Catch Rates for Sturgeon Chubs and Sicklefin Chubs in the Upper Missouri River 2004–2016 and Correlations with Biotic and Abiotic Variables

Patrick J. Braaten,* David B. Fuller, Tyler M. Haddix, John R. Hunziker, Michael E. Colvin, Luke M. Holmquist, Ryan H. Wilson

P.J. Braaten, L.M. Holmquist

U.S. Geological Survey, Columbia Environmental Research Center, Fort Peck Project Office, P.O. Box 165, Fort Peck, Montana 59223

Present address of L.M. Holmquist: Montana Fish, Wildlife and Parks, 205 W Aztec Drive, Lewistown, Montana 59457

D.B. Fuller, T.M. Haddix, J.R. Hunziker

Montana Fish, Wildlife and Parks, P.O. Box 165, Fort Peck, Montana 59223

Present address of D.B. Fuller: 1 Airport Road, Glasgow, Montana 59230

M.E. Colvin

Mississippi State University, Department of Wildlife, Fisheries, and Aquaculture, Mississippi State, Mississippi 39762

R.H. Wilson

U.S. Fish and Wildlife Service, 3425 Miriam Avenue, Bismarck, North Dakota 58501

*Corresponding author: pbraaten@usgs.gov
Abstract

A multiweek standardized sampling regime during 2004–2016 in a 60-km reach of the Upper Missouri River assessed reproduction and catch rates for Sturgeon Chub *Macrhybopsis gelida* and Sicklefin Chub *Macrhybopsis meeki*. We sampled age-0 *Macrhybopsis* (primarily Sturgeon Chubs, but potentially including Sicklefin Chubs) all years to indicate successful reproduction, but noted an inverse correlation of catch per unit area (CPUA) with year. There was an inverse correlation for CPUA of age-1+ Sturgeon Chubs with year. There was no correlation for CPUA of age-1+ Sicklefin Chubs with year, but we noted a depression in CPUA during 2010 and 2012. The study reach includes restoration directives for federally endangered Pallid Sturgeon *Scaphirhynchus albus*, with 245,000 hatchery-origin Pallid Sturgeon (HOPS) stocked since 1998 to supplement the declining wild stock. Pallid Sturgeon longer than 350 mm transition to piscivory and are known to prey on Sturgeon Chubs and Sicklefin Chubs. We examined the hypothesis that mass additions of HOPS to the existing predator community could have population-level effects on the two chub species. Population modeling for the stocked HOPS through time yielded estimates of nearly 1,300 piscivore-sized HOPS in 2004, an increase to 26,000 HOPS in 2012, and decreasing numbers through 2016 (14,500). Candidate variables that also included discharge and water temperature best supported a negative correlation between HOPS abundance and age-0 *Macrhybopsis* CPUA. We found an inverse correlation for CPUA of age-1+ Sturgeon Chubs and estimated HOPS abundance, and there was also evidence of an inverse association between age-1+ Sicklefin Chub CPUA and HOPS in the study area. Results for a 60-km reach of the Upper Missouri River suggest declining CPUA for age-0 *Macrhybopsis* and Sturgeon Chubs during 2004–2016 and modest recovery of Sicklefin Chubs after 2012. Although causative factors driving CPUA changes through time are not known, correlative
analyses suggest that large numbers of HOPS added to the Missouri River predator community potentially influence CPUA of Sturgeon Chubs and Sicklefin Chubs in the study area. Testing this hypothesis will require expanded quantification of chub populations and HOPS numbers through time.

Keywords: *Macrhybopsis gelida*; *Macrhybopsis meeki*; *Scaphirhynchus albus*; reproduction; recruitment

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**Introduction**

The Sturgeon Chub *Macrhybopsis gelida* and Sicklefin Chub *Macrhybopsis meeki* are members of Leuciscidae that have a native range inclusive of the Yellowstone River, Missouri River, Mississippi River downstream from the Missouri River confluence, and tributaries adjoining these large river systems (U.S. Fish and Wildlife Service [USFWS] 1993a, 1993b). Both species have short lives (≤4 y depending on location [Stewart 1981; Werdon 1992; Grisak 1996; Braaten and Guy 2002; Everett et al. 2004]), are relatively small (maximum length ~93 mm for Sturgeon Chub [Stewart 1981; Duncan et al. 2016]; ~120 mm for Sicklefin Chub [Welker and Scarnecchia 2004]), and highly specialized for existence in turbid river systems.
(Davis and Miller 1967). Sturgeon Chubs and Sicklefin Chubs tend to be sampled in main channel habitats (Welker and Scarnecchia 2006; Duncan et al. 2016), and although they exhibit niche overlap, slight differences in habitat use exist (e.g., depth, velocity, substrate) between the two species (Everett et al. 2004; Welker and Scarnecchia 2004, 2006). Information suggests that Sturgeon Chubs and Sicklefin Chubs also exhibit similarities in their reproductive ecology. They attain sexual maturity after 2 y (Sicklefin Chub [Grisak 1996; Dieterman et al. 2006, but see Albers and Wildhaber 2017]; Sturgeon Chub [Stewart 1981; Werdon 1992]). Ovaries of mature females contain eggs in various developmental stages to indicate that females are multiple batch spawners (Stewart 1981; Werdon 1992; Dieterman et al. 2006; Albers and Wildhaber 2017) with the potential to perform multiple spawning events during the summer over an extended period (e.g., several weeks [Starks et al. 2016; Albers and Wildhaber 2017]). Reproduction in Sturgeon Chubs and Sicklefin Chubs includes the broadcast of nonadhesive eggs that rapidly become semibuoyant; thus, the developing embryos are subject to current-mediated downstream transport during incubation (Perkin and Gido 2011; Albers and Wildhaber 2017). Developing embryos and hatched free embryos may drift for 4–5 d, depending on water temperature; during the drift period, progeny from upstream spawning events may travel several hundred kilometers downstream, depending on current velocities (Perkin and Gido 2011; Albers and Wildhaber 2017).

Sturgeon Chub and Sicklefin Chub have experienced localized extirpations and diminished distribution and abundance throughout their native range (Hesse 1994; USFWS 2001; Galat et al. 2005; Hoagstrom et al. 2011); the USFWS (2001) estimated that Sturgeon Chub and Sicklefin Chub occupy 55 and 54%, respectively, of their historic range. Collectively, both species belong to a larger group of river-dwelling leuciscids that have experienced
substantial declines in distribution and abundance throughout the Great Plains (Hoagstrom and Turner 2015; Worthington et al. 2018). Based on known or suspected reproductive attributes, researchers report that many imperiled Great Plains fishes share modes of reproduction similar to those of Sturgeon Chub and Sicklefin Chub, wherein species are either pelagic broadcast spawners or lithopelagic broadcast spawners with propagules that drift several days over an extended distance (Perkin and Gido 2011; Hoagstrom and Turner 2015). Altered hydrology and river fragmentation are threats to this reproductive guild (Worthington et al. 2018), and Sturgeon Chubs and Sicklefin Chubs require approximately 300 km of free-flowing river (Dieterman and Galat 2004; Perkin and Gido 2011) to reproduce successfully and persist, given the long-distance dispersal attributes of developing embryos.

