

DISTRIBUTION, PHENOLOGY, GROWTH, AND OVERWINTER MORTALITY OF
AGE-0 SMALLMOUTH BASS IN THE YELLOWSTONE RIVER, WITH
IMPLICATIONS FOR UPSTREAM RANGE EXPANSION

by

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ABSTRACT

Non-native fish introductions are a leading threat to freshwater biodiversity, and accurate assessments of future impact are often hindered by the challenge of anticipating future range expansion. Successful introductions of non-native Smallmouth Bass *Micropterus dolomieu* have occurred globally and often exhibit secondary spread to upstream habitat. This has occurred in the Yellowstone River, Montana (USA). Observations of adults in socio-economically valuable trout habitat have highlighted a need to better understand the controls on the upstream distribution of Smallmouth Bass in this system, particularly the influence of cold upstream climates on first-year growth and size-selective overwinter mortality (a potential life history bottleneck at northern latitudes). We documented the phenology, growth, and survival of age-0 Smallmouth Bass in relation to water temperature between the uppermost distribution of adults, and downstream regions where they are abundant. Successful reproduction (i.e., age-0 presence) was rare or absent throughout the uppermost 150 km of the upstream distribution of adults, suggesting that something currently prevents or discourages successful reproduction farther upstream. Surprisingly, the mean late-autumn body size of age-0 Smallmouth Bass did not differ significantly among the uppermost 200 km of their distribution, despite upstream declines in ambient water temperature. Although water temperature was a key attribute affecting age-0 growth, upstream shifts towards earlier hatching mediated the expected negative effect of colder upstream climates. Furthermore, surveys of overwinter survivors and simulations of age-0 starvation mortality indicated that age-0 individuals at the upstream extent of their distribution successfully recruited to the age-1 year-class in four consecutive years. Taken together, our results suggest that Smallmouth Bass have not yet reached the thermal limit of their upstream distribution, and that first-year growth, survival, and consequent spread by this non-native predator are probably driven by the complex interactions of spawn timing and ambient thermal and hydrologic regimes in the Yellowstone River.

CHAPTER 1

DISTRIBUTION, PHENOLOGY, GROWTH, AND OVERWINTER MORTALITY OF
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[A]Abstract

Non-native fish introductions are a leading threat to freshwater biodiversity, and accurate assessments of future impact are often hindered by the challenge of anticipating future range expansion. Successful introductions of non-native Smallmouth Bass *Micropterus dolomieu* have occurred globally and often exhibit secondary spread to upstream habitat. This has occurred in the Yellowstone River, Montana (USA). Observations of adults in socio-economically valuable trout habitat have highlighted a need to better understand the controls on the upstream distribution of Smallmouth Bass in this system, particularly the influence of cold upstream climates on first-year growth and size-selective overwinter mortality (a potential life history bottleneck at northern latitudes). We documented the phenology, growth, and survival of age-0 Smallmouth Bass in relation to water temperature between the uppermost distribution of adults, and downstream regions where they are abundant. Successful reproduction (i.e., age-0 presence) was rare or absent throughout the uppermost 150 km of the upstream distribution of adults, suggesting that something currently prevents or discourages successful reproduction farther upstream. Surprisingly, the mean late-autumn body size of age-0 Smallmouth Bass did not differ significantly among the uppermost 200 km of their distribution, despite upstream declines in ambient water temperature. Although water temperature was a key attribute affecting age-0 growth, upstream shifts towards earlier hatching mediated the expected negative effect of colder upstream climates. Furthermore, surveys of overwinter survivors and simulations of age-0 starvation mortality indicated that age-0 individuals at the upstream extent of their distribution

successfully recruited to the age-1 year-class in four consecutive years. Taken together, our results suggest that Smallmouth Bass have not yet reached the thermal limit of their upstream distribution, and that first-year growth, survival, and consequent spread by this non-native predator are probably driven by the complex interactions of spawn timing and ambient thermal and hydrologic regimes in the Yellowstone River.

[A]Introduction

Non-native fish introductions are among the most damaging and least reversible threats to aquatic biodiversity (Vitousek et al. 1996; Cucherousset and Olden 2011). Widespread introductions have been particularly common among fishes with edible, aesthetic, or recreational value (Gozlan 2008). Although only a small proportion of introductions lead to establishment (i.e., consistent reproduction by naturally-reproduced adults leading to survival of early life stages of offspring; Cudmore et al. 2017; Kocovsky et al. 2018), high rates of introduction have led to severe and widespread impacts on many aquatic ecosystems (Parker 1999; Marchetti et al. 2004; Gallardo et al. 2016). Even when mechanisms of impact such as predation or competition are well understood, difficulty in predicting secondary spread (i.e., range expansion) following establishment often obscures the potential consequences of successful introductions (Cucherousset and Olden 2011; Kulhanek et al. 2011; Trumpickas et al. 2011). Accurate assessments of current and future distributions are therefore critical to decision-making because the farther a non-native species spreads, the greater potential it has to impact the host ecosystem (Parker 1999).

Smallmouth Bass *Micropterus dolomieu* are native to central and eastern portions of the USA and Canada and exhibit many traits associated with successful establishment and spread by non-native species (Marchetti et al. 2004). For example, Smallmouth Bass have broad thermal tolerances, are feeding and habitat generalists, can disperse long distances, often exhibit high rates of nest success, and have been widely introduced because of their recreational value as sportfish (Loppnow et al. 2013; Brewer and Orth 2015). These traits have allowed Smallmouth Bass to establish and spread from their native range in the eastern Mississippi River Basin into their current distribution spanning 47 U.S. states and more than 20 countries (Marchetti et al. 2004; Brown et al. 2009).

Smallmouth Bass are regarded as “invasive” (Beck et al. 2008) across much of their expanding distribution (Loppnow et al. 2013). Compiled evidence from disparate watersheds, countries, and continents shows that they tend to spread rapidly following initial introductions, outcompete and prey on juvenile fish, reduce the abundance and diversity of small-bodied fishes, and alter aquatic and terrestrial food webs (Jackson 2002; Carey et al. 2011; Loppnow 2013). Notably, age-0 individuals can be highly piscivorous, and small size classes (i.e., 150–199 mm total length) can cumulatively consume more fish than all other size classes combined (George and Hadley 1979; Fritts and Pearsons 2006; Brown et al. 2009). Consequently, the full effect of non-native Smallmouth Bass is not realized until all age classes are present. Today, Smallmouth Bass are established across a broad extent of western North America, where they negatively impact many native fish species (Carey et al. 2011; Loppnow et al. 2013; Rubenson and Olden 2020).

The growing distribution and potential impact of non-native Smallmouth Bass in the Yellowstone River (Montana; Figure 1) have caused concern (Lamborn and Smith 2019). The upstream range limit of Smallmouth Bass was initially expected to be limited to warm reaches of the lower Yellowstone River Basin, where Smallmouth Bass were stocked to provide sportfishing opportunities by Montana Fish, Wildlife & Parks between the mid-1960s and the early 1990s (Montana Fish, Wildlife & Parks 2020). Instead, Smallmouth Bass expanded their upstream range limit. For example, an adult was recently documented as far upstream as Emigrant, Montana (Figure 1), which is > 375 km upstream of the nearest stocking location, < 50 km downstream of Yellowstone National Park, and well within the socio-economically valuable Paradise Valley trout fishery (Sage 2016). However, whether this occurrence is the result of local establishment or merely seasonal habitat use by adults (as seen in other watersheds, e.g., Langhurst and Schoenike 1990; Rubenson and Olden 2017) remains unknown.

The factors that control secondary spread (hereafter “spread”) by Smallmouth Bass in the Yellowstone River are similarly unknown, although some mechanisms have been identified in other systems. Cold climates often constrain Smallmouth Bass distributions at northern latitudes by preventing survival to the age-1 year class (hereafter “recruitment,” a prerequisite for local establishment; Cudmore et al. 2017), whereby cold water temperatures delay spawning, slow first-year growth, and ultimately cause size-selective overwinter mortality (Shuter et al. 1980; Shuter and Post 1990; Lawrence et al. 2015). However, limited research on the role of temperature in limiting non-native Smallmouth Bass spread in lotic environments has been conducted outside of the

Columbia River Basin (but see Lyons 1997). Furthermore, juvenile and adult densities, turbidity, and diet can also mediate first-year growth and survival (Miller and Storck 1984; Dong and DeAngelis 1998; Sweka and Hartman 2003). Lastly, feeding and spawning habitat, seasonal hydrology, and movement barriers can also limit the spread of Smallmouth Bass (Lawrence et al. 2012; Rubenson and Olden 2016, 2019). Whether upstream declines in water temperature currently constrain spread by preventing recruitment in upstream areas of the hydrologically, geomorphically, and ecologically distinct Yellowstone River (Reinhold et al. 2016), or whether farther upstream range expansion into salmonid habitat should be expected, is therefore unclear.

We addressed these uncertainties by investigating the influence of water temperature on Smallmouth Bass recruitment. We focused on the effects of temperature on age-0 phenology, growth, and overwinter mortality due to starvation because these life history attributes are sensitive to temperature and strongly influence recruitment success in other northern-latitude waterbodies (Shuter et al. 1980; Lawrence et al. 2015; Rubenson and Olden 2019). We hypothesized that a longitudinal gradient in water temperature currently limits upstream recruitment in the Yellowstone River by constraining age-0 overwinter survival. We predicted that relative to conspecifics in downstream areas, age-0 cohorts in progressively colder upstream areas would hatch later, experience shorter and colder growing seasons, and attain smaller body sizes (i.e., lengths and conditions) by the onset of winter. We further predicted that progressively longer upstream winters, combined with declining body sizes, would result in increasingly severe age-0 overwinter mortality

that approaches 100% at the upstream range extent (as seen in other northern-latitude rivers; Rubenson and Olden 2019).

We tested our predictions by satisfying four objectives. First, we identified the upstream extent of age-0 Smallmouth Bass presence (an indicator of successful reproduction and precursor to recruitment, establishment and spread), where age-0 cohorts presumably experience the coldest water temperatures. Second, we determined broad-scale longitudinal patterns in age-0 size and condition at the onset of winter, which are indices of internal energy reserves and determinants of overwinter survival. Third, we determined broad-scale longitudinal patterns in the timing of Smallmouth Bass hatching and assessed the collective influence of spawning phenology and rearing temperatures on age-0 body size at the onset of winter. Fourth, we used a size- and temperature-dependent model to simulate age-0 overwinter mortality due to starvation across all combinations of locations and years in which we measured body sizes at the onset of winter, and supplemented model results with surveys of overwinter survivors. Our research adds to the growing knowledge of mechanisms driving regional and global lotic Smallmouth Bass invasions, and informs regional fisheries management.

[A]Methods

[B]Study area

The Yellowstone River (Figure 1) is the longest river without major impoundments in the contiguous USA. It is an 8th-order snowmelt-driven stream that begins in the high-

elevation headwaters of the Greater Yellowstone Area (i.e., protected lands including and surrounding Yellowstone National Park) in northwest Wyoming, flows north into central Montana, and winds northeast to its confluence with the Missouri River in western North Dakota. Winters are typically long, cold, and experience high levels of precipitation, and spring snowmelt causes strong peaks in discharge that gradually decline to baseflow through the short, warm, and dry summers (e.g., 10-year average annual maximum of 1,321 m³/s on June 8, to an average daily mean of 100 m³/s on September 10; Supplementary Figure S.1). Moving upstream from Custer, Montana, at river kilometer (hereafter rkm) 481 (as measured from the Missouri River confluence; Figure 1), the river gradually transitions from a warm, turbid, anabranching river that supports diverse prairie fish assemblages and abundant Smallmouth Bass (Duncan et al. 2016; Reinhold et al. 2016), to a cold, clear, single-channel river that supports a celebrated blue-ribbon trout fishery (Figures 1, 2). Our study area spanned 364 km of the middle Yellowstone River and extended from Custer (rkm 481), which is adjacent to the uppermost historic Smallmouth Bass stocking source, upstream to Emigrant (rkm 845), which is adjacent to the uppermost recent observation of an adult (Figure 1).

[B]Data collection

[C]*Upstream extent.*— We estimated the upstream extent of successful Smallmouth Bass reproduction by sampling to detect the presence of age-0 individuals between August 1 and September 31 from 2016 through 2019 (hereafter “distribution surveys”). First, we delineated 11 equally spaced sections of the Yellowstone River that each contained 8 km and were spaced about 16 km apart. We later included a section adjacent

to historic stocking locations where adults are abundant (near Custer, Montana; rkm 500; Figure 1). Lastly, we confirmed the location of the upstream extent in 2016 and 2018 by sampling “extent-confirmation sections” centered between the uppermost positive and adjacent upstream negative detection locations in each year ($n = 2$ total; Figure 1).

We focused our sampling within each section on side channels because they provide high-quality nesting and nursery habitat for Smallmouth Bass in rivers (Simonson and Swenson 1990; Orth and Newcomb 2002), and to minimize disruptions to public recreation on this high-use waterbody (Sage 2016). We randomly selected three reaches (i.e., stretches of river between two main channel crossover points; Welker and Drobish 2010) within each section that contained at least one side channel. We then randomly selected one side channel within each reach for passive overnight sampling using three fyke nets, a level of effort that previously provided a 90% detection probability for all small-bodied fishes present in side channels in the middle and lower Yellowstone River (Duncan 2019).

Logistical constraints limited us to setting fyke nets within the lowest 300 m of selected side channels, which we divided into three contiguous 100-m segments. We set one fyke net in each segment. Each fyke net contained two 1.2×0.6 -m metal frames spaced 0.6 m apart, two 0.6-m diameter hoops spaced 0.6 m apart, a 6-cm diameter throat with no restriction starting at the first hoop, and a 4.5×0.7 -m lead with floats on top and a lead-core rope on the bottom. All netting was 3.2-mm Ace knotless black mesh. We set fyke nets by staking the lead to a randomly selected location along the wetted edge and anchoring it perpendicular to shore. To minimize catch interference, we never set nets

closer than 30 m apart. We also limited net locations to cod-end depths < 0.6 m and water velocities < 0.4 m/s to minimize mortality among fish and air-breathing animals. As a result, our inferences are limited to shallow areas with slow current velocity, which is optimal nursery habitat for age-0 Smallmouth Bass in rivers (Orth and Newcomb 2002). When candidate locations did not meet these criteria, we randomly selected nearby suitable locations within the same segment. Nets soaked overnight, and we measured the total length (mm; hereafter “length”) and wet weight (g; hereafter “weight”) of each captured individual.

