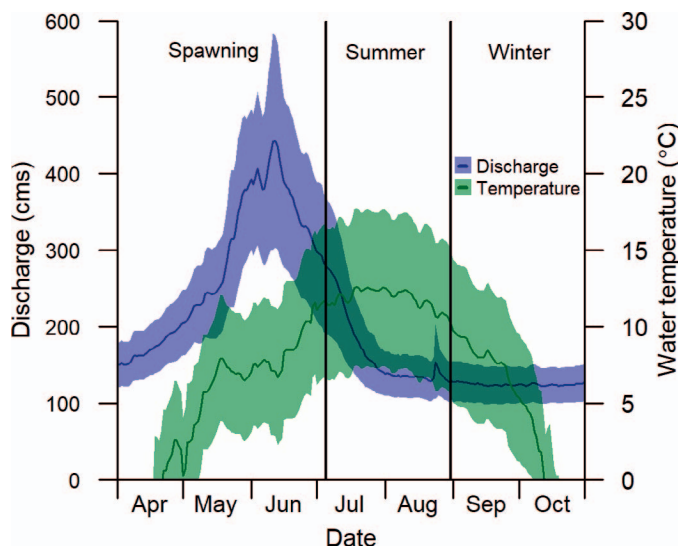
Fig. 2. Delineation of seasons (vertical lines) and average discharge and water temperature with 95% confidence bands (2006–2014 and averaged among all monitoring stations) on the Missouri River in Montana within our study area when environmental covariates were measured (1 April–24 October) for movement distance and probability modeling.

2012). We radio transmittered and tracked 62 individual Blue Suckers from 2006–2014. Most fish were transmittered in 2006 ($n = 28$) and 2007 ($n = 21$), but we added additional fish in 2008 ($n = 6$) and 2009 ($n = 7$). We weighed and measured total length of each individual. We determined sex of each individual by assessing the presence (male) or absence (female) of tubercles on the anterior of the individual, and the presence of milt or eggs. We surgically implanted 26 g radio transmitters (model MCFT-3L; Lotek Wireless, Inc., St. John's, New Foundland, Canada) using a shielded-needle technique (Fig. 3; Ross and Kleiner, 1982). We implanted transmitters through a small incision anterior to the pelvic fin and threaded the antenna through the body wall, posterior to the transmitter. We closed the incision with surgical staples. Following implantations of transmitters, we held fish for a short recovery period in a holding tank with recirculating water before releasing them at their point of capture. Each radio transmitter had a frequency of 149.700 MHz, unique factory-programmed code for individual identification, and estimated battery life of 3–5 y.

We attempted to manually locate each fish about every two weeks from April–October with a boat-mounted Yagi antenna and receiver (model SRX-400, Lotek, Inc.). Additionally, we recorded when fish passed any of ten fixed radio telemetry stations, herein remote stations, from 2006–2014 (Fig. 1). We also recorded passing of fish from three additional remote stations that were operational from 2011–2014. Remote stations included two four-element Yagi antennas (one pointed upstream and the other pointing downstream) connected to receivers (model SRX-400, Lotek, Inc.) and installed on river banks. Remote stations were placed strategically throughout the study area about 30 km apart from one another (mean = 27.4 rkm; range = 4.4–52.3 rkm) and often near access points (Fig. 1).

Movement and home range.—We calculated weekly movement rates (river kilometer [rkm]/wk; herein, movement

rates) between successive telemetry fixes by subtracting the subsequent rkm location from the previous rkm location, and dividing by the number of weeks (7 d per week) elapsed between telemetry fixes. Positive values indicated upstream movements and negative values indicated downstream movements. We calculated weekly (compared to daily) rates to account for the variation in days and weeks between successive telemetry fixes among individuals. These rates represent minimum estimates because other movement may have occurred between sampling events (Rogers and White, 2007). For each telemetry fix, we also determined if fish had moved (yes or no) from their previous river-kilometer location (>500 m) to calculate probabilities of movement. We calculated linear home range of each fish by subtracting its furthest downstream rkm location from its furthest upstream rkm location both overall (length of home range per fish throughout the study period) and by season within each year.

We delineated seasons into three temporal periods differentiated by streamflow, thermal patterns, and the natural history of Blue Suckers in the study area (Fig. 2; AET and WMG, unpubl. data). The spawning season began at about river ice-off (mid-April) and was characterized by increasing-to-peak then decreasing discharge, increasing water temperature, and included the period when spawning-related movements and spawning occurs in our study system (spawning in early May; AET and WMG, unpubl. data). The summer season began in early July, continued to September, and was characterized by decreasing-to-base discharge and peak water temperature. The winter period was characterized by baseflow discharge, decreasing to minimum water temperatures, and ice-cover starting in November. For each telemetry fix, we assigned discharge and water temperature (mean daily) data from the nearest U.S. Geological Survey discharge gauges or water temperature recorder sites, which were spread throughout the study area and typically near remote stations.

Statistical analyses.—We investigated relationships between home range sizes, movement probabilities, or movement rates and individual (sex, length, mass, tagging location, and monitoring period) and abiotic (discharge, water temperature, and photoperiod) covariates. We also compared home ranges and movement of Blue Suckers among seasons. We conducted all analyses in program R (v3.5.0; R Core Team, 2017).

