PHYSICOCHEMICAL INFLUENCES ON THE SPAWNING AND REARING HABITAT OF RIVERINE NEOSHO SMALLMOUTH BASS

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Abstract: Stream fishes are vulnerable to a range of natural and anthropogenic stressors. Information on fish movements and habitat use is essential to conserve and manage these populations, and is particularly limited for populations that occupy range boundaries and novel habitats. Neosho Smallmouth Bass *Micropterus dolomieu velox* occurs only in the southwestern Ozark Highlands ecoregion, where the riverscape is highly dissected by impoundments. I sought to broaden the knowledge of Neosho Smallmouth Bass (NSMB) ecology by evaluating movement patterns, nesting and rearing habitat use at multiple scales, and spawning phenology in relation to physicochemical conditions. Adult NSMB movements were greatest during the spring spawning period and were positively related to discharge and fish size, though I also observed considerable variability among individuals and streams. Tagged fish did not use the reservoir or associated interface habitats. I also documented nest "clustering" by NSMB in response to local habitat conditions; cluster presence was more likely in warmer streams with wide, shallow channels, and less likely in groundwater-gaining reaches. Nest abundance was greater in warmer streams and reaches with deeper pools. I observed spatiotemporal variation in the hatch timing and growth rate of age-0 NSMB in response to discharge and stream temperature conditions. I showed the importance of warmer streams and of deep pools in small streams for NSMB rearing. I also demonstrated the harm of July floods for first-year survival in these populations, and showed the importance of stream proximity (i.e., adjacency to larger streams) for mitigating this effect and modifying the habitat relationships of age-0 NSMB. Lastly, we observed juvenile NSMB movements were greater for larger individuals and with warmer water temperatures. Individual variation was high for both movement and microhabitat use. The variability in movement, habitat use, and response to physicochemical conditions among individuals and populations (i.e., in different streams) underscores the importance of maintaining habitat heterogeneity and streamflow sufficient to connect important habitats, especially in small streams. Protecting the inherent diversity of these populations is crucial for their persistence in a changing environment.

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CHAPTER I

INTRODUCTION AND RESEARCH OBJECTIVES

Riverine ecosystems experience a wide range of human stressors. Among the most well-known and detrimental of these stressors are land development for agriculture and urbanization, and the impoundment of free-flowing rivers for flood control or hydroelectric generation (Vörösmarty et al. 2010). Agricultural and urban landscapes often generate nonpoint sources of pollution that result in excessive influxes of nutrients, sediment and contaminants to flowing waters (Allan et al. 2004). Furthermore, these land-use conversions typically affect soil infiltration capacity, which in turn leads to altered hydrology (e.g., larger floods, lower base flows) and instream habitat (Peterson and Kwak 1999; Wang et al. 2001). Impoundments fragment riverine habitat and create discontinuities in longitudinal environmental gradients along the river corridor (Ward and Stanford 1983). For example, dams alter flow regimes (Poff et al. 1997), thermal patterns (Caissie 2006), and instream habitat (Ligon et al. 1995) in ways that typically favor tolerant, generalist fish species at the expense of endemic, locally-adapted species (Poff and Zimmerman 2010).

An outsized amount of fish biodiversity is concentrated in freshwater ecosystems, but several major threats put this diversity at risk. Globally, 40% of fish species are found in freshwater, despite these systems covering less than 2% of the Earth's surface (Lundberg et al. 2000; Allan and Castillo 2007). This diversity of fishes provides value to humans via fisheries and ecosystem services (e.g., nutrient subsidies), and confers resistance and resilience to biota in dynamic environments (Schindler et al. 2010). Biodiversity declines across all taxa are greatest in freshwater ecosystems (Sala et al. 2000). Among the abiotic threats to freshwater biodiversity are habitat loss and flow modification (Richter et al. 1997; Dudgeon et al. 2006). Species with specialized habitat needs and limited physiographic ranges are particularly vulnerable to extirpation (Moyle and Leidy 1992; Angermeier 1995). Altered flow regimes drastically change the physicochemical environment, influence the quantity and quality of stream habitat, and disrupt the timing of key life-history events in fishes (Poff et al. 1997; Bunn and Arthington 2002). Despite this, basic ecological information (e.g., natural history, migrations, and flow-ecology relationships) is often lacking for vulnerable species such as narrow-range endemics (Jelks et al. 2008; Cooke et al. 2012).

Stream habitats and fish populations are affected by factors operating at multiple spatiotemporal scales (Schlosser 1991; Allan et al. 1997; Fausch et al. 2002). Stream habitat is ultimately a product of the surrounding landscape (Hynes 1975), and exists in a spatial hierarchy wherein smaller spatial units are nested within larger units (Frissell et al. 1986). This creates stream habitat heterogeneity that spans multiple dimensions in space – horizontal, lateral, vertical – and time (Wiens 1989). Integrating habitat factors across scales has potential to provide a more mechanistic understanding of how catchment conditions structure habitats, populations, and assemblages. For example, hierarchical approaches indicate the importance of coarse-scale factors such as climate, land use, and groundwater input on stream temperatures and fish populations and assemblages (Torgersen et al. 2006; Wehrly et al. 2006; Brewer 2013). Work at intermediate scales, such as stream reaches and segments, will also help bridge the gap between coarse-scale natural and anthropogenic processes and finer-scale conservation and management of stream fish (Frissell et al. 1986; Fausch et al. 2002). Incorporating novel habitat factors at intermediate scales (e.g., groundwater controls, geomorphic and hydrologic conditions) may also improve our understanding of the processes that develop and maintain species-habitat relationships, thereby benefitting management (e.g., environmental flow designations) and stream restoration efforts (Newson and Newson 2000; Lake et al. 2007). As stream fish move between multiple habitats based on changing needs throughout their life cycles (i.e., spawning, rearing, feeding, growth, and refuge; Schlosser 1991), it is important to consider the entire range of important habitats for a species when prescribing management actions.

Smallmouth Bass *Micropterus dolomieu* is an important ecological and recreational component of many warmwater systems in North America. Smallmouth Bass plays a critical role in aquatic food webs by acting as a top predator and conferring top-down effects (Power et al. 1985; Vander Zanden et al. 1999; MacRae and Jackson 2001), making them highly problematic invasive species in some regions (Whittier and Kincaid 1999; Carey et al. 2011). Smallmouth Bass is a common target species of recreational anglers (Long et al. 2015), known for strong fighting ability relative to body size (Henshall 1881). Smallmouth Bass fisheries (i.e., combination of subspecies and unique strains) are economically important and are found in rivers, lakes, and impoundments (Martin and Fisher 2008; Carey et al. 2011).

Populations of Smallmouth Bass in the southwestern Ozark Highlands ecoregion are of special interest to scientists and managers due to their unique genetics and importance as sportfish, but they also face several threats. First described by Hubbs and Bailey (1940), the Neosho subspecies *M. d. velox* (hereafter “Neosho Smallmouth Bass”) is one of three genetically-distinct clades of Smallmouth Bass (Stark and Echelle 1998). Neosho Smallmouth Bass is endemic to streams in the Ozark Highlands of Oklahoma, Missouri, Arkansas, and Kansas, comprising the extreme southwestern extent of the native range of Smallmouth Bass (Brewer and Long 2015). Neosho Smallmouth Bass are popular angler targets both regionally and nationally (i.e., “bass slams”) and experience particularly high catch and harvest rates (Martin and Fisher 2008; Long et al. 2015; Taylor et al. 2019). Annual economic benefits of angling in eastern Oklahoma streams, where 70% of licensed anglers pursue black bass (i.e., Smallmouth Bass, Spotted Bass *M. punctulatus*, and Largemouth Bass *M. salmoides*), were approximately $24 million in 1993 (Fisher et al. 2002).

Throughout much of the range of the Neosho subspecies, reservoirs fragment the landscape (Brewer and Long 2015) and create challenges for the persistence of these populations (e.g., reduced gene mixing, Taylor et al. 2018). Furthermore, Ozark streams are naturally flashy (Leasure et al. 2016), and many smaller streams containing Neosho Smallmouth Bass are seasonally disconnected (e.g., Hafs et al. 2010). This loss of habitat connectivity at multiple scales may force diminutive populations in some stream fragments to use suboptimal habitat conditions during critical life events (e.g., use of bedrock substrate for spawning; S. K. Brewer and J. Burroughs, personal observations).

Relative to the well-studied northern subspecies (see review by Brewer and Orth 2015), we lack general information on many aspects of Neosho Smallmouth Bass life history (e.g., seasonal movements, life history diversity, habitat needs, and growth; Brewer and Long 2015). The role of connected habitats is also of interest given the many smaller, seasonally disconnected streams and reservoir-connected systems throughout the range of the subspecies. There is uncertainty regarding the influence of coarse-scale landscape factors on spawning and rearing habitat use and on movement patterns (Brewer and Long 2015). Information on seasonal movement patterns, hierarchical influences on nesting and juvenile habitat, and growth of juveniles will allow for more relevant management actions to be developed (e.g., protection and enhancement of important spawning and rearing habitats, defining management objectives for different streams, and delineation of important movement corridors).

The goal of my dissertation was to advance our understanding of Neosho Smallmouth Bass ecology, thereby benefitting conservation and management efforts across their native riverscape. My dissertation comprises five objectives related to this goal:

1. Quantify seasonal movements and microhabitat use of adult Neosho Smallmouth Bass in reservoir-river connected systems.

2. Determine the habitat factors at multiple spatial scales related to suitable spawning habitat for Neosho Smallmouth Bass.

3. Quantify the role of environmental variation on hatch timing and growth of age-0 Neosho Smallmouth Bass.

4. Determine abundance and multi-scale habitat use of age-0 Neosho Smallmouth Bass in tributary systems.

5. Quantify movements and microhabitat use of juvenile Neosho Smallmouth Bass in a tributary stream.

For my first objective, I documented movements across the riverscape to highlight the range of habitats used, identify movement corridors, and help define manageable populations. In the second objective, I focused on habitat use during the spawning period. This period is of considerable importance for fish recruitment and population persistence. I explored multi-scale influences on spawning habitat, given the potential for coarse-scale conditions to influence finer-scale habitat quality and quantity. This work helped explain potential spawning habitat limitations and their variation across the riverscape. For the third objective, I quantified the role of environmental conditions (i.e., discharge and water temperature) on the hatch timing and daily growth of age-0 Neosho Smallmouth Bass. This information is useful for understanding how spawning phenology reflects dynamic environmental conditions and its consequences for fish growth. Building on the third objective, I focused my fourth objective on the survival and associated multi-scale habitat of age-0 Neosho Smallmouth Bass near the end of the first growing season. I also considered the potential for stream network position and hydrology to modify these relationships given they varying hydrology and relative connectivity of different stream reaches throughout the riverscape. These results emphasized the role of habitat in age-0 Smallmouth Bass survival and highlight beneficial habitat conditions during this critical period. For my final objective, I measured the fine-scale movement and habitat use of juvenile Neosho Smallmouth Bass in an Ozark tributary stream. Other studies (e.g., Humston et al. 2010; Brewer et al. 2019) have demonstrated the ability of juvenile Smallmouth Bass to disperse within and among stream segments, but no one has looked at how these patterns respond to environmental conditions on short time scales and throughout the diel cycle.

CHAPTER II

SEASONAL HABITAT USE AND MOVEMENT OF ADULT NEOSHO SMALLMOUTH BASS IN A DYNAMIC RIVERSCAPE OF THE OZARK HIGHLANDS ECOREGION

ABSTRACT

Stream fish movements reflect changing resource use and habitat needs in a dynamic environment. The ability to respond to these changes is important for growth, survival, and reproduction. I used radio-telemetry to evaluate daily movement rates, home ranges, and habitat-use characteristics of riverine Smallmouth Bass *Micropterus dolomieu velox* in three Ozark streams from June 2016 to February 2018. My objective was to quantify variation in movement and habitat use across seasons and among streams with varying physicochemical conditions and proximities to large rivers and impoundments. I also examine relations with select environmental cues (i.e., temperature and discharge) that might influence these patterns. I used linear mixed models and AIC_c to rank models that describe variation in daily movement rate of adult Smallmouth Bass. Movement rates were greatest and most variable in spring and lowest in winter. Spring movement rate was positively associated with increasing discharge while autumn and winter movement rates were lower and occurred under relatively homogeneous discharge conditions. Temperature and movement rate were positively related in Elk River in all seasons except winter, though temperature was less important for movement in smaller streams. Increased variation in discharge had a small but positive effect on movement rate. Movement rate was greater for larger fish across all streams and seasons. Home ranges were highly variable among individuals, ranging 45–15,061 m (median: 773 m). Home range size was not related to fish size, sex, season, or specific stream. My data indicated tagged fish did not use the reservoir or associated interface habitat throughout the study. Some variation in habitat use was apparent relative to season and stream, but individual variability in habitat use was considerable. Deeper-water habitats were used in Buffalo Creek and in winter across all study streams. Velocity use was greatest in Elk River independent of season and lowest in autumn across all streams. These results indicate that considerable heterogeneity in movement and habitat-use exists within and among lotic populations of Smallmouth Bass. These findings highlight the importance of natural flow conditions (i.e., spring high flows) and connected habitats for this endemic sport fish, particularly in small streams.

INTRODUCTION

Generalizing movement and habitat-use patterns for many stream fishes is difficult due to the timing and availability of resources and population differences among catchments. Stream habitats reflect processes operating at multiple spatial and temporal scales resulting in substantial heterogeneity in resources across the riverscape (Frissell et al. 1986). The resulting patchy stream conditions likely dictate changes in movement behaviors and habitat use by fishes (Warren 2009). Higher movement rates due to especially patchy environments may be more common among isolated populations or those occurring on the edge of the range that may be more vulnerable to human disturbances (e.g., climate change, Radinger et al. 2017; Rubenson and Olden 2017). Population differences may reflect mobile and non-mobile individuals and divergent life-history strategies (Barthel et al. 2008; Chapman et al. 2012; Radinger and Wolter 2014). A common observation is variation in habitat use among stream populations that may lead to conflicting conclusions about a species' designation as a "generalist" versus "specialist" (e.g., Pert et al. 2002); the reality is movement among habitat patches may relate to specific resource needs that are not continuously available in space or time.

Riverine fish movements reflect changing resources and habitat needs throughout their life cycle. Resources such as prey availability and critical habitats (e.g., spawning, rearing and refuge) are often life-stage dependent and dynamic in space and time, thereby necessitating movement by many stream fishes (Schlosser 1991; Thurow 2016). Typical movement cues include water temperature, discharge, and combinations thereof, and often correspond to shifts in resource availability (Taylor and Cooke 2012). For example, many stream fishes migrate to thermal environments beneficial for overwinter growth and survival, but the timing of these movements can vary widely (Peterson and Rabeni 1996; Westhoff et al. 2016). Movements associated with the reproductive period are often pronounced, with many species demonstrating potamodromy (i.e., migration within freshwater environments) to reach distinct spawning habitats (Northcote 1997; Lucas and Baras 2001; Thurow 2016). Movement cues may vary within and among catchments, and failure to support these habitat needs can cause maladaptive movement behavior and declines in stream fish populations (Pelicice and Agostinho 2008; Nagrodski et al. 2012; Benitez and Ovidio 2018). Understanding movement patterns is crucial for the effective conservation and management of stream fishes (e.g., defining critical habitats, movement corridors, and management units; Schlosser 1991; Cooke et al. 2016; Thurow 2016).

Black bass of the genus *Micropterus* are both recreationally and ecologically important, but our ecological knowledge of the narrow-range endemics is lacking relative to the quickly-evolving species designations (Birdsong et al. 2015). Black basses are among the most highly-sought game species in North American freshwater ecosystems, including stream ecosystems. These top-level predators play a critical role in aquatic food webs by conferring top-down effects (Power et al. 1985, MacRae and Jackson 2001). Although the taxonomic status of black basses is controversial (Taylor et al. 2019), we know little about the ecological needs of some of these endemic fishes such as the Neosho subspecies of Smallmouth Bass *M. dolomieu velox* (hereafter, “Neosho Smallmouth Bass”). Management agencies acknowledge the conservation need for this subspecies (Boxrucker et al. 2004; Quinn et al. 2004). Further, its geographic range (southwest Ozark Highlands, Stark and Echelle 1998; Brewer and Long 2015) makes it ideal for examining interactions among different ecosystems (e.g., streams, large rivers, and reservoirs) across a landscape that is highly variable with respect to hydrology, water temperature, and physical habitat (The Nature Conservancy 2003; Hafs et al. 2010; Leasure et al. 2016). Understanding how this subspecies uses resources across the riverscape through multiple years may provide insight into useful conservation strategies that will be faced by other endemic black basses as environmental conditions continue to change due to a variety of factors including development and climate change (Birdsong et al. 2015; Taylor et al. 2019).

Migration responses by Smallmouth Bass are not well studied in highly modified riverscapes (i.e., connected rivers and reservoirs). Potamodromous behavior is evident for many warmwater fishes in natural systems (e.g., Golden Perch *Macquaria ambigua* and Silver Perch *Bidyanus bidyanus*, Mallen-Cooper and Stuart 2003; Shoal Bass *M. cataractae*, Sammons 2015). For example, in a connected lotic-lentic system in Ontario, Canada, Smallmouth Bass populations overwinter in a lake, but spawn in either the lake or use connected river habitats (Barthel et al. 2008). The use of connected habitats in human-modified systems (e.g., impoundments) is less clear, though such modifications appear to create barriers to movement by native fishes in some cases (Herbert and Gelwick 2003; Pelicice et al. 2015). Correspondingly, the goal of this study is to provide information on the extent of Neosho Smallmouth Bass movement in streams with highly variable physicochemical conditions and part of an impounded riverscape. The objectives of this study were: 1) describe seasonal movement and habitat-use patterns of Neosho Smallmouth Bass in three streams with varying physicochemical conditions; and 2) relate common drivers (i.e., temperature and discharge) of movement relative to the spawning season. I build on previous studies that examined Neosho Smallmouth Bass movement in three forks of the Illinois Bayou, Arkansas during summer drought conditions (Hafs et al. 2010) and discrete sampling that identified relationships with select aspects of seasonal habitat (Dauwalter et al. 2007; Dauwalter and Fisher 2008; Brewer 2013).

METHODS

Study area

I tracked radio-tagged adult Smallmouth Bass from three populations occupying different lotic-lentic interfaces: 1) a small creek (Sycamore Creek) that terminates at Grand Lake O' the Cherokees (hereafter Grand Lake), 2) a large tributary (Buffalo Creek) that terminates at the confluence of a larger river-transient reservoir interface, and 3) a large river population situated between a low-head dam and Grand Lake (Elk River; Figure 1). Sycamore Creek is a third-order stream (Strahler 1952) that flows 18 km, draining a 133-km^2 catchment, before reaching Grand Lake, Oklahoma. A road crossing 4 km upstream of the lake creates a barrier to fish movement on Sycamore Creek. Buffalo Creek is also a third-order stream and flows 42 km southwest from Missouri to Oklahoma and drains a 293-km^2 catchment before terminating in the transient river-reservoir interface of Grand Lake and the Elk River. The fifth-order Elk River flows west for 41 km from Pineville, Missouri to Grand Lake, draining a 2,524-km^2 catchment. A low-head dam in Noel, Missouri disconnects the lower 23 km of the Elk River, though this barrier may be passable during higher flows (i.e., ~2-year return interval discharge, R. Horton, Missouri Department of Conservation, pers. comm.). These streams are characteristic of the Ozark Highlands ecoregion, and contain distinct riffle-pool sequences and some off-channel habitats. Substrates are predominately gravel, pebble and cobble with some exposed bedrock and groundwater inputs are common but spatially variable (Brewer 2013; Zhou et al. 2018).

Environmental measurements

I collected water temperature and discharge data for each stream throughout the study period to determine their influence on movement and habitat-use patterns. I placed temperature loggers (HOBO Pro v2; Onset Corp., Bourne, Massachusetts) in two equally spaced, well-mixed locations (~0.75 m deep) along the thalweg in each stream and recorded temperature every 30 min. I averaged temperature data across loggers within streams to calculate mean daily temperatures for comparison with fish movements. Mean daily discharge data were compiled from U.S. Geological Survey (USGS) stream gages on Buffalo Creek (gage 07189100) and Elk River (gage 07189000) near Tiff City, Missouri. I characterized Sycamore Creek discharge patterns by developing a rating curve. Briefly, I deployed a HOBO U20 Water Level Data Logger (Onset Corp.) to continuously record stream stage, and compared stage values to measured cross-sectional discharge (Gordon et al. 2004):

$$Q = aS^b$$

Where Q is the discharge [m^3/s], S is the stage height [m], and a and b are system-specific coefficients. The rating curve coefficients for Sycamore Creek were: a = 5.11 and b = 6.66 and the modeled relationship had an R^2 = 0.63. Gaps in discharge data were estimated using least-squares regression with discharge values from the USGS gage on nearby Honey Creek (gage 07189542; R^2 = 0.94).

Fish tagging

I conducted initial capture and tagging of Smallmouth Bass in May 2016. All collection and tagging procedures were conducted under the auspices of Oklahoma State University Animal Care and Use Protocol number AG-16-8. I used boat and tow-barge (Stealth Mini-Boat; Midwest Lake Management, Polo, Missouri) electrofishing and angling to sample 99 individuals weighing ~400 g or greater across the three study streams (n = 40 in Buffalo Creek, n = 30 in Elk River, n = 29 in Sycamore Creek). Boat electrofishing was conducted from a 4.3-m boat with a Smith-Root 5.0 generator-powered pulsator and one boom-mounted anode using pulsed-DC electricity. For each of the three study streams, tagging occurred in 4–6 locations of varying distance from major confluences and the reservoir interface (Figure 1). I anesthetized fish by immersing them in a 30-mg/L bath of Aqui-S 20E (Aqui-S, Lower Hutt, New Zealand) until fish lost equilibrium, typically 2–5 min, and then recorded total length (TL, 1 mm) and weight (1 g). Anesthetized fish were placed ventral side up on a V-shaped surgical table fish and had a low-dose (15 mg/L) of Aqui-S 20E continuously flushed across the gills. I made a ~15 mm incision slightly lateral to the ventral midline and inserted MCFT2 radio transmitters (Model 3BM: 11 × 43 mm, 8 g in air, and Model 3EM: 12 × 53 mm, 10 g in air; Lotek Wireless, Newmarket, Ontario) into the coelom (Cooke and Bunt 2001). I trailed the antenna out of a secondary incision to reduce risk of tag loss (Ross and Kleiner 1982) and trimmed the antenna to the caudal fin to reduce the potential for biofouling (Thorstad et al. 2001). I closed the incision using absorbable material (Unify PGA; AD Surgical, Sunnyvale, California) and a pair of simple interrupted sutures (Cooke and Bunt 2001). Following surgeries, fish were placed in flow-through containers in a shaded portion of the stream and allowed to recover for a minimum of 30 min prior to release near the site of capture.

I conducted additional tagging of Smallmouth Bass in October 2016 and March–April 2017 using transmitters recovered during tracking efforts. If recovered transmitters were in good condition, they were cleaned and sterilized prior to implantation into new fish. I performed tagging in autumn and spring to avoid warmer water temperatures associated with greater handling stress, mortality, and transmitter loss (Bunnell and Isely 1999; Walsh et al. 2000). These tagging efforts combined with initial tagging brought the total number of tagged fish to 152 over the study (*n* = 62 in Buffalo Creek, *n* = 50 in Elk River, *n* = 40 in Sycamore Creek).

Fish movement and habitat use

I tracked radio-tagged Smallmouth Bass from June 2016 to February 2018. I waited a minimum of 48 h after surgery before re-locating fish. I tracked approximately weekly from March–October and monthly from November–February. All tracking was conducted during daylight hours (~0700-1900). I conducted manual tracking from a kayak or on foot using an SRX800 VHF receiver (Lotek Wireless) and a three-element Yagi antenna. I tracked in a downstream direction covering the lower 9.3 km of Sycamore Creek, the lower 14.3 km of Buffalo Creek, and the lower 23.4 km of the Elk River (Figure 1). Following the initial detection of a tagged fish, I slowly approached the area of strongest signal and gradually reduced receiver gain to improve directionality (i.e., homing; Koehn et al. 2012; Westhoff et al. 2016; Heim et al. 2018). Location accuracy was within ~1.5 m based on dummy tag relocations, and I visually confirmed tagged fish presence for 23% (505/2,233) of relocations.

I obtained GPS coordinates and recorded several habitat characteristics at each fish location. I recorded channel unit type as riffle, run, pool, or slackwater based on current velocity, depth, gradient, and substrate (simplified from Rabeni and Jacobson 1993). I also measured focal depth (0.01 m), water-column velocity (0.6× depth, 0.1 m/s; FP111 Flow Probe, Global Water, Sacramento, California), and water temperature (0.1˚C; Ultrapen PT1, Myron L, Carlsbad, California). I noted the nearest cover type: woody debris, boulder, rootwad, undercut bank or bedrock, vegetation, man-made cover, and combinations of these types. Man-made cover consisted of miscellaneous structures in the stream (e.g., bridge pilings, broken concrete, fencing). I also quantified distance to cover (0.5 m) for each location; fish were considered to be using cover if cover occurred within 1 m of their location (Probst et al. 1984). I visually estimated dominant substrate class within a 1-m^2 area surrounding each fish location using a modified Wentworth scale (Bain 1999): silt (< 0.06 mm), sand (> 0.06–2 mm), gravel (> 2–16 mm), pebble (> 16–64 mm), cobble (> 64–256 mm), boulder (> 256 mm) and bedrock (Brewer 2011). If a fish demonstrated a fright response to tracking efforts (indicated by a sudden, drastic decrease in received signal strength), I recorded a waypoint at the initial fish location but did not collect microhabitat information.

After evaluating fish location data, I summarized fish movement in two ways and estimated their home range. I plotted fish locations in ArcMap 10.3.1 (ESRI, Redlands, California) and used field-collected information on recovered transmitters and visual confirmation of tagged fish to evaluate the validity of each fish location (Schwarz and Arnason 1990). For example, if a transmitter was recovered or a fish was found in the same location over multiple consecutive tracking events, I used prior locations and visual confirmations of tagged fish to identify and remove spurious "fish" locations. I combined the updated fish location waypoints and manually digitized stream lines in ArcMap and used the "Locate Features Along Routes" tool to measure the distance (1 m) along the stream between relocations. I calculated daily movement rate as: the distance moved between consecutive locations divided by the number of days between locations. This metric accounted for varying amounts of time between fish locations and was particularly useful for evaluating the role of daily changes in environmental conditions (i.e., water temperature, stream discharge; see *analyses* section). I also calculated home ranges for each fish as the distance between the maximum upstream and downstream locations (Hill and Grossman 1987; Young 1994).

Analyses

Several variable calculations, transformations, and standardizations were necessary prior to modeling to meet assumptions and improve interpretation. The response variable, movement rate, was natural-log transformed to account for skewness; I added a constant (i.e., y + 1) to all values to facilitate the transformation in cases of no apparent movement. I used stream and season as categorical predictors with three and four levels, respectively. I used water temperatures to define the following seasons: spring (rising between 10–20°C; approximately March–May), summer (> 20°C; approximately June–September), autumn (decreasing between 20–10°C; approximately October–November), and winter (< 10°C; approximately December–February). I quantified both mean water temperature and the change in water temperature over the period between consecutive fish locations. To account for differences in stream size, discharge data were first scaled by the median streamflow values for each stream during the study (McCune and Grace 2002) using the following values: Buffalo Creek (0.43 m^3/s), Elk River (6.68 m^3/s) and Sycamore Creek (0.38 m^3/s). I then calculated both mean discharge and the coefficient of variation (CV: $\frac{\sigma}{\mu} \times 100$) of discharge for the period between successive locations. Lastly, I included fish TL as a predictor. I natural-log transformed mean discharge and fish TL to account for skewness and standardized all continuous predictors (mean = 0; SD = 1) to improve model interpretation (McCune and Grace 2002).

I combined linear mixed models (LMMs) with a model selection approach to determine the relationship between Smallmouth Bass daily movement, stream, season, environmental conditions, and fish size. All analyses were conducted in R version 3.5.1 (R Core Team 2018). I considered all subsets of the model containing terms for stream, season, mean water temperature, change in water temperature, mean discharge, CV of discharge, fish TL, and the following interactions: stream × mean temperature, stream × mean discharge, season × mean temperature, season × mean discharge, and season × stream. Pairwise correlations between predictor variables were < |0.44|, so all combinations were included in the candidate model set (n = 563 models). All models included a random effect for individual fish to account for unequal sampling and the lack of independence among measurements (Otis and White 1999; Wagner et al. 2006). I assumed a normal distribution $N(0, \tau^2)$ for random effects, where τ^2 represents the population variance among random effect levels (e.g., among individual fish). Candidate LMMs were coded using the ‘lme4’ package (Bates et al. 2015) in R. I used the R package ‘AICcmodavg’ (Mazerolle 2017) to rank my models using Akaike’s information criterion adjusted for small sample size (AIC_c, Sugiura 1978). For this and all subsequent model-selection efforts, I did not consider models within 2 AIC_c of the top model to have support if they contained more parameters than the top model; this approach avoids unnecessary model complexity and reduces the inclusion of uninformative predictors (Arnold 2010). I evaluated residual and Normal Q-Q plots for the top model to ensure homogeneity of variance and the normal distribution of residuals and random effects. To assess the relative amount of variation explained by fixed and random effects in the top model, I calculated marginal and conditional R^2 as described by Nakagawa and Schielzeth (2013) using R package 'MuMIn' (Bartoń 2018). Marginal R^2 (R^2_m) describes the variance explained by fixed effects, whereas conditional R^2 (R^2_c) reflects the variance explained by fixed and random effects (Vonesh et al. 1996).

I used model selection on a set of generalized linear models (GLMs) to evaluate the influence of stream, fish sex, and fish TL on home range size. I compared home range size with the number of observations for each fish to determine an appropriate cutoff for estimating home range (Todd and Rabeni 1989). With $n \geq 12$ observations, home range estimates showed no relationship with the number of observations, so this cutoff was used to identify $n = 72$ home ranges for summary and subsequent analysis. I natural-log transformed home range size to reduce skewness. Stream was a categorical predictor with levels for Sycamore Creek, Buffalo Creek, and Elk River. Fish sex was determined for individual fish during radio transmitter implantation. Sex could not be determined for all fish, including all autumn-tagged individuals, so I created a third category for unknown sex. Fish TL was natural-log transformed and standardized (mean = 0; SD = 1). All interactive and additive combinations of predictors were included in a candidate model set ($n = 14$ models) and AIC_c was used to compare models (Sugiura 1978).