Petitions filed in 1994 to list the Sturgeon Chub and Sicklefin Chub as endangered (USFWS 1995) under the US Endangered Species Act (ESA 1973, as amended) were unwarranted after review, as new collections in the upper and lower portions of the Missouri River basin yielded increased numbers of chubs, a result used to infer wider distributions than previously thought (USFWS 2001). A portion of the Upper Missouri River basin including reaches of the Missouri River downstream from Fort Peck Dam, the Yellowstone River, and some tributaries supports populations of Sturgeon Chubs and Sicklefin Chubs, and information indicates some level of reproduction and recruitment occurs. Short-term studies conducted during the mid- to late-1990s indicated the presence of age-0 and older age groups (Braaten and Guy 2002; Everett et al. 2004; Welker and Scarnecchia 2004; Dieterman et al. 2006). Similarly, longer term, more recent monitoring programs for this portion of the Missouri River basin depict a range of size groups and ages to indicate some level of successful spawning and recruitment by Sturgeon Chubs and Sicklefin Chubs (Herman et al. 2008a, 2008b; Hunziker et al. 2016a, 2016b;
Wilson and Sandness 2016). However, the presence of recruitment cannot be used as a sole indicator of status and trend as species can maintain some level of spawning and recruitment while in a state of population decline.

A comprehensive understanding of recent population status and trends for Sturgeon Chubs and Sicklefin Chubs is lacking. Moreover, some information is contradictory. For Sturgeon Chub, the Powder River (a tributary to the Yellowstone River) historically serves as a stronghold for the species (Stewart 1981; Werdon 1992; USFWS 1993a), with this tributary delineated as a range-wide Sturgeon Chub refuge (Hoagstrom et al. 2011). Senecal et al. (2015) identified a substantial decrease in Sturgeon Chubs in the Powder River since 1980, with the species noted as rare by 2008. By contrast, Stagliano (2014) indicated that Sturgeon Chubs in the Powder River rebounded from low collection frequencies during 2005–2011 (present at 13% of sites) to increased occurrence during 2012–2013 (present at 65% of sites). Perkin and Gido (2011) reported that Sturgeon Chubs were extirpated from a section of the Yellowstone River downstream from the Powder River; however, Duncan et al. (2016) collected Sturgeon Chubs in this section and further noted that Sturgeon Chubs were common in lower sections of the Yellowstone River. The status of Sturgeon Chubs in the Upper Missouri River is similarly uncertain, as Oldenburg et al. (2010) did not identify a declining trend, but Perkin and Gido (2011) and Wildhaber et al. (2016) did observe a declining trend. However, data series for these studies spanned through only 2010. For Sicklefin Chub, the Upper Missouri and Yellowstone rivers were delineated as range-wide refuges for this species (Hoagstrom et al. 2011). In both river systems, Sicklefin Chubs remain present and are regularly caught, although catch records suggest longitudinal trends where increased catches occur in more downstream river sections (Duncan et al. 2016; Hunziker et al. 2016a, 2016b; Wilson and Sandness 2016). Similar to the
Sturgeon Chub analysis, Oldenburg et al. (2010) did not detect a declining trend for Sicklefin Chubs in the Upper Missouri River during 2006–2008, but additional analysis from Wildhaber et al. (2016) indicated a declining trend for Sicklefin Chubs during 2006–2010. Sturgeon Chub and Sicklefin Chub are currently being evaluated as candidates for a threatened or an endangered designation (USFWS 2017); thus, information on population status and trajectories is needed to assist the evaluation process.

Sturgeon Chubs and Sicklefin Chubs in the Upper Missouri River basin are subject to stressors (e.g., fragmentation, altered flow and temperature regimes [Worthington et al. 2018]), similar to other declining Great Plains fishes. In addition, since 1998, both of these species faced potential increased predation pressure in the Missouri and Yellowstone river drainages due to the stocking of large numbers of Pallid Sturgeon *Scaphirhynchus albus*—a top level predator. From 1998 to 2016, supplementation of the stock of wild Pallid Sturgeon in the joined Missouri–Yellowstone river systems (2001 population estimate of 178 individuals [Kapuscinski 2002]; most recent population estimate of 125 individuals in 2008 [Jaeger et al. 2009]) occurred with more than 245,000 hatchery-origin Pallid Sturgeon (HOPS; Rotella 2017) produced from wild broodstock. During their initial few years, Pallid Sturgeon feed primarily on macroinvertebrates, but then initiate the transition to piscivory at lengths of 300–600 mm (Grohs et al. 2009; Dutton 2018). Sturgeon Chubs and Sicklefin Chubs may comprise a significant portion of the piscine diet of Pallid Sturgeon (Gerrity et al. 2006), but *Macrhybopsis* chubs along with several other species are found in the gut of Pallid Sturgeon (e.g., Channel Catfish *Ictalurus punctatus*, Flathead Chub *Platigobio gracilis*, Sand Shiner *Notropis stramineus*, Johnny Darter *Etheostoma nigrum*, Emerald Shiner *Notropis atherinoides*, Stonecat *Noturus flavus* [Gerrity et al. 2006; Wanner et al. 2007; Grohs et al. 2009; Winders et al. 2014; Dutton 2018]). Although the
potential existed for large numbers of piscivorous Pallid Sturgeon to influence populations of Sturgeon Chubs and Sicklefin Chubs and their population status over the past 2 decades, there has been no examination of this potential in the Upper Missouri River basin.

We implemented a trawling regime during 2004–2016 to assess reproduction and quantify catches of Sturgeon Chubs and Sicklefin Chubs in the Upper Missouri River system. Designed within the multiyear assessment, sampling also spanned several weeks within each year to match protracted spawning attributes of the *Macrhybopsis* reproductive guild. The objectives were to 1) compare catches of age-0 *Macrhybopsis*, age-1+ Sturgeon Chubs, and age-1+ Sicklefin Chubs among years; 2) examine the potential influence of environmental conditions on catch rates of age-0 *Macrhybopsis*; and 3) test for the potential influence predator abundance (HOPS and Sauger *Sander canadensis*) on the three chub groups.

