Growth and Recruitment of Nonnative Smallmouth Bass Along the Upstream Edge of its Riverine Distribution

Abstract

Nonnative species have been widely introduced, and once established, often exhibit secondary spread to new areas. For instance, after its initial introduction in the John Day River, Oregon, smallmouth bass (Micropterus dolomieu) has expanded upstream into headwater habitats. Recruitment is a key component of successful range expansion and has been highlighted as a potential bottleneck to continued expansion by smallmouth bass. We explored growth, body lengths, and survival of young-of-the-year (YOY) smallmouth bass in the North Fork John Day River to better understand the recruitment dynamics near its invasion boundary. In 2014–2015, we collected YOY across the upstream 63 km of smallmouth bass distribution at the end of the first growth season and after a winter starvation period. We found that growth, body length, and survival showed varied correspondence with patterns in water temperature. Specifically, body lengths matched temperature predictions in upstream sites (after accounting for spawning delays) where smallmouth bass density is low. By contrast, individuals achieved smaller than predicted body lengths in downstream sites where density is relatively high. Model selection revealed that temperature and age ≥ 1 density were the most important predictors of body length. Additionally, individuals predicted to be too small to survive a winter starvation period were present. Our findings reveal nuanced recruitment dynamics at the invasion boundary, where departures from temperature-based predictions point to multiple mechanisms affecting growth and survival. Understanding mechanisms operating at invasion boundaries may help develop management strategies to prevent future spread of smallmouth bass into headwater salmon habitat.

Keywords: secondary spread, range expansion, invasive species, headwater, young-of-the-year

Introduction

Nonnative species have been widely introduced, including into freshwater ecosystems of the northwestern United States (Sanderson et al. 2009). Although rates of intentional introductions by agencies have generally slowed in recent decades, many species are continuing, or have the potential, to expand their range in response to continued environmental change (Vander Zanden and Olden 2008). One of the primary determinants for a species to successfully expand its range is the ability for young-of-the-year (YOY) to survive (i.e., recruit) in new habitat (Angert et al. 2011, Blackburn et al. 2011). Examining patterns of YOY growth and survival near range boundaries may provide useful insight into mechanisms, and thus management strategies that constrain species’ range expansion.

In the Columbia River basin, nonnative smallmouth bass (Micropterus dolomieu) was introduced in the early 20th century and now supports a multi-million-dollar sport fishing industry (Carey et al. 2011). Smallmouth bass, a cool water predator native to central and part of the eastern United States and Canada, has also been implicated in the decline of wild populations of native Pacific salmon (Fritts and Pearsons 2004, Carey et al. 2011). Recent decades have seen smallmouth bass expand its range into headwater habitats of the Columbia River basin, calling attention to the need to understand mechanisms that enable successful range expansion (Lawrence et al. 2012).

The John Day River is the largest undammed tributary of the Columbia River and home to a prized smallmouth bass fishery. Initially, smallmouth bass from the Columbia River were unable to colonize the John Day River due to an impass-
able (for smallmouth bass) waterfall near the John Day River mouth (Tumwater Falls at river kilometer [RKM] 16). In 1971, however, 80 individuals were introduced upstream of that barrier at a location approximately 42 km downstream of the mouth of the North Fork John Day River (Shrader and Gray 1999). Smallmouth bass have since expanded approximately 150 km upstream into the North Fork John Day River and have encroached on endangered, wild, juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*) rearing habitat (Lawrence et al. 2012).

The spatial congruence of smallmouth bass populations and Chinook salmon rearing habitat varies across time in the North Fork John Day River (Lawrence et al. 2012, Rubenson and Olden 2017). Recent surveys indicate that the invasion edge of smallmouth bass shifts both seasonally and inter-annually, but that there has been an overall trend of upstream expansion since 2009 (Rubenson and Olden 2017). Each spring, some adult smallmouth bass move upstream, spawn, and then return downstream in the late summer and early fall. Although there are detailed data on the adult movement and spawning patterns, little is known about the growth and survival dynamics of the resultant YOY. Based upon previous modeling, it is hypothesized that the growth potential in the most upstream habitats (i.e., ≥ RKM 90) is insufficient to provide adequate energy reserves for YOY to survive the winter (i.e., cold-water period) (Lawrence et al. 2015), but this hypothesis has yet to be tested.

