Dynamism in the upstream invasion edge of a freshwater fish exposes range boundary constraints

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Abstract Studying the dynamics of species’ borders can provide insight into the mechanisms limiting or promoting range expansion in response to environmental change. In the John Day River, Oregon (USA), rising stream temperatures are facilitating the upstream expansion of invasive smallmouth bass *Micropterus dolomieu*. Here, where smallmouth bass occupy the upstream limit of its thermal tolerance, we explore population structure and seasonal movement patterns to elucidate the environmental conditions and individual traits that define front edge (where individuals reside year-round) and leading edge (where individuals colonize, but may not establish) limits to its upstream distribution. Reporting on a multi-year, spatially extensive riverscape survey, our results show dramatic ebbs and flows of seasonal occupancies due to individual movement with an overall trend of upstream expansion. We revealed distinct front and leading edge invasion extents, each constrained by different ecological conditions. The front edge is largely constrained by the ability for juveniles to survive an overwinter starvation period, whereas the leading edge is associated with adult growth potential and seasonal hydrological conditions. We also found key morphological traits associated with more mobile individuals.

By providing mechanistic insight into the factors that promote or limit range expansion of an invasive riverine species, our study enhances the ability to predict future range shifts and provides critical information to managers tasked with restricting further expansion.

Keywords Climate change · Secondary spread · Range dynamics · Connectivity · Morphology

Introduction

Environmental change, including shifts in climate and habitat conditions, has required many species to move to avoid extinction (Parmesan 2006; Ackerly et al. 2010). In recent history, dramatic shifts to species’ ranges have been documented throughout the world (Chen et al. 2011), creating challenges for conserving native species (Lawson et al. 2012) and for slowing the spread and impact of non-native invasions (Diez et al. 2012). Predicting the rate and magnitude of range shifts, however, has proven difficult—in part because of unexpected responses of individuals to novel environmental conditions at the edge of their range (Dytham 2009; Chuang and Peterson 2016).

Investigating the dynamics of individuals that inhabit the edge of an ongoing expansion presents a unique opportunity to understand the factors that promote or inhibit species’ ranges. At range boundaries, species reside at the limit of their physiological tolerances and tend to experience large fluxes in habitat suitability caused by changing seasonal and inter-annual variability in environmental conditions (Holt et al. 2005; Sexton et al. 2009). These range boundary conditions can impose novel selection pressures on individuals, often resulting in different dispersal, life-history, or ecological strategies relative to conspecifics in the core distribution.

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Key points:
- Rising stream temperatures facilitate upstream expansion of invasive smallmouth bass *Micropterus dolomieu*.
- Study reveals distinct front and leading edge invasion extents, constrained by different ecological conditions.
- Front edge limits by juvenile survival during overwinter starvation period.
- Leading edge associated with adult growth potential and seasonal hydrological conditions.
- Key morphological traits associated with more mobile individuals.

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(Dytham 2009; Burton et al. 2010; Volis et al. 2016). Examining the patterns, behaviors, and traits of individuals in the expanding edge, therefore, can provide valuable insight into the mechanisms that determine the rate and magnitude of future range shifts (Lindstrom et al. 2013).

Range boundaries are characterized by repeated colonization attempts, successes, and failures through time (Sexton et al. 2009; Kubisch et al. 2010). By examining the ebb and flow of species’ edges in both space and time, it is possible to differentiate areas where populations persist and grow (i.e., core population and front edges, respectively) from areas that are being actively colonized but are not yet established (i.e., leading edge) (Lenoir and Svenning 2013). This distinction provides insights into the conditions that enhance or restrict colonization success, and ultimately better inform conservation and management practices at critical boundary regions (Rehm et al. 2015).

Freshwater fishes face unique movement and range expansion challenges. Streams and rivers constrain fishes into the wetted boundaries of their dendritic network (Grant et al. 2007), and individuals can only respond to environmental change within these confines (Olden et al. 2010). As a result, fish have demonstrated longitudinal shifts toward more upstream habitats in response to climate warming (Heino et al. 2009; Comte and Grenouillet 2013). However, understanding range expansion dynamics in riverine systems is constrained by how little is known about the movement patterns of nonanadromous freshwater fishes (Radinger and Wolter 2014). Natural history data, for example, have limited ability to reveal the mechanisms that underpin range changes, as they cannot directly assess the environmental conditions that initiate movements or account for failed colonization attempts. Here, we leverage animal tracking technology and the study of invasive species to address some of these knowledge gaps.

Invasive species can act as large-scale experiments that enable real-time investigation of the ecological processes influencing range expansion (Sax et al. 2007; Moran and Alexander 2014). The colonization dynamics of secondary spread from an initial introduction location and natural colonization are biologically similar (Hoffman and Courchamp 2016), and consequently represent a powerful, yet still under-utilized, opportunity to advance our understanding of range expansion in changing environments. Recognizing that established nonnative species are often, by definition, good dispersers, they still face ecological and biological constraints that limit their range and contribute to a greater understanding of range boundary dynamics (Moran and Alexander 2014; Hoffman and Courchamp 2016).

In the present study, we examine an established, yet actively expanding, invasive population of smallmouth bass Micropterus dolomieu at the upstream extent of its range boundary in a major Columbia River tributary. Smallmouth bass is a popular sport fish native to central and eastern North America that has been widely introduced throughout the world (Loppnow et al. 2013). As a voracious predator, there is concern about the rate and magnitude of climate-driven range expansion into headwaters of Pacific Northwest rivers that provide critical rearing habitat for several endangered and threatened salmonids (Carey et al. 2011; Lawrence et al. 2014).