I evaluated and summarized habitat use in relation to season, stream, fish sex, and fish TL. Based on apparent seasonal, among-stream, and individual differences in depth and velocity use, I modeled predictors of depth use and velocity use using separate candidate LMM sets that differed only in their response term. I natural-log transformed velocity values (i.e., y + 0.001) to address skewness. Categorical predictors included stream (three levels), season (four levels), and fish sex (three levels). I natural-log transformed and standardized (mean = 0; SD = 1) the continuous predictor, TL. Each candidate model set included all additive combinations of these fixed effect predictors (*n* = 16 models). I added a random individual fish effect to all candidate models to address correlation between measurements and unequal sampling of individuals (Otis and White 1999; Wagner et al. 2006). I ranked candidate models using AIC_c (Sugiura 1978). I assessed top model fit and assumptions using residual and Normal Q-Q plots and calculated the amount of variation explained by the model using marginal and conditional R^2 (Nakagawa and Schielzeth 2013). Because the use of different cover and substrate types appeared to vary only with categorical predictors, I calculated proportional use of cover types and substrate classes for each season and stream.

RESULTS

The size of tagged fish varied within and among study systems. The largest fish were generally tagged in the larger streams. Fish that were tagged following capture from the Elk River had a mean TL of 349 mm (range: 290–464 mm) and a mean weight of 600 g (range: 368–1,603 g). Comparatively, fish sampled and tagged in Buffalo Creek were shorter (mean TL: 327 mm; range: 278–408 mm) and lighter (mean weight: 518 g; range: 370–1,010 g). Smallmouth Bass sampled and tagged from Sycamore Creek were the smallest fish by both TL (mean: 322 mm; range: 290–370 mm) and weight (mean: 481 g; range: 376–765 g). Over the duration of the study, I recovered 71 transmitters; I re-implanted 53 into new fish (*n* = 22 in Buffalo Creek, *n* = 20 in Elk River, and *n* = 11 in Sycamore Creek). Tracking efforts from the 21-month study period resulted in *n* = 2,362 individual locations from *n* = 130 fish.

Discharge conditions and water temperature during the study followed typical seasonal patterns and reflected groundwater variability of these Ozark Highland streams (Figure 2). High flows typically occurred during spring for all three streams. There was one major flood event in late April 2017 representing a substantial extreme relative to flows during the remainder of the study period. In late summer and autumn 2016–2017, low flow conditions were common in both Buffalo and Sycamore creeks. Stream drying of riffles and pool isolation were common across many reaches of both streams during these periods. Over the study period, discharge was greatest in Elk River (median: 6.68 m^3/s) and similar for Buffalo Creek (median: 0.43 m^3/s) and Sycamore Creek (median: 0.38 m^3/s). Mean water temperatures during the study period were warmer in Elk River (19.0 °C) than in Sycamore Creek (17.0 °C) and Buffalo Creek (16.9 °C). Thermal variability was greatest in Sycamore Creek (CV: 38.2) and lowest in Elk River (CV: 30.2).

Movements of tagged Smallmouth Bass were highly variable among seasons, streams, and individuals. Movement rates were greatest (median: 3.8 m/d) and most variable (CV: 450.7) during spring, lowest (median: 0.3 m/d) in winter, and least variable (CV: 184.0) in autumn. Tagged fish tended to be more mobile in Elk River (median: 5.2 m/d), followed by Buffalo Creek (median: 2.3 m/d) and Sycamore Creek (median: 1.3 m/d). The greatest individual movements were an order of magnitude greater in Elk River (17.0 km) and Buffalo Creek (12.9 km) compared to movements of tagged fish in Sycamore Creek (1.7 km). Of 73 individual movements > 1.0 km, 43 (59%) occurred during the spring. Movement rates > 1,000 m/d were observed on nine occasions in Elk River (56%) and Buffalo Creek (44%) and were concentrated during the spring season (89%). I did not observe any tagged fish using Grand Lake or its associated river-reservoir interface zones during the study, but three tagged fish moved between Elk River and Buffalo Creek when reservoir levels were low and there was flowing water at the confluence.

The top model for movement rate included several interaction terms (season × mean discharge, season × mean temperature, season × stream, stream × mean temperature) and two main effects: CV of discharge and fish TL (Table 1). Movement rate was positively associated with increasing discharge during spring, but this relationship was negligible over the smaller range of flows that occurred during summer (Figure 3). Predicted movement rates were consistent and comparatively low during relatively homogenous discharge conditions associated with both autumn (mean: 3.4 m/d) and winter (mean: < 0.1 m/d). The effect of mean water temperature on movement rate varied by stream and by season (Figure 4). Movement rates in Elk River were positively related to mean temperature in all seasons except winter, and this relationship was particularly evident in spring. Movement rates of tagged fish in Buffalo Creek were similar regardless of mean water temperature in spring and autumn. Interestingly, movement rates of these fish also decreased as temperature increased in both summer and winter. In Sycamore Creek, there was a small but positive relationship between mean temperature and movement rate in all seasons except winter. Across all streams and seasons, larger fish were predicted to have greater movement rates (Figure 5). Increasing flow variability, as measured by the CV of discharge, had a small but positive effect on movement rate. The fixed effects in this model explained 16% of the variation in movement rate (R^2_m = 0.16), and the addition of the random individual effect led to a total of 29% of the variation being explained (R^2_c = 0.29).

Linear home range sizes were highly variable and were not related to stream, fish sex, or fish TL (Table 2). Home range size differed substantially among individuals, ranging from 45–15,061 m. Median linear home range size was 773 m. Each stream and sex contained individuals ranging from sedentary to highly mobile (Table 2). The top-ranked linear model for home range size included only an intercept term. No other candidate models were within 2 ΔAIC_c of the null model.

Several aspects of habitat use varied among streams and seasons (Table 3). Model-predicted depth use varied by stream, with deeper habitats used in Buffalo Creek. Season also affected depth use, with greater depth use in winter, followed by spring, autumn, and summer. The fixed effects of stream and season explained 10% of the variability in depth use (R^2_m = 0.10), and the addition of a random individual effect increased the variance explained by the model to 41% (R^2_c = 0.41). The top model for velocity use included stream and season predictors (Table 3). Modeled velocity use was greater in Elk River regardless of season and lower during autumn across all streams. These fixed effects explained 7% of the variation in velocity use ($R^2_m = 0.07$), and the random effect for individual brought total variance explained to 15% ($R^2_c = 0.15$). Qualitative plots indicate that proportional use of different substrate and cover types was slightly different across streams and seasons (Figure 6). A greater proportion of tagged Smallmouth Bass in Elk River used bedrock substrates compared to fish in the smaller streams, and tagged fish in all streams used gravel substrates to a greater degree during spring. Observations of fish not associated with any cover type were common in all study streams, particularly Elk River, and the use of woody debris was more frequent in Buffalo Creek. No seasonal differences were apparent regarding use of different cover types.

DISCUSSION

Neosho Smallmouth Bass exhibit a considerable degree of heterogeneity in seasonal movement behavior. As expected, tagged fish exhibited greater mobility associated with spawning in the spring and reduced movement in winter (Todd and Rabeni 1989; Lyons and Kanehl 2002; Barthel et al. 2008). I did not observe a seasonal concentration of movements to overwinter habitats; however, movements to overwinter habitats sometimes occur over a protracted period (i.e., summer–autumn, Robbins and MacCrimmon 1977). Movement magnitudes were not as large as those observed in some northern populations. For example, Langhurst and Schoenike (1990) observed radio-tagged Smallmouth Bass movements of 69–87 km from a tributary to downstream mainstem habitat prior to the overwinter period. I would not expect movements of this magnitude given the dissected study river-reservoir landscape. The only way tagged fish could move such distances would be if they traversed the reservoir or river-reservoir interface.

I did not observe any evidence of fish using Grand Lake or transient river-reservoir interfaces during the study suggesting lentic habitats may act as a barrier to movement for the

Neosho subspecies. In fact, when the pool level of Grand Lake rose 3.1 m in spring 2017 and flooded the lower 1.7 km of Buffalo Creek, tagged fish in the affected area (*n* = 3) moved just far enough upstream to remain in lotic habitat. The avoidance of lentic habitat by the subspecies is further supported by the high degree of genetic uniqueness within the smaller stream populations (Taylor et al. 2018). Some mixing of genetics with the Tennessee strain of Smallmouth Bass is evident in the Elk River and thought to be related to angler movement of fish to Grand Lake (Taylor et al. 2018). Interestingly, Smallmouth Bass use both lotic and lentic habitats in natural connected river-lake systems (Webster 1954; Gerber and Haynes 1988; Barthel et al. 2008). The movements that I observed by the Neosho subspecies did reflect relationships with environmental drivers and were often stream-specific with noticeable differences between the large river and smaller stream populations.

I found movement rates of Smallmouth Bass reflected both season- and stream-specific environmental cues. As expected, increasing movement during the spring spawning season was positively related to discharge (Cleary 1956; Lyons and Kanehl 2002). Slightly higher movement rates by larger individuals may correspond with greater movement among older individual Smallmouth Bass (Dauwalter and Fisher 2008) with more experience locating suitable habitat patches (Orth and Newcomb 2002). Discharge was less variable and unrelated to fish movement outside the spring season. In general, I found lower movement rates and dampened relationships between environmental cues and movement rates in the two smaller streams (Buffalo Creek and Sycamore Creek). The movement patterns associated with the smaller streams may relate to restricted movement potential due to seasonal drying (i.e., loss of habitat connectivity). The slight but positive effect of flow variability on movement rate may be due to small flow pulses that increase habitat connectivity when flows are otherwise low (Bradford and Heinonen 2008). Similar to discharge patterns, I found the effect of water temperature on fish movement was positive in the Elk River but appeared less important in the smaller streams. The effects of temperature on freshwater fish movements are variable but increasing spring temperatures are a common movement cue for Smallmouth Bass (Lyons and Kanehl 2002; Barthel et al. 2008). Reduced movements across all streams in winter may reflect use of thermal refugia or sedentary behavior to reduce loss of energy stores (Westhoff et al. 2016). The slightly greater movement rates in all systems at lower temperatures during winter may reflect movements to refuge habitats in response to harsher temperatures (Lyons and Kanehl 2002). Buffalo Creek has a higher contribution of groundwater (Zhou et al. 2018); thus, local groundwater inputs may offer refuge locations that minimize the need for winter movements. Although seasonal and stream-specific patterns emerged, there was still high individual variability in movements within these populations.

Individual variation and unexplained residual variability in movement rates among tagged Smallmouth Bass were apparent in my results. This variation may reflect individual differences (e.g., condition, inherent movement propensity, reproductive status) and their interactions with measured or unmeasured extrinsic ecological factors (e.g., habitat, predation risk, presence of mates, Rasmussen and Belk 2017). A mix of mobile and non-mobile individuals within a population has been observed in many studies of Smallmouth Bass in riverine and connected environments (e.g., Gerber and Haynes 1988; Gunderson VanArnum et al. 2004; Barthel et al. 2008). Additional individuality may reflect fidelity to specific spawning or overwinter habitats, which I observed for a few individuals in this study. This behavior occurs in some Smallmouth Bass populations (Ridgway et al. 1991; Barthel et al. 2008) but not others (Gerber and Haynes 1988; Lyons and Kanehl 2002).

Linear home ranges of tagged Smallmouth Bass were also highly variable among individuals and not related to sex, stream, or fish size. In an interior Ozark Highlands stream, Todd and Rabeni (1989) likewise found no relationship between fish length and home range size. Individuality in home range size has been reported for Smallmouth Bass populations in Kentucky

(Gunderson VanArnum et al. 2004) and Ontario (Barthel et al. 2008). Individual variation is also the primary driver of home range size in other riverine fish species (e.g., Flathead Catfish *Pylodictis olivaris*, Vokoun and Rabeni 2005).

I observed seasonal and stream-specific patterns in habitat use by Smallmouth Bass. I observed fish using deeper-water habitats during winter, regardless of stream size. Use of deeper-water during winter is consistently reported for Smallmouth Bass populations (Munther 1970; Lyons and Kanehl 2002; Ettinger-Dietzel et al. 2016). Interestingly, tagged fish in Buffalo Creek also used deeper habitats compared to tagged fish in the other study streams. This may relate to several factors: 1) the availability of deeper water, 2) the association of pools with thermal refugia at a patch scale that I did not measure, and 3) the regular disconnection of surface flows during the summer and autumn seasons in Buffalo Creek (see Hafs et al. 2010). Modeled velocity use by tagged Smallmouth Bass was greatest in the largest river I examined (Elk River) and generally the lowest across all streams during autumn. This result may reflect that Smallmouth Bass were more often associated with run habitats in Elk River than in the other streams. Elk River is much wider and faster when compared to the other two streams in this study. Use of low-velocity habitats in autumn is likely important for conserving energy prior to the overwinter period when fish subsist primarily on accumulated energy stores (Coble 1975). Considerable individual variation remained in explaining patterns of depth and velocity use across the three streams I examined. Use of gravel substrates increased in spring, consistent with the reproductive period and known spawning habitat preferences (Dauwalter and Fisher 2007; Miller, Chapter 3). Many tagged fish were not associated with cover, which seems common among adult Smallmouth Bass (Todd and Rabeni 1989; Lyons and Kanehl 2002). Cover used by tagged fish in this study did not differ among seasons, in contrast to previous studies (Todd and Rabeni 1989; Ettinger-Dietzel et al. 2016).

One potential factor complicating this study was the loss of transmitters by tagged fish. Transmitter loss is often unavoidable in telemetry studies, but may arise due to mortality of tagged individuals, stress related expulsion, or poor tagging practices (Jepsen et al. 2002). Natural mortality may explain some of the lost transmitters, as tag loss peaked when natural mortality was expected to be greatest (i.e., summer, winter, Hurst 2007; Dauwalter and Fisher 2008) and several recovered tags showed signs of predation (e.g., chew marks). Harvest can greatly reduce numbers of tagged fish (Westhoff et al. 2016) and several of my fish were caught by anglers during the study. I specifically know of one tagged fish that was harvested by anglers (and the transmitters returned). Several catch-and-release anglers I encountered while tracking mentioned catching and releasing tagged bass suggesting post-release mortality or tag expulsion may have occurred throughout the study. On two occasions, I tracked fish to anglers' stringers and convinced the angler to release the fish; in both instances, the transmitter was found by itself during the following tracking period (i.e., shed). Surgically, I followed best practices by moving the inserted transmitter away from the incision site and by trailing the antenna out a separate incision to reduce pressure on the sutures (Ross and Kleiner 1982; Jepsen et al. 2002). As most tag loss occurred several months after tagging surgeries and multiple relocations and/or visual confirmations of fish survival, I am confident that surgical technique or post-release mortality was not the underlying cause of transmitter loss. The main complication of frequent tag loss to this study was the lower number of tagged Smallmouth Bass with sufficient observations to evaluate home range size. Transmitter loss had a lesser effect on the analysis of movement rate and habitat use because each observation was treated as a unique response (i.e., with individual fish treated as a random effect).

Accounting for fish movements is essential for defining the appropriate scale for effective conservation and management actions. Movement data provide insight into the range of habitats needed for the completion of the life cycle and the corridors that connect these habitats (i.e., the functional habitat unit, Schlosser 1991; Cooke et al. 2016; Thurow 2016). Because the tagged fish in smaller streams moved primarily during the spawning season and in response to higher discharge levels, efforts to limit further alteration of the flow regime (e.g., groundwater pumping) would seem warranted. Because local populations appear to exhibit some variation in their movement tendencies, tailoring management actions to specific population units may also be a useful approach. It is important to limit the introgression of nonnative Smallmouth Bass genetics into these populations, as this poses a conservation threat to the native form by compromising locally-adapted genotypes (Koppelman 2015). There is evidence of some introgressive hybridization with nonnative forms in both the Elk River and Buffalo Creek populations (Taylor et al. 2018); curiously, introgression appears to be lacking in the smallest stream I evaluated despite connection to the same reservoir. Educating stakeholders about the value of endemic Neosho Smallmouth Bass may help discourage future unauthorized introductions (e.g., Cambray 2003). Although the Sycamore Creek population of Neosho Smallmouth Bass is effectively isolated by Grand Lake from other populations, connectivity between the Elk River and Buffalo Creek populations could be increased by keeping Grand Lake pool levels low during winter and spring when possible. This would improve access to warmer mainstem winter habitats and to a wider range of spawning habitats between the two systems. Efforts to protect this narrow-rage endemic black bass could be valuable to scientists and managers dealing with similar issues (e.g., endemism, human alteration of the environment, scale of management) and strategies may be transferrable to other endemic black basses in the face of environmental change. Movement of individuals represents an important mechanism for coping with environmental changes and reduces vulnerability to the myriad effects of climate change (Pörtner and Peck 2010). Therefore, it is essential that we protect or enhance the physical conditions that allow stream fish to move in response to changing environmental conditions and biological needs.

Table 1. Rankings of models within 2 AIC_c of the top model from candidate set of linear mixed models of movement rate (natural-log transformed) by adult Smallmouth Bass in Ozark streams ($n = 563$ models). Y_{ij} is daily movement rate at relocation i for fish j, β_0 is the grand intercept, γ is the random fish intercept, X_1 is season, X_2 is stream, X_3 is the mean discharge (m^3/s) between relocations, X_4 is the coefficient of variation (CV) for discharge between relocations, X_5 is the mean water temperature (°C) between relocations, X_6 is the CV of water temperature between relocations, X_7 is the change in mean daily water temperature (°C) between relocations, X_8 is fish TL (mm). Main effects involved in interactions are included but not shown for each model. K is the number of model parameters, LL is log-likelihood, AIC_c is Akaike's information criterion corrected for small sample size, and $\Delta\mathrm{AIC}_c$ is the difference in AIC_c score between a given model and the top model. Akaike weight (w_i) indicates the relative support for each model. Marginal R^2 (R^2_m) describes variance explained by fixed effects and conditional R^2 (R^2_c) describes variance explained by both fixed and random effects.

Model	K	LL	AIC_c	$\Delta\mathrm{AIC}_c$	w_i	R^2_m	R^2_c
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i}\cdot X_{3i} + \beta_2 X_{1i}\cdot X_{5i} + \beta_3 X_{2i}\cdot X_{5i} + \beta_4 X_{1i}\cdot X_{2i} + \beta_5 X_{4i} + \beta_6 X_{8j}$	26	-3671.84	7396.31	0.00	0.27	0.16	0.29
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i}\cdot X_{3i} + \beta_2 X_{1i}\cdot X_{5i} + \beta_3 X_{2i}\cdot X_{5i} + \beta_4 X_{1i}\cdot X_{2i} + \beta_5 X_{4i} + \beta_6 X_{8j} + \beta_7 X_{2i}\cdot X_{3i}$	28	-3670.44	7397.62	1.31	0.14	0.16	0.29
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i}\cdot X_{3i} + \beta_2 X_{1i}\cdot X_{5i} + \beta_3 X_{2i}\cdot X_{5i} + \beta_4 X_{1i}\cdot X_{2i} + \beta_5 X_{4i} + \beta_6 X_{8j} + \beta_8 X_{7i}$	27	-3671.78	7398.24	1.93	0.10	0.16	0.29

Table 2. Summary statistics of estimated linear home ranges of radio-tagged adult Smallmouth Bass in three Ozark streams by stream and fish sex. I define linear home range as the distance between the most extreme upstream and downstream locations for each fish.

Predictor	*n*	Mean ± SD (m)	Median (m)	Range (m)
Elk River	20	2,799 ± 4,251	742	45 – 15,061
Buffalo Creek	32	1,858 ± 2,238	883	53 – 9,933
Sycamore Creek	20	806 ± 573	503	167 – 2,046
Female	14	1,176 ± 1,476	604	82 – 5,220
Male	20	1,974 ± 2,392	1,194	53 – 9,933
Unknown	38	1,990 ± 3,289	714	45 – 15,061
Overall	72	1,827 ± 2,770	773	45 – 15,061

Table 3. Models within 2 AIC$_c$ of the top model from candidate sets of linear mixed models of depth and velocity use (natural-log transformed) by adult Smallmouth Bass in Ozark streams (*n* = 16 models each). Y_{ij} is the depth (or velocity) at location *i* for fish *j*, β_0 is the grand intercept, γ is the random fish intercept, X_1 is season, X_2 is stream, X_3 is fish sex, and X_4 is fish TL (mm). *K* is the number of model parameters, LL is log-likelihood, AIC$_c$ is Akaike's information criterion adjusted for small sample size, and ΔAIC$_c$ is the difference in AIC$_c$ score between each model and the top model. Relative support for each model is given by Akaike weight (w_i). Variance explained by fixed effects is given by marginal R^2 (R^2_m) while the variance explained by both fixed and random effects is described by conditional R^2 (R^2_c).

Model	*K*	LL	AIC$_c$	ΔAIC$_c$	w_i	R^2_m	R^2_c
Depth							
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2i}$	8	-501.84	1019.75	0.00	0.41	0.10	0.41
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3j}$	10	-500.31	1020.71	0.96	0.26	0.11	0.41
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_4 X_{4j}$	9	-501.48	1021.03	1.29	0.22	0.10	0.41
Velocity							
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2i}$	8	-5227.77	10471.59	0.00	0.48	0.07	0.15
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3j}$	10	-5226.43	10472.95	1.36	0.24	0.07	0.15
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_4 X_{4j}$	9	-5227.73	10473.53	1.94	0.18	0.07	0.15

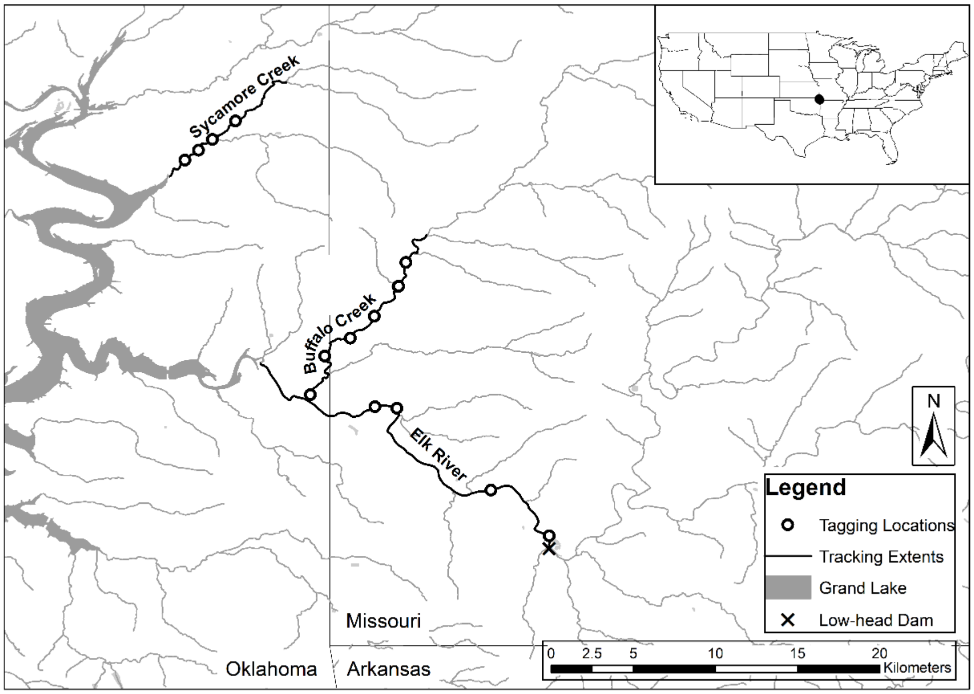


Figure 1. Tagging locations and tracking extents (bolded) for three Ozark streams where I evaluated movement and habitat use of adult Smallmouth Bass.

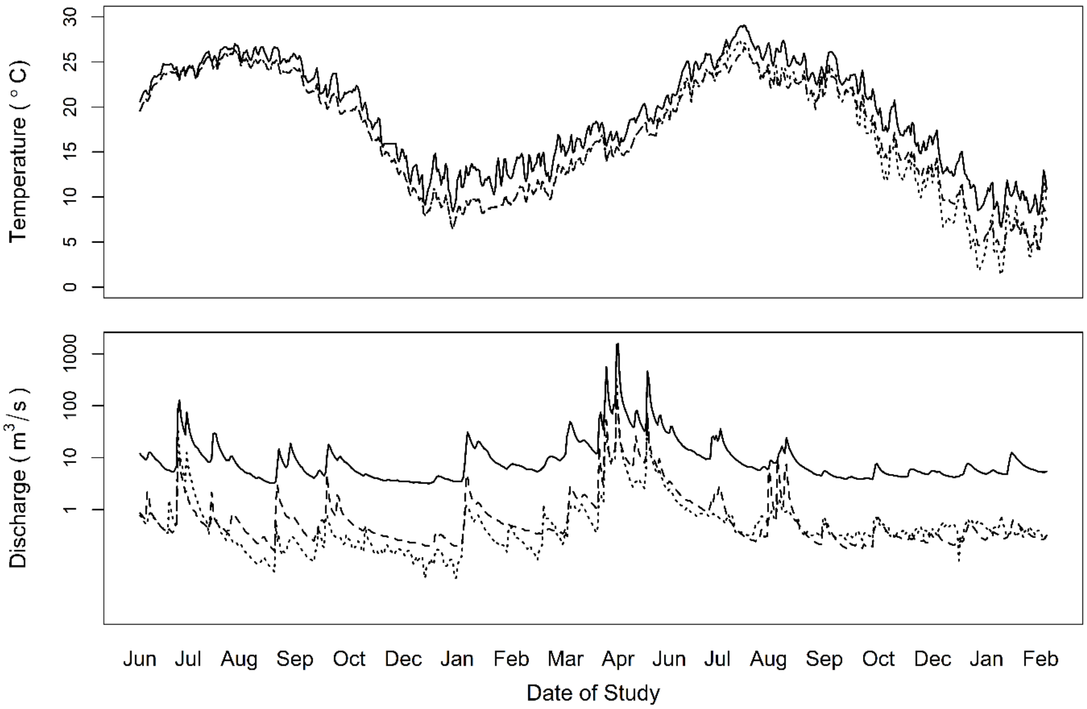


Figure 2. Daily mean water temperature (top) and discharge (bottom) conditions for Elk River (solid line), Buffalo Creek (dashed) and Sycamore Creek (dotted) during the June 2016–February 2018 study of adult Smallmouth Bass movement and habitat use. For reference, 1.0 m^3/s equals 35.3 ft^3/s. Note that discharge is plotted using a $\log_{10}$ scale and that the y-axis ranges from 0.01 m^3/s to the maximum discharge during the study period (1,557 m^3/s on 30 April 2017 in Elk River).

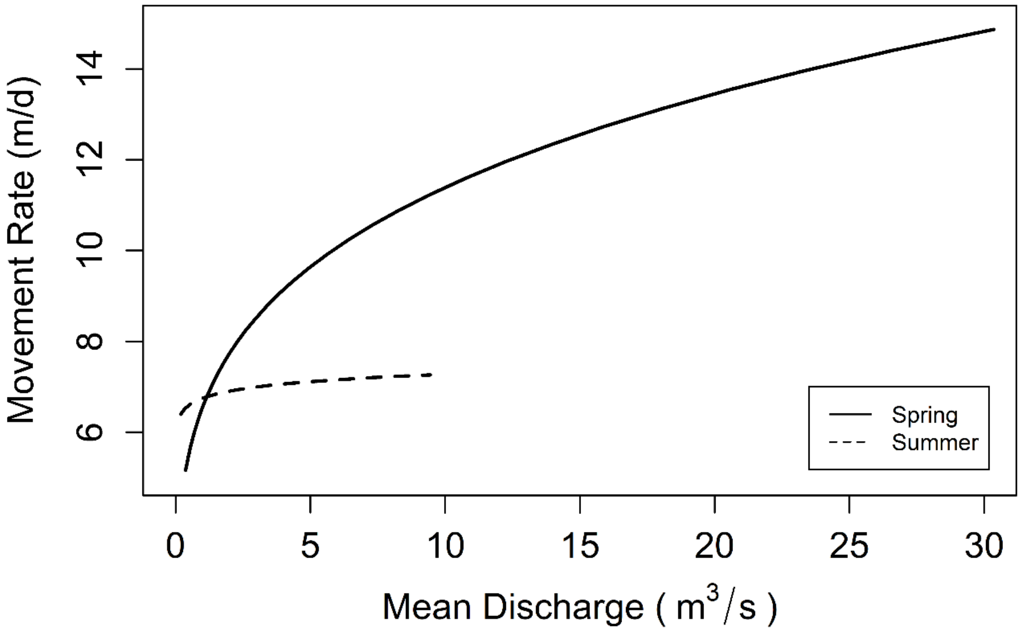


Figure 3. Predicted relationship between Smallmouth Bass movement rate (m/d) and mean discharge (m^3/s) in spring and summer. Predicted movement rates are not pictured for autumn (mean: 3.4 m/d) or winter (mean: < 0.1 m/d) as these predictions do not vary over the small range of discharge values (0.29–0.92 m^3/s) for which they are valid. Predicted movement rates are made for back-transformed mean discharge values in Buffalo Creek with all additional continuous predictors held constant at their mean values.