We did not conduct distribution surveys in each section each year. Pilot sampling in 2016 only included sections between rkm 603 and 779 (Figure 1), whereas in 2017 we expanded distribution sampling to sections between rkm 570 and 817 (Figure 1). In contrast, we focused our efforts in 2018 and 2019 on sections proximal to the farthest-upstream detection during the preceding year. We did so by sampling the uppermost section where age-0 Smallmouth Bass were captured the year before, and sampling upstream until no individuals were detected in two consecutive sections (not including extent-confirmation sections; Figure 1).

As a check on the probability of type-II error (i.e., false negative) where age-0 individuals may be rare, we collected environmental DNA (hereafter eDNA) samples in conjunction with 2019 distribution surveys using methods described in Franklin et al. (2018) and Rubenson and Olden (2019). Briefly, we filtered three 5-L field samples paired with one 1-L field control (i.e., reverse-osmosis water) through 1.5- μ m fiberglass filters near the downstream mouth of each side channel, as well as in the adjacent main

stem. We also collected eDNA samples in the same manner immediately following 2019 electrofishing surveys (see below), which allowed us to confirm that our eDNA sampling methods could detect Smallmouth Bass in side channels with confirmed presence.

We extracted eDNA from filters using the Investigator Lyse & Spin Basket Kit (Qiagen, Hilden, Germany) with the DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's instructions. We included an extraction blank, with no filter of any kind, to detect possible contamination from extraction equipment and reagents. We analyzed eDNA extract using the Smallmouth Bass COI-assay developed by Franklin et al. (2018), which included a 4- μ L eDNA extract, 0.5- μ m forward and reverse primer, and 0.25- μ m FAM-labeled probe. We analyzed five reactions per sample and included an internal positive control (Exogenous Internal Positive Control kit; Thermo Fisher Scientific, Waltham, Massachusetts) in each reaction following the manufacturer's instructions. We ran one no-template control (reverse-osmosis water) and one tissue-derived positive control per plate. We processed samples using a BioRad CFX96 thermocycler (Bio-Rad Laboratories, Hercules, California) with the following thermal cycles: 95°C for 15 min \times 1, and 95°C for 15 s followed by 60°C for 1 min \times 40. We processed all samples at the United States Geological Survey (USGS) Northern Rocky Mountain Science Center.

[C]*Size and condition at the onset of winter.*— Age-0 size and condition at the onset of winter reflect internal energy stores assimilated during the prior growing season and are important predictors of overwinter survival (i.e., successful recruitment), a prerequisite for local establishment (Shuter et al. 1980). We determined longitudinal

patterns in size and condition by intensively sampling three equally spaced sections at the onset of winter in 2018 and 2019. Each section contained 8 rkm and was previously sampled during distribution surveys. The uppermost section was located at rkm 700 (i.e., encompassing rkm 696– 704; hereafter “Upper section”; Figure 1) and contained the probable upstream extent of successful reproduction. The lowermost section was 200 km downstream of the Upper section and near historic stocking locations where adult abundances were high (rkm 500, hereafter “Lower section”; Figure 1), and the “Middle section” was centered between the two (rkm 603; Figure 1). We sampled age-0 Smallmouth Bass within these three sections in the late autumns of 2018 and 2019, after daily mean water temperatures declined below 10°C and active feeding was assumed to cease (Shuter et al. 1980). We randomly selected one side channel from each of five randomly selected reaches within each section for sampling.

We electrofished both banks of the lowest 300 m of each randomly selected side channel with a fixed-electrode electrofishing boat following Montana Fish, Wildlife & Parks guidelines. We measured the length and weight of every captured age-0 Smallmouth Bass, and retained a subset of randomly selected individuals from each side channel in 2018 (69 to 100 per section) by immersing them in a 500 mg/L solution of MS-222 and freezing carcasses for otolith extraction at a later date. We attempted to collect an equal number of fish from each side channel in a section to avoid over-representing individual family groups.

We supplemented our age-0 size data with length and weight measurements made during pilot sampling late in the autumns of 2016 and 2017, which experienced warmer

temperatures and lower discharges than in 2018 or 2019 (Figures S.1, S.2). We used the same methods as described above, except that we did not weigh fish or collect otoliths in 2016, and we did not sample areas that we judged to be poor overwintering habitat (i.e., lacking large rocky substrate or woody debris; Munther 1970; Paragamian 1981) in both 2016 and 2017. The inclusion of these data added temporal context to the longitudinal patterns we evaluated in 2018 and 2019.

[C]*Hatch date.*— Hatch timing can influence the length of the age-0 growing season, and may therefore be critical to first-year growth (Miller and Storck 1984; Bestgen and Hill 2016). We used otolith microstructure analysis (Stevenson and Campana 1992) to estimate the hatch dates of 30 individuals collected from each of the Upper, Middle, and Lower sections late in the autumn of 2018. We attached otoliths to glass microscope slides using thermoplastic glue (Crystalbond 509 Mounting Adhesive, Electron Microscopy Sciences, Hatfield, Massachusetts), and polished otoliths in the sagittal plane using 15.0–0.1 μm lapping film. We stopped polishing when the innermost rings of the nucleus, which begin to deposit upon hatching (Hill and Bestgen 2014), were visible. We photographed prepared otoliths at $120\times$ magnification under a stereomicroscope (Leica Application Suite v4.1, Leica Camera AG, Wetzlar, Germany), and counted daily growth rings from the images. The lead author read each otolith on two non-consecutive days and averaged the two ring counts to estimate hatch date.

We assessed the precision of hatch-date estimates using CV (i.e., $100\cdot\text{SD}/\text{mean}$; Campana et al. 1995). If the CV of a pair of ring counts was $> 5\%$ we conducted a third count, averaged the three, and rejected the otolith if the mean CV remained $> 5\%$; 3% of

aged otoliths required a third count, none were rejected, and the mean CV among all final estimates was 1.78% ($n = 120$). We assessed reader bias by having a second reader age a length-based systematic subsample of 10 otoliths, and we graphically contrasted the two sets of estimates using an age-bias plot (Campana et al. 1995). We also used Wald tests to determine whether a simple linear regression between the estimates of the two readers deviated from a 1:1 relationship (Campana et al. 1995). Neither the slope ($T = 0.599$; $P = 0.407$) nor intercept ($T = 0.658$; $P = 0.566$) was significantly different from values expected under a 1:1 relationship, and the age-bias plot did not indicate bias among readers (Figure S.3).

[C]*Water temperature.*— We monitored water temperatures across our study area to describe the upstream declines that we hypothesized would drive longitudinal patterns in age-0 hatch timing, body size, and overwinter mortality. However, rapid sedimentation and falling water levels prevented us from accurately monitoring temperatures in many of the shallow side channels we sampled for age-0 Smallmouth Bass. We therefore used mean daily temperatures derived from hourly measurements made in the main stem to approximate the typical thermal conditions that fish experienced within each section. We obtained main-stem temperature data from USGS stream gages (<https://waterdata.usgs.gov/mt/nwis/rt>; Figure 1), maintained temperature loggers (HOBO pendant; Onset Electronics, Onset, Massachusetts) in the main stem of the Upper section between the late summer and early winter of 2017, and attempted to maintain loggers in the Upper, Middle, and Lower sections between the spring of 2018 and summer of 2020. Unfortunately, all loggers deployed in spring 2018 were lost or buried during high spring

runoff (Figure S.1), so we deployed replacement loggers in each section on July 30. We accounted for this lost data by applying lapse rate corrections to water temperatures measured at Big Timber, Montana (USGS gage 06195950; Figure 1), using longitudinal lapse rates observed between it and each section during the same months the following year. Comparisons of observed to expected temperatures suggested that these estimates were adequately precise and accurate (Supplementary methods).

Because continuous autumn, winter, and spring temperatures are needed to estimate overwinter mortality (Shuter et al. 1980), we filled gaps in our four-year Upper section dataset using a predictive stream temperature model. We used a non-linear regression model to predict 2016 and spring 2017 and 2018 stream temperatures from air temperature and discharge data using least squares regression (Mohseni et al. 1998; R version 3.6.2; Supplementary methods).

[C]*Spring size distributions.*— We sampled age-0 Smallmouth Bass in the Upper, Middle, and Lower sections in the early spring of 2019 to determine if overwinter survival occurred, to identify minimum size requirements for survival, and to detect shifts in length distributions, a key feature of size-selective overwinter mortality (Ludsin and DeVries 1997; Post et al. 1998). We sampled as water temperatures rose to 10°C, and electrofished the same side channels using the same methods as during the preceding autumn. However, high turbidities limited the capture efficiency and sample size of spring surveys, particularly in the Upper section where rain and snowmelt runoff the previous night reduced water clarity.

[B]Data analysis

[C]*Modeling approach.*— We used linear mixed-effects models to evaluate spatial and temporal patterns in age-0 Smallmouth Bass distribution, length, condition, hatch date, and thermal history. We began each analysis by fitting a maximal model that included random-effects terms for each grouping of potentially non-independent observations (i.e., within side channels, sections, or years). We fit random-intercept terms when the fixed effect of interest was categorical, and additionally included random-slope terms when the fixed effect was continuous. We fit maximal models with individual side channel as a random effect nested within section. We removed random-effects terms that caused singular fit or nonconvergence (Barr et al. 2013; Bates et al. 2014). We assessed the fit of fixed-effects terms using marginal R^2 , a measure of the proportion of overall variance explained only by fixed effects (package MuMIn, Nakagawa and Schielzeth 2013; Barton 2019). We assessed the significance of fixed-effect terms using ANOVAs with Satterthwaite's approximation (package lmerTest, Kuznetsova et al. 2017), and used a threshold probability of type-I error (α) of 0.10 to mediate loss of power due to observed high individual variability in phenology and growth. When a categorical fixed effect was significant, we conducted post-hoc tests of pairwise differences among levels using the Bonferroni-Holm correction for multiple comparisons (package multcomp; Hothorn et al. 2014). We conducted all statistical analyses using program R version 3.6.2 (R Core Team 2019).

[C]*Objective 1: upstream extent.*— We estimated the age-0 upstream extent by fitting a generalized linear mixed-effects regression with a binomial distribution (hereafter GLMER; package lme4, Bates et al. 2014) to the presence or absence of age-0

Smallmouth Bass from multi-year distribution sampling. In addition to the results from equally spaced sampling sections, we also included data from fyke-net sampling for small-bodied fish assemblages that occurred in the Lower section using the same methods as elsewhere. We modeled the probability of age-0 presence within a section as a function of the fixed effect of distance upstream (i.e., rkm), and included random slope and intercept terms for year. This maximal model encountered singular fit due to the random slope and intercept terms for year (i.e., almost no variation was explained by the relationship between age-0 presence and distance upstream across years), and as a result our final model estimated the probability of age-0 presence solely as a function of the fixed effect of distance upstream.

Given the unequal number of presences ($n = 14$) and absences ($n = 17$) in our age-0 distribution data, we used an optimized probability threshold to predict age-0 Smallmouth Bass presence or absence in each section (Figure 1) by maximizing the proportion of the area under the curve (AUC) of receiver operating characteristic plots (package ROCR; Sing et al. 2005). Given the prevalence of positive detections in our data (45.2%; Manel et al. 2001), AUC is an effective and unbiased indicator of model performance and was maximized (0.962) by an optimal probability threshold of 0.546. We estimated the age-0 upstream extent at the rkm where model predictions switched from age-0 presence to age-0 absence (i.e., where the probability of presence began falling below the optimal probability threshold).

[C]*Objective 2: size and condition at the onset of winter.*— We calculated the relative condition (hereafter “condition”) of each captured individual because this index

approximates whole-body lipid content in juvenile fishes and is strongly associated with starvation mortality in age-0 Smallmouth Bass (Shuter et al. 1989; Schloesser and Fabrizio 2017). We divided the measured weight of each individual by an expected weight based on a “standard” length-weight regression (Pope 2007). In the absence of a population- or species-level standard regression appropriate for Smallmouth Bass < 150 mm (Blackwell et al. 2000), we developed a linear regression using \log_{10} -transformed late-autumn length (mm) and weight (g) data pooled across the Upper, Middle, and Lower sections ($n = 447$; Pope 2007). The resulting equation was

$$\log_{10}(\text{weight}) = -4.88097 + 3.00204 \cdot \log_{10}(\text{length}). \quad (1)$$

We evaluated spatial patterns in age-0 size and condition by using linear mixed-effects ANOVAs (package `lmerTest`; Kuznetsova et al. 2017) to separately model length and condition at the onset of winter as a function of the fixed effect of section, random-intercept terms for side channel nested within section, and a random-intercept term for year. However, both models encountered non-convergence due to the random-intercept term for section, which we then removed. The resulting model structure fit the length data (Table 1, Model 1), but when modeling condition we were forced to remove the random-intercept term for year because it caused singular fit. As such, we assessed condition by modeling it as a function of the fixed effect of section and a random-intercept term for side channel (Table 1, Model 2).

In addition to spatial data, we also considered the implications of temperature on age-0 size and condition using data collected across years. We predicted that age-0 body lengths in the Upper section (2016–2019) would be longer on average in warmer and

lower-discharge years than in cooler and higher-discharge years (Figures S.1, S.2). We tested for differences in mean length in the Upper section across years using a linear mixed-effects ANOVA, wherein we modeled length as a function of the fixed effect of year and a random-intercept term for side channel (Table 1, Model 5).

[C]*Objective 3: drivers of age-0 size at the onset of winter.*— We used age and temperature data to evaluate how age-0 phenology (i.e., hatch timing) and main-stem temperature influenced longitudinal patterns in size at the onset of winter. We investigated longitudinal patterns in age-0 hatch dates by using a linear mixed-effects ANOVA to model hatch date as a function of the fixed effect of section and random-intercept terms for side channel nested within section. This model encountered nonconvergence due to the random-intercept term for section, which we then removed. Consequently, we tested our prediction by modeling hatch date as a function of the fixed effect of section and a random-intercept term for side channel (Table 1, Model 3).