Smallmouth bass in riverine ecosystems are generally described as a sedentary species (Todd and Rabeni 1989) that establish home ranges and exhibit strong interannual homing tendencies (Ridgway and Shuter 1996). Populations subjected to large fluctuations of habitat suitability—such as range boundary populations—however, have exhibited dramatic differences in dispersal behaviors, undertaking long journeys to attempt colonization in novel habitats (Lyons and Kanehl 2002; Tabor et al. 2012). In the Pacific Northwest, evidence suggests that such large seasonal movements occur each year at the upstream extent of smallmouth bass’ riverine range (Lawrence et al. 2012).

The goal of our study is to explore the environmental conditions (i.e., extrinsic factors) and individual traits (i.e., intrinsic properties) that initiate and inhibit movement responses. We examine two range boundary populations of smallmouth bass in the North Fork and Middle Fork John Day River, Oregon (USA), employing spatially extensive surveys to monitor population and individual movement patterns over four years. Our objectives were (1) to quantify spatiotemporal changes in abundance and the extent of smallmouth bass at inter-annual and seasonal time scales, (2) to characterize individual movement patterns of adults and assess individual traits associated with movement, (3) to determine the consistency of the front edge (where individuals reside year-round) and leading edge (where individuals colonize, but may not establish) over time, and (4) to evaluate the potential environmental drivers of invasion edge dynamics. We specifically define the front edge as the most upstream portion of the river in which smallmouth bass are present each spring after a winter (cold-water) period (i.e., spring invasion edge), whereas the leading edge is defined by the most upstream location of smallmouth bass during any time of the year (i.e., summer invasion edge). Through these objectives, we investigate the effect of seasonal movement on range boundary dynamics and evaluate the mechanisms that promote and limit smallmouth bass range in Pacific Northwest rivers.
Methods

Study area description

Our study examines range boundary dynamics at the upstream extent of smallmouth bass distributions in the North Fork (NFJDR) and Middle Fork (MFJDR) tributaries of the John Day River (JDR) (Fig. 1). The JDR basin originates in the Blue Mountains of northeastern Oregon and drains an area of 21,000 km². It is the largest undammed tributary of the Columbia River and is the third longest free-flowing river in the contiguous United States. The JDR is also home to a population of endangered wild-only, spring Chinook salmon *Oncorhynchus tshawytscha* and threatened steelhead *Oncorhynchus mykiss*. In 1971, smallmouth bass was introduced into the JDR, approximately 42 km downstream of the NFJDR confluence (Shrader and Gray 1999). Since that time, smallmouth bass has expanded its range over 150 km upstream and is now resident in both the NFJDR and MFJDR (Lawrence et al. 2012).

Flowing through colluvial and alluvial canyons and valleys, the NFJDR is characterized by channel gradients ranging from 2.4 to 30 m/km, and the less steep MFJDR ranging from 0.6 to 15 m/km. As a result, the NFJDR also has a steeper thermal gradient (cools ca. 0.3 °C every 5 km gained in an upstream direction) than the MFJDR (cools ca. 0.2 °C every 5 km). Discharge in both systems peak in April and May in response to snowmelt, decline through Jun and Jul, and generally exhibit summer base flow until late Sep (Online Resource 1). Water temperatures range from 0 °C in winter (partial ice coverage) to mean summer temperatures >25 °C that generally peak in Jul, with a 4.5 °C (NFJDR) or 3 °C (MFJDR) difference between the most upstream and most downstream temperatures of our survey extent (Lawrence et al. 2012; Rubenson and Olden 2016).

Temperature and discharge monitoring

Water temperature was measured from June 2009 to September 2010 (Lawrence et al. 2012) and again from May 2014 to June 2016 using an array of 15 Hobo temperature loggers (Onset Electronics, Onset, MA, USA) in the NFJDR and 13 loggers in the MFJDR. Each logger was placed approximately 5 km apart and distributed over 66 and 58 river kilometers (RKMs) in the NFJDR and MFJDR, respectively. Additionally, water temperatures for 2008–2009 and 2013–2014 were obtained from an array of temperature loggers managed by the US Forest Service.
and MFJDR Intensively Monitored Watershed program. Water temperatures for individual RKMs (the study units) were assigned 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 \( P < 0.001 \)). Growing degree-days for young-of-the-year were calculated by summing mean daily temperatures exceeding a 10 °C threshold (the temperature at which smallmouth bass initiate feeding; Shuter et al. 1980) for each day beyond when daily mean temperature first exceeded 15 °C (the temperature at which smallmouth bass initiate spawning: Shuter et al. 1980; Lawrence et al. 2015). Days of winter were calculated by summing the number of days less than 10 °C beginning when first achieved in late fall the year prior to the survey until temperatures again first attained 10 °C in the spring. Discharge was measured from a US Geological Survey (USGS) long-term flow gauge (station 14046000) located on the NFJDR at RKM 24 and a gauge (station 14044000) located at RKM 24 on the MFJDR. The number of days of low discharge during the spring and summer was calculated by summing the number of days below mean daily discharge thresholds of 28 m\(^3\)/s for NFJDR and 9 m\(^3\)/s for MFJDR between 1 April and 1 August. These thresholds were determined by the mean daily discharge observed at the time of first smallmouth bass spawning activity for each study year. These values generally represent the receding limb of the hydrograph and demarcate a shift from high-magnitude snowmelt discharge to lower flow conditions amenable to smallmouth bass spawning and movement (Online Resource 2).