Our objectives were to 1) characterize the growth and body length distributions of YOY across the upstream-most 63 km of riverine smallmouth bass distribution, 2) explore potential determinants of YOY length, 3) examine post winter length distributions, and 4) compare observed lengths (pre- and post-winter) with lengths predicted by temperature-dependent models of growth and survival (Shuter et al. 1980).

**Methods**

**Study Area**

Our study examined the growth and survival of YOY smallmouth bass in the upstream 63 km of its distribution in the North Fork John Day River (i.e., upstream of RKM 54) (Figure 1). The John Day River is an undammed major tributary of the Columbia River that originates in the Blue Mountains of northeastern Oregon. The hydrology is characterized by a snowmelt flow regime, resulting in peak discharges in the spring that decline to a summer base flow that remain low until early winter (Figure 2). In the North Fork John Day River, mean daily water temperature ranges from 0 °C (i.e., ice over) in winter to > 25 °C in summer (Figure 2). Channel gradients range from 2.4 m km\(^{-1}\) to 30 m km\(^{-1}\), producing a thermal gradient that cools approximately 0.3 °C every 5 km. This results in a 4.5 °C difference in daily mean temperature between the most upstream (RKM 117) and downstream (RKM 54) temperature of our study extent (Figure 2). Guided by previous snorkel surveys, our study area encompassed portions of the river that have had year-round presence of smallmouth bass since at least 2009 (i.e., below RKM 72) and continued upstream to 5 km beyond the most upstream presence of smallmouth bass observed in 2014 (Rubenson and Olden 2016).

**Temperature and Discharge**

Water temperature was recorded using a series of pendant temperature loggers (HOBO pendant, Onset Electronics, Onset, Massachusetts) distributed across the upstream 63 km of smallmouth bass distribution in the North Fork John Day River. Loggers were placed approximately 5 km apart. Temperatures were recorded at 1-hour intervals from June 2014 to October 2015. Linear models were then fit to estimate hourly water temperature at a 1-RKM scale ($R^2 = 0.958$ to 0.992, all $P < 0.001$). Smallmouth bass are considered to rarely feed once temperatures drop below 10 °C (Shuter et al. 1980). As such, we quantified the winter starvation period by tallying the number of days below a mean daily temperature of 10 °C, generally beginning in fall and ending in spring. Daily mean temperature for tributaries of the North Fork John Day River were obtained from the Integrated Status and Effectiveness Monitoring Program database (ISEMP 2018), which measured daily temperature using loggers from June to October 2001–2003.

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gers in tributaries and their confluence with the mainstem North Fork John Day River. Finally, discharge \( \text{m}^3\text{s}^{-1} \) was collected from the USGS gauge station 14046000, located at RKM 24 of the North Fork John Day River.

Collection and Processing of YOY

Individuals spawned in spring 2014 were collected at pre-selected glides distributed approximately every 3–7 km along the upstream-most 63 km of smallmouth bass distribution (Figure 1). Glides were selected to be similar in length (between 100–200 m), width (20–40 m), and to have substrate and vegetation characteristics conducive to smallmouth bass spawning. Upstream of RKM 90, smallmouth bass occurrence was extremely rare, and surveys in 2014 indicated only four smallmouth bass nests that received eggs (Rubenson and Olden 2016). As such, the sample sites upstream of RKM 90 were aligned with nest locations. The spring 2014 fish cohort were collected twice; once as YOY during the fall of 2014 as mean daily temperatures declined toward 10 °C—the threshold below which feeding reportedly stops (Table 1; Figure 3a) and again as age-1 fish in the spring of 2015 as mean daily temperatures warmed above 14 °C—the threshold at which growth begins (Table 2; Figure 3b). Between 10–14 °C, feeding occurs, but not at sufficient levels to achieve growth (Shuter et al. 1980). Two attempts were made to capture age-1 fish during the spring; one in May and one in June. During the May survey, water temperatures were below 14 °C, but the water was too deep and discharge too swift to efficiently capture age-1 fish. In addition, a two-week rain event increased the discharge and water depths during the survey, preventing further sampling at that time (Figure 2). As such, only 18 individuals were captured in four glides. These 18 individuals, however, provided a useful baseline for body lengths before spring growth could occur. A growth correction was applied to individuals captured in June (see below), and resultant sizes were compared with the 18 individuals captured in May.

Two survey methods were used in every unit to capture the spring 2014 cohort. For shallow (depth < 0.5 m) areas characterized by cobble, silt, or vegetated substrate, we used a 3-m beach seine (3-mm bar mesh) to capture individuals. In depths > 0.5 m or areas with boulder substrate, we set dog-food baited Gee minnow-traps (23 x 44 cm, 2.5 cm opening, 0.6 cm mesh) overnight. Traps were set between 0.5 m and 1 m depths approximately every 10 m along both shorelines.