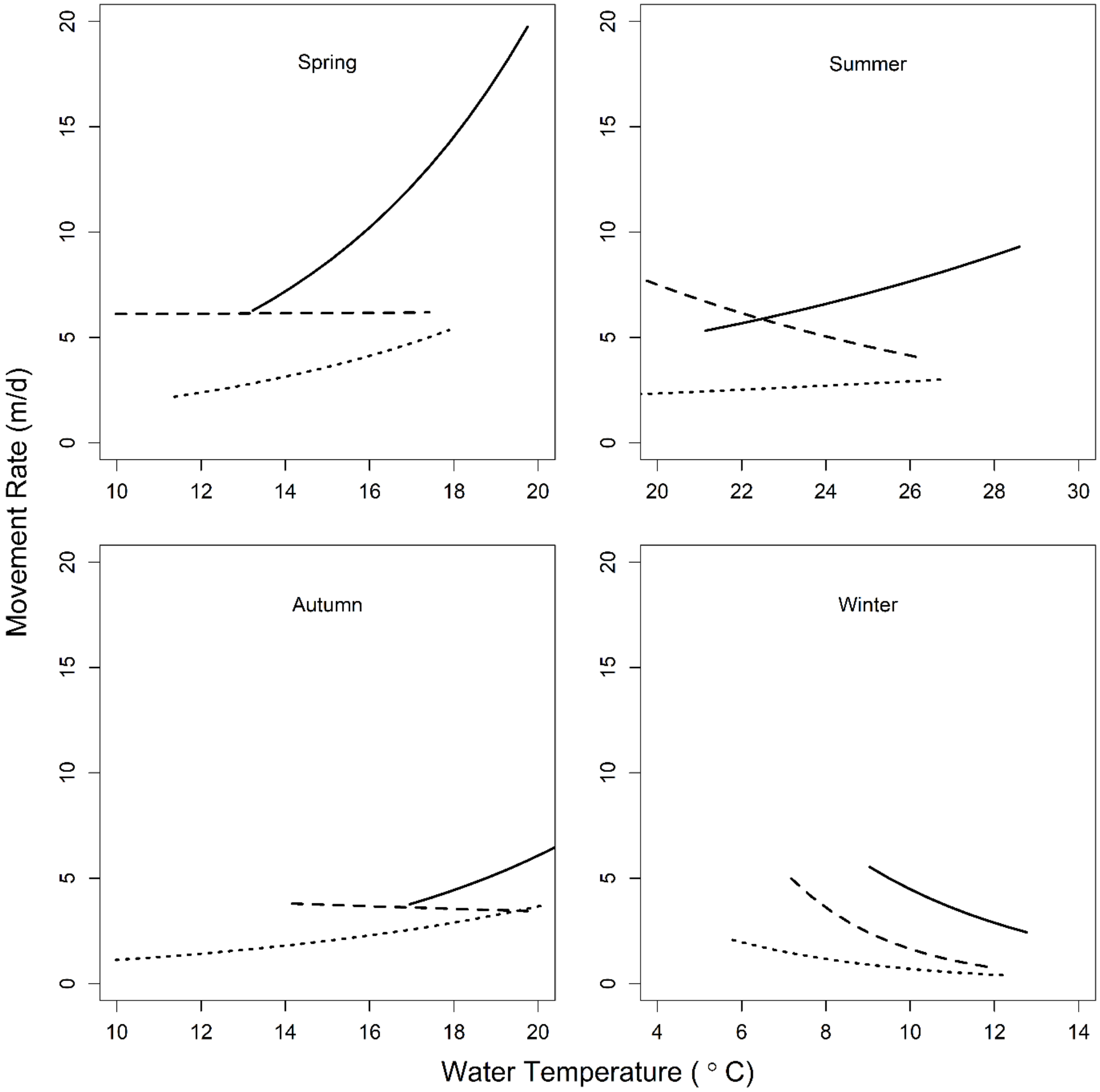


Figure 4. Modeled relationship between movement rate (m/d) of Smallmouth Bass and mean water temperature (°C) across three study streams and four seasons. The study streams are Elk River (solid line), Buffalo Creek (dashed), and Sycamore Creek (dotted). Predictions represent changes in water temperature with all other continuous model predictors held constant at their mean values.

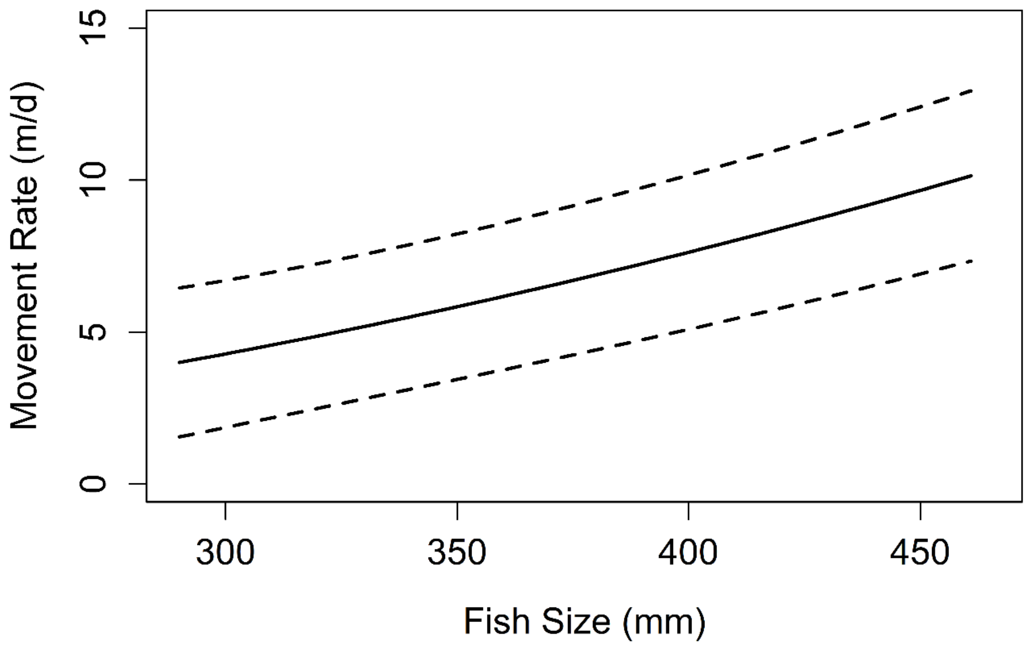


Figure 5. Relationship between movement rate (m/d) and fish size (TL, mm) from the top-ranked model of movement rate. Dashed lines indicate 95% confidence intervals. Predictions are made with all other continuous predictors at mean levels and with Elk River as the reference stream and summer as the reference season.

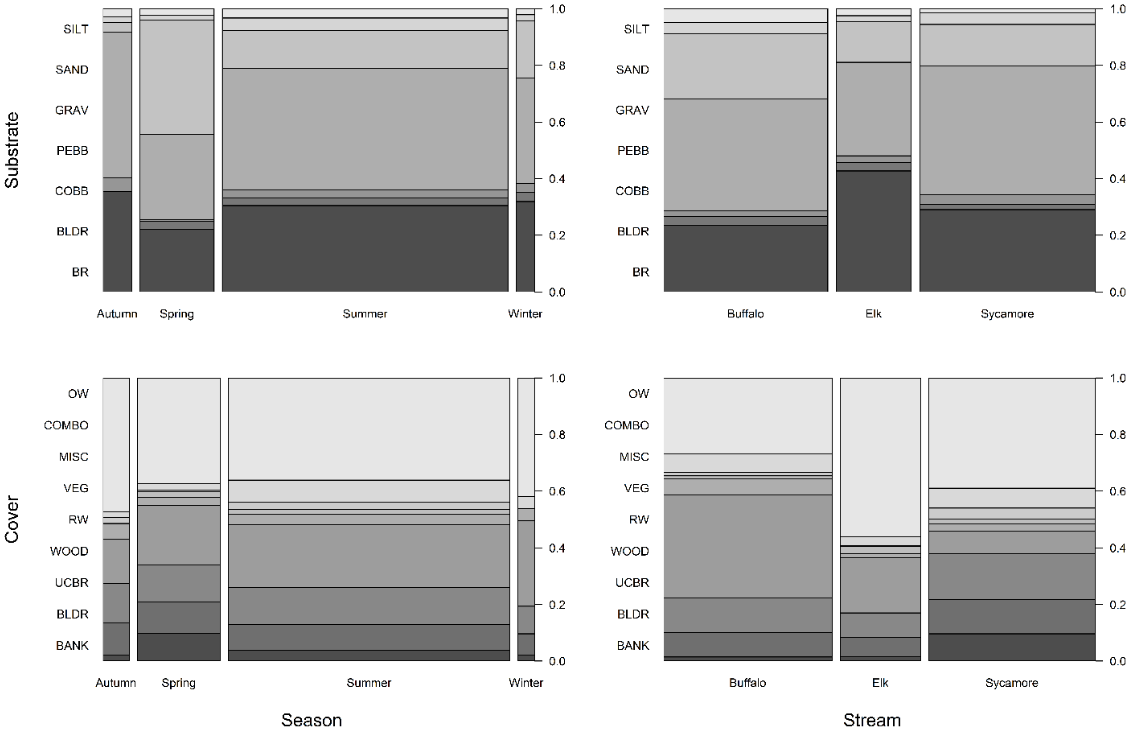


Figure 6. Summaries of proportional substrate and cover use across seasons and streams based on *n* = 2,362 observations of radio-tagged Smallmouth Bass. Column widths are proportional to sample size. Substrate types include silt (< 0.06 mm), sand (> 0.06–2 mm), gravel (> 2–16 mm; GRAV), pebble (> 16–64 mm; PEBB), cobble (> 64–256 mm; COBB), boulder (> 256 mm; BLDR) and bedrock (BR). Cover types are open water/no cover (OW), woody debris (WOOD), boulder (BLDR), rootwad (RW), undercut bank (BANK) or bedrock (UCBR), vegetation (VEG), man-made (MISC) and combinations of these types (COMBO). Man-made cover includes miscellaneous structures such as bridge pilings, broken concrete, and fencing.

CHAPTER III

RIVERSCAPE NESTING DYNAMICS BY AN ECOLOGICALLY AND ECONOMICALLY-IMPORTANT SUBSPECIES OF SMALLMOUTH BASS

ABSTRACT

Hierarchical stream habitat conditions influence patterns of fish abundance and population dynamics. The spawning period is important for stream fish populations but coincides with dynamic environmental conditions and myriad natural and anthropogenic stressors. Thus, identifying the habitat conditions that confer suitable spawning areas is crucial to managing vulnerable stream fish populations, including narrow-range endemics. I conducted snorkel and habitat surveys from 2016–2018 to determine the influence of multi-scale habitat features on nest abundance of Smallmouth Bass Micropterus dolomieu velox. I documented nest aggregations (“clusters”) that are scarcely known for other Smallmouth Bass populations. Nest cluster presence was more likely in warmer stream reaches with wide, shallow channels and less likely in reaches experiencing a net gain in streamflow due to groundwater. The abundance of Smallmouth Bass nests was related to several local habitat conditions, with greater abundances in warmer streams and reaches with deeper pool habitats. Regardless of cluster inclusion, nesting Smallmouth Bass used similar microhabitats, including a range of depths (0.26–1.85 m), low velocities, and gravel substrates. These relationships highlight the need to consider multiple aspects of stream habitat when developing conservation and management plans. The unique nest clustering of Smallmouth

Bass in these streams represents a potential vulnerability to human influence but also an opportunity to proactively protect these diverse populations during vulnerable life history periods.

INTRODUCTION

Lotic ecosystems are organized in a spatially nested hierarchy, resulting in complex patterns of fish distribution and abundance. Stream habitat reflects patterns and processes operating at several spatiotemporal scales from microhabitats to catchments (Frissell et al. 1986). Coarse-scale processes such as climate, geology, and topography influence finer-scale habitat patterns, creating a complex mosaic of stream habitat and thus providing context for observed relationships between fish and the physical environment (Frissell et al. 1986; Snelder and Biggs 2002; Allan 2004). For example, coarse-scale thermal patterns may limit the abundance of stream fish in sample reaches, overriding the influence of suitable local habitat features (e.g., depth, substrate, mesohabitat composition, Martin and Petty 2009; Lawrence et al. 2012; Brewer 2013). Because the perceived habitat needs of stream fish vary with the scale of investigation, a multi-scale approach to determining important habitats is necessary for appropriate conservation and management (Schlosser 1991; Fausch et al. 2002). This could be particularly important during the spawning period if nest site selection and mate acquisition are influenced by factors operating at different spatiotemporal scales.

Spawning habitat is a critical component of the life history of fishes, and appropriate physicochemical conditions are required for successful spawning and incubation of eggs (Schlosser and Angermeier 1995). Eggs and larval fish are particularly vulnerable to both biotic and abiotic stressors including starvation, predation, and physicochemical extremes (e.g., floods, severe temperatures, Jennings and Philipp 1994; Lukas and Orth 1995; Knotek and Orth 1998). Appropriate habitat confers added protection from these threats by providing physical cover that obstructs stream currents and serves as refuge from predators (Schlosser 1987, 1991).

Additionally, nest habitats must provide favorable growing conditions for developing offspring until they are capable of seeking out other profitable locations (Lawrence et al. 2015). These constraints collectively influence stream fish demographic patterns in heterogeneous lotic environments.

There is tremendous diversity in life-history traits and behaviors among fishes, and spawning habitat choice and associated species-nesting behavior may vary along environmental gradients. Life-history diversity reflects trade-offs among demographic parameters (e.g., survival, fecundity, time to reproductive maturity), which in turn reflect phylogenetic and biogeographic constraints (Winemiller and Rose 1992; Mims et al. 2010). Understanding diversity among spawning populations is useful to predict differences in demographic responses among populations (Ensign et al. 1997; Winemiller 2005). Intraspecific variation in use of spawning habitats and spawning behavior may relate to differences in habitat quality and quantity (Blanck and Lamouroux 2007; Isaak et al. 2007; Senay et al. 2015). Aggregations form when spawning individuals are mutually attracted to resources such as food or habitat (Freeman and Grossman 1992; Helfman et al. 2009); this behavior may confer advantages such as improved mate attraction and protection from predators. Diversity in spawning behavior of fishes and use of habitat can confer population resistance and resilience to disturbance and changing environmental conditions (Reusch et al. 2005; Schindler et al. 2010; Thorson et al. 2014) and should be considered in developing conservation strategies for freshwater fishes (Fausch et al. 2002; White et al. 2014; Schindler et al. 2015).

Although the general nesting ecology of Smallmouth Bass is well-studied, unique genetic lineages occupying the southwest edge of the native range offer opportunities for examination of geographic variation in nesting habitat and behavior across a highly-altered landscape. Spawning by the more-common northern subspecies is typically preceded by migrations (Todd and Rabeni 1989; Barthel et al. 2008) with nesting occurring from April to mid-July when water temperatures reach ~15°C (Shuter et al. 1980). Males excavate shallow substrate depressions in low-velocity areas near cover (Pflieger 1966). Post spawn, parental males vigorously defend eggs and larvae from nest predators (Scott et al. 1997). Territoriality by male Smallmouth Bass typically leads to ample spacing (i.e., > 17 m) between nests in both lakes and rivers (Winemiller and Taylor 1982; Wiegmann et al. 1992; Scott 1996). In addition to the well-studied northern populations, Smallmouth Bass has two known genetic variants at the southwest edge of the native range including the Neosho subspecies *M. d. velox* (Hubbs and Bailey 1940; Stark and Echelle 1998; Brewer and Long 2015). The range of this subspecies (hereafter referenced as Neosho Smallmouth Bass) is characterized by impoundments that appear to limit gene mixing among riverine subpopulations (Taylor et al. 2018) and may result in distinct subpopulation habitat use. Our current understanding of Neosho Smallmouth Bass nesting ecology is limited to results from one river (Dauwalter and Fisher 2007), but results indicate high nest densities (i.e., 100–147 km^{-1}), microhabitat use consistent with the northern subspecies, and notes on nest failures (i.e., angling and human physical disturbance) and nest predation. Field observations associated with unrelated stream fish surveys suggest nesting behaviors by this subspecies that appear to reflect aggregations that are rarely reported and never quantified (S. K. Brewer, pers. obs.; J. Burroughs, pers. comm.), though Pflieger (1966) reports a single instance of northern subspecies nests ~1.1 m apart in an interior Ozark Highland ecoregion stream.

My objective was to quantify the multi-scale nest habitat use by Neosho Smallmouth Bass and to describe factors related to nest aggregations within the subspecies. Multi-scale approaches are increasingly applied to examination of warmwater stream-fisheries research (e.g., Brewer et al. 2007; Dauwalter et al. 2008; Dunn and Angermeier 2019; Wellemeyer et al. 2019). For example, Dunn and Angermeier (2019) show that persistence of the imperiled Candy Darter *Etheostoma osburni* is limited to refugia defined by habitat conditions at multiple spatial scales. However, most efforts to understand hierarchical controls on warmwater stream fish abundance focus on adult fish outside of the reproductive period (but see Peoples et al. 2014). This lack of research belies the importance of the spawning period for population dynamics and the often-narrow environmental tolerances of spawning fish (e.g., temperature, Grabowski and Isely 2007; Asch and Erisman 2018). Thus, it is imperative to evaluate multi-scale spawning habitat relationships for warmwater stream fish, in particular those populations that occupy novel riverscapes such as those on range boundaries.

METHODS

Study area

I sampled 120 stream reaches across the Neosho Smallmouth Bass range within the Ozark Highlands ecoregion (hereafter “Ozarks”) to determine the physicochemical factors associated with nesting (Figure 1). The Ozarks receive an average of 108 cm of precipitation annually and annual hydrographs reflect typical spring floods followed by much lower baseflow conditions in summer and autumn (Nigh and Schroeder 2002). The Neosho Smallmouth Bass range is restricted to the southwest Ozarks comprising southwest Missouri, northeast Oklahoma, northwest Arkansas, and southeast Kansas, USA (Brewer and Long 2015). Lithology of the southwest Ozarks is primarily cherty limestone. The karst topography and associated springs confer spatially variable groundwater inputs with substrate comprised primarily of gravels and cobbles (Nigh and Schroeder 2002). Land use is generally forest or pasture, with the latter more common in valleys and the southwest portion of the Ozarks (Nigh and Schroeder 2002). Widespread damming in the southwest Ozarks has resulted in alteration to the naturally flashy flow regime (Graf 2006; Leasure et al. 2016) and altered the stream morphology such that streams are relatively wider and shallower (Splinter et al. 2010; Brewer 2011). My sample reaches (~20 times mean wetted stream width, Flosi et al. 1998) were chosen using a combination of criteria: high water clarity, representation of available habitat across the region, and access to privately-owned lands (Figure 1). Streams in this region are generally clear under base-flow conditions and reach-scale habitat typically comprises pools, riffles, runs, and off-channel habitats (simplified from Rabeni and Jacobson 1993).

Nest surveys

I examined habitat conditions used by individual nesting Neosho Smallmouth Bass and nest aggregations (hereafter referenced as “clusters”). Smallmouth Bass nests are typically defined by individual depressions made in gravel-cobble substrates in low-velocity areas (Warren 2009); however, anecdotal observations suggest the subspecies may also spawn on solid rock where a depression or fanned area is not obvious (S. K. Brewer and B. Brown, pers. comm.) and they may aggregate in clusters (J. Burroughs, pers. comm.). Thus, I used multiple characteristics to define nests. First, I observed Neosho Smallmouth Bass to identify territorial guarding behaviors such as quick swimming bursts toward perceived threats to the nest (e.g., other fishes and surveyors) and nest circling. In addition, I thoroughly searched any substrate depressions for the presence of eggs or larvae. I defined nest clusters as groups of at least two nests within 2 m of one another. The distances between neighboring nests of spawning riverine bass are usually far greater (e.g., 77.9 m, Winemiller and Taylor 1982). I only quantified guarded nests or those that contained eggs or fry because Smallmouth Bass sometimes excavate multiple nests in close proximity before choosing their nesting location (Cleary 1956).

I surveyed nesting Neosho Smallmouth Bass (i.e., nests and nest clusters) from 120 stream reaches during late spring and early summer (May–early July) of 2016–2018. Sampling began after water temperatures reached ~15°C (Pflieger 1966; Dauwalter and Fisher 2007) and continued throughout the spawning period until fry dispersed from nests. The beginning and end dates of sampling each year depended on spring and summer hydrologic patterns because bass may abandon existing nests or re-nest following flood events (Warren 2009). At least one flood event prevented sampling for ~7 d each sampling year and frequent high flows resulted in continued spawning activity by the fish into early July.

I surveyed each sample reach with a crew of 2–5 snorkelers (depending on wetted width and complexity) during daylight hours (0900-1700 hours) to maximize visibility. Lane widths per snorkeler were adjusted to reflect visibility and habitat complexity; in areas with reduced visibility or more-complex habitat, narrower lanes were used (Dunham et al. 2009; Thurow et al. 2012). Snorkelers slowly moved upstream in parallel lanes (e.g., left, middle, right), avoiding sudden movements and carefully searching complex habitats for guarding male bass or groups of eggs or fry in small depressions or near cover. As soon as a guarding male bass was observed, I slowly approached the area to determine nest location. If a potential guarding bass was spooked, I swam further away from the location and waited for the fish to return to determine if the fish was guarding a nest and estimate fish size (5.0 mm increments, total length [TL]). Snorkelers were trained to estimate fish sizes using a bass model (i.e., silhouettes of different sizes that resembled Smallmouth Bass, 150-305 mm TL, Mueller 2003; Dunham et al. 2009). Communication between observers was required to prevent the double-counting of nests. Because I surveyed some reaches twice to evaluate sample efficiency (see below), I uniquely marked individual nests with numbered flags on the last snorkel pass for later microhabitat quantification (Dunham et al. 2009; Brewer 2011). After each snorkeling pass, I measured water clarity (0.1 m), defined as the distance at which an observer could distinguish a bass-shaped silhouette underwater (Dunham et al. 2009). Visibility during all snorkel surveys was at least 1.5 m (Goldstein 1978).

I conducted a second snorkeling pass at 60 reaches to assess detection efficiency. I define detection efficiency as the proportion of nests detected among those present (*sensu* Peterson and Paukert 2009). I allowed a minimum of one hour between surveys so the stream could return to a relatively undisturbed state (Peterson and Cederholm 1984; O’Neal 2007). If the same snorkelers surveyed the second pass, each observer switched lanes so there would be no prior information on nests from the previous pass. Count data were not shared between observers between snorkel passes. The second survey was conducted using the aforementioned approach and individual nests were marked with numbered flags.

Habitat

I quantified the physicochemical conditions associated with nesting habitat at multiple spatial scales. First, I measured microhabitat conditions at each individual nest and cluster within each reach. Then, I quantified reach-scale attributes describing conditions among reaches where fish chose to nest. Because of the inherent nested structure of streams, I also quantified attributes associated with stream segments (i.e., sections of stream between tributary confluences) where multiple stream reaches were nested within stream segments (see also Analyses). Lastly, I measured conditions associated with the catchment draining to each stream segment (i.e., hereafter catchment) due to the influence of the upstream drainage on local conditions (Hynes 1975).

I recorded microhabitat conditions at each nest and recorded size characteristics of nest clusters. I measured microhabitat at individual nests and size attributes of nest clusters across n = 88 stream reaches in 2017–2018, whereas I documented the presence of nest clusters in all surveys completed from 2016–2018 (n = 120 reaches). For each nest observed, I measured water depth (0.01 m) and velocity (0.1 m/s) at the nest surface. For every cluster, I counted the number of nests in the cluster and measured both length and width to calculate cluster area (0.1 m^2). Lastly, I measured the center-to-center distance of each nest in the cluster to the nearest neighboring nest.

I measured additional physicochemical characteristics to determine the relative importance of reach-scale factors on nest abundance (Table 1). I used a thermometer (Ultrapen PT1, Myron L, Carlsbad, CA) to measure water temperature (0.1 °C) at mid-pool depth. Because water temperature represented only a point measure at the sampling event and there was a natural break in the data, I converted stream temperature to a factor with two levels (cool: ≤ 19.5°C, warm: > 19.5°C). I classified channel units using a simplified version of Rabeni and Jacobson (1993) and calculated percent area of each (Thurow 1994). Briefly, riffles were erosional units with relatively high gradient and coarse substrate, pools were depositional channel units in the main channel, runs were transitional habitats of intermediate depth and velocity, and off-channel habitats were low-velocity habitats adjacent to the main channel (i.e., backwaters or forewaters). Mean wetted channel width (0.1 m) was calculated when measuring channel units due to its expected influence of sampling efficiency (Schill and Griffith 1984; Hicks and Watson 1985) and relationship with land use (Clifton 1989). I measured residual pool depth (RPD; 0.01 m) as the difference between maximum pool depth and the downstream riffle crest (Lisle 1987). Thalweg depth (0.01 m) was measured every 50 m and averaged across each reach. I quantified high-flow characteristics of channel hydrology by measuring bankfull width-depth ratios (0.1 m; Gordon et al. 2004) and by estimating median substrate size (D_{50}) as a proxy for channel shear stress (Shields 1936). To estimate D_{50}, I measured intermediate diameters (1 mm) of ≥ 100 substrate particles collected from a single transect across a run that included the floodplain (Wolman 1954; Leopold 1970). I also conducted seepage runs (Harvey and Wagner 2000; Zhou et al. 2018) using an acoustic Doppler current profiler (RiverSurveyor M9, SonTek, San Diego, CA) to quantify discharge (0.01 m^3/s) at the upstream and downstream ends of each reach; I used the difference in discharge to define reach-scale groundwater flow. I categorized groundwater flow into three categories based on longitudinal gain or loss of streamflow relative to discharge measurement uncertainty (~0.03 m^3/s; Zhou et al. 2018): losing streams (net loss of streamflow), neutral streams (no change) and gaining streams (net gain).

I used terrain analysis and existing geospatial data in ArcMap 10.3.1 (ESRI, Redlands, California) to calculate characteristics describing each stream segment (i.e., section of stream between tributary confluences, *n* = 69; Table 1). Using a 30-m resolution raster digital elevation model (USGS National Elevation Dataset [NED]), I defined overland flow-direction pathways (O'Callaghan and Mark 1984; Jenson and Domingue 1988) and upstream catchment areas (Betz et al. 2010) for each stream segment. I calculated in-stream flow direction using rasterized 1:100,000 flowlines (USGS National Hydrography Dataset [NHD]) and overlaid this grid on the landscape flow-direction grid to ensure that flow pathways agreed with mapped streams (Betz et al. 2010). I used the in-stream flow direction raster to calculate two metrics of stream topology: link magnitude (Shreve 1966) and downstream link (Osborne and Wiley 1992). Link magnitude and downstream link describe both stream size and segment location within the stream network (e.g., a similar-sized stream may be located in the headwaters or adjacent to a large mainstem river). I considered spatial location to describe proximity to different habitat types or resources that might influence nesting location.

I calculated metrics describing landscape disturbance, topography, soils, geology, runoff, and baseflow conditions for each catchment (Table 1). I calculated an index of landscape disturbance using land cover data from the 2011 National Land Cover Dataset (NLCD; Homer et al. 2015) and disturbance coefficients (modified from Brown and Vivas 2005; Mouser et al. 2019; Table S1). Because the land use types used by Brown and Vivas (2005) are finer-resolution than NLCD categories, I use the average of multiple coefficient values from Brown and Vivas (2005) if a single NLCD category comprised more than one land use type (e.g., Mouser et al. 2019). As an example, I used a coefficient for the NLCD "pasture/hay" category (2.99) that reflects the average of woodland pasture (2.02), improved pasture without livestock (2.77), improved pasture low-intensity with livestock (3.41) and improved pasture high-intensity with livestock (3.74) land use types from Brown and Vivas (2005). The lowest coefficient (1.00) described undisturbed habitats (e.g., forests, wetlands), whereas habitats subject to greater degrees of disturbance were assigned larger coefficients (e.g., 7.92, high-intensity development). Brown and Vivas (2005) used land-cover categories of a finer-resolution than the NLCD, so I averaged their coefficients to make them applicable to the NLCD (Mouser et al. 2019). Then, I calculated an area-weighted average of these coefficients across the upstream contributing area for each stream segment. I characterized topography using an instream measure of stream gradient from the NHDPlus V2 and calculated average landscape slope in the upstream catchment of each stream segment. I calculated percent hydrologic soil group D (i.e., indicative of high runoff potential) and percent carbonate lithology for each catchment using existing data (Stoeser et al. 2005; NRCS 2017). Hydrologic soils groups (A-D) describe soil permeability characteristics and are highly correlated with one another (i.e., total 100% across groups). Thus, I quantified soil group D because it negatively influences Smallmouth Bass presence and relative abundance in Ozark streams (Brewer et al. 2007). Likewise, lithology data were highly correlated, so I chose to quantify carbonate lithology because of its association with karst topography and springs. Lastly, I used data from Hill et al. (2016) to summarize variation in long-term mean annual runoff and relative baseflow contribution (i.e., percent of total flow attributable to groundwater) for the contributing segment catchment.

Nest cluster analysis

I used a mixed-effects logistic regression model to evaluate the multi-scale habitat features associated with nest cluster presence. First, I modeled the presence of nest clusters at n = 120 stream reaches in relation to a subset of predictors based on hypothesized explanations for clustering behavior (i.e., habitat limitation, groundwater, disturbance, progression of spawning season; Table 2). Habitat features influence aggregations and behavior of spawning fish in stream systems (e.g., Beard and Carline 1991; Baxter and Hauer 2000; Grabowski and Isely 2007). I included late-summer young-of-year (YOY) densities collected from the same reach in the same year (see Chapter 5) as a predictor to assess whether nest-clustering behavior results in increased offspring survival. I also added a sample-area term to the model to account for differences in snorkeling effort among stream reaches. I natural-log transformed continuous variables and logit-transformed proportions (after adding a constant of 0.001 to channel unit proportions and YOY densities to facilitate transformation when these values were zero) to reduce skewness and standardized all predictors to simplify interpretation of model terms (Warton and Hui 2011). Mean values of YOY density were used in place of missing observations to avoid data loss. I also included a random effect for stream segment to account for non-independent observations and address unexplained variability among reaches (Wagner et al. 2006; Gelman and Hill 2007). Coefficient and standard error estimates were used to determine which predictor slopes differed from zero. Lastly, I calculated marginal R^2 (i.e., amount of variance explained by the fixed effects) and conditional R^2 (i.e., amount of variance explained by both fixed and random effects, Vonesh et al. 1996; Nakagawa and Schielzeth 2013) to evaluate model fit. Logistic regression modeling and R^2 calculations were implemented in R packages ‘lme4’ (Bates et al. 2015) and ‘MuMIn’ (Bartoń 2018), respectively.