**Study Area**

The study area was in a 64-km reach of the Missouri River extending from river kilometer (rmk; distance measured from the confluence of the Missouri and Mississippi rivers) 2,499 in western North Dakota upstream to rkm 2,563 in eastern Montana (Figure 1). Regulated flows on the Missouri River and hydrologic inputs from the Yellowstone River influence the study reach. Regulated releases through Fort Peck Dam (located at rkm 2,852; Figure 1) mostly eliminated natural peak flow events associated with snow-melt conditions (Bowen et al. 2003). There is substantially diminished water temperature below the dam due to hypolimnetic releases, and although longitudinal warming occurs, water temperature in the Missouri River remains suppressed 300 km downstream (Erwin et al. 2018). The Yellowstone River (confluence located at rkm 2,547; Figure 1) maintains mostly natural flow and water temperature patterns, owing to the absence of flow-regulation dams on the mainstem (White and Bramblett 1993; Bowen et al.)
2003), but two river-width irrigation diversion dams are present on the lower mainstem (Cartersville diversion, Intake diversion; Figure 1). Elevated flows from precipitation events and snow-melt occur primarily during May and June (White and Bramblett 1993; Bowen et al. 2003). Impacts to flow on the Yellowstone River result from tributary dams and irrigation withdrawals (Eddy-Miller and Chase 2015). The lower portion of the Missouri River study area transitions from a mixing zone of the two rivers to the headwater reservoir environment of Lake Sakakawea (formed by completion of Garrison Dam on the Missouri River in 1953 at rkm 2,237). The full-pool headwater of Lake Sakakawea is at rkm 2,523 (Galat et al. 1996), and although considered the full-pool headwaters at this point, the reservoir headwater environment is riverine as average channel velocities greater than 0.4 m/s (Erwin et al. 2018) persist downstream to at least the study area terminus at rkm 2,499; Figure 1).

Methods

Environmental conditions

For the 2004–2016 duration of this study, we quantified discharge and temperature data for the Missouri River upstream from the Yellowstone River confluence and for the Yellowstone River as environmental conditions in both rivers had the potential to influence reproduction and chub populations within the study area. We used data from the U.S. Geological Survey streamflow gaging station at rkm 2,739 (gage 06177000) near Wolf Point, Montana (Figure 1), to assess flow conditions in the Missouri River upstream from the Yellowstone River confluence. We assessed water temperature in the Missouri River upstream from the Yellowstone River confluence with water temperature loggers deployed at two sites: an upper site located at rkm 2,814 near Frazer, Montana, and a lower site located at rkm 2,561. The U.S. Geological Survey streamflow gaging station at rkm 47.0 (gage 06329500) near Sidney, Montana (Figure 1), was
used to characterize discharge in the Yellowstone River. We obtained water temperature data for the Yellowstone River from a water temperature logger deployed at rkm 4.0.

**Fish sampling**

We sampled Sturgeon Chubs and Sicklefin Chubs following standard protocols during 2004–2016, excluding 2011 when flooding occurred in the Missouri River basin. We conducted sampling at eight fixed-site river bend stations extending from rkm 2,499 to rkm 2,563 (Figure 1). We sampled Sturgeon Chubs and Sicklefin Chubs in three macrohabitats associated with each river bend station: inside bend, outside bend, and channel crossover (Wildhaber et al. 2012). We included one variation to the river bend sampling regime in standard protocols for all years whereby nine samples were distributed through inside bend, outside bend, and channel crossover macrohabitats at the lowermost river bend (rkm 2,499). We conducted sampling at five weekly intervals (late July through late August) common to all years. We accomplished sampling of the eight river bend stations over a 2- to 3-d period each week. Under this sampling regime, we obtained a maximum of 30 samples each week (seven river bend stations × three macrohabitat samples per river bend station plus one river bend station × nine macrohabitat samples).

Sturgeon Chubs and Sicklefin Chubs were sampled using a benthic beam trawl (2.0 m wide × 0.5 m high steel frame with curved runners to ride along the river bed) supporting two nets (outer 5.5-m-long chafe net, 3.81-cm mesh; inner fish-retaining net, 0.32-cm mesh [Welker and Scarnecchia 2004; Braaten and Fuller 2007]). We attached ropes to the trawl frame and to the port and starboard supports of the boat bow, and while motoring in reverse with the current, we lowered the trawl to the river bed and fished moving downstream for a target duration of 4 min. Trawl distance (in meters) was recorded using an on-board global positioning system trip odometer from which we calculated trawl effort (in square meters) as the product of trawl width
(2.0 m) times trawl distance (in meters). The boat operator failed to record trawl distance in 28 trawls (1.6% of 1,775 total trawls conducted). For these 28 trawls, we applied a trawl distance of 299.0 m to the sample, as this distance represented the average trawl distance for the other 1,747 trawls conducted. After completing a sample, we emptied the trawl contents into a bucket and sieved. We extracted the fishes and enumerated and measured Sturgeon Chubs and Sicklefin Chubs (total length, in millimeters), but in situations when large numbers of small (e.g., <40-mm) fish were captured, we performed length measurements on a subsample and we counted the remaining fish. We identified small individuals mostly as Sturgeon Chubs, but similar to findings by Grisak (1996), species identification for small individuals (e.g., <45 mm) was not always certain due to similarities between Sturgeon Chubs and Sicklefin Chubs at small sizes. Therefore, we pooled small Sturgeon Chubs and Sicklefin Chubs as a single group (see below).

We constructed length–frequency plots by year and date to facilitate partitioning chubs into age groups corresponding to individuals presumed age-0 fish and individuals presumed greater than age-0 fish. For nearly all dates in all years, we could discern length gaps between the small fish group (pooled Sturgeon Chubs and Sicklefin Chubs mentioned above) and larger Sturgeon Chubs and Sicklefin Chubs; we used the length gaps to delineate chubs as age-0 or greater than age-0, such that we assigned individuals below the length gap as age-0 and individuals above the length gap as age-1+. If an individual length did not clearly associate with the age-0 group or age-1+ group, we randomly assigned the individual to either group. We delineated three groups of chubs from the length–frequency plots: age-0 *Macrhybopsis* (pooled group of small Sturgeon Chubs and small Sicklefin Chubs), age-1+ Sturgeon Chubs (Sturgeon Chubs that exceeded lengths of age-0 *Macrhybopsis*), and age-1+ Sicklefin Chubs (Sicklefin
Chubs that exceeded lengths of age-0 *Macrhybopsis*. We did not conduct partitioning of age-1 and older chubs to additional ages due to overlapping lengths for the older age groups.

**Statistical analysis**

We summarized discharge and water temperature conditions potentially related to spawning and catches of age-0 *Macrhybopsis* for the period spanning from June 1 to August 31. Although we did not specifically identify time of spawning for Sturgeon Chubs and Sicklefin Chubs, this time frame likely encompassed much of the spawning time frame based on earlier studies of these species (Stewart 1981; Werdon 1992; Grisak 1996; Dieterman et al. 2006). We quantified median discharge and median temperature for the Missouri and Yellowstone rivers. In addition, we calculated the number of days that daily water temperature equaled or exceeded 18.0°C (approximate baseline temperature for spawning [Werdon 1992; Grisak 1996]) to provide an estimate of suitable spawning conditions specific to each river.