**Growth and survival models**

Predicted size of young-of-the-year smallmouth bass was calculated using mean daily temperatures and the daily growth equations in Shuter et al. (1980):

\[
G = 0.0, \quad T < 14 \, ^\circ\text{C} ; \quad T > 35 \, ^\circ\text{C} ;
\]
\[
G = -1.7 + 0.127T, \quad 14 \, ^\circ\text{C} \leq T < 25.5 \, ^\circ\text{C} ;
\]
\[
G = 1.4, \quad 25.5 \, ^\circ\text{C} \leq T < 31.5 \, ^\circ\text{C} ,
\]

where \( T \) is the temperature (°C) and \( G \) is the daily growth (mm). The average starting length of fry was assumed to be 9.1 mm, to which the summed daily growth increments were added at the end of each season. Additionally, we used the Shuter et al. (1980) survival index that describes the minimum size young-of-the-year smallmouth bass need to attain to survive a winter (cold-water) starvation period:

\[
L_0 = 0.188d + 14.8
\]
\[
L_1 = 0.328d + 33.9
\]

where \( L_0 \) represents the length (mm) below which survival is predicted to be 0%, \( L_1 \) represents the length above which survival is predicted to be 100%, and \( d \) is the duration of winter in days. Previous smallmouth bass bioenergetics modeling has demonstrated the validity of the daily growth and survival equations of Shuter et al. (1980) in the JDR (Lawrence et al. 2015).

**Longitudinal surveys**

In 2009, 2010 (Lawrence et al. 2012), and 2014, seasonal spatially continuous snorkel surveys were conducted in the NFJDR; one in the spring as temperatures warmed above 15 °C—when smallmouth bass typically initiate spawning (Shuter et al. 1980; Lawrence et al. 2015)—and the second in the late summer as temperatures began to decline (late July to early August). The MFJDR was similarly surveyed in 2009 and 2014. Surveys consisted of two snorkelers on opposite shorelines simultaneously assessing each reach in an upstream direction. Snorkelers reported the number and size class (<100 mm, 100–200 mm, 200–300 mm, >300 mm total length) of all observed smallmouth bass to an above-water data recorder. In 2015, glide-like pool habitats in both the NFJDR and MFJDR were selected at approximately 5-km intervals. In these subsampled reaches, snorkel surveys were repeated four times (4 to 5 June, 19 to 22 June, 08 to 12 July, and again 16 to 18 September) to monitor seasonal changes in abundance of smallmouth bass populations. Additionally, the four most upstream reaches in each river were snorkeled twice more (22 to 23 July and 12 to 14 August) to gain resolution at the upstream extent during peak summer temperatures.

**Movement study**

During 15 to 19 May and 6 to 9 June 2015, a total of 100 adult smallmouth bass (195–353 mm total length) were captured between RKM 57 and 69 of the NFJDR using hook-and-line sampling. Fish were anesthetized using a 30 mg/L dosage of AQUI-S® 20E until surgical plane was achieved (measured by loss of equilibrium, lack of response to external stimulus, and slowing of operculum movement), which took ca. 5 min. Fish were then connected to a flowing anesthesia solution to irrigate the gills, and a ca. 15-mm shallow incision was made on the ventral surface just anterior to the pelvic girdle offset of the linea alba. A shielded catheter needle was inserted through the incision aft into the abdominal cavity and guided through the lateral side body of the fish. The transmitter antenna was then guided through the catheter shield and transmitter placed in the incision. Incisions were closed using three simple interrupted sutures (PDS 3-0 absorbable monofilament) placed 3–5 mm apart.
Fish were then placed in a recovery bath, photographed, weighed, and measured. Additionally, 5–7 scales were removed from behind the pectoral fin for aging. Scales were placed directly onto a wax paper and stored until laboratory processing. 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). Once fish were fully processed post-surgery (5–7 min), fish were monitored in the bath until full recovery (ability to maintain body equilibrium and resumption of normal coordinated swimming) (15–20 min). Once fully recovered, fish were released in slow-moving water with ample cover.

Smallmouth bass were implanted with an ATS F1440 body implant transmitter with trailing whip antenna (Advanced Telemetry Systems, Inc. Isanti, MN, USA). Each transmitter weighed 2.1 g (dry weight) and had a battery life of 68–158 days. Tagged fish were tracked using an ATS 4500C telemetry receiver (Advanced Telemetry Systems Inc., Isanti, MN, USA) and a three- or six-element yagi antenna from a truck, canoe, or on foot. Tracking occurred every 3–16 days from June to October and once in November (n = 18 total periods). Using signal gain, fish were pinpointed to within 100 m, and location was recorded using a handheld Global Positioning System (GPS).

To calculate movement, GPS locations of individual fish were translated into RKM using a Geographic Information System (ArcGIS, version 10.2). Distance moved was then calculated as the change in RKM between each tracking period (upstream indicated by positive values and downstream as negative values). At the end of the season, the absolute values of all movements were summed to determine cumulative movement distance over a season for each individual.

**Fish morphology**

Geometric morphometrics were used to characterize body shape of tagged individuals. When anesthetized, each fish was placed on a photo board, straightened with fins extended, and photographed. Landmark coordinates were sampled from the digital photographs using tpsDig version 2.18 (Rohlf 2006) and input into R using the geomorph (Adams and Otarola-Castillo 2013) package. Only fish that were consistently tracked throughout the season (n = 87) were used for the analysis. An additional 21 specimens were removed due to lack of proper alignment in the photograph (i.e., tail not straight, body bent, etc.). Of the remaining 66 specimens, 11 fixed landmarks were selected to represent overall body morphology. A single person digitized all landmarks to reduce the potential for systematic biases.

