Transactions of the American Fisheries Society 151:527–542, 2022

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1002/tafs.10364

ARTICLE

The Importance of Phenology and Thermal Exposure to Early Life History Success of Nonnative Smallmouth Bass in the Yellowstone River

Nicholas S. Voss*
Montana Cooperative Fishery Research Unit, Department of Ecology, Montana State University, Post Office Box 173460, Bozeman, Montana 59717, USA

Robert Al-Chokhachy and Adam J. Sepulveda
U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, Montana 59715, USA

Christine E. Verhille
Department of Ecology, Montana State University, Post Office Box 173460, Bozeman, Montana 59717, USA

Michael P. Ruggles
Montana Fish, Wildlife and Parks, 2300 Lake Elmo Drive, Billings, Montana 59105, USA

Alexander V. Zale
U.S. Geological Survey, Montana Cooperative Fishery Research Unit, Montana State University, Post Office Box 173460, Bozeman, Montana 59717, USA

Abstract

Knowledge of potential spread by introduced species is critical to effective management and conservation. The Smallmouth Bass *Micropterus dolomieu* is an example of a fish that has been introduced globally, often spreads after introduction, and has substantial predatory impacts on fish assemblages. Nonnative Smallmouth Bass in the free-flowing Yellowstone River, Montana, have expanded from warmer, downstream sections of river into colder, upstream sections containing socio-economically valuable trout fisheries. We sought insight into mechanisms controlling upstream spread by evaluating whether progressively colder upstream climates physiologically constrained successful recruitment by limiting age-0 growth and preventing overwinter survival (i.e., population establishment). We documented the phenology, growth, and overwinter survival of age-0 Smallmouth Bass across a temperature gradient leading to their upstream extent in the Yellowstone River. The upstream extent of population establishment did not appear limited by water temperature alone. Age-0 body size at the onset of winter did not differ significantly between colder, upstream reaches and warmer, downstream reaches. Instead, the earlier hatch timing exhibited by some age-0 individuals in upstream sections allowed them to experience longer growing seasons than many individuals in downstream sections. This counter-intuitive hatching phenology mediated much of the expected decreases in growth in colder, upstream climates. Furthermore, evidence of successful overwinter survival and simulations of age-0 starvation mortality indicated that age-0 individuals at the upstream extent of their distribution successfully recruited to the age-

---

*Corresponding author: 12nvoss@gmail.com
Received September 30, 2021; accepted April 20, 2022

1 year-class during four consecutive years. However, age-0 individuals were rare or absent throughout the uppermost upstream distribution of adults, suggesting that something other than temperature limits or discourages reproduction farther upstream. Taken together, our results suggest that Smallmouth Bass have not yet reached the thermal limit of their upstream distribution in the Yellowstone River and that future spread may challenge fisheries managers tasked with management of coldwater trout fisheries in this river.

Nonnative fish introductions have led to severe and widespread impacts on many aquatic ecosystems (Parker et al. 1999; Marchetti et al. 2004; Gallardo et al. 2016). Even when the mechanisms of impact, such as predation or competition, are well understood, difficulty in predicting secondary spread (i.e., range expansion; hereafter, "spread") often obscures the potential consequences of successful introductions (Cucherousset and Olden 2011; Kulhanek et al. 2011; Trumpickas et al. 2011). Accurate assessments of secondary spread are therefore critical to decision making because the farther a nonnative species spreads, the greater potential it has to impact the host ecosystem (Parker et al. 1999).

The extent of secondary spread in systems with high connectivity depends on the ability of propagules to establish (characterized by consistent reproduction leading to survival of early life stages; Cudmore et al. 2017; Kocovsky et al. 2018), after which new generations can disperse to more distant locations (Lodge et al. 2006). Consequently, physiological limitations determine the availability of suitable reproductive habitat and eventually constrain range expansion in unfragmented systems. Physiological tolerance is therefore a major control on range boundaries, which are often characterized by repeated colonization attempts and year-class failures caused by interannual variability in abiotic conditions (Holt et al. 2005; Sexton et al. 2009; Kubisch et al. 2010).

Species that can tolerate a wide range of abiotic conditions are among the most successful aquatic invaders (Marchetti et al. 2004), and widespread invasions by Smallmouth Bass *Micropterus dolomieu*, which are native to central and eastern portions of the United States and Canada, provide one such example. Smallmouth Bass exhibit broad thermal tolerances, are resource generalists, can disperse long distances, often exhibit high rates of nest success, and have been widely introduced because of their recreational value as sport fish (Loppnow et al. 2013; Brewer and Orth 2015). They tend to spread after 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 et al. 2013). Nonnative Smallmouth Bass are now present in 24 U.S. states and 18 countries (Marchetti et al. 2004; Brown et al. 2009), where they are often regarded as invasive (Carey et al. 2011; Loppnow et al. 2013).

The growing distribution and potential impact of nonnative Smallmouth Bass on salmonid populations in the Yellowstone River, Montana (Figure 1), have caused concern among fisheries managers and stakeholders (Lamborn and Smith 2019). The upstream range of Smallmouth Bass was initially expected to be limited to warm reaches of the lower Yellowstone River basin, where stocking to provide sportfishing opportunities occurred between the mid-1960s and early 1990s (Montana FWP 2020). Instead, Smallmouth Bass spread to cooler reaches upstream of historical stocking locations (M. P. Ruggles, personal communication). Although the specific timing of historical Smallmouth Bass spread is unclear due to limited long-term monitoring, adults were recently captured by anglers as far upstream as Emigrant, Montana (Figure 1), which is over 375 km upstream of the nearest stocking location, less than 50 km downstream of Yellowstone National Park, and well within the socio-economically valuable Paradise Valley trout fishery (Sage 2016). However, whether recent observations signify the full impacts of an established population versus the minimal impact of seasonal habitat use by migratory adults as documented in other watersheds (e.g., Langhurst and Schoenike 1990; Rubenson and Olden 2017) remains unknown.

Cold climates often constrain Smallmouth Bass establishment at northern latitudes. Because age-0 Smallmouth Bass are less cold tolerant than older age-classes (Whitledge et al. 2003), sufficiently cold climates can prevent survival to the age-1 year-class (hereafter, "recruitment," a prerequisite for local establishment; Cudmore et al. 2017) by delaying spawning, slowing first-year growth, and causing size-selective overwinter mortality (Shuter et al. 1980; Shuter and Post 1990; Lawrence et al. 2015). For example, age-0 Smallmouth Bass at the upstream extent of their distribution in the John Day River basin, Oregon, experienced negligible overwinter survival because delayed spawning and reduced growth in these colder habitats resulted in age-0 sizes that were too small to survive the winter starvation period (Rubenson and Olden 2019). However, the nuances and consistency of how temperature limits the spread of Smallmouth Bass in the Yellowstone River remain unclear because large rivers (i.e., >100 m^3/s) have been underrepresented in the literature. Water temperatures that inhibited establishment in the John Day River basin are present in the Yellowstone River, but the relative importance of temperature therein remains uncertain because first-year growth and survival can be mediated by many other variables (e.g., reproductive phenology, turbidity, adult densities, prey availability, and diet; Miller and Storck 1984; Dong and DeAngelis 1998; Sweka and Hartman 2003; Rubenson and Olden 2019). Furthermore, limited adult feeding and