Figure 1. The location and watershed of the North Fork John Day River, Oregon. The survey extent is highlighted in the lower box, with river kilometer (RKM) and large tributaries annotated. The gray circles indicate the distribution of sample sites where young-of-the-year and age-1 smallmouth bass were collected in 2014–2015.
Smallmouth bass were extracted from the nets or traps, and all other fishes released. Smallmouth bass were killed using an overdose of MS-222 and total length (mm) (hereafter, body length) was measured. Individuals were then placed in individual bags and frozen on dry ice until transport back to the laboratory.

**Aging and Growth of YOY**

The otoliths from 100 YOY were extracted for aging (Table 1), 95 of which had daily increments successfully enumerated. These YOY were subsampled from the total number of smallmouth bass collected during the fall surveys in select sample sites distributed across the survey extent (RKM 57 [n = 24], RKM 69 [n = 25], RKM 78–87 [n = 24], RKM 102–110 [n = 22]) (Table 1). Otoliths were extracted by Washington Department of Fish and Wildlife (WDFW) and mounted in thermoplastic resin, ground using successive grits of lapping film (30–5 μm grit size), and polished using aluminum oxide slurry (1 μm grit size). Otoliths were imaged (20X) using a Leica DM100 compound scope paired with a DFC 450 camera and increments enumerated using Image Pro software. Daily increments were independently enumerated by two readers beginning at the hatch check out to the dorsal edge (Hill and Bestgen 2014). The average percent error index (Beamish and Fournier 1981) between readers was 2.2% and the mean difference between readers was 3 days (d) (min = 0 d, max = 9 d). After completing increment analysis, days from hatch date was calculated as the mean of all reads for each fish, rounded to the nearest integer. Growth rate (mm d⁻¹) was then calculated for each fish based on number of days from hatch date (d) and body length at capture.

**Predicted Length and Survival**

Predicted body length (mm) was calculated using the smallmouth bass YOY daily growth model from Shuter et al. (1980):

\[ G = \begin{cases} 
0.0, & T < 14 \degree C; \\
-1.7 + 0.12T, & 14 \degree C \leq T < 25.5 \degree C; \\
1.4, & 25.5 \degree C \leq T < 31.5 \degree C; \\
1.4 - 0.04T, & 31.5 \degree C \leq T \leq 35 \degree C 
\end{cases} \]

where T is daily mean temperature (°C) and G is daily growth (mm). This model assumes maximum feeding rates, and therefore reflects the maximum body length achievable based upon the thermal conditions. It also accounts for limitations to
growth at high temperatures (i.e., > 35 °C). To determine predicted lengths at the end of the growth season (i.e., fall 2014), modeled daily growth was summed over the growing season, ending at YOY capture date, using daily mean temperatures at each sample site.

Three curves predicting the potential growth of YOY smallmouth bass across the study area were developed. The first curve calculated potential growth assuming that spawning began on the first day mean daily water temperatures warmed above 15 °C (the temperature at which spawning is typically initiated) (Rubenson and Olden 2016). We use this curve to provide a benchmark for the maximum size that could be attained had spawning occurred as soon as conditions became amenable. Here, we also assumed immediate brood development, adding 9.1 mm to the summed daily growth increments to account for the average length of fry when they rise from the nest (Shuter et al. 1980). The second and third curves calculated potential growth from the first and last date of observed spawning, which were often delayed relative to when water temperatures first exceeded 15 °C. To determine this timing, a comprehensive assessment of spawning events was conducted. Spawning was assessed via repeat snorkel surveys by two snorkelers on opposite shorelines (Rubenson and Olden 2016). All nests were geo-referenced, enumerated, and then monitored for success throughout the spawning season (i.e., June to August) (Table 1). Spawning initiation was defined as the date a nest received eggs. When there was a discrepancy between observed spawning dates and spawning dates calculated from otolith ages (Table 1), the most conservative date was used. Again, we added 9.1 mm to the summed daily growth increments based on early spawn timing but elected to not make this correction for the estimates for late spawn timing. This delivers a more conservative estimate of minimum body length predicted at that location. Predicted body lengths were then compared with observed body lengths.