We examined the influence of covariates using generalized linear models (GLM) for overall home range size or generalized linear mixed models (GLMM) for seasonal home range sizes. We implemented models using the functions "lmer" and "glmer" in the R package "lme4" (Bates et al., 2014). For seasonal home ranges (SHR), we accounted for repeated measures within and among seasons by nesting multiple observations for each individual as a random effect. We also accounted for variation among years, which was not of primary interest in this investigation, by including this variable as a random effect and fit models with a Laplace approximation (Bates et al., 2014). To fit the final model for seasonal home range, we used backwards selection by including all possible variables and removing variables until all were significant ($P < 0.05$) using a Wald's Z-test (Zuur et al., 2009). We investigated relationships between home range sizes and monitoring period (number of days) and number of
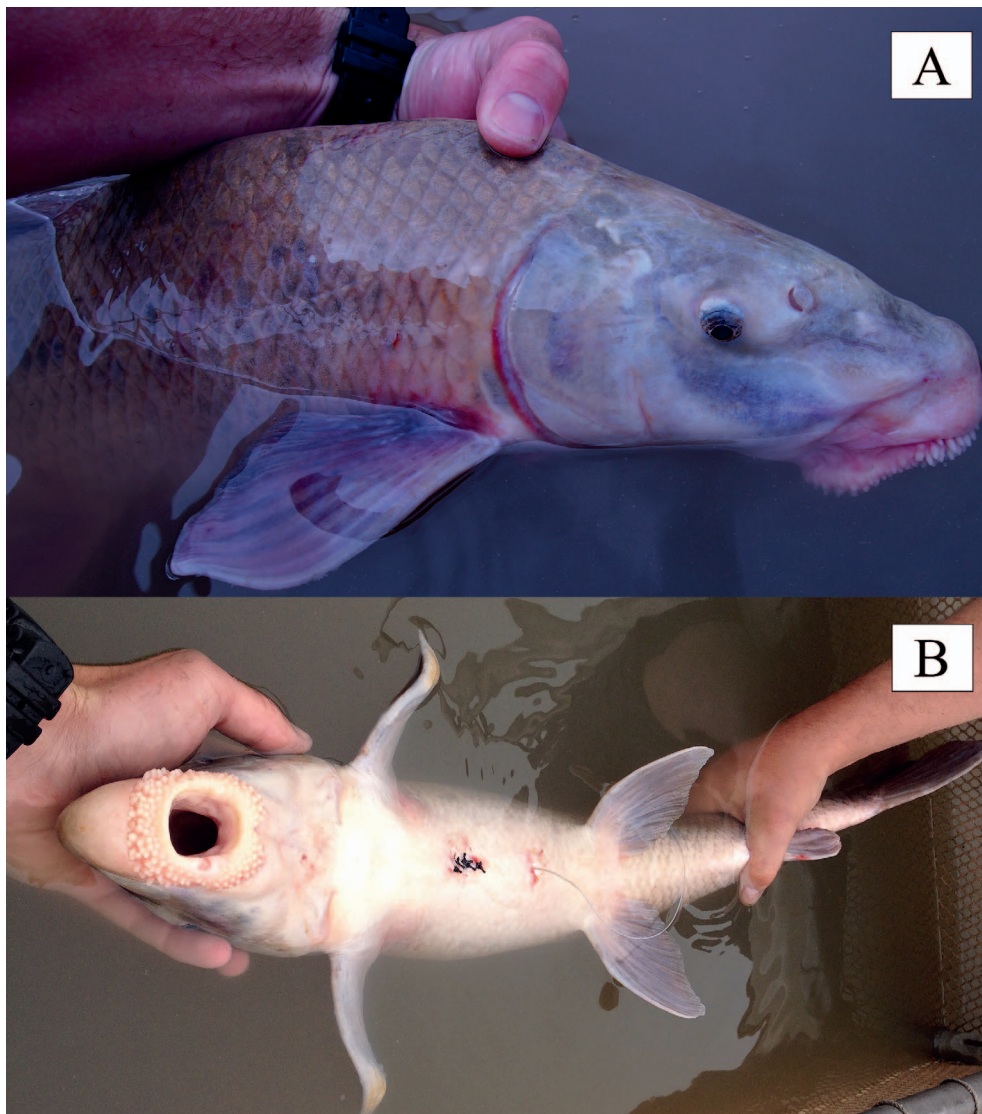
Fig. 3. Blue Sucker, *Cycleptus elongatus*, following (A) capture with electrofishing and (B) implantation of radio transmitter with tail of transmitter exiting body cavity. Photographed by T. David Ritter.

telemetry fixes, which can influence home range estimates, by calculating Pearson product-moment correlation coefficients. We used Welch's t-tests to compare the absolute movement rates in either an upstream or downstream direction within each season separately because this test is robust to differences in sample size and variance that we observed (Ruxton, 2006).

We used GLMMs to examine the influence of individual and abiotic covariates on movement rate and movement probability. For movement rate, we used the absolute value of rates such that all distances were positive and could be log-transformed to achieve normality. For both movement response variables, we accounted for repeated measures on individual fish as described above. We also accounted for type of telemetry fix (by remote station or hand) and yearly variation in both movement models by including these parameters as random effects. Variation can occur in these variables, but this was not of primary interest in our analyses. We centered and scaled all continuous variables to improve numerical stability and facilitate comparisons of coefficients among predictor variables (Bartón, 2010). We also removed observations with incomplete covariate data (i.e., missing water temperature or discharge data).

We began model selection for movement analyses by individually investigating the influence of 12 covariates on movement rate and probability with univariate GLMMs fitted with Gaussian or binomial (yes or no, 1 or 0) distributions with a logit link, respectively. To keep global models (i.e., full models) tractable, we only included predictor variables that had $P < 0.10$ in univariate analyses into subsequent movement rate and probability analyses. We did not include interactions in global models because we did not expect strong interactions among predictor variables. However, we did include quadratic terms for discharge, water temperature, and photoperiod covariates because these variables generally increase and decrease throughout the year and movement response curves could mimic this behavior.

Following univariate analyses and the elimination of nonsignificant variables, we used the "dredge" function in the R package "MuMIn" to separately create sets of all possible sub-models from global models for movement rate or probability and determine the best-supported model or models (Burnham and Anderson, 2004; Bartón, 2010). We compared sub-models separately for movement rate and probability using Akaike's information criterion (Burnham
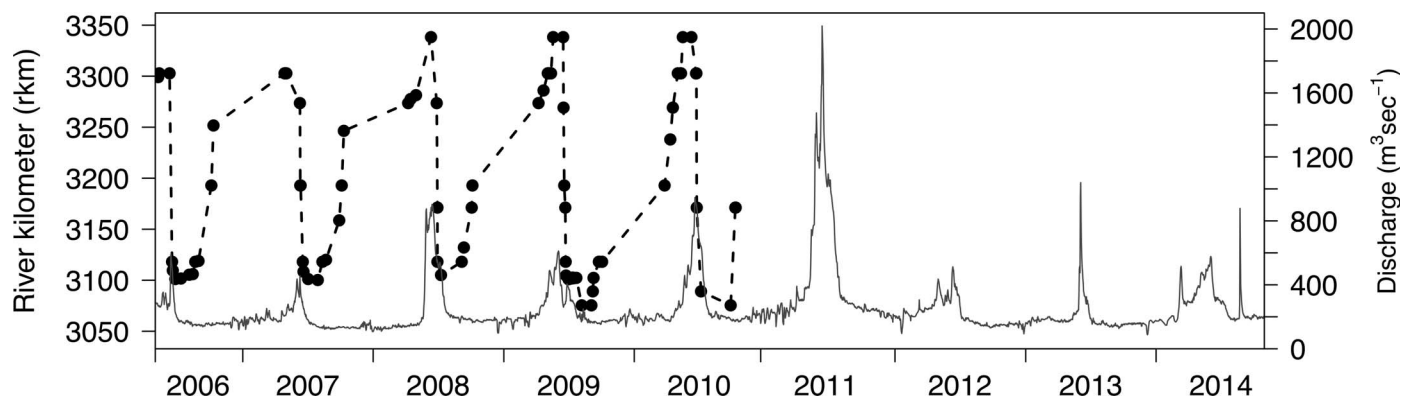
Fig. 4. Example of movement patterns of one *Cycleptus elongatus* in the Missouri River in Montana from 2006–2010. This individual (code 14 with 89 telemetry fixes; solid circles and dotted line referring to left y-axis) made clear long-distance movements upstream during spawning and moved back downstream after peak discharge (gray solid line refers to right y-axis). River kilometer represents distance from the confluence with the Mississippi River (river kilometer 0).