Next, we determined how hatching timing interacted with main-stem temperatures to influence size at the onset of winter. We tested the prediction that age-0 cohorts in upstream areas would attain smaller sizes due to shorter and colder growing seasons using growing degree days $> 10^{\circ}\text{C}$ (Rubenson and Olden 2017). The sum of growing degree days $> 10^{\circ}\text{C}$ (hereafter GDD) is a holistic index of the duration and intensity of exposure to temperatures at which Smallmouth Bass actively feed (i.e., $>10^{\circ}\text{C}$; Shuter et al. 1980), and is calculated by subtracting 10°C from all daily mean water temperatures between two dates and taking the cumulative sum of all positive values. However, because the thermal history of each individual begins at hatching, we calculated GDD for

each aged individual using the main-stem temperatures measured between the otolith-estimated hatch date and date of capture. The resulting “first-year GDD” is an index of the cumulative exposure to temperatures that allow active feeding (i.e., $>10^{\circ}\text{C}$), and allowed us to assess whether antecedent thermal history alone explained longitudinal patterns in age-0 size. We calculated first-year GDD using temperature data specific to each section, so we did not include section as a fixed effect in the same model as first-year GDD. We consequently modeled section as a random effect and used parameter estimates to evaluate differences in the relationship between length and GDD across sections and years.

We tested the hypothesis that first-year GDD was the principal driver of longitudinal patterns in age-0 size at the onset of winter using a linear mixed-effects regression analysis (package lmerTest). We modeled age-0 length as a function of the fixed effect of first-year GDD, with random slope and intercept terms for side channel nested within section. This maximal model encountered singular fit due to both random slope terms, which we then removed. As a result, we modeled length as a function of the fixed effect of first-year GDD, with random intercepts for side channel nested within section (Table 1, Model 4).

[C]*Objective 4: overwinter mortality.*— Because overwinter mortality due to starvation is size-selective (Shuter et al. 1980), we assessed evidence for overwinter mortality in the Upper, Middle, and Lower sections by comparing age-0 length distributions between autumn 2018 and spring 2019. We did so by using a one-sided Kolmogorov-Smirnov test, which makes no assumption of the underlying sample size or

data distribution (Massey 1951; R version 3.6.2), to separately detect shifts towards longer body lengths within each section between the autumn of 2018 and spring of 2019 (Ludsin and DeVries 1997; Post et al. 1998). However, we only captured one age-0 Smallmouth Bass in the Upper section during spring sampling, which prevented any formal tests in this section.

Next, we estimated the probability of overwinter mortality due to starvation for every age-0 individual captured at the onset of winter in the Upper (2016–2019), Middle (2018, 2019), and Lower (2018, 2019) sections using a temperature- and size-dependent survival model specific to overwintering age-0 Smallmouth Bass (Shuter et al. 1980),

$$L_0 = 0.188d + 14.8 \quad (2)$$

$$L_{100} = 0.328d + 33.9 \quad (3)$$

where the probability of surviving a starvation period of d days in duration increases linearly from the estimated length below which survival is 0% (L_0), up to the length above which survival is 100% (L_{100}). In the original model (Shuter et al. 1980), d is determined by tallying the number of days with mean daily temperatures $< 10^\circ\text{C}$.

However, Rubenson and Olden (2019) found overwinter survivors in the John Day River Basin that were shorter than L_0 . Consequently, they suggested that calculating d using days $< 7^\circ\text{C}$ may avoid under-estimating survival (i.e., over-estimating mortality) in rivers, as the limited feeding that is known to occur between 7°C and 10°C may allow fish to maintain existing energy stores (Shuter et al. 1980, 1989), and the transition between cold and warm temperatures is more gradual in northwestern rivers than in lakes (Rubenson and Olden 2019). We attempted to corroborate the findings of Rubenson and

Olden (2019) by comparing L_0 based on both proposed definitions of d (i.e, using days $< 7^\circ\text{C}$ versus $< 10^\circ\text{C}$) to the minimum length of overwinter survivors captured during spring 2019 sampling.

We calculated survival probabilities for each age-0 individual measured at the onset of winter, and subtracted percent values from 100 to convert them to probabilities of mortality due to overwinter starvation. We estimated “cohort mortality” within each section and year by taking the mean percent mortality of 100,000 simulated trials. Each trial assigned a binary outcome (i.e., survival or death) to each measured individual, and calculated a single percent cohort mortality for each cohort by dividing the number of deaths by the starting cohort size. Given current uncertainties in the conditions that cause winter starvation, we duplicated all of the above calculations using d generated from both days $< 7^\circ\text{C}$, and days $< 10^\circ\text{C}$.

[A]Results

[B]Upstream extent

The estimated annual upstream extent of age-0 Smallmouth Bass presence in the Yellowstone River (2016–2019) was located within the Upper section at rkm 702 (95% confidence limits of 645 and 726; Figure 2). Thirteen of the 14 observations made downstream of rkm 702 were positive detections, whereas 16 of the 17 observations made upstream were negative detections. The single positive detection above the

predicted upstream extent occurred at rkm 725 (near Big Timber; Figure 1), where we captured two age-0 individuals in 2016.

Smallmouth Bass eDNA detections in 2019 supported the results of our distribution surveys. We never detected Smallmouth Bass eDNA where we did not capture age-0 individuals in fyke nets ($n = 15$ side channels; Table S.1), whereas we always detected Smallmouth Bass eDNA where we captured individuals by electrofishing in 2019 ($n = 9$ side channels; Table S.2). We also detected Smallmouth Bass eDNA in every main-stem sample collected in the Lower and Middle sections, two-thirds of samples in the Upper section, and none farther upstream (Tables S.1, S.2).

[B]Water temperature

Mean August 2018 water temperatures differed by 2.5°C between the Lower and Upper sections in 2018, and differed by 2.7°C in 2019. This corresponded to a 25% decline in ambient GDD between the two sections in both years (Figures S.4, S.5).

[B]Size and condition at the onset of winter

[C]*Longitudinal patterns.*— Contrary to our prediction, neither mean age-0 length ($F = 0.10$, $P = 0.91$, marginal $R^2 < 0.01$, Table 1) nor condition ($F = 0.91$, $P = 0.44$, marginal $R^2 = 0.01$, Table 1) at the onset of winter varied significantly among sections (Figures 3A, 3B, 3C, 3D), despite colder upstream temperatures (Figures S.4, S.5). However, variation in length and condition were consistently higher in downstream sections. For example, both the longest and shortest fish, as well as the highest- and lowest-condition fish, were all observed in the lower section in each year (Figures 3A, 3B, 3C, 3D).

[C]*Temporal patterns.*— Age-0 length at the onset of winter varied among years in the Upper section (2016–2019; $F = 13.34$, $P < 0.01$, marginal $R^2 = 0.47$; Table 1). The mean length in 2016 was longer than in any other year sampled, whereas the mean lengths in all other years were not significantly different from one another (Table 2).

[B]Drivers of age-0 size at the onset of winter

Contrary to our prediction, estimated 2018 hatch dates broadly overlapped within our study area, and mean hatch date did not vary significantly among sections ($F = 1.88$, $P = 0.23$, marginal $R^2 = 0.12$; Table 1). However, estimated hatching occurred over a narrower window of time and ended substantially earlier moving upstream, such that estimated hatching ceased in the Upper section before it even peaked in the Lower (Figure 4A; Table 3).

First-year GDD was positively associated with age-0 length in all sections ($F = 157.87$, $P < 0.01$, marginal $R^2 = 0.56$; Table 1), and individuals that hatched in the colder Upper section accumulated 24 to 28% fewer GDD than those hatched on the same date in the warmer Lower section (Figures 4B, S.4). However, earlier-hatching individuals always accumulated more GDD than late-hatching individuals in the same section (Figure 4B). Consequently, an earlier start and end to the hatching season in the Upper section resulted in mean GDD there being only 12% lower than in the Lower section, despite the GDD of individuals hatched on the same date differing by up to 28% between the two locations (Figures 4B, 5).

[B]Overwinter mortality

[C]*Spring size distributions.*— Spring 2019 electrofishing was hampered by high turbidity, particularly in the Upper section. As a result, we captured one age-0 overwinter survivor in the Upper section, 12 in the Middle section, and 16 in the Lower section (Figure 6). Despite small spring 2019 sample sizes relative to the previous autumn, we detected a significant shift towards longer age-0 lengths between autumn and spring sampling in the Middle ($D = 0.57$, $P < 0.01$) and Lower sections ($D = 0.54$, $P < 0.01$; Figure 6). No overwinter survivor in any section was shorter than L_0 estimated from winter temperatures $< 7^\circ\text{C}$, or $< 10^\circ\text{C}$ (Figure 6).

[C]*Mortality simulations.*— The estimated mortality due to overwinter starvation among age-0 cohorts hatched in 2018 and 2019 was never lower than 31.9%, nor higher than 81.9%, in any section under either proposed method for estimating the duration of winter starvation (i.e., tallying days $< 7^\circ\text{C}$ versus days $< 10^\circ\text{C}$; Figure 7). Winters were always longer in upstream areas, but winters in the Upper section were only 11–24 days longer than in the Lower, corresponding to an increase in L_0 of only 2.1–4.5 mm across 200 km of the Yellowstone River (Figure 1; Shuter et al. 1980). Consequently, cohort mortality was estimated to be slightly higher in upstream sections, but never approached 100% (Figure 7). Estimates of overwinter mortality in the Upper section varied widely across four years of available data (2016–2019), and ranged from a maximum cohort mortality of 50.3–81.9% in 2018, to a minimum of 0.2–11.2% in 2016 (Figure 8).

[A]Discussion

Understanding the interplay among environmental conditions, life history, and species range limits is crucial to the effective management of non-native fishes (Ricciardi and Rasmussen 1998; Lodge et al. 2006). Our multi-year study of non-native Smallmouth Bass in the Yellowstone River identified a wide spatial disconnect between the upstream extent of adults and that of successful reproduction, which we estimated to be within the Upper section based on age-0 capture data. Although age-0 growth was positively associated with cumulative exposure to warm temperatures, mean age-0 body size at the onset of winter did not vary across a 200-km study area spanning warmer, downstream strongholds and the cooler, age-0 upstream extent. Reproductive phenology determined the overall extent of the growing season (i.e., GDD), and was thereby critical determinant of growth that allowed early-hatching individuals in upstream habitat to reach satisfactory body sizes by the onset of winter. Furthermore, a weak longitudinal gradient in the duration of winter starvation resulted in a similarly weak gradient in estimated cohort mortality, which both simulations and field observations suggest failed to cause 100% starvation mortality at the age-0 upstream extent across four years of available data (2016–2019). Taken together, our results indicate that first-year growth and overwinter starvation do not appear to be preventing farther upstream establishment by this non-native population.

[B]Upstream extent: spatial disconnect between adults and juveniles.

The upstream extent of age-0 Smallmouth Bass in the Yellowstone River, which we estimated was located within the Upper section, lagged behind the uppermost observation of an adult (near Emigrant; Figure 1) by up to 150 river km. Similar spatial disconnects in

other populations were associated with upstream declines in temperature, where adults migrate to feed in upstream habitat that offers energetic benefits during the summer, but individuals do not successfully recruit there because the cold climates prevent first-year survival of offspring (Langhurst and Schoenike 1990; Lawrence et al. 2015; Rubenson et al. 2019). Other limitations to spawning habitat appear less probable, as ample gravel substrate and shallow, calm, clear water are abundant throughout upper reaches of the Yellowstone River (Orth and Newcomb 2002; Dalby and Robinson 2003; Holnbeck 2005). Alternatively, upstream establishment may instead be limited by low densities of adults near the range boundary. Reduced fitness at high population densities (i.e., density dependence) is a major driver of animal dispersal (Marchetti et al. 2004; Matthysen 2005), and Smallmouth Bass in the Yellowstone River may currently lack the density-driven competition needed to motivate colonization of even colder upstream areas. Furthermore, the inability to locate mates at low population densities, particularly in discrete, patchy reproductive habitat such as side channels, can delay establishment and limit the speed of ongoing invasions (Keitt et al. 2000; Taylor and Hastings 2005; Gregory et al. 2010). This may play a role in the Yellowstone River because side channels serve as critical reproductive habitat, and our eDNA sampling indicates that Smallmouth Bass of all size classes (let alone reproductive adults) are probably rare at and above the age-0 upstream extent (Tables S.1, S.2). Consequently, the absence of age-0 Smallmouth Bass from the uppermost distribution of adults does support the general hypothesis that something limits upstream recruitment, but the specific mechanisms remain unclear.

[B]Phenology, temperature, and first-year growth

The positive association between first-year GDD (i.e., degree days $> 10^{\circ}\text{C}$ experienced by age-0 individuals) and body size within every age-0 cohort we aged indicates that both the magnitude and duration of suitable temperatures following hatching are important drivers of first-year growth by Smallmouth Bass. This relationship affects Smallmouth Bass populations across a wide range of environments (Armour 1993), and is a causal mechanism in the northward range expansion of Smallmouth Bass in North America facilitated by climate change (Shuter and Post 1990; Sharma et al. 2007). The importance of the length of the growing season is particularly relevant to the Yellowstone River region as the duration of warm temperatures is expected to continue increasing (Al-Chokhachy et al. 2013; Sepulveda et al. 2015), suggesting greater potential for first-year growth and recruitment in the future (Shuter and Post 1990).

Surprisingly, mean body size at the onset of winter did not differ across our 200-km study area, despite positive intra-cohort associations between GDD and growth, and substantial spatial differences in ambient GDD (Figure S.4; Fry 1971). Similarities in mean size at the onset of winter across a broad gradient of main-stem temperatures suggest that additional biotic and abiotic controls on age-0 growth are present in the Yellowstone River.