Predicted survival was calculated using the Shuter et al. (1980) survival index. This index describes the probability that a YOY smallmouth bass will survive a winter (i.e., cold-water) starvation period based upon its body length at the end of the growing season. It was calculated as:

\[ L_0 = 0.188d + 14.8 \]

where \( L_0 \) represents the length (mm) below which survival is predicted to be 0% and \( d \) is the duration.

<table>
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<tr>
<th>RKM</th>
<th>Sampled @ Sampling</th>
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<th>T &lt; 14 °C</th>
<th># YOY</th>
<th># Otoliths</th>
<th>Observed Spawn</th>
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TABLE 1. Fall 2014 survey data at each sample site, including river kilometer (RKM), sampling date, mean daily temperature (°C) at time of sampling, date when growth ceased (i.e., when daily mean temperature fell below 14 °C), number of young-of-the-year (YOY) captured, number of captured YOY that also had otoliths analyzed, observed spawn timing, calculated spawn timing from aged YOY, and the number of observed nests that produced swim-up fry.
of winter (daily mean temperature < 10 °C) in days. Observed body lengths (mm) of age-1 fish collected in the spring of 2015, after a winter starvation period, were compared with the predicted minimum body length required for survival ($L_0$) to test the accuracy of this model in predicting survival in this system. In some sample sites, the age-1 fish were collected after temperatures were sufficiently warm for post-winter growth to occur. In these cases, a length correction was applied using sizes calculated from the modeled growth equations (Table 2). Specifically, the potential growth incurred during spring 2015 was subtracted from size at capture. Resultant lengths were then compared with individuals collected in May 2015 (i.e., before temperatures warmed to above 14 °C when growth begins) to validate the use of this correction.

Smallmouth Bass Density

The linear density of smallmouth bass YOY was measured using quantitative surveys in the fall of 2014. Each sample site was divided into 20 m transects within 5 m of both shorelines. Surveys were conducted a minimum of 20 m from the previous transect to ensure independent counts. The number of transects surveyed was proportional to the length of the sample site (105–250 m), with a maximum of 10 transects surveyed (divided evenly between both shorelines). For each transect, a snorkeler swam in the center and reported counts of YOY smallmouth bass to an above water observer. Density was then calculated by dividing the sum of the YOY smallmouth bass observed by the total length surveyed in each sample site.

The linear density of smallmouth bass age ≥ 1 was estimated using two separate snorkel surveys in the spring and fall of 2014. Two snorkelers sampled individual sample sites on opposite shorelines, surveying in an upstream direction. Snorkelers reported the number of age ≥ 1 smallmouth bass (> 100 mm) in each sample site to an above water observer. Counts between the two surveys were averaged, and density was calculated by dividing the average count by the length of the sample site surveyed.
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Statistical Analysis

All statistical analyses were conducted in R version 3.3.2 (R Development Core Team 2016). We used linear modeling to examine the determinants of body length (mm) at each sample site as a function of age estimated from otoliths (days), mean temperature (calculated for each individual based upon its age and sample site) (°C), and intraspecific density of both age ≥ 1 and YOY. Models were built using the 95 individuals that had age determined via otoliths. All possible candidate models (n = 15) were considered, and model support was evaluated using Akaike’s information criterion (AIC) (Burnham and Anderson 2002). Residual and diagnostic plots were examined for evidence of departures from model assumptions. Piecewise linear regression was applied to assess longitudinal trends in mean body lengths (n = 13) and mean growth rates estimated from otoliths (n = 8) using the segmented library in R (Muggeo 2008). Piecewise linear regression identifies breakpoints at which an abrupt change in slope occurs, highlighting departures from linearity.

Results

Contrary to our prediction of a linear, temperature-determined decrease of YOY smallmouth bass lengths from downstream to upstream, we found a more nuanced pattern at the upstream distribution of smallmouth bass (Figure 3a). We captured 426 YOY smallmouth bass across its upstream distribution in the fall of 2014 (Table 1) and 233 age-1 smallmouth bass the following spring (2015) (Table 2). No individuals were captured at RKM 95 or 117, so these sample sites were not included in our analyses. In contrast to an upstream linear decrease in body lengths as predicted by the temperature-dependent growth models, we found a significant breakpoint at RKM 90 (piecewise regression $R^2 = 0.870, P = 0.0003, n = 13$) with a non-significant slope downstream of this breakpoint ($P = 0.693; y = 49.6 + 0.05x$). This result appears to be caused by the majority of individuals in downstream sample sites not achieving the predicted body length based upon spawn timing (Figure 3a). Upstream of RKM 90, individuals achieved the predicted body length based upon observed spawn timing, but appeared constrained by a delay in spawn timing relative to when water temperatures warmed above 15 °C (Figure 3a).