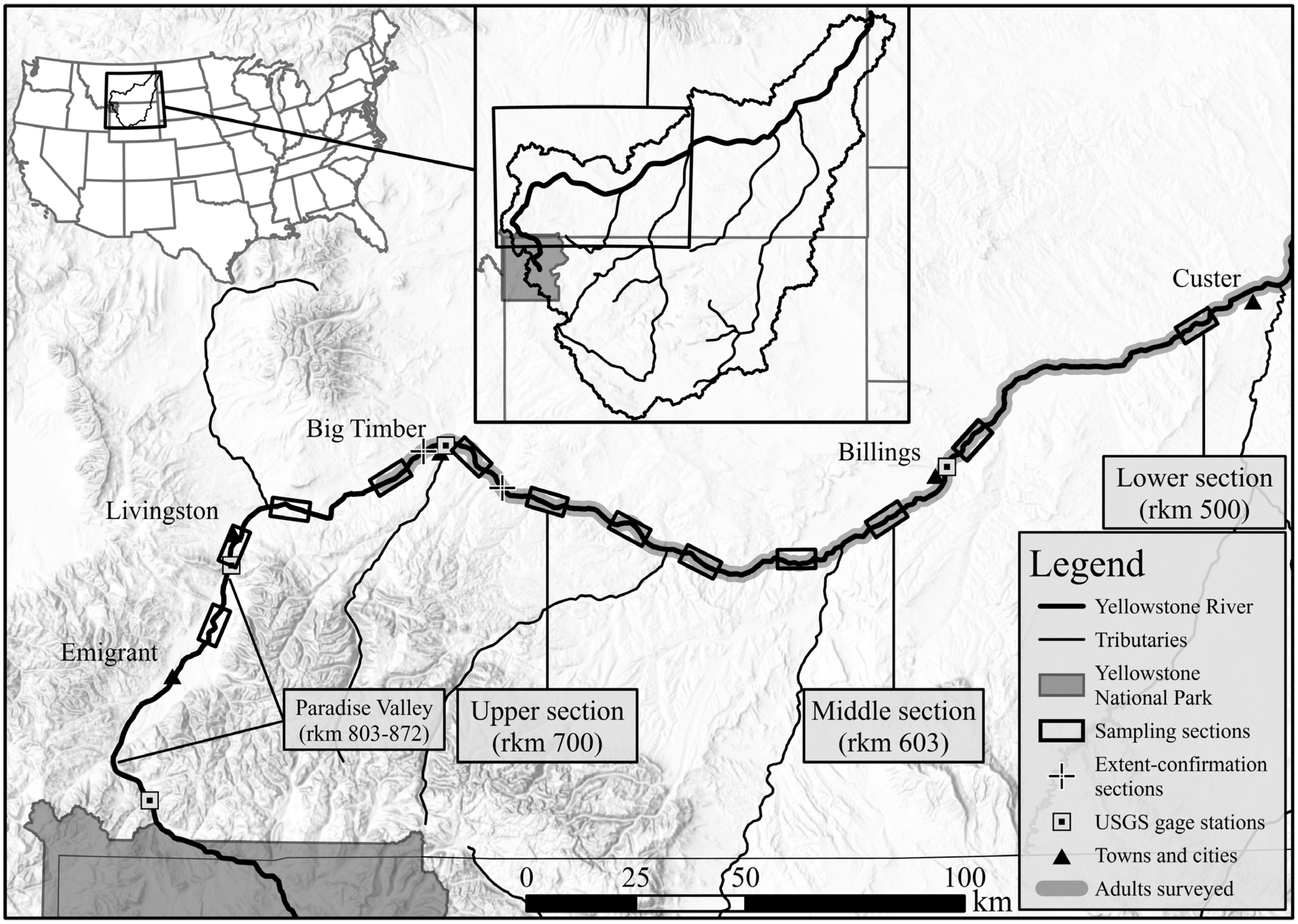

FIGURE 1. Map of the study area on the Yellowstone River, with inset maps illustrating the Yellowstone River basin regionally and within the United States. Labeled sampling sections consist of the 11 sections sampled during distribution surveys (2016–2019) in addition to one downstream-most section adjacent to historical stocking locations. "Extent confirmation" sections immediately upstream of the uppermost age-0 detection were sampled once in 2016 and 2018. U.S. Geological Survey (USGS) stream gauges that monitor Yellowstone River water temperatures in Montana include USGS station 06191500 at Corwin Springs (operating continuously), station 06192500 near Livingston (operating April–September), station 06195950 at Big Timber (operating July–September), and station 06214500 at Billings (operating continuously since October 2018). The gray buffer labeled "Adults surveyed" links the locations where adult Smallmouth Bass were captured during Montana Fish, Wildlife and Parks monitoring surveys (Montana FWP 2020).

spawning habitat, seasonal hydrology, and movement barriers can also constrain the spread of Smallmouth Bass (Lawrence et al. 2012; Rubenson and Olden 2016, 2019). Whether upstream declines in water temperature currently prevent farther upstream establishment in the large, unimpounded, and geomorphically complex Yellowstone River is therefore unclear. Such uncertainty inhibits proactive fisheries management because it obscures whether continued expansion into upstream trout habitat should be expected under current climate conditions.

We sought to understand (1) whether upstream establishment (i.e., consistent recruitment) by Smallmouth Bass in the Yellowstone River was physiologically constrained by cold water temperatures and (2) whether the uppermost distribution of adults was representative of an established population. Because water temperatures near the upstream limit of Smallmouth Bass detections in the Yellowstone River were comparable to thermally limited range boundaries studied elsewhere (Table S.1 available in the Supplement in the online version of this article; Figure 1; Lawrence et al. 2015; Rubenson and Olden 2017), we hypothesized that cold temperatures currently prevent farther upstream establishment by limiting age-0 overwinter survival. Specifically, we predicted that age-0 cohorts in progressively colder upstream areas would eventually fail to reach sufficient body sizes needed to survive the winter starvation period because growing seasons would be progressively shorter and colder in upstream areas. We therefore predicted that the farthest upstream observations of cold-tolerant adults represented seasonal habitat use instead of successful establishment. As such, our first objective was to identify the upstream extent of age-0 Smallmouth Bass in the Yellowstone River (objective 1). We then sought to characterize age-0 size by the onset of winter (objective 2), how phenology and temperature collectively influenced age-0 growth (objective 3), and age-0 overwinter mortality (objective 4) across a broad longitudinal gradient leading up to the age-0 upstream extent. Our research informs regional fisheries management and represents a novel study system within which to test our understanding of the thermal controls on nonnative Smallmouth Bass invasions.

METHODS

Study Area

The Yellowstone River (Figure 1) is the longest river without major impoundments in the contiguous United States. It is an eighth-order, snowmelt-driven stream that begins in the high-elevation headwaters of the Greater Yellowstone Area 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 and cold, with high levels of precipitation, and spring snowmelt causes strong peaks in discharge (e.g., 10-year-average annual maximum = 1,321 m^3/s) that gradually decline to base flow through the short, warm, and dry summers (e.g., average daily mean = 100 m^3/s; Figure S.1 available in the Supplement in the online version of this article). Moving upstream from Custer, Montana, at river kilometer (rkm) 481 (as measured from the Missouri River confluence [rkm 0]; Figure 1), the Yellowstone River gradually transitions from a warm, turbid, anabranched 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 trout fishery (Figures 1, 2).

Our study area spanned 364 km of the middle Yellowstone River and extended from Emigrant (rkm 845), which is adjacent to the uppermost recent observation of an adult (Figure 1), downstream to Custer (rkm 481), which is adjacent to the uppermost historical Smallmouth Bass stocking source. Thermal gradients derived from stream gauge data available prior to our study indicated that summer water temperatures between Custer and the upstream extent of age-0 Smallmouth Bass (see below) differed by about 3.2°C (U.S. Geological Survey [USGS] station 06192500 near Livingston, Montana; USGS station 06192500 at Billings, Montana; Figure 1), which is enough to almost halve expected juvenile Smallmouth Bass growth rates if all else is held equal (Horning and Pearson 1973; Armour 1993).

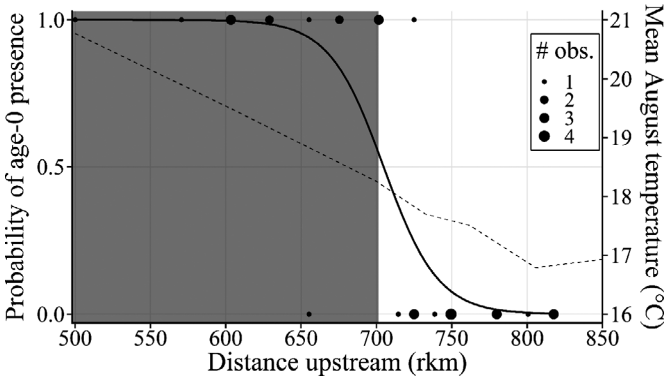

FIGURE 2. Section-level results for age-0 Smallmouth Bass presence (1) and absence (0) during annual distribution (i.e., fyke-net) surveys of Yellowstone River side channel habitat as a function of distance upstream from the Missouri River confluence (2016–2019; $n = 31$ observations). Point size represents the number of surveys (i.e., observations [# obs.]) where age-0 individuals were present or were not detected in a section. The solid line shows the probability of age-0 presence estimated by a binomial generalized linear mixed-effects regression, with gray shading indicating the areas of predicted presence (age-0 upstream extent predicted at rkm 702). The dashed line connects mean August 2018 mainstem water temperatures at seven monitoring sites within our study area.

Data Collection

Upstream extent.— We estimated the upstream extent of successful Smallmouth Bass reproduction by using mini-fyke nets (hereafter, "fyke nets"; dimensions described by Duncan et al. 2016) to sample for the presence of age-0 individuals between August 1 and September 30 from 2016 through 2019 (hereafter, "distribution surveys"; $n = 31$ total). Distribution surveys occurred in 8-km sections of the Yellowstone River, within which we randomly selected three reaches (i.e., stretches of river between two main-channel crossover points; Welker and Drobish 2010) 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 in the middle and lower Yellowstone River (Duncan 2019). We divided the lowest 300 m of all selected side channels into three contiguous 100-m segments and randomly set one fyke net with 3.2-mm knotless mesh in each segment. Nets soaked overnight, and we measured the TL (mm) and wet weight (g; hereafter, "weight") of each captured individual. We conducted distribution surveys within (1) 11 equally spaced sections that were 16 km apart, (2) an additional section adjacent to historical stocking locations (near Custer; Figure 1), and (3) "extent confirmation sections" that we delineated between the uppermost section where age-0 Smallmouth Bass were captured in a given year and the next section upstream (Figure 1).

We did not sample each section in each year. Sampling in 2016 only included sections between rkm 603 and 779, 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 that were proximal to the farthest upstream section where age-0 individuals were captured during the preceding year. We did so by sampling the uppermost section where age-0 Smallmouth Bass were captured the year before and then sampling upstream until no individuals were detected in two consecutive sections. Lastly, logistical constraints only allowed us to delineate and sample the extent confirmation sections in 2016 and 2018.