and Anderson, 2004; Mazerolle, 2016). We used AIC corrected for small sample sizes (AICc) because it converges with AIC at large sample sizes (Anderson and Burnham, 2002; Burnham and Anderson, 2004). We report model-averaged parameter estimates and adjusted standard errors of predictor variables averaged from best-supported models (ΔAICc < 4 AICc units). We ensured the assumptions of all models, tested for correlations between covariates by calculating Pearson's correlation coefficients, and tested for multicollinearity among covariates for each best-supported model by calculating variance inflation factors in the R package "car" with the function "vif.lme" (Fox and Weisberg, 2011). Variance inflation factors ∼2 are generally acceptable (Fox and Weisberg, 2011).

We assessed aggregation of Blue Suckers in mainstem locations and tributaries, and individual- and population-level fidelity to these locations among years (i.e., inter-annual fidelity), to determine critical habitat areas for Blue Suckers in our study area. We randomly selected one telemetry fix per individual per week for aggregation and fidelity analyses. We defined aggregations as three or more individuals within 100 m of each other within 1 wk. We tabulated aggregations and subsequently determined if, and how many of, the locations were used in consecutive years. We also determined when fish entered tributaries, how long they remained there, and fidelity of individuals to tributaries among years.

RESULTS

Radio telemetry.—We obtained 1,690 precise hand fixes (within ∼20 m) from boat and 2,621 fixes from remote stations for a total of 4,311 telemetry fixes on 62 Blue Suckers from 2006–2014. The mean monitoring period per individual was 1,536 d (95% CI = 1,396–1,676 d) and number of telemetry fixes was 69 (95% CI = 59–79 fixes) per individual. The mean number of days between telemetry fixes per individual was 2.7 wk (95% CI = 2.4–3.0 wk). Mean monitoring period and number of fixes did not differ between sexes and was not associated with mean length or mass of individuals ($P > 0.195$). We removed 1,441 observations from models considering the influence of individual and abiotic variables on movement because of missing environmental data (discharge or water tempera-

ture). These observations were outside the range of collection dates for water temperature or during flows that interrupted USGS discharge-monitoring stations. Nearly two thirds of telemetry fixes we removed were from remote stations (64%, $n = 922$) where individuals can spend considerable time and accumulate multiple fixes.

Home range and movement.—Overall home ranges of Blue Suckers were large (∼88 km) and length of home ranges used was greatest during the spawning season. Ranges were not related to monitoring period or number of fixes ($P > 0.291$). Additionally, overall and seasonal home ranges were not associated with length, mass, sex, original tagging location, or year ($P > 0.265$). Mean overall home range was 87.89 km (95% CI = 77.07–98.71 km). Mean home range sizes differed among all three seasons ($P < 0.001$, t < 12.01) and were highest during spawning (mean = 31.62 km, 95% CI = 30.18–33.05 km), lower in winter (7.19 km, 5.75–8.64 km), and lowest in summer (4.34 km, 2.89–5.78 km).

Most individuals made large movements up and down-stream or vice versa each year (Fig. 4), primarily during the spawning season. Blue Suckers primarily moved upstream during spawning (90.4%, $n = 56$), but some (9.6%, $n = 6$) moved downstream. Spawning-related movements began during the winter period, continued into spawning, and were often followed by immediate movements in the opposite direction. Overall, downstream rates (mean = 38.09 rkm/wk, 95% CI = 32.00–44.18 rkm/wk) were about 1.3 times greater than upstream rates (mean = 30.41 rkm/wk, 95% CI = 26.85–33.97 rkm/wk; $P_{-2.14} = 0.033$; subscript indicates the t-value). During spawning, downstream move-ment rates (45.63 rkm/wk, 37.07–54.19 rkm/wk) were about 1.4 times greater than upstream (mean = 34.12 rkm/wk, 95% CI = 29.78–38.45 rkm/wk; $P_{-2.36} = 0.012$). However, distance of upstream and downstream movement rates did not differ in summer or winter ($P_{1.04} = 0.298$ and $P_{0.16} = 0.871$). The maximum upstream movement detected was 71.3 km and the maximum downstream movement was 131.6 km; both occurred in less than a 24 h period.

Univariate analyses determined that seven covariates were associated with movement rate (discharge, discharge^2, sea-son, water temperature, water temperature^2, photoperiod, and photoperiod^2) at $P < 0.10$ (Table S1; see Data Accessi-bility). We included all seven covariates in the global model

Table 1. Model-averaged coefficients for log-transformed, centered, and scaled predictor variables from the generalized linear model of movement rate (river kilometer per week) of transmittered *Cycleptus elongatus* in the Missouri River in Montana from 2006–2014. "Num. mod." is the number of top models that include that predictor variable, "Importance" is the proportion of top models that contain that variable, and "Adj. SE" is model-adjusted standard error. Coefficients with $P < 0.05$ have an asterisk (*). "Season–Spawn" is the intercept term in the model; other seasons are in comparison to this season.

Variable	Num. mod.	Importance	Estimate	Adj. SE	z	P
*Discharge	2	1.00	0.93	0.11	8.73	<0.001
*Discharge^2	2	1.00	−0.70	0.10	6.88	<0.001
*Season–Spawn	2	1.00	1.46	0.14	10.55	<0.001
*Season–Summer	2	1.00	−0.45	0.09	5.12	<0.001
*Season–Winter	2	1.00	−0.25	0.09	2.87	0.004
Water temperature^2	1	0.13	−0.07	0.04	1.65	0.099

for this response variable except for photoperiod and photoperiod^2. We removed photoperiod variables from subsequent movement rate models because they were strongly correlated with discharge (Pearson's $r = 0.41$, $P < 0.001$) and we had greater interest in the influence of discharge. However, only five covariates were associated with movement probability (discharge, discharge^2, season, water temperature, and water temperature^2) at $P < 0.10$ and included in the global model for this response variable (Table S1; see Data Accessibility). From the global models, the dredge function produced 32 sub-models for movement rate and 32 sub-models for movement probability. Despite a dredge approach, all models were ecologically relevant and represented realistic hypotheses predicting movement rate and probability. Two and six models for movement rate and movement probability, respectively, had high support (within < 4 AICc units of the best-supported models) and were included in multimodel inference (i.e., separately for rate and probability).