We used a generalized linear mixed effects model (GLMM) to evaluate differences in catches of age-0 *Macrhybopsis*, age-1+ Sturgeon Chubs, and age-1+ Sicklefin Chubs among years. We modeled fish counts from individual trawls assuming a Poisson distribution and trawl area as an offset. An offset in a GLMM accounts for a known effect of a variable such as area trawled (Maunder and Punt 2004). The GLMM allowed us to model catch directly with area trawled as an offset assuming a Poisson distribution, thereby allowing the analysis of individual trawls with 0 catch. In addition, we used the GLMM to account for the extra variation due to the nested design for trawls nested within week, weeks nested within stations, and stations (i.e., three additional variance components). We modeled catch data as follows:

$$\log(\lambda_{ijk}) = \beta_0 + \beta_1 \times \text{year}_{ijk} + \nu_k + \gamma_{jk} + \delta_{jk} + \log(f_{ijk}),$$
where $\lambda_i$ is the expected catch, $\beta_0$ is the intercept, $\beta_1$ is the fixed effect of year, $\nu_i$ is a random effect of station, $\gamma_{ij}$ is a random effect of week within station, $\epsilon_{ijk}$ is a random effect of trawl within week and station, $i$ indexes each trawl within a station and week, $j$ indexes each week within station, $k$ indexes each station, and $\log(f_{ijk})$ is the offset defined as the area trawled (in square meters). We fit the GLMM to observed catch by maximum likelihood by using the glmer function from the lme4 package in R (Bates et al. 2015; R Core Development Team 2019).

We evaluated the analysis assumptions visually. We evaluated model specification by plotting observed and predicted catches compared with a 1:1 line for departures of linearity (e.g., curvature). We plotted the residuals vs. the predicted values to evaluate whether they were centered around 0. The analysis assumes a Poisson distribution where the variance is equal to the mean; therefore, the assumption is heteroscedasticity. We assumed the random effects to be normally distributed with mean 0, and we assessed them visually for departures with histograms. We evaluated fitted model residuals for potential temporal autocorrelation visually by examining residual plots for patterns (i.e., consistently above or below 0; see Figure S1, Supplemental Material) by trawls within year, station, and week and used Durbin–Watson (DW) tests for correlated errors through time. Similarly, we assessed potential for spatial correlation among stations visually by plotting residuals by rkm for each year (see Figure S1, Supplemental Material). Spatial correlation, if present, will be apparent with patterns in the residuals by rkm (i.e., residuals not centered at 0, increasing or decreasing by rkm). In addition, we tested spatial correlation in the residuals by using Moran’s $I$ (Moran 1950). We used the Anova function from the car package (Fox and Weisberg 2019) to perform the omnibus test for differences in mean catch among years. We calculated expected catch (expressed as catch per unit area [CPUA]; fish per square meter) and 95% confidence intervals for each year by using the LSMEANS function...
from the emmeans package (Leanth 2021). We assessed temporal trends for age-0 *Macrhybopsis*, age-1+ Sturgeon Chubs, and age-1+ Sicklefin Chubs by correlating CPUA with year.

We estimated the relative abundance of HOPS and Sauger as potential predators on the three chub groups for 2004–2016. Hatchery-origin Pallid Sturgeon have been stocked in the Missouri and Yellowstone rivers nearly every year since 1998. For this analysis, we used 350 mm as the base length for initiation of potential piscivory in HOPS, and we estimated yearly abundance of HOPS greater than 350 mm as follows. We obtained the annual abundance of all age classes of HOPS originally stocked as fall fingerlings, spring yearlings, and summer yearlings from Rotella (2017), where the Rotella estimates included survival rates for the different groups of fish stocked through time. Although Rotella (2017) provided estimates for the number of HOPS of different ages alive each year, the data did not contain information on lengths. We used the linear growth model for HOPS in the Upper Missouri River basin (Shuman et al. 2011) and growth data from 2005 to 2016 monitoring of HOPS in the Upper Missouri River basin (Wilson et al. 2017) to estimate mean length at age and the standard deviation (SD) of length at age for the population of stocked HOPS. Based on mean length at age, the associated SD of length at age, and the estimated number of HOPS alive at each age, we generated normal distributions of length at age from which we estimated the number of HOPS greater than 350 mm by year. The Missouri River supports several species in addition to HOPS that could be predaceous on chubs; however, long-term relative abundance data for these species do not exist or are extremely limited. We examined compilations of relative abundance data for Sauger since 2005 (Wilson et al. 2017) within the current study area. We quantified the Sauger data by year as mean catch per effort (number of Sauger/100 m drifted) from 2.54-cm trammel nets fished during the summer [Wilson et al. 2017]).
We used correlation analysis to examine associations between yearly mean CPUA of age-0 *Macrhybopsis* in the study area and estimated abundance of HOPS, relative abundance of Sauger, and discharge and temperature conditions in the Missouri and Yellowstone rivers. We also used the second-order Akaike’s Information Criterion for small sample sizes (*AICc*; Burnham and Anderson 2002) to evaluate candidate variables correlated with age-0 *Macrhybopsis* CPUA. Because of the small data set (12 y), the *AICc* selection process extended to only three-variable models with interaction terms. We used correlation analysis to examine associations between yearly mean CPUA of age-1+ Sturgeon Chubs and age-1+ Sicklefin Chubs in the study area and abundance metrics for HOPS and Sauger.

**Results**

Discharge and water temperature from June 1 to August 31 in the Missouri and Yellowstone river systems varied substantially across years within and among rivers (Table 1). Median discharge for the Missouri River was lowest in 2005 (178.0 m³/s) and highest in 2012 (317.0 m³/s). The Yellowstone River exhibited elevated discharge in 2008 (736.0 m³/s) and 2014 (749.0 m³/s) and lowest flows in 2007 (median = 117.0 m³/s). Median water temperature at the Upper Missouri River site varied 3.5°C among years (2015, 12.9°C; 2007, 16.4°C), and over the 12-y study period, mean daily water temperature equaled or exceeded 18.0°C in 3 y (2005, 2007, and 2010) for only 2–7 d. At the lower Missouri River site, median water temperature varied 3.7°C across years (2012, 17.9°C; 2010, 21.6°C). Water temperature equaled or exceeded 18°C all years at the lower Missouri River site (47–93% of the dates). In the Yellowstone River, median water temperature varied 2.7°C across years, with coolest and warmest temperatures occurring in 2004 (20.3°C) and 2013 (23.0°C), respectively. Daily water temperature equaled or exceeded 18.0°C all years in the Yellowstone River (76–97% of the dates).
In total, 7,079 *Macrhybopsis* chubs were sampled during the five late-July through late-August sampling events in 2004–2016. Length distributions by date indicated length gaps between presumed age-0 and older chubs to facilitate partitioning chubs by age group (Figure 2). Age group assignment based on length was less certain for 18 individuals (0.3% of all fish), and these fish were randomly assigned as age-0 or age-1+ by year (number of cases in parentheses): 2004 (1), 2005 (0), 2006 (2), 2007 (4), 2008 (0), 2009 (1), 2010 (0), 2012 (1), 2013 (1), 2014 (1), 2015 (6), and 2016 (1). Collectively, the species identification and age-assignment processes yielded the following: 4,425 age-0 *Macrhybopsis* (mean length = 32.0 mm, SD = 6.0 mm, minimum length = 12.0 mm, maximum length = 54.0 mm, \(N = 3,291\) measured individuals); 869 age-1+ Sturgeon Chubs (mean length = 62.0 mm, SD = 9.0 mm, minimum length = 43.0 mm, maximum length = 93.0 mm); and 1,785 age-1+ Sicklefin Chubs (mean length = 73.0 mm, SD = 10.0 mm, minimum length = 49.0 mm, maximum length = 114.0 mm). Samples of age-0 *Macrhybopsis* across dates identified prolonged spawning and continual or near-continual additions of young fish to the population as evidenced by minimum lengths that were less than lengths on earlier dates in most years (Figure 2).