Nest abundance modeling

First, I evaluated the influence of water clarity, wetted channel width, and thalweg depth on sampling efficiency (p) among sites using an N-mixture model (Royle 2004). I scaled wetted width by the number of observers for each sample reach to account for differences in personnel among sites. I natural-log (continuous variables) or logit-transformed (proportions; +0.001 for channel units) and standardized all predictors to mean = 0 and SD = 1 to help with model convergence and simplify interpretation (Warton and Hui 2011). I used the ‘unmarked’ package (Fiske and Chandler 2011) in Program R (Version 3.5.1, R Core Team 2018) to build a zero-inflated Poisson (ZIP) model with a three-way interaction among detection covariates and four univariate abundance predictors (area sampled, drainage area, water temperature, and amount of pool habitat; Table 3). I evaluated model fit by calculating overdispersion ($\hat{c}$, where values > 1 indicate overdispersion) using the chi-square test described by MacKenzie and Bailey (2004) with

1,000 bootstrap replications in the R package ‘AICcmodavg’ (Mazerolle 2017). I used model coefficients and empirical Bayes methods to adjust nest abundance estimates for variable detection efficiency among sites (Royle and Dorazio 2008) so that these adjusted counts could be evaluated in a mixed-model framework, which is not currently possible in ‘unmarked’ (A. Royle, pers. comm.). Empirical Bayes methods use observed data to estimate unknown prior parameters to determine the posterior distribution of random variables, such as latent detection efficiency (Carlin and Louis 1996).

I evaluated the predictor variable distribution and various potential generalized linear mixed model (GLMM) forms for comparing adjusted Smallmouth Bass nest abundances and habitat. I transformed all continuous (natural-log) and proportion (logit) variables to reduce skewness (Warton and Hui 2011) and then standardized all independent variables (mean = 0 and SD = 1) to improve model convergence and simplify interpretation. Initial evaluation of the nest count data suggested overdispersion and zero inflation. I modeled adjusted nest abundance (scaled by area sampled) and zero inflation in relation to 16 predictors (Table 1) using several model forms (i.e., Poisson, negative binomial, ZIP, zero-inflated negative binomial [ZINB]). All models included a random effect for stream segment to account for non-independence among observations (Wagner et al. 2006; Gelman and Hill 2007). Comparison of model forms revealed that a ZINB model best fit these data (AIC_c weight > 0.99).

To reduce my set of predictor variables, I compared a set of ZINB GLMMs with each univariate predictor variable ($n = 18$) and ecologically-sensible two-way interaction terms ($n = 46$) to a random-intercept only (null) model using AIC_c (Sugiura 1978; Hurvich and Tsai 1989). If $\Delta AIC_c < 2$ compared to the intercept-only model, I retained that model predictor (Burnham and Anderson 2002). I also filtered my variable set by removing covariates with pairwise correlations $\geq |0.7|$, retaining only the predictor variable with greater model support (Dormann et al. 2013).

The reduced set of variables consisted of 12 univariate predictors and 31 two-way interaction terms (Table 1).

I used the reduced variable set to create a candidate set of nest abundance models. This exploratory approach used AIC_c to determine the set of predictors with the most support from an ecologically-sensible candidate model set (Dochtermann and Jenkins 2011; Grueber et al. 2011). Model comparisons during variable reduction indicated that three predictors (i.e., stream temperature and two interaction terms: stream temperature × RPD and stream temperature × drainage area) were especially important. Using these three terms and an additive combination of the interaction terms, I built a base set of four models. I built my full candidate set of 172 GLMMs by adding the remaining univariate and two-way interaction terms from the reduced set (see Table 1) to this base model set. To ensure appropriate degrees of freedom for model performance and avoid overfitting, I capped fixed-effect predictors at 11 per model (in addition to one random effect; Peduzzi et al. 1995; Harrell 2001). I included a random effect for stream segment in all models to address the nested structure of reach-scale observations (Wagner et al. 2006; Gelman and Hill 2007). I assumed the random effect was normally distributed $N(0, \tau^2)$, where τ^2 represented population variance among levels of a random effect (e.g., among stream segments). I built all ZINB models in the R package 'glmmTMB' (Magnusson et al. 2018) and conducted model selection (AIC_c) using the 'bbmle' package (Bolker 2017).

I assessed model fit of my top model by calculating marginal R^2 (i.e., amount of variance explained by the fixed effects) and conditional R^2 (i.e., amount of variance explained by both fixed and random effects, Vonesh et al. 1996; Nakagawa and Schielzeth 2013). I performed these calculations in the 'sjstats' (Lüdecke 2018) package in R.

RESULTS

Nest surveys

I observed Neosho Smallmouth Bass nests in 77 of 120 sampled reaches (64%). An additional 15 reaches were occupied by age-1 and older Smallmouth Bass even though no nests were present. In reaches where nests were present, nest counts ranged 1–79 (mean = 11.5; SD = 13.7) and nest densities ranged 1.2–90.0 ha^{-1} (mean = 19.4 ha^{-1}; SD = 16.3). Nest counts per stream length ranged 2.4–140.1 km^{-1} (mean = 26.8 km^{-1}; SD = 26.7) at these sites.

Habitat

Habitat conditions varied among nest survey sites (Table 1). Temperature varied spatially and temporally among sampled reaches, but warm streams were more common (n = 85 warm, n = 35 cool). Pool habitat was typically abundant in sample reaches (mean = 64%; SD = 17) but was variable among reaches (range: 3–92%). Channel morphology also varied considerably among streams, with clear differences in residual pool depth (range: 0.35–3.14 m) and bankfull width-depth ratio (range: 7.9–122.7). Groundwater flow was emblematic of karst topography (range: -0.70–1.13 m^3/s) and indicated a mix of losing (n = 48), neutral (n = 33), and gaining (n = 39) reaches. Coarse-scale habitat reflected a wide range of stream sizes, spatial metrics, and catchment characteristics. Drainage area of sample sites ranged 18.0–886.6 km^2. Downstream link ranged from 3–874, suggesting that some reaches were adjacent to larger streams, whereas others were in more isolated, upstream portions of the river network. Catchment slope ranged 1–15% and the amount of hydrologic soil group D ranged from 6–70% across the study area. Disturbance index values ranged 1.5–3.9 (mean = 2.3; SD = 0.4).

Nest clusters and nest microhabitat

The model of nest cluster habitat indicated relationships with stream temperature, groundwater flow, sample timing, and channel morphology on cluster presence (Table 2). The presence of nest clusters was less likely in cooler stream segments (≤ 19.5°C) and in gaining stream reaches. Clusters were more likely to be present earlier in the sampling period, and in reaches with wide, shallow channels. Sampling effort (i.e., area sampled) was not a significant predictor of nest cluster presence (95% CI: -0.10–1.60). Nest clusters were not associated with higher or lower offspring densities at the reach scale relative to regular nesting behavior (95% CI: -1.71–4.49). For this model, fixed effects explained 72% of the variability in nest cluster presence (marginal $R^2 = 0.72$), while the random stream segment effect did not explain any additional variability (conditional $R^2 = 0.72$).

Nest cluster microhabitat was measured for $n = 66$ clusters in $n = 22$ stream reaches. Nest clusters contained 2–6 nests (mean = 2.4; SD = 0.8). Center-to-center spacing between clustered nests ranged from 0.5–2.0 m (mean = 1.5 m; SD = 0.3). Average area encompassed by nest clusters was 2.4 m^2 (SD = 2.6, range = 0.5–14.0 m^2).

Nest microhabitat measures ($n = 646$ nests in $n = 55$ reaches) were similar for nests regardless of cluster inclusion, and reflected variability in nesting Smallmouth Bass size, a range of nesting depths and predominate use of low-velocity areas with gravel substrates. In total, 160 of the 646 nests measured (25%) were part of a nest cluster. Guarding male Smallmouth Bass ranged in size from 130–400 mm TL and average TL of male fish associated with and without nest clusters was 269 mm (SD = 45) and 253 mm (SD = 46), respectively. Nests were constructed in 0.26–1.85-m deep water; average water depth of nest clusters and single nests were 0.84 m (SD = 0.29) and 0.83 m (SD = 0.31), respectively. Nest-surface water velocities ranged from 0.0–0.2 m/s, though most cluster nests (96%) and regular nests (96%) occurred in zero-velocity habitats. Nest substrate was predominately gravel (98% of cluster nests, 97% of regular nests), though use of bedrock (2% of cluster nests, 3% of regular nests) and other substrates (i.e., roots, < 1% of cluster nests) was observed.

Nest abundance

Average sampling efficiency of my nest surveys was relatively high at 72% and varied across sites in response to water clarity, depth, and lane width surveyed per observer (Table 3). As expected, nest detection efficiency was positively related to water clarity and average stream depth. Sampling efficiency also decreased in reaches where snorkelers were responsible for wider sampling lanes. Adjusted non-zero nest counts ranged 1–86 (mean = 14.7; SD = 16.0) and mean adjusted nest density in reaches with nests was 24.1 ha^{-1} (SD = 17.6).

The top-ranked model for Smallmouth Bass nest abundance included a zero-inflation term, an interaction, and two main effects that highlight the importance of multiple reach-scale habitat features, though there is similar support for several models (Table 4). Zero inflation in the top model suggests that zero nest counts are expected at 13% of stream reaches, though no single predictor variable explained this phenomenon. Nest abundance was positively related to residual pool depth and this relationship was dependent on stream temperature (Figure 2). Although the relationship between nest abundance and increasing pool depth was similar in magnitude and direction between the two temperature categories, nest abundances were lower for a given residual pool depth in cooler stream reaches. A main effect of the proportion of pool habitat was included in the top model of Smallmouth Bass nest abundance and indicated a positive relationship between nest abundance and pool habitat amount. Similarly, a main effect for bankfull width-depth ratio in the top model showed a positive relationship between nest abundance and relatively wide, shallow stream reaches. The fixed effects in the top model explained 80% of the variability in nest abundance (marginal R^2 = 0.80), while the random stream segment effect did not explain any additional variability in nest abundance (conditional R^2 =

0.80). There is additional support based on AIC_c for simpler forms of the top-ranked model, one without the bankfull width-depth ratio main effect and another without the percent pool habitat main effect. Similarly, there is some support for a more complex model containing the residual pool depth × stream temperature interaction from the top-ranked model along with a percent pool habitat × median substrate size interaction. In the latter interaction, nest abundance has a positive relationship with pool habitat when substrate is small-to-average (i.e., when shear stress is low-to-average), with this relationship changing to slightly negative when substrate is larger than average (i.e., when shear stress is greater).

DISCUSSION

Nest clustering by Smallmouth Bass appears to be unique to the Neosho subspecies and may relate to high nesting densities even though microhabitat use was comparable to the nominal species. Smallmouth Bass are territorial nest guarders in lakes and rivers throughout most of their range, resulting in considerable spacing between nests (i.e., > 17–77.9 m, Winemiller and Taylor 1982; Scott 1996). This may reflect territorial males interfering with courtship by neighboring males (Beeman 1924; Wiegmann et al. 1992). Clusters, where neighboring nests were within 2 m of one another, accounted for 25% of the observed Neosho Smallmouth Bass nests in 2017–2018. Clustering by nesting Smallmouth Bass is rare elsewhere in the species range, though Pflieger (1966) observed one instance of neighboring nests within 1.1 m for the northern subspecies *M. d. dolomieu* in a central Missouri stream. Clustering behavior may explain why my greatest observed nest densities (i.e., 140.1 km^{-1}) and those from another study of the Neosho subspecies (i.e., 100–147 km^{-1}, Dauwalter and Fisher 2007) are much greater than nest densities reported in the literature for the nominal species (maximum = 75.3 km^{-1}, Reynolds and O'Bara 1991). I observed nests built across a range of water depths (i.e., 0.26–1.85 m), as has been documented for both the Neosho and northern subspecies (Reynolds and O'Bara 1991; Knotek and Orth 1998; Orth and Newcomb 2002; Dauwalter and Fisher 2007). The use of low-velocity nesting habitats and of gravel and occasional bedrock nesting substrate is consistent with previous work on the Neosho (Dauwalter and Fisher 2007) and northern subspecies (Pflieger 1966; Winemiller and Taylor 1982; Sabo and Orth 1994).

Several physicochemical factors correlated with the occurrence of Smallmouth Bass nest clusters. Nest clusters and individual nests were more likely to occur in warmer streams (> 19.5°C), possibly reflecting favorable development and growing conditions for offspring in these reaches. Developing Smallmouth Bass generally use warmer temperatures than adult fish (Armour 1993; Brewer 2013) and optimal growth of juvenile Smallmouth Bass occurs around 27–28°C (Peek 1965; Coutant and DeAngelis 1983). The greater abundance of nests in general in warm streams may explain the positive relationship between cluster presence and warm water temperature. The presence of nest clusters was less likely in gaining reaches, though groundwater flow did not affect individual nest abundance. The magnitude of groundwater flow varied considerably among reaches, and there was no consistent relationship between groundwater flow and water temperature class. In summer, age-0 Smallmouth Bass show greater occurrence and abundance and slower growth in stream segments with high spring-flow influence (Brewer 2013). Complex patterns of groundwater exchange, wherein upwelling and downwelling occur at different spatial scales, may further complicate nest-groundwater relationships (e.g., Baxter and Hauer 2000). Alternatively, lower abundances of a potential nest predator, Longear Sunfish *Lepomis megalotis*, associated with gaining stream reaches (R. Mollenhauer, unpubl. data) may help explain the lower incidence of nest clusters despite normal nest abundances in these reaches. I found relatively wide, shallow stream reaches were more likely to contain nest clusters. These reaches tend to have more open-water habitat and high abundances of Longear Sunfish (R. Mollenhauer, unpubl. data), thereby increasing the risk of nest predation. Aggregations of guarding male fish help to deter potential predators (Dominey 1981, 1983) and may have thus been beneficial for nest success in these systems.

Sample timing also explained nest cluster presence, with clusters more common earlier in the spawning season. This may reflect coincident nesting efforts following delays in spawning due to high flows or cool temperatures (e.g., Sabo and Orth 1994), as I observed in 2016–2017 and 2018, respectively. Furthermore, although many bass build new nests if earlier broods are destroyed (e.g., due to flooding or predation, Cleary 1956; Knotek and Orth 1998) or successfully disperse (Pflieger 1966), not all bass make multiple nesting attempts (Lukas and Orth 1995; Orth and Newcomb 2002), potentially alleviating habitat limitation that leads to nest clustering. The threat of predation may also influence this relationship, as Longear Sunfish are potential nest predators early in the Smallmouth Bass nesting season but begin their own spawning activities in late May (Warren 2009). In summary, it seems possible clustering behavior by Neosho Smallmouth Bass reflects both habitat conditions conducive to greater nest densities and a response to the threat of highly abundant nest predations, primarily Longear Sunfish.

Multiple reach-scale habitat factors influenced the presence and abundance of Neosho Smallmouth Bass nests in Ozark streams. Absences of nests from stream reaches were expected for 13% of stream reaches, though the specific factors underpinning these absences remains unclear. The absence of nests at these sites could reflect habitat features at various scales that were not measured. Nest abundance increased with residual pool depth in both warm and cool streams, though nest abundances, in general, were much higher in warm streams. The positive relationship between nest abundance and increasing pool depths may reflect better protection from terrestrial predators (Orth and Newcomb 2002) or from scour during high flows (Lukas and Orth 1995). Nest abundance also reflected the availability of low-velocity pool habitat and wide, shallow channels. Based on my observations of nest microhabitat and on existing literature, there is a clear preference by nesting Smallmouth Bass for low-velocity areas such as those common in pools (Pflieger 1966; Winemiller and Taylor 1982; Dauwalter and Fisher 2007). Wide, shallow stream reaches receive more solar radiation due to relatively less riparian overhang, which may benefit adults and developing offspring via increased water temperatures and primary productivity (Vannote et al. 1980; Whitledge et al. 2006). One potential mechanism underlying the interactive relationship between pool habitat and substrate size is a lack of suitable velocity refugia available for nesting, regardless of pool habitat amount, under increased shear stress conditions (Knighton 1998; Schwendel et al. 2010).

I used a separate model to account for variable nest detection efficiency among sample sites prior to modeling relationships between habitat and nest abundance. I accounted for site-specific variation in detection efficiency using repeat surveys of unmarked nests and *N*-mixture modeling in the R package ‘unmarked’ (Royle 2004; Fiske and Chandler 2011). This time- and cost-effective approach permitted adjustment of raw nests counts. Detection efficiency was positively related to water clarity and depth. The relationship with water clarity is unsurprising, and the relationship with depth may reflect high water clarity relative to the greatest nest depths (i.e., 1.85 m) and the territorial behavior of nesting Smallmouth Bass. As expected, detection efficiency and width surveyed by each observer had a negative relationship. One limitation of *N*-mixture models in ‘unmarked’ is that they do not permit the inclusion of random effects (e.g., stream segment) to account for correlations among reach-scale observation (A. Royle, pers. comm.). Ignoring this correlation increases the chance of incorrect inferences (Wagner et al. 2006). Thus, I felt the best approach was to adjust nest counts for variable detection efficiency and use these adjusted counts in a mixed model to include random effects.

The unique clustering behavior and influence of multi-scale habitat features on Neosho Smallmouth Bass nest abundance create unique conflicts for the management of an endemic sportfish. Fish management and biodiversity conservation typically represent conflicting interests in freshwater systems, but combined approaches (e.g., protected areas) may provide disproportionate conservation benefits when focused on spawning aggregations (Erisman et al. 2015). In contrast to the northern subspecies, Neosho Smallmouth Bass often construct nests in close proximity to neighboring nests. These aggregations may be more susceptible to anglers targeting nesting males given the vulnerability of neat-guarding males to anglers (Philipp et al. 1997; Steinhart et al. 2004). Males with greater quantities of eggs tend to be more aggressive toward potential predators and more vulnerable to angling, suggesting that angling disproportionately affects individuals with the greatest potential to contribute to annual recruitment (Suski and Philipp 2004). Angling also frequently results in nest predation and nest failure even with catch and release angling (Philipp et al. 1997; Suski et al. 2003). Regulations vary throughout the range of Neosho Smallmouth Bass (i.e., closed season March–late May in Missouri, no closed season in Oklahoma or Arkansas), and could be modified to cover the early part of the nesting season in all streams or specifically applied to areas that support nesting aggregations to alleviate angling vulnerability (Kubacki et al. 2002; Noble 2002). The consequences of clustered nesting to subsequent growth and survival of larval Neosho Smallmouth Bass presents an interesting avenue for future research, as density-dependent effects on juvenile survival have been observed for other warmwater stream fish due to habitat limitation or in the absence of strong density-independent effects (Jennings and Philipp 1994; Schlosser 1998). Disentangling the multi-scale influences on spawning habitat is important for conserving existing habitat and for guiding stream restoration efforts (Lawrence et al. 2012). Although cooler water temperatures broadly restrict nesting habitat potential of Neosho Smallmouth Bass, cooler streams, especially those with deeper pools, provide additional spawning habitat. As deeper pools are beneficial to nest abundance regardless of stream temperature, efforts to limit landscape and channel modification that alter natural geomorphology (e.g., bedform, sedimentation, channel dimensions) would be beneficial (Rabeni and Jacobson 1993; Leasure et al. 2016). The ability of nesting Neosho Smallmouth Bass to use various low-velocity refugia helps explain their presence across streams with varying hydraulic conditions and availabilities of low-velocity mesohabitat. Habitat plasticity in general provides resistance to environmental changes (Goniea et al. 2006; Beever et al. 2017) and has been observed for age-0 Smallmouth Bass (Pert et al. 2002; Fore et al.

2007). With several subpopulations of Neosho Smallmouth Bass that appear isolated due to very little gene mixing (Taylor et al. 2018), observed habitat plasticity may reflect adaptation to specific habitat types among drainages. My results highlight the unique nesting behavior of Neosho Smallmouth Bass and the myriad habitat features that influence clustering, presence, and abundance of nests during this critical period of fish life history.

Table 1. Summary statistics and data sources for ancillary and habitat predictor variables used to model Neosho Smallmouth Bass nest detection efficiency and nest density-habitat relationships. I measured reach-scale (~20 times channel width) variables in the field and calculated segment-scale (tributary confluence to tributary confluence) variables in ArcMap 10.3.1 (ESRI, Redlands, California). I retained 43 terms following variable reduction: 12 univariate terms (bolded) and 31 two-way interaction terms.

Variable	**Mean ± SD**	**Range**	**Data source**
Detection efficiency			
Water clarity (m)	3.1 ± 1.2	1.3 – 7.6	Field-collected
Mean thalweg depth (m)	0.72 ± 0.27	0.22 – 1.70	Field-collected
Wetted width/observer (m)	5.4 ± 2.0	2.4 – 11.6	Field-collected
Reach scale			
Sampling date (day of year)[ab]	155.5 ± 19.2	122 – 190	Field-collected
Stream temperature (°C)[a]	19.7 ± 2.4	15.1 – 24.6	Field-collected
Residual pool depth (m)[a]	1.03 ± 0.53	0.35 – 3.14	Field-collected
Pool habitat (%)[a]	63.6 ± 17.0	3.0 – 92.0	Field-collected
Off-channel habitat (%)	5.7 ± 6.3	0.0 – 30.0	Field-collected
Riffle habitat (%)	12.5 ± 8.5	0.0 – 41.0	Field-collected
Median substrate size (mm)[ab]	25.1 ± 5.3	10.0 – 40.0	Field-collected
Bankfull width-depth ratio[a]	42.0 ± 21.8	7.9 – 122.7	Field-collected
Groundwater flow (m^3/s)[a]	-0.01 ± 0.24	-0.70 – 1.13	Field-collected
Area sampled (m^2)	4771.9 ± 3887.6	565.9 – 20127.3	Field-collected
Segment scale			
Link magnitude	23.5 ± 37.9	1 – 264	USGS NHD[c]
Downstream link[a]	69.2 ± 132.5	3 – 874	USGS NHD[c]
Stream gradient (%)[a]	0.34 ± 0.16	0.03 – 0.73	NHD Plus Version 2[d]
Drainage area (km^2)[ab]	172.2 ± 176.0	18.0 – 886.6	USGS NED[ef]

Catchment slope (%)	7.2 ± 3.3	1.4 – 15.4	USGS NED[ef]
Disturbance index	2.3 ± 0.4	1.5 – 3.9	NLCD 2011[eg]
Hydro soil group D (%)	33.5 ± 14.4	5.9 – 70.3	USDA NRCS SSURGO 2.2[eh]
Carbonate geology (%)[a]	96.8 ± 8.9	17.3 – 100.0	USGS, USDA NRCS[ei]
Base flow/total flow (%)[a]	46.0 ± 4.1	34.4 – 53.3	USEPA StreamCat[ej]
Runoff (mm)[a]	350.4 ± 17.8	316.0 – 381.6	USEPA StreamCat[ej]

a: Variables (*n* = 16) used to evaluate model form.

b: Variables for which quadratic effects were used to evaluate model form.

c: http://nhd.usgs.gov/

d: http://www.horizon-systems.com/nhdplus/nhdplusv2_home.php

e: These variables were summarized for the entire catchment draining to the downstream end of each stream segment.

f: http://ned.usgs.gov/

g: Homer et al. 2015, https://www.mrlc.gov/nlcd11_data.php

h: NRCS 2017, https://websoilsurvey.sc.egov.usda.gov

i: Stoeser et al. 2005, https://datagateway.nrcs.usda.gov/

j: Hill et al. 2016, https://www.epa.gov/national-aquatic-resource-surveys/streamcat

Table 2. Coefficients, standard errors (SE), and 95% confidence intervals (CI) for mixed-effects logistic regression describing presence of Smallmouth Bass nest clusters in Ozark streams. Hypothesized explanations for including each predictor variable are also included. Model coefficients are presented on a logit scale, and predictors were standardized to mean = 0 and standard deviation = 1 prior to model specification. The reference condition for stream temperature is warm (> 19.5°C) and the reference condition for groundwater flow is losing (i.e., longitudinal decrease in stream discharge). Area sampled is included to account for differences in sampling effort among stream reaches.

Predictor variable	Coefficient ± SE	95% CI	Hypotheses
Intercept	-1.35 ± 0.58	-2.49, -0.21	
Stream temperature	-2.32 ± 1.04	-4.36, -0.27	Habitat limitation
Pool habitat	0.54 ± 0.32	-0.09, 1.17	Habitat limitation
Off-channel habitat	0.59 ± 0.40	-0.20, 1.38	Habitat limitation
Stream gradient	-0.50 ± 0.34	-1.17, 0.17	Habitat limitation
Bankfull width-depth ratio	0.79 ± 0.39	0.04, 1.55	Habitat limitation, Disturbance
Disturbance index	0.26 ± 0.33	-0.39, 0.92	Disturbance
Neutral groundwater flow	0.11 ± 0.73	-1.32, 1.55	Groundwater
Gaining groundwater flow	-1.55 ± 0.76	-3.04, -0.06	Groundwater
Sampling date	-1.04 ± 0.41	-1.84, -0.24	Progression of spawning season
Young-of-year abundance	1.39 ± 1.58	-1.71, 4.49	Increased offspring survival
Area sampled	0.75 ± 0.44	-0.10, 1.60	Sampling effort

Table 3. Coefficient estimates, standard errors (SE) and 95% confidence intervals (CI) for the model of Smallmouth Bass nest detection efficiency in Ozark streams. I adjusted SE and CI to account for model overdispersion ($\hat{c}$ = 2.18). Detection model coefficients are on a logit scale, and abundance model coefficients are on a natural-log scale. Continuous predictors were standardized to mean = 0 and standard deviation = 1. Warm streams (> 19.5°C) are the reference condition for stream temperature. Model-estimated zero inflation was -1.40 ± 0.45 (logit scale).

Predictor variable	Coefficient ± SE	95% CI
Detection model		
Intercept	0.94 ± 0.39	0.17, 1.72
Width × Clarity × Depth	-0.09 ± 0.13	-0.35, 0.17
Width × Clarity	-0.18 ± 0.21	-0.60, 0.23
Width × Depth	-0.19 ± 0.12	-0.43, 0.05
Clarity × Depth	-0.03 ± 0.20	-0.43, 0.36
Width	-0.46 ± 0.19	-0.83, -0.09
Clarity	0.84 ± 0.23	0.40, 1.28
Depth	0.53 ± 0.20	0.14, 0.92
Abundance model		
Intercept	2.28 ± 0.12	2.04, 2.52
Area sampled (effort)	0.74 ± 0.10	0.55, 0.93
Drainage area	0.03 ± 0.10	-0.17, 0.23
Stream temperature	-1.73 ± 0.32	-2.36, -1.09
Pool habitat	0.20 ± 0.07	0.06, 0.34

Table 4. Rankings of top (i.e., within 2 AIC_c) candidate linear mixed models of Smallmouth Bass nest abundance in Ozark streams. Y_{ij} is nest abundance of stream reach i in stream segment j, β_0 is the grand intercept, and γ_j is the random stream segment intercept. X_1 is water temperature class, where warm (> 19.5°C) is the reference condition. X_2 is residual pool depth (m), X_3 is percent pool habitat, X_4 is bankfull width-depth ratio, and X_5 is median substrate size (mm). *K* is the number of model parameters, LL is log-likelihood, AIC_c is Akaike's information criterion adjusted for small sample size, and ΔAIC_c is the difference in AIC_c score between the given model and the top model. Akaike weight (w_i) indicates the relative support for the given model. Marginal R^2 (R^2_m) and conditional R^2 (R^2_c) values represent the amount of variance explained by fixed effects only and by both fixed and random effects, respectively. All models containing interaction terms also include main effects for predictors involved in interactions.

Model	*K*	LL	AIC_c	ΔAIC_c	w_i	R^2_m	R^2_c
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} \cdot X_{2i} + \beta_2 X_{3i} + \beta_3 X_{4i}$	9	-289.5	598.6	0.0	0.12	0.80	0.80
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} \cdot X_{2i} + \beta_2 X_{3i}$	8	-291.0	599.3	0.7	0.08	0.80	0.81
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} \cdot X_{2i} + \beta_4 X_{3i} \cdot X_{5i}$	10	-288.7	599.4	0.8	0.08	0.81	0.83
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} \cdot X_{2i} + \beta_3 X_{4i}$	8	-291.6	600.5	1.9	0.05	0.79	0.79

Table S1. Disturbance coefficients used in relation to 2011 National Land Cover Dataset (Homer et al. 2015, https://www.mrlc.gov/nlcd2011.php) land cover categories for calculating disturbance index, where greater values equate to a greater degree of disturbance. The large coefficient used for barren land reflects the association of such lands with mining activities in this region (Smart et al. 1981), although overall this cover class was uncommon.

Land cover type	NLCD Class	Coefficient
Open water	11	1.00
Perennial ice/snow	12	1.00
Developed, open space	21	1.83
Developed, low intensity	22	6.90
Developed, medium intensity	23	7.64
Developed, high intensity	24	7.92
Barren land (rock/sand/clay)	31	8.32
Deciduous forest	41	1.00
Evergreen forest	42	1.00
Mixed forest	43	1.00
Shrub/scrub	52	1.00
Grassland/herbaceous	71	1.00
Pasture/hay	81	2.99
Cultivated crops	82	4.54
Woody wetlands	90	1.00
Emergent herbaceous wetlands	95	1.00

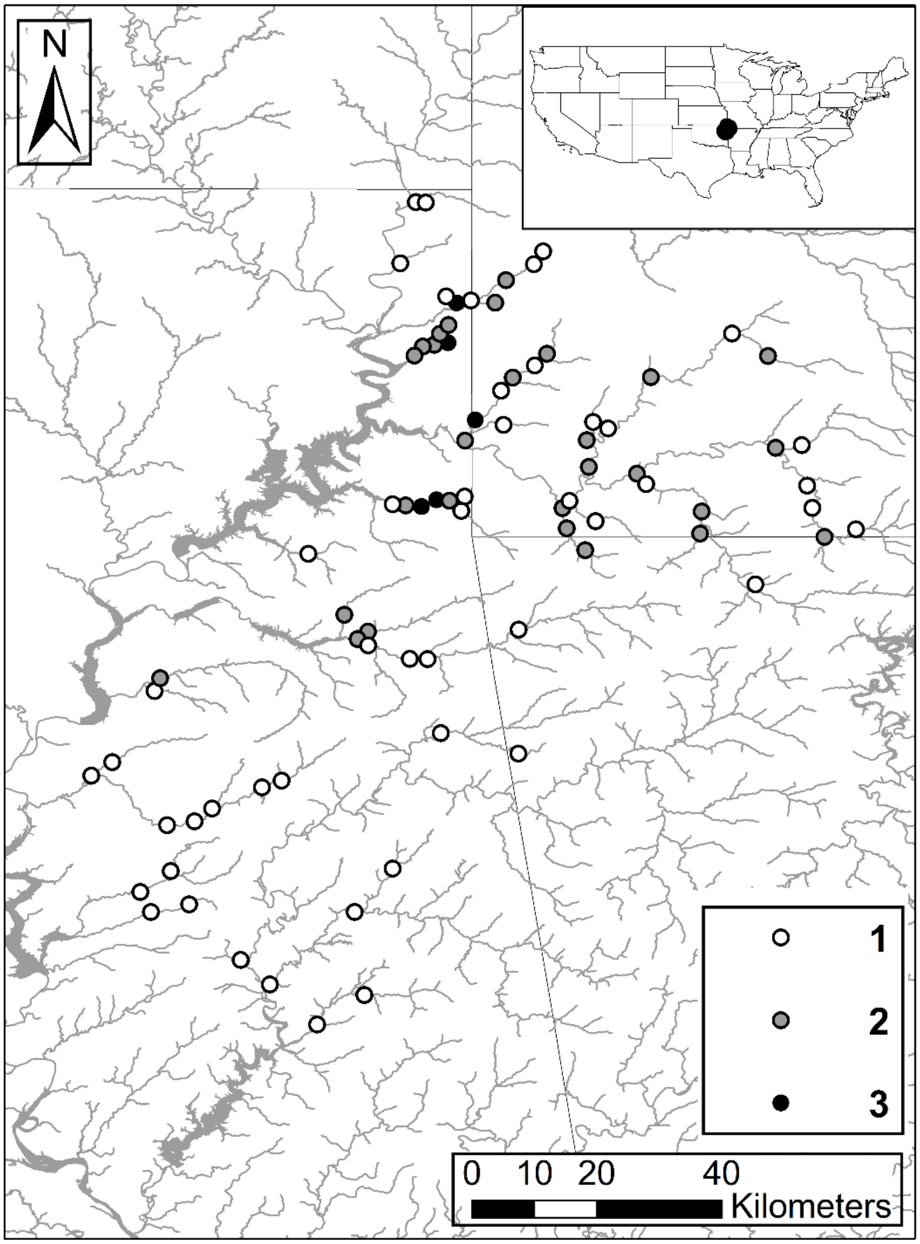


Figure 1. Map of stream reaches (*n* = 120) surveyed for Neosho Smallmouth Bass nests. Dot color indicates the number of years during the study (2016–2018) in which a stream reach was sampled.