Because cold water temperatures are known to delay or slow Smallmouth Bass spawning behavior, egg deposition, and incubation (Armour 1993), we predicted that age-0 cohorts in colder upstream sections would exhibit delayed hatch timing and reach smaller mean body sizes as a result. Instead, the onset of hatching exhibited no

longitudinal pattern and hatching ended earlier moving upstream, which allowed upstream cohorts to accumulate more GDDs and reach larger sizes on average than expected based on differences in ambient temperature. The importance of hatch timing to age-0 growth in black bass (*Micropterus* spp.) populations appears regionally variable, with some showing little to no variation in size with hatch date (e.g., Phillips et al. 1995; Sabo and Orth 1995; Phelps et al. 2008), whereas in others it is strongly associated with first-year growth (e.g., Miller and Storck 1984; Isely and Noble 1987; Bestgen and Hill 2016). Our GDD analysis suggests that the overlap of spawning with rising early-summer temperatures may determine the influence of phenology on growth (Sabo and Orth 1995). If temperatures remain low after hatching begins, the advantage of hatching early in sub-optimal conditions may, by the onset of winter, be inconsequential to first-year GDD and growth. In contrast, the earliest-hatching individuals in our study emerged as summer temperatures peaked, and attained larger sizes by rapidly gaining GDD during the narrow window of temperatures $> 20^{\circ}\text{C}$ that late hatchers had less exposure to (Figures 5, S.5; Bestgen and Hill 2016). As a result, early hatching and the absence of late-season hatching in colder upstream areas have thus far allowed age-0 cohorts reared therein to reach mean body sizes comparable to those reared in warmer downstream habitats. However, the earliest probable onset of successful reproduction depends on the timing of rapid early-summer snowmelt runoff, a phenomenon that this species did not evolve with that causes high turbidities and depresses water temperatures within our study area (Figures S.1, S.6; Winemiller and Taylor 1982, Orth and Newcomb 2002; Rubenson and Olden 2016). Although early hatching in upstream areas can lead to favorable growth and

size at the onset of winter, the extent to which it can offset the effects of cold climates even farther upstream remains unclear.

[B]Overwinter mortality

The synchrony of frontal weather patterns across our study area in late autumn and early spring (Figure S.6) produced a weak longitudinal gradient in the minimum size needed for overwinter survival (e.g., L_0 differed by only 2.1–4.5 mm across 200 rkm). This gradient, combined with broad-scale similarities in age-0 body size across sections, resulted in our simulations predicting a similarly weak gradient in starvation mortality. Estimates of substantial size-selective mortality in all sections (e.g., never less than 31.9% in 2018 or 2019; Figure 7) suggest that age-0 growth and factors affecting it are important determinants of Smallmouth Bass recruitment success in much of the Yellowstone River, particularly as the duration of winter starvation varied so little across our 200-km study area. Furthermore, post-hoc simulations showed that cohorts observed at the age-0 upstream extent (i.e., the Upper section) in 2018 would not have experienced recruitment failure even if placed 185 rkm farther upstream (i.e., at Corwin Springs, Montana, USGS gage 06191500; Figures 1, S.7). These results suggest that age-0 growth scope is probably a more important determinant of upstream habitat suitability and recruitment success than upstream increases in the duration of starvation conditions, which exhibited comparatively little variation across our 200-km study area.

The fact that even liberal estimates of cohort mortality at the age-0 upstream extent never exceeded 82% in four consecutive years (2016–2019) suggests that age-0 overwinter mortality due to starvation is not currently preventing recruitment above the

current range boundary in the Yellowstone River. Range boundaries constrained by environmental conditions are characterized by intermittent reproductive success and frequent year-class failures (Holt et al. 2005; Sexton et al. 2009; Kubisch et al. 2010). In contrast, successful reproduction in the Upper section occurred in four consecutive years, estimates of starvation mortality over the coldest of those years ranged from only 50.3–81.9% percent, and starvation mortality in the Upper section was probably negligible in 2016 (i.e., 0.2–11.2%; Figure 8). Post-hoc simulations also demonstrated that the weak longitudinal gradient in L_0 extends at least to Corwin Springs (i.e., 185 rkm above the Upper section), and ambient GDD measured at Corwin Springs suggests that early hatching individuals spawned there may be able to reach body sizes needed to survive the winter (i.e., exceed L_0 ; Figures 1, 5, S.4, S.7). Probable recruitment at the upstream range boundary across four consecutive years, combined with weak gradients in L_0 and sufficient GDD above the range boundary, suggest that this population has not yet expanded to its thermal limit in the Yellowstone River Basin.

[B]Study limitations

Logistical and public-use considerations constrained our sampling frame in the Yellowstone River to side channels; consequently, our scope of inference outside of this high-quality nursery habitat is limited. Movement of larger age-0 individuals than we observed into deep main-stem habitat is unknown, but could have biased the size distributions we observed in side channels and led us to over-estimate cohort mortality, as well as the barrier imposed by overwinter starvation on upstream recruitment. However, many of our side channels contained deep pools and overwintering habitat (i.e., large

rocky substrate; Orth and Newcomb 2002), and consistent differences in maximum size among sections suggest that some large individuals remain in side channels through their first winter. Large, fast-swimming individuals could also have evaded our electrofishing surveys. However, any undetected presence of larger age-0 individuals than we observed would further reinforce evidence that size-selective age-0 overwinter mortality is not preventing recruitment beyond their current upstream extent.

We also acknowledge that the temperature data in our analyses imperfectly approximated the thermal conditions that each age-0 Smallmouth Bass may have experienced. Off-channel habitats can provide areas of high thermal heterogeneity (Arscott et al. 2001; Baldock et al. 2016), and juvenile and small-bodied fishes can diurnally migrate into warm-water refugia to increase growth (e.g., Neverman and Wurtsbaugh 1994; Ward et al. 2010; Armstrong et al. 2013). Such movements, although not known to occur in Smallmouth Bass, could have allowed greater growth than expected from main-stem temperatures if habitable warm-water refugia were present. Logistical challenges limited our understanding of thermal variation in these habitats, but our capture results from passive fyke nets do suggest some diel movement by age-0 Smallmouth Bass within individual side channels.

Lastly, we recognize that the coarse scale of our distribution surveys (i.e., 16-km spacing between sections) may not have allowed us to identify the exact uppermost point that any age-0 individual hatched in a given year, and that conditions there could have more severely affected age-0 growth and survival than in the Upper section. Although some age-0 individuals could have been present above the Upper section, we find it

unlikely that age-0 growth, overwintering conditions, or overwinter mortality would be substantially different < 16 rkm upstream because each of these exhibited very shallow or no longitudinal gradient across a much broader spatial extent (i.e., 200 rkm).

Furthermore, finer-resolution “extent-confirmation” sampling suggested that in 2016 and 2018, the upstream extent was accurate to within 8 rkm. We recognize the inherent limitations of coarse-scale surveys, but argue that given our findings, the resolution of our distribution surveys had little influence on our results.

[B] Implications for upstream range expansion

Despite upstream declines in temperature and positive linear associations between antecedent thermal history and age-0 size by the onset of winter, first-year growth and overwinter starvation appear unlikely to prevent Smallmouth Bass recruitment beyond the current age-0 upstream extent in the Yellowstone River (i.e., the Upper section). Mean body size and simulated cohort mortality in the Upper section were comparable to that of conspecifics in downstream sections where Smallmouth Bass are abundant, in contrast with population characteristics at similar range boundaries where age-0 growth rapidly declines, and overwinter mortality rapidly increases, approaching the upstream extent of the species (Lawrence et al. 2015; Rubenson and Olden 2019). Furthermore, the high variability in hatch dates and body sizes observed even in the Upper section, combined with weak longitudinal gradients in L_0 , suggests that early-spawning adults could continue to ensure favorable age-0 growth and recruitment success farther upstream. This may be particularly true where geothermally-heated groundwater increases water temperatures upstream of Emigrant (Figure 1; Taylor and Hinds 1976).

Taken together, our results cast doubt on the importance of age-0 overwinter starvation in directly preventing upstream recruitment by non-native Smallmouth Bass in the Yellowstone River.

Even if habitat beyond the current age-0 upstream extent is warm enough to allow successful recruitment, anomalously warm growing seasons could still facilitate farther and more rapid upstream establishment by increasing overwinter survival, adult abundances, and density-dependent dispersal (Neubert and Caswell 2000; Diez et al. 2012). Remarkably high survival among a single year-class (which probably occurred in 2016 following a very warm early summer; Figures 8; <https://waterdata.usgs.gov/mt/nwis/rt>) can cause pronounced increases in adult Smallmouth Bass density (Armour 1993). Consequently, warm years that minimize overwinter starvation may lead to more upstream dispersal due to overcrowding. Furthermore, because early spawning in the Yellowstone River is particularly beneficial to age-0 survival, and because historic trends towards warmer springs and earlier peak runoffs are expected to continue (Sepulveda et al. 2015; Al-Chokhachy et al. 2017), climate warming may thereby accelerate upstream establishment even if those upstream areas are already habitable.

Although range size is a critical determinant of non-native impact (Parker 1999), the nature of Smallmouth Bass impact in the Yellowstone River depends on how they interact with other aquatic organisms. Smallmouth Bass are capable of preying on and competing with a wide variety of aquatic organisms (Brown et al. 2009; Loppnow et al. 2013), making the specific effects of these opportunistic predators on host ecosystems

unclear. Because farther upstream establishment may even occur under the current climate regime, future research efforts should focus on Smallmouth Bass predation and competition with other species before future range expansion further amplifies their impact in the ecologically distinct Yellowstone River Basin.

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[A]Tables

TABLE 1. Summary of the final linear mixed-effects models used to evaluate age-0 Smallmouth Bass length (mm) at the onset of winter (Length), relative condition (Condition), hatch date (HD), and first-year growing degree days (GDD) using multiple years of data (Years) collected at three sampling sections (Sections) in the Yellowstone River. Final models included the fixed- and random-effects terms listed below.

Model	Response	Years	Sections ^a	Fixed effects	Random effects ^b	R^2_m ^c	R^2_c ^d	F	P
1	Length	2018,2019	U,M,L	Section	SC+Yr	<0.01	0.23	0.10	0.91
2	Condition	2018,2019	U,M,L	Section	SC	0.01	0.03	0.91	0.44
3	HD	2018	U,M,L	Section	SC	0.12	0.35	1.88	0.23
4	Length	2018	U,M,L	GDD	Sec/SC	0.56	0.77	157.87	<0.01
5	Length	2016–2019	U	Year	SC	0.47	0.62	13.34	<0.01

^aSections: “U” is the Upper, “M” is the Middle, and “L” is the Lower sampling section.

^bRandom Effects: “SC” is side channel, “Yr” is year, “Sec” is section “+” denotes additional uncorrelated intercept terms, and “/” denotes nested random intercepts.

^c R^2_m denotes marginal R^2 , a measure of variance explained by all fixed effect terms.

^d R^2_c denotes conditional R^2 , a measure of variance explained by fixed and random effects terms.

TABLE 2. Summary of the post-hoc multiple comparisons test conducted on Model 5 (Table 1), which tested for pairwise differences in the mean total length (mm) of age-0 Smallmouth Bass at the onset of winter in the Upper sampling section in the Yellowstone River (2016–2019). We reported the raw differences in means, as well as standard errors (SE), Z-score (*Z*), and associated *P*-values (*P*) for each comparison.

Response	Fixed-effect term	Linear hypothesis:	Difference in means	SE	<i>Z</i>	<i>P</i>
Length	Year	2016 = 2017	-21.64	5.02	-4.31	< 0.001
Length	Year	2016 = 2018	-27.77	5.19	-5.36	<0.001
Length	Year	2016 = 2019	-25.30	5.52	-4.59	<0.001
Length	Year	2017 = 2018	-6.13	4.32	-1.42	0.468
Length	Year	2017 = 2019	-3.66	4.72	-0.78	0.876
Length	Year	2018 = 2019	2.47	4.89	0.51	0.876

TABLE 3. Summary of 2018 otolith-estimated age-0 Smallmouth Bass hatch dates by sampling section in the Yellowstone River, including sample size (*n*), the onset of the age-0 hatch (Start), median (Median) and mean hatch date (Mean), the end of the hatch (End), the duration of the hatch in days (Range), and standard deviation (SD) in days.

Year	Section	<i>n</i>	Start	Median	Mean	End	Range (days)	SD
2018	Upper	30	19-Jul	28-Jul	28-Jul	5-Aug	17	4.4
	Middle	30	13-Jul	1-Aug	30-Jul	13-Aug	31	7.1
	Lower	30	23-Jul	3-Aug	4-Aug	16-Aug	24	7.6

[A]Figures

FIGURE 1. Map of the study area on the Yellowstone River. We sampled “extent-confirmation” sections immediately upstream of the uppermost age-0 detection a single time in 2016 and 2018. USGS stream gages that monitor Yellowstone River water temperatures in Montana include USGS 06191500 at Corwin Springs (operating continuously), USGS 06192500 near Livingston (operating April–September), USGS 06195950 at Big Timber (operating July–September), and USGS 06214500 at Billings (operating continuously since October 2018).