Discharge and season were included in both best-supported models for movement rate, but water temperature was only included in one. Discharge had the strongest associations with movement rate of Blue Suckers ($P < 0.001$; Tables 1, S2; see Data Accessibility). The relationship between movement rate and discharge had a quadratic form wherein movement rate increased with increasing discharge until discharge reached ~600 cms and movement rate peaked at a mean of ~6 rkm/wk. This was followed by declining movement rates with increasing discharge ($\beta = 0.93 \pm 0.11$ [adj. SE] and -0.70 ± 0.10, for discharge and discharge^2, respectively; Fig. 5). Movement rate and water temperature were only weakly associated, but movement rate generally decreased with increasing water temperature ($\beta = -0.07 \pm 0.04$; $P = 0.099$; Table S2; see Data Accessibility). Movement rates were highest (mean = 6.2 km/wk, 95% CI = 5.4–7.0 rkm/wk) when water temperature was ~1°C. Movement rates also varied by season when they were highest during spawning (mean = 44.21 rkm/wk, 95% CI = 40.59–47.83 rkm/wk), lower in winter (36.27 rkm/wk, 31.47–41.07 rkm/wk; $P = 0.065$), and lowest in summer (34.16 rkm/wk, 31.14–37.18 rkm/wk; $P = 0.002$). Movement rates were not significantly different from each other in summer and winter ($P = 0.666$). We did not detect multicollinearity in our best-supported movement rate model (VIF = 2.19).

The influences of covariates on movement probability were similar to their influences on movement rate. Both discharge variables were included in all best-supported models for movement probability, but water temperature variables were only included in four and season was only included in three best-supported models (Fig. 5, Tables 2, S3; see Data Accessibility). The relationship with movement probability and discharge also had a quadratic form. Movement probability peaked (mean = 0.92, 95% CI = 0.75–1.0) when discharge was ~650 cms and declined thereafter ($\beta = 1.06 \pm 0.15$ and -0.81 ± 0.14, respectively; $P < 0.001$). Movement probability was only marginally related to water temperature, was highest at ~1°C (mean = 0.98, 95% CI = 0.27–1.0), and declined by ~50% at ~15°C (mean = 0.40, 95% CI = 0.29–0.50; $\beta = -0.41 \pm 0.22$; $P = 0.07$). However, movement probability had wide confidence intervals at temperatures <10°C which reflects the marginal relationship we observed. Movement probability was highest during spawning, but was not different from in winter ($P = 0.631$), and lowest in summer when movement probability was different from spawning and winter ($\beta = 0.30 \pm 0.15$; $P = 0.043$). We did not detect multicollinearity in our best-supported movement probability model (VIF = 1.90).

Tributary use, aggregation, and fidelity.—Throughout our study, we observed 25 unique Blue Suckers occupying the Marias River. A mean of 13 transmittered Blue Suckers (95% CI = 6–20; 10–32% of transmittered fish) were relocated in the Marias River each year. Blue Suckers were only detected in the Judith and Teton rivers during the spawning season but were detected in the Marias River throughout the year. Most Blue Suckers entered the Marias River in early May, but could enter as early as mid-April, and remained there a mean of 11 d (95% CI = 7–15 d). Only two individuals were detected in the Teton River in 2011 and a different Blue Sucker was detected in the Judith River in 2008, 2009, and 2012.

Aggregations (three or more fish within 100 m of each other within 1 wk) occurred in each season, but mostly during spawning. Most aggregations occurred during spawning (74%), but some occurred in winter and summer (17 and 9%, respectively). Blue Suckers aggregated at 23 unique locations throughout our study area. The average number of transmittered fish in aggregations during the spawning season was four (range 3–9). The average number of fish in aggregations was highest from 1–7 May and declined thereafter. We observed the most aggregations during spawning at sections of the river where rapids, braided channels, and shallows occurred. We observed two areas in our downstream reach, near the transition from lotic to lentic
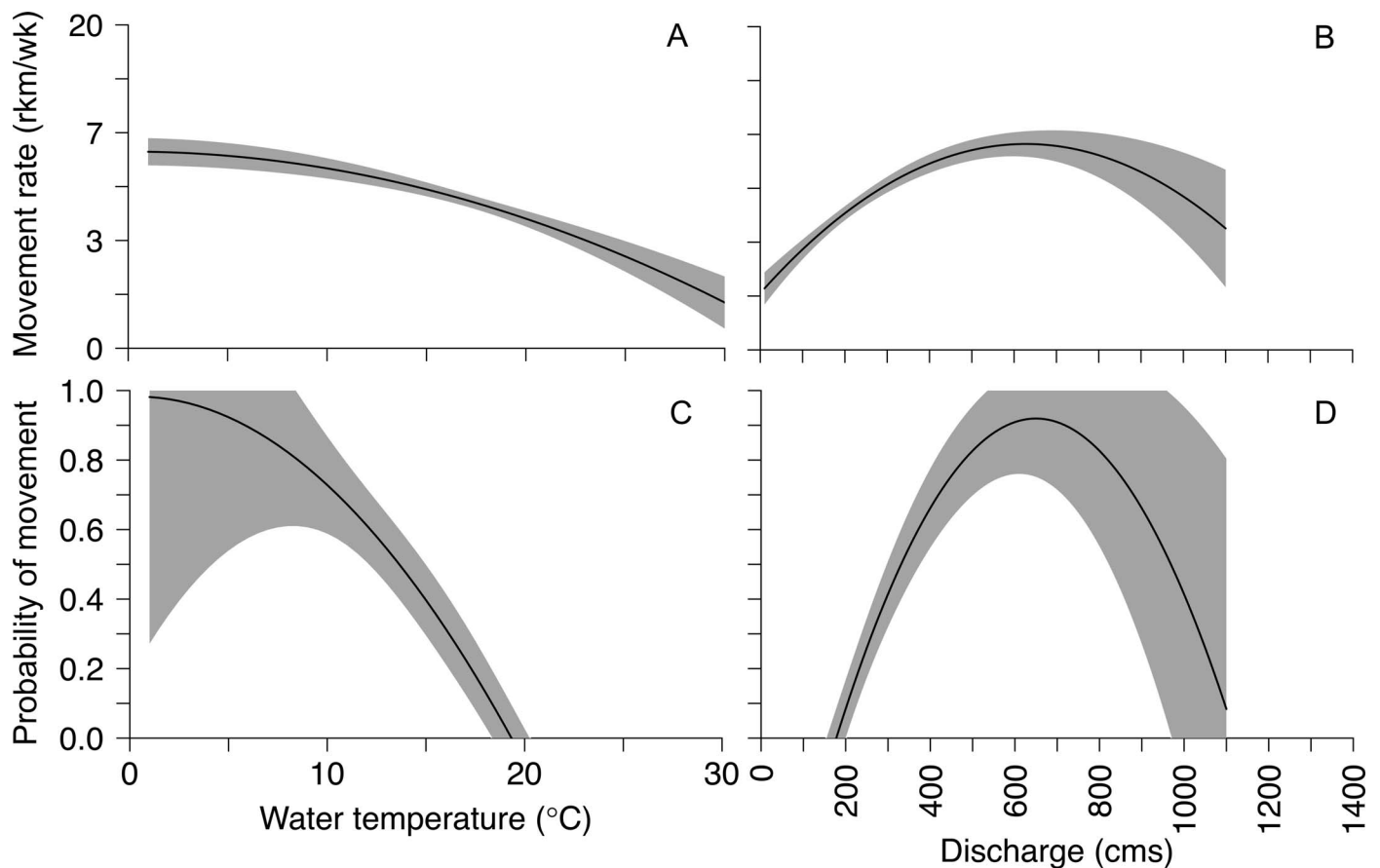
Fig. 5. Log-transformed and model averaged movement rate (river kilometer per week, rkm/wk; with 95% confidence bands) and predicted probability of movement (with 95% confidence bands) with increasing water temperature (°C; 'A' and 'C,' respectively) and discharge (cubic meters per second, cms; 'B' and 'D,' respectively) for transmittered *Cycleptus elongatus* in the Missouri River in Montana from 2006–2014. For 'A' and 'B,' the y-axis has been back-transformed for clarity.