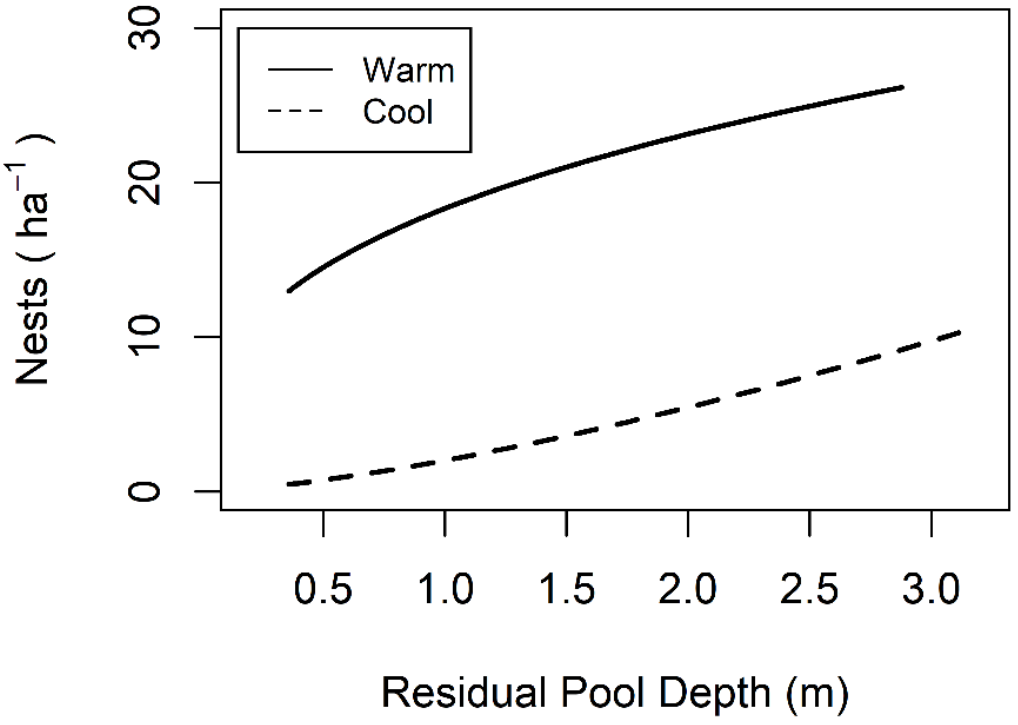


Figure 2. Influence of residual pool depth (m) on Smallmouth Bass nest density in streams of two temperature classes: warm (> 19.5°C midday) and cool (≤ 19.5°C). Cool streams include those with relatively higher groundwater influence and those sampled earlier in the May–July study period.

CHAPTER IV

EFFECTS OF HYDROLOGY AND TEMPERATURE ON HATCH TIMING AND DAILY GROWTH OF AGE-0 SMALLMOUTH BASS ACROSS OZARK STREAMS

ABSTRACT

Spawning phenology and growth rate of age-0 stream fish reflect environmental conditions and have important implications for subsequent survival and recruitment. I determined daily age and back-calculated hatch date and daily growth rate for 794 age-0 Smallmouth Bass *Micropterus dolomieu velox* collected from five Ozark streams in 2017 and 2018. My objective was to assess variability in hatch timing among streams and years and to determine the influence of water temperature and streamflow conditions on growth rate. I used AIC_c to rank a candidate set of linear mixed models describing variation in daily growth rate of age-0 Smallmouth Bass. My data indicate that streamflow magnitude, streamflow variability, and water temperature variability relate to age-0 growth rate and reflect landscape heterogeneity in these relationships. I also observed differences in hatch timing between years and among streams, which I attribute to different streamflow and temperature patterns. My results suggest that environmental variability influences both spawning phenology and age-0 Smallmouth Bass growth, and that these relationships are spatially variable across the landscape. These findings highlight the role of riverscape-level variation in creating among-population heterogeneity, which in turn confers resistance to extreme environmental conditions. As climate change and human alteration create

increasingly unpredictable riverine environments, protecting the inherent diversity of these populations is vital for their persistence.

INTRODUCTION

Growth during the first year of life is critical for the survival and recruitment of juvenile stream fishes. Two periods of particularly high vulnerability are the period between egg fertilization and larval dispersal and the first winter (Shuter et al 1980; Coleman and Fausch 2007). Acquisition and energy storage are important during the first year of life, as growth of juvenile stream fish confers resistance to many sources of mortality including predation and starvation. Larger age-0 individuals are more likely to survive the overwinter period when activity and feeding are greatly reduced, and fish subsist on accumulated energy reserves (Oliver et al. 1979). Because of the relationships between fish size and survival, the drivers of spatiotemporal variation in fish growth are of considerable interest to fish biologists.

Spawning phenology and growth patterns among larval and juvenile fishes are tightly coupled to physicochemical conditions such as temperature and streamflow, though biotic factors may also be important. High flows and warming temperatures trigger spawning activity in many stream fishes (Graham and Orth 1986; Falke et al. 2010; Lisi et al. 2013). Subsequent extreme flows often have negative effects on spawning success and larval survival via nest destruction, desiccation, and larval displacement (Pflieger 1975; Harvey 1987; Grabowski and Isely 2007). Extreme temperatures during early development can indirectly cause mortality by increasing the likelihood of infection and by prompting nest abandonment by guarding males, in turn allowing predation of eggs and larvae (Shuter et al. 1980; Knotek and Orth 1998). Among temperate warmwater fishes, earlier-hatched fish have a longer growth period during the first year of life, whereas later-hatched fish experience warmer temperatures during the earliest larval stages. Earlier-hatched individuals have been shown to maintain their size advantage in some species (e.g., Largemouth Bass *Micropterus salmoides*, Phillips et al. 1995; some Cyprinidae, Durham and Wilde 2005), but not in others (e.g., Smallmouth Bass *M. dolomieu*, Sabo and Orth 1995). In years with relatively stable physicochemical conditions, biotic factors such as predation and competition may play a greater role in determining spawning success, individual growth, and survival (Jennings and Philipp 1994).

Smallmouth Bass is an important component of riverine ecosystems with a life history well-suited to these dynamic environments. Smallmouth Bass spawn from April to early July, beginning when water temperatures exceed ~15 °C, and males aggressively guard their eggs and larvae a period of 2–7 weeks until larval dispersal (Shuter et al. 1980; Brewer and Orth 2015). Mortality is greatest from swim-up to metamorphosis as larvae feed more actively but are less able to escape predators (Knotek and Orth 1998; Brewer et al. 2019). Individuals are capable of repeat spawning in response to early nest destruction or brood loss (Brewer and Orth 2015). First-year survival reflects variation in thermal and hydrologic conditions, which affect age-0 bass directly via nest destruction and displacement and indirectly via diminished growth potential and reduced disease resistance (Pflieger 1975; Lukas and Orth 1995; Knotek and Orth 1998). There is no apparent correlation between age-0 fish size and swim-up date in one Virginia stream (Sabo and Orth 1995). The lack of a consistent relationship may reflect individual variability (DeAngelis and Coutant 1979; Phelps et al. 2008) or density-dependence, which has been observed in simulations of age-0 Smallmouth Bass growth at high fish densities (DeAngelis et al. 1991).

Little is known about the life history of genetically-distinct populations of Neosho Smallmouth Bass *M. d. velox* in the southwestern Ozark Highlands (Stark and Echelle 1998; Brewer and Long 2015). These populations occur on the edge of the native range and are vulnerable to warming water temperatures and hydrologic alteration due to climate change and groundwater pumping (Brewer and Long 2015). Additionally, streams in this region naturally encompass a wide range of thermal and hydrologic conditions (Brewer 2013; Leasure et al. 2016). Yet, whether spawning phenology and first-year growth of Neosho Smallmouth Bass vary across this heterogeneous riverscape is unclear. Thus, my objectives are to 1) back-calculate hatch date and determine mean daily growth rate of age-0 Smallmouth Bass and 2) evaluate the relationships between hatch timing, growth rate, streamflow and water temperature in Ozark streams. I hypothesize that temperature will influence hatch date and growth rate, but that hydrology will alter the relative abundance of fish hatched at different times due to flood-induced nest failure and larval mortality. We, therefore, expect that hatch timing and growth rate will be more tightly coupled with stream temperature during years of more stable hydrology. Knowledge of Smallmouth Bass hatch phenology, growth, and their relationship with environmental factors is essential to conserving this species across heterogeneous riverscapes and increasingly extreme habitat conditions due to climate change and anthropogenic disturbances (e.g., groundwater pumping, flow modification).

METHODS

Study sites

I collected age-0 Smallmouth Bass from five streams with disparate flow and temperature regimes in the Ozark Highlands ecoregion (Figure 1). The Smallmouth Bass populations in these streams are predominately the Neosho subspecies, though some hybridization with non-native Tennessee ‘lake strain’ Smallmouth Bass does occur in the Elk River (Taylor et al. 2018). Cherty limestone geology and karst topography are prevalent in the Ozark Highlands ecoregion, resulting in spatially variable hydrology and groundwater contributions (Brewer 2013; Leasure et al. 2016; Zhou et al. 2018). The study streams vary by an order of magnitude with respect to both catchment area and streamflow (Table 1). In addition to among-stream differences, conditions during the pre-spawn through rearing period (March 1–July 13) were generally wetter in 2017 (median daily discharge: 2.2 m^3/s) than in 2018 (median: 1.7 m^3/s; Figure 2). Relative to 2017, water temperatures in 2018 were colder at the start and warmer at the end of the pre-spawn through rearing period (Figure 2).

Hydrology and temperature

I collected discharge and temperature data concurrent with the nesting and early growing periods. Discharge data (0.1 m^3/s), collected at 15-minute intervals, were obtained from U.S. Geological Survey (USGS) stream gages located within 3.5 rkm of each fish sampling location (Table 1). I summarized streamflow patterns by calculating mean daily discharge and its coefficient of variation (CV: $\frac{\sigma}{\mu} \times 100$) for each stream in each year. I measured water temperature (0.1 °C) using temperature loggers (HOBO Pro v2; Onset Corp., Bourne, Massachusetts) placed at my study sites or nearby USGS stream gages (Spavinaw Creek, gage 071912213; Beaty Creek, gage 07191222). I calculated mean daily water temperature and the CV of mean daily water temperature from logger and stream gage data recorded at 30-min intervals. To account for temperature data gaps due to logger tampering, I used least-squares regression to predict Elk River and Buffalo Creek temperature values from Spavinaw Creek ($R^2 = 0.80$) and Beaty Creek ($R^2 = 0.89$) data, respectively. I used temperature data to calculate accumulated growing degree-days > 15 °C (GDD, °C·day) by summing mean daily temperatures for all days that exceed 15 °C (Graham and Orth 1986; Trudgill et al. 2005). Thermal integral metrics such as the GDD can explain a considerable amount of variation in growth rates among ectotherms such as fishes (Neuheimer and Taggart 2007). The base temperature of 15 °C reflects the temperature that typically initiates Smallmouth Bass spawning activity (Shuter at al. 1980).

Fish collection and aging

I collected age-0 Smallmouth Bass in late June and early July 2017–2018 to assess hatch date distributions among streams. Sampling dates were July 12–13, 2017 and June 25–26, 2018, several weeks after spawning was observed in these systems and coinciding with observations of juvenile Smallmouth Bass. I collected 58–101 individuals on one occasion from each stream in each year by seining (3.5 x 1.2 m, 3-mm mesh) shallow, low-velocity habitats (Table 2). Multiple habitats (i.e., pools, runs, backwaters) at each site were sampled to ensure collection of individuals from multiple and earlier broods. All fish were humanely euthanized in a 30 mg/L solution of Aqui-S 20E (Aqui-S, Lower Hutt, New Zealand) and stored on ice. Individual fish were patted dry and measured (total length [TL], 1 mm) in the field immediately after they were euthanized. In the laboratory, I extracted sagittal otoliths and mounted them convex-side-down on glass microscope slides using thermoplastic cement (Miller and Storck 1982; Graham and Orth 1987). I polished the mounted otoliths with wetted 1500- and 2000-grit sandpaper until daily rings were visible at 180–200x magnification. Daily rings were counted by two independent observers. Each observer independently aged otoliths twice, non-consecutively, and in a random order. If mean counts by each observer were within 10% or three rings for an individual fish, the average of these values was used as the final age; otherwise, the readers jointly recounted daily rings to determine a consensus final age (Miller and Storck 1982). If a consensus age could not be agreed upon, those fish were excluded from subsequent calculations (n = 7). A total of n = 794 fish were retained for my analyses (Table 2). I estimated hatch date using the following equation (Graham and Orth 1986):

$$Hatch\ date = Collection\ date - Age - FDI$$

Where, collection date was the date of sample collection, age was the final daily ring count, and FDI was the number of days between hatching and first daily increment formation. I assumed a constant FDI of 7 d for Smallmouth Bass, which coincides with swim-up (Graham and Orth 1986, 1987). I estimated mean daily growth rates (mm/day) during the period from swim-up to capture as follows (Miller and Storck 1984; Phelps et al. 2008):

$$Daily\ growth\ rate = \frac{(TL\ at\ capture - TL\ at\ swim\text{-}up)}{Mean\ daily\ ring\ count}$$

Where, TL at capture is measured during field collection and TL at swim-up is assumed constant at 8.4 mm (Graham and Orth 1987; Warren 2009).

Analyses

Prior to the analyses, I made necessary transformations and standardizations to the predictor variables. I defined stream as a categorical predictor with five levels. My continuous predictors were the means and CVs of daily streamflow and water temperature summarized over the period between hatching and collection for each fish. I scaled mean streamflow by the long-term median discharge for each stream (see Table 1) to permit meaningful comparisons among streams of different sizes (McCune and Grace 2002). Skewed independent variables were natural-log transformed, and all predictors were standardized (mean = 0; SD = 1) to simplify model coefficient interpretation.

I used a model-selection approach to assess the relative support for candidate models describing average daily growth rate as a function of study stream and both streamflow and water temperature. I built a set of 97 candidate linear mixed models (LMMs) which included a null model and all subsets of the full model that included the following interaction effects: stream × mean streamflow, stream × streamflow CV, stream × mean water temperature, stream × water temperature CV. Pairwise correlations between continuous predictor variables were $< |0.55|$; thus, all were considered simultaneously for modeling. Each model included a random effect for sample year. The inclusion of the random year effect in the model accounts for unequal sample sizes among levels, the lack of independence among observations, and unexplained variability among years (Wagner et al. 2006; Gelman and Hill 2007). I assumed the random effect was normally distributed as $N(0, \tau^2)$, where τ^2 represents the variance among levels (e.g., among years). I used Akaike's information criterion corrected for small sample size (AIC_c, Sugiura 1978; Hurvich and Tsai 1989) to rank competing models and calculate relative model support (i.e., Akaike weights, w_i; Wagenmakers and Farrell 2004). Candidate models within 2 AIC_c of the top model were only considered to have support if they contained an equal or lesser number of parameters than the top model; this approach favors model simplicity by excluding uninformative predictors (Arnold 2010). I viewed residual histograms and plotted residuals against fitted values to ensure that top model residuals were normally distributed with constant variance. I calculated the amount of variance explained by the top model as described by Nakagawa and Schielzeth (2013). Briefly, variance explained by fixed effects is represented by the marginal R^2, whereas variance collectively explained by fixed and random effects is given by the conditional R^2 (Vonesh et al. 1996). All analyses were conducted in R 3.5.1 (R Core Team 2018) using the 'lme4' (Bates et al. 2015) and 'MuMIn' (Bartoń 2018) packages.

RESULTS

Hydrology and temperature

I observed considerable variability in hydrology and water temperature patterns during the spawning and rearing period among years and streams (Figure 2). Streamflow magnitudes were greater, on average, and more variable in 2017. These patterns reflect several discrete high-flow events, including one in late April 2017 (~30-year flood) that generated peak flows an order of magnitude greater than 2018 peak flows in all study streams. In contrast, 2018 hydrology mostly remained below long-term median levels with only a ~3-year flood in early May on Beaty Creek and Spavinaw Creek. Mean water temperatures were consistent (within 1 °C) for each stream across years. Honey Creek (mean = 20.6; SD = 3.7) and Elk River (mean = 20.4; SD = 4.3) were the warmest streams and Spavinaw Creek (mean = 18.3 °C; SD = 3.4) was the coldest. Variability in daily mean water temperatures was greater in 2018 compared to 2017, with more extreme temperatures at the start and end of the spawning and rearing period. GDD across all study streams on May 1 ranged from 19.3–107.4 in 2017 and from 1.1–22.2 in 2018.

Fish collection and aging

Individual age-0 Smallmouth Bass collected for this study varied in size and age among years and streams (Table 2). Despite making collections 16–18 d earlier in 2018, sampled fish were both larger (by 9 mm) and older (by 5 days), on average, than fish sampled in 2017. I also observed a wider range of TLs among fish collected in 2018 (25–86 mm) compared to 2017 (19–57 mm). The largest individuals in a given year, on average, were collected from the Elk River (2017 mean = 37 mm; SD = 5), with this trend being especially pronounced in 2018 (mean = 50 mm; SD = 7). Buffalo Creek and Honey Creek had the oldest (i.e., earliest-spawned) fish, on average, over both sample years, while Spavinaw Creek had particularly young (mean = 27 days; SD = 4) and small (mean = 26 mm; SD = 4) fish in 2017.

Hatch timing

Hatch date distributions were unimodal and of similar average duration in both years (Figure 3). Hatch timing differed across years, covering a later period in 2017 (range: May 22–June 17) relative to 2018 (range: April 29–May 23; Figure 3). Within each year, hatching began earlier in Buffalo Creek and Honey Creek relative to the other study streams. In both years, the hatching period was latest in Spavinaw Creek, and this was particularly evident in 2017. Hatch date durations varied among streams but were more consistent in 2018. Duration of hatching ranged from 12 days (Buffalo Creek) to 24 days (Spavinaw Creek) in 2017, and from 15 days (Elk River) to 19 days (Honey Creek) in 2018. The onset of hatching in 2017 corresponded with accumulated GDD of 54.0–195.6 across all streams, whereas GDD were 1.7–17.1 at the onset of 2018 hatching.

Growth rate

Mean daily growth rates of age-0 Smallmouth Bass varied among years and streams (Figure 4). Growth rates across all streams were generally higher and more variable in 2018 (mean = 0.84 mm/day; SD = 0.20) than in 2017 (mean = 0.70 mm/day; SD = 0.15). Among streams, Elk River growth rates were particularly high (mean = 1.02 mm/day; SD = 0.18).

The top-ranked growth rate model ($w_i = 0.32$) contained three interactive effects: stream × mean streamflow, stream × streamflow CV, and stream × water temperature CV (Figure 5). The effect of increased streamflow on growth rate was negative in all streams, but this relationship was most pronounced in Honey Creek and least pronounced in Buffalo Creek. Growth rate was positively related to increased streamflow variability (CV) in Honey Creek and especially in Elk River, whereas no relationship was apparent in the other streams. Growth rate was positively related to water temperature variation (CV) in Spavinaw Creek, but this relationship was negative in both Elk River and Honey Creek. Across observed values of these environmental variables, fish in Elk River typically exhibited the greatest predicted growth rates. The fixed effects in this model explained 55% of the variation in age-0 Smallmouth Bass growth rate (marginal $R^2 = 0.55$), including all random variation among years (conditional $R^2 = 0.55$).

DISCUSSION

Age-0 Smallmouth Bass hatch timing and growth rate patterns varied across the riverscape, suggesting that system-specific responses to environmental stimuli may produce spatially divergent patterns of fish growth and year-class strength. Although streamflow and temperature conditions explained much of the variation in age-0 Smallmouth Bass growth rate in Ozark streams, these relationships varied among streams. My findings emphasize the importance of local variation in creating population-level heterogeneity that provides resistance in the face of environmental stochasticity, even in naturally dynamic systems. Efforts to protect and maintain the inherent diversity of these populations will benefit their persistence under increasingly unpredictable environmental scenarios.

Growth rate of age-0 Smallmouth Bass was influenced by several stream-dependent environmental conditions including streamflow magnitude and variability and water temperature variability. The observed negative relationship between streamflow magnitude and growth rate may reflect the loss of optimum velocity habitat for age-0 Smallmouth Bass under elevated flow conditions (Swenson et al. 2002). Additionally, at high flows, substrate scour reduces invertebrate prey production and increased turbidity reduces foraging efficiency of juvenile stream fish (Cushman 1985; Sweeten 1996). The positive relationship between flow variability and growth rate that I observed in two study streams has been noted for some riverine fish populations (e.g., Central Stoneroller *Campostoma anomalum*, Spranza and Stanley 2000; Humpback Chub *Gila cypha*, Finch et al. 2013). Mechanisms by which variable flows benefit growth include increasing drift of invertebrate prey (Poff and Ward 1991; Vinson 2001) and access to floodplain food sources or warmer microhabitats (i.e., warmer floodplain waters) that benefit juvenile growth (Junk et al. 1989; Sommer et al. 2001). Growth responses to variability in water temperature were mixed among streams (positive, negative, and no relationship). Thermal variability may affect growth rate by altering prey quality or quantity, and via deviations from optimal foraging and metabolic temperatures (Elliott 1976; Wootton 1990; Lawrence et al. 2015). The way I quantified temperature (i.e., at the reach scale), of course, does not account for fine-scale thermal refugia (e.g., springs, seeps) important for fish growth. Groundwater inputs create thermally complex habitats that allow individual fish to behaviorally thermoregulate and reduce the influence of temperature changes (Fullerton et al. 2017). Observed differences in growth rates among stream populations may reflect variation in stream size and productivity (Vannote et al. 1980). Biotic factors (e.g., predation, density dependence, interspecific competition) may also contribute to observed differences in growth rate among streams (Knotek and Orth 1998; Vøllestad et al. 2002; Xu et al. 2010).

The growth rate model also reflected unexplained variation among individual fish. Individual variability in behaviors is common among studies examining stream fish populations (Magurran 1986). Individual variation in growth rate may reflect differences in behavior (e.g., foraging or predator avoidance, Fraser et al. 2001; Mangel and Stamps 2001) or metabolism (Auer et al. 2018). For example, the switch to piscivory by larval fishes greatly benefits growth and can occur when Smallmouth Bass are quite small (i.e., 15–18 mm TL, Easton and Orth 1992), though this behavior varies among individuals and with temporal prey availability (Steinhart et al. 2004; Dauwalter and Fisher 2008). Individuals also exhibit differences in their propensity to move to exploit favorable habitats or resources (Merciai et al. 2017; Tattam et al. 2017; Miller et al. 2019). It is likely that several physicochemical factors interact to determine individual variability in growth including environmental factors associated with hatch timing.

The observed patterns of hatch timing suggest that extreme flows during the spawning period may limit the contribution of earlier-hatched individuals to these populations. Many populations show a high degree of adaptation to local flow regimes (Lytle and Poff 2004). Although flow regimes in Ozark streams tend to be flashy (Leasure et al. 2016), large floods can be devastating to larval stream fish by scouring nests and substrates and by displacing eggs and fry (Pflieger 1975; Jennings and Phillip 1994; Lukas and Orth 1995). One evolutionary response to high flows is the protracted spawning window of Smallmouth Bass (i.e., 12.5–23.5 °C, Graham and Orth 1986) and the ability of fish to repeat spawning under favorable conditions or when earlier broods are lost (Pflieger 1966; Shuter et al. 1980). I observed spawning and nest-guarding by Smallmouth Bass early in 2017 (i.e., April 12–13) in Elk River and Buffalo Creek (see Chapter 2), but these nests and larvae were apparently lost in subsequent floods as I did not collect any juveniles that reflected successful spawning during that period. Sustained elevated flows in 2017 appeared to limit successful spawning until mid-May. Under benign flow conditions, hatch timing was positively associated with temperature though spatially variable.

Coupling of temperature and spawning phenology in fishes is common (Wootton 1990). Thermal cues are associated with spawn timing (Shuter et al. 1980) and egg development (Warren 2009) of Smallmouth Bass, but these cues can vary among streams in close spatial proximity (Graham and Orth 1986). Alternatively, conditions at finer spatial scales may have influenced observed spawning phenology. Environmental conditions interact with stream and individual heterogeneity to produce diverse reproductive phenology in other regions. For example, geomorphology and hydrology drive patterns of thermal heterogeneity in Pacific Northwest streams that influence Pacific salmon *Oncorhynchus* sp. spawn timing within and among basins (Lisi et al. 2013).

I found average hatch durations in Ozark streams typically mirrored the findings of others (e.g., 6–10 d, Scott and Crossman 1973; 19–27 d, Phelps 2008); however, spawning phenology varied among years and streams (e.g., hatching began relatively early under relatively stable flow conditions). Flooding after the onset of spawning can create an extended, bimodal range of hatch dates in northern rivers (e.g., late April to mid-July, Graham and Orth 1986). The onset of hatching I observed in late April 2018 was consistent with the spawn timing in other regional streams (Dauwalter and Fisher 2007). Slightly earlier hatching in Buffalo Creek and Honey Creek compared to other streams during both years may reflect relatively warmer water temperatures (e.g., Honey Creek) or the expected quick return of a smaller stream (Knighton 1998) to moderate discharge levels following flooding (e.g., Buffalo Creek).

This study demonstrates interannual and spatial variation in hatch distributions and growth rates by age-0 Smallmouth Bass, but additional efforts would be helpful in developing a more comprehensive evaluation of these patterns. The study sites were selected based on spatial proximity to available stream gages but increasing the number of sites through the addition of gages or use of multi-state data would help increase our understanding of these patterns. Additionally, combining spring and autumn sampling to determine hatch date distributions and growth rates along with size distributions and condition following the growing season would provide a clearer picture of the role that spawning phenology and environmental conditions play in age-0 Smallmouth Bass populations. It would seem advantageous to collect individuals on multiple occasions during the spawning and rearing period to describe spawning phenology and the relative contribution of different cohorts to the year-class (Pine et al. 2000); however, I completed nest surveys (Chapter 3) and tracked fish during the spawning period (Chapter 2) so I had more information on spawn timing at the landscape scale. Collectively, I provide data that suggests ecological novelty in spawning and rearing by the Neosho subspecies of Smallmouth Bass (e.g., nest clustering, plasticity of habitat use across the riverscape, the importance of confluences for rearing).

Conservation and management strategies would benefit from protection of individual and across-stream variability in spawning behaviors. Spawning heterogeneity among streams is important for the adaptability of populations in the face of changing environmental conditions (e.g., climate change and other human alterations). Smallmouth Bass in these streams appear well adapted to deal with naturally flashy hydrology, though unpredictable and late occurring extreme flows remain problematic for their reproductive success (Chapter 5). Thus, limiting further modification of the flow regime (e.g., groundwater pumping) and working to mitigate extreme flows would be beneficial for Smallmouth Bass hatching and rearing success. Given the naturally dynamic streams which they inhabit and their ability to thrive across a variety of stream sizes, managers would benefit from protecting the genetic uniqueness of Smallmouth Bass in this region (e.g., Stark and Echelle 1998; Taylor et al. 2018). Although the Tennessee strain of Smallmouth Bass may grow faster than juvenile Neosho fish (i.e., some of the fish in Elk River may be Tennessee strain or hybrids), the Neosho subspecies shows complex relationships with the physicochemical environment of smaller streams (this and Chapter 5) that are atypical of other populations. The genetic structure of the Neosho subspecies suggests that these fish are highly adapted to their local environment, particularly in small streams (Taylor et al. 2018). Genetic variation in Smallmouth Bass among these streams may drive observed stream-specific responses of spawning phenology and growth to environmental variability. Genetic variability coupled with ecological variability may work in concert to stabilize overall population dynamics at the riverscape level (i.e., portfolio effect, Schindler et al. 2010). Thus, maintaining the genetic integrity of these populations is essential for ensuring resilient Smallmouth Bass populations in a changing environment.

Table 1. U.S. Geological Survey (USGS) stream gage information and hydrologic characteristics for five Ozark Highland streams used in this study of age-0 Smallmouth Bass hatch date distributions and growth rates. Coordinates are given in the NAD83 datum. DA is contributing drainage area at the gage location. Mean daily and median daily discharge for the period of record are given by Q_{mean} and Q_{med}, respectively. Period indicates the years of discharge data available at each USGS stream gage. Data accessed 22 March 2018.