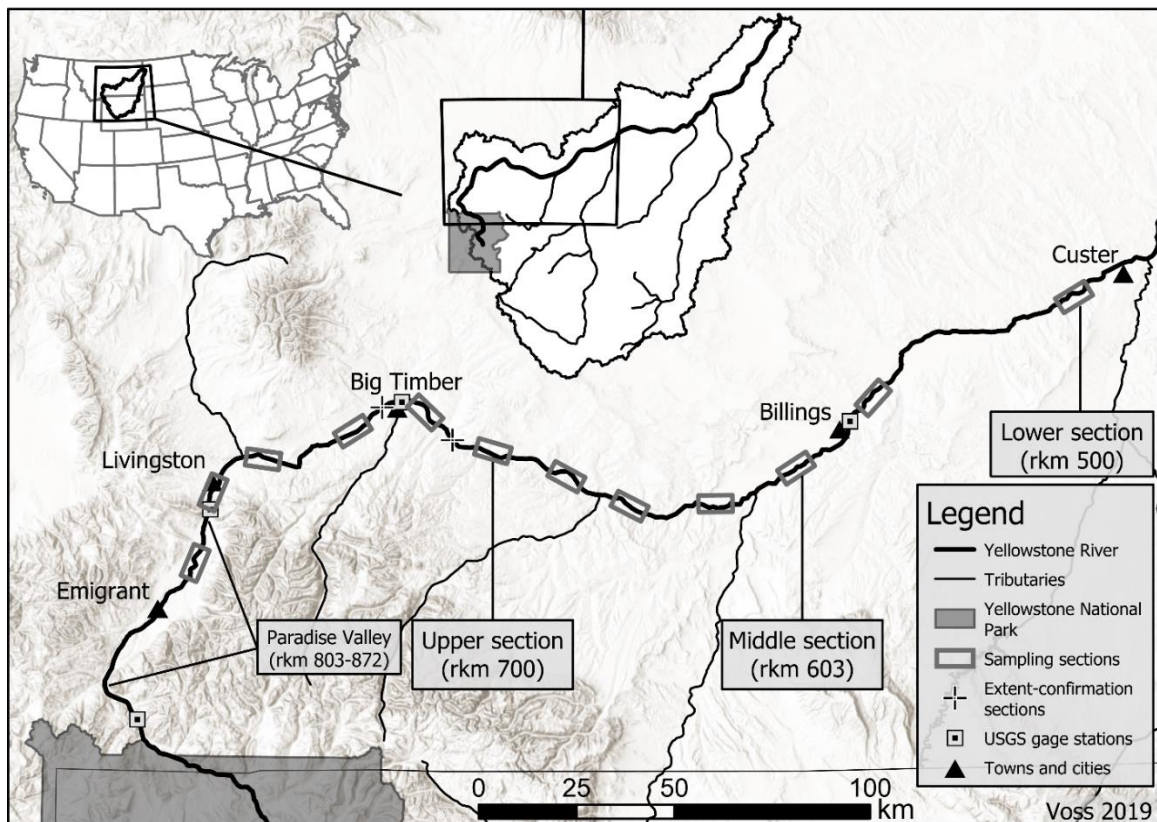


FIGURE 2. Section-level age-0 Smallmouth Bass detections from annual distribution (i.e., fyke net) surveys of Yellowstone River side channel habitat as a function of distance upstream from the Missouri River confluence (2016–2019; $n = 31$ observations). Point size represents the number of surveys (i.e., observations; # obs.) where age-0 individuals were present (1) or were not detected (0) in a section. The solid line shows the modeled probability of age-0 presence, with grey shading showing areas of predicted presence (age-0 upstream extent predicted at rkm 702). The dashed line connects mean August 2018 main-stem water temperatures at seven monitoring sites within our study area.

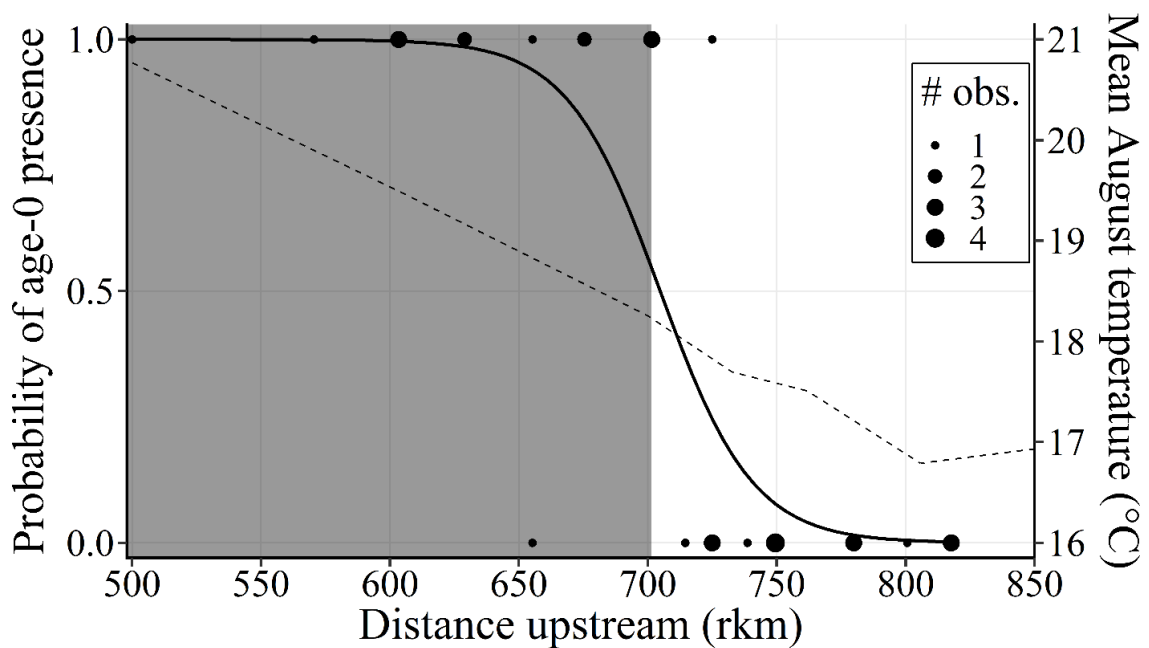


FIGURE 3. Total length (A, B) and relative condition (Pope 2007; C, D) of age-0 Smallmouth Bass captured at the onset of winter in side channels within the Upper, Middle, and Lower sampling sections in the Yellowstone River in 2018 ($n = 116, 69,$ and 139) and 2019 ($n = 30, 24,$ and 68). Boxes are drawn using the 25th, 50th, and 75th percentiles, diamonds are mean values, whiskers extend to the highest and lowest values within 1.5 times the interquartile range, and open circles are outliers.

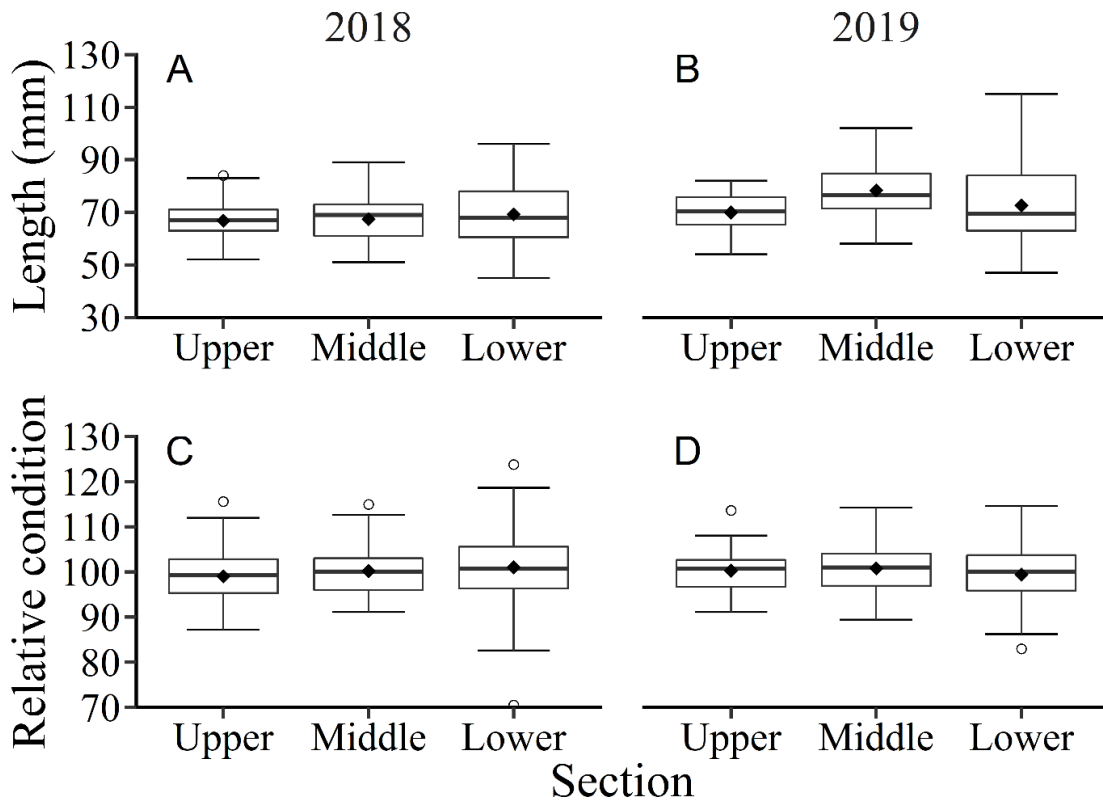


FIGURE 4. Frequency of otolith-estimated hatch dates (A), and first-year growing degree days (GDD) by hatch date (B) for 30 age-0 Smallmouth Bass captured at the onset of winter (2018) in each of the Upper, Middle, and Lower sampling sections in the Yellowstone River. Hatch date frequencies are plotted with a four-day bin width for the same individuals depicted in (B).

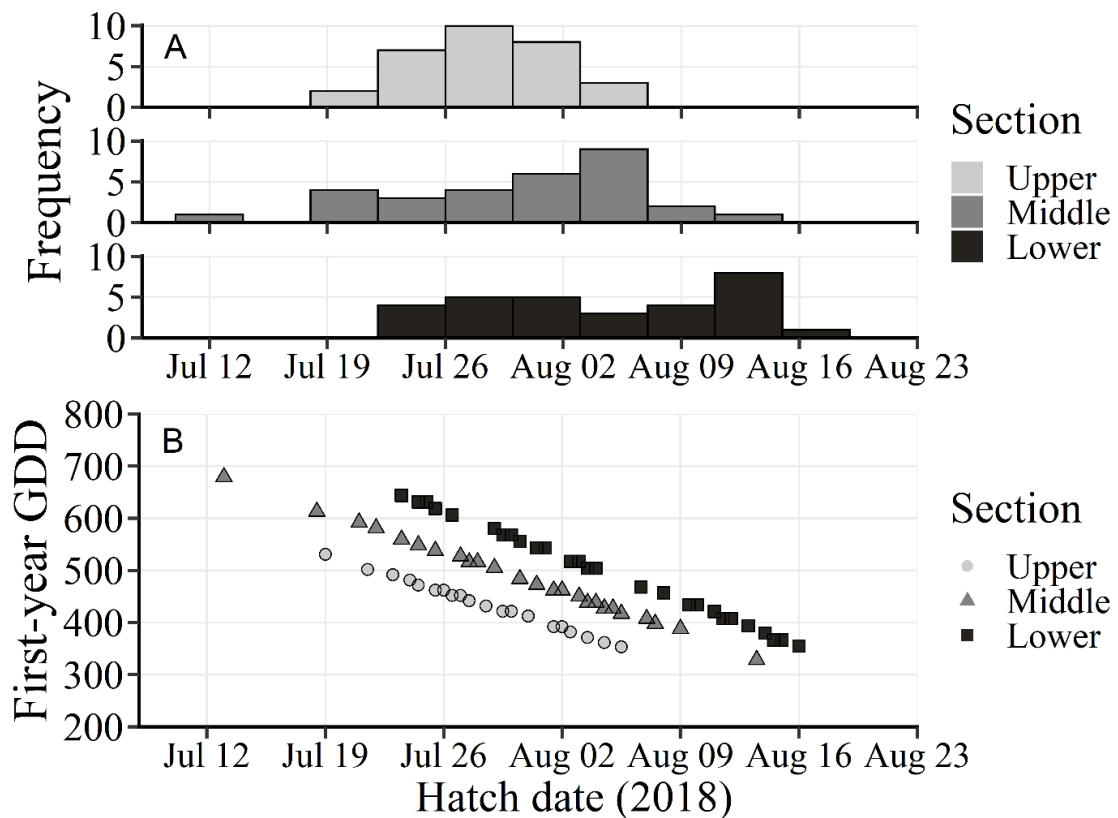


FIGURE 5. Total length of age-0 Smallmouth Bass in the Yellowstone River at the onset of winter versus first-year growing degree days (GDD) estimated in the Upper, Middle, and Lower sampling sections in 2018 ($n = 30$ each), Linear regressions for the Upper (dotted line), Middle (dashed line), and Lower (solid line) sections were estimated by the mixed-effects “equal-slopes” Model 4 (Table 1).

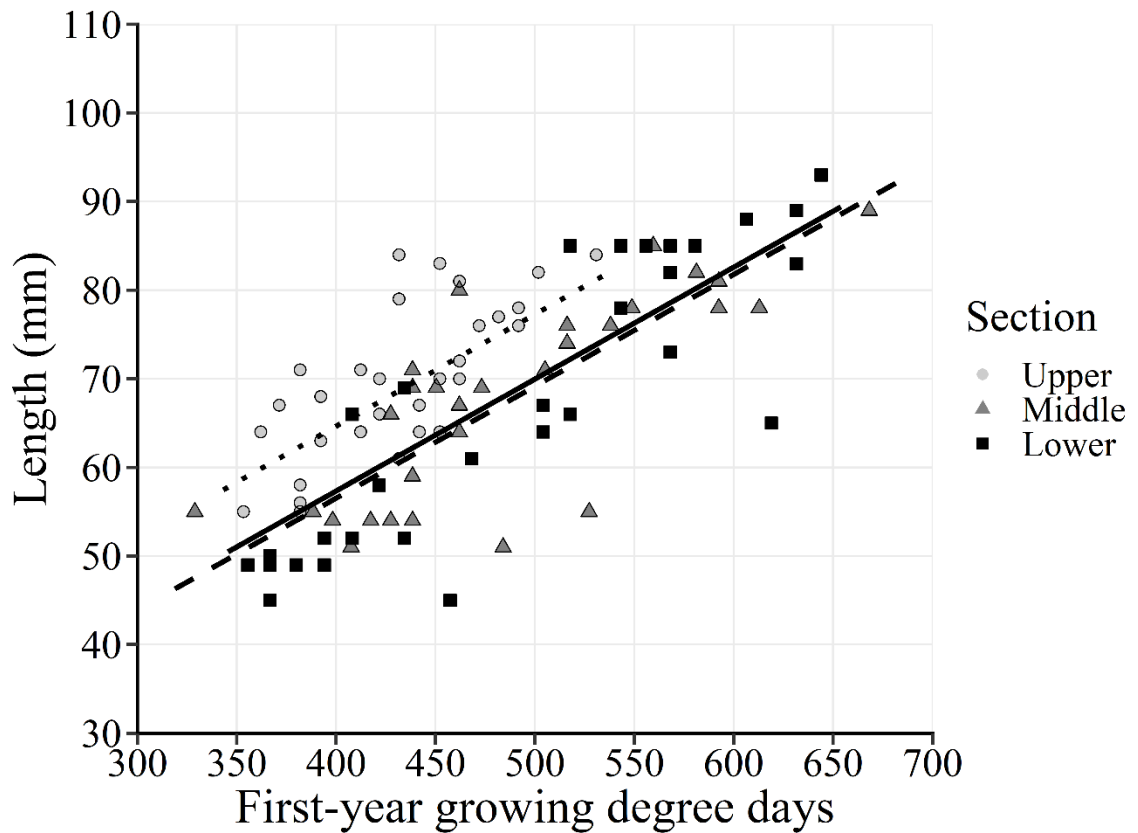


FIGURE 6. Cumulative frequency distributions of the total lengths of age-0 Smallmouth Bass in the Yellowstone River measured at the onset of winter (late autumn 2018) and early the following spring (2019). Sample sizes for fall and spring sampling were 119 and 1 in the Upper sampling section, 69 and 12 in the Middle section, and 139 and 16 in the Lower section. Asterisks indicate significant shifts toward longer total lengths. Vertical dashed lines represent the late-autumn body length below which overwinter mortality is estimated to be 100% given a winter duration of days $< 7^{\circ}\text{C}$ (grey), and days $< 10^{\circ}\text{C}$ (black).