Three elements of the sampling scheme described above limit our scope of inference. First, we focused 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). Furthermore, this focus met the limitations of our permitting, which was aimed at minimizing disruptions to public recreation on this high-use waterbody. Second, logistical constraints limited our sampling to the lowest 300 m of side channels, which typically contain the majority of slow-velocity habitat that consistently retains connectivity to the main stem. Lastly, we limited net locations to cod-end depths less than 0.6 m and water velocities less than 0.4 m/s to minimize mortality among fish and air-breathing animals. Consequently, our scope of inference is limited to shallow areas with slow current velocity and consistent connectivity to the main stem, which constitute optimal nesting and nursery habitat for age-0 Smallmouth Bass in rivers (Orth and Newcomb 2002).

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 (eDNA) samples in conjunction with all 2019 surveys using the field sampling and laboratory methods described by Franklin et al. (2018) and Rubenson and Olden (2019). Field and laboratory methods are described in the Supplementary Methods available in the online version of this article.

Size and condition at the onset of winter.— Age-0 size and condition at the onset of winter reflect internal energy stores that were assimilated during the prior growing season, and they are important predictors of overwinter survival (i.e., successful recruitment), which is a prerequisite for local establishment (Shuter et al. 1980). We determined longitudinal patterns in age-0 size and condition by intensively sampling three equally spaced sections at the onset of winter in 2018 and 2019. Each section encompassed 8 rkm and was previously sampled during distribution surveys. The uppermost section was located at rkm 700 (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 historical 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 sections during late autumn in 2018 and 2019, after daily mean water temperatures declined below 10°C and active feeding was assumed to have ceased (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 and Parks (FWP) guidelines. We measured the TL and weight of every captured age-0 Smallmouth Bass, and we retained a subset of randomly selected individuals from each side channel in 2018 (69–100 fish/section) by immersing them in a 500-mg/L solution of tricaine methanesulfonate (MS-222) and freezing the carcasses for otolith extraction and age determination to be conducted 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 TL and weight measurements obtained during previous sampling in the late autumn 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 (1) did not weigh fish or collect otoliths in 2016 and (2) 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.

We calculated the relative condition (hereafter, "condition") of captured individuals because condition in juvenile fish approximates the whole-body lipid content, which is strongly associated with starvation mortality in age-0 Smallmouth Bass (Shuter et al. 1980; Pope 2007; Schloesser and Fabrizio 2017). We calculated condition using a length–weight regression that we developed using late-autumn TL (mm) and weight (g) data pooled across the Upper, Middle, and Lower sections ($n = 447$; Supplementary Methods).

Phenology.— 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 section (Upper, Middle, and Lower) during the late autumn of 2018. We acknowledge that otoliths were collected well outside of the 30-d period within which daily deposition has been validated for age-0 Smallmouth Bass (Hill and Bestgen

2014). However, daily deposition by closely related Spotted Bass *M. punctulatus* has been validated for up to 94 d after swim-up (exceeding the estimated age of all age-0 Smallmouth Bass sampled here; Dicenzo and Bettoli 1995), supporting our use of daily aging approaches. Furthermore, other studies have found that reliable aging of Smallmouth Bass is possible during the growing season (i.e., as long as water temperatures are >10°C; Graham and Orth 1987; Hill and Bestgen 2014). However, our interest in ensuring that individuals were at their maximum size prior to the starvation period resulted in otolith collection occurring 9–11 d after main-stem temperatures fell below 10°C, potentially resulting in underestimates of fish age. However, this potential bias is systematic and minimally affects relative differences in hatch date estimates among individuals and cohorts, which are the principal interest of this study.

We attached otoliths to glass microscope slides using thermoplastic glue (Crystalbond 509 Mounting Adhesive; Electron Microscopy Sciences, Hatfield, Massachusetts) and polished the otoliths in the sagittal plane using 0.1–15.0-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 the prepared otoliths at 120× magnification under a stereomicroscope (Leica Application Suite version 4.1; Leica Camera AG, Wetzlar, Germany), and we counted daily growth rings from the images. The lead author read each otolith on two nonconsecutive days and averaged the two ring counts to estimate hatch date. We assessed the precision of hatch date estimates using the coefficient of variation ($CV = 100 \cdot [SD/mean]$; Campana et al. 1995). If the CV of a pair of ring counts was greater than 5%, we conducted a third count, averaged the three, and rejected the otolith if the mean CV still exceeded 5%. Three percent of aged otoliths required a third count, none was rejected, and the mean CV among all final estimates was 1.78% ($n = 120$). We assessed reader bias by having a second reader estimate ages for 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 the 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).

Water temperature.— We monitored water temperatures across our study area to describe the upstream declines that we hypothesized would drive spatial patterns in age-0 hatch timing, body size, and overwinter mortality. Logistical challenges prevented us from using fixed temperature loggers to accurately monitor temperatures in many of the shallow side channels that were sampled for age-0 Smallmouth Bass. Instead, we 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 gauges (https://waterdata.usgs.gov/mt/nwis/rt; Figure 1), maintained temperature loggers (HOBO pendant; Onset Computer, Bourne, 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 spring 2018 and summer 2020. Loss of loggers due to winter and spring scour prevented acquisition of continuous temperature data within each section. We accounted for these lost data by applying lapse rate corrections to water temperatures measured at Big Timber, Montana (USGS station 06195950; Figure 1), using longitudinal lapse rates observed between the USGS gauge and each section during the same months in 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 4-year Upper section data set using a predictive stream temperature model. We used a nonlinear regression model to predict 2016 and spring 2017 and 2018 stream temperatures from air temperature and discharge data using least-squares regression in R version 3.6.2 (Mohseni et al. 1998; R Core Team 2019; Supplementary Methods).

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

Data Analysis

Modeling approach.— We used mixed-effects models to evaluate spatial and temporal patterns in age-0 Smallmouth Bass distribution, length, condition, hatch date, and thermal history. Each model contained a single fixed-effects term used to evaluate the prediction in question. We determined random-effects structures using the Barr method, wherein all groupings of potentially non-independent observations are included as random-effects terms (i.e., side channels, sections, and years), and terms that cause nonconvergence or singular fit (i.e., almost no variation explained) are removed (Barr et al. 2013; Bates et al. 2014). Random intercepts for side channel were nested within section when the two terms co-occurred, and random slopes were additionally included when the response variable was continuous. Details regarding random-effects structure determination for each model are described in the Supplementary Methods. All final models are numbered, with final structures reported in Table 1.

We assessed the significance of fixed-effect terms using ANOVAs with Satterthwaite's approximation (lmerTest package; Kuznetsova et al. 2017), and the threshold probability of type I error (α) was set at 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 assessed the significance of pairwise differences among levels using the Bonferroni–Holm correction for multiple comparisons (multcomp package; Hothorn et al. 2014). We conducted all statistical analyses using R version 3.6.2.

Objective 1: upstream extent.— We estimated the upstream extent of age-0 individuals in the Yellowstone River by using a binomial generalized linear mixed-effects regression (lme4 package; Bates et al. 2014) to model the probability of age-0 presence in sampling sections as a function of the fixed effect of rkm (Table 1, model 1.1). Because the numbers of age-0 presences ($n = 14$) and absences ($n = 17$) in our data set were unequal, we assigned presence versus absence using an optimal probability threshold that maximized the proportion of the area under the curve of receiver operating characteristic plots (hereafter, "area under the curve"; ROCR package; Sing et al. 2005). This approach is an effective and unbiased indicator of model performance (Manel et al. 2001), and the area under the curve was maximized (0.962) by a probability threshold of 0.546. We contrasted the upstream extent of age-0 presence with the locations of adults encountered during Montana FWP monitoring surveys (Figure 1; Montana FWP 2020).

Objective 2: size and condition at the onset of winter.— We tested the prediction that within years, age-0 Smallmouth Bass would attain smaller body sizes and poorer body condition in upstream sections. We accomplished this by using linear mixed-effects ANOVAs (lmerTest package; Kuznetsova et al. 2017) to separately model TL and condition at the onset of winter as a function of the fixed effect of section (Table 1, models 2.1 and 2.2).

In addition to spatial data, we also considered the effect 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 TL 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 (Table 1, model 2.3).

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 date) and main-stem temperature collectively influenced longitudinal patterns in size at the onset of winter. First, we tested the prediction that age-0 individuals would hatch later in cooler, upstream sections by using a linear mixed-effects ANOVA to model hatch date as a function of the fixed effect of section (Table 1, model 3.1).

Next, we tested the prediction that age-0 cohorts in upstream sections would experience shorter and colder growing seasons using growing degree-days greater than 10°C (Rubenson and Olden 2017). The sum of growing degree-days greater than 10°C (hereafter, GDDs) is a holistic index of the duration and intensity of exposure to temperatures at which Smallmouth Bass actively feed

TABLE 1. Summary of the final linear mixed-effects models used to evaluate age-0 Smallmouth Bass presence (p[presence]), TL (mm; Length) and relative condition (Condition) at the onset of winter, hatch date (HD), and first-year growing degree-days (GDDs) using multiple years of data (Years) collected at three sampling sections in the Yellowstone River. Final models included the fixed- and random-effects terms listed below. Marginal R^2 (R^2_m) is a measure of variance explained by all fixed-effects terms. Conditional R^2 (R^2_c) is a measure of variance explained by fixed- and random-effects terms.