Ages of YOY generally reflected the protracted spawning season observed in 2014. Spawning was initiated in early June in downstream sample sites as water temperatures reached 15 °C, with a progressive delay (relative to water temperature) with increased RKM (Figure 3a). The latest spawning event was observed 10 August at RKM 110, well after water temperatures reached 15 °C (Table 1, Figure 2). Individual YOY aged from

### TABLE 2. Spring 2015 survey data at each sample site, including the river kilometer (RKM), sampling date, mean daily temperature (°C) at time of sampling, date when growth began (i.e., when daily mean temperature increased above 14 °C), number of young-of-the-year (YOY) captured, and a length correction for the potential growth may have occurred prior to sampling.

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<th>RKM</th>
<th>Sampling</th>
<th>T (°C) @ Sampling</th>
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otoliths ranged from 56 to 99 days old (mean = 73 d, SD = 6 d), corresponding to spawning dates of 22 June–5 August. When comparing the ages in each sample site, however, there were some exceptional divergences from the spawn timing observed (Table 1). Specifically, spawning surveys indicated that spawning ceased in June or early July, but otolith ages suggest additional spawning that was not detected in snorkeling surveys.

The density of both age ≥ 1 and YOY smallmouth bass declined in an upstream direction (Figure 4). The maximum observed density of YOY was 0.6 fish m⁻¹, which declined exponentially toward < 0.1 fish m⁻¹ in the uppermost sample sites (y = 1.8 – 0.03x + 0.0002x², R² = 0.525). The maximum observed density of age ≥ 1 fish was 0.3 fish m⁻¹, which declined toward 0.0 fish m⁻¹ moving upstream (y = 0.9 – 0.02x + 0.00009x², R² = 0.834). The top-performing models that predicted individual lengths included mean daily water temperature (°C) over the growth season and the density of age ≥ 1 smallmouth bass (Table 3). This highlights a potential interaction between the length of a growth season and the temperature experienced, but also suggests a negative relationship between the density of age ≥ 1 smallmouth bass and YOY growth in downstream sample sites.

Contrary to our predictions, growth rates did not exhibit a consistent longitudinal pattern (Figure 5). Across the sample sites in which YOY were aged, growth rates ranged from 0.4–0.7 mm d⁻¹ (mean = 0.6 mm d⁻¹, SD = 0.1 mm d⁻¹). We hypothesized that there would be a decreasing linear trend in growth across the study sites based upon growth scope (Figure 3a). Instead, piecewise regression revealed a significant breakpoint at RKM 86 (R² = 0.974; P = 0.0019, n = 8), with a non-significant slope downstream from this breakpoint (P = 0.833; y = 0.7 – 0.0003x). This matches the trend observed in body lengths, with similar lengths in sample sites downstream of RKM 90 and smaller individuals upstream.

We found that the length of the winter starvation period (i.e., the number of days < 10 °C) did not predict the minimum size of age-1 fish post-winter. Instead, 23% of the age-1 fish collected in the spring (after the cold-water winter period) were smaller than the size below which we predicted 0% survival (Figure 3b). In the sample sites upstream of RKM 100, however, no recruitment was observed, which matched the modeled prediction. By contrast, mean and maximum sizes remained relatively unchanged after winter. In all but one sample site (RKM 90), measurements of mean and maximum body lengths of YOY before and age-1 after winter were within 5 mm of each other (Figure 3b). At RKM 90, however, we found that age-1 individuals were on average 9 mm larger than YOY captured the previous fall.
and we found a difference of 21 mm between the maximum length of YOY and age-1.

### Discussion

Our study presents the first assessment of smallmouth bass YOY growth and recruitment at its upstream-most distribution. We show that the factors that influence growth rates, body length, and overwinter survival vary considerably across the upstream 63 km of its distribution. The most upstream sample sites were predictably constrained by season length and temperature, but were also substantially influenced by a delay in spawn timing (Figure 3a). By contrast, the most downstream sample sites were not well predicted by season length and temperature, but instead revealed evidence for additional constraints on growth related to bass density. Furthermore, we found that some small individuals were able to survive an overwinter starvation period despite not attaining the predicted minimum survival size ($L_0$) according to temperature-dependent growth models (Figure 3b).