Stream	Gage No.	Latitude	Longitude	DA (km^2)	Q_{mean} (m^3/s)	Q_{med} (m^3/s)	Period (years)
Buffalo Creek	07189100	36.67093	-94.60429	157.5	1.44	1.08	17
Elk River	07189000	36.63090	-94.58689	2204.1	40.21	21.29	78
Honey Creek	07189542	36.54899	-94.68369	126.1	0.99	0.79	20
Beaty Creek	07191222	36.35542	-94.77600	153.1	1.13	0.93	19
Spavinaw Creek	071912213	36.32297	-94.68517	422.2	3.29	2.61	16

Table 2. Total length and daily age summaries for age-0 Smallmouth Bass collected from study streams in 2017 and 2018. Sample size for each site is denoted by *n*.

		Total Length (mm)		Age (days)	
Stream	*n*	Mean ± SD	Range	Mean ± SD	Range
2017					
Buffalo Creek	101	32 ± 3	25 – 44	37 ± 2	32 – 43
Elk River	60	37 ± 5	30 - 57	31 ± 3	24 – 40
Honey Creek	99	35 ± 4	27 - 43	38 ± 2	29 – 43
Beaty Creek	58	32 ± 4	26 – 43	37 ± 3	27 – 45
Spavinaw Creek	62	26 ± 4	19 – 42	27 ± 4	19 – 42
Total	380	33 ± 5	19 – 57	35 ± 5	19 – 45
2018					
Buffalo Creek	98	42 ± 5	33 – 60	44 ± 3	35 – 50
Elk River	93	50 ± 7	37 – 86	39 ± 3	31 – 45
Honey Creek	73	43 ± 6	33 – 61	42 ± 4	33 – 51
Beaty Creek	83	36 ± 5	27 – 48	37 ± 3	31 – 47
Spavinaw Creek	67	37 ± 6	25 – 52	35 ± 3	26 – 41
Total	414	42 ± 8	25 – 86	40 ± 4	26 – 51

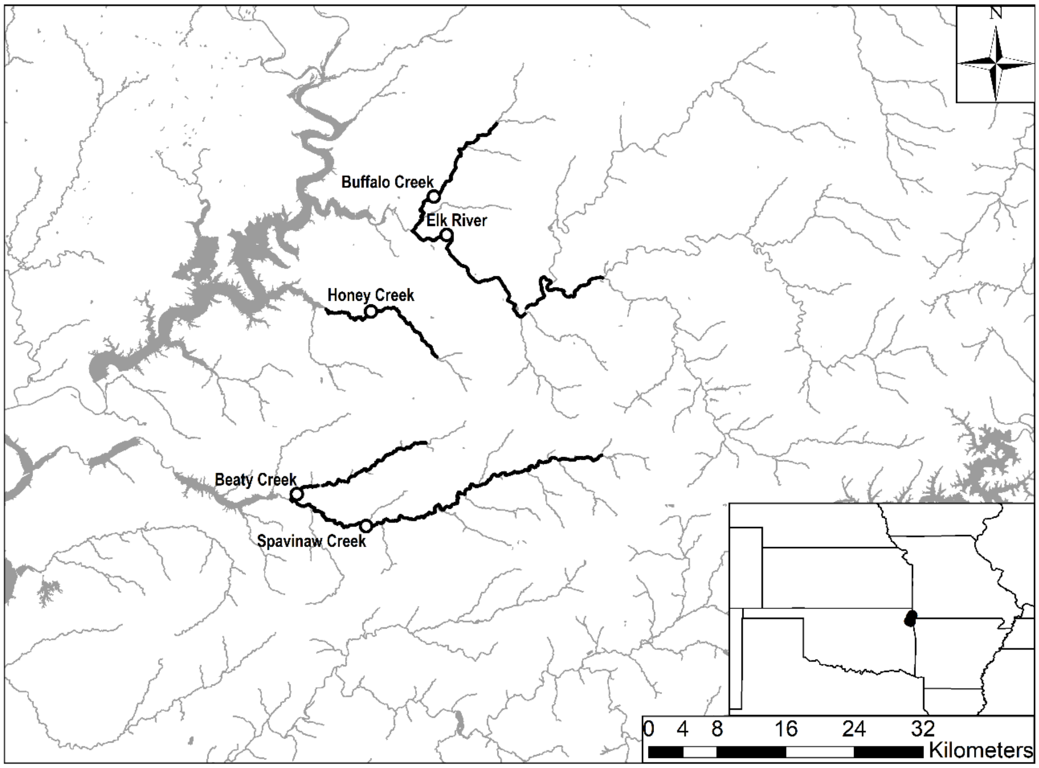


Figure 1. Stream reaches where U.S. Geological Survey stream gages were located (circles) and where I collected age-0 Smallmouth Bass for daily aging in late June and early July 2017–2018. All sample reaches were within 3.5 rkm of the associated stream gage.

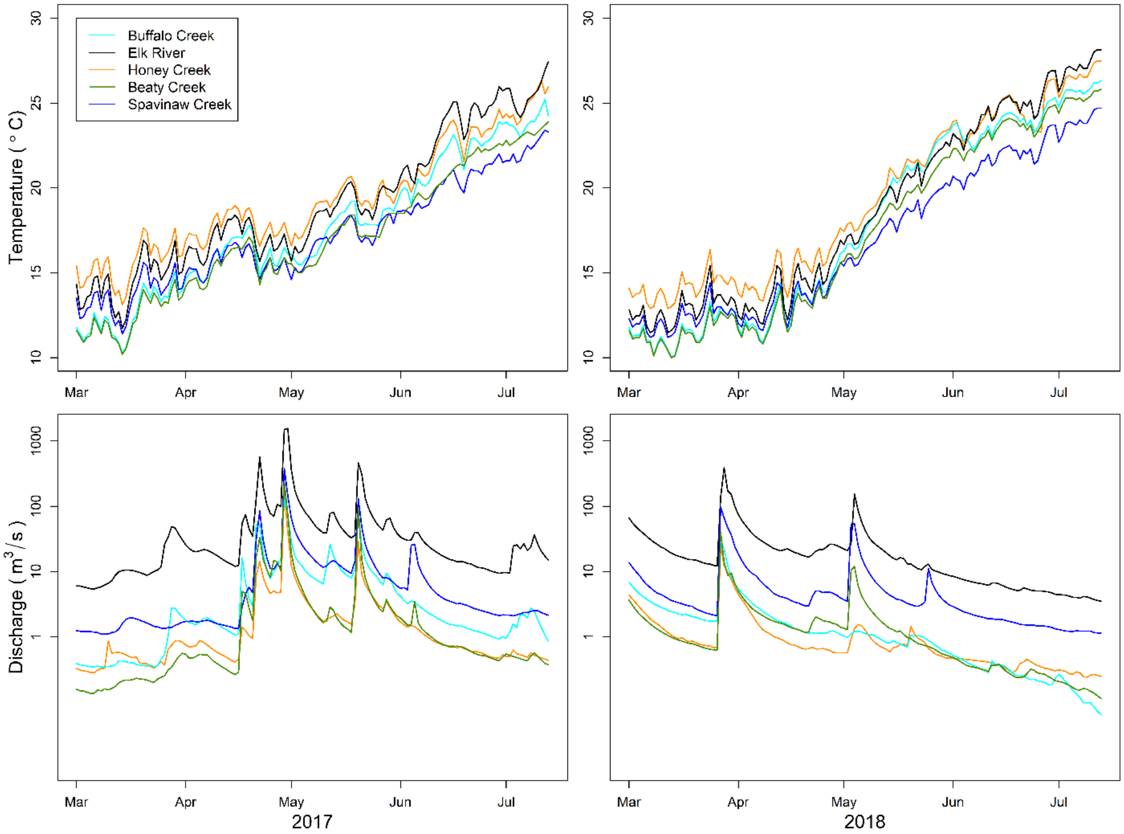


Figure 2. Mean daily water temperature and discharge patterns for the 2017–2018 pre-spawn through rearing periods in five Ozark Highland streams. These five streams were sampled to determine age-0 Smallmouth Bass hatch date distributions and growth rates. Note $\log_{10}$ scale was used to plot discharge.

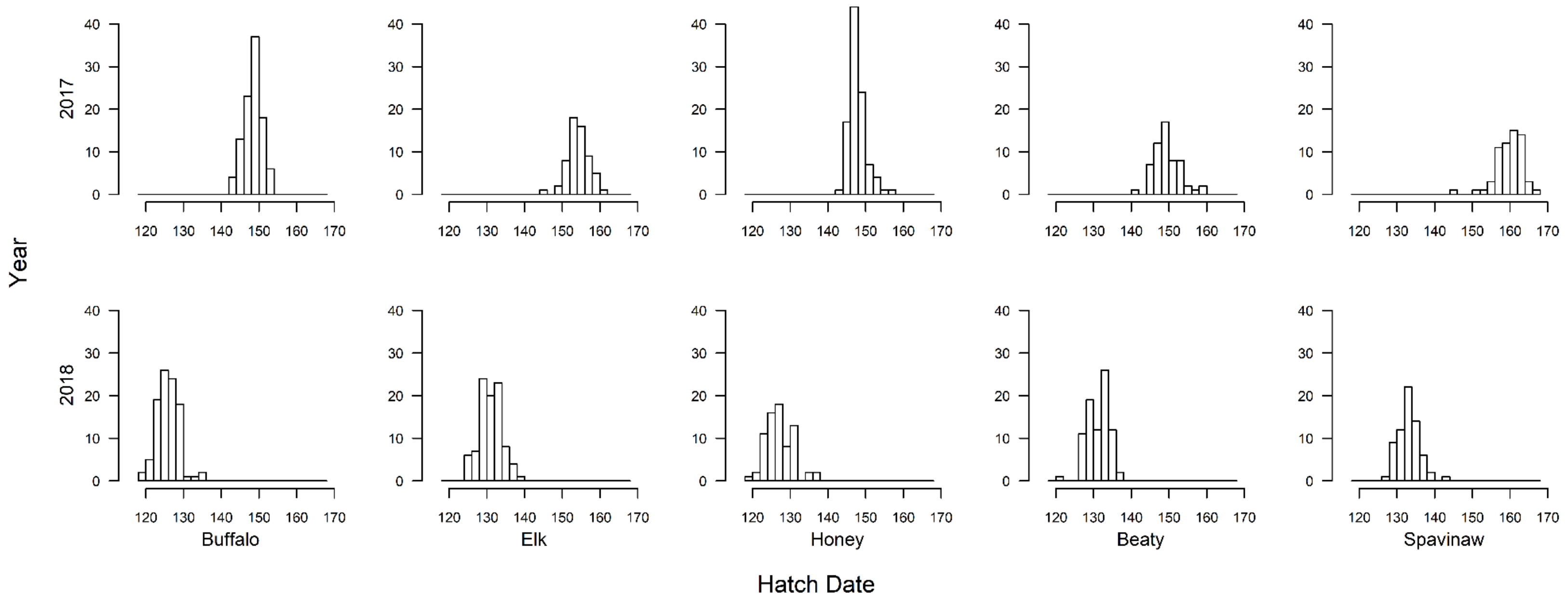


Figure 3. Distribution of hatch dates (day of year) for age-0 Smallmouth Bass collected across five Ozark streams in late June and early July 2017 and 2018. For reference, hatch day 120 corresponds to April 30 and hatch day 150 corresponds to May 30.

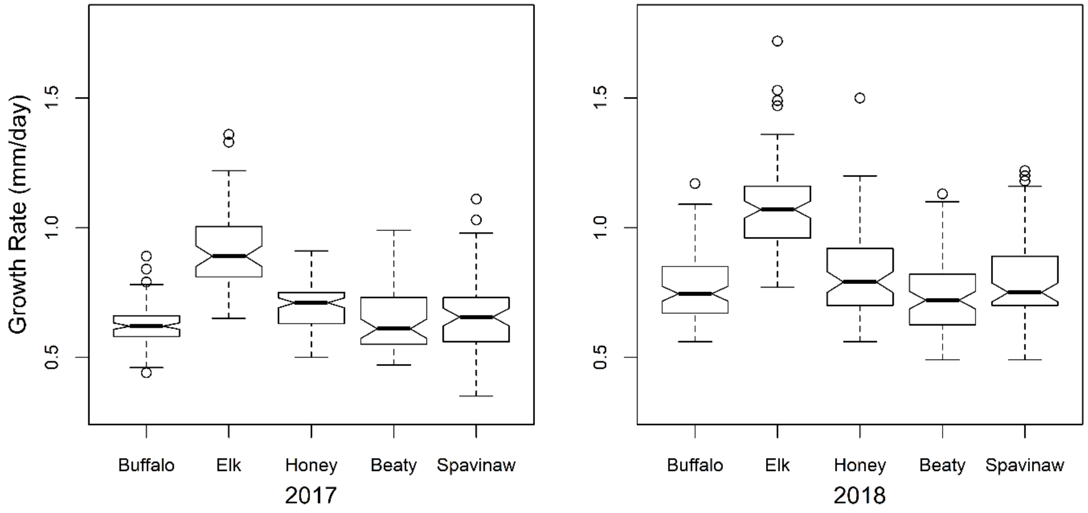


Figure 4. Boxplots of age-0 Smallmouth Bass daily growth rate (mm/day) across two years and five streams. Boxes reflect the interquartile range (IQR) of these data, whereas whiskers equal 1.5× IQR. Notches approximate 95% confidence intervals for each median.

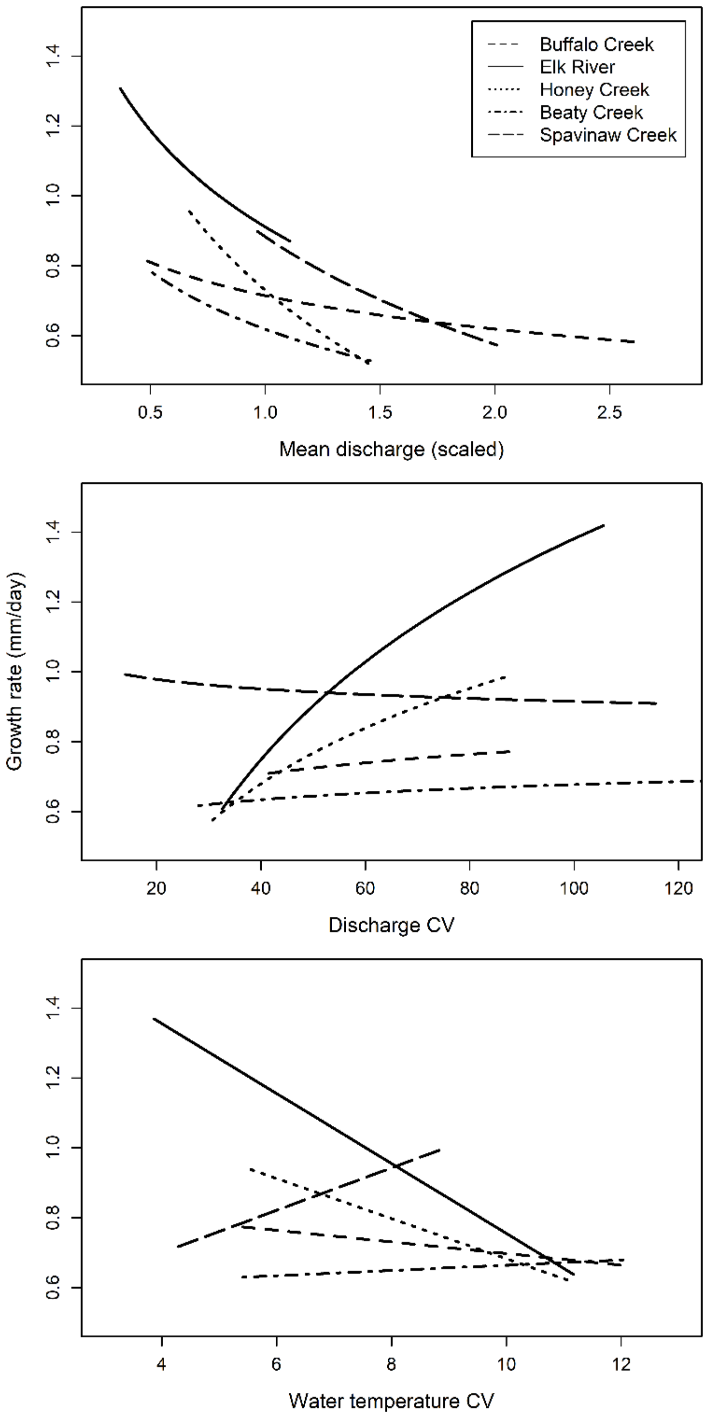


Figure 5. Predicted relationships between age-0 Smallmouth Bass growth rate (mm/day) and environment by stream interactions from the top candidate model. Mean discharge values are scaled by the long-term median discharge for each stream (see Table 1). Coefficient of variation (CV) is calculated as: $\frac{\sigma}{\mu} \times 100$. Predictions for each interaction effect are made with other continuous predictors held constant at their mean values.

CHAPTER V

INFLUENCE OF HYDROLOGY, MULTI-SCALE HABITAT, AND STREAM NETWORK POSITION ON AGE-0 SMALLMOUTH BASS ABUNDANCE

ABSTRACT

Stream fish survival and recruitment are products of the physicochemical environment that benefit growth and provide refuge; yet, drivers of spatiotemporal variation in fish abundance and habitat remain unclear. Using snorkel and habitat surveys from 2015-2017, I evaluated the relationships among multiscale habitat features, hydrology, and age-0 Smallmouth Bass (*Micropterus dolomieu velox*) abundance. I found occurrence and abundance of age-0 bass were spatiotemporally variable and correlated with stream temperature, a July streamflow-network position interaction, a pool depth-stream size interaction, and a stream-temperature dependent effect of network position. High flows at the end of the nesting season reduced age-0 abundance, but this effect was mitigated in reaches located close to larger streams. In small streams, deeper-water habitat supported higher bass abundances. Generally, colder streams had lower age-0 Smallmouth Bass abundance, though this trend was less apparent in reaches adjacent to larger streams. My findings suggest improved rearing conditions could result from limiting flow alteration and land-use practices that exacerbate extreme flows and alter channel morphology, particularly in select portions of the stream network.

INTRODUCTION

The first growing season of life represents a critical population bottleneck for many stream fishes and is influenced by a variety of factors. Both abiotic (e.g., extreme flows, temperatures), and biotic pressures (e.g., predation, starvation, disease) reduce survival of developing eggs and fry during the first growing season (Cleary 1956; Fajen 1975; Schlosser 1982; Lukas and Orth 1995; Knotek and Orth 1998). For example, predation and fungal infection are common causes of Smallmouth Bass (*Micropterus dolomieu*) nest failure and larval mortality even when abiotic conditions are favorable (Knotek and Orth 1998; Dauwalter and Fisher 2007). Seasonal floods also influence age-0 fish survival and subsequent recruitment (Lukas and Orth 1995; Smith et al. 2005); however, flood timing, fish size, and available refuge habitats all influence fish susceptibility to flood disturbances (Harvey 1987; Pearsons et al. 1992; Lobón-Cerviá 1996). The nature of both disturbances and refuges vary with environmental conditions and the degree of local adaptation by fishes (Gelwick 1990; Schlosser and Angermeier 1995), and multi-scale habitat features may further influence these relationships (Kennard et al. 2007; Arthington et al. 2010). Because these factors lead to considerable spatiotemporal variability in recruitment and, thus, population dynamics (Schlosser 1982; Elliott 1989; Schlosser 1991; Schlosser 1998), efforts to elucidate these relationships are essential for effective conservation and management of stream fishes.

Stream habitats are arranged in a spatially-nested hierarchy, wherein coarse-scale landscape features modify finer-scale abiotic and biotic conditions (Hynes 1975; Frissell et al. 1986; Schlosser 1991) and create habitat heterogeneity (Wiens 1989; Allan et al. 1997). The relationship between local fish assemblages and habitat conditions is related to a variety of coarse-scale factors including climate (Eaton and Scheller 1996; Comte and Grenouillet 2013), geology (Neff and Jackson 2012), soils (Brewer et al. 2007), and land use (Allan 2004; Brewer and Rabeni 2011). Intermediate-scale patterns in hydrology, water temperature, and groundwater influence are dictated by coarse-scale features and further modify local stream habitat, fish occupancy and fish abundance (Jowett and Duncan 1990; Wehrly et al. 2003; Torgersen et al.

2006; Brewer et al. 2007; Falke et al. 2010). For example, flow conditions influence spawn timing of Brassy Minnow (*Hybognathus hankinsoni*) in Great Plains streams, thereby affecting growth rates and larval survival (Falke et al. 2010). Similarly, greater spring-flow volume is associated with increased occurrence and density of age-0 Smallmouth Bass, likely due to increased hatch or survival rates (Brewer 2013a). Understanding how physicochemical conditions drive spatial and temporal patterns in fish abundances provides insight about how stream networks influence fish population success, including economically and ecologically important sportfish such as Smallmouth Bass (Brewer and Orth 2015).

My study objective was to determine the physicochemical factors that relate to spatial and temporal variation in age-0 Smallmouth Bass (*M. d. velox*) abundance across stream networks of the Ozark Highland ecoregion. Previous evaluations of age-0 Smallmouth Bass abundance focused on their use of microhabitat features (e.g., Aadland 1993; Sabo and Orth 1994; Orth and Newcomb 2002; Pert et al. 2002; Fore et al. 2007), with some examination of coarser-scale influences emphasizing relationships with land use (e.g., Dauwalter et al. 2007; Brewer and Rabeni 2011; Brewer 2013b). My study is the first extensive landscape evaluation of rearing habitat across the range of the Neosho subspecies of Smallmouth Bass, a genetically-distinct population (Brewer and Long 2015). Further, the study is novel because 1) I examine several physicochemical characteristics typically overlooked in warmwater streams (i.e., groundwater, sheer stress index), and 2) I place my habitat relationships in the context of stream network position. Because age-0 Smallmouth Bass abundance is frequently used as an index of reproductive success (Pflieger 1975; Smith et al. 2005), I specifically identified factors that both correspond to the scale most relevant to fisheries management evaluations (i.e., reach scale; Fausch et al. 2002) and those that would facilitate use of existing geospatial and hydrologic data.

METHODS

Study area

My study area represented a variety of streams across the Neosho subspecies' range in the southwest Ozark Highlands ecoregion (Fig. 1). I selected representative sample reaches though final site location was influenced by permission to access privately-owned lands. The landscape of the Ozark Highlands is characterized by cherty limestone lithology, karst topography, and numerous springs, resulting in variable groundwater inputs within and among streams (Brewer 2013a; Zhou et al. 2018), low suspended sediment loads under baseflow conditions, and predominately gravel-cobble substrates (Nigh and Schroeder 2002). The climate is relatively humid (average annual rainfall: 106–110 cm; Nigh and Schroeder 2002), and stream flow regimes are classified as flashy to stable with substantial variation in groundwater contributions (Turton et al. 2008; Leasure et al. 2016; Zhou et al. 2018). Predominant land-use in this region is a mix of forest and pasture (Nigh and Schroeder 2002). Impoundments across the basins create a number of river-reservoir complexes and river fragments that support distinct subpopulations of the Neosho subspecies (Taylor et al. 2018).

Fish surveys

I conducted snorkel surveys for age-0 Smallmouth Bass in 120 stream reaches (i.e., 20 times average channel width; Flosi et al. 1998; Dauwalter and Fisher 2008a) nested within 70 stream segments (i.e., stream area between two tributary junctions; Frissell et al. 1986) in late summer and early autumn 2015–2017. My sample timing was chosen to avoid periods of significant, but expected mortality (e.g., larval bass; Brewer et al. 2019) and major changes in sampling efficiency due to water clarity (minimum 1.5 m using a fish silhouette, Goldstein 1978; Dunham et al. 2009), water temperature, and fish activity (Oliver et al. 1979). All surveys were conducted during daylight hours (approximately 0900–1700 hours) to maximize visibility. At each stream reach, a team of 2–5 snorkelers moved upstream in parallel lanes spending additional time searching complex or deep habitats and communicating to prevent double-counting of individual fish (Dunham et al. 2009; Brewer 2011). Lanes were defined by both visibility and habitat complexity where areas of lower visibility and highly complex habitat resulted in much narrower sample lanes (Hillman et al. 1992; Thurow et al. 2012). Age-0 Smallmouth Bass were distinguished from other sympatric basses (Spotted Bass *M. punctulatus* and Largemouth Bass *M. salmoides*) via the lack of horizontal black bars and the presence of a tri-colored tail (Brewer and Ellersieck 2011).

At a subset of stream reaches (*n* = 78), I snorkeled a second pass to assess sampling efficiency (i.e., the proportion of individuals detected among those present; Peterson and Paukert 2009) of age-0 Smallmouth Bass. Observers did not discuss fish counts between each pass, and observers changed survey lanes in the stream between passes. I waited a minimum of one hour between the start of each pass to allow the stream to return to a reasonably undisturbed state (O’Neal 2007; Thurow et al. 2012). The second pass was conducted in the same manner as the first snorkel pass.

Habitat

I quantified habitat characteristics at each stream reach immediately following my fish survey(s) (Table 1). Discharge (0.01 $m^3 \cdot s^{-1}$) was measured at each site using the velocity-area method (Gordon et al. 2004). Channel units were classified following a simplified version of Rabeni and Jacobson (1993) and quantified by percent area (Thurow 1994). Briefly, pools were depositional units, riffles were high-gradient erosional habitats with swift water and coarse substrate, runs were transitional habitats of moderate velocity, and off-channel habitats included both forewaters and backwaters. Average width of the channel (0.1 m) was also calculated while mapping channel units due to hypothesized influences of stream morphology on fish abundance

(Jowett et al. 1996; Rosenfeld et al. 2000). I measured residual pool depth (0.01 m) as the maximum pool depth minus depth of downstream riffle crest (Lisle 1987) and thalweg depth (0.01 m) at 50-m intervals along the study reach. I measured water temperature (0.1 °C) at mid-pool depth with a thermometer (Ultrapen PT1, Myron L, Carlsbad, CA). Because I only has a point measure from the time of sampling and these data reflected a natural break in temperature conditions, I converted stream temperature to a categorical variable with two levels (≤ 19.5 °C and > 19.5 °C).

I combined terrain analysis with existing data using Spatial Analyst Tools in ArcMap 10.3.1 (ESRI, Redlands, California) to summarize habitat attributes for each stream segment (*n* = 70; Table 1). Following the methods of Jenson and Domingue (1988), I delineated overland flow-direction pathways (O'Callaghan and Mark 1984) and upstream contributing areas (Betz et al. 2010) for each segment using a 30-m resolution raster digital elevation model (U.S. Geological Survey [USGS] National Elevation Dataset [NED]). I restricted in-stream flow pathways by calculating flow direction within the rasterized 1:100,000 stream network (USGS National Hydrography Dataset [NHD]) and overlaying this grid on the landscape-flow direction grid (Betz et al. 2010). Using my in-stream flow-direction grid, I calculated two topology metrics: link magnitude (Shreve 1966) and downstream link (Osborne and Wiley 1992). The first metric reflected stream size, whereas the latter was useful for understanding spatial position within the stream network.

I then calculated metrics of landscape disturbance, topography, soils, geology, annual runoff, and baseflow contribution for the upstream contributing area of each stream segment (Table 1). To quantify landscape disturbance, I calculated an index modified from Brown and Vivas (2005) and Mouser et al. (2019). First, I assigned coefficients in order of increasing hypothesized severity to land cover classes from the 2011 National Land Cover Dataset (NLCD; Homer et al. 2015; Table S1). Brown and Vivas (2005) used finer-resolution land use types than those in the NLCD; therefore, I averaged coefficient values from Brown and Vivas (2005) when a single NLCD category contained more than one land use type (e.g., Mouser et al. 2019). For example, my coefficient for the NLCD “pasture/hay” category (2.99) was the average of four categories from Brown and Vivas (2005): woodland pasture (2.02), improved pasture without livestock (2.77), improved pasture low-intensity with livestock (3.41) and improved pasture high-intensity with livestock (3.74). The lowest coefficient (1.00) represented undisturbed habitats (e.g., forests, wetlands), whereas more disturbed habitats, where I hypothesized Smallmouth Bass would be most affected by land use, had greater values (e.g., 7.92 for high-intensity development). Many categories described in Brown and Vivas (2005) were of finer resolution than the NLCD, so I averaged the values from Brown and Vivas (2005) to determine my coefficients (sensu Mouser et al. 2019). Next, I averaged the coefficients across the upstream contributing area so one value represented each stream segment. I also calculated area-weighted percent impervious cover using 30-m imperviousness data from Xian et al. (2011); I considered impervious cover as a predictor given its disproportionate negative influence on stream biota in many systems (Allan 2004; Brewer and Rabeni 2011; King et al. 2011). I calculated the local slope for each 30-m raster cell across the landscape, and used the area-weighted average of these cells to characterize topography for each stream segment. I calculated area-weighted measures of soil conditions (i.e., percent hydrologic soil group D, soil permeability) and geology (i.e., percent carbonate lithology) using existing data (Stoeser et al. 2005; Hill et al. 2016; NRCS 2017). Variability in annual runoff and baseflow contributions (i.e., groundwater) was quantified by averaging data from Hill et al. (2016) across the upstream contributing area of each stream segment.

Annual Hydrology

I characterized annual hydrology (i.e., 2015–2017) to represent a coarse resolution of the flow conditions during the spawning and early growth period of Smallmouth Bass. Because many streams I sampled did not have stream gages, I summarized available data using 11 representative stream gages (USGS gages: 07189100, 07188653, 07188838, 07188885, 07189540, 07189542, 07191222, 071912213, 07196000, 07197000, and 07197360; Table S2). Using daily streamflow data, I calculated mean discharge from April–July for each year (2015–2017). I also calculated monthly (April–July) maximum daily discharge and corresponding flow exceedance probability (EP, the relative frequency of a given streamflow magnitude based on historical flows) for each gage. Because I averaged discharge across all streams in each sample year, I used monthly flow EP due to its relative independence from stream size. Lastly, I calculated the average frequency of higher flow events (> 10 $m^3 \cdot s^{-1}$) and the average number of days (duration) with mean daily streamflow above this threshold from April–July of each year. I used 10 $m^3 \cdot s^{-1}$ as a threshold given its association with Smallmouth Bass nest failure (Lukas and Orth 1995) and with observed reductions in spawning activity in streams of similar size (A. D. Miller and S. K. Brewer, unpublished data). In addition to these streamflow metrics, I also summarized April–July precipitation trends across the study area for each year using data from the Oklahoma Mesonet (https://www.mesonet.org/, accessed April 2018; Table S3).

