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ARTICLE

Spatiotemporal Spawning Patterns of Smallmouth Bass at Its Upstream Invasion Edge

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Abstract
Climate change and land-use practices are causing widespread warming of streams, forcing resident species to adapt or migrate. For instance, in the John Day River, Oregon (Columbia River basin), rising temperatures are facilitating the range expansion of Smallmouth Bass *Micropterus dolomieu* into critical salmon rearing habitat. Understanding Smallmouth Bass reproductive ecology at its range boundaries is integral to understanding and ultimately predicting its upstream range expansion. We addressed this knowledge gap by exploring potential temperature-mediated effects on Smallmouth Bass reproduction at the leading edge of its nonnative riverine distribution in the Pacific Northwest. We used continuous snorkel surveys to characterize its upstream extent in the North Fork John Day River, where we observed spawning patterns and measured adult nest-guarding male size, fecundity, brood development, habitat attributes, and nest success over 2 years (2014, 2015). We found a pattern of asynchronous and protracted spawn timing across the leading invasion edge, >90% nest success, and few changes in reproductive attributes (e.g., fecundity, brood development) as the thermal regime became increasingly colder. We also found increased selectivity of nest substrata and decreased guarding requirements in upstream habitats. These results suggest that reproductive success does not limit the upstream range expansion of Smallmouth Bass and highlight potential ecological benefits that may offset the energetic demands associated with dispersing upstream. Overall, our findings enhance the current understanding of how reproduction influences range expansion of nonnative Smallmouth Bass populations in streams, enabling us to better guide managers tasked with minimizing the spread of this nonnative species in the future.

Temperature is a key ecological attribute in freshwater ecosystems, influencing productivity, water quality, habitat availability, and the metabolism, abundance and distribution of ectothermic organisms (Magnuson et al. 1979; Caissie 2006). In recent years, rising air temperatures, changing hydrologic regimes and increasing land-use change have acted synergistically to cause widespread stream warming (Kaushal et al. 2010; Carpenter et al. 2011). Elevated stream temperature is now one of the most pervasive water quality issues in the Pacific Northwest region of the USA, and ongoing climate change and loss of riparian vegetation is predicted to exacerbate this problem (Isaak et al. 2012; Wu et al. 2012; Arismendi et al. 2013). Warming temperatures threaten native coldwater fish species, including Pacific salmon, both in potential loss of thermally suitable habitat (Wenger et al. 2011; Ruesch et al. 2012) as well as through facilitating range expansion of nonnative warmwater predators such as Smallmouth Bass *Micropterus dolomieu* (Rahel and Olden 2008; Lawrence et al. 2014). Smallmouth Bass have both direct predation impacts on salmonids as well as indirect nonconsumptive impacts such as through effects on behavior, growth and stress (e.g., Carey et al. 2011; Kuehne et al. 2012).

The Smallmouth Bass is a warmwater sportfish native to central and parts of eastern USA that has been routinely stocked outside its native range, both throughout North America and globally (Carey et al. 2011; Loppnow et al. 2013). In the Pacific Northwest, Smallmouth Bass has been purposefully introduced since the early 20th century, beginning in 1923 with a couple hundred fish stocked in the Willamette River, Oregon, followed by several thousand fish

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in the Yakima River, Washington, in 1925 (Lampman 1946). Intentional stocking by state natural resource agencies continued throughout the middle and late parts of the century and in recent decades has generally slowed. However, illegal transplants by the public and secondary spread of individuals continues to contribute to a potentially growing distribution throughout the Pacific Northwest (Carey et al. 2011).

Smallmouth Bass has recently been found in cooler headwater habitats that contain endangered subyearling Pacific salmon (Lawrence et al. 2012), heightening concerns about its distributional potential and ecological impacts. Despite emerging evidence that Smallmouth Bass range is expanding upstream, little is known about the critical mechanisms that may promote or inhibit this expansion in the Pacific Northwest. As a known predator and competitor with proven negative implications for native species (Fritts and Pearsons 2006; Tabor et al. 2007; Sanderson et al. 2009; Kuehne et al. 2012), it is essential to have a detailed understanding of these critical drivers to better forecast future range expansion and guide management and education efforts.

The ability to successfully reproduce and recruit in novel habitats is perhaps the most fundamental determinant of range expansion by invasive species (Ibáñez et al. 2014). Smallmouth Bass reproductive success is contingent on a number of factors that include temperature-mediated processes such as spawn timing (Ridgway et al. 1991), parental care (Ridgway and Friesen 1992), offspring development rates (Shuter et al. 1980), and brood survival (Lukas and Orth 1995). Despite a wealth of research on these processes in their native range (e.g., Raffetto et al. 1990; Rejwan et al. 1997; Scott et al. 1997; Wiegmann et al. 1997; Phelps et al. 2008; Steinhart and Lunn 2011), surprisingly little is known for nonnative populations in headwater rivers that are subjected to thermal regimes defined by short growing seasons, variable summer growth temperatures, and long winters. Such environmental conditions in its native range can cause Smallmouth Bass to exhibit significant variation in reproductive strategies (Dunlop et al. 2005), and current models that predict reproductive success often perform poorly outside of the native populations for which they were developed (Dunlop and Shuter 2006). These differences necessitate regional assessments (and ultimately specific parameterization of models) to better inform managers tasked with minimizing Smallmouth Bass spread and impacts.

We investigated mechanisms of Smallmouth Bass range expansion by exploring potential temperature-mediated effects on reproduction at its upstream leading edge of invasion. Rivers draining the Cascade Range of western North America are characterized by a steep temperature gradient over a relatively small spatial scale, providing a powerful opportunity to examine the direct effects of temperature on spawn timing, adult size, fecundity, and overall reproductive success. We first defined the upstream leading edge of Smallmouth Bass spawning distribution in the John Day River basin, then characterized reproductive patterns, and finally assessed nest success along the continuous spatial extent over 2 years. We specifically explored whether reproduction in the leading edge limits the successful establishment of new upstream populations. Suitable temperatures for Smallmouth Bass spawning have been documented to be 12–25°C, and average daily water temperature has been shown to be the single most important variable to predict spawn timing in streams (Graham and Orth 1986). Brood development is also directly related to water temperature (Shuter et al. 1980), with broods developing more slowly in cooler temperatures, thus increasing nest-guarding requirements for males (Ridgway and Friesen 1992). We therefore hypothesized that the gradient of decreasing upstream temperatures would result in (1) a decrease in size and, in turn, a decrease in fecundity of reproductive adults due to relatively shorter growing seasons, (2) slight delays to spawning initiation in response to later water warming, (3) slower brood development rates, and (4) declines in nest success as thermal regimes become colder.