In the most downstream sample sites, YOY body length at the end of the growth season fell short of model benchmarks (Figure 3a). Models predicted that YOY in downstream sample sites would receive growth benefits from warmer temperatures and a longer growth season (Figure 3a). Instead, the majority of observed body lengths were either below or near the minimum predicted lengths, creating a departure from the hypothesized linear relationship between body length and RKM (Figure 3a). This was also exhibited in the non-significant slope across growth rates in the downstream sample sites (Figure 5). Although it is not surprising that some individuals fell below the modeled predictions (due to the assumption of maximum consumption and potential errors in calculating the last spawning date), this result suggests that other mechanisms may be in operation. One explanation could be that smaller YOY from upstream sample sites were displaced into lower sample sites, potentially confounding the data. Dispersal of YOY was not measured and recent research indicates that smallmouth bass juveniles may undergo frequent, albeit short-distance, movements in lotic systems (Humston et al. 2017). In addition, passive dispersal during high flow conditions can force YOY downstream (Humston et al. 2010). Although there were no high discharge events between 01 June 2014 (before spawning began) and 27 September 2014 (the last collection date in the fall) (Figure 2), even small discharge events could displace fry or small individuals (Simonson and Swenson 1990). The potential that YOY were mobile could also explain some of the discrepancies between observed spawn timing and calculated ages. The influence of YOY movement on our results remains an open line of research. Dispersal from upstream, however, would also not explain the paucity of large individuals in the most downstream sample sites and research suggests that YOY generally remain within a few hundred meters from their natal nest site (Langhurst and Schoenike 1990, Scott et al. 1997). Another explanation for the lack of a longitudinal relationship could be that biological interactions—specifically competition or risk of predation—may be limiting growth in this region of the invasion boundary. We show that intra-specific density declines from downstream to upstream (Figure 4), which corresponds with our observations that body lengths are smaller than predicted in downstream sample sites. This hypothesis is supported by our modeling exercise, which indicated a significant negative relationship.

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### Table 3

Summary of the top five regression models predicting body length (mm) of aged young-of-the-year (YOY) smallmouth bass ($n = 95$) collected in the fall 2014 as a function of mean daily water temperature ($^\circ C$), age (days), and density of YOY and adult smallmouth bass at each sample site. The null model AIC is 740.3. All candidate models provided in Supplemental Table 1.

<table>
<thead>
<tr>
<th>Model</th>
<th>$R^2$</th>
<th>AIC$_i$</th>
<th>$\Delta$AIC$_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp*, Adult Density*, Age</td>
<td>0.597</td>
<td>656.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Temp*, Adult Density*</td>
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<td>657.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Temp*, Adult Density*, YOY Density</td>
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<td>657.6</td>
<td>0.7</td>
</tr>
<tr>
<td>Temp*, Adult Density*, Age, YOY Density</td>
<td>0.594</td>
<td>658.4</td>
<td>1.5</td>
</tr>
<tr>
<td>Temp*, Age</td>
<td>0.563</td>
<td>663.6</td>
<td>6.7</td>
</tr>
</tbody>
</table>

* $P < 0.05$
between adult density and YOY body lengths (Table 3). This mechanism is supported by Ridgway et al. (2002) who found that first year growth was negatively correlated with abundance of age 1–4 smallmouth bass. In addition, pools with high densities of largemouth bass juveniles have been shown to reduce juvenile growth when compared to low density pools (Ludsin and DeVries 1997), and results from individual based modeling of smallmouth bass show that high densities consistently lead to smaller juvenile size (DeAngelis et al. 1991). The potential that adult abundance in downstream sample sites has a negative effect on YOY growth could have important management implications. Specifically, any efforts to remove adults in these sites could result in increased growth of YOY, potentially confounding control efforts. By contrast, adult removals further upstream is these sample sites might be in close proximity to a thermal refuge. For instance, RKM 90 is located at the confluence of a warm water tributary (i.e., Camas Creek) (Figure 1). On average, the mouth of Camas Creek is approximately 0.6 °C warmer than the North Fork John Day River just upstream of the confluence with Camas Creek. This suggests that warm water tributaries may confer growth benefits to individuals assuming adequate access to these habitats. The growth opportunities provided by warm water refuges during the winter may provide a number of advantages, such as reduced risk of predation (Miller et al. 1988, Post et al. 1998), quicker transition to piscivory (Ludsin and DeVries 1997, Phelps et al. 2008) and lower risk of mortality from starvation (Shuter et al. 1980, Post et al. 1998). In addition, perennial tributaries, such as Camas Creek,
may provide overwinter refuges where growth is still possible despite cold temperatures in the main channel. Smallmouth bass has been shown to use thermal refuges in other streams during cold-water periods, demonstrating a propensity for thermoregulation (Peterson and Rabeni 1996, Carter et al. 2012, Westhoff et al. 2014). Refuges can act to buffer populations from fluctuations in inter-annual conditions, potentially acting as a source population after prohibitively cold winters (Peterson and Rabeni 1996). In addition to warm water tributaries, groundwater upwelling and deep pools may also provide thermal refuge in the North Fork John Day River (Torgersen et al. 1999). It is unknown if a thermal refuge exists near RKM 69 and 72.