Analyses

I used data from 78 sites with two snorkel surveys to assess my sampling efficiency (Royle 2004). My multiple-survey data showed high concordance at each site (Pearson's r = 0.97), suggesting that my Smallmouth Bass counts were precise. With the large number of sites examined, a lack of variability in repeated counts also suggests high sampling efficiency, with the correlation coefficient between passes providing a rough estimate of average real-world detection probability (Kéry and Royle 2015). I, therefore, proceeded with my habitat analyses using unadjusted abundance data, using the greater of my counts at sites where multiple surveys were conducted.

I assessed the distribution of my predictor variables and compared generalized linear mixed models (GLMMs) with different probability distributions prior to evaluating the relationship between age-0 Smallmouth Bass abundance and habitat. To reduce skewness, I transformed continuous (natural-log) and proportion (logit) variables (Warton and Hui 2011). All independent variables were then standardized to mean = 0 and SD = 1 to ease model interpretation and improve model convergence (Gelman and Hill 2007). Transformations and standardizations were done using the 'MuMIn' (Bartoń 2018) and 'psych' (Revelle 2018) packages in Program R (Version 3.5.1, R Core Team 2018). Examination of my count data suggested both overdispersion and zero inflation. I compared several model forms (i.e., Poisson, negative binomial, zero-inflated Poisson, zero-inflated negative binomial [ZINB]) for modeling abundance (scaled by area sampled) as a function of 11 predictors (Table 1). These models included random effects for both stream segment and sample year to account for unexplained variability among reaches and lack of independence among observations (Wagner et al. 2006; Gelman and Hill 2007). Model comparison indicated that a ZINB model with zero inflation modeled in relation to stream temperature provided the best model fit (AIC_c weight > 0.99).

To reduce the number of possible explanatory variables, I first compared ZINB models with each univariate predictor variable ($n = 25$) and two-way interaction term of *a priori* interest ($n = 22$) to a random-intercept only (null) model using Akaike's information criterion adjusted for small sample size (AIC_c; Sugiura 1978; Hurvich and Tsai 1989). I retained terms from all models with $\Delta AIC_c < 2$ relative to the null model (Burnham and Anderson 2002). To minimize issues with interpretation, I reduced any remaining covariates with pairwise correlations $\geq |0.7|$ by retaining the predictor variable with better model fit (Dormann et al. 2013). The reduced variable set contained 10 univariate predictors and 11 two-way interaction terms (Table 1).

Using my reduced variable set, I developed a set of candidate models. Initial model comparisons suggested that July flow EP and several two-way interaction terms (i.e. July flow EP

× Drainage area, July flow EP × Downstream link, July flow EP × Stream temperature, and Drainage area × Residual pool depth) were particularly influential predictors. I used all additive combinations of these terms to build a base set of 17 models. I then added the remaining univariate and two-way interaction terms (Table 1) to this base model set to build my candidate set of 261 models. I limited the number of fixed-effect predictors to 10 (in addition to two random effects) to maintain appropriate degrees of freedom for model performance (Peduzzi et al. 1995; Harrell 2001). All candidate models included stream-segment and year random effects to account for the non-independence among reach-scale observations (Wagner et al. 2006; Gelman and Hill 2007). I assumed a normal distribution for all random effects as $N(0, \tau^2)$, where τ^2 was the population variance among levels of a random effect (e.g., among stream segments). All models were built in the R package 'glmmTMB' (Magnusson et al. 2018), and I used the 'bbmle' package (Bolker 2017) to calculate AIC_c for my candidate set to determine the variable set that had the most support. This approach, though exploratory, limited candidate models to those that were ecologically sensible (Dochtermann and Jenkins 2011; Grueber et al. 2011).

I calculated the amount of variation explained by the top model using marginal R^2 (amount of variance explained by the fixed effects) and conditional R^2 (amount of variance explained by both fixed and random effects; Vonesh et al. 1996; Nakagawa and Schielzeth 2013). For zero-inflated mixed models, this formula considers only the conditional (abundance) model and ignores the zero-inflation model (B. Bolker, personal communication, 2018). These calculations were performed using the 'sjstats' (Lüdecke 2018) package in R.

RESULTS

Snorkel surveys

Smallmouth Bass occurrence and abundance varied among study reaches. I observed age-0 Smallmouth Bass in 103 of 120 surveyed stream reaches, with an average of 181.3 ± 182.5 ha^{-1}

(mean ± SD) at occupied sites (range: 1–1,347 ha^{-1}). Age-0 Smallmouth Bass were disproportionately absent from streams I classified as cold (≤ 19.5 °C). Stream temperature explained some absences of age-0 Smallmouth Bass, with model-predicted zero-inflation probabilities of 29.5% for cold streams and 8.0% for warm streams. I observed age-0 Smallmouth Bass in streams of all sizes within my study range (drainage area range: 16.9–772.7 km^2).

Habitat and annual hydrology

Habitat conditions and hydrology varied considerably among sites and years (Table 1, Table S2). As expected, pools made up the majority of habitat in sampled reaches (mean ± SD: 73.7 ± 15.8%), though residual pool depths differed considerably across study streams (range: 0.20–2.37 m). Sample reaches differed greatly in their spatial position relative to larger streams, with downstream link values ranging from 4–694. Thus, while some reaches were adjacent to large mainstem rivers, others were located in upstream, more isolated parts of the river network. Flows during the nesting period were particularly high and variable in 2015 and 2017, though the timing of flood events varied. In 2015, high flows occurred May–July but in 2017, high flows occurred earlier in the season (April–May). In contrast, precipitation was lower and flow conditions more benign, on average, in 2016 (Table S2, Table S3).

Smallmouth Bass abundance

The top model explaining conditional abundance of age-0 Neosho Smallmouth Bass (i.e., after accounting for zero inflation in cold study reaches) contained several interaction terms for reach and segment-scale predictors and hydrology (Table 2). Late-summer abundances of age-0 Smallmouth Bass were positively associated with higher July flow EP (i.e., more benign July flows), though this relationship was more pronounced in reaches located further upstream relative to reaches adjacent to larger streams (Fig. 2). The influence of residual pool depth on age-0 Smallmouth Bass abundance was dependent on stream size (Fig. 3). In smaller streams, deeper pool habitat was associated with greater age-0 Smallmouth Bass abundance. There was no clear relationship between abundance and pool depth in average-size streams (~117.0 km^2), whereas abundance and pool depth were inversely related in larger streams. The relationship between age-0 Smallmouth Bass abundance and downstream link magnitude was minimal in warm (> 19.5 °C) stream reaches, but a positive trend was observed for cold streams (Fig. 4). Thus, although cold stream reaches generally had much lower numbers of age-0 Smallmouth Bass, this relationship was less apparent in reaches adjacent to larger streams. Collectively, fixed effects in my model explained 57% of the variability in age-0 Smallmouth Bass abundance (marginal $R^2 = 0.57$). No additional variability was explained by random stream segment or year effects in the final model (conditional $R^2 = 0.57$), with all remaining unexplained variability at the residual (i.e., reach) level.

DISCUSSION

I found several relationships between age-0 Smallmouth Bass abundance and abiotic conditions that were modified by stream network position and stream size, suggesting that large and small streams serve as complementary refuge habitats under different abiotic scenarios. The relative influences of water temperature, July flow magnitude, and pool depth on age-0 abundance were variable across the riverscape. These findings highlight the importance of movement corridors that allow fish to seek refuge from natural disturbances and environmental variability. Although age-0 Smallmouth Bass use a diverse range of habitats throughout their range, often in response to coarse-scale conditions (Orth and Newcomb 2002; Pert et al. 2002; Dauwalter et al. 2007; Brewer 2013b), current conservation and management efforts often fail to account for this variability. Efforts to preserve and rehabilitate complementary habitats and areas that provide natural habitat diversity (e.g., tributary junctions) across riverscapes would be beneficial for the persistence of the Neosho subspecies under varying environmental conditions.

Occurrence and abundance of age-0 Smallmouth Bass were lower in colder (i.e., ≤ 19.5 °C) stream reaches, though the latter relationship varied with stream network position. Optimum growth of juvenile Smallmouth Bass occurs between 25–28 °C (Peek 1965; Coutant and DeAngelis 1983), though development and growth are possible at 20–32 °C (Wrenn 1980). As these warmer stream temperatures accelerate larval development, they confer added resistance against predation and environmental disturbance (e.g., displacement during floods; Harvey 1987; Armour 1993). Growth of age-0 Smallmouth Bass also creates an important buffer against starvation during the overwinter period, which often serves as a recruitment bottleneck (Oliver et al. 1979; Shuter et al. 1980). Thus, it was not surprising that model-predicted absence was nearly four times more likely in cold streams. Despite this, I observed age-0 Smallmouth Bass in 58% of cold stream reaches, suggesting that these habitats are important for reasons other than growth or that thermal refugia exist at finer scales. Groundwater contributions are common in the Ozark Highlands and confer fine-scale thermal heterogeneity (Peterson and Rabeni 1996; Brewer 2013a). This variation may confer a favorable mix of habitats for feeding and growth (e.g., colder stream reaches often lacked larger piscivores; personal observations), which can be exploited by juvenile stream fishes across considerable distances (Armstrong et al. 2013). Age-0 Smallmouth Bass are capable of fine-scale movements between habitats in search of refuge (Brewer et al. 2019; Miller et al. 2019), and larger migrations of age-0 among tributaries occur elsewhere in their range (Humston et al. 2010; Humston et al. 2017). Short-term movements to exploit favorable foraging conditions in warmer, more productive habitats may explain how network position mitigates the influence of colder streams on age-0 Smallmouth Bass abundance. Access to larger, more productive streams may benefit growth (Vannote et al. 1980; Gorman 1986) and in turn confer resistance to size-dependent displacement and mortality during floods (Larimore 1975; Jager et al. 1993).

Flood magnitude and timing during spawning and post-nesting periods are important predictors of age-0 Smallmouth Bass abundance at the end of the first summer, though I found this relationship was influenced by stream network position. Late-summer abundance of age-0 Smallmouth Bass was greater in years where July flow EP was greater (i.e., July flows were more benign). Considerable inter-annual variability in age-0 stream fish abundance and recruitment is common and often reflects the timing of high flows, with floods that occur during nesting and larval development being particularly detrimental (Pearsons et al. 1992; Smith et al. 2005; Kanno et al. 2016; Blum et al. 2018). For example, autumn abundance of age-0 Smallmouth Bass in large Virginia rivers is inversely related to the magnitude of June streamflow (Smith et al. 2005). Similarly, extreme winter floods exert a strong negative influence on young-of-year Brook Trout (*Salvelinus fontinalis*; Blum et al. 2018). In streams throughout their range, floods destroy and displace Smallmouth Bass eggs and larvae (Larimore 1975; Winemiller and Taylor 1982; Lukas and Orth 1995). Flood timing was important in this study, which likely reflects the protracted nature of Smallmouth Bass spawning. Early spring flooding, as was observed in 2017, destroys nests but allows for ample re-nesting opportunities over the following months (Lukas and Orth 1995). Conversely, large floods later in this period, as I observed in 2015, preclude re-nesting attempts as stream temperatures become too warm (i.e., > 25 °C, Robbins and MacCrimmon 1977; Graham and Orth 1986). The observed abundance-flow relationship was modified by proximity of the study reach to larger streams, with the relationship less pronounced in reaches adjacent to larger streams. This suggests that nearby large streams serve as a buffer against flow-related mortality, possibly by providing refuge habitats (e.g., logs, boulders, eddy pools; Todd and Rabeni 1989). Indeed, use of low-velocity refuge habitats (e.g., forewaters and backwaters) by age-0 Smallmouth Bass increases under elevated flow conditions (Brewer et al. 2019). The abundance-flow relationship was more pronounced in more isolated streams (i.e., those located upstream), suggesting that the importance of these streams for age-0 Smallmouth Bass is greater when flow conditions are moderate. Regardless of relative network position, smaller streams may serve as important refugia from predators when flow conditions allow (Meyer et al. 2007; Richardson and Danehy 2007). While my findings are informative, the reliance on limited hydrology data (i.e., gaged streams only) only allowed the use of coarse metrics that could overlook variability that drives additional landscape and local habitat relationships. Similarly, my choice of 10 $m^3 \cdot s^{-1}$ for calculating high-flow frequency and duration metrics likely overlooks stream-size dependent variability in this threshold. I chose this value from observations of Smallmouth Bass nest failure in similarly sized streams (Lukas and Orth 1995), though many of my study streams were smaller and were likely vulnerable to substrate mobility and nest failure at lower flows (Pflieger 1975). My use of annual averages across all gaged streams was a conservative approach that I feel best represented the range of study stream given the available data. Future work focusing on finer-scale modeling of streamflow dynamics and developing mechanistic linkages between hydrology, habitat, on age-0 abundance would be beneficial.

An interactive effect of residual pool depth and drainage area also explained variation in age-0 Smallmouth Bass abundance. Age-0 Smallmouth Bass are often associated with intermediate depths, but deep habitats can also contain high densities (Aadland 1993; Sabo and Orth 1994; Dauwalter et al. 2007; Fore et al. 2007) and considerable plasticity in depth use has been observed (Pert et al. 2002; Brewer 2011). My modeled relationship between depth and abundance was positive in smaller streams and negative in larger streams, and may reflect habitat limitations and some of the discrepancy observed among streams (see overview by Pert et al. 2002). Greater habitat area, whether due to deeper pools or larger streams, provides habitat heterogeneity and associated thermal variability (Arrigoni et al. 2008; Westhoff and Paukert 2014), diverse foraging opportunities (Aadland et al. 1991; Sabo et al. 1996), and refuge from disturbance, predation, and density-dependent effects (Lukas and Orth 1995; Nislow et al. 2004). Age-0 Smallmouth Bass use a range of prey types during their first growing season (Dauwalter and Fisher 2008b), and foraging rates increase in faster habitats (Simonson and Swenson 1990;

Sabo et al. 1996) where their prey is typically more common (Aadland et al. 1991). Larger streams, independent of pool depth, provide greater total riffle habitat areas that disproportionately contribute to prey production (Rabeni 1992; Zweifel et al. 1999) and Smallmouth Bass abundance (Sowa and Rabeni 1995; Brewer 2013b). Heterogeneous microhabitat conditions provide greater refuge from abiotic disturbance and can reduce nest failure and brood loss (Lukas and Orth 1995). Predator avoidance is important for diminutive fishes such as age-0 Smallmouth Bass, and risks are often greatest at depth extremes (Power 1987; Orth and Newcomb 2002). Deeper habitats may be favorable in small streams where avian predators predominate (Power et al. 1989; Harvey and Stewart 1991), while deeper habitats are less favorable in larger streams due to larger fish predators (Harvey 1991; Steinmetz et al. 2008). Density-dependent effects on age-0 Smallmouth Bass survival and growth have been documented in simulation studies (DeAngelis et al. 1991, 1993; Dong and DeAngelis 1998), though evidence for such dynamics in natural systems is lacking (Serns 1982; Orth and Newcomb 2002). However, loss of habitat area due to drying in late summer and autumn, a common feature of Ozark streams, may drive temporal variation in abundance and density-dependence for age-0 and adult Smallmouth Bass (Dauwalter and Fisher 2008a; Hafs et al. 2010).

Age-0 Smallmouth Bass survival is influenced by habitat characteristics that operate at different spatiotemporal scales, and is important for the conservation and management of these populations. Despite the inherent stochasticity in age-0 Smallmouth Bass survival due to flashy hydrology (Lukas and Orth 1995; Smith et al. 2005), Smallmouth Bass populations are behaviorally adapted to such dynamics (e.g., protracted spawning season, building nests in current refugia; Lukas and Orth 1995; Orth and Newcomb 2002). Nevertheless, juvenile rearing conditions would be improved by limiting further flow alteration and land use practices that exacerbate extreme flows and result in wider and shallower streams (e.g., deforestation, urbanization, groundwater pumping; Poff et al. 1997; Paul and Meyer 2001). Gravel-bed streams emblematic of the Ozark Highlands are frequently reorganized during high, flashy flows (Rabeni and Jacobson 1993; Leasure et al. 2016), and these geomorphic changes (e.g., bedform change, sedimentation, channel shallowing and widening) can lead to decreases in age-0 stream fish survival and abundance (Nislow et al. 2002; Harvey et al. 2009). The removal of riparian buffers and gravel mining exacerbate the geomorphic consequences of high flows (Rabeni and Jacobson 1993; Rabeni and Smale 1995; Naiman and Décamps 1997) and would be expected to negatively affect rearing habitat. Maintaining existing stream connectivity patterns is important for permitting fish movement to refuge and foraging habitats and may offset negative influences on survival in different portions of basins depending on the threat (Peterson and Rabeni 1996; Labbe and Fausch 2000). For example, many warmwater fishes use thermal refuge in the winter, as these environments provide relatively warmer conditions that benefit fish growth and survival (Langhurst and Schoenike 1990; Peterson and Rabeni 1996). These efforts will be especially important in light of changing climate that is expected to result in more extreme weather and hydrology patterns (Mulholland et al. 1997; Döll and Zhang 2010; Singh et al. 2013). My work shows how network position would be useful when examining landscape-scale approaches to stream management (Rabeni and Sowa 2002) or restoration (Roni et al. 2002; Bond and Lake 2003) though considerable efforts to acquire available resources and avoid conflicts of interest in smaller watersheds may be necessary (i.e., Lake et al. 2007).

Table 1. Predictor variables used for modeling age-0 Smallmouth Bass abundance-habitat relationships in Ozark Highland streams, along with summary statistics for *n* = 120 stream reaches and data sources. Reach-scale (~20 times wetted channel width) variables were measured in the field, segment-scale (tributary confluence to tributary confluence) variables were calculated using ArcMap 10.3.1 (ESRI, Redlands, California). I also calculated several coarse-resolution hydrologic variables to describe annual trends in streamflow patterns across the study area. The 25 variables were considered in an initial screening process to determine which variables to retain in the modeling process. I retained 10 univariate terms (bolded) and 11 two-way interactions (all combinations of Drainage area, July flow EP, Downstream link, and Stream temperature; Drainage area × Residual pool depth, Drainage area × April-July precip, Drainage area × Pool habitat, July flow EP × Soil permeability, and Stream temperature × April-July precip) following variable reduction. I scaled abundance by wetted area sampled by including the latter as a model offset.

Variable	Mean ± SD	Range	Data source
Reach scale			
Sampling date (day of year)[a]	258.4 ± 19.1	215 – 312	Field-collected
Water clarity (m)[b]	4.0 ± 1.6	1.5 – 8.7	Field-collected
Discharge ($m^3 \cdot s^{-1}$)[b]	0.46 ± 0.61	0.01 – 3.68	Field-collected
Stream temperature (°C)[a]	21.6 ± 2.7	15.1 – 27.5	Field-collected
Wetted width (m)[a]	9.9 ± 4.0	3.8 – 21.8	Field-collected
Residual pool depth (m)[a]	0.92 ± 0.40	0.20 – 2.37	Field-collected
Thalweg depth (m)[b]	0.54 ± 0.21	0.16 – 1.08	Field-collected
Pool habitat (%)[a]	73.7 ± 15.8	9.9 – 100	Field-collected
Riffle habitat (%)	9.4 ± 7.8	0.0 – 35.3	Field-collected
Wetted area sampled (m^2)	4046.5 ± 4195.7	295.2 – 28415.1	Field-collected
Segment scale			
Link magnitude	26.2 ± 34.3	1 – 215	USGS NHD[c]
Downstream link[a]	73.3 ± 127.0	4 – 694	USGS NHD[c]
Drainage area (km^2)[a]	171.8 ± 165.9	16.9 – 772.7	USGS NED[de]
Catchment slope (%)	7.33 ± 3.31	2.59 – 18.02	USGS NED[de]

Disturbance index	2.21 ± 0.32	1.48 – 2.90	NLCD 2011[df]
Impervious cover (%)	0.93 ± 0.64	0.17 – 3.64	NLCD 2011[dg]
Hydro soil group D (%)	33.04 ± 14.60	5.93 – 72.49	USDA NRCS SSURGO 2.2[dh]
Carbonate geology (%)	94.45 ± 11.07	43.76 – 100	USGS, USDA NRCS[di]
Baseflow/total flow (%)	44.58 ± 5.13	31.43 – 53.26	USEPA StreamCat[dj]
Runoff (mm)	345.8 ± 21.3	316.0 – 383.7	USEPA StreamCat[dj]
Soil permeability (cm/hour)[a]	4.08 ± 0.31	3.08 – 4.90	USEPA StreamCat[dj]
Precipitation and streamflow metrics			
April-July precip (mm)[a]	646.4 ± 179.2	417.6 – 1069.6	Oklahoma Mesonet[k]
Mean April-July flow ($m^3 \cdot s^{-1}$)[a]	8.5 ± 6.2	3.0 – 11.7	USGS NWIS[l]
Mean April flow EP (%)	3.76 ± 3.06	0.04 – 6.43	USGS NWIS[l]
Mean May flow EP (%)	2.90 ± 2.93	0.32 – 6.23	USGS NWIS[l]
Mean June flow EP (%)	14.13 ± 9.00	0.84 – 23.86	USGS NWIS[l]
Mean July flow EP (%)[a]	13.43 ± 7.75	0.34 – 21.79	USGS NWIS[l]
Mean flood frequency	3.32 ± 1.33	1.82 – 4.73	USGS NWIS[l]
Mean flood duration (d)	17.13 ± 10.93	5.27 – 33.00	USGS NWIS[l]

a: Predictors (*n* = 11) used in evaluation of model distribution.

b: Ancillary variables (*n* = 3) not considered in analyses.

c: http://nhd.usgs.gov/

d: Variables summarized for the entire catchment at the downstream end of every stream segment.

e: http://ned.usgs.gov/

f: Homer et al. 2015, https://www.mrlc.gov/nlcd11_data.php

g: Xian et al. 2011, https://www.mrlc.gov/nlcd11_data.php

h: NRCS 2017, https://websoilsurvey.sc.egov.usda.gov

i: Stoeser et al. 2005, https://datagateway.nrcs.usda.gov/

j: Hill et al. 2016, https://www.epa.gov/national-aquatic-resource-surveys/streamcat

k: https://www.mesonet.org/

l: https://nwis.waterdata.usgs.gov/nwis/sw

Table 2. Coefficient estimates and 95% confidence intervals (CI) from the top-ranked candidate model of age-0 Neosho Smallmouth Bass abundance in Ozark streams. Conditional (abundance) model coefficients are on the natural-log scale and reflect unit increments of one standard deviation and mean levels of all other continuous predictors. Zero-inflation coefficients are on a logit scale. Warm streams (> 19.5 °C) are the reference condition for water temperature. EP is exceedance probability, D-link is downstream link, and pool depth is residual pool depth.

	Coefficient ± SE	95% CI
Conditional model		
Intercept	-4.03 ± 0.09	-4.21, -3.85
July flow EP x D-link	-0.22 ± 0.08	-0.38, -0.06
Drainage area x Pool depth	-0.41 ± 0.10	-0.59, -0.22
Stream temperature x D-link	0.56 ± 0.30	-0.03, 1.16
July flow EP	0.54 ± 0.08	0.38, 0.70
Drainage area	0.24 ± 0.12	0.01, 0.47
Stream temperature	-1.18 ± 0.41	-1.98, -0.38
Downstream link	0.04 ± 0.10	-0.15, 0.24
Pool depth	-0.01 ± 0.09	-0.20, 0.17
Zero-inflation model		
Intercept	-2.45 ± 0.44	-3.31, -1.58
Stream temperature	1.57 ± 0.90	-0.19, 3.34

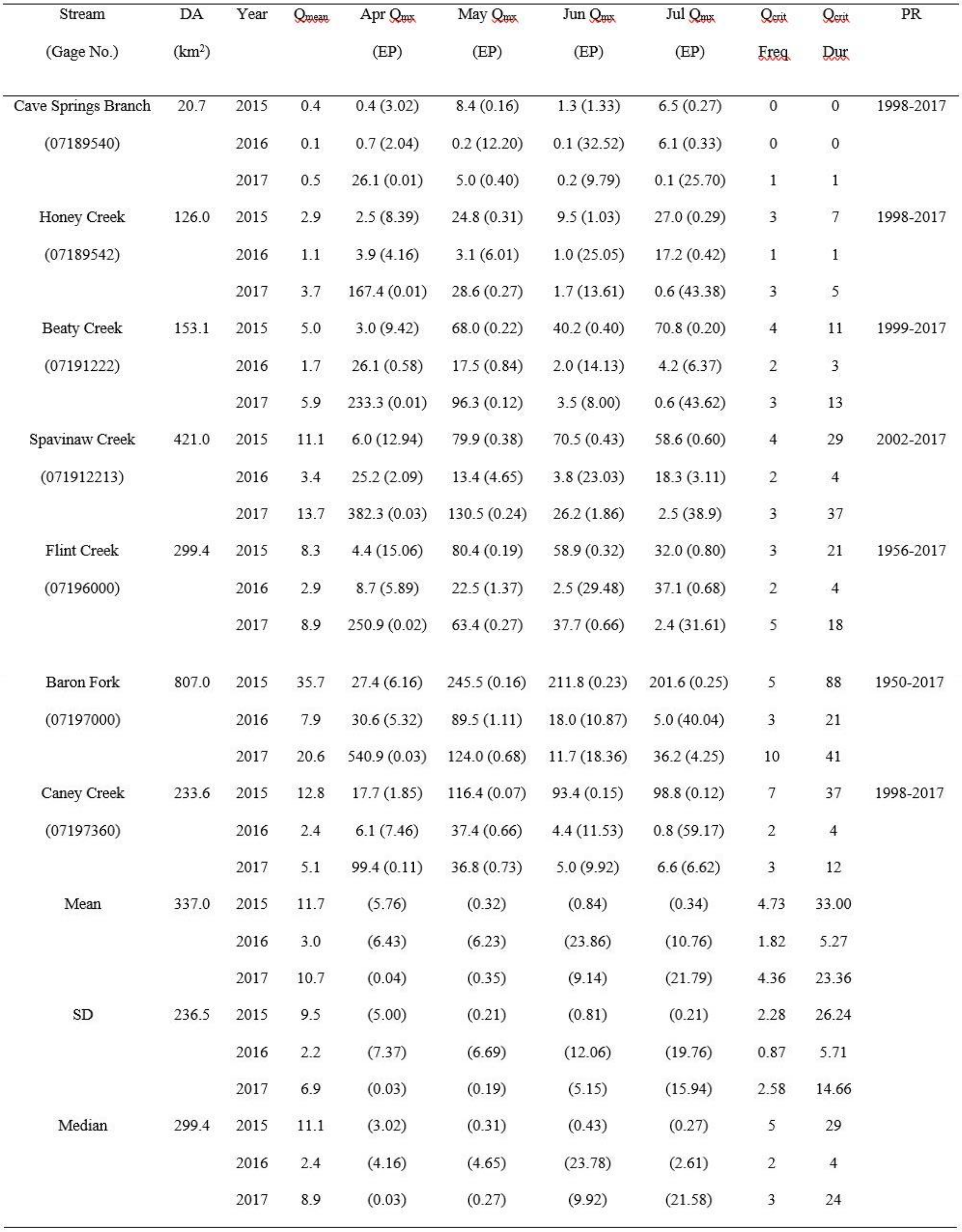
Table S1. Land cover types from 2011 National Land Cover Dataset (Homer et al. 2015, https://www.mrlc.gov/nlcd2011.php) and associated disturbance coefficients for calculating disturbance index, where greater coefficients indicate a greater degree of disturbance. Barren land was uncommon in my study region, but was typically associated with mining activities (Smart et al. 1981).

Land cover type	NLCD Class	Coefficient
Open water	11	1.00
Perennial ice/snow	12	1.00
Developed, open space	21	1.83
Developed, low intensity	22	6.90
Developed, medium intensity	23	7.64
Developed, high intensity	24	7.92
Barren land (rock/sand/clay)	31	8.32
Deciduous forest	41	1.00
Evergreen forest	42	1.00
Mixed forest	43	1.00
Shrub/scrub	52	1.00
Grassland/herbaceous	71	1.00
Pasture/hay	81	2.99
Cultivated crops	82	4.54
Woody wetlands	90	1.00
Emergent herbaceous wetlands	95	1.00

Table S2. Characteristics and hydrology statistics for 11 stream gages (U.S. Geological Survey, gage numbers provided below each stream name) used to describe annual hydrology patterns during the nesting and early growing period for Smallmouth Bass (April-July) in 2015-2017. DA is drainage area, Q_{mn} is mean April-July discharge ($m^3 \cdot s^{-1}$), Q_{mx} is maximum monthly discharge ($m^3 \cdot s^{-1}$), and EP is annual exceedance probability for Q_{mx} during the period of record. I also summarize the overall frequency (Freq) and duration (Dur) of flow events during the study period with a mean daily discharge capable of causing nest failure and limiting nesting behavior, Q_{cr}, assumed to be 10 $m^3 \cdot s^{-1}$ (Lukas and Orth 1995; A. D. Miller and S. K. Brewer, unpublished data). Period of record (PR) gives the water years of record used in calculations of exceedance probability. All data downloaded from https://nwis.waterdata.usgs.gov/nwis/sw. (April 2018).

Stream (Gage No.)	DA (km^2)	Year	Q_{mean}	Apr Q_{mx} (EP)	May Q_{mx} (EP)	Jun Q_{mx} (EP)	Jul Q_{mx} (EP)	Q_{crit} Freq	Q_{crit} Dur	PR
Buffalo Creek	157.5	2015	7.9	22.8 (1.34)	58.3 (0.32)	14.5 (2.53)	98.3 (0.17)	5	23	2001-2017
(07189100)		2016	1.9	35.1 (0.75)	17.6 (1.97)	4.8 (8.73)	10.9 (3.66)	2	4	
		2017	7.9	140.7 (0.08)	75.0 (0.27)	4.2 (9.98)	2.8 (15.58)	5	24	
Big Sugar Creek	365.2	2015	12.2	29.2 (1.43)	61.4 (0.63)	145.0 (0.23)	105.1 (0.35)	6	30	2001-2017
(07188653)		2016	2.3	3.1 (26.11)	3.6 (21.72)	1.6 (47.46)	40.2 (0.92)	1	2	
		2017	14.5	368.1 (0.05)	116.9 (0.27)	11.4 (4.86)	14.5 (3.62)	7	33	
Little Sugar Creek	505.0	2015	15.4	43.9 (1.52)	73.9 (0.80)	99.1 (0.55)	97.7 (0.57)	8	55	2005-2017
(07188838)		2016	4.6	9.2 (12.47)	9.2 (12.62)	5.6 (23.78)	26.9 (2.61)	3	7	
		2017	16.7	393.6 (0.06)	169.6 (0.36)	9.4 (12.02)	17.5 (4.80)	6	29	
Indian Creek	619.0	2015	17.1	30.3 (2.27)	135.1 (0.32)	32.3 (2.04)	257.7 (0.16)	7	62	2001-2017
(07188885)		2016	5.0	22.3 (3.85)	18.0 (5.41)	4.1 (35.85)	49.0 (1.01)	2	8	
		2017	20.4	492.7 (0.02)	166.5 (0.27)	10.7 (11.47)	6.6 (21.58)	2	44	

Table S2. Continued.