settings directly upstream of the reservoir, where Blue Suckers aggregated and ostensibly spawned.

Blue Suckers aggregated and showed interannual and individual- and population-level fidelity to several sites in all seasons but had the strongest fidelity to locations during spawning. We detected aggregations of Blue Suckers at six sites during spawning in four or more consecutive years. Blue Suckers aggregated in the Marias River in all seasons throughout the study (2006–2014). However, Blue Suckers only showed population and individual-level interannual fidelity to the Marias River during spawning. We also observed aggregations and population-level interannual fidelity to four sites in the winter season through four years. We only observed population-level interannual fidelity during the summer season at three sites for less than three years. Thirty-six percent ($n = 9$) of individuals that occupied the Marias River did so in two consecutive years, 20% did so in three consecutive years ($n = 5$), 4% ($n = 1$) did so in five consecutive years, and the remainder (40%, $n = 10$) occupied the river in only one year ($n = 8$) or multiple non-consecutive years ($n = 2$, both in three non-consecutive years).

Table 2. Model-averaged coefficients for log-transformed, centered, and scaled predictor variables from the generalized linear model of movement probability of transmittered *Cycleptus elongatus* in the Missouri River in Montana from 2006–2014. "Num. mod." is the number of top models that include that predictor variable, "Importance" is the proportion of all models that contain that variable, and "Adj. SE" is model-adjusted standard error. Coefficients with $P < 0.05$ are have an asterisk (*). "Season–Spawn" is the intercept term in the model; other seasons are in comparison to this season.

Variable	Num. mod.	Importance	Estimate	Adj. SE	z	P
*Discharge	6	1.00	1.06	0.15	7.17	<0.001
*Discharge^2	6	1.00	−0.81	0.14	5.73	<0.001
*Season–Summer	3	0.65	−0.32	0.16	2.02	0.043
Season–Spawn	3	0.65	0.55	0.36	1.50	0.132
Season–Winter	3	0.65	0.06	0.13	0.48	0.631
Water temperature	4	0.82	−0.41	0.22	1.83	0.068
Water temperature^2	4	0.46	0.01	0.41	0.03	0.974

DISCUSSION

Blue Suckers in the Upper Missouri River above Fort Peck Reservoir moved long distances each year putatively for spawning, movements were cued by environmental variables, and individuals aggregated and showed interannual fidelity to specific locations during each season. However, movements and home ranges were smaller than for populations in other North American rivers. Similar to other systems, we observed that trends in discharge and water temperature cued Blue Sucker movements, likely related to spawning, with discharge as the strongest cue. Fort Peck and Tiber dams reduce accessible habitat and the potential home range size for this population. However, Blue Suckers above Fort Peck still have the opportunity to respond to pseudo-natural cues provided by discharge and water temperature. In contrast, flow regimes have been substantially altered in some of the spawning tributaries. Blue Suckers living in more extensively modified systems may no longer have these cues. Natural trends in discharge and water temperature, including occasional flood pulses, are likely critical environmental cues necessary for Blue Suckers to complete their life histories.

Home range and movement.—Blue Suckers in this study exhibited similar movement patterns to those seen in other North American rivers, with large home ranges that were highly variable among individuals (Neely et al., 2009; Mayes, 2015; Adams et al., 2017; M. E. Jaeger, unpubl. data). Prior to peak spring discharge, Upper Missouri River Blue Suckers typically made large movements upstream and moved downstream in summer. In other systems, observed movement patterns are greater than what is available to this population (Rupprecht and Jahn, 1980; Morey and Berry, 2003; Mayes, 2015). For example, home ranges in the Yellowstone River were more than twice those in our study (mean home range ~230 km; M. E. Jaeger, unpubl. data). The Upper Missouri and the Yellowstone rivers are influenced by upstream (Bighorn and Tongue river dams on the Yellowstone River) and downstream dams (Garrison Dam); however, Blue Suckers in the Yellowstone River have a much longer river reach available (M. E. Jaeger, unpubl. data). Blue Suckers in the Upper Missouri River may have historically made much longer movements but fragmentation by Tiber and Fort Peck dams have reduced the available reach length.

Most Blue Suckers made upstream movements during spawning, but some moved downstream. We posit that downstream movement rates were higher during spawning, despite most fish moving upstream to spawn, because Blue Suckers began their spawning movements before mid-April (the purported beginning of their spawning run, and the timeframe used to define our spawning season) and this was followed by relatively rapid movement in the opposite direction after spawning. Therefore, downstream movement rates appeared higher despite most spawning sites being located upstream of overwintering and summer sites. Contrary to previous observations (Eitzmann et al., 2007; Neely et al., 2009; M. E. Jaeger, unpubl. data), some Blue Suckers made downstream migrations to putative spawning sites in the mainstem Missouri River. These movements occurred in the lowest section of our study area, approximately ~25 rkm upstream of Fort Peck Reservoir, but these individuals also spent the majority of their time in the lower reach throughout the years. Sauger (*Sander canadensis*) and Shovelnose Sturgeon (*Scaphirhynchus platorynchus*) in this

reach of the Missouri River also made downstream movements during spawning (Bellgraph, 2006; Richards et al., 2014). Downstream spawning migrations may result from meeting unfavorable conditions during initial upstream migrations (Richards et al., 2014) or the distribution of potential spawning habitat relative to overwintering and summer habitats. Some fish may also abstain from spawning in some years (i.e., alternate year spawners) and remain in downstream reaches.