In the most upstream sample sites (i.e., > RKM 90), body lengths matched our modeled predictions according to temperature-dependent growth, but were also heavily constrained by spawn timing (Figure 3a). In 2014, adults did not spawn upstream of RKM 90 until late July; a month after temperatures had exceeded 15 °C (Rubenson and Olden 2016). This delayed initiation of spawning truncated the length of the overall growing season and reduced the maximum body length that YOY could achieve entering into the winter. Had spawning occurred as temperatures warmed above 15 °C, the YOY upstream of RKM 90 could have potentially grown 5–15 mm larger before water temperatures began to cool in the fall (Figure 3a). This highlights the interaction between adult overwintering location and spawning habitat. Specifically, a previous survey found that adults abandon the upper reaches of the North Fork John Day River in the early fall—overwintering downstream (Rubenson and Olden 2017). Adult smallmouth bass often exhibit strong site fidelity to overwinter sites that, in cold-water habitats, are characterized by deep pools or nearby lakes. This suggests a high metabolic cost of remaining resident in spawning and summer feeding habitats in the upstream edge of smallmouth bass distribution. The mismatch between overwintering habitat and spawning habitat likely contributed to spawning delays, therefore a better understanding of limitations to adult overwintering locations may provide a key piece to the recruitment potential of smallmouth bass at its invasion boundary.

The observed minimum body length required to survive an overwinter starvation period did not match modeled predictions according to the survival equations of Shuter et al. (1980) downstream of RKM 90 (Figure 3b). At least two reasons may explain this result. First, our analysis relied on daily mean temperatures measured at a single location in the channel, thus not accounting for small-scale thermal refuges for fishes caused by groundwater upwelling, vegetation, interstitial spaces in the substrate, stratified pools, and/or tributaries (Torgersen et al. 1999, 2006; Peterson and Rabeni 1996; Westhoff et al. 2014). There are multiple deep pools, rock crevices, and thick vegetation in the North Fork John Day River that may support warm water microhabitats important to overwintering fish. Second, it is possible that the survival equations of Shuter et al. (1980) are not appropriate for rivers, specifically in the Pacific Northwest. These equations are based on temperate populations of lacustrine smallmouth bass in Canada, which may have different physiological responses based on adaptive differences (Shuter et al. 1980). For instance, populations of largemouth bass from high, intermediate, and low latitudes were shown to be locally adapted to winter severity, causing low-latitude juvenile largemouth bass to experience increased mortality over high-latitude juveniles under the same winter conditions (Fullerton et al. 2000). Even if local adaptation cannot account for differences in survival, however, the severity of the winter may play some role in the observed differences. Specifically, the winters in the John Day River do not exhibit rapid declines in temperature below 10 °C, but instead hover between 7–10 °C for 30–60 days (Figure 2). This is in sharp contrast to lacustrine habitats that often show rapid temperature shifts post turnover of the lake water column. There is evidence that although smallmouth bass activity level declines rapidly below 10 °C, it is not until 7 °C that they remain completely inactive and do not feed. Shuter et al. (1980) states that, “Experiments showed that the activity of the young of year drops markedly as the temperature falls below 10 °C. At 7 °C and below, the fish seek shelter, remain inactive for
long periods, and do not feed.” Although the 10 °C threshold is typically used in the models, the starvation experiments conducted by Shuter et al. (1989) used temperatures less than 7 °C. We found that using a 7 °C threshold better predicted survival in 2015, with the estimated 0% survival line (L₀) falling reasonably close to the smallest observed age-1 fish that survived to the spring (Figure 3b). This suggests that the survival equations are appropriate and effective for YOY smallmouth bass in the North Fork John Day River, but that 7 °C is a more accurate temperature threshold to use when calculating winter length. Examining the mechanism of mortality, however, remains an open line of research in the leading edges of riverine invasions.