METHODS

In 2014 and 2015, we conducted snorkel surveys of Smallmouth Bass distribution and spawning behavior in a Columbia River tributary, the North Fork John Day River (hereafter the "North Fork"), which originates in the Blue Mountains (Cascade Range) of northeastern Oregon. It is the third longest free-flowing (undammed) river in the contiguous USA, is snowmelt fed, and supports one of the last remaining wild-only Chinook Salmon *Oncorhynchus tshawytscha* Evolutionary Significant Units (Figure 1) south of the Canadian border. Guided by previous snorkel surveys (Lawrence et al. 2012) that defined the upstream leading edge of Smallmouth Bass, our survey extent included 65 km (river kilometers [rkm] 53–117) in 2014 and 70 km (rkm 53–123) in 2015. This represented the spatially variable upstream leading edge of adult Smallmouth Bass distribution and spawning activity. The surveys began at the initiation of spawning and continued throughout the summer until spawning activity ceased (June 10 to August 26, 2014, and May 27 to July 29, 2015).

Thermal regime.—Water temperatures were monitored using an array of 15 temperature loggers (HOBO pendant, Onset Electronics, Onset, Massachusetts) recording at 1-h intervals from May 28, 2014, to October 5, 2015. Water temperatures were assigned to individual nests using a linear extrapolation of recorded temperatures as a function of river kilometer; R^2 values for all models ranged from 0.958 to 0.992 (all $P < 0.001$). Because nest initiation most often occurs as temperatures rise above 15°C (Carlander 1977; Shuter et al. 1980), we used degree days >15°C to describe the thermal history of the adult fish prior to spawning. Spawning degree days were calculated by summing average daily temperatures for all days that exceeded the 15°C threshold beginning each spring.

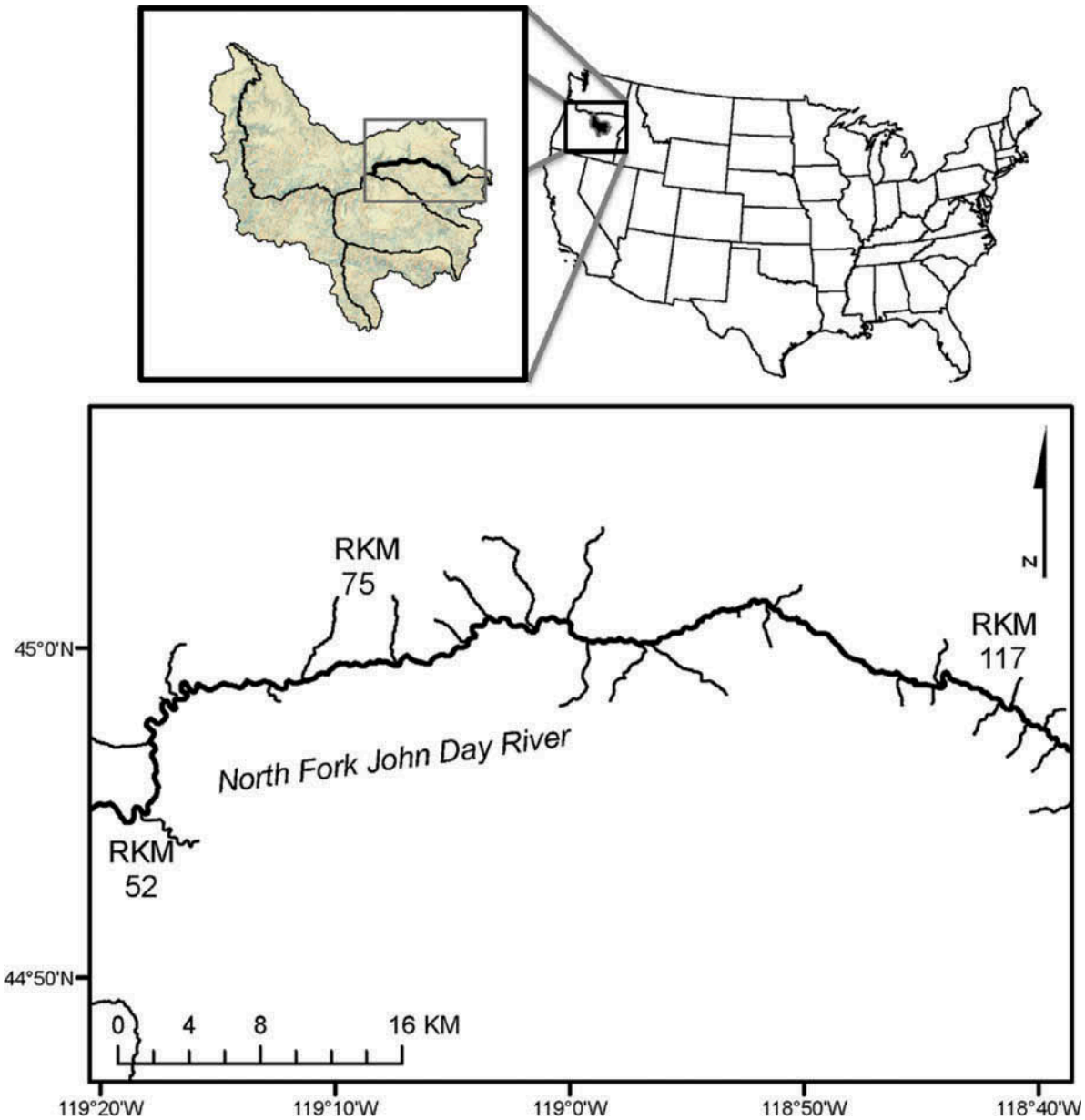

FIGURE 1. Map of the North Fork John Day River and its location in Oregon. The study section with river kilometer (RKM) demarcations are denoted in the lower map.