Using geomorph, specimens were superimposed using a Generalized Procrustes analysis (Rohlf and Slice 1990). From the superimposed specimens, 22 principal components (PC) were extracted, representing the overall change in shape between all specimens. The top 5 PC from the morphometric analysis (representing 68% of the total shape variation) were then each analyzed for relationships with cumulative movement using linear regression analysis.

Aspect ratio of the caudal fin is often used as a proxy for swimming performance and has been suggested to be a significant predictor of dispersal distance in fishes (Radinger and Wolter 2014). Aspect ratio of the caudal fin is defined by the equation:

\[ AR = \frac{h^2}{s}, \]

where \( h \) is the height of the caudal fin and \( s \) is the surface area of the caudal fin. To determine the aspect ratio of the caudal fin, photos for the 87 tracked fish were re-examined to determine which had caudal fins that were properly spread for analysis (n = 47). In order to ensure that the subsample of 47 fish was a random and representative sample, Mann–Whitney U tests of all body measurements and movement metrics were conducted between the 47 subsampled individuals and the remaining 40 individuals. No differences were found between the groups (all \( P > 0.2 \)).

In addition to photographs, direct measurements were taken of individual fish. While anesthetized, total length (mm), weight (g), body depth (mm) (dorsal to ventral measurement at pectoral fin), caudal peduncle depth (mm) (dorsal to ventral measurement at narrow point in caudal peduncle), head height (mm) (dorsal to ventral measurement at head insertion to jaw opening), and girth (mm) (side to side measurement at pectoral fin) were measured (Online Resource 3). For statistical analyses, body measurements were standardized by total length to account for the influence of allometry.

**Statistical analysis**

Statistical analyses were conducted in R version 3.2.2 (R Foundation for Statistical Computing, Vienna). Pearson’s correlation coefficients were computed to assess the relationships between environmental variables (i.e., temperature and discharge) and upstream distributional limits. We used linear modeling to determine the relationship between individual movement and morphology. We considered 59 candidate models, including every combination of six body shape predictor variables (i.e., weight, body depth, caudal peduncle depth, head height, girth, and aspect ratio of the caudal fin). Akaikes’s information criterion (AIC) was then used to evaluate the support for each model. As movement data were not normally distributed, we used
Mann–Whitney U tests to compare groups of fish that moved at different time periods.

**Results**


Across all years and both rivers, a seasonal shift in upstream distribution was revealed. Each year, the upstream extent of distribution increased between spring surveys (conducted as temperatures increased above 15 °C) and late summer snorkel surveys (conducted as temperatures began to decline from peak summer temperatures). In the NFJDR, the spring invasion edge (i.e., front edge) was closely associated with minimum young-of-the-year growth requirements (Table 1). By contrast, the spring invasion edge in the MFJDR remained highly consistent despite inter-annual variability in conditions. In late summer, the distribution of smallmouth bass in both rivers increased 5–33 km upstream, depending on the year. This summer invasion edge (i.e., leading edge) in the NFJDR was correlated with the number of days of low discharge during the spring and early summer (1 April to 1 August) ($r = 0.941, P = 0.058, n = 4$) and was consistently located at a longitudinal position exhibiting mean daily July temperatures of 19.4–21 °C (Table 1). These trends hold in the MFJDR, but statistical analyses were not possible due to limited sample size ($n = 3$ years). Finally, a pattern of steady increase to all distributional limits (i.e., spring and summer) was observed, indicating that smallmouth bass successfully expanded both its inter-annual and seasonal range in both the NFJDR and MFJDR during the study period (Fig. 1). The two exceptions were (1) late summer 2010, which was characterized by low temperatures and late recession of peak discharge relative to other years (Table 1; Online Resource 2), and (2) early spring 2014, which was preceded by a season of cold upstream temperatures relative to 2010.

In 2015, repeat snorkel surveys revealed that both abundance and upstream extent increased throughout the season, peaking in late July (Fig. 2a, b). Initial shifts upstream of the spring invasion edge occurred as mean daily stream temperatures increased above 15°C and spawning was initiated (simultaneous in 2015). Each subsequent survey revealed higher numbers of smallmouth bass in each sub-sampled reach with more reaches occupied. In mid-August, mean daily temperatures began a steady downward trend from the summer seasonal highs (Online Resource 1). After this time, smallmouth bass abandoned upstream reaches of both rivers and abundances began to decline in downstream reaches. By the middle of September, no smallmouth bass were observed above RKM 84 in the NFJDR and RKM 39 in the MFJDR.

A marked longitudinal trend in the distribution of size classes was also revealed during the snorkel surveys. Downstream of the spring invasion edge, all size classes of smallmouth were represented in the abundance counts, with individuals <100 mm constituting 25–43% of the population. By contrast, individuals <100 mm were notably absent from the summer invasion edges. Instead, 100- to

<table>
<thead>
<tr>
<th>Table 1 Environmental variables associated with the location of the front and leading edges in the North Fork John Day River (NFJDR) and Middle Fork John Day River (MFJDR)</th>
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</thead>
<tbody>
<tr>
<td>River</td>
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<tr>
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</tr>
<tr>
<td>NFJDR</td>
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<td>MFJDR</td>
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$RKM$ represents the river kilometer where the front or leading edge of smallmouth bass occurred during that year. $GDD$ represents the number of growing degree-days >10 °C accumulated the year prior to the survey. $Days of winter$ represents the number of days <10 °C accrued the year prior to the survey. $Size$ represents the predicted size (mm) young-of-the-year should achieve given the GDD available the year prior. $L_0$ represents the minimum size (mm) a young-of-the-year bass would need to be in order to survive the winter. $L_1$ represents the size (mm) above which the probability of overwinter survival is 100%. $July mean T$ is the mean monthly temperature (°C) for July at the corresponding $RKM$.