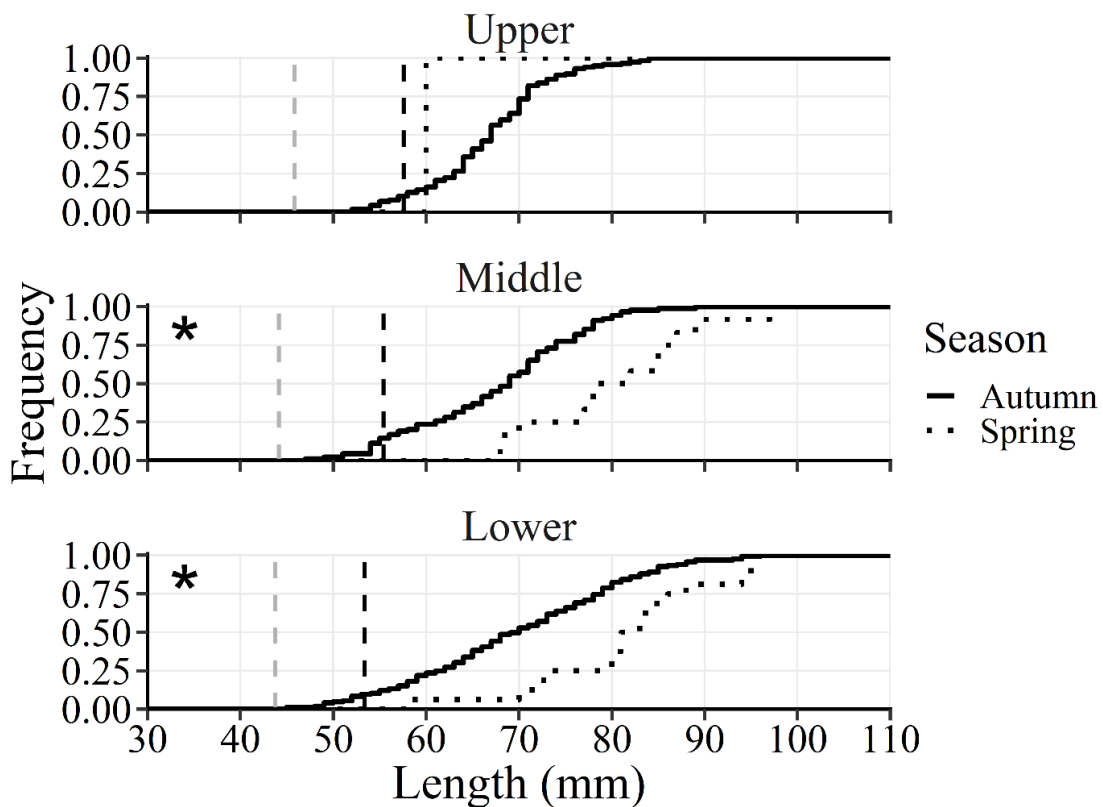


FIGURE 7. Normalized histograms depicting the probability of overwinter mortality due to starvation estimated for each age-0 Smallmouth Bass measured at the onset of winter in the Upper ($n = 119$), Middle ($n = 69$), and Lower ($n = 139$) sampling sections in the Yellowstone River in 2018 ($n = 119, 69,$ and 139) and 2019 ($n = 30, 24,$ and 68). Grey bars show individual mortality probabilities based on a winter duration of days $< 7^{\circ}\text{C}$, black bars show estimates based on days $< 10^{\circ}\text{C}$, and corresponding dashed lines show the mean percent cohort-level mortality of 100,000 simulated outcomes.

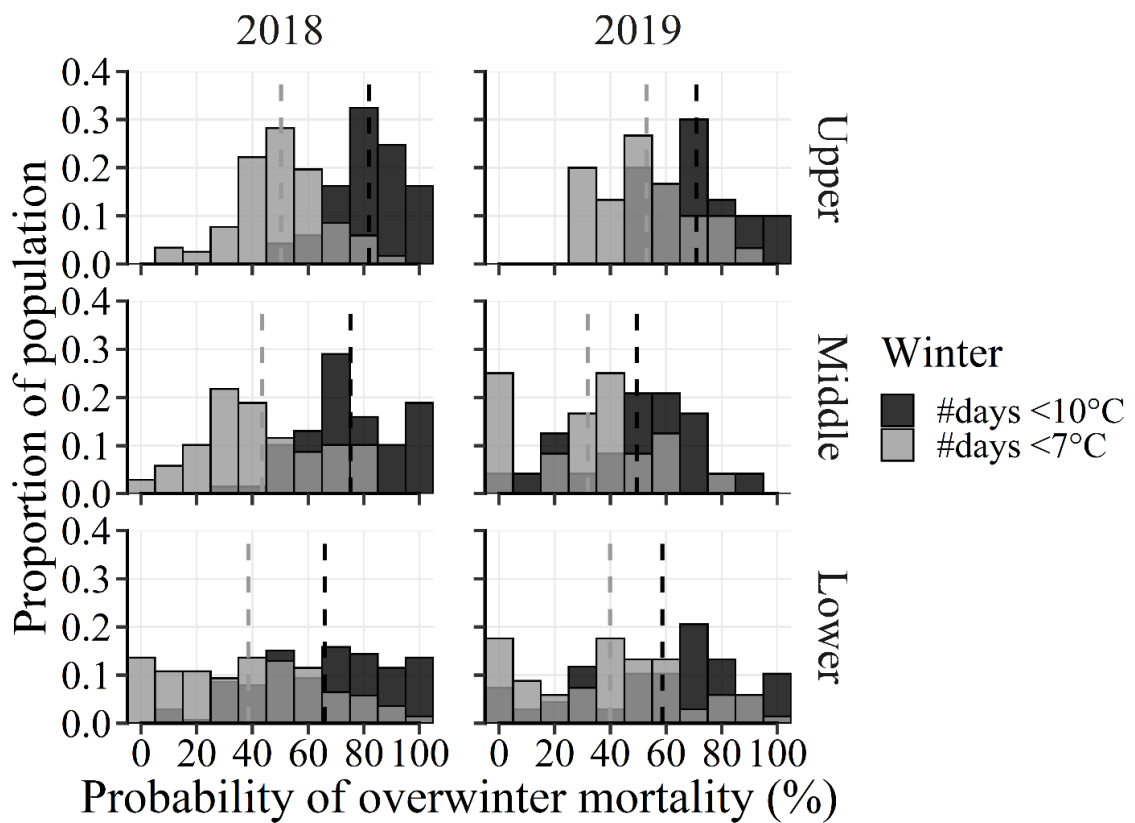
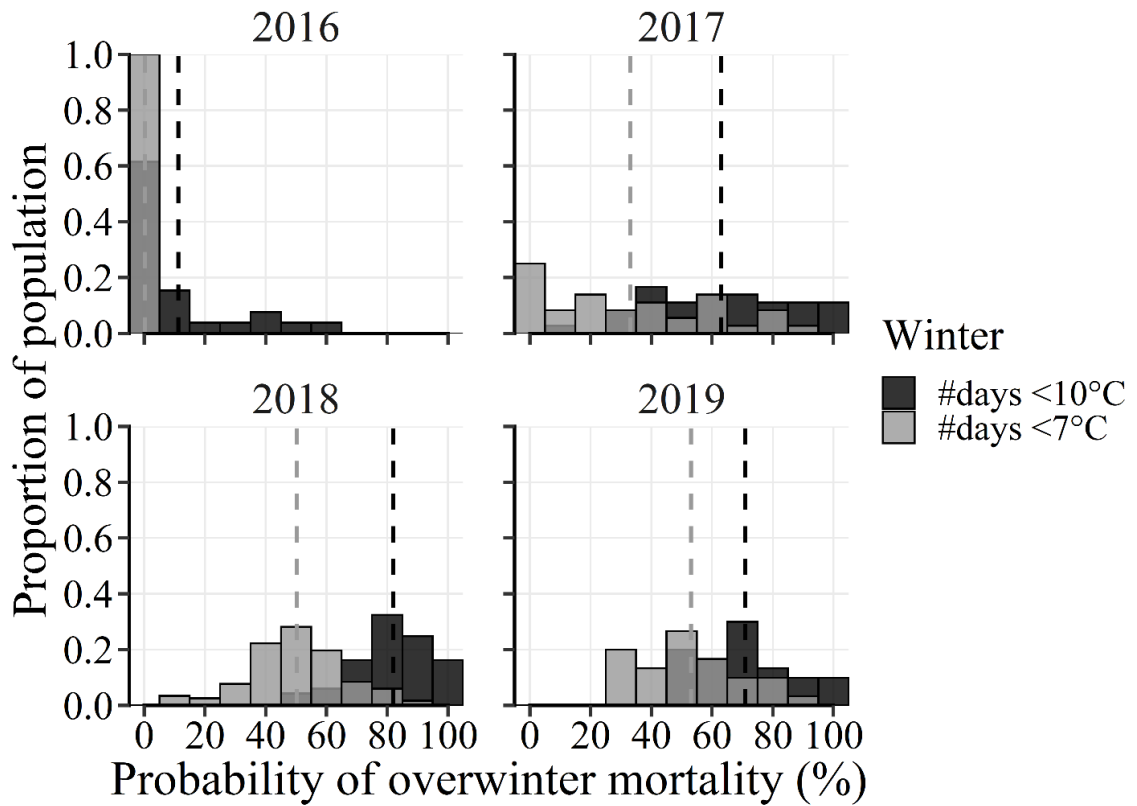


FIGURE 8. Normalized histograms depicting the probability of overwinter mortality due to starvation for each age-0 Smallmouth Bass measured at the onset of winter in the Upper sampling section in the Yellowstone River in 2016 ($n = 26$), 2017 ($n = 36$), 2018 ($n = 119$), and 2019 ($n = 30$). Grey bars show individual mortality probabilities based on a winter duration of days $< 7^{\circ}\text{C}$, black bars show estimates based on days $< 10^{\circ}\text{C}$, and corresponding dashed lines show the mean percent cohort-level mortality of 100,000 simulated outcomes.



[A]Supplementary materials

[B]Supplementary methods

[C]*Stream temperature estimation.*— We estimated July 2018 temperatures in the main stem of the Upper, Middle, and Lower sections by multiplying July 2018 temperatures measured at Big Timber, Montana (USGS gage 06195950; Figure 1) by the average percent difference in daily mean water temperatures measured at Big Timber and each section in July 2019, which experienced discharges and temperatures that were very similar to the year before (Figures S.1, S.4). The root-mean-squared errors (hereafter RMSE) of predicted minus observed July 2019 temperatures at the Upper, Middle, and Lower sections were 0.18, 0.32, and 0.62°C, and a mean daily difference < 0.003°C in all sections suggests little systematic bias.

Empirical measurements of Upper section water temperatures were not available in 2016 or the spring of 2018, but were needed to estimate overwinter mortality in these years (Shuter et al. 1980). We filled gaps in our Upper section dataset using a predictive stream temperature model. Stream and air temperatures are correlated by heat-transfer processes (Mohseni and Stefan 1999), and readily-available air temperature data are frequently used by aquatic biologists to estimate water temperatures (e.g., Al-Chokhachy et al. 2013). We obtained air temperatures from a National Oceanic and Atmospheric Association weather station located in the valley bottom about 28 km downstream of the Upper section (www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00241938). Correlations between stream and air temperature are mediated by stream depth, surface area, and velocity, all of which

vary with discharge (Stefan and Preud'homme 1993; Mohseni and Stefan 1999; Webb et al. 2003). Because seasonal fluctuations in Yellowstone River discharge regularly exceed an order of magnitude (Figure S.1), we included daily mean discharges measured near Livingston, Montana (USGS gage 06192500; Figure 1) as an additional correlate in our temperature model (van Vliet et al. 2011).

We used a non-linear regression model to predict stream temperatures from air temperature and discharge data. Non-linear models can accurately capture non-linear relationships between stream and air temperature that occur at warm (i.e., $>20\text{ }^{\circ}\text{C}$), cold (i.e., $<0\text{ }^{\circ}\text{C}$), or geothermally-influenced water temperatures (Mohseni et al. 1998; Mohseni and Stefan 1999), and can further incorporate stream discharge as an interaction (van Vliet et al. 2011; Piotrowski and Napiorkowski 2019). We fit the van Vliet et al. (2011) non-linear regression model for temperature and discharge data using non-linear least squares regression (R version 3.6.2).