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Fish distribution and nest surveys.—In 2014, spatially continuous snorkel surveys were conducted in a manner to allow for a comprehensive spatial assessment of spawning, as well as detailed temporal monitoring of nest progression. Snorkel surveys were continued 5 km beyond the most upstream Smallmouth Bass observation, regularly checking further upstream for seasonal shifts in distribution. The resultant 65-km survey extent was delineated into channel units (i.e., riffle, glide-like riffle, glide, glide-like pool, pool) according to changes in current velocity and mean and maximum channel depth profiles following Lawrence et al. (2012). Every channel-unit was sampled, excluding shallow riffles <0.25 m deep. Two snorkelers on opposite shorelines simultaneously surveyed each channel-unit in an upstream direction. Snorkelers reported the number and size-class (<10 cm, 10–20 cm, 20–30 cm, >30 cm) of all observed Smallmouth Bass in each channel unit to an above-water data recorder and geo-referenced the exact location of individual nests. In 2015, glide-like pool habitats were subsampled at 5-km intervals, and the survey extent increased to rkm 123 to match the observed increase in distribution.

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Nest attributes in 2014 were characterized by a consistent observer who measured length and width of swept area (cm), length and width of area in which eggs were present (cm), water depth (m), distance from shore (m), and dominant and subdominant substratum (%) of each nest. Substratum was represented as a composite score determined by multiplying the field-measured substrata data (i.e., percentage of dominant and subdominant substratum) by a score (7 = bedrock, 6 = boulder, 5 = cobble, 4 = gravel, 3 = sand, 2 = silt, 1 = organic matter) and then summing across substratum types (following Lawrence et al. 2012). Nest substratum compositions were then contrasted with available habitat (channel-unit habitat surveys completed in 2009 and 2010 by Lawrence et al. 2012, 2014) to determine substratum selectivity relative to habitat availability across the survey extent. Total body length (cm) of nest-guarding males was visually estimated for 183 occupied nests. Visual size estimates were verified by a subsample of 21 adult males captured; the average difference between actual and estimated total length was 0.71 cm (SD = 2.5). Five scales were also removed from behind the pectoral fin of every captured fish and placed directly on wax paper and stored in coin envelopes for aging. In the laboratory, impressions of the scales were made on acetate slides and viewed under a dissecting microscope at 48× magnification. Scale annuli were then counted to determine age (DeVries and Frie 1996).

Nest progression was monitored via visits to each nest at 3–6-d intervals, averaging four visits per nest. Date, time, and stage of development were annotated at each visit. Following Ridgway and Friesen (1992), nest development was divided into four stages (eggs, hatched embryos, swim-up, and metamorphosis), and nests were considered successful if swim-up fry were produced. Due to the extensive nature of the survey, a small number of nests were discovered after the initiation of hatching. If nests were discovered mid-development cycle, the date of egg deposition was back-calculated using development rates in surrounding nests in comparison to the stage when the new nest was discovered. If no other nests were discovered in near proximity, the egg deposition date was back-calculated using recorded water temperature and the development equations published in Shuter et al. (1980). In a few cases, nests were checked 1–2 d after swim-up occurred. In these rare cases, however, the swim-ups had not yet dispersed and the channel-unit nest density was sufficiently low to confidently assign the group of swim-ups to the marked nest location underneath. We also characterized and monitored nests that were swept and guarded by a male but never received eggs from a female.

In 2014, eggs were collected from 59 nests across the survey extent using a turkey baster (pointed plastic tube with squeeze bulb attached). A 2 × 2-cm gridded quadrat was placed over each nest, and eggs were collected from 10 random cells within the quadrat. The total number of eggs was then estimated using an area-density calculation (validated by counting all eggs from one nest). From the eggs collected, 10 eggs were blot dried and weighed to the nearest 0.1 g in the field and then frozen for laboratory processing. In the laboratory, mean radius of five eggs and their oil droplets were measured from each nest using a digital dissection microscope, and average radius of egg and oil droplet calculated from the five measurements (Gingerich and Suski 2011).

Statistical analysis.—Univariate statistical approaches were conducted in R version 3.2 (R Foundation for Statistical Computing, Vienna). Piecewise (or segmented) linear regression was used to assess differences in spawn timing along the longitudinal gradient using the segmented library in R. This package was designed to fit regression models with broken-line relationships (Muggeo 2008). Given apparent nonlinearity in some relationships, we used segmented linear regression to quantify an abrupt change in the response variable, identifying a specific breakpoint or threshold beyond which the slope of the relationship significantly changes.

RESULTS

Spawning Patterns and Brood Development

The upstream extent of Smallmouth Bass adults was highly concordant with the leading edge of spawning activity in both years. Adult abundance and upstream extent consistently increased from June to August, similar to patterns observed by Lawrence et al. (2012). In early June of both years, the leading edge of adults were concentrated below rkm 66, but as temperatures warmed above 15°C, a portion of the adult population moved upstream, demonstrating a seasonal shift in upstream distribution. Upstream extent peaked in August when adults were recorded up to rkm 110 (2014) and rkm 117 (2015).

A total of 271 nests were discovered in 2014 over the 65-km river stretch representing the leading edge of Smallmouth Bass. Of those, 75% (202) received eggs and 25% (69) did not. Spawning was first initiated on June 10, 2014 (downstream of rkm 66), corresponding with water temperatures increasing above 15°C. With time, nest density increased in downstream habitats and nest activity simultaneously expanded upstream (Figure 2a). Successive nest initiation progressed continuously through July 16, 2014, at which time the most upstream nest was spawned at rkm 90. No Smallmouth Bass were observed above rkm 90 until August. In August, adult distributions expanded into upstream units and four additional nests were observed 10–20 km beyond the previous most upstream nest, extending the upstream limit of reproductive behavior to rkm 110. Spatiotemporal patterns in 2015 were similar to 2014, except that spawning was initiated 2 weeks earlier (May 27, 2015) in response to earlier warming, and the upstream progression of nest activity occurred more rapidly (Figure 3). In total, 144 nests were found in the subsampled habitat, 67% (96) of which received eggs. In comparison, 107 nests were recorded in the same subsampled habitats in 2014.