$Days of low discharge$ represents the number of days (between 1 April and 1 August) in which discharge was less than 28 m³/s (NFJDR) and 9 m³/s (MFJDR). The discharge threshold levels were chosen based upon the mean discharge observed when spawning was first initiated in each system. This generally represents the receding limb of the hydrograph and demarcates a shift from high-magnitude snowmelt discharge to lower flow conditions amenable to smallmouth bass spawning and movement.
300-mm-size fish made up the majority (83–100%) of total observed individuals each year, with the remainder being in the >300 mm size class.

**Individual movement patterns (2015)**

Smallmouth bass were found to make considerable seasonal movements in the NFJDR. In total, 87 individuals were tracked from early June through late November 2015, represented by 1450 valid tracks, averaging 17 locations out of 18 tracking periods per individual. The tracked fish ranged from 195 to 311 mm (SD = 26 mm) in total length and 105 to 375 g (SD = 62.5 g) in wet mass. Total (cumulative) distance moved varied substantially between individuals, ranging from 0 km (i.e., fish that remained within the same 100-m pool throughout the entire study) to 109 km. Distributions of individual movements were such that there was no clear distinction between a mobile and a stationary component of the population. Specifically, 25% (n = 22) moved less than 1 km, 16% (n = 14) moved 1–5 km, 24%
(n = 21) moved 5–20 km, 15% (n = 13) moved 20–40 km, and 20% (n = 17) moved 40–109 km.

Age structure in the headwaters of the NFJDR and MFJDR was relatively young compared to the main-stem JDR (unpublished data, Oregon Department of Fish and Wildlife) and native smallmouth bass populations (Beamesderfer and North 1995). Of the 100 fish caught using angling and implanted with a tracking device, 66% were age 3 (n = 66), 25% age 4 (n = 25), 1% age 5 (n = 1), and less than 5% age 6–8 (n = 5) (3 individuals could not be conclusively aged due to scale regrowth). An additional 41 individuals were captured that were too small to tag (<200 mm), and presumed to be predominantly age 2 based on consistent size–age relationships in the system. Similarly, fish >300 mm (representing older age classes) were rarely observed during snorkel surveys. The fish that were tracked through the season (n = 87) had a distribution of ages similar to all aged fish. There were no significant differences in cumulative movement between age 3 and age 4+ individuals (Mann–Whitney U = 556, n₁ = 61, n₂ = 24, P = 0.086), the only two age classes with sufficient sample size to analyze.

Individuals that moved >1 km generally exhibited complex movement patterns. Specifically, two-thirds (68%, n = 44) of individuals moved in an upstream direction in the spring and downstream direction in the late summer (Fig. 3). The remaining one-third (32%) either moved only upstream (n = 11), primarily in the spring, or only downstream (n = 10) at different times during the study. Tagged individuals were observed as far upstream as RKM 107 and as far downstream as RKM 22. Only 9% (n = 6), however, exhibited site fidelity to the initial tagging location (i.e., returned to within 500 m of where they were tagged). Instead, 46% (n = 30) of individuals were last observed downstream and 45% (n = 29) upstream from the initial tagging location. All fish that occupied habitats upstream of RKM 81 (n = 15), however, eventually returned to a location downstream of RKM 81 later in the year.

Upstream movement throughout the system was highly coordinated, occurring predominantly in two main phases (Fig. 3a, b). Upstream movement was first observed in early June and generally ceased the second week in July when peak summer water temperatures were reached. The vast majority of individuals that moved greater than 1 km upstream (n = 43) initiated movement either in the period spanning 2 to 18 June (n = 23) (Fig. 3a) or a second period spanning 24 June to 7 July (n = 17) (Fig. 3b) (only 3 fish initiated upstream movement between 18 and 24 June). The first period encapsulates mean daily temperatures above 15 °C (and the initiation of spawning), whereas the second period correlates with the cessation of spawning for the year and an increased rate of stream warming (Online Fig. 3).
Resource 1). There was a slight, but not significant, size difference between fish that initiated movement 2 to 18 June (mean TL = 240 mm, n = 28) and those that waited until 24 June to 7 July (mean TL = 249, n = 17) (Mann–Whitney U = 143, n₁ = 28, n₂ = 17, P = 0.090). When comparing fish that made large upstream movements (i.e., >5 km) (n = 39), however, the trend becomes significant. Specifically, fish that initiated large upstream movements in the first time period (2 to 18 June) (n = 21) were significantly smaller (mean = 237 mm) than those in the second period (24 June to July) (n = 11) (mean = 258 mm) (Mann–Whitney U = 37, n₁ = 21, n₂ = 11, P = 0.0020). Additionally, there was an anomalous period 6 to 22 October in which six individuals initiated large upstream movements (Fig. 3f). Of these, three individuals returned to their tagging location after having initiated downstream movements earlier in the season. The other three individuals moved into deep (i.e., >4 m) pool habitat upstream of where they had been previously located in the season.