Objective	Model	Response	Years	Section[a]	Fixed effects	Random effects[b]	R^2_m	R^2_c	P
1	1.1	p(presence)	2016–2019	*	rkm	None	NA	NA	0.01
2	2.1	Length	2018, 2019	U, M, L	Section	SC + Yr	<0.01	0.23	0.91
	2.2	Condition	2018, 2019	U, M, L	Section	SC	0.01	0.03	0.44
	2.3	Length	2016–2019	U	Year	SC	0.47	0.62	<0.01
3	3.1	HD	2018	U, M, L	Section	SC	0.12	0.35	0.23
4	4.1	Length	2018	U, M, L	GDDs	Sec/SC	0.56	0.77	<0.01

[a] Asterisk (*) denotes the use of all sections included during distribution sampling ($n = 14$ sections); U = Upper sampling section; M = Middle section; and L = Lower section.

[b] SC = side channel; Yr = year; Sec = section; plus symbol (+) denotes additional uncorrelated intercept terms; and forward slash (/) denotes nested random intercepts.

(Shuter et al. 1980). However, because the thermal history of each individual begins at hatching, we calculated GDDs for each aged individual using the main-stem temperatures measured between the otolith-estimated hatch date and the date of capture. The resulting "first-year GDDs" allowed us to assess whether antecedent thermal history alone explained longitudinal patterns in age-0 size. We calculated first-year GDDs using temperature data that were specific to each section, so we did not include section as a fixed effect in the same model as first-year GDDs. We consequently modeled section as a random effect and used parameter estimates to evaluate differences in the relationship between TL and first-year GDDs across sections and years.

Lastly, we tested the prediction that shorter and colder growing seasons (collectively summarized by first-year GDDs) were the principal drivers of longitudinal patterns in age-0 size at the onset of winter using a linear mixed-effects regression analysis (package lmerTest), wherein we modeled age-0 TL as a function of the fixed effect of first-year GDDs (Table 1, model 4.1).

Objective 4: overwinter mortality.— We assessed evidence for longitudinal patterns in overwinter mortality, which we hypothesized would ultimately prevent upstream recruitment, by first comparing age-0 length distributions in the Upper, Middle, and Lower sections between autumn 2018 and spring 2019 (as other studies have done; Ludsin and DeVries 1997; Post et al. 1998). We did so by using a one-sided Kolmogorov–Smirnov test, which makes no assumption of the underlying sample size or data distribution (R version 3.6.2; Massey 1951), to separately detect shifts toward longer body lengths within each section between autumn 2018 and spring 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 for this section.

Next, we estimated the probability of overwinter mortality due to starvation for every age-0 individual captured at the onset of winter. Mortality probabilities (i.e., 1 – probability of survival) in the Upper (2016–2019), Middle (2018, 2019), and Lower (2018, 2019) sections were estimated using a temperature- and size-dependent survival model that was specific to overwintering age-0 Smallmouth Bass (Shuter et al. 1980):

$$L_0 = 0.188d + 14.8$$

$$L_{100} = 0.328d + 33.9$$

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 less than 10°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 with mean daily temperatures less than 7°C may avoid underestimating survival (i.e., overestimating 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; Shuter and Post 1990). Furthermore, 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 days less than 7°C (d_7) and days less than 10°C (d_{10}) to the minimum length of overwinter survivors that were captured during spring 2019 sampling.

We estimated the percentage of age-0 Smallmouth Bass that starved to death within each section in a given year (hereafter, "cohort mortality") using simulations. We estimated cohort mortality for each simulation by performing a single Bernoulli trial (i.e., resulting in survival or death) on each measured individual given its length-dependent mortality probability and then dividing the resulting number of deaths in each cohort by the starting cohort size. We took the average of 100,000 simulations as our official estimate of cohort mortality. Given current uncertainties in the conditions that cause winter starvation, we duplicated all of the above calculations using d_7 and d_{10}.

RESULTS

Objective 1: Upstream Extent

Our generalized linear mixed-effects regression had excellent model fit (area under the curve = 0.962) and estimated that the upstream extent of age-0 Smallmouth Bass in the Yellowstone River between 2016 and 2019 was located within the Upper section at rkm 702 (95% confidence limits = rkm 645 and 726; Figure 2). In contrast, adults were surveyed by Montana FWP as far upstream as rkm 751 (Montana FWP 2020; Figure 1), and repeated anecdotal captures by anglers extend up to rkm 787 (S. Opitz, Montana FWP, personal communication). These results supported our prediction of a disparity between the uppermost distribution of juveniles and that of adults.

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.2), whereas we always detected Smallmouth Bass eDNA where we captured individuals by electrofishing in 2019 ($n = 122$ individuals across nine side channels; Table S.3). 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.2, S.3).

Objective 2: Size and Condition at the Onset of Winter

Despite consistent upstream declines in temperature (Table 2; Figure S.4), neither mean age-0 length ($n = 446$, $P = 0.91$, marginal $R^2 < 0.01$; Table 1, model 2.1) nor condition ($n = 446$, $P = 0.44$, marginal $R^2 = 0.01$; Table 1, model 2.2) at the onset of winter varied significantly among sections (Figure 3A–D). However, variation in TL and condition was consistently higher in downstream sections, with both the maximum and minimum observed values for TL and condition occurring in the Lower section during both 2018 and 2019. These results did not support our prediction that declining upstream temperatures would lead to consistently shorter age-0 sizes and poorer body condition in upstream sections.

In contrast, mean TLs in the Upper section did vary among years (2016–2019; $n = 209$, $P < 0.01$, marginal $R^2 = 0.47$; Table 1, model 2.3). Mean length at the onset of winter was greater in 2016 than in any other year sampled, whereas the mean lengths in all other years were not significantly different from one another (Table 3).

Objective 3: Drivers of Age-0 Size at the Onset of Winter

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 (Table 2; Figure S.4). This corresponded to a 25% difference in ambient GDDs between the two sections in both years (Table 2).

Although the onset of temperatures associated with Smallmouth Bass spawning occurred considerably later in upstream sections (Table 2), 2018 hatch dates broadly overlapped within our study area and the mean hatch date did not vary significantly among sections ($n = 90$, $P = 0.23$, marginal $R^2 = 0.12$; Table 1, model 3.1). However, estimated hatching occurred over a narrower window of time and ended substantially earlier in areas farther upstream (Table S.4), such that estimated hatching ceased in the Upper section before 47% of aged fish had hatched in the Lower section (Figure 4A). These results did not support our prediction that declining upstream temperatures would delay hatching in upstream sections.

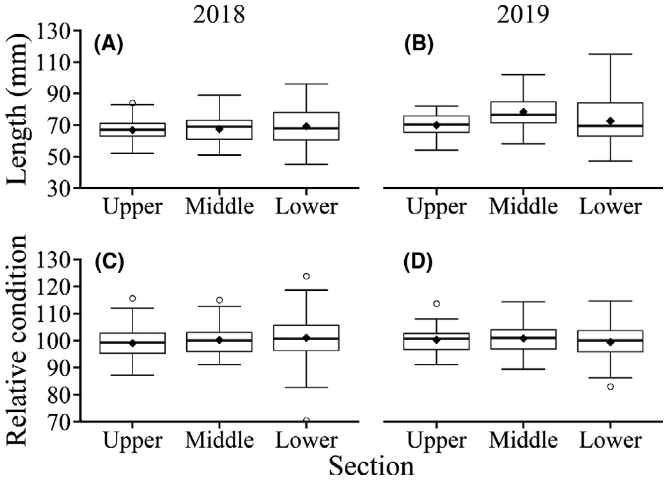

FIGURE 3. **(A)**, **(B)** Total length and **(C)**, **(D)** relative condition of age-0 Smallmouth Bass captured at the onset of winter in side channels within the Upper, Middle, and Lower sampling sections of the Yellowstone River in 2018 ($n = 116$, 69, and 139) and 2019 ($n = 30$, 24, and 68). Boxes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

First-year GDDs were positively associated with age-0 length in all sections ($n = 90$, $P < 0.01$, marginal $R^2 = 0.56$; Table 1, model 4.1), and individuals that hatched in the colder Upper section accumulated 24–28% fewer GDDs than those hatched on the same date in the warmer Lower section (Table 2; Figures 4B, S.4). However, an earlier start and end to the hatching season in the Upper section resulted in mean GDDs therein being only 12% lower than the mean in the Lower section, despite ambient

TABLE 2. Summary of 2019 water temperatures measured in three sampling sections within the main-stem Yellowstone River, in addition to U.S. Geological Survey gauging station 06192500 near Livingston, Montana (Figure 1), including the first date at which the mean daily temperature exceeded 15°C (MDT > 15°C; a temperature frequently associated with Smallmouth Bass spawning behavior; Armour 1993), the first date at which the 7-d average exceeded 15°C (7DAD > 15°C), mean August temperature (°C), summer maximum temperature (°C), and cumulative degree-days greater than 10°C (CDD > 10°C) calculated between July 6 (approximating the earliest onset of spawning in 2018; Figure 4B) and September 30.

Location	rkm	MDT > 15°C	7DAD > 15°C	Mean Aug temperature	Summer maximum temperature	CDD > 10°C
Lower section	500	May 13	May 16	22.1	24.9	857.7
Middle section	603	May 13	Jun 30	20.5	22.8	731.7
Upper section	700	Jun 28	Jul 3	19.4	21.8	645.7
Livingston station	806	Jul 12	Jul 14	17.6	19.4	512.6

TABLE 3. Summary of the post hoc multiple comparison tests conducted on model 2.3 (Table 1), which examined for pairwise differences in the mean TL (mm; Length) of age-0 Smallmouth Bass at the onset of winter in the Upper sampling section of the Yellowstone River (2016–2019). We report the raw difference in means, as well as the SE, Z-score, and associated P-value for each comparison.