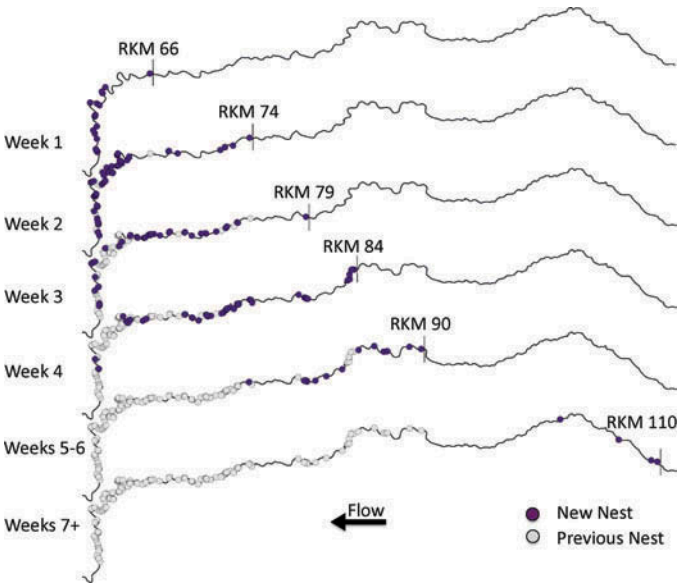

FIGURE 2. Spatiotemporal spawning patterns in the North Fork John Day River for 2014 (June 10 to August 26, 2014). Each panel represents the location of active (old and new) nests during each week of the spawning season. The line demarcates the river kilometer (RKM) of the most upstream nest during the associated week.

In both years, discharge decreased and average daily water temperatures steadily increased beginning in mid-May. Average daily temperatures peaked in July and began decreasing in mid-August. On average, a 3°C temperature differential existed between the most downstream (rkm 53) and most upstream (rkm 117) unit. Average daily temperatures in 2015, however, were approximately 2–4°C warmer from 29 May to 7 July across the entire survey extent (Figure 4), likely in response to considerably lower discharge relative to historical conditions. Regression analysis revealed a significant association between spawning degree days (>15°C) and the date of nest initiation ($R^2 = 0.567$, $P < 0.001$ for 2014; $R^2 = 0.248$, $P < 0.001$ for 2015; Figure 5a, b). The decrease in explained variability in 2015 is probably due to average daily water temperatures rapidly rising above 15°C at the beginning of spawning season, resulting in faster accumulation of degree days (and therefore greater dispersion of points) relative to 2014. Evidence for potential nonlinear relationships in 2014 prompted a piecewise regression to be conducted; this analysis revealed a significant change in slope occurring at rkm 73 ($R^2 = 0.784$, $P = 0.049$) demonstrating that spawning was increasingly delayed in time upstream of rkm 73 in 2014. This threshold response demarcates a shift in reproductive patterns and suggests a secondary mechanism in addition to temperature that may

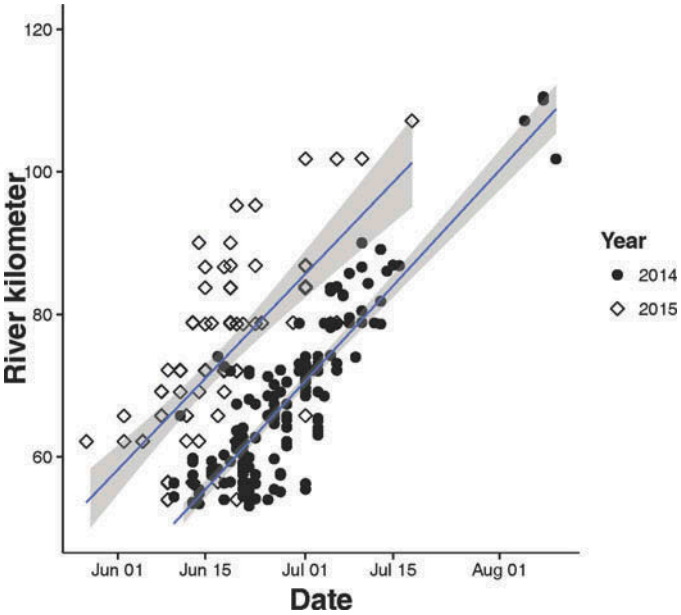

FIGURE 3. Comparison of spatiotemporal spawning patterns in the North Fork John Day River for 2014 and 2015 with associated linear regression lines. Gray shading represents the 95% confidence interval for each regression line. Spawning date and spatial location were significantly correlated in both 2014 ($R^2 = 0.761$, $P < 0.001$) and in 2015 ($R^2 = 0.498$, $P < 0.001$). Note that spawning began and ended earlier and that nests occurred further upstream at an earlier date in 2015 than in 2014.

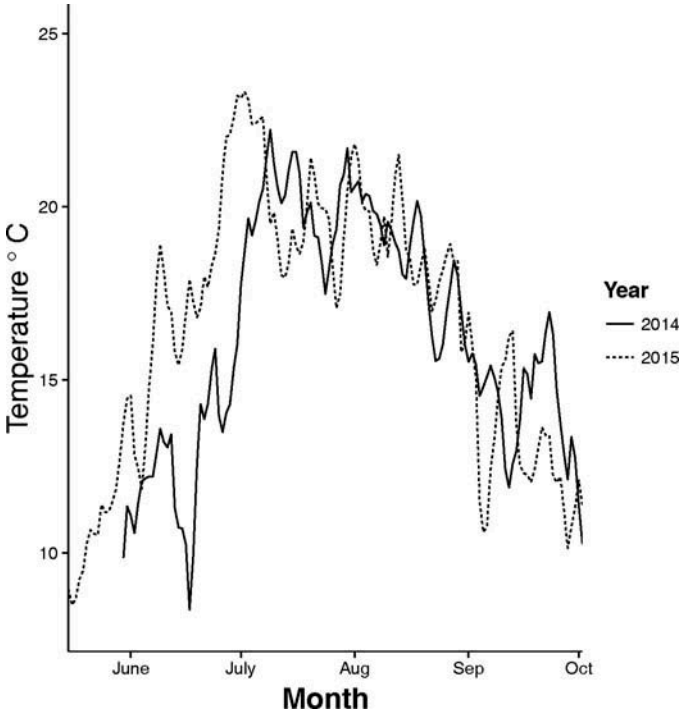

FIGURE 4. Average daily temperature profile at river kilometer 110, highlighting the 2–4°C warmer temperatures in 2015 (dashed line) relative to 2014 (solid line) from May through early July observed throughout the North Fork John Day River.