Analogous with previous observations, we observed that movement rates were highest from winter–spring and decreased in the summer when discharge, water temperature, and photoperiod increase to peak (Mayes, 2015; AET and WMG, unpubl. data; M. E. Jaeger, unpubl. data from Yellowstone River). Indeed, many fishes in lotic systems have periodic life history characteristics and are adapted to natural flow regimes (Winemiller and Rose, 1992; Mims and Olden, 2012). Therefore, they respond to natural pulses in discharge and changes in other environmental variables (Lytle and Poff, 2004; Benson et al., 2007; King et al., 2016).

Both temperature (Bauer et al., 2011) and discharge (Næsje et al., 1995; Mims and Olden, 2013) can cue riverine fish migrations (Clarkson et al., 1994). Previous studies have suggested that temperatures influences migration timing (Vokoun et al., 2003; Neely et al., 2009), high discharge increases capture rates at spawning locations (Moss et al., 1983; Morey and Berry, 2003), and movement may be initiated by increasing discharge (Mayes, 2015). This is the first study to directly evaluate environmental movement cues of Blue Suckers and detect correlations between movement variables and discharge and water temperature. We found that discharge was most influential on Blue Sucker movements consistent with previous studies (Neely et al., 2009). However, our investigation also supports the assertion that multiple environmental variables may influence movement and spawning behavior of riverine fishes and should be considered for management purposes.

Although water temperature only marginally influenced movement rate and probability, we observed colder temperatures associated with peak movement than reported for other systems. Movement rates and movement probability in our study system were highest between ~1–5°C. However, peak movement rates of Blue Suckers in the Middle Missouri River in South Dakota occurred when temperatures were 10–12°C (Morey and Berry, 2003; Neely et al., 2009) and spawning occurred between 13–17°C in other southern rivers (Rupprecht and Jahn, 1980; Peterson et al., 1999; M. E. Jaeger, unpubl. data). Despite differences in temperature during spawning-related movements, previous studies have determined that Blue Sucker spawned at water temperatures between about 10–15°C in our system (AET and WMG, unpubl. data), similar to other populations (Rupprecht and Jahn, 1980; Peterson et al., 1999). This suggests that Blue Suckers in our system begin migrations and arrive early, then stage at spawning locations until suitable conditions occur.

Aggregation, fidelity, and spawning.—We observed that Blue Suckers aggregated and showed high interannual fidelity to presumed spawning habitats, but to a lesser degree for summer habitats. Blue Suckers are difficult to observe spawning because they prefer riffles in rapid flows with high turbidity. However, we did observe Blue Suckers surfacing near rocky outcrops during the spawning season, which

suggests spawning behavior (Coker, 1930; Moss et al., 1983; Adams et al., 2006; Neely et al., 2009; AET and WMG, unpubl. data). We monitored aggregations from telemetry data to identify spawning sites. Previous studies of the same population also identified repeated aggregations of Blue Suckers at specific locations among years (AET and WMG, unpubl. data). In contrast to previous studies in other systems, we observed the lowest rates of site fidelity during the summer season (Neely et al., 2009; Adams et al., 2017).

Blue Suckers aggregated to the highest degree during the spawning season in the Marias River and to sites in the mainstem of the Missouri River that were braided, near rapids, and in shallow-water areas. Aggregations were probably easier to identify at remote station locations because they are constantly scanning at a fixed location, but we randomly selected points for aggregation analyses to account for this. However, remote stations were also serendipitously located in areas with habitats that Blue Suckers often use for spawning (braided channels, rapids, and shallow areas). While aggregations during this period suggest spawning at these sites, it is unclear whether the aggregations we observed resulted in spawning or subsequent recruitment. For example, only three juvenile Blue Suckers <400 mm were observed in the same area from 2001–2017 (AET and WMG, unpubl. data). Whether the absence of young fish is related to sterility of adults, drift distances necessary for eggs and larvae, or habitat quality (for spawning or larval rearing) is unknown and investigating this should be a priority in future research.

High fidelity to the Marias River may suggest that spawning habitats are more abundant there compared to other mainstem or tributary habitats, or were prior to construction of Tiber Dam. Spawning habitats in mainstem and other tributaries may only be accessible or optimal during certain discharge conditions. For example, in the Neosho River in Kansas and Oklahoma, Blue Suckers abandoned certain spawning sites during drought years when the areas were too shallow or dry (Moss et al., 1983). The consistent occupation of sites among years at the population and individual level during spawning may suggest that optimal spawning habitats are patchy throughout the study area. Our identification of these sites should be useful for managers to preserve these critical habitats and enhance the conservation of Blue Suckers in the Missouri River in Montana.

We observed several aggregations in the lower portion of the river near the transition from a lotic to lentic setting where the Missouri River meets Fort Peck Reservoir. Spawning near the headwaters of the reservoir could be an ecological sink for Blue Sucker larvae because, although eggs are adhesive, larvae must drift to optimal habitats following hatching. Upstream spawning migrations are thought to benefit Blue Sucker larvae because they drift downstream into rearing habitats that benefit recruitment (Neely et al., 2009). Indeed, reservoirs can be sinks for larval recruitment of riverine fish (e.g., Pallid Sturgeon in our study area) because of the extensive hypoxic transition zones where the river transitions to reservoir (Braaten et al., 2012; Guy et al., 2015). More research is necessary to determine the drift distances required for Blue Sucker larvae and the possibility for these spawning sites to be ecological sinks.

Tributary occupation.—Blue Suckers occupied the Marias River to a higher degree than the Teton and Judith rivers. Given the number of fish that aggregated in the Marias River, and the fidelity with which they do so, this suggests that the Marias River contains some of the most important spawning habitat in our study area. Since 1997, the Bureau of Reclamation releases spring flows in the Marias River when environmental conditions permit for the benefit of fisheries (WMG, unpubl. data). This attempt to mimic natural flow regimes may be responsible for suitable spawning habitat and environmental cues to migrate into the Marias River. Indeed, Blue Suckers are known to opportunistically spawn in tributaries when discharge is high and environmental cues are present (Moss et al., 1983; Vokoun et al., 2003; Neely et al., 2010). Blue Suckers only used the Teton River in 2011 during a flood year, but the Teton River is usually chronically dewatered throughout most of the year—including the spring migration period—for agricultural use (Montana Fish, Wildlife and Parks and Montana Department of Natural Resources and Conservation, unpubl. data). Prior to chronic dewatering (~1979), more Blue Suckers were captured in the Teton River than the lower Marias River and it was identified as an important spawning tributary (R. Berg, unpubl. data). Managing the Teton River to reflect a more-natural flow regime may benefit Blue Sucker spawning and recruitment in this system. Similarly, Blue Suckers have historically been observed in the Judith River during the spawning season (AET, WMG, and R. Berg, unpubl. data), but not to the degree observed for the Marias and Teton rivers. During this study, we only observed three individuals in the Judith River during the spawning season; however, this could be due in part to limited monitoring of this tributary compared to others. Future work investigating Blue Sucker spawning and recruitment requirements could benefit management and conservation of Blue Suckers in the Upper Missouri River and other systems.