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

GDDs differing by up to 28% between the two locations (Figure 4B, C).

Objective 4: Overwinter Mortality

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 overwinter survivors in the Middle section, and 16 overwinter survivors in the Lower section (Figure 5). However, we still detected a significant overwinter shift toward longer body lengths in the Middle (one-sided Kolmogorov–Smirnov test statistic $D = 0.57$, $P < 0.01$) and Lower ($D = 0.54$, $P < 0.01$; Figure 5) sections, as would be expected if overwinter mortality among smaller individuals had occurred. No overwinter survivor in any section was shorter than L_0 (i.e., the length below which mortality was expected to be 100%) estimated from winter temperatures less than 7°C or less than 10°C (Figure 5).

Our simulations predicted considerable overwinter mortality due to starvation across our study area in 2018 and 2019. Estimated starvation mortality among age-0 cohorts hatched in these years was never lower than 31.9% and was never higher than 81.9% in any section based on d_7 or d_{10} (Figure 6). However, longitudinal gradients in

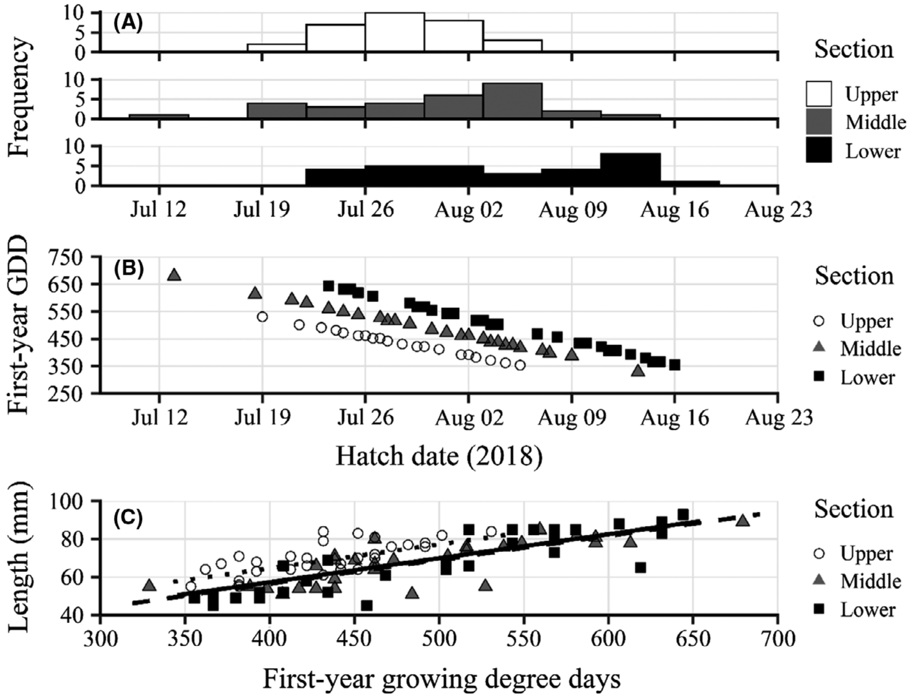

FIGURE 4. **(A)** Frequency of otolith-estimated hatch dates, **(B)** first-year growing degree-days (GDDs) by hatch date, and **(C)** TL by first-year GDDs of 30 age-0 Smallmouth Bass captured at the onset of winter (2018) in each sampling section (Upper, Middle, and Lower) within the Yellowstone River. Hatch date frequencies in panel A are plotted with a 4-d bin width for the same individuals depicted in panel B. Linear regressions for the Upper (dotted line), Middle (dashed line), and Lower (solid line) sections in panel C were estimated by the mixed-effects "equal-slopes" model (Table 1, model 4.1).

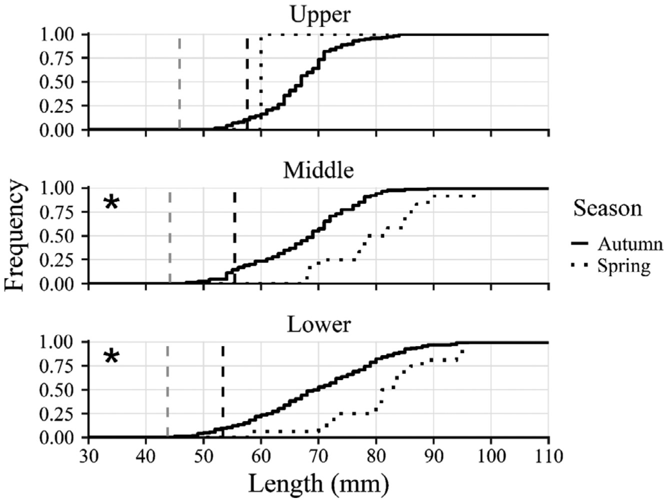

FIGURE 5. Cumulative frequency distributions of TLs for age-0 Smallmouth Bass in the Yellowstone River, as measured at the onset of winter (late autumn 2018) and early the following spring (2019). Sample sizes for autumn and spring were 119 and 1 in the Upper sampling section, 69 and 12 in the Middle section, and 139 and 16 in the Lower section. Asterisks indicate significant shifts toward longer TLs. Vertical dashed lines represent the late-autumn body lengths below which overwinter mortality is estimated to be 100% given a winter duration of days less than 7°C (gray) or days less than 10°C (black).

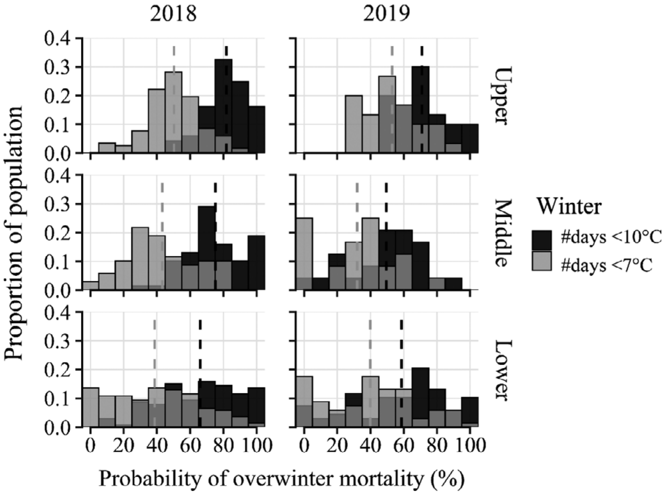

FIGURE 6. Normalized histograms depicting the probability of overwinter mortality due to starvation estimated for each age-0 Smallmouth Bass measured at the onset of winter in the Upper ($n = 119$), Middle ($n = 69$), and Lower ($n = 139$) sampling sections of the Yellowstone River during 2018 ($n = 119$, 69, and 139) and 2019 ($n = 30$, 24, and 68). Gray bars show individual mortality probabilities based on a winter duration of days less than 7°C, black bars show estimates based on days less than 10°C, and corresponding dashed lines show the mean percent cohort-level mortality from 100,000 simulated outcomes.

mortality appeared weak. Winters were always longer in upstream areas, but winters in the Upper section were only 11–24 d longer than those in the Lower section, 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 it never approached 100% as we predicted (Figure 6). Estimates of overwinter mortality varied more widely across years in the Upper section (2016–2019) than across sections 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 7).

DISCUSSION

In this multi-year study, we sought to understand whether upstream establishment by nonnative Smallmouth Bass in the Yellowstone River was physiologically constrained by progressively colder upstream climates and whether the uppermost distribution of adult detections was representative of an established population. Although age-0 Smallmouth Bass were likely absent from the uppermost distribution of adults, the cold upstream temperatures that we hypothesized would limit age-0 growth and overwinter survival did not appear to physiologically constrain establishment farther upstream. Instead, the earlier hatch timing exhibited by some age-0 individuals in colder, upstream sections allowed them to attain sizes that were equal to or larger than those of many individuals in warmer, downstream sections; as a result, many fish at the current estimated age-0 upstream extent exceeded the minimum size needed to survive the winter in four consecutive years. Our findings underscore that an understanding of the interactions between environmental conditions and Smallmouth Bass life history is crucial for evaluating potential spread by this nonnative predator. This knowledge may help to direct future management efforts to stream reaches where they are likely to provide the greatest benefits (Ricciardi and Rasmussen 1998; Lodge et al. 2006; Vander Zanden and Olden 2008).