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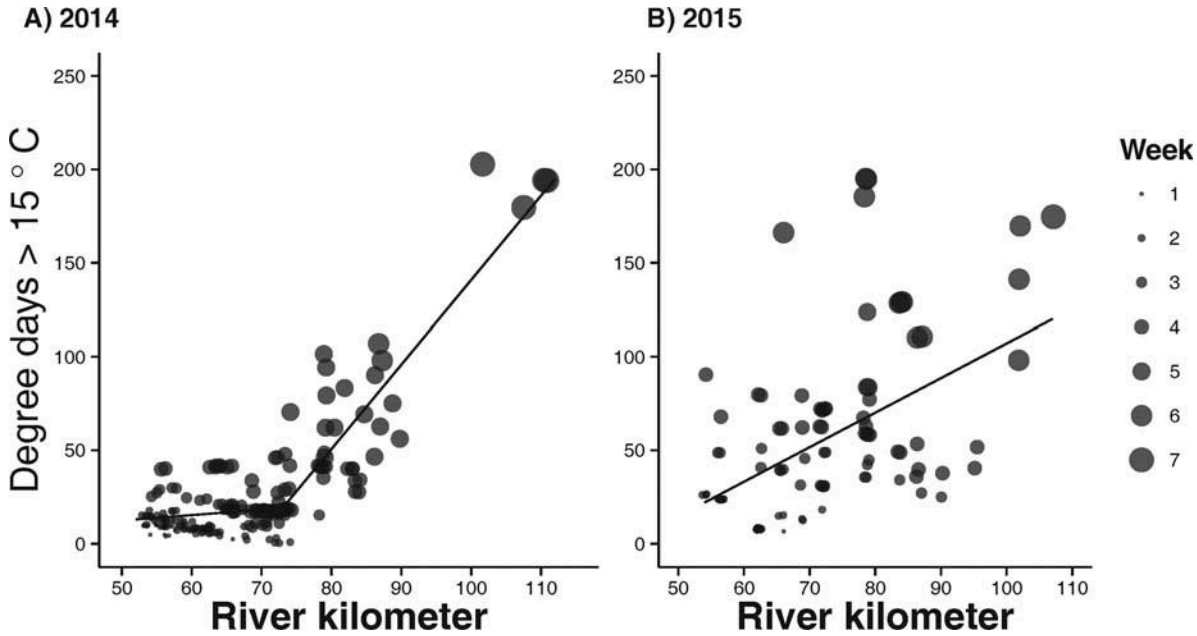

FIGURE 5. The number of degree days >15°C accumulated prior to the initiation of spawning along the spatial extent of the survey in the North Fork John Day River for **(A)** 2014 and **(B)** 2015. Each point represents a nest (points scaled by the week in which each nest received eggs) over the survey period (May–August). Lines of best fit according to the piecewise regression analysis are reported for 2014 ($y = 0.26x - 1.10$ and $y = 4.54x - 312.20$), and linear regression analysis is reported for 2015 ($y = 1.88x - 79.81$).

influence Smallmouth Bass spawning at the leading edge of its upstream distribution.

Brood development rates varied considerably along the longitudinal extent and between years. On average, broods in 2014 were fully developed (eggs to swim-up) in 14 d (range: 7–26 d, SD = 4.357, n = 184) and 9 d (range: 5–14 d, SD = 1.849, n = 89) in 2015. Contrary to our hypothesis, a significant negative linear trend was detected in 2014, indicating that nests in more upstream reaches had broods that developed faster than nests in downstream reaches ($R = -0.634$, $P < 0.001$). In 2015, when warmer water conditions existed through the river, the same declining trend was not observed, but instead the entire survey extent showed rapid brood development and no significant differences between downstream and upstream segments.

Characteristics of Reproductive Adults

Estimated sizes of 183 adult nest-guarding males in 2014 ranged from 180 to 345 mm TL (mean = 253 mm; SD = 30) and measured sizes (n = 21) ranged from 203 to 325 mm TL (mean = 247 mm; SD = 32). Ages ranged from 2 to 6, representing 9%, 62%, 5%, 19% and 5% of spawners, respectively. Similar adult sizes were observed in 2015 (results not shown). Although it is often reported that larger males tend to nest earlier (Ridgway et al. 1991), we found no significant correlations between male size and spawn timing in the North Fork. The maximum size of nesting males did, however, decline from 345 mm to 280 mm, and average size declined from 258 mm (SD = 31) to 237 mm (SD = 22) in upstream segments, indicating a tendency for the largest males to nest downstream (Figure 6a).

Reproductive females were rarely seen spawning; therefore we report patterns in egg size and quantity. Across the spatial extent, egg volume averaged 5.517 mm^3 (SD = 0.856) and egg weight averaged 0.007 g (SD = 0.002). Egg counts ranged from 1,597 to 8,850 (mean = 4,526; SD = 2289). No trend, however, was observed for egg counts or egg size over the spatiotemporal extent of the survey (Figure 6b), suggesting a consistent body size distribution of females.

Habitat Characteristics of Nests

The majority of Smallmouth Bass nests were constructed in either glide-like pool (43%) or glide habitat (36%) at an average depth of 0.57 m (SD = 0.34) and a distance from shore of 1.4 m (SD = 1.7). The remaining nests were in shallow portions of pools or in protected shoreline habitat adjacent to higher flow units. Nests were primarily located in habitats containing cobble and gravel substrate (mean substrata score = 4.3, SD = 1.0). The predominant substrate in the North Fork is cobble (55%) and boulder (36%; Lawrence et al. 2012, 2014). There were no significant longitudinal changes in substrate availability across the survey extent, with the exception of bedrock. Bedrock, however, was less than 15% of any channel reach and represented less than 2%