Conservation implications.—Blue Suckers are adapted to natural flow regimes, including flood events that are common in large rivers, and require large expanses of unfragmented river to complete their life history (Coker, 1930; Moss et al., 1983). Blue Sucker movements are influenced by discharge and temperature and are therefore sensitive to alterations resulting from dams and river management. Management of dam releases often influences discharge patterns, flood events, and fluctuations in water temperatures (e.g., hypolimnetic releases). Furthermore, the management of tributaries to mimic natural conditions can benefit Blue Suckers by providing additional spawning and feeding habitats. Although the Upper Missouri River in Montana is altered, it remains pseudo-natural compared to other rivers that are more highly fragmented and likely have greater influences on Blue Sucker movement and spawning. Mimicking natural flows in the Missouri River and its tributaries will continue to benefit the conservation and persistence of Blue Suckers and other riverine biota (Richards et al., 2014; Tornabene et al., 2018; WMG, unpubl. data).

Future research should investigate four aspects of Blue Sucker ecology to enhance their conservation and management in the Missouri and other large rivers. (1) Investigating the movement and spawning patterns of Blue Sucker populations in more highly flow-altered systems may help determine the influence of river regulation on Blue Suckers

and other spring-spawning fishes. (2) Studies in other systems suggest that recruitment of Blue Suckers is variable and generally low (Bednarski and Scarnecchia, 2006; Eitzmann et al., 2007). Understanding how river management and habitat length required for adequate larval drift distances influence Blue Sucker recruitment would enhance conservation efforts. Additionally, taxonomic keys for larval Blue Suckers are poor; therefore, genetic identification of sucker larvae may be useful. (3) Genetic analyses may also be useful to determine the viability and heritage of the Upper Missouri River population. (4) Population estimates would be beneficial in determining the age and viability of this disjunct population given that they may be vulnerable to anthropogenic influences such as fragmentation.

Our investigation provides support that natural trends in discharge and water temperature (including occasional high flow events) should be preserved to maintain habitats and environmental cues that initiate movement and spawning of fishes in large rivers. Dam operations can have strong influences on water temperature and discharge, and the ecology of riverine biota. Given that these variables were most important in predicting Blue Sucker movements, dam operations that have strong effects on discharge or temperature trends could alter timing of spawning and influence annual recruitment. Maintaining natural discharge conditions that influence turbidity, geomorphology, and water temperature is critical to cue spawning-related movements, maintain natural habitats, and ensure the persistence of Blue Suckers and many other fishes in large rivers throughout North America.

DATA ACCESSIBILITY

Supplemental information is available at https://www.copeiajournal.org/ci-19-256.

LITERATURE CITED

Adams, J. D., C. L. Bergthold, J. D. Haas, M. A. Pegg, and G. E. Mestl. 2017. Blue sucker summer utilization distributions and inter-annual fidelity to summering habitats. Transactions of the Nebraska Academy of Sciences 37:18–27.

Adams, S., M. Flinn, B. Burr, M. Whiles, and J. Garvey. 2006. Ecology of larval Blue Sucker (_Cycleptus elongatus_) in the Mississippi River. Ecology of Freshwater Fish 15:291–300.

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management 66:912–918.

Bartón, K. 2010. MuMIn: multi-model inference. R package version 1.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bauer, S., B. A. Nolet, J. Giske, J. W. Chapman, S. Åkesson, A. Hedenström, and J. M. Fryxell. 2011. Cues and decision rules in animal migration, p. 68–87. _In_: Animal Migration: A Synthesis. J. M. Fryxell, A. R. E. Sinclair, and E. J. Milner-Gulland (eds.). Oxford University Press, Oxford.

Bednarski, J., and D. L. Scarnecchia. 2006. Age structure and reproductive activity of the Blue Sucker in the Milk River, Missouri River drainage, Montana. Prairie Naturalist 38:167–182.

Bellgraph, B. J. 2006. Competition potential between sauger and walleye in non-native sympatry: historical trends and resource overlap in the Middle Missouri River, Montana. Unpubl. M.S. thesis, Montana State University, Bozeman, Montana.

Benson, R. L., S. Turo, and B. W. McCovey Jr. 2007. Migration and movement patterns of green sturgeon (_Acipenser medirostris_) in the Klamath and Trinity rivers, California, USA. Environmental Biology of Fishes 79:269–279.

Braaten, P. J., D. B. Fuller, R. D. Lott, M. P. Ruggles, T. F. Brandt, R. G. Legare, and R. J. Holm. 2012. An experimental test and models of drift and dispersal processes of Pallid Sturgeon (_Scaphirhynchus albus_) free embryos in the Missouri River. Environmental Biology of Fishes 93:377–392.

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

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference—understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Burr, B. M., and R. L. Mayden. 1999. A new species of _Cycleptus_ (Cypriniformes: Catostomidae) from Gulf Slope drainages of Alabama, Mississippi, and Louisiana, with a review of the distribution, biology, and conservation status of the genus. Bulletin of the Alabama Museum of Natural History 20:19–57.

Buzby, K. M., and L. A. Deegan. 2000. Inter-annual fidelity to summer feeding sites in Arctic grayling. Environmental Biology of Fishes 59:319–327.

Clarkson, R. W., O. T. Gorman, D. M. Kubly, P. C. Marsh, and R. A. Valdez. 1994. Management of discharge, temperature, and sediment in Grand Canyon for native fishes. Unpublished manuscript available from the authors.

Coker, R. E. 1930. Studies of common fishes of the Mississippi River at Keokuk. US Govt. Print. Off.

Eitzmann, J., A. Makinster, and C. Paukert. 2007. Distribution and growth of Blue Sucker in a Great Plains river, USA. Fisheries Management and Ecology 14:255–262.

Fox, J., and S. Weisberg. 2011. An R Companion to Applied Regression. SAGE Publications, Thousand Oaks, California.

Galat, D. L., C. R. Berry, W. M. Gardner, J. C. Hendrickson, G. E. Mestl, G. J. Power, C. Stone, and M. R. Winston. 2005. Spatiotemporal patterns and changes in Missouri River fishes. American Fisheries Society Symposium 45: 249–291.

Graf, W. L. 1999. Dam nation: a geographic census of American dams and their large-scale hydrologic impacts. Water Resources Research 35:1305–1311.

Graf, W. L. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. Geomorphology 79:336–360.

Guy, C. S., H. B. Treanor, K. M. Kappenman, E. A. Scholl, J. E. Ilgen, and M. A. Webb. 2015. Broadening the regulated-river management paradigm: a case study of the forgotten dead zone hindering Pallid Sturgeon recovery. Fisheries 40: 6–14.