Objective 1: Upstream Extent

The upstream extent of age-0 Smallmouth Bass in the Yellowstone River (rkm 702) lagged behind the uppermost observations of adults by up to 85 rkm. Longitudinal differences in distributions of the age-0 and adult life stages appear to be common with Smallmouth Bass. For example, research outside of the Yellowstone River found that adults often seasonally migrated from warmer, downstream habitat to colder, upstream habitat that offered energetic benefits during the summer, and the adults then returned to warmer, downstream habitat to overwinter (Langhurst and Schoenike 1990; Rubenson and Olden 2017). In other systems, cold climates interact with nuanced recruitment dynamics (e.g., temperature and

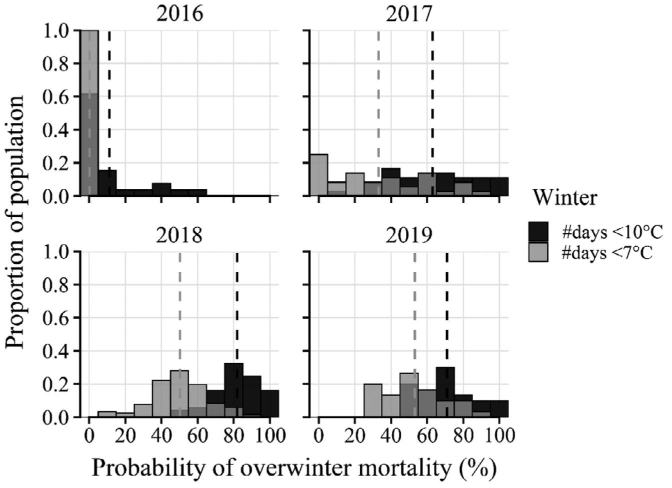

FIGURE 7. Normalized histograms depicting the probability of overwinter mortality due to starvation for each age-0 Smallmouth Bass measured at the onset of winter in the Upper sampling section of the Yellowstone River during 2016 ($n = 26$), 2017 ($n = 36$), 2018 ($n = 119$), and 2019 ($n = 30$). Gray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

foraging limit; Lawrence et al. 2015) to prevent first-year survival of offspring in the upstream habitats (Langhurst and Schoenike 1990; Rubenson and Olden 2019). In contrast, our results suggest that factors other than water temperature alone must be limiting farther upstream establishment in the Yellowstone River.

Spawning habitat quality and longitudinal patterns in adult Smallmouth Bass density and distribution can also influence where reproduction and recruitment occur. While not specifically assessed herein, spawning habitat in the upstream reaches of the Yellowstone River appears to be suitable, with relatively low gradients (Lawrence et al. 2012), an abundance of gravel substrate, and shallow, calm, clear water (Orth and Newcomb 2002; Dalby and Robinson 2003; Holnbeck 2005). Alternatively, the spatial disconnect between juvenile and adult distributions may be caused by a temporal mismatch in upstream dispersal versus spawning temperature cues (Rubenson and Olden 2016) or density dependence, a major driver of animal dispersal (Marchetti et al. 2004; Matthysen 2005). Adult Smallmouth Bass near the Upper section may currently lack the density-driven competition needed to motivate dispersal to upstream areas. The inability to locate mates at low population densities (an Allee effect), particularly in discrete, patchy reproductive habitat such as side channels, can also delay establishment and limit the speed of ongoing invasions (Keitt et al. 2001; Taylor and Hastings 2005; Gregory et al. 2010). The potential for Allee effects is suggested by our eDNA results, which indicated that Smallmouth Bass were rare at and above the age-0 upstream extent (Tables S.2, S.3), and warrants further investigation.

Objective 2: Size by the Onset of Winter

We predicted that Smallmouth Bass growth in the Yellowstone River would be determined by temperature because it is a principal driver of fish growth (Fry 1971) in addition to Smallmouth Bass spawning phenology and incubation (Graham and Orth 1986; Armour 1993). Given that observed differences in temperature across our study area were enough to almost halve the expected growth rates if all else was held equal (Table 2; Figure S.4; Horning and Pearson 1973; Armour 1993), the similarities in the size of age-0 Smallmouth Bass at the onset of winter were surprising. Furthermore, our results from the Yellowstone River were inconsistent with findings from the smaller North Fork John Day River, Oregon (i.e., about 40× smaller at base flow; Figure S.1; USGS station 14,046,000 at Monument, Oregon), where upstream declines in temperature were compounded with delays in spawning and hatch timing to result in rapid declines in age-0 size approaching the upstream range boundary (Rubenson and Olden 2016, 2019). There, spawning was delayed in upstream habitats because adults overwintered downstream and had not yet dispersed to the upstream habitats. Indeed, the relationship between stream temperature and age-0 size by the onset of winter appears complex and context dependent and may be illuminated by additional research on rivers of varying sizes and abiotic conditions.

Objective 3: Drivers of Age-0 Growth

The positive association between first-year GDDs and body size in our study supports past findings, which indicated that both the magnitude and the duration of suitable temperatures after hatching are important drivers of first-year growth by Smallmouth Bass (Bestgen and Hill 2016; Rubenson and Olden 2019). Indeed, climate warming is considered a primary factor in the northward range expansion of Smallmouth Bass in North America because age-0 individuals can both hatch earlier and grow faster than historical conditions may have allowed (Shuter and Post 1990; Sharma et al. 2007). In the unimpounded Yellowstone River, the onset of successful reproduction probably depends on the timing of early summer snowmelt runoff—a phenomenon with which this species did not evolve—that rapidly depresses water temperatures and causes high turbidities (Figures S.1, S.5; Winemiller and Taylor 1982; Orth and Newcomb 2002; Rubenson and Olden 2016). The broadly synchronous occurrence of snowmelt runoff across our study area could explain why the onset of hatching was more similar across the Upper, Middle, and Lower sections than we expected; it could also explain why the onset of hatching probably occurred well after mean daily temperatures associated with Smallmouth Bass spawning first appeared (15°C; Table 2; Figure 4A; Armour 1993). Although this apparent delay in hatching across all sections could be partially explained by underestimates of fish age, we note that the first occurrences of 15°C in the unimpounded Yellowstone River are typically short in duration and are followed by pulses of snowmelt runoff that depress temperatures below levels associated with nest failure (10–14°C; Figure S.5; Armour 1993). The importance of discharge for first-year growth and recruitment may also be apparent in the 2016 cohort, which attained the largest mean body size observed in our study during an anomalously low-discharge growing season, despite exposure to below-average stream temperatures (Table 3; Figures S.1, S.2). Climate change-driven shifts to both earlier runoff and longer durations of warm temperatures are expected to continue in the Yellowstone River (Al-Chokhachy et al. 2013, 2017; Sepulveda et al. 2015), suggesting a greater potential for first-year growth, recruitment, and range expansion in the future (Shuter and Post 1990; Rubenson and Olden 2019). The influence of temperature and hydrology on Smallmouth Bass reproduction is therefore a logical place for future research aimed at understanding how Smallmouth Bass near their upstream extent might deviate from the expected effects of water temperature in the Yellowstone River and elsewhere.

Objective 4: Overwinter Mortality

Range boundaries constrained by environmental conditions (e.g., temperature) are characterized by intermittent reproductive success and frequent year-class failures (Holt et al. 2005; Sexton et al. 2009; Kubisch et al. 2010). Our estimates of size-selective mortality in all sections (Figure 6), combined with widespread similarities in the duration of winter starvation, suggest that age-0 growth is an important determinant of Smallmouth Bass recruitment success in much of the Yellowstone River. Longitudinal differences in overwintering conditions appeared less important (sensu Lyons 1997), as the small variation in L_0 across sites was eclipsed by the effect of intra-cohort variation in age-0 size (ranges of 28–68 mm; Figure 3A, B). 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 winter starvation. Furthermore, age-0 growth remained high at the upstream extent of their distribution in the Yellowstone River despite temperatures being comparable to thermally limited range boundaries described elsewhere (Table S.1; Figure 1; Lawrence et al. 2015; Rubenson and Olden 2017). Nevertheless, probable recruitment at the age-0 upstream extent across four consecutive years, combined with weak gradients in L_0 and sufficient GDDs upstream, suggests that this population has not yet expanded to its thermal limit in the Yellowstone River basin.

Study Limitations

We acknowledge limitations to our study. First, 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 into main-stem habitat by larger age-0 individuals than we observed is unknown but possible. However, many of the side channels we sampled exceeded 70 m in width and contained deep pools and overwintering habitat (i.e., large rocky substrate; Orth and Newcomb 2002). Furthermore, consistent differences in maximum age-0 size among sections suggest that at least some large individuals remained in side channels through their first winter. Lastly, any undetected presence of larger individuals than we observed would further reinforce evidence that size-selective age-0 overwinter mortality is not preventing recruitment of age-0 Smallmouth Bass beyond their current upstream extent.

We also acknowledge that empirical and modeled temperature data imperfectly approximate 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 move into warmwater refugia to increase growth (e.g., Neverman and Wurtsbaugh 1994; Ward et al. 2010; Armstrong et al. 2013). Although we consider it improbable that availability and use of these habitats would differ across our study area where off-channel habitat was abundant, we acknowledge that access to increased thermal heterogeneity may allow enhanced growth opportunities and could provide a fruitful direction for future research on nonnative species invasions.

Implications for Upstream Range Expansion

Range size is a critical determinant of nonnative impacts (Parker et al. 1999), but it can be difficult to predict. We found that upstream spread by Smallmouth Bass in the Yellowstone River is not presently constrained by water temperature and cannot be accurately predicted by temperature alone. Smallmouth Bass spawning and hatching phenology allowed age-0 individuals at their current upstream extent to reach body sizes necessary to survive overwinter starvation, and farther upstream recruitment appears possible under current climate conditions. Nevertheless, climate change will probably accelerate future spread by bolstering overwinter survival (e.g., Al-Chokhachy et al. 2017). However, for reasons that remain unclear, Smallmouth Bass recruitment did not progress upstream between 2016 and 2019 despite adult dispersal upstream of this point.

Our results track those of other nonnative Smallmouth Bass studies, which showed that endogenous and exogenous factors interact with physiological restrictions imposed by water temperature to influence invasion dynamics.