In comparing the size of fish before and after the winter, it is important to note that the winter period in the North Fork John Day River in 2014 was characterized by several high discharge events that could have displaced individuals downstream (Figure 2). During these periods, however, water temperatures were cold, which affects smallmouth bass behavior. In temperatures below 7 °C, YOY seek shelter and remain inactive (Shuter et al. 1980)—behavior that was observed during our surveys. The benthic nature of YOY during cold temperatures may make them less susceptible to passive transport during high discharge events in the winter. This, however, remains an open line of research. Even if YOY were displaced downstream, however, it does not explain how fish predicted to have insufficient lipid reserves to survive a winter starvation period (i.e., fish smaller than L₀) were present in downstream sample sites. Had the smaller individuals been displaced from upstream units, they still should have accumulated additional days of winter to survive based on models using a 10 °C threshold.

In the most upstream sample sites (i.e., > RKM 90), we were unable to locate any YOY post-winter, suggesting little to no survival. The individuals in these locations were the smallest and experienced the longest winter (Figure 3b). Several mechanisms can account for high mortality rates. First, these small individuals had vastly insufficient energy reserves available to survive a long winter, regardless of whether the winter threshold was at 10 °C or 7 °C, falling well below the predicted 0% survival line (Figure 3b). In addition, small size also likely increased their susceptibility to predation. Smaller individuals are more prone to predation risk due to being within the gape limitation of more predators and having reduced mobility than larger conspecifics (Post et al. 1998, Hurst 2007). These two factors were coupled with very low reproductive activity upstream of RKM 90, leading to low abundances relative to downstream. Specifically, only four nests were observed over the most upstream 27 km of our survey extent (Rubenson and Olden 2016). Between these four nests, the two closest singular nests were distributed at least 300 m apart, leading to extremely low densities of YOY fishes (Figure 4). These low abundances made complete mortality more likely.

One major limitation to our study is the scarcity of data above RKM 80. Although the sample sizes are small, they are representative of the density of smallmouth bass, particularly above RKM 80. There were very low abundances of adults upstream of RKM 80 and only a few successful nests (Figure 4, Table 1). We present these data to highlight potential differences in mechanisms that affect growth and survival at the upstream distribution of invasive smallmouth bass. In downstream sample sites, we depict an environment in which there is likely a complex interaction of factors influencing the growth scope of YOY. By contrast, growth in upstream sample sites is more easily predicted from spawn timing and the thermal regime alone. These differences are important to understand to appropriately tailor future management strategies.

Although there is some evidence that the temperature threshold most appropriate to predict 100% overwinter mortality was closer to 7 °C than 10 °C based on fish collections in May and June (as discussed above), combining a calculation of predicted lengths and the minimum size predicted to survive based on local daily mean temperature can potentially predict the edge of recruitment to within 10–20 km (Rubenson and Olden 2017). Thus, using only temperature data, managers
have access to an easy, inexpensive, and quick method to locate the approximate recruitment boundary in an unstudied system where smallmouth bass has been introduced. This may hold utility when predicting the invasion extent of a long-established population where data are scarce or if predicting the potential invasion extent of a newly introduced population of smallmouth bass. Knowing the potential for invasion can provide incentives for control or eradication efforts before an expanding population achieves the physiological range boundary.

Conclusion
Managers throughout the Pacific Northwest are charged with conservation of native fishes in addition to supporting a healthy and economically viable smallmouth bass fishery (Carey et al. 2011). Understanding recruitment dynamics may provide new management tools that can protect critical headwater habitats from range expansion of smallmouth bass while still preserving fishing opportunities downstream. Here we demonstrate that growth potential at the most upstream edge of smallmouth bass distribution is strongly influenced by temperature, although mediated by biotic conditions such as spawn timing and the density of age ≥ 1 smallmouth bass. This highlights the sensitivity of the YOY life-history stage to temperature. Initiatives that reduce the growing season such as riparian zone restoration (which can cool streams) (Lawrence et al. 2014), timing dam releases of cold water to deter or delay spawning (Olden and Naiman 2010), and other control strategies, including inducing spawning failure via nest destruction (Loppnow et al. 2013) may deter recruitment in new habitat. Understanding the mechanisms that enable the secondary spread of nonnative species can ultimately improve our ability to manage streams that are now home to both native and nonnative species.

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