Estimations of age-0 overwinter mortality require daily temperature data (Shuter et al. 1993), however autocorrelation of stream temperatures at this resolution can potentially violate the assumption of non-independence in least-squares regression. We addressed this issue in three ways. First, we fit our model to weekly mean temperatures and discharges, which are less autocorrelated and provide superior model fit relative to daily values (Mohseni and Stefan 1999). Second, we fit separate logistic curves to the rising and falling limbs of the thermograph (i.e., before and after air temperatures peak), which reduces directional autocorrelation caused by broad-scale shifts in temperature (Mohseni et al. 1998). Third, we converted water temperature estimates to seven-day moving

averages, which smooths unrealistically rapid changes in daily estimates, adds a degree of temporal autocorrelation that may reflect real-world conditions (Stefan and Preud'homme 1993), and has a negligible effect on survival estimates for age-0 Smallmouth Bass (Lawrence et al. 2015). These measures reduce, but do not eliminate, autocorrelation in our temperature data. The resulting non-linear regression model had an R^2 of 0.955, and a visual inspection of residuals only suggested bias at temperatures below 2°C , which is unlikely to affect estimates of overwinter mortality based on the duration of temperatures below $7\text{-}10^{\circ}\text{C}$ (Suter et al. 1980; Rubenson and Olden 2019).

[B]Supplementary references

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[B]Supplementary tables

TABLE S.1. Negative (0) detections of Smallmouth Bass environmental DNA (eDNA) and presence based on simultaneous fyke-net surveys (Fyke detection) within five systematically-spaced sampling sections in the Yellowstone River (denoted by rkm upstream from the Missouri River confluence). Sampling began above the uppermost site where an age-0 individual was captured in 2018, and proceeded upstream. We filtered two 5-L water samples from each of three reaches (Reach) within each section, where one sample was drawn from the downstream mouth of a side channel (SC), and the other from adjacent main-stem (Main) habitat.

rkm	Reach	Habitat	eDNA detection	Fyke detection
725	1	Main	0	NA
		SC	0	0
	2	Main	0	NA
		SC	0	0
	3	Main	0	NA
		SC	0	0
749	1	Main	0	NA
		SC	0	0
	2	Main	0	NA
		SC	0	0
	3	Main	0	NA
		SC	0	0
780	1	Main	0	NA
		SC	0	0
	2	Main	0	NA
		SC	0	0
	3	Main	0	NA
		SC	0	0
801	1	Main	0	NA
		SC	0	0
	2	Main	0	NA
		SC	0	0

65

	3	Main	0	NA
		SC	0	0
818	1	Main	0	NA
		SC	0	0
	2	Main	0	NA
		SC	0	0
	3	Main	0	NA
		SC	0	0

TABLE S.2. Positive (1) and negative (0) detections of Smallmouth Bass environmental DNA (eDNA) and presence based on simultaneous electrofishing surveys (Electrofishing detection) in the Lower, Middle, and Upper sampling sections in the Yellowstone River. We filtered two 5-L water samples from each of three reaches (Reach) within each section, where one sample was drawn from the downstream mouth of a side channel (SC), and the other from adjacent main-stem (Main) habitat.

Section	Reach	Habitat	eDNA detection	Electrofishing detection
Lower	1	Main	1	NA
		SC	1	1
	2	Main	1	NA
		SC	1	1
	3	Main	1	NA
		SC	1	1
Middle	1	Main	1	NA
		SC	1	1
	2	Main	1	NA
		SC	1	1
	3	Main	1	NA
		SC	1	1
Upper	1	Main	0	NA
		SC	1	1
	2	Main	1	NA
		SC	1	1
	3	Main	0	NA
		SC	1	1

[B]Supplementary figures

FIGURE S.1. Mean daily discharge (m^3/s) in the Yellowstone River measured by USGS gage 06214500 at Billings, Montana (Figure 1) in 2016, 2017, 2018, and 2019, and contrasted with the 10-year average daily (10yr avg), and 10-year average annual maximum (solid diamond).

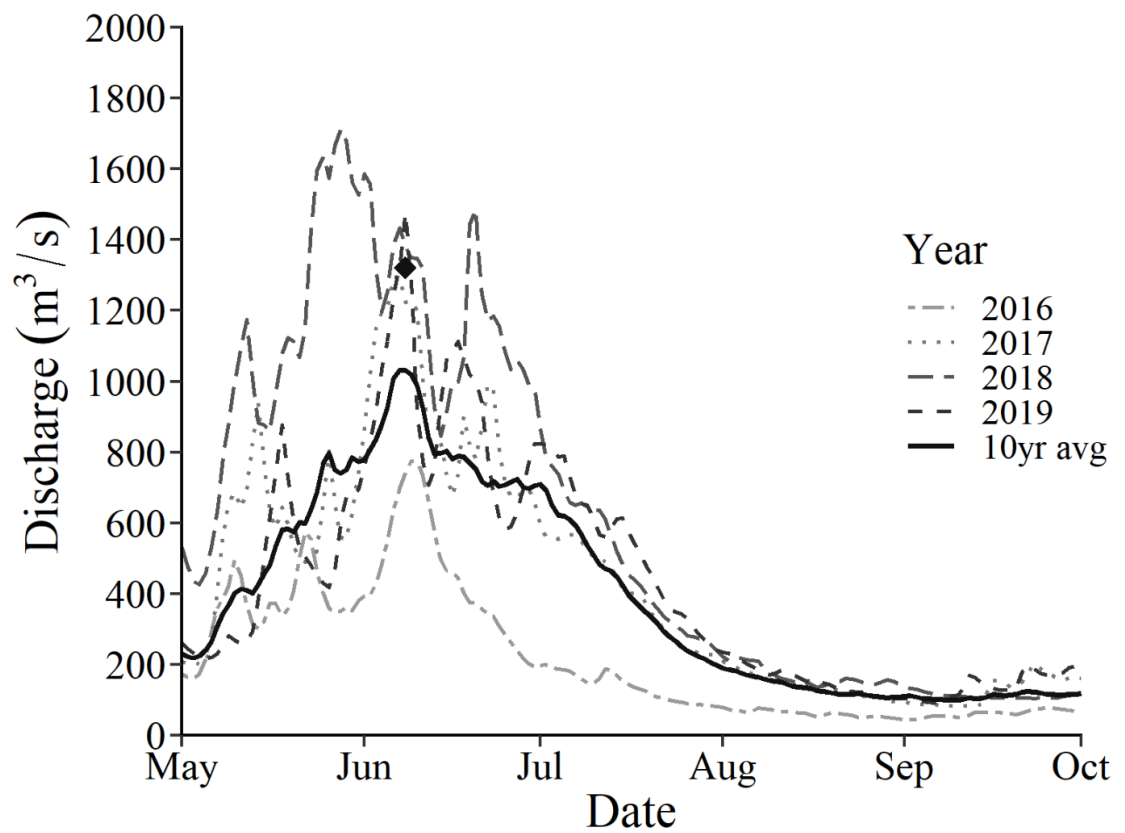


FIGURE S.2. Growing degree days (i.e., cumulative degree days $>10^{\circ}\text{C}$) calculated between July 6 (approximating the earliest onset of spawning in 2018; Figure 4B; Shuter et al. 1980), and September 30 (2016–2019), and contrasted with the 10-year average (10yr avg), at USGS gage 06192500 on the Yellowstone River near Livingston, Montana (Figure 1).

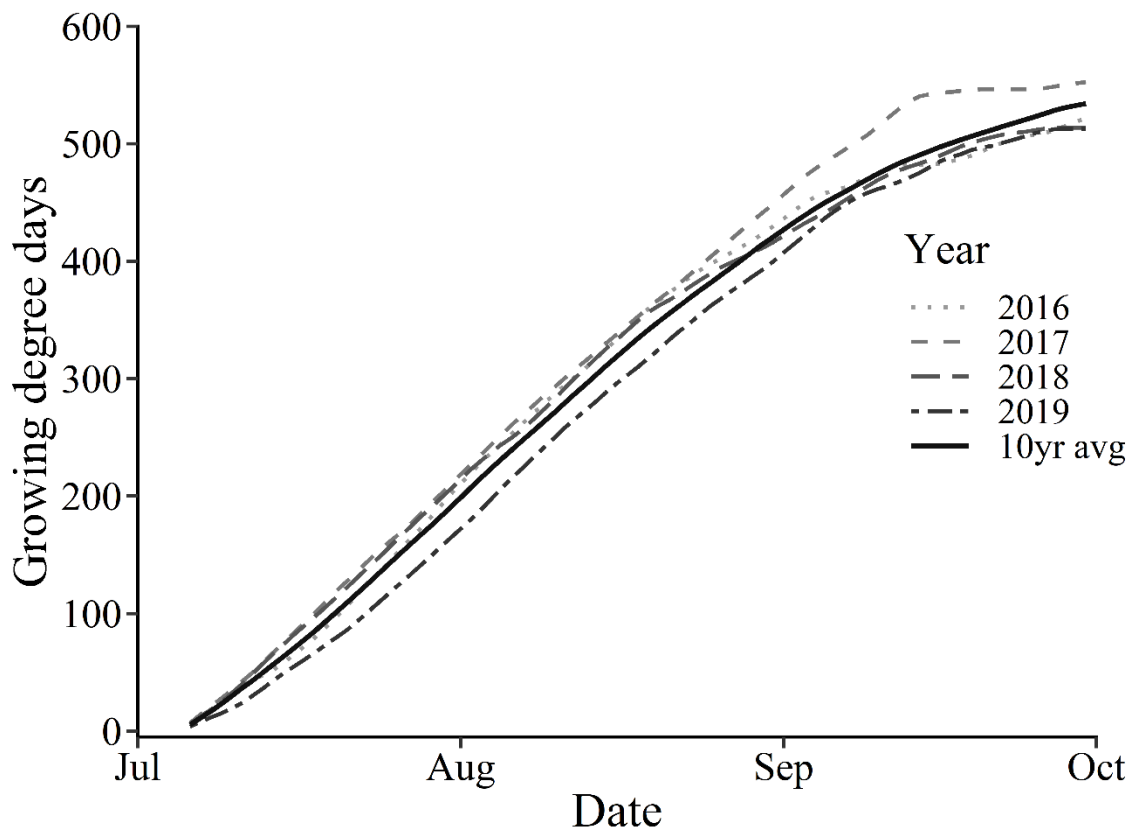


FIGURE S.3. Age-bias plot depicting the mean ring count of a series of three reads made on a single otolith from each of 10 age-0 Smallmouth Bass collected from the Yellowstone River (closed circles), with whiskers extending to the 95% confidence intervals around each estimate. The solid line represents a 1:1 relationship, and the dashed line represents a simple linear regression of the two sets of ring count estimates.

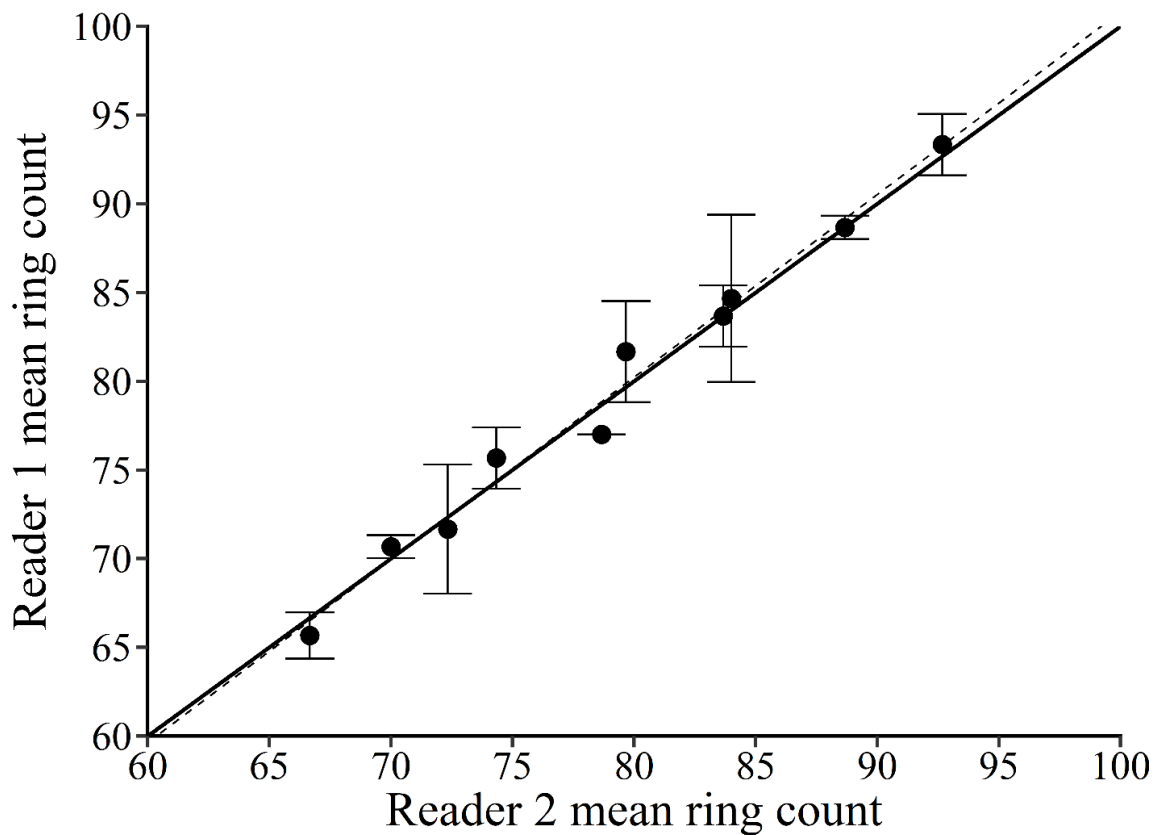


FIGURE S.4. Growing degree days (i.e., cumulative degree days $>10^{\circ}\text{C}$) calculated between July 6 (approximating the earliest onset of spawning in 2018; Figure 4B; Shuter et al. 1980), and September 30, in the Lower, Middle, and Upper Yellowstone River sampling sections and at USGS gage 06191500 near Corwin Springs, Montana, in 2018 and 2019.