Moreover, Smallmouth Bass are highly adaptable and capable of life history divergence in novel environments (Dunlop et al. 2005). Site-specific nuances, interactions, and lag times (e.g., Breton et al. 2014) therefore make it difficult to develop generalizations about Smallmouth Bass invasion dynamics so as to proactively manage recently invaded systems. These types of complications underscore why "an ounce of prevention is worth a pound of cure" (Leung et al. 2002); after a nonnative species is established, it can be difficult and costly to manage. For example, Smallmouth Bass introductions in tributaries to the Columbia River ultimately resulted in invasions and substantial predation on juvenile salmonids across most of the lower and middle Columbia River basin, wherein widespread prevention of future spread may now be challenging (Carey et al. 2011; Rubenson and Olden 2020). For nonnative species that were intentionally introduced but can have unintended consequences for fish assemblages (e.g., Smallmouth Bass and Rainbow Trout *Oncorhynchus mykiss*; Shelton et al. 2015; Tiffan et al. 2020), managers will have to consider the tradeoffs of controlling adults and juveniles near the upstream extent versus the uncertainty of future spread and amplification of their consumptive impacts.

ACKNOWLEDGMENTS

We thank Patrick Hutchins (USGS), Benjamin Bailey (Montana FWP), and Earl Radonski (Montana FWP) for logistical support. Funding for this project came from the USGS Ecosystem Mission Area's Invasive Species Program, Montana State University, the Jim Belsey Endowment, SITKA Gear (Bozeman, Montana), and the Montana Cooperative Fishery Research Unit. The Montana Cooperative Fishery Research Unit is jointly sponsored by the USGS, Montana FWP, Montana State University, and U.S. Fish and Wildlife Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was performed under the auspices of the Institutional Animal Care and Use Committee (Protocols 2016-26 and 2019-113) at Montana State University. There is no conflict of interest declared in this article.

ORCID

Robert Al-Chokhachy https://orcid.org/0000-0002-2136-5098

REFERENCES

Al-Chokhachy, R., J. Alder, S. Hostetler, R. Gresswell, and B. Shepard. 2013. Thermal controls of Yellowstone Cutthroat Trout and invasive fishes under climate change. Global Change Biology 19:3069–3081.

Al-Chokhachy, R., A. J. Sepulveda, A. M. Ray, D. P. Thoma, and M. T. Tercek. 2017. Evaluating species-specific changes in hydrologic regimes: an iterative approach for salmonids in the Greater Yellowstone Area (USA). Reviews in Fish Biology and Fisheries 27:425–441.

Armour, C. L. 1993. Evaluating temperature regimes for protection of Smallmouth Bass. U.S. Fish and Wildlife Service, Resource Publication 191, Washington, D.C.

Armstrong, J. B., D. E. Schindler, C. P. Ruff, G. T. Brooks, K. E. Bentley, and C. E. Torgersen. 2013. Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. Ecology 94:2066–2075.

Arscott, D. B., K. Tockner, and J. Ward. 2001. Thermal heterogeneity along a braided floodplain river (Tagliamento River, northeastern Italy). Canadian Journal of Fisheries and Aquatic Sciences 58:2359–2373.

Baldock, J. R., J. B. Armstrong, D. E. Schindler, and J. L. Carter. 2016. Juvenile Coho Salmon track a seasonally shifting thermal mosaic across a river floodplain. Freshwater Biology 61:1454–1465.

Barr, D. J., R. Levy, C. Scheepers, and H. J. Tily. 2013. Random effects structure for confirmatory hypothesis testing: keep it maximal. Journal of Memory and Language 68:255–278.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S2. R package version 1.7.1.

Bestgen, K., and A. Hill. 2016. River regulation affects reproduction, early growth, and suppression strategies for invasive Smallmouth Bass in the upper Colorado River basin. Colorado State University, Department of Fish, Wildlife, and Conservation Biology, Larval Fish Laboratory Contribution 187, Fort Collins.

Breton, A. R., D. L. Winkelman, J. A. Hawkins, and K. R. Bestgen. 2014. Population trends of Smallmouth Bass in the upper Colorado River basin with an evaluation of removal effects. Colorado State University, Department of Fish, Wildlife, and Conservation Biology, Larval Fish Laboratory Contribution 169, Fort Collins.

Brewer, S. K., and D. J. Orth. 2015. Smallmouth Bass *Micropterus dolomieu* Lacepède, 1802. Pages 9–26 *in* M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.

Brown, T. G., B. Runciman, S. Pollard, A. D. Grant, and M. J. Bradford. 2009. Biological synopsis of Smallmouth Bass (*Micropterus dolomieu*). Canadian Manuscript Report of Fisheries and Aquatic Sciences 2887.

Campana, S. E., M. C. Annand, and J. I. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124:131–138.

Carey, M. P., B. L. Sanderson, T. A. Friesen, K. A. Barnas, and J. D. Olden. 2011. Smallmouth Bass in the Pacific Northwest: a threat to native species; a benefit for anglers. Reviews in Fisheries Science 19:305–315.

Cucherousset, J., and J. D. Olden. 2011. Ecological impacts of nonnative freshwater fishes. Fisheries 36:215–230.

Cudmore, B. C., L. A. Jones, N. E. Mandrak, J. M. Dettmers, D. C. Chapman, C. S. Kolar, and G. Conover. 2017. Ecological risk assessment of Grass Carp (*Ctenopharyngodon idella*) for the Great Lakes basin. Canada Department of Fisheries and Oceans, Ottawa.

Dalby, C., and J. Robinson. 2003. Historic channel changes and geomorphology of the upper Yellowstone River, Gardiner to Springdale, Montana. Montana Department of Natural Resources and Conservation, Water Resources Division, Helena.

Dicenzo, V. J., and P. W. Bettoli. 1995. Verification of daily ring deposition in the otoliths of age-0 Spotted Bass. Transactions of the American Fisheries Society 124:633–636.

Dong, Q., and D. L. Deangelis. 1998. Consequences of cannibalism and competition for food in a Smallmouth Bass population: an individual-based modeling study. Transactions of the American Fisheries Society 127:174–191.

Duncan, M. B. 2019. Distributions, abundances, and movements of small, nongame fishes in a large Great Plains river network. Doctoral dissertation. Montana State University, Bozeman.

Duncan, M. B., R. G. Bramblett, and A. V. Zale. 2016. Distributions of small nongame fishes in the lower Yellowstone River. American Midland Naturalist 175:1–24.

Dunlop, E. S., J. A. Orendorff, B. J. Shuter, F. H. Rodd, and M. S. Ridgway. 2005. Diet and divergence of introduced Smallmouth Bass (*Micropterus dolomieu*) populations. Canadian Journal of Fisheries and Aquatic Sciences 62:1720–1732.

Franklin, T. W., J. C. Dysthe, E. S. Rubenson, K. J. Carim, J. D. Olden, K. S. McKelvey, M. K. Young, and M. K. Schwartz. 2018. A non-invasive sampling method for detecting non-native Smallmouth Bass (*Micropterus dolomieu*). Northwest Science 92:149–157.

Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish. Pages 1–98 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume 6. Academic Press, New York.

Gallardo, B., M. Clavero, M. I. Sánchez, and M. Vilà. 2016. Global ecological impacts of invasive species in aquatic ecosystems. Global Change Biology 22:151–163.

Graham, R. J., and D. J. Orth. 1986. Effects of temperature and streamflow on time and duration of spawning by Smallmouth Bass. Transactions of the American Fisheries Society 115:693–702.

Graham, R. J., and D. J. Orth. 1987. Otolith aging of young-of-the-year Smallmouth Bass. Pages 483–491 *in* R. C. Summerfelt and G. E. Hall, editors. The age and growth of fish. Iowa State University Press, Ames.

Gregory, S. D., C. J. Bradshaw, B. W. Brook, and F. Courchamp. 2010. Limited evidence for the demographic Allee effect from numerous species across taxa. Ecology 91:2151–2161.

Hill, A. A., and K. R. Bestgen. 2014. Otolith daily increment deposition in age-0 Smallmouth Bass reared in constant and fluctuating water temperatures. North American Journal of Fisheries Management 34:774–779.

Holnbeck, S. R. 2005. Sediment-transport investigations of the upper Yellowstone River, Montana, 1991 through 2001: data collection, analysis, and simulation of sediment transport. U.S. Geological Survey, Scientific Investigations Report 2005–5234, Reston, Virginia.

Holt, R. D., T. H. Keitt, M. A. Lewis, B. A. Maurer, and M. L. Taper. 2005. Theoretical models of species' borders: single species approaches. Oikos 108:18–27.

Horning, W. B., and R. E. Pearson. 1973. Growth temperature requirements and lower lethal temperatures for juvenile Smallmouth Bass (*Micropterus dolomieu*). Journal of the Fisheries Research Board of Canada 30:1226–1230.

Hothorn, T., B. Frank, P. Westfall, R. M. Heiberger, A. Schuetzenmeister, and S. Scheibe. 2014. Multcomp: simultaneous inference in general parametric models. R package version 1.2.

Jackson, D. A. 2002. Ecological effects of *Micropterus* introductions: the dark side of black bass. Pages 221–232 *in* D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Keitt, T. H., M. A. Lewis, and R. D. Holt. 2001. Allee effects, invasion pinning, and species' borders. American Naturalist 157:203–216.