**Chub CPUA comparisons among years**

The CPUA of age-0 *Macrhybopsis* differed among years (Wald \(\chi^2 = 2,623.0; P = 0.001\)), as CPUA declined after 2005 to significantly lower values from 2008 to 2016 (Figure 3). An inverse correlation was found for the CPUA with year, and the trend through time exhibited little evidence of autocorrelation (DW = 1.71; \(P = 0.40\); Figure 3). There was no spatial correlation between replicate river bends based on analysis of residuals (Moran’s \(I = -0.006; P = 0.38\)).

Significant differences in the CPUA of age-1+ Sturgeon Chubs occurred among years (Wald \(\chi^2 = 385.8, P = 0.001\)). The CPUA declined from a maximum in 2004 to significantly
lower values in later years (Figure 3). There was an inverse correlation between CPUA of age-1+ Sturgeon Chubs with year, and although time trends were suggestive of cyclical reductions in CPUA every 3–4 y (e.g., 2007, 2010, 2014; Figure 3), the data set exhibited little evidence for temporal autocorrelation (DW = 1.86; \( P = 0.50 \)). Residual analysis indicated little evidence for spatial correlation among river bends (Moran’s \( I = -0.008; \ P = 0.19 \)).

The CPUA of age-1+ Sicklefin Chubs differed among years (Wald \( \chi^2 = 514.1; \ P = 0.001 \)), as CPUA was greatest in 2009 and least in 2010 and 2012 (Figure 3). There was no significant correlation of CPUA of age-1+ Sicklefin Chubs with year (Figure 3), and significant autocorrelation through time was not evident in the data set (DW = 2.6; \( P = 0.46 \)). Similar to age-0 Macrhybopsis and Sturgeon Chubs, residuals from the Sicklefin Chub analysis exhibited little evidence of spatial correlation among river bends (Moran’s \( I = -0.006; \ P = 0.37 \)).

**Chub CPUA correlations with biotic and abiotic variables**

The estimated total abundance of HOPS greater than 350 mm increased from 1,323 fish in 2004 to a maximum of 26,003 fish in 2012 (Figure 4). After 2012, the number of HOPS greater than 350 mm declined to 14,515 fish in 2016, likely due to a combination of factors including cumulative mortality through time coupled with reductions in the number of fish stocked later in the stocking program. The mean number of HOPS greater than 350 mm by year followed a trend similar to total abundance and correlated with total abundance (\( r = 0.96; \ P < 0.0001; \ N = 13 \) y; Figure 4). Whereas mean abundance quantified the average number of HOPS across individual age classes, total abundance summed numbers across age classes to yield estimates that were 5–16 times greater than average abundance. Mean catch per effort for Sauger during 2005–2016 varied between 0.08 and 0.52 fish/100 m, but catch per effort did not exhibit a trend with year (\( r = 0.36; \ P = 0.25; \ N = 12 \)).
The CPUA of age-0 *Macrhybopsis* was significantly and inversely correlated with HOPS abundance (Figure 5), and HOPS abundance was the top-ranked candidate model in the model selection process (Table 2). Candidate models also contained support for a positive influence of water temperature in the Missouri and Yellowstone rivers, but in almost all cases, candidate models with temperature also contained HOPS abundance. There was an inverse correlation of CPUA of age-1+ Sturgeon Chubs with HOPS abundance, and there was also evidence ($P = 0.068$) of an inverse association between age-1+ Sicklefin Chubs and HOPS abundance (Figure 5). Sauger catch per effort was not significantly correlated with CPUA of age-0 *Macrhybopsis* ($r = -0.13; P = 0.70; N = 11$), age-1+ Sturgeon Chubs ($r = -0.22; P = 0.51; N = 11$), and age-1+ Sicklefin Chubs ($r = -0.23; P = 0.50; N = 11$).

**Discussion**

Sturgeon Chubs and Sicklefin Chubs in the Upper Missouri River basin—and more broadly throughout the historic range of both species—have been the subject of debate in past assessments (USFWS 2001). More recently, efforts were underway to summarize population trajectories for the two species as potential candidates for threatened or endangered designations (USFWS 2017). Initial studies on Sturgeon Chubs and Sicklefin Chubs in the Upper Missouri River basin centered on short-term assessments (Everett et al. 2004; Welker and Scarnecchia 2004, 2006; Oldenburg et al. 2010), and although providing point-in-time quantification on relative abundance, such investigations did not provide information on long-term population trajectories incorporating natural or anthropogenic-induced variations in population size. Moreover, discerning population status and trends from multiple short-term studies over the long-term are confounded if study objectives, habitats sampled, or sampling gears differ among studies. For example, seining surveys of shallow-water habitats provided initial concerns for
diminishing populations of chubs, but trawling surveys in deeper water identified additional catches (USFWS 2001). In contrast to short-term investigations, the present 12-y study yielded longer term trends in CPUA of Sturgeon Chubs and Sicklefin Chubs with data collected under common objectives, with consistent sampling gear, and in consistent sampling areas. In addition, sampling persisted over several weeks each year to quantify spatial and temporal trends in abundance related to reproduction, addition of age-0 individuals through the summer sampling regimes, and presence of older age groups.

We detected reproduction by *Macrhybopsis* chubs in all years, as evidenced by the collection of age-0 individuals each year. Although we primarily identified small chubs as age-0 Sturgeon Chubs, we categorized all small fishes as age-0 *Macrhybopsis*, owing to the potential that some individuals may have been Sicklefin Chubs. Welker and Scarnecchia (2004) identified few small Sicklefin Chubs (e.g., <60 mm) during their research; however, similar to our study, they also noted an abundance of small Sturgeon Chubs (i.e., <40 mm). We did not discern spawn timing in this study, but it likely spanned from mid-July through at least mid-August based on the occurrence of small individuals through late August and elevated catches of small age-0 *Macrhybopsis* through late August in some years (e.g., 2005, 2008, and 2015).