Downstream movements were less coordinated than upstream movement. These movements occurred over a more protracted period beginning in late July and ending in early October (Fig. 3c–f). During the first 4 weeks, 3–5 individuals per week moved downstream (n = 15), with some individuals moving multiple times. During this period, no large temperature deviations were observed (daily mean temperatures oscillated around 22–25 °C in downstream segments and 17–20 °C in upstream segments) (Online Resource 1). In the middle of August, daily mean temperatures began trending downward. At this time, increased numbers of individuals (7–15) moved downstream each week for the remainder of the season (n = 48) (Fig. 3d, e). By early October, most downstream movements ceased (except one fish that moved downstream in November), at which point mean daily temperatures were below 10 °C upstream and 15 °C downstream (Fig. 3f). When comparing individuals that moved each week, those that moved downstream earliest were the largest with a steady decline in average size over each subsequent week. There was a significant difference in size and a slight difference in age between individuals that initiated downstream movement in late July (n = 9) (mean size = 265 mm, mean age = 3.8 years) and those that first initiated downstream movement in October (n = 5) (mean size = 228 mm, mean age = 3.0 years; Mann–Whitney U = 42.5 (size), n₁ = 9, n₂ = 5, P = 0.0092; Mann–Whitney U = 35 (age), n₁ = 9, n₂ = 5, P = 0.058).

Several body size metrics were significantly correlated to cumulative movement, but the top performing model included only body depth (standardized by total length) and aspect ratio \( R^2 = 0.287 \) (multiple regression),

### Table 2 Summary of the top five ranked regression models predicting cumulative individual movement as a function of body morphology

<table>
<thead>
<tr>
<th>Model</th>
<th>( R^2 )</th>
<th>P</th>
<th>AIC</th>
<th>∆AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>BD + AR</td>
<td>0.287</td>
<td>0.0006</td>
<td>429.4</td>
<td>0</td>
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<td>2</td>
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<tr>
<td>W + G + BD + AR</td>
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<td>0.0028</td>
<td>431.6</td>
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</tbody>
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Total movement distance (km) (response variable) was calculated as the cumulative sum of the absolute values of change in river kilometers between each tracking period (upstream indicated by positive values and downstream as negative values). Morphological metrics (predictor variables) included in the analysis were body depth (BD), aspect ratio of the caudal fin (AR), girth (G), caudal peduncle depth (CPD), head height (HH), and weight (W).

All measurements, with the exception of aspect ratio of the caudal fin, were standardized by total length to minimize the effects of allometry...
Body depth and aspect ratio were included in all top candidate models (Table 2), whereby deeper bodied fish were positively correlated (Fig. 4a) and fish with larger aspect ratios of the caudal fin were negatively correlated (Fig. 4b) to cumulative movement. PC 2 from the Generalized Procrustes Analysis was also significantly correlated with cumulative movement. PC 2 primarily described shape variation in body depth (Fig. 5), with deeper body depths again correlated with increased movement distance \( r^2 = 0.103 \) (single regression), \( P = 0.0085 \).

Discussion

Through detailed longitudinal monitoring of range boundary dynamics of smallmouth bass, we reveal an overall trend of range expansion over time in response to changing ecological conditions and intrinsic traits (i.e., body shape) that predispose some individuals to be more exploratory of the riverscape. At an inter-annual scale, we expose distinct front (i.e., spring invasion edge) and leading (i.e., summer invasion edge) edges (sensu Lenoir and Svenning 2013), each limited by different ecological conditions that restrict upstream establishment of smallmouth bass. The front and leading edges of the NFJDR and MFJDR demonstrate a clear trend of upstream progression during the 7-year study period (2009–2015) (Fig. 1), responding to favorable environmental conditions. The NFJDR population of smallmouth bass with its steeper thermal gradient, however, was found to be considerably more sensitive to seasonal environmental conditions leading to increased distributional volatility relative to the MFJDR population.

A key attribute of front edges is population growth (Lenoir and Svenning 2013). Although recruitment was not directly measured, a unique characteristic of this region in the NFJDR and MFJDR was the consistent presence of all size classes up through the front edge, but not beyond. Additionally, the front edge location was associated with the combination of antecedent growing degree-days and the length of the preceding winter. Combined, these metrics

![Fig. 5 Ordination plot from a Principal Component Analysis describing shape variation among Procrustes-aligned specimens. The circles are scaled by cumulative movement distances (km) moved by individuals. Principal Component (PC) 1 is associated with curvature in the caudal peduncle [not correlated to cumulative movement (\( P = 0.71 \))] and PC 2 is associated with changes in body depth. PC 2 is significantly correlated to cumulative movement (\( r^2 = 0.103, P = 0.0085, n = 66 \)). The warp grids are visual representations of the hypothetical shapes created from the extreme differences between the minimum (lower) and the maximum (upper) PC2 values.](image-url)
describe the requirements for young-of-the-year to grow to a sufficient size to survive an overwinter starvation period (Shuter et al. 1980), a pattern consistent with bioenergetics modeling suggesting that age-0 survival constrains the upstream distribution limits of smallmouth bass (Lawrence et al. 2015). Indeed, predicted size based on available growing degree-days generally fell just above the minimum size required to survive the upcoming winter for all study years except 2009 (Table 1). Improved conditions in 2015—characterized by a late cooling period at the end of 2014 (i.e., extended growing season) and temperatures rising much earlier in the spring of 2015 (i.e., shorter winter)—resulted in a 6-RKM increase to the front edge in the NFJDR and a 1-RKM increase in the MFJDR. Here, increased duration of the growing season and decreased duration of the winter starvation period appear to have removed perhaps the most important environmental constraint to establishment, especially in the NFJDR, which has a steeper thermal gradient than the MFJDR. By contrast, colder temperatures and a longer winter in 2014 (relative to 2010) resulted in a decrease to the front edge in the NFJDR (no data available for MFJDR in 2010).