Kocovsky, P. M., R. Sturtevant, and J. Schardt. 2018. What it is to be established: policy and management implications for non-native and invasive species. Management of Biological Invasions 9:177–185.

Kubisch, A., T. Hovestadt, and H. J. Poethke. 2010. On the elasticity of range limits during periods of expansion. Ecology 91:3094–3099.

Kulhanek, S. A., A. Ricciardi, and B. Leung. 2011. Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species? Ecological Applications 21:189–202.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest package: tests in linear mixed effects models. Journal of Statistical Software 82(13).

Lamborn, C. C., and J. W. Smith. 2019. Human perceptions of, and adaptations to, shifting runoff cycles: a case-study of the Yellowstone River (Montana, USA). Fisheries Research 216:96–108.

Langhurst, R. W., and D. L. Schoenike. 1990. Seasonal migration of Smallmouth Bass in the Embarrass and Wolf rivers, Wisconsin. North American Journal of Fisheries Management 10:224–227.

Lawrence, D. J., D. A. Beauchamp, and J. D. Olden. 2015. Life-stage-specific physiology defines invasion extent of a riverine fish. Journal of Animal Ecology 84:879–888.

Lawrence, D. J., J. D. Olden, and C. E. Torgersen. 2012. Spatiotemporal patterns and habitat associations of Smallmouth Bass (*Micropterus dolomieu*) invading salmon-rearing habitat. Freshwater Biology 57:1929–1946.

Leung, B., D. M. Lodge, D. Finnoff, J. F. Shogren, M. A. Lewis, and G. Lamberti. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London Series B: Biological Sciences 269:2407–2413.

Lodge, D. M., S. Williams, H. J. MacIssac, K. R. Hayes, B. Leung, S. Reichard, R. N. Mack, P. B. Moyle, M. Smith, and D. A. Andow. 2006. Biological invasions: recommendations for U.S. policy and management. Ecological Applications 16:2035–2054.

Loppnow, G. L., K. Vascotto, and P. A. Venturelli. 2013. Invasive Smallmouth Bass (*Micropterus dolomieu*): history, impacts, and control. Management of Biological Invasions 4:191–206.

Ludsin, S. A., and D. R. DeVries. 1997. First-year recruitment of Largemouth Bass: the interdependency of early life stages. Ecological Applications 7:1024–1038.

Lyons, J. 1997. Influence of winter starvation on the distribution of Smallmouth Bass among Wisconsin streams: a bioenergetics modeling assessment. Transactions of the American Fisheries Society 126:157–162.

Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. Journal of Applied Ecology 38:921–931.

Marchetti, M. P., P. B. Moyle, and R. Levine. 2004. Alien fishes in California watersheds: characteristics of successful and failed invaders. Ecological Applications 14:587–596.

Massey, F. J. Jr. 1951. The Kolmogorov–Smirnov test for goodness of fit. Journal of the American Statistical Association 46:68–78.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403–416.

Miller, S. J., and T. Storck. 1984. Temporal spawning distribution of Largemouth Bass and young-of-year growth, determined from daily otolith rings. Transactions of the American Fisheries Society 113:571–578.

Mohseni, O., H. G. Stefan, and T. R. Erickson. 1998. A nonlinear regression model for weekly stream temperatures. Water Resources Research 34:2685–2692.

Montana FWP (Fish, Wildlife and Parks). 2020. FishMT [online database]. Montana FWP, Helena. Available: http://fwp.mt.gov/fish/stocking.html. (August 2021).

Munther, G. L. 1970. Movement and distribution of Smallmouth Bass in the middle Snake River. Transactions of the American Fisheries Society 99:44–53.

Neverman, D., and W. A. Wurtsbaugh. 1994. The thermoregulatory function of diel vertical migration for a juvenile fish, *Cottus extensus*. Oecologia 98:247–256.

Orth, D., and T. Newcomb. 2002. Certainties and uncertainties in defining essential habitats for riverine Smallmouth Bass. Pages 251–264 *in*

D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Paragamian, V. 1981. Some habitat characteristics that affect abundance and winter survival of Smallmouth Bass in the Maquoketa River, Iowa. Pages 45–53 *in* L. A. Krumholz, editor. The warmwater streams symposium. American Fisheries Society, Bethesda, Maryland.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, and J. E. Byers. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1:3–19.

Pope, K. 2007. Condition. Pages 423–471 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Post, D. M., J. F. Kitchell, and J. R. Hodgson. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of Largemouth Bass in a northern lake. Canadian Journal of Fisheries and Aquatic Sciences 55:2588–2600.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reinhold, A. M., R. G. Bramblett, A. V. Zale, D. W. Roberts, and G. C. Poole. 2016. Comparative use of side and main channels by small-bodied fish in a large, unimpounded river. Freshwater Biology 61:1611–1626.

Ricciardi, A., and J. B. Rasmussen. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences 55:1759–1765.

Rubenson, E. S., and J. D. Olden. 2016. Spatiotemporal spawning patterns of Smallmouth Bass at its upstream invasion edge. Transactions of the American Fisheries Society 145:693–702.

Rubenson, E. S., and J. D. Olden. 2017. Dynamism in the upstream invasion edge of a freshwater fish exposes range boundary constraints. Oecologia 184:453–467.

Rubenson, E. S., and J. D. Olden. 2019. Growth and recruitment of nonnative Smallmouth Bass along the upstream edge of its riverine distribution. Northwest Science 93:1–15.

Rubenson, E. S., and J. D. Olden. 2020. An invader in salmonid rearing habitat: current and future distributions of Smallmouth Bass (*Micropterus dolomieu*) in the Columbia River basin. Canadian Journal of Fisheries and Aquatic Sciences 77:314–325.

Sage, J. L. 2016. Economic contributions of the Yellowstone River to Park County, Montana. University of Montana, Institute for Tourism and Recreation Research Publication 346, Missoula.

Schloesser, R. W., and M. C. Fabrizio. 2017. Condition indices as surrogates of energy density and lipid content in juveniles of three fish species. Transactions of the American Fisheries Society 146:1058–1069.

Sepulveda, A. J., M. T. Tercek, R. Al-Chokhachy, A. M. Ray, D. P. Thoma, B. R. Hossack, G. T. Pederson, A. W. Rodman, and T. Olliff. 2015. The shifting climate portfolio of the Greater Yellowstone Area. PLoS (Public Library of Science) One [online serial] 10: e0145060.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. Annual Review of Ecology, Evolution, and Systematics 40:415–436.

Sharma, S., D. A. Jackson, C. K. Minns, and B. J. Shuter. 2007. Will northern fish populations be in hot water because of climate change? Global Change Biology 13:2052–2064.

Shelton, J. M., M. J. Samways, and J. A. Day. 2015. Predatory impact of non-native Rainbow Trout on endemic fish populations in headwater streams in the Cape Floristic region of South Africa. Biological Invasions 17:365–379.

Shuter, B., J. MacLean, F. Fry, and H. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of Smallmouth Bass. Transactions of the American Fisheries Society 109:1–34.

Shuter, B., and J. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314–336.

Simonson, T. D., and W. A. Swenson. 1990. Critical stream velocities for young-of-year Smallmouth Bass in relation to habitat use. Transactions of the American Fisheries Society 119:902–909.

Sing, T., O. Sander, N. Beerenwinkel, and T. Lengauer. 2005. ROCR: visualizing classifier performance in R. Bioinformatics 21:3940–3941.

Stevenson, D. K., and S. E. Campana. 1992. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

Sweka, J. A., and K. J. Hartman. 2003. Reduction of reactive distance and foraging success in Smallmouth Bass, *Micropterus dolomieu*, exposed to elevated turbidity levels. Environmental Biology of Fishes 67:341–347.

Taylor, C. M., and A. Hastings. 2005. Allee effects in biological invasions. Ecology Letters 8:895–908.

Tiffan, K. F., J. M. Erhardt, R. J. Hemingway, B. K. Bickford, and T. N. Rhodes. 2020. Impact of Smallmouth Bass predation on subyearling fall Chinook Salmon over a broad continuum. Environmental Biology of Fishes 103:1231–1246.

Trumpickas, J., N. E. Mandrak, and A. Ricciardi. 2011. Nearshore fish assemblages associated with introduced predatory fishes in lakes. Aquatic Conservation: Marine and Freshwater Ecosystems 21:338–347.

Vander Zanden, M. J., and J. D. Olden. 2008. A management framework for preventing the secondary spread of aquatic invasive species. Canadian Journal of Fisheries and Aquatic Sciences 65:1512–1522.

Ward, A., E. Hensor, M. Webster, and P. Hart. 2010. Behavioral thermoregulation in two freshwater fish species. Journal of Fish Biology 76:2287–2298.

Welker, T., and M. Drobish. 2010. Missouri River standard operating procedures for fish sampling and data collection, volume 1.5. U.S. Army Corps of Engineers, Omaha District, Yankton, South Dakota.

Whitledge, G. W., R. S. Hayward, R. D. Zweifel, and C. F. Rabeni. 2003. Development and laboratory evaluation of a bioenergetics model for subadult and adult Smallmouth Bass. Transactions of the American Fisheries Society 132:316–325.

Winemiller, K. O., and D. H. Taylor. 1982. Smallmouth Bass nesting behavior and nest site selection in a small Ohio stream. Ohio Journal of Science 82:266–273.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.