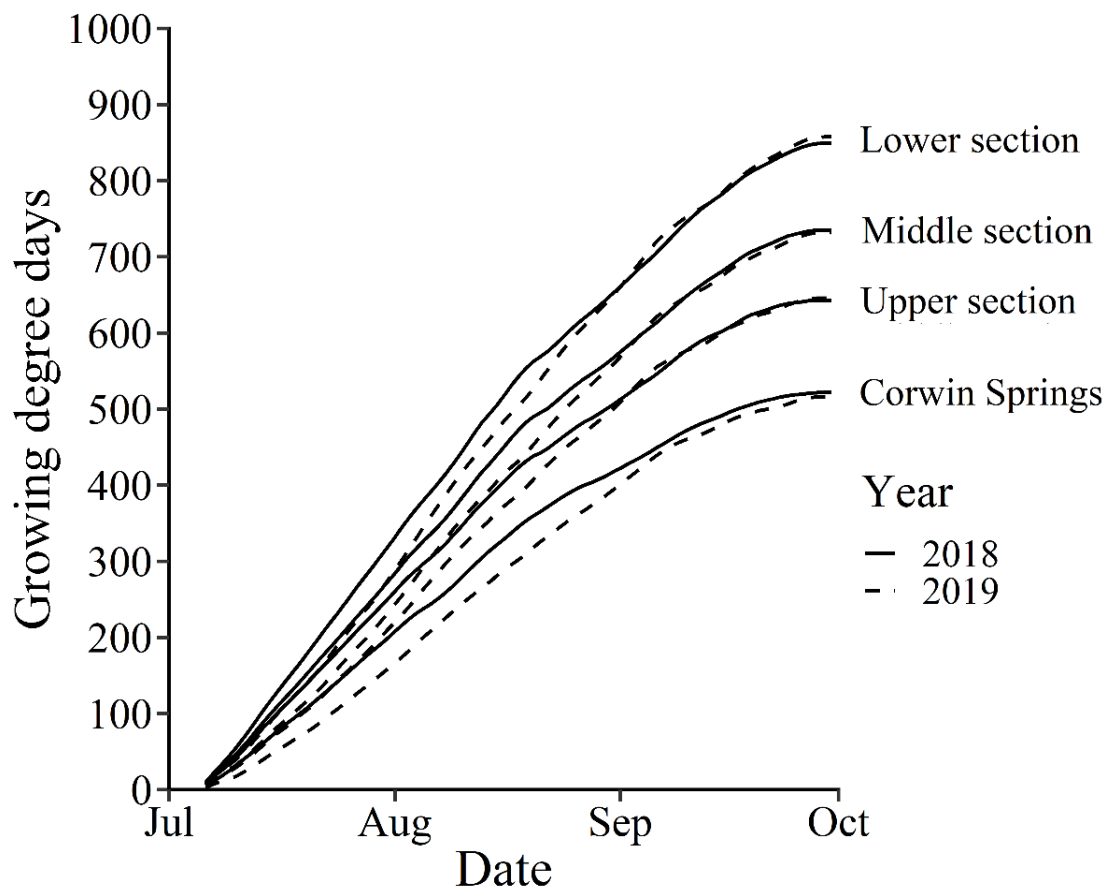


FIGURE S.5. Daily mean water temperatures in the Yellowstone River measured between July 1, and September 30, in the Upper, Middle, and Lower sampling sections in 2018 and 2019.

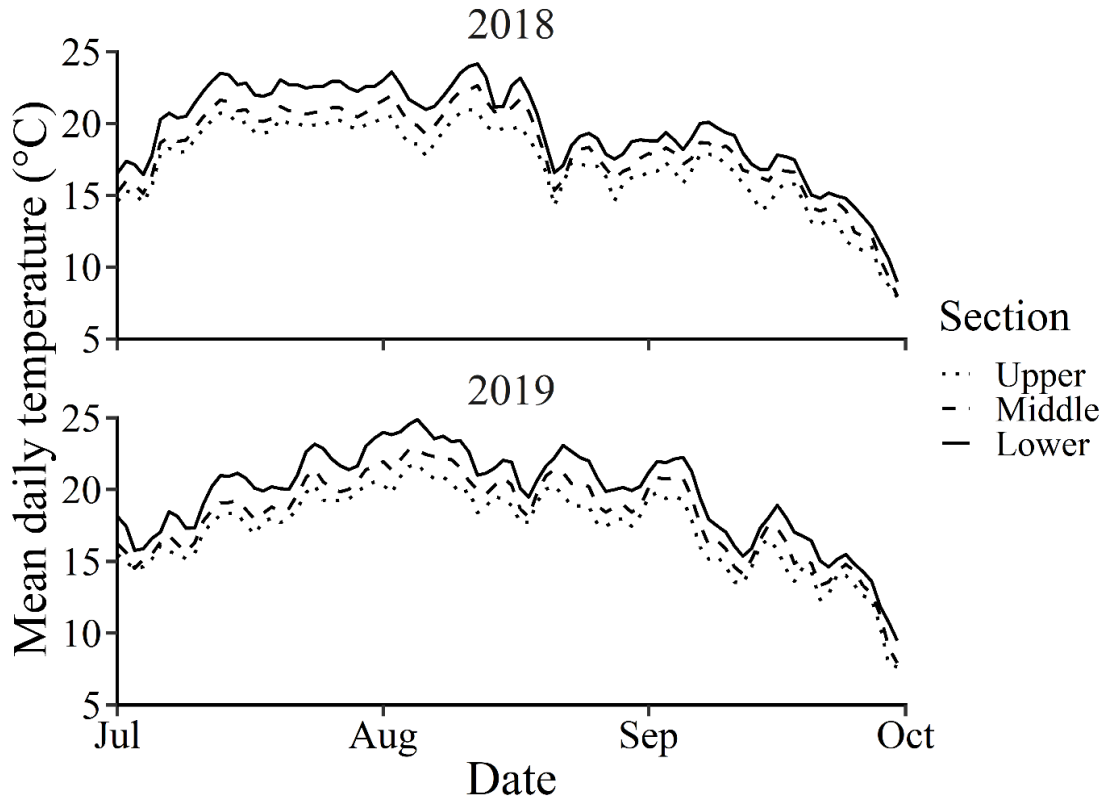


FIGURE S.6. Daily mean water temperatures measured between the autumn of 2018 and the early summer of 2019 in the Upper, Middle, and Lower sampling sections in the Yellowstone River. The horizontal dashed lines represent two proposed water temperatures below which feeding by age-0 Smallmouth Bass does not occur (Shuter et al. 1980; Rubenson and Olden 2019).

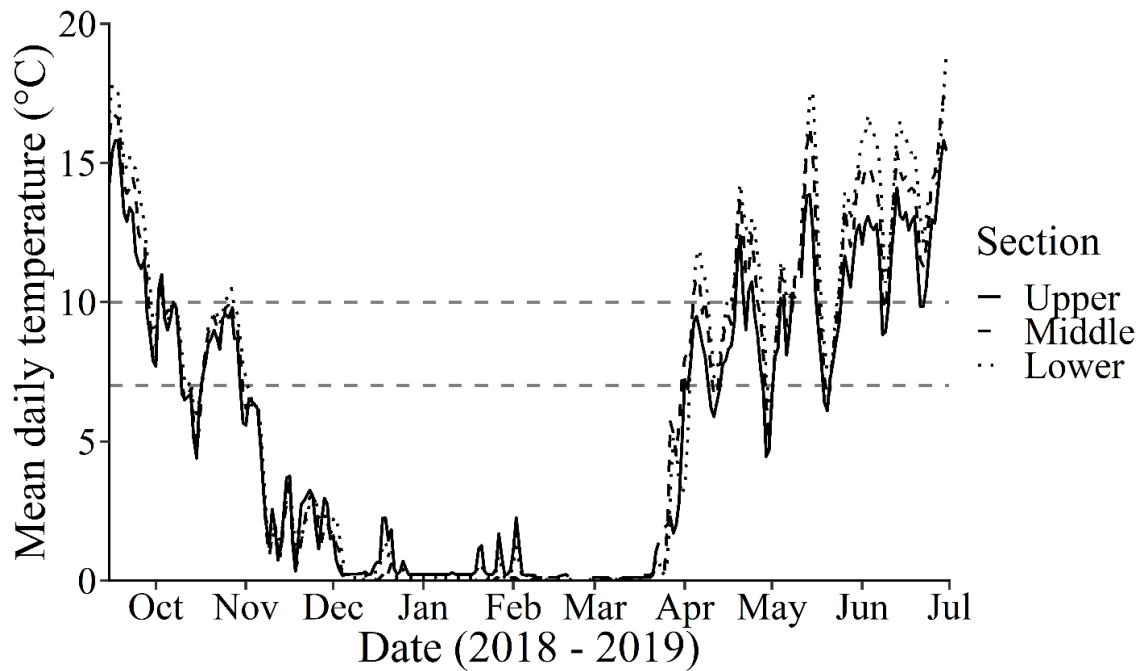


FIGURE S.7. Normalized histograms depicting the probability of starving to death over the winter conditions of 2018 in the Upper Yellowstone River sampling section (rkm 700), versus conditions at USGS gage 06191500 near Corwin Springs, Montana (rkm 885; Figure 1), for all age-0 Smallmouth Bass measured at the onset of winter in the Upper section in 2018 ($n = 119$). Grey bars show estimates given a proposed winter duration of days $< 7^{\circ}\text{C}$, black bars show estimates based on days $< 10^{\circ}\text{C}$, and corresponding dashed lines show the mean cohort-level mortality of 100,000 simulated outcomes.

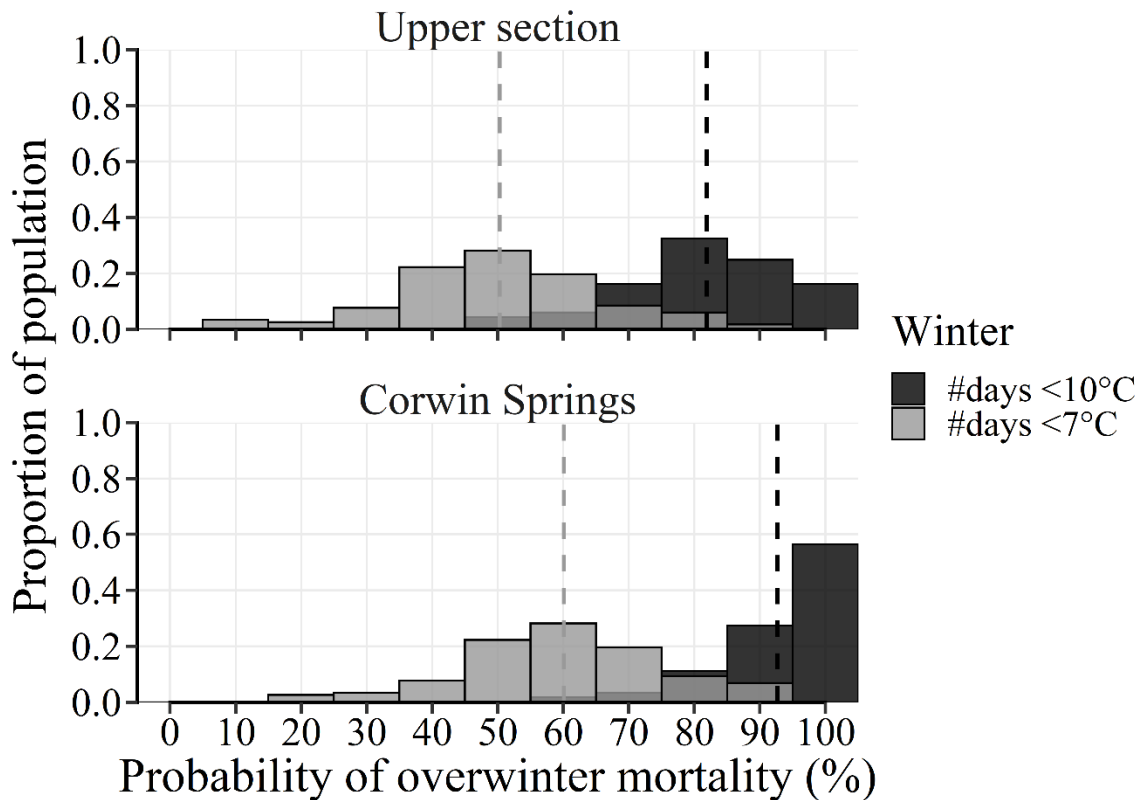


Figure S.8. Screenshot of code (program R version 3.6.2; R Core Team 2019) used to estimate the percent mortality of age-0 Smallmouth Bass cohorts measured in the Yellowstone River at the onset of winter. Line 1 specifies that the output table will be formatted as a data frame. Line 2 specifies the input file, a CSV file where each age-0 Smallmouth Bass measured at the onset of winter is represented by two rows, each containing a probability of overwinter mortality (0-1) based on their measured total length and one of two winter durations based on days < 7°C, and days < 10°C). Individual fish (i.e., rows) are then grouped into cohorts by sample year, section, and winter duration. Line 4 specifies that the following calculations (i.e., “n” and “MeanCohortMort”) be performed for each cohort of age-0 Smallmouth Bass. Line 5 specifies that column “n” in the output table reports the sample size of each cohort. Line 6 specifies that column “MeanCohortMort” report 100 times the mean outcome of 100,000 repetitions of the calculation that follows, which specifies how cohort mortality is estimated within each iteration. Line 7 specifies that for each repetition, each fish in each cohort is randomly assigned a binary outcome based on their individual probability of mortality 'pM', with 1 representing death, and 0 representing survival. The sum of all outcomes within a cohort is then (line 8) divided by the starting number of fish, thereby calculating the proportion of fish that died in that iteration.

```

cohort_mort <- as.data.frame(                                     #[1]
  autumn_dat %>%                                               #[2]
  group_by(Year, Section, starv_thresh) %>%                   #[3]
  dplyr::summarise(                                           #[4]
    n = length(pM),                                           #[5]
    MeanCohortMort = 100*mean(replicate(100000,                #[6]
                                     sum(rbinom(length(pM), size=1, prob=(pM))) #[7]
                                     / length(pM))))          #[8]
  MeanMort_b1c                                               #[9]

```

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