The presence of age-0 *Macrhybopsis* through the eight river bends sampled suggests that reproduction occurred in the Missouri River upstream from the Yellowstone River confluence, and in the Yellowstone River system. Sturgeon Chubs and Sicklefin Chubs have semibuoyant eggs that drift in the river currents, and although all aspects of embryonic drift and ontogenetic development are not known, total drift duration may span 3–5 d including 1–2 d for incubation and an additional 2–3 d of larval drift after hatch (Perkin and Gido 2011; Albers and Wildhaber 2017). The extended downstream drift duration for embryos and larvae before settling on benthic
habitats has been integrated in two converging models, in that both Sicklefin Chubs (Dieterman and Galat 2004) and Sturgeon Chubs (Perkin and Gido 2011) have been estimated to require at least 300 km of river habitat between barriers to complete early ontogenetic development and exhibit population persistence. The 303-km length of river between Fort Peck Dam (rkm 2,852) and the most upstream river bend sampled (rkm 2,549) is similar to the 300-km minimum recruitment threshold posited by Dieterman and Galat (2004) and Perkin and Gido (2011); however, owing to the suppressed thermal regime of the Missouri River downstream from Fort Peck Dam, results suggest that ontogenetic development during the embryonic and initial larval drift phases is completed in less than 300 km. Specifically, the upper 38 km of the Missouri River between Fort Peck Dam (rkm 2,852) and the Upper Missouri River temperature monitoring site (rkm 2,814) rarely attained (i.e., 2–7 d in only 3 of 12 y) the hypothesized lower spawning threshold of 18.0°C (Werdon 1992; Grisak 1996) across the range of hypolimnetic releases and additive tributary contributions observed during the 12-y study. Excluding this 38-km river reach as unsuitable spawning habitat for Sturgeon Chubs and Sicklefin Chubs leaves approximately 250 km of river between the Upper Missouri River temperature site and the most upstream sampling bend. Gradual warming of the river progresses longitudinally as quantified by the two Missouri River water temperature loggers. Spawning locations for chubs are not known, but samples of age-0 *Macrhybopsis* in the upper sampling bends suggest that spawning, incubation of drifting embryos, initial drift of hatched free embryos, and initial settlement of larvae to benthic habitats can occur in river reaches of approximately 250 km. Warm tributaries contributing to the thermally impacted Missouri River downstream from Fort Peck Dam have potential to serve as spawning areas; however, these tributaries are not likely sources of chub
propagules, as surveys during 1999–2007 did not find Sturgeon Chubs or Sicklefin Chubs in tributaries downstream from Fort Peck Dam (Bramlett 2014).

Whereas age-0 *Macrhybopsis* collected from Missouri River bends upstream from the Yellowstone River resulted from spawning events and drift processes in the Missouri River, age-0 *Macrhybopsis* sampled from downstream bends likely included progeny produced from spawning events and drift processes involving both rivers. Sturgeon Chubs range nearly 300 km upstream in the Yellowstone River, but are most common downstream from the Powder River (confluence at rkm 240; Duncan et al. 2016) identified as a spawning tributary for Sturgeon Chubs (Stewart 1981; Werdon 1992; USFWS 1993). Sturgeon Chub progeny sourced from spawning events in the mainstem Yellowstone River downstream from the Powder River confluence would have a maximum distance of 240 km of Yellowstone River habitat plus at least an additional 48 km of Missouri River habitat (i.e., most downstream river bend sampled) to complete ontogenetic development before settling. Drifting embryos and free embryos of Sturgeon Chubs produced from spawning events in the Powder River would have greater dispersal distances, depending on spawning locations within the Powder River. Although we did not identify spawning sources, Welker and Scarnecchia (2004) noted the abundance of small (<40 mm) Sturgeon Chubs in the Yellowstone River, indicating that at least some fish produced in the upstream reaches of the Yellowstone River system are retained in the lower Yellowstone River. Sicklefin Chubs are present in the mainstem Yellowstone River up to approximately rkm 200, but are most abundant downstream from an irrigation diversion at rkm 117 (Intake Diversion Dam; Duncan et al. 2016). Mainstem spawning by Sicklefin Chubs near Intake Diversion Dam would provide 165 km of longitudinally connected habitat (117 km of Yellowstone River plus 48 km of Missouri River to the most downstream river bend) for
completion of ontogenetic development and settling—less than the 300 km suggested in
dispersal and population persistence models (Dieterman and Galat 2004; Perkin and Gido 2011).

Identifying natal origin of age-0 *Macrybopsis* would be beneficial in future
investigations. Results would lend support toward quantifying the proportion of young Sturgeon
Chubs and Sicklefin Chubs sourced from spawning events among the potential natal rivers and
aid in testing spawning-dispersal distance hypotheses (Dieterman and Galat 2004; Perkin and
Gido 2011) relevant to the mostly natural Yellowstone River and the regulated Missouri River.

Catch trends in the study area were not consistent among the three chub groups. The
CPUA for age-1+ Sicklefin Chubs differed among years, but there was little evidence for a
consistent trend through time. By contrast, the CPUA of age-0 *Macrybopsis* and age-1+
Sturgeon Chubs differed among years and exhibited negative correlations through time to
suggest declines in CPUA from 2004 through 2016. Working with a short-term data set (2005–
2010) based on otter trawl sampling, Wildhaber et al. (2016) noted a trend of declining relative
abundance of Sturgeon Chubs and Sicklefin Chubs through 2010 in the Upper Missouri River
that included areas examined in our study. Longer term trends from the present study suggest
decreasing CPUA for age-0 *Macrybopsis* and age-1+ Sturgeon Chubs in the study area, and there
is some indication of a CPUA rebound for Sicklefin Chubs following the extremely low CPUA
years (2010 and 2012).

Factors influencing chub populations through time in the Upper Missouri River basin are
not specifically known. Median discharge and water temperature during June–August received
little to no support as correlates of age-0 *Macrybopsis* CPUA in the model selection process.
Contrasting with the annually varying discharge and thermal regimes, HOPS abundance was a
system-wide common factor that had the potential to affect populations of Sturgeon Chubs and
Sicklefin Chubs throughout the 60-km study reach. The stocking of HOPS in the Missouri and Yellowstone rivers was initiated in 1998 when approximately 180 individuals (Kapuscinski 2002) comprised the stock of wild Pallid Sturgeon. Whereas Pallid Sturgeon are one of several potential piscivorous species present in the Upper Missouri River, the stocking of large numbers of HOPS and their growth progressions to predatory sizes presented the potential for additive predation pressure on Sturgeon Chubs, Sicklefin Chubs, and other prey species across the aquatic community. Specifically, growth progressions of HOPS resulted in a 7 times (2004) to 144 times (2012) greater number of potentially piscivorous Pallid Sturgeon in the system than the number of wild adults. Data are unavailable to assess population changes for the entire community of potential piscivore species in the Missouri River during 2004–2016, but for Sauger, there was little evidence of significant population change through time, as indexed by trammel net catch per effort.

The negative correlations between HOPS abundance and CPUA for the three chub groups are suggestive of a potential influence of HOPS predation on chub populations in the study area. Past studies documented Pallid Sturgeon predation on Sturgeon Chubs and Sicklefin Chubs within the study area during 2013–2016, but other fish species were also prey (e.g., Emerald Shiner, Channel Catfish, Stonecat [Dutton 2019]). Verification (Gerrity et al. 2006) or listing (Winders et al. 2014) of Sturgeon Chubs and Sicklefin Chubs in other areas of the Missouri River as likely prey in the diet of Pallid Sturgeon, along with other prey fish species, is known.