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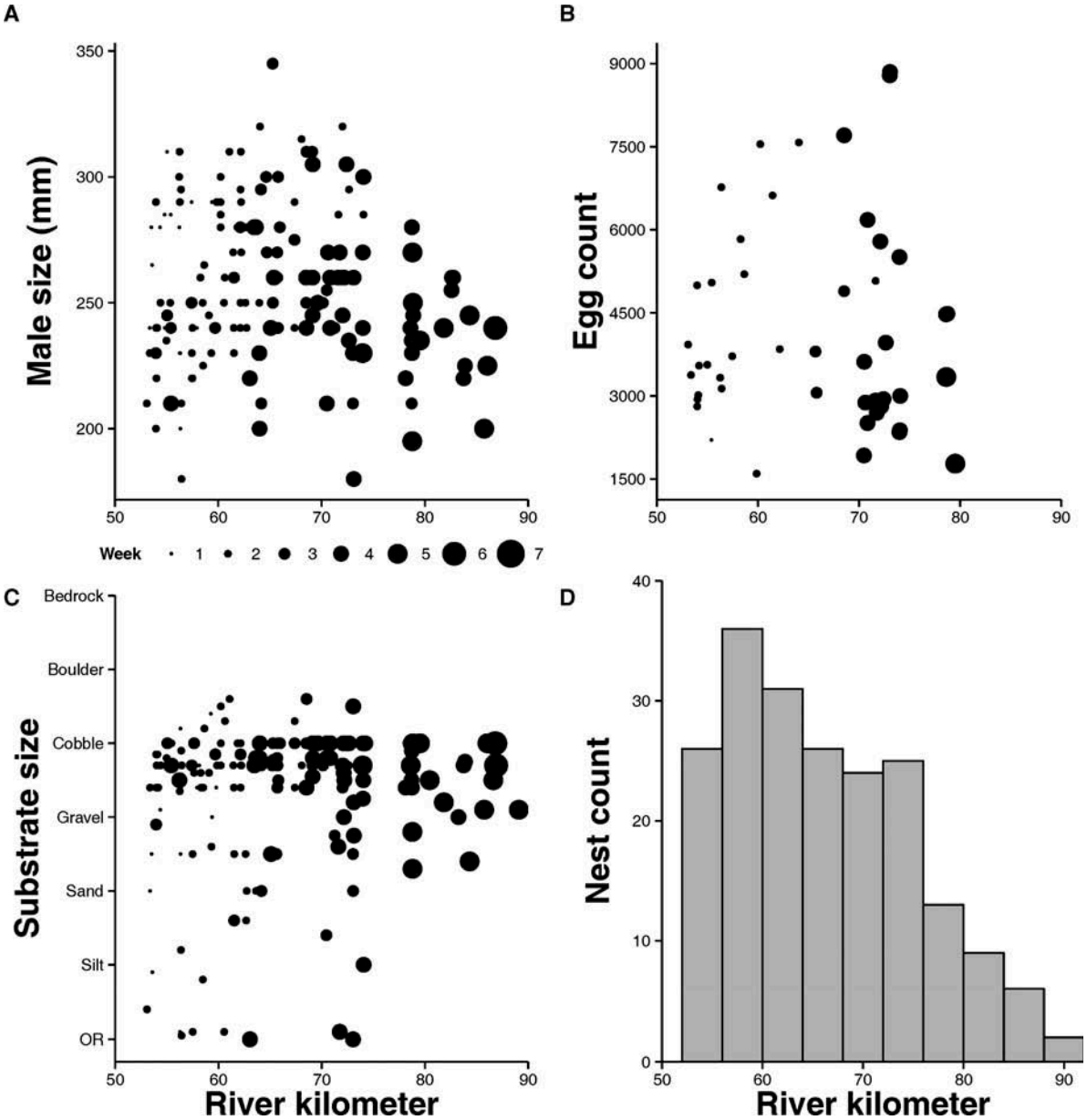

FIGURE 6. Smallmouth Bass reproductive attributes from nests in the North Fork John Day River in 2014. Data points are scaled by week in which the nest received eggs for **(A)** adult nest-guarding male size (n = 183), **(B)** distribution of egg counts for nests (n = 59), **(C)** average substrate composition represented as a composite score determined by multiplying the field-measured substrata percentage (i.e., percentage of dominant and subdominant substratum) by a score for each substrata type, where scores are 7 = bedrock, 6 = boulder, 5 = cobble, 4 = gravel, 3 = sand, 2 = silt, 1 = organic matter (OR), **(D)** number of nests.

of overall available substrate. Although habitat and nest characteristics showed similarity across the spatial extent, a slight shift in habitat selection did occur in the upstream habitats (Figure 6c). In downstream reaches, a wide variety of substrata including vegetation, organic matter, and sand were used to construct nests indicated by a large variation in nest substrata scores (range, 1.0–5.6). By contrast, nest construction in upstream reaches was more confined to cobble and gravel (score range, 3.3–5.0).

Nest Success

Overall nest success rates were high in the North Fork. Of the 202 total nests that received eggs in 2014 (Figure 6d), 184 were confirmed as successful (achieving swim-up stage), 8 as failed (no swim-ups produced), and 10 were not confirmed. Conservatively, we assumed the 10 nonconfirmed nests also failed, making 18 total failed and resulting in a 91% nest success rate. Nest success rates were similar (93%; n = 89) in 2015, and all nests were verified as either successful or

failed. In contrast to our hypothesis that increasingly cooler thermal regimes in upstream habitat would lead to an increase in nest failure, 94% (17) of the failed nests in 2014 and 86% (6) of the failed nests in 2015 were located in more downstream reaches of the survey extent.

DISCUSSION

Our study represents the first broad-scale survey of riverine Smallmouth Bass spawning in its nonnative range. We determined the leading edge of distribution in the North Fork John Day River using snorkel surveys and compared reproductive attributes along the steep thermal gradient. The leading edge of Smallmouth Bass distribution changed seasonally, with spatial extent and number of individuals in upstream channel-units increasing throughout the summer months. In concert with distributional expansion, we revealed a striking pattern of asynchronous and protracted spawn timing across the spatial extent. Broadly, Smallmouth Bass capitalize on a constantly expanding thermal regime as temperatures warm over the spawning season.

Temperature alone, however, did not consistently explain spawn timing or nest success. We suggest that temperature defines reproduction at a local scale but that the seasonal change in adult distribution may play a more important role in shaping spawning dynamics in the extreme leading edge. For instance, in 2014 we revealed a significant spatial threshold at rkm 73 that delineated a pronounced shift in spawn timing relative to growing degree days. In the core distribution of spawning (downstream of rkm 73), we found that accumulation of degree days >15°C reasonably predicted spawn timing, whereas spawn timing in the upstream edge was substantially delayed relative to degree days >15°C. It is revealing that this pattern was not observed in 2015. One explanation for the observed delay in spawn timing in 2014 and not 2015 may involve an interaction between adult seasonal movement patterns (unpublished data) and the timing and magnitude of spring high-flow events. Discharge (measured at rkm 24, USGS gauge station 14046000) in late June 2014 averaged 2–3 times higher than June 2015 (mean daily discharge of 23.1 m^3/s versus 8.4 m^3/s). The high discharge in 2014 may have delayed spawning adults in downstream reaches during winter months from dispersing upstream until after the temperatures were above 15°C, delaying spawning initiation. By contrast, we hypothesize that the considerably lower discharge in 2015 did not restrict upstream movement, thus allowing adults to reach upstream habitat in time to spawn as temperatures reached a daily average of 15°C. Additional investigation is warranted to determine the overwinter location of adult Smallmouth Bass and track seasonal movement patterns relative to flow and temperature.