There are obvious exceptions to these patterns and differences in association strength between rivers. In the MFJDR, the consistency of the edge location across different years (and hence, different environmental conditions) suggests a strong secondary mechanism that restricts front edge expansion. This could include limited habitat suitable for reproduction, strong Allee effects associated with mate limitation, competitive interactions with other fish species, and low prey availability. Smallmouth bass were also located farther upstream than expected (based on stream thermal conditions) in 2009. One explanation is that the complex depth profile and thermal heterogeneity of the NFJDR and MFJDR provided warm-water thermal refugia during the winter (Torgersen et al. 1999). Although a secondary mechanism seems to be exhibiting influence on the location of the front edge in the MFJDR, we demonstrate that climatological events alone do play a primary role in defining the invasion edge, portending future expansion under certain climate change scenarios (Lawrence et al. 2014).

The location of leading edges between years was much more dynamic compared to the front edges. Depending on current year environmental conditions, the leading edge extended from as little as 5 km to as much as 33 km beyond the front edge during summer months (June through August) (Fig. 1). The location of the leading edge was correlated with the number of days of low spring discharge, where earlier spring runoff timing was associated with greater increases to the front edge (Online Resource 2). This, along with the individual movement patterns observed, lends support to the idea that the leading edge is recolonized each year by smallmouth bass during the receding limb of the spring hydrograph. The absence of individuals <100 mm at the leading edge suggests that recolonization is limited to larger-bodied individuals demonstrating greater dispersal abilities. This mechanism is further supported by the observation that earlier timing of peak spring runoff leads to earlier spawning in both the NFJDR and MFJDR (Rubenson and Olden 2016), thus providing a longer time period for spawning-initiated movement.

The location of the leading edge was also highly associated with water temperature. For both rivers across all years, the respective edge locations occurred at different longitudinal positions but were consistently found where the mean July temperatures were 19.4–21 °C (Table 1). This temperature window corresponds to the optimal growth temperature for adult bass of 20–22 °C (Lawrence et al. 2015), suggesting that adult growth potential plays an important role in determining the location of the leading edge. Although a direct comparison between growth rates of individuals that over-summered in the front versus the leading edge is not available, bioenergetics modeling predicts age 3 bass to maintain growth scope and age 4 and above to increase growth scope in cooler habitats during summer months (Lawrence et al. 2015). In support, we saw the greatest increases to leading edge extent in 2015, which had warmer upstream July temperatures compared to previous years. It is important to note, however, that although temperatures upstream of the leading edge are colder (decreasing by ca. 0.5 °C every 5 km), temperature alone is not a constraint to farther expansion. Further research into additional constraints such as habitat availability, resource limitations, and biotic interactions is required to more fully understand the constraints to leading edge populations of smallmouth bass in temperate streams.

Our study provides strong evidence that large seasonal movements by individuals are a dominant component of range boundary demographics in the headwaters of the JDR. The increased rate and magnitude of dispersal relative to other core population movement dynamics (Todd and Rabeni 1989) is a distinctive trait of population edges (Burton et al. 2010; Chuang and Peterson 2016) and is typically influenced by environmental variability, competition, and potential for kin inbreeding (Dytham 2009). Previous research in the NFJDR and MFJDR demonstrated that abundances of smallmouth bass and nest densities are high in the front edge relative to the leading edge and that there was no reduction of nesting success along the longitudinal gradient (Rubenson and Olden 2016). These conditions paired with the alignment of upstream movement with spawning initiation and the tendency for smaller sexually mature individuals (therefore less competitive) to initiate large upstream movements early suggest that competition for spawning habitat is a critical driver influencing
distribution changes at the range boundary. This is not unexpected as nesting smallmouth bass males aggressively defend their nests, potentially excluding less dominant mature males from spawning nearby (Ridgway et al. 1991). If these outcompeted individuals disperse upstream, they can receive reproductively benefits of available spawning habitat and less competition. Reproductive benefits, such as these, can outweigh the costs and risks associated with dispersal and are considered a key component of successful range expansion (Dytham 2009; Chuang and Peterson 2016).

Upstream movement, however, was not solely confined to spawn timing, but instead continued until temperatures began to decline off summer maximums. In 2015, a rapid rise in temperature occurred as broods were dispersing off nests, which was paired with a second mass initiation of upstream movement (Fig. 3b; Online Resource 1). These movements, in addition to the continuous increase in upstream abundances observed during single-season repeat snorkel surveys (Fig. 2a, b), suggest some level of behavioral thermoregulation, which has been demonstrated in other smallmouth bass populations (Westhoff et al. 2016). Above 22 °C, growth scope for smallmouth bass begins to decline due to high costs of metabolic activity (Whitledge et al. 2002). In the front edge, mean daily temperatures regularly reach 25–27 °C (maximum temperatures >31 °C), whereas mean daily temperatures in the leading edge are 20–22 °C (maximum temperatures <26 °C). This temperature gradient may be sufficient to select for upstream movement and further supports the hypothesis that adult growth scope drives the location of the leading edge (Lawrence et al. 2016). The ability to thermoregulate and track areas of suitable habitat is advantageous for species to respond to climate change (Henry et al. 2013). Under continued warming scenarios, selection would benefit those individuals better able to disperse into the leading edge and escape the high metabolic costs of warmer temperatures downstream.

After a period of expansion in the spring and summer, the range boundaries in the NFJDR and MFJDR contracted in the fall. Elastic boundaries, such as those demonstrated here, tend to occur when mortality and growth rate at the leading edge no longer benefit the individuals that dispersed (Kubisch et al. 2010). Evidenced by the abandonment of upstream habitats as temperature drops, it appears that declining temperatures trigger movement downstream. The habit in the leading edges of the NFJDR and MFJDR experience partial to full ice cover in the winter months and have only a few deep pools (Lawrence et al. 2012), which may limit overwinter survival in the leading edge. The specific trigger that initiates downstream movement, however, is still unclear. It is interesting that larger, older individuals were prone to move earlier. One potential explanation is that previous years’ experience influenced current behavior, or perhaps, more simply, that larger individuals are in better condition earlier to make another large seasonal movement compared to smaller individuals.