The Upper Missouri and Yellowstone river systems serve as refuges for Sturgeon Chubs and Sicklefin Chubs (Hoagstrom et al. 2011), where populations of both species have persisted under a heterogeneous landscape including annually varying environmental conditions associated with the relatively natural Yellowstone River and annually varying environmental
conditions characteristic of the altered Missouri River. During the course of this study, we documented consistent declining trends through time in the bends sampled for Sturgeon Chubs and the age-0 *Macrhybopsis* group. Sicklefin Chubs in the study area also experienced periods of reduced abundance, but have moderately rebounded since 2012. The correlative analyses in this study do not point to causal factors driving reproduction or population changes through time for either Sturgeon Chubs or Sicklefin Chubs, but provide hypotheses to address in subsequent years. Specifically, we anticipate that the number of HOPS in the study area will continue to decline, owing to natural mortality through time and reduced numbers of HOPS stocked in recent years. If the number of HOPS in the connected river systems has an influence on populations of Sturgeon Chubs and Sicklefin Chubs, both species may potentially increase, owing to diminished predation pressure from HOPS in future years. Alternatively, although we expect the abundance of HOPS to decrease through time, similar or perhaps elevated predation pressure on both chub species and all life stages may still occur as the surviving HOPS increase food intake to meet energetic demands of growth and gamete production after attainment of sexual maturity.

Consistent and focused studies addressing reproductive output and abundance of Sturgeon Chubs and Sicklefin Chubs in the Upper Missouri River basin are essential to discern not only trends related to HOPS numbers through time but also to evaluate population persistence and functionality of the Upper Missouri River basin as a refuge for both species.

**Supplemental Material**

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.
Data S1. Trawling data set of fish counts by trawl to calculate catch per unit area (number per square meter) for age-0 *Macrhybopsis*, age-1+ Sturgeon Chub *Macrhybopsis gelida*, and age-1+ Sicklefin Chub *Macrhybopsis meeki* in the Upper Missouri River, Montana and North Dakota, during 2004–2016.

Found at DOI: https://doi.org/10.3996/JFWM-20-086.S1 (468 KB XLSX).

Data S2. Water temperature data set for two sites in the Upper Missouri River, Montana, and one site in the lower Yellowstone River, North Dakota, during 2004–2016.

Found at DOI: https://doi.org/10.3996/JFWM-20-086.S2 (51 KB XLSX).

Figure S1. Residual plots from generalized linear mixed effects models for age-0 *Macrhybopsis*, age-1+ Sturgeon Chub *Macrhybopsis gelida*, and age-1+ Sicklefin Chub *Macrhybopsis meeki* collected during 2004–2016 from eight river bend stations in the Upper Missouri River, Montana and North Dakota.

Found at DOI: https://doi.org/10.3996/JFWM-20-086.S3 (1.5 MB PDF).

Reference S1. Herman P, Plauck A, Utrup N, Hill T. 2008a. Three year summary age and growth report for sicklefin chub (*Macrhybopsis meeki*). Prepared for the U.S. Army Corps of Engineers–Northwest Division. U.S. Fish and Wildlife Service, Columbia, Missouri.

Found at DOI: https://doi.org/10.3996/JFWM-20-086.S4 (3.1 MB PDF).

Reference S2. Herman P, Plauck A, Utrup N, Hill T. 2008b. Three year summary age and growth report for sturgeon chub (*Macrhybopsis gelida*). Prepared for the U.S. Army Corps of Engineers–Northwest Division. U.S. Fish and Wildlife Service, Columbia, Missouri.

Found at DOI: https://doi.org/10.3996/JFWM-20-086.S5 (2.0 MB PDF).

Reference S3. Hunziker J, Haddix T, Holte L. 2016a. 2015 annual report, pallid sturgeon population assessment and associated fish community monitoring for the Missouri River:
segment 2 report prepared for the U.S. Army Corps of Engineers–Missouri River Recovery Program. Montana Fish, Wildlife and Parks, Fort Peck.

Found at DOI: https://doi.org/10.3996/JFWM-20-086.S6 (757 KB PDF).

**Reference S4.** Hunziker J, Haddix T, Holte L. 2016b. 2015 annual report, pallid sturgeon population assessment and associated fish community monitoring for the Missouri River: segment 3 report prepared for the U.S. Army Corps of Engineers–Missouri River Recovery Program. Montana Fish, Wildlife and Parks, Fort Peck.

Found at DOI: https://doi.org/10.3996/JFWM-20-086.S7 (731 KB PDF).

**Reference S5.** Jaeger M, Ankrum A, Watson T, Hadley G, Rotella J, Jordan G, Wilson R, Camp S, Thatcher T, Boyd K. 2009. Pallid sturgeon management and recovery in the Yellowstone River. Unpublished report. Montana Fish, Wildlife and Parks, Glendive.

Found at DOI: https://doi.org/10.3996/JFWM-20-086.S8 (216 KB PDF).

**Reference S6.** Rotella J. 2017. Upper Basin pallid sturgeon survival estimation project. Report prepared for the Upper Basin Pallid Sturgeon Workgroup. Montana State University, Bozeman.

Found at DOI: https://doi.org/10.3996/JFWM-20-086.S9 (1.9 MB PDF).

**Reference S7.** U.S. Fish and Wildlife Service. 1993a. Status report on sturgeon chub (*Macrhybopsis gelida*), a candidate endangered or threatened species. U.S. Fish and Wildlife Service, North Dakota State Office, Bismarck.

Found at DOI: https://doi.org/10.3996/JFWM-20-086.S10 (1.1 MB PDF).

**Reference S8.** U.S. Fish and Wildlife Service. 1993b. Status report on sicklefin chub (*Macrhybopsis meeki*), a candidate endangered or threatened species. U.S. Fish and Wildlife Service, North Dakota State Office, Bismarck.
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**Figure 1.** Upper Missouri River of western North Dakota and eastern Montana, including the Missouri River between Fort Peck Dam and Lake Sakakawea, and the lower Yellowstone River.
The rectangle in the broad-coverage locator map identifies the spatial coverage of the fish sampling area. The reduced-coverage map shows the eight river bends (gray ovals) where trawling was conducted during 2004–2016 (excluding 2011 when no standardized sampling was undertaken). River kilometer labels for the Yellowstone River denote distance upstream from the confluence of the Missouri and Yellowstone rivers. River kilometer labels for the Missouri River denote distance upstream from the confluence of the Missouri and Mississippi rivers.

**Figure 2.** Length plots by date and year for age-0 *Macrhybopsis* (triangles), age-1+ Sturgeon Chub *Macrhybopsis gelida* (squares), and age-1+ Sicklefin Chub *Macrhybopsis meeki* (circles) sampled from the eight river bends in the Upper Missouri River during 2004–2016 (excluding 2011 when no standardized sampling was undertaken).

**Figure 3.** Mean catch per unit area (CPUA; number/m² ± 95% confidence intervals) of age-0 *Macrhybopsis*, age-1+ Sturgeon Chub *Macrhybopsis gelida*, and age-1+ Sicklefin Chub *Macrhybopsis meeki* sampled in the Upper Missouri River during 2004–2016 (excluding 2011 when no standardized sampling was undertaken). Correlation statistics in each graph identify associations between CPUA and year.