Hand, G., and D. Jackson. 2003. Blue Sucker stock characteristics in the upper Yazoo River basin, Mississippi, USA. Fisheries Management and Ecology 10:147–153.

Helfrich, L. A., C. Liston, S. Hiebert, M. Albers, and K. Frazer. 1999. Influence of low-head diversion dams on fish passage, community composition, and abundance in the Yellowstone River, Montana. Rivers 7:21–32.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems, p. 110–127. In: Proceedings of the International Large River Symposium. D. P. Dodge (ed.). Canadian Special Publication of Fisheries and Aquatic Sciences, Volume 106.

King, A. J., D. C. Gwinn, Z. Tonkin, J. Mahoney, S. Raymond, and L. Beesley. 2016. Using abiotic drivers of fish spawning to inform environmental flow management. Journal of Applied Ecology 53:34–43.

Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams. BioScience 45: 183–192.

Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19:94–100.

Mayes, K. B. 2015. Blue Sucker movement and habitat use in the Lower Sabine River, Texas. Final Report. Texas Parks and Wildlife Department River Studies, Inland Fisheries San Marcos, Texas.

Mazerolle, M. J. 2016. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). https://CRAN.R-project.org/package=AICcmodavg

Mims, M. C., and J. D. Olden. 2012. Life history theory predicts fish assemblage response to hydrologic regimes. Ecology 93:35–45.

Mims, M. C., and J. D. Olden. 2013. Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. Freshwater Biology 58:50–62.

Morey, N. M., and C. R. Berry. 2003. Biological character-istics of the Blue Sucker in the James River and the Big Sioux River, South Dakota. Journal of Freshwater Ecology 18:33–41.

Moss, R. E., J. W. Scanlan, and C. S. Anderson. 1983. Observations on the natural history of the Blue Sucker (Cycleptus elongatus Le Sueur) in the Neosho River. American Midland Naturalist 109:15–22.

Næsje, T., B. Jonssons, and J. Skurdal. 1995. Spring flood: a primary cue for hatching of river spawning Coregoninae.

Canadian Journal of Fisheries and Aquatic Sciences 52: 2190–2196.

Neely, B., M. Pegg, and G. Mestl. 2009. Seasonal use distributions and migrations of Blue Sucker in the Middle Missouri River. Ecology of Freshwater Fish 18:437–444.

Neely, B., M. Pegg, and G. Mestl. 2010. Seasonal resource selection by Blue Suckers Cycleptus elongatus. Journal of Fish Biology 76:836–851.

Nilsson, C., F. Lepori, B. Malmqvist, E. Törnlund, N. Hjerdt, J. M. Helfield, D. Palm, J. Östergren, R. Jansson, and E. Brännäs. 2005. Forecasting environmental respons-es to restoration of rivers used as log floatways: an interdisciplinary challenge. Ecosystems 8:779–800.

Pegg, M. A., C. L. Pierce, and A. Roy. 2003. Hydrological alteration along the Missouri River basin: a time series approach. Aquatic Sciences 65:63–72.

Peterson, M. S., L. C. Nicholson, D. J. Snyder, and G. L. Fulling. 1999. Growth, spawning preparedness, and diet of Cycleptus meridionalis (Catostomidae). Transactions of the American Fisheries Society 128:900–908.

Pflieger, W. L. 1970. A distributional study of Missouri fishes. University of Kansas Museum of Natural History Publica-tions 20:225–570.

Poff, N. L., and D. D. Hart. 2002. How dams vary and why it matters for the emerging science of dam removal: an ecological classification of dams is needed to characterize how the tremendous variation in the size, operational mode, age, and number of dams in a river basin influences the potential for restoring regulated rivers via dam removal. BioScience 52:659–668.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Com-puting, Vienna, Austria. https://www.R-project.org/

Ramey, M., D. Reiser, and S. Beck. 1993. Supplemental report determination of flushing flow needs Madison and Upper Missouri Rivers. Project completion report prepared by R2 Resource Consultants under contract to EA Engi-neering. Science, and Technology for Montana Power Company, Redmond, Washington.

Richards, R. R., C. S. Guy, M. A. Webb, W. M. Gardner, and C. Jensen. 2014. Spawning related movement of shovel-nose sturgeon in the Missouri River above Fort Peck Reservoir, Montana. Journal of Applied Ichthyology 30:1–13.

Rogers, K. B., and G. C. White. 2007. Analysis of movement and habitat use from telemetry data, p. 625–676. In: Analysis and Interpretation of Freshwater Fisheries Data. C. S. Guy and M. L. Brown (eds.). American Fisheries Society, Bethesda, Maryland.

Ross, M. J., and C. F. Kleiner. 1982. Shielded-needle technique for surgically implanting radio-frequency trans-mitters in fish. The Progressive Fish-Culturist 44:41–43.

Rupprecht, R. J., and L. A. Jahn. 1980. Biological notes on Blue Suckers in the Mississippi River. Transactions of the American Fisheries Society 109:323–326.

Ruxton, G. D. 2006. The unequal variance t-test is an underused alternative to Student's t-test and the Mann–Whitney U test. Behavioral Ecology 17:688–690.

Sanford, J. P. 2007. Dam regulations effects on sand bar migration on the Missouri River: southeastern South Dakota. Unpubl. M.A. thesis, University of Montana, Missoula, Montana.

Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. Ecological Applications 7: 677–690.

Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533–555.

Tockner, K., and J. A. Stanford. 2002. Riverine flood plains: present state and future trends. Environmental Conservation 29:308–330.

Tornabene, B. J., R. G. Bramblett, A. V. Zale, and S. A. Leathe. 2017. Spatiotemporal ecology of *Apalone spinifera* in a large, Great Plains river ecosystem. Herpetological Conservation and Biology 12:252–271.

Tornabene, B. J., R. G. Bramblett, A. V. Zale, and S. A. Leathe. 2018. Factors affecting nesting ecology of *Apalone spinifera* in a northwestern Great Plains river of the United States. Chelonian Conservation and Biology 17:63–77.

USFWS (U.S. Fish and Wildlife Service). 2012. Biological procedures and protocols for researchers and managers handling pallid sturgeon. U.S. Fish and Wildlife Service, Billings, Montana.

Vokoun, J. C., T. L. Guerrant, and C. F. Rabeni. 2003. Demographics and chronology of a spawning aggregation of Blue Sucker (*Cycleptus elongatus*) in the Grand River, Missouri, USA. Journal of Freshwater Ecology 18: 567–575.

Ward, J., and J. Stanford. 1995. The serial discontinuity concept: extending the model to floodplain rivers. River Research and Applications 10:159–168.

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

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer-Verlag, New York.