We hypothesize that Smallmouth Bass may accrue reproductive benefits at the extreme upstream edge of their distribution. First, we found that although habitat availability was similar across our entire survey extent, upstream nests were less likely to be placed in suboptimal substrata, suggesting a decrease in competition for nesting locations. Second, when delayed upstream spawning was more pronounced in 2014, eggs from nests in upstream reaches experienced higher temperatures during incubation than nests further downstream (18–21°C versus 12–15°C in downstream nests). This resulted in faster brood development rates and ultimately demanded less time and energetic investment by nest-guarding males. Decreased guarding requirement by adult male Smallmouth Bass has been linked to increases in nest success (Lukas and Orth 1995) and may explain the high rate of upstream nest success. By contrast, temperatures in 2015 were conducive to rapid brood development across the survey extent, contributing to high nest success across all habitats.

Taken together our results indicate that reproductive adults in upstream reaches may experience lower competition for spawning habitats and decreased guarding requirements, which together could outweigh the energetic demands associated with dispersing upstream. It is important to note, though, that the largest males spawned in downstream reaches, suggesting that habitat in downstream reaches may be preferred. If downstream spawning habitat is limited, then smaller fish may be being outcompeted and therefore forced upstream to spawn. Although the mechanism responsible for fish using habitat in upstream reaches to spawn is still unclear, those fish that did attempt to reproduce upstream demonstrated high spawning success. This suggests that, on the whole, reproduction is not a primary limiting factor in defining the leading upstream edge of Smallmouth Bass invasion in coldwater streams.

Despite potential ecological benefits for upstream nests, the delay in spawn timing also resulted in a shorter first-summer growing season. Considerable research suggests that young-of-the-year Smallmouth Bass must achieve a size sufficiently large to survive a winter starvation period (Shuter et al. 1980) in order to recruit into the population. Excessive delays in spawning could result in insufficient growing degree days for overwinter survival. Furthermore, the lower average summer temperatures in upstream habitats are likely to reduce growth potential for young of the year (Lawrence et al. 2015), probably impacting following-year recruitment rates. For instance, although the most upstream nests (above rkm 90) were successful in rearing eggs to swim-up fry, the late date and short growing season produced small-sized young of the year (23–36 mm as measured September 27, 2014) that are unlikely to survive a winter starvation period (Shuter et al. 1980). In support of this, there were no age-1 Smallmouth Bass discovered above rkm 90 in 2015 (unpublished data). In this case, recruitment, not reproduction, limited successful establishment in upstream habitat. Future research is needed to explore whether or not recruitment largely limits Smallmouth Bass range expansion in the Pacific Northwest.

Contrary to the expectation of progressive changes to reproductive patterns with declining upstream temperature, we found a slight decline in maximum size of reproductive males in

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upstream habitat but no change in fecundity and consistently high (>90%) nest success rates across the survey extent. Although nest success rates >90% have been documented in other systems, more typical are rates of approximately 50% (Cooke et al. 2003). Common reasons for nest abandonment are angling (Kieffer et al. 1995), stochastic environmental events (Lukas and Orth 1995), rapid temperature fluctuations (Cooke et al. 2003), low prey availability, and high predator abundance (Steinhart et al. 2004). In 2014 and 2015, th North Fork had only moderate angling pressure and no notable flood events or rapid temperature changes. We did observe potential predators near nests during monitoring surveys, but very few attempts were made by predators to consume the eggs even if nests were left unguarded for an extended period (results not published). The potential predators most commonly noted were conspecifics and typically were low in numbers, if present at all. We also observed low numbers of Northern Pikeminnow *Ptychocheilus oregonensis*, Redside Shiner *Richardsonius balteatus*, Speckled Dace *Rhinichthys osculus*, and Bridgelip Sucker *Catostomus columbianus*. In short, the angling pressure, flow regime, and resident community of predators in the headwaters of the North Fork John Day River are highly conducive to successful reproduction.

CONCLUSION

We demonstrated that reproductive success in cool headwater streams is probably not limiting future range expansion potential of Smallmouth Bass in the Pacific Northwest. The spatiotemporal spawning patterns along the range boundary created both ecological costs and benefits, dependent on when spawning occurred relative to summer growing conditions, but these trade-offs did not affect overall nest success rates. Indeed, Smallmouth Bass had high nest success relative to native populations and fecundity did not vary along the longitudinal gradient. Instead, delayed spawn timing in upstream habitats benefitted from warmer temperatures during brood development and decreasing nest-guarding time. These delays, however, also afforded a shorter growing season to young of the year that could potentially impact the ability for successful overwinter survival and restrict establishment of self-sustaining populations.

Management agencies in the Pacific Northwest are charged with both conservation of native fishes and supporting a recreational Smallmouth Bass fishery (Carey et al. 2011). Limited information on the distribution and ecology of Smallmouth Bass in Pacific Northwest streams, however, provides little guidance to support the complex management decisions regarding nonnative fish stocking regulations, angling restrictions, and riparian shading restoration efforts aimed to reduce stream warming trends. Overall, our study contributes to an enhanced understanding of how reproduction influences range expansion of nonnative Smallmouth Bass populations in headwater streams, better informing management agencies tasked with minimizing future spread and impacts. Research exploring other mechanisms of range expansion, such as recruitment and dispersal, is suggested to improve future range predictions and to provide managers with new information on specific processes that might be targeted to limit further expansion of Smallmouth Bass.

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REFERENCES

Arismendi, I., S. L. Johnson, J. B. Dunham, and R. Haggerty. 2013. Descriptors of natural thermal regimes in streams and their responsiveness to change in the Pacific Northwest of North America. Freshwater Biology 58:880–894.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51:1389–1406.

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.

Carlander, K. D. 1977. Handbook of freshwater fishery biology, volume 2. Iowa State University Press, Ames.

Carpenter, S. R., E. H. Stanley, and M. J. Vander Zanden. 2011. State of the world's freshwater ecosystems: physical, chemical, and biological changes. Annual Review of Environmental Resources 36:75–99.