**Figure 4.** Estimated total abundance (sum of all age classes, open bars) and mean abundance (average across all age classes, black points ± 1 standard error) of stocked hatchery-origin Pallid Sturgeon *Scaphirhynchus albus* (HOPS) more than 350 mm in the Upper Missouri River basin during 2004–2016.

**Figure 5.** Bivariate plots and correlation statistics for associations between estimated total abundance of hatchery-origin pallid sturgeon *Scaphirhynchus albus* (HOPS) more than 350 mm and catch per unit area (CPUA; number/m² ± 95% confidence intervals) of age-0 *Macrhybopsis*, age-1+ Sturgeon Chub *Macrhybopsis gelida*, and age-1+ Sicklefin Chub *Macrhybopsis meeki* in
the Upper Missouri River during 2004–2016 (excluding 2011 when no standardized sampling was undertaken).
Table 1. Median discharge and median water temperature during June–August ($N = 92$ d; 2004–2010, 2012–2016) for the Missouri and Yellowstone rivers used in correlation analysis of catch per unit area (CPUA; number/m²) of age-0 *Macrhybopsis*, age-1+ Sturgeon Chub *Macrhybopsis gelida*, and age-1+ Sicklefin Chub *Macrhybopsis meeki*. Numbers in parentheses are the first and third quartiles of the data distributions; for temperature, D indicates the number of days within the year that water temperature equaled or exceeded 18.0°C. Discharge data were obtained from Missouri River U.S. Geological Survey (USGS) gaging station 06177000 located at river kilometer mile (rkm) 2,739 and Yellowstone River USGS gaging station 06329500 at rkm 47.0. (The 0-rkm point was the confluence of the Missouri and Mississippi rivers.) Water temperature data were obtained from water temperature loggers deployed in the Upper Missouri River (rkm 2,814), lower Missouri River (rkm 2,561), and Yellowstone River (rkm 4.0).

| Year | Missouri River discharge (m³/s) | Upper Missouri River Temperature (°C) | D | Lower Missouri River Temperature (°C) | D | Yellowstone River discharge (m³/s) | Yellowstone River Temperature (°C) | D |
|------|--------------------------------|-------------------------------------|---|-------------------------------------|---|-----------------------------------|-----------------------------------|---|
| 2004 | 208 (198–219)                  | 14.9 (14.1–15.6)                   | 0 | 18.4 (17.1–20.5)                   | 55 | 193 (122–371)                     | 20.3 (18.2–22.2)                  | 71 |
| 2005 | 178 (169–189)                  | 15.5 (14.6–16.3)                   | 2 | 20.9 (19.0–22.7)                   | 82 | 345 (124–621)                     | 22.1 (19.7–23.9)                  | 82 |
| 2006 | 217 (214–220)                  | 15.7 (14.8–16.2)                   | 0 | 21.2 (19.7–23.0)                   | 86 | 191 (78–427)                      | 21.8 (20.2–24.2)                  | 89 |
| 2007 | 190 (185–203)                  | 16.4 (15.7–17.0)                   | 3 | 21.0 (19.5–23.9)                   | 83 | 117 (77–497)                      | 21.5 (19.9–23.2)                  | 89 |
Table 2. Model selection results for highest ranked candidate models correlating annual mean catch per unit area (CPUA; number/m²) of age-0 *Macrhybopsis* in the Upper Missouri River (2004–2010, 2012–2016) from six variables. Variables included in the model selection process are median June–August discharge (m³/s) in the Missouri and Yellowstone rivers; median June–August daily water temperature (°C) for the Upper Missouri River (river kilometer [rkm] 2,814), lower Missouri River (rkm 2,561), and Yellowstone River (rkm 4.0); and estimated total abundance of hatchery-origin Pallid Sturgeon *Scaphirhynchus albus* (HOPS). (The 0-rkm point was the confluence of the Missouri and Mississippi rivers.) Models contain the variable names and correlative trend (+ or − in

| Year | CPUA (min–max) | Median June–August Discharge (m³/s) | Median June–August Daily Water Temperature (°C) | Median Total Abundance HOPS (range) | Model AIC Score |
|------|----------------|------------------------------------|-----------------------------------------------|-----------------------------------|-----------------|
| 2008 | 199 (195–210)  | 15.6 (14.7–16.2)                   | 0.0 (16.2–22.4)                               | 72.8 (736–1204)                   | 21.0 (19.3–23.8) |
| 2009 | 195 (180–206)  | 13.3 (12.6–13.9)                   | 0.0 (18.9–21.3)                               | 76.1 (699–1121)                   | 21.0 (19.5–21.7) |
| 2010 | 210 (200–248)  | 15.0 (14.3–16.3)                   | 0.0 (19.1–23.0)                               | 80.4 (543–1163)                   | 21.9 (18.7–23.6) |
| 2012 | 317 (308–323)  | 14.2 (13.6–14.6)                   | 0.0 (17.3–19.0)                               | 43.3 (124–573)                    | 22.7 (20.7–24.6) |
| 2013 | 260 (246–320)  | 14.4 (13.8–15.0)                   | 0.0 (18.8–21.3)                               | 76.1 (234–607)                    | 23.0 (21.5–24.5) |
| 2014 | 244 (224–287)  | 13.6 (12.0–14.1)                   | 0.0 (17.4–21.6)                               | 58.5 (749–1,071)                  | 22.3 (18.1–23.7) |
| 2015 | 238 (229–248)  | 12.9 (12.1–13.5)                   | 0.0 (18.9–21.8)                               | 81.7 (276–991)                    | 22.8 (20.8–24.6) |
| 2016 | 272 (260–286)  | 14.2 (13.4–15.3)                   | 0.0 (19.3–21.1)                               | 82.3 (177–419)                    | 22.7 (21.5–23.7) |
parentheses), the number of parameters ($K$), second-order Akaike’s Information Criterion for small sample sizes ($AIC_c$), the difference in $AIC_c$ between the specified model and model containing the lowest $AIC_c$ ($\Delta AIC_c$), and the $AIC_c$ model weight.

| Model | Variable | $K$ | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ weight |
|-------|----------|-----|--------|----------------|----------------|
| 1     | HOPS (−) | 3   | −118.0 | 0              | 0.13           |
| 2     | HOPS (−) | 4   | −117.4 | 0.6           | 0.09           |
|       |          |     |        |               |                |
| 3     | HOPS (+) | 4   | −117.3 | 0.7           | 0.09           |
|       |          |     |        |               |                |
| 4     | Upper Missouri River temperature (+) | 3   | −117.1 | 0.9           | 0.08           |
| 5     | HOPS (−) | 4   | −116.8 | 1.2           | 0.07           |
|       | Lower Missouri River temperature (+) |     |        |               |                |
| 6     | HOPS (−) | 5   | −116.4 | 1.6           | 0.06           |
|       | Upper Missouri River temperature (+) |     |        |               |                |
|       | Yellowstone River temperature (+) |     |        |               |                |
HOPS (+)

Lower Missouri River temperature (+)

HOPS × Lower Missouri River temperature (−)