In addition to environmental influences and body size, morphology may provide important clues into the intrinsic factors that promote movement at range boundaries (Hudina et al. 2012). Individuals in the upper NFJDR and MFJDR smallmouth bass populations are relatively homogenous in size (<350 mm) and age (<age 6), suggesting that our study area did not include the core population. Even so, we found significant differentiation between movement and individual body shape. Movement was significantly positively correlated to individuals that were deeper bodied with smaller aspect ratios of the caudal fin. Other fish movement studies have also shown body depth to be a significant predictor of movement in centrarchids (Hanson et al. 2007) and aspect ratio a significant predictor of movement in fishes (Radinger and Wolter 2014). However, the direction of the association with body depth and aspect ratio in our study is opposite to that shown in previous studies. In terms of aspect ratio of the caudal fin, most studies compare movement and aspect ratio between species—highlighting differences in function between extremely different forms (Webb 1984, Radinger and Wolter 2014). When comparing intraspecific differences in the aspect ratio of the caudal fin, more nuanced results are to be expected—especially in a species such as smallmouth bass that is labeled as a locomotor generalist (Webb 1984). Our results may provide a key clue for determining the dominant drivers behind dispersal along an invasion gradient. On the invasion front, advantageous morphology for movement is only one factor selecting for dispersal—along with competition for resources and spawning habitat (Henry et al. 2013). In smallmouth bass, nest guarding requires burst acceleration and quick turning ability (Cooke et al. 2002). These specific swimming traits have been correlated with individuals with narrow bodies and large caudal regions (Hanson et al. 2007). As such, the individuals with these morphological traits may be those better able to compete for spawning habitat downstream, thus selecting for the subdominant forms (i.e., individuals with deeper bodies and smaller aspect ratio) to disperse upstream. The combination of subdominant forms moving farther and the timing of movement aligning with spawning again supports that range expansion is driven, in part, by competitive pressure to spawn.

Another hypothesis that warrants further exploration is that differences in body shape of mobile individuals are the result of longitudinal genetic differentiation. Several studies have shown a single population of smallmouth bass to contain two groups of individuals that exhibit distinct life-history patterns year-to-year, suggesting the potential for genetic differentiation within a single population. For
instance, Barthel et al. (2008) reported that a population of smallmouth bass that overwintered in a common lake habitat contained individuals that spawned in an adjoining river and those that spawned in the lake. Similarly, Tabor et al. (2012) found distinct evidence of reproductive isolation between individuals that were residents of Lake Washington (Washington, USA) from those that migrated into connected tributaries. Our findings of significant morphological differences in a relatively homogenous group of individuals suggest that selection for movement traits may be occurring at relatively confined spatial scales located at the range boundary. We encourage additional research to fully understand the costs and benefits of differing body morphologies in range boundary populations.

Although the habitat at the leading edges of the NFJDR and MFJDR does not, yet, maintain self-sustaining populations, the elasticity at the range boundary may have both ecological and evolutionary benefits. Ecologically, dynamics at the range boundary provide opportunities for individuals to establish in new upstream habitat. Specifically, we found that close to half (45%) of the individuals that moved remained upstream of their initial tagging location. Interestingly, all of these individuals settled inside the front edge boundary, and there were no tagged individuals that attempted to remain upstream of this boundary. This implies strong selection for successful overwinter survival of juvenile bass. From an evolutionary perspective, seasonal movement dynamics may predispose the invasive population for future upstream secondary spread. The NFJDR and MFJDR are predicted to experience stream warming under various climate change scenarios (Lawrence et al. 2014), which may provide opportunities for continued range expansion. High dispersal characteristics enable individuals to exploit new habitat and benefit from fewer competitive pressures relative to core populations (Dytham 2009; Burton et al. 2010).

Conclusion

Understanding the movement patterns of species is essential for the accurate prediction of future range shifts and forecasting the speed of invasion (Kokko and Lopez-Sepulcre 2006; Radinger and Wolter 2014). As streams continue to warm into the future, smallmouth bass are well poised to take advantage of improving conditions in these headwater streams. This has important implications for managers that are tasked with minimizing the impact of this top predator on juvenile salmonids that use these headwater habitats to rear (Carey et al. 2011). Understanding the mechanisms of expansion, however, may help mitigate this challenge. Here we show that seasonal adult movement occurs at a predictable time. This presents a unique opportunity to find means to delay or inhibit these movements, be that through restricting movement itself or perhaps increasing fishing pressure to reduce downstream densities. By contrast, expansion might be restricted through efforts to cool streams through riparian restoration that increases channel shading (Lawrence et al. 2014) or by altering the timing or temperature of water released from dams when feasible (Olden and Naiman 2010). Cooler water deters movement, spawning, decreases the growing season, and increases the length of winter cold-water conditions. Ultimately, understanding the intrinsic and extrinsic factors that influence individual movement patterns within the range boundary at multiple timescales is critical to understanding the mechanisms behind range expansion. With these data, we can both improve predictions of future range expansion and better prevent secondary spread of an invasive species.

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Author contribution statement ESR and JDO conceived and formulated the project questions. ESR conducted the fieldwork and data analysis. ESR and JDO wrote the manuscript.

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