Cooke, S. J., J. F. Schreer, D. P. Philipp, and P. J. Weatherhead. 2003. Nesting activity, parental care behavior, and reproductive success of Smallmouth Bass, *Micropterus dolomieu*, in an unstable thermal environment. Journal of Thermal Biology 28:445–456.

DeVries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483–512 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

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.

Dunlop, E. S., and B. J. Shuter. 2006. Native and introduced populations of Smallmouth Bass differ in concordance between climate and somatic growth. Transactions of the American Fisheries Society 135:1175–1190.

Fritts, A. L., and T. N. Pearsons. 2006. Effects of predation by nonnative Smallmouth Bass on native salmonid prey: the role of predator and prey size. Transactions of the American Fisheries Society 135:853–860.

Gingerich, A. J., and C. D. Suski. 2011. The role of progeny quality and male size in the nesting success of Smallmouth Bass: integrating field and laboratory studies. Aquatic Ecology 45:505–515.

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.

Ibáñez, I., J. M. Diez, L. P. Miller, J. D. Olden, C. J. B. Sorte, D. M. Blumenthal, B. A. Bradley, C. M. D'Antonio, J. S. Dukes, R. I. Early, E. D. Grosholz, and J. J. Lawler. 2014. Integrated assessment of biological invasions. Ecological Applications 24:25–37.

Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980–2009 and implications for salmonid fishes. Climatic Change 113:499–524.

Kaushal, S. S., G. E. Likens, N. A. Jaworski, M. L. Pace, A. M. Sides, D. Seekell, K. T. Belt, D. H. Secor, and R. L. Wingate. 2010. Rising stream and river temperatures in the United States. Frontiers in Ecology and the Environment 8:461–466.

Kieffer, J. D., M. R. Kubacki, F. J. S. Phelan, D. P. Philipp, and B. L. Tufts. 1995. Effects of catch-and-release angling on nesting male Smallmouth Bass. Transactions of the American Fisheries Society 124:70–76.

Kuehne, L. M., J. D. Olden, and J. J. Duda. 2012. Costs of living for juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in an increasingly warming and invaded world. Canadian Journal of Fisheries and Aquatic Sciences 69:1621–1630.

Lampman, B. H. 1946. The coming of the pond fishes: an account of the introduction of certain spiny-rayed fishes, and other exotic species, into the waters of the lower Columbia River region and the Pacific coast states. Binfords and Mort, Portland, Oregon.

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.

Lawrence, D. J., B. Stewart-Koster, J. D. Olden, A. S. Ruesch, C. E. Torgersen, J. J. Lawler, D. P. Butcher, and J. K. Crown. 2014. The interactive effects of climate change, riparian management, and a nonnative predator on stream-rearing salmon. Ecological Applications 24:895–912.

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.

Lukas, J. A., and D. J. Orth. 1995. Factors affecting nesting success of Smallmouth Bass in a regulated Virginia stream. Transactions of the American Fisheries Society 124:726–735.

Magnuson, J. T., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. American Zoologist 19:331–343.

Muggeo, V. M. R. 2008. Segmented: an R package to fit regression models with broken-line relationships. R News 8:20–25.

Phelps, Q. E., D. A. Isermann, and D. W. Willis. 2008. Influence of hatch duration and individual daily growth rates on size structure of age-0 Smallmouth Bass cohorts in two glacial lakes. Ecology of Freshwater Fish 17:363–373.

Raffetto, N. S., J. R. Baylis, and S. L. Serns. 1990. Complete estimates of reproductive success in a closed population of Smallmouth Bass (*Micropterus dolomieu*). Ecology 71:1523–1535.

Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. Conservation Biology 22:521–533.

Rejwan, C., B. J. Shuter, M. S. Ridgway, and N. C. Collins. 1997. Spatial and temporal distributions of Smallmouth Bass (*Micropterus dolomieu*) nests in Lake Opeongo, Ontario. Canadian Journal of Fisheries and Aquatic Sciences 54:2007–2013.

Ridgway, M. S., and T. G. Friesen. 1992. Annual variation in parental care in Smallmouth Bass (*Micropterus dolomieu*). Environmental Biology of Fishes 35:243–255.

Ridgway, M. S., B. J. Shuter, and E. E. Post. 1991. The relative influence of body size and territorial behavior on nesting asynchrony in male Smallmouth Bass (*Micropterus dolomieu*). Journal of Animal Ecology 60:665–681.

Ruesch, A. S., C. E. Torgersen, J. J. Lawler, J. D. Olden, E. E. Peterson, C. J. Volk, and D. J. Lawrence. 2012. Projected climate-induced habitat loss for salmonids in the John Day River network, Oregon, USA. Conservation Biology 26:873–882.

Sanderson, B. L., K. A. Barnas, and A. M. Wargo Rub. 2009. Nonindigenous species of the Pacific Northwest: an overlooked risk to endangered salmon? BioScience 59:245–256.

Scott, R. J., M. S. Ridgway, and D. L. G. Noakes. 1997. The nest range of Smallmouth Bass (*Micropterus dolomieu*): parental care after swim-up. Canadian Journal of Zoology-Revue 75:2058–2062.

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

Steinhart, G. B., and B. D. Lunn. 2011. When and why do Smallmouth Bass abandon their broods? The effects of brood and parental characteristics. Fisheries Management and Ecology 18:1–11.

Steinhart, G. B., E. A. Marschall, and R. A. Stein. 2004. Round Goby predation on Smallmouth Bass offspring in nests during simulated catch-and-release angling. Transactions of the American Fisheries Society 133:121–131.

Tabor, R. A., B. A. Footen, K. L. Fresh, M. T. Celedonia, F. Mejia, D. L. Low, and L. Park. 2007. Smallmouth Bass and Largemouth Bass predation on juvenile Chinook Salmon and other salmonids in the Lake Washington basin. North American Journal of Fisheries Management 27:1174–1188.

Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences of the USA 108:14175–14180.

Wiegmann, D. D., J. R. Baylis, and M. H. Hoff. 1997. Male fitness, body size and timing of reproduction in Smallmouth Bass, *Micropterus dolomieui*. Ecology 78:111–128.

Wu, H., J. S. Kimball, M. M. Elsner, N. Manua, R. F. Adler, and J. Stanford. 2012. Projected climate change impacts on the hydrology and temperature of Pacific Northwest rivers. Water Resources Research [online serial] 48: W11530.

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