Stream (Gage No.)	DA (km^2)	Year	Q_{mean}	Apr Q_{mx} (EP)	May Q_{mx} (EP)	Jun Q_{mx} (EP)	Jul Q_{mx} (EP)	Q_{crit} Freq	Q_{crit} Dur	PR
Cave Springs Branch	20.7	2015	0.4	0.4 (3.02)	8.4 (0.16)	1.3 (1.33)	6.5 (0.27)	0	0	1998-2017
(07189540)		2016	0.1	0.7 (2.04)	0.2 (12.20)	0.1 (32.52)	6.1 (0.33)	0	0	
		2017	0.5	26.1 (0.01)	5.0 (0.40)	0.2 (9.79)	0.1 (25.70)	1	1	
Honey Creek	126.0	2015	2.9	2.5 (8.39)	24.8 (0.31)	9.5 (1.03)	27.0 (0.29)	3	7	1998-2017
(07189542)		2016	1.1	3.9 (4.16)	3.1 (6.01)	1.0 (25.05)	17.2 (0.42)	1	1	
		2017	3.7	167.4 (0.01)	28.6 (0.27)	1.7 (13.61)	0.6 (43.38)	3	5	
Beaty Creek	153.1	2015	5.0	3.0 (9.42)	68.0 (0.22)	40.2 (0.40)	70.8 (0.20)	4	11	1999-2017
(07191222)		2016	1.7	26.1 (0.58)	17.5 (0.84)	2.0 (14.13)	4.2 (6.37)	2	3	
		2017	5.9	233.3 (0.01)	96.3 (0.12)	3.5 (8.00)	0.6 (43.62)	3	13	
Spavinaw Creek	421.0	2015	11.1	6.0 (12.94)	79.9 (0.38)	70.5 (0.43)	58.6 (0.60)	4	29	2002-2017
(071912213)		2016	3.4	25.2 (2.09)	13.4 (4.65)	3.8 (23.03)	18.3 (3.11)	2	4	
		2017	13.7	382.3 (0.03)	130.5 (0.24)	26.2 (1.86)	2.5 (38.9)	3	37	
Flint Creek	299.4	2015	8.3	4.4 (15.06)	80.4 (0.19)	58.9 (0.32)	32.0 (0.80)	3	21	1956-2017
(07196000)		2016	2.9	8.7 (5.89)	22.5 (1.37)	2.5 (29.48)	37.1 (0.68)	2	4	
		2017	8.9	250.9 (0.02)	63.4 (0.27)	37.7 (0.66)	2.4 (31.61)	5	18	
Baron Fork	807.0	2015	35.7	27.4 (6.16)	245.5 (0.16)	211.8 (0.23)	201.6 (0.25)	5	88	1950-2017
(07197000)		2016	7.9	30.6 (5.32)	89.5 (1.11)	18.0 (10.87)	5.0 (40.04)	3	21	
		2017	20.6	540.9 (0.03)	124.0 (0.68)	11.7 (18.36)	36.2 (4.25)	10	41	
Caney Creek	233.6	2015	12.8	17.7 (1.85)	116.4 (0.07)	93.4 (0.15)	98.8 (0.12)	7	37	1998-2017
(07197360)		2016	2.4	6.1 (7.46)	37.4 (0.66)	4.4 (11.53)	0.8 (59.17)	2	4	
		2017	5.1	99.4 (0.11)	36.8 (0.73)	5.0 (9.92)	6.6 (6.62)	3	12	
Mean	337.0	2015	11.7	(5.76)	(0.32)	(0.84)	(0.34)	4.73	33.00	
		2016	3.0	(6.43)	(6.23)	(23.86)	(10.76)	1.82	5.27	
		2017	10.7	(0.04)	(0.35)	(9.14)	(21.79)	4.36	23.36	
SD	236.5	2015	9.5	(5.00)	(0.21)	(0.81)	(0.21)	2.28	26.24	
		2016	2.2	(7.37)	(6.69)	(12.06)	(19.76)	0.87	5.71	
		2017	6.9	(0.03)	(0.19)	(5.15)	(15.94)	2.58	14.66	
Median	299.4	2015	11.1	(3.02)	(0.31)	(0.43)	(0.27)	5	29	
		2016	2.4	(4.16)	(4.65)	(23.78)	(2.61)	2	4	
		2017	8.9	(0.03)	(0.27)	(9.92)	(21.58)	3	24	

Table S3. Oklahoma Mesonet monthly precipitation data during the study period. Data accessed from https://www.mesonet.org/index.php/weather/station_monthly_summaries. (April 2018).

Station	Year	April (mm)	May (mm)	June (mm)	July (mm)	Total (mm)
Miami	2015	95.3	328.9	124.0	145.0	693.2
	2016	155.2	142.2	66.0	138.2	501.7
	2017	277.1	223.6[a]	124.2	86.6	711.5
Jay	2015	83.1	297.4	80.8	207.8	669.0
	2016	131.6	114.6	51.3	180.8	478.3
	2017	320.3	219.7	98.6	108.5	747.0
Westville	2015	95.8	329.4	190.8	231.5	847.9
	2016	106.9	127.5	10.7	172.5	417.6
	2017	362.7	160.0	136.4	78.5	737.6
Tahlequah	2015	96.5	458.2	202.9	311.9	1069.6
	2016	126.5	128.0	85.3	101.9	441.7
	2017	395.2	136.9	200.7	83.3	816.1

a: Average of values for Jay and Vinita stations, due to incomplete record at Miami station.

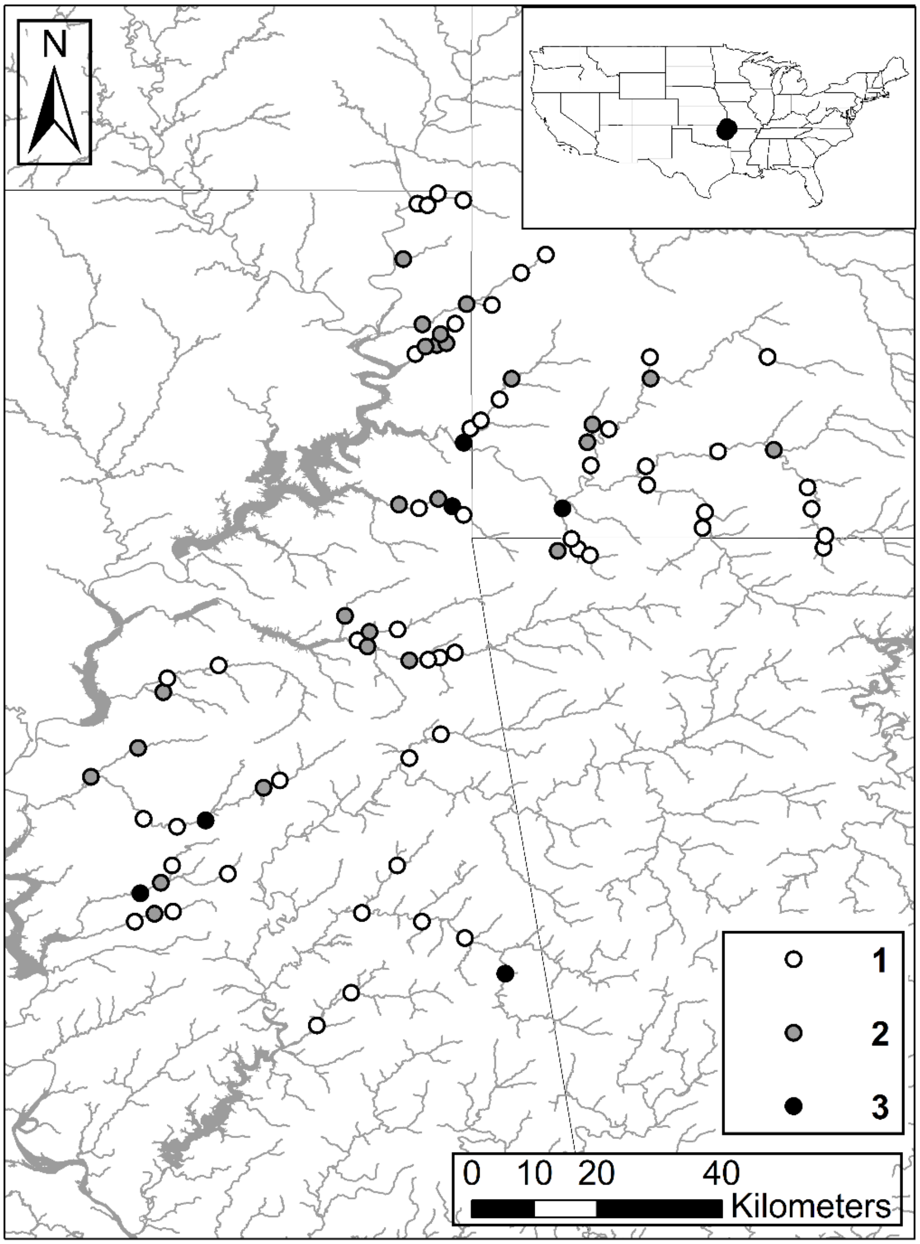


Figure 1. Location of stream reaches surveyed for age-0 Smallmouth Bass. The open or shaded circles represent the number of years a reach was sampled (from 2015-2017). I did not sample reaches twice within a given year, and reaches sampled in different years were treated as unique sites.

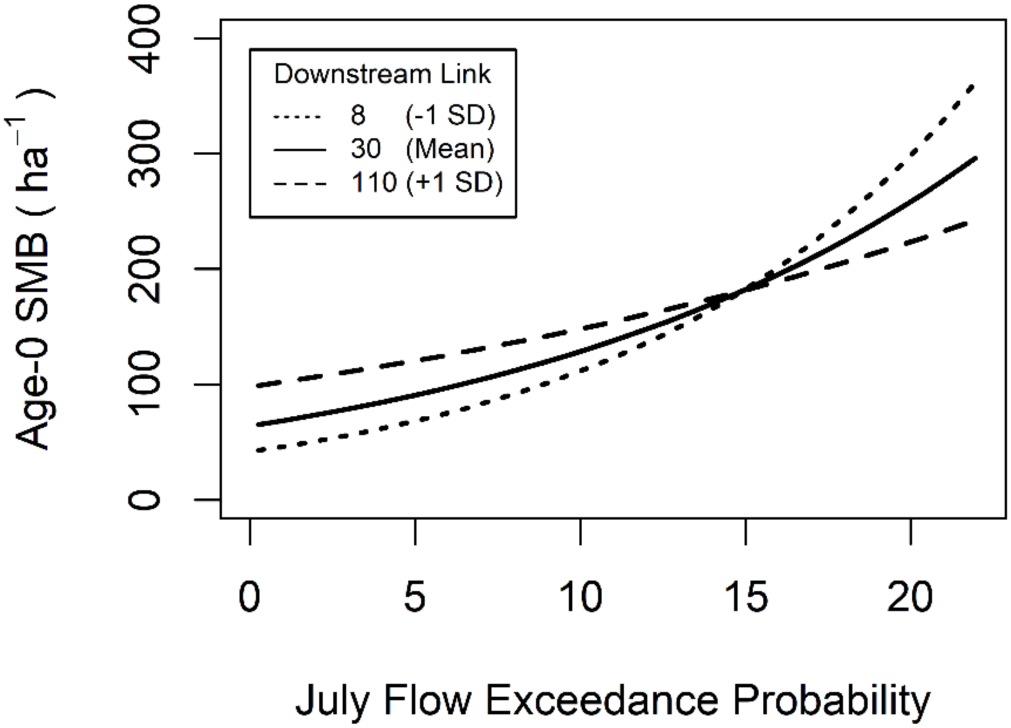


Figure 2. Model-predicted relationship between July flow exceedance probability and age-0 Smallmouth Bass abundance in stream reaches with varying downstream link magnitudes. Modeled relationships are at mean values of other continuous predictors and at the reference stream temperature (i.e., warm; > 19.5 °C).

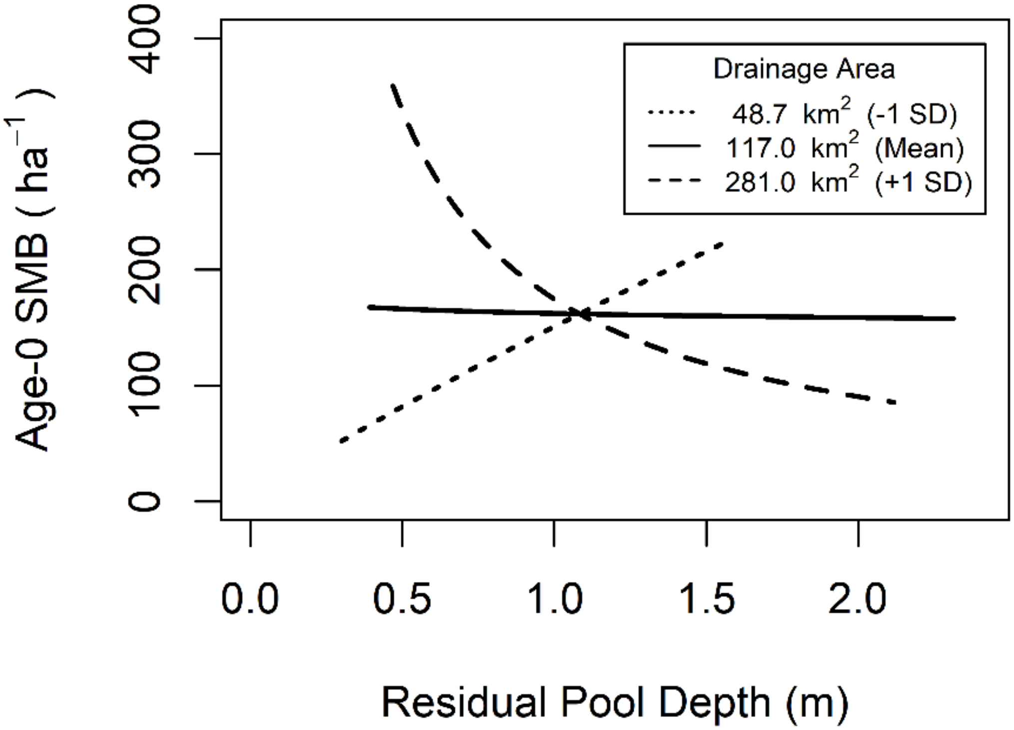


Figure 3. Model-predicted effect of residual pool depth (m) on age-0 Smallmouth Bass abundance across three representative stream sizes (drainage areas [km^2]). Predictions are only included for combinations of residual pool depth and drainage area that co-occur in the dataset. Relationships are modeled with other continuous predictors held at mean levels and for the reference stream temperature (i.e., warm; > 19.5 °C).

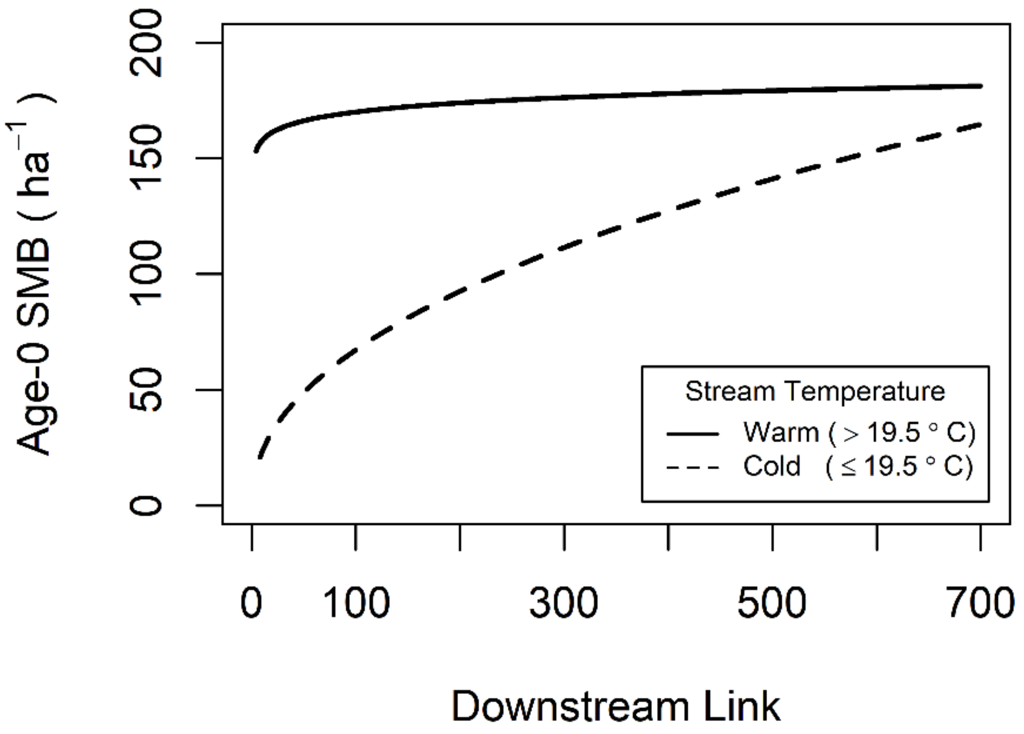


Figure 4. Relationship between downstream link magnitude and age-0 Smallmouth Bass abundance in relation to stream temperature based on my top model. Stream temperature consists of two levels, cold (≤ 19.5 °C) and warm (> 19.5 °C), based on a natural break in my data.

CHAPTER VI

MOVEMENT AND DIEL HABITAT USE OF JUVENILE NEOSHO SMALLMOUTH BASS IN AN OZARK STREAM

ABSTRACT

Movement and habitat-use patterns of juvenile Smallmouth Bass Micropterus dolomieu in streams are poorly understood, particularly near the end of the first growing season and across the diel cycle. My study objectives were to quantify movement and diel habitat use of juvenile Smallmouth Bass and to determine how they are influenced by water temperature, fish size, and time of day. I surgically implanted radio transmitters in 13 juvenile Smallmouth Bass in Honey Creek, Oklahoma, during autumn 2016. I tracked fish using radio telemetry on 41 occasions over the 26-day tag life, and located fish throughout the diel cycle to characterize movement patterns and habitat use. Movement patterns varied among individual fish, with average daily movements ranging from 7 m to 52 m. Incremental movement magnitude was slightly greater at warmer water temperatures and for larger fish. There was considerable individual variation in habitat-use patterns throughout the diel cycle. Tagged fish used deeper habitats diurnally, and depth use also increased with fish size. Greater velocities were used during the day and later in the study. Tagged fish were typically situated several meters from the channel edge in pool and slackwater habitats, with some use of run habitats during the day. My results suggest that considerable variation in movement and habitat use exists among individual fish and that some aspects of habitat use vary across the diel cycle. This study demonstrates the feasibility of using radio-

telemetry to assess the movement and habitat use patterns of small-bodied warmwater stream fish.

INTRODUCTION

The early ontogeny of stream fishes is a time of heightened vulnerability to abiotic and biotic stressors. Environmental conditions that fluctuate naturally (e.g., temperature and discharge) can facilitate or compromise juvenile fish survival (Knotek and Orth 1998; Smith et al. 2005), and may influence population persistence (Brewer and Rabeni 2011). Juveniles may also be limited by food availability during critical developmental periods, reducing individual survival and thus, year-class strength (Hjort 1914; Blaxter and Hempel 1963). Additionally, eggs, larvae, and juveniles are vulnerable to a variety of predators (Dahlberg 1979; Johnson and Ringler 1981). This suite of abiotic and biotic factors generally results in a rapid decline in age-0 fish abundance after hatching, before abundances stabilize (Brewer et al. 2019). How individuals respond to these challenges, including differences in movement or use of refuge habitats, may help explain variation in year-class strength across streams.

Stream fishes display a wide range of inter- and intra-specific movement behaviors in response to physicochemical and biotic stimuli. Differences in movement are well documented among fishes (Matthews 1998), ranging from highly migratory salmonids (Quinn 2005) to relatively restricted movement in many benthic species (Scalet 1973; Petty and Grossman 2004; Hicks and Servos 2017). Several studies have reported individual differences in the movement patterns of stream fishes (Mollenhauer et al. 2013; Ettinger-Dietzel et al. 2016), and the presence of ‘stationary’ and ‘mobile’ subsets within fish populations (Fraser et al. 2001; Rodríguez 2002; Booth et al. 2013). Moreover, movement patterns within a species can change with ontogeny (Young 2011). Movements of juvenile stream fishes may be influenced by water temperature (Bjornn 1971; Dugdale et al. 2016), discharge (Irvine 1986; Boavida et al. 2017), the availability of shelter (Bjornn 1971; Simpkins et al. 2000; Larranaga and Steingrímsson 2015), food availability (Junk et al. 1989, Winemiller and Jepsen 1998), and predator avoidance (Schlosser 1987). For example, juvenile Coho Salmon *Oncorhynchus kisutch* display diel longitudinal movements ranging from 350-1,300 m to exploit heterogeneity in both temperature and prey availability, thereby maximizing energy assimilation (Armstrong et al. 2013).

Plastic habitat use is common among stream fishes (e.g., Fore et al. 2007; Brewer and Rabeni 2008) and relates to predator avoidance, feeding habits, refuge use, habitat partitioning, and inherent individual variability (Moyle and Vondracek 1985; Schlosser 1987; Salas and Snyder 2010; Giller and Greenberg 2015). For example, some salmonids and cyprinids use deeper habitats at night (Banish et al. 2008; Salas and Snyder 2010), but shallower habitats with cover during the day to avoid diurnal predators such as wading birds and sight-feeding fishes (Grossman and Freeman 1987; Kadye and Booth 2014). Ontogenetic shifts in habitat use may correspond to changing foraging strategies (Mittelbach and Persson 1998) and the spatial distribution of prey. Refuge habitats are commonly used by juvenile fish in response to changes in flow (Armstrong et al. 1998; Magoulick and Kobza 2003; Schwartz and Herricks 2005) and temperature (Fraser et al. 1995; Brewitt and Danner 2014). Plastic habitat use drives both intra- and inter-specific habitat partitioning (Armstrong and Griffiths 2001; Salas and Snyder 2010). Individual variation in habitat use has been reported for several salmonid species, wherein environmental stimuli, such as reduced streamflow and changes in prey availability, do not appear to elicit fixed responses among individuals (Armstrong et al. 1998; Giller and Greenberg 2015).

Smallmouth Bass *Micropterus dolomieu* is an ecologically and recreationally important component of many warm-water streams in North America and comprises several genetically-distinct populations (Brewer and Orth 2015). Smallmouth Bass plays a critical role in aquatic food webs, acting as a top predator and often conferring top-down effects (Power et al. 1985;

Vander Zanden et al. 1999; MacRae and Jackson 2001). Smallmouth Bass is also a common target of recreational anglers, and are known for strong fighting ability relative to body size (Henshall 1881). The Neosho subspecies *M. d. velox* (hereafter referred to as Neosho Smallmouth Bass) is one of three genetically-distinct clades (Stark and Echelle 1998) and is endemic to the southwest Ozark Highlands at the southwest extent of the native range of Smallmouth Bass (Brewer and Long 2015).

Juvenile Smallmouth Bass exhibit a variety of movement and habitat-use patterns in rivers across their range, though little is known about fine-scale movements or nocturnal trends. In one riverine population, approximately 50% of age-1 Smallmouth Bass captured in the main stem of the James River, Virginia were spawned in an upstream tributary the year before, but there was no evidence of reciprocal movements (Humston et al. 2010). Juvenile Smallmouth Bass habitat use is described as plastic, varying spatially and with ontogeny, but is limited to diurnal observations (Pert et al. 2002). Studies of microhabitat use by age-0 Smallmouth Bass indicate typical use of low-velocity areas (Fore et al. 2007; Brewer 2011) and cover (Olson et al. 2003; Brown and Bozek 2010), with deeper water used in smaller streams (Brewer 2011). My study objectives were to 1) describe general movement and diel habitat-use patterns of juvenile Smallmouth Bass and 2) identify relationships between juvenile Smallmouth Bass movement and habitat use and both environmental and individual fish characteristics. As Smallmouth Bass fisheries are characterized by substantial spatiotemporal variation in recruitment (Pflieger 1975; Paragamian 1984; Smith et al. 2005), this work could allow for the development of management actions that benefit juvenile recruitment.

METHODS

Study area

I radio tracked juvenile Smallmouth Bass over a 1.5-km reach of Honey Creek in Oklahoma. The Smallmouth Bass population in Honey Creek predominately comprises the pure Neosho subspecies (Taylor et al. 2018). Honey Creek is a third-order stream (mean annual discharge = 1.16 m^3/s, U.S. Geological Survey [USGS] stream gauge 07189542), draining a 174.5-km^2 catchment of the Ozark Highlands ecoregion (Figure 1). The Ozark Highlands ecoregion covers the majority of the Neosho Smallmouth Bass range (Brewer and Long 2015), and is characterized by cherty limestone and karst topography (Nigh and Schroeder 2002). The study reach was located 3.0 km upstream of the interface with Grand Lake O' the Cherokees (Figure 1). The wetted channel within my study reach was 5–21 m wide, mean thalweg depth was 0.50 m, water clarity was excellent (~3.0 m), and the substrates were primarily gravel and cobble with occasional bedrock outcroppings.

Stream discharge and temperature data were collected throughout the study period. Discharge (USGS stream gauge 07189542) was relatively low and varied little during my study, ranging from 0.29–0.57 m^3/s (mean = 0.35 m^3/s; SD = 0.04). This range of discharge values exceeded the long-term median (20 years, 0.45 m^3/s) for the study period on only two occasions of < 24-h duration (Figure 2). Water temperatures (HOBO Pro v2; Onset, Bourne, Massachusetts) in Honey Creek ranged from 11.9–23.0 °C (mean = 17.9 °C; SD = 2.1) and showed a slow and expected seasonal decline across the study period.

Fish sampling and tagging

I captured and radio-tagged 13 juvenile Smallmouth Bass ranging from 79 to 106 mm (mean = 89.8 mm; SD = 8.7) total length (TL) and from 5.7 to 14.0 g (mean = 8.6 g; SD = 2.6) to characterize movement and habitat use (Table 1). Individuals in this size range are typically age-0 or age-1 (Balkenbush and Fisher 1999; Brewer 2011; Brewer and Long 2015). I captured juvenile Smallmouth Bass using both seining and tow-barge electrofishing (Stealth Mini-Boat; Midwest

Lake Management, Polo, Missouri) on October 15–17, 2016. Fish were anesthetized in a 2-L bath of Aqui-S® 20E at a concentration of 30 mg/L until loss of equilibrium (typically 2-4 min), then weighed (0.1 g) and measured (TL; 1.0 mm). I then moved fish to a shallow tub containing low-dose anesthetic (15 mg/L) and held them ventral-side-up as I surgically implanted NanoTag NTQ-1 radio transmitters (5 x 3 x 10 mm, 0.26 g in air, 33-d lifespan, Lotek Wireless, Newmarket, Ontario) into the body cavity (Liedtke et al. 2012). I used the shielded-needle technique to create an exit for the trailing antenna (Ross and Kleiner 1982). The incision was closed with a pair of simple interrupted sutures (Adams et al. 2012) using absorbable material (Unify® PGA; AD Surgical, Sunnyvale, California) and the antenna was trimmed (40–64 mm, depending on fish length) to reduce fouling (Brown et al. 1999). The tag burden of marked fish ranged from 1.9–4.6% (mean = 3.4%; SD = 0.9). Following surgery, fish were moved to a flow-through chamber in a shaded region of the creek and held for 24 h to assess respiration and swimming behavior. Upon recovery, I released each juvenile Smallmouth Bass near its point of capture (i.e., same channel unit).

Movement and habitat use

I tracked the tagged juvenile Smallmouth Bass on multiple occasions during four 6-h blocks that encompassed the diel cycle during autumn 2016 (October 19–November 13). The time blocks were 0100–0659, 0700–1259, 1300–1859, and 1900–1259 hours. I surveyed my stream reach at least twice weekly during each time block, on haphazardly-selected days, with each block surveyed 9-12 times over the 26-d study period. While tracking, I walked the bank in a downstream direction and relocated fish using an SRX 800 VHF receiver (Lotek Wireless) and 3-element Yagi antenna. I tracked from the bank until I determined the channel unit occupied by my tagged fish. I categorized channel units as riffle, run, pool, or slackwater based on gradient, depth, velocity, and substrate using a simplified version of the hydraulic classification developed by Rabeni and Jacobson (1993). Though slackwaters are considered a sub-type of pool by Rabeni and Jacobson (1993), I distinguished slackwater habitats by their off-channel location (e.g., backwaters, forewaters) and differences in substrate (e.g., silt). After the occupied channel unit was identified, I carefully entered the water to identify the location of the fish within the channel unit. I used homing (Hafs et al. 2010; Koehn et al. 2012; Westhoff et al. 2016) while slowly and quietly approaching the fish to assign located individuals to a ~ 6-m^2 habitat patch. In the event fish were not located within my 1.5-km tracking reach (three occasions), I searched up to approximately 300 m beyond the regular upstream and downstream tracking extents. Fish locations were recorded using a handheld GPS unit. I conducted 'hide and seek' trials (Koehn et al. 2012) using dummy tags, which indicated my location accuracy was within 1 m, but I maintained my ~ 6-m^2 resolution to avoid scaring fish during the tracking process. On six occasions, I visually confirmed the locations of the tracked fish.

I characterized habitat patches occupied by tagged Smallmouth Bass using depth, velocity, cover, substrate, and distance to the nearest bank. After locating the fish via homing, I placed a 6-m^2 grid at each fish relocation and divided the grid into six 1-m^2 cells in a 2-m long x 3-m wide pattern. I averaged water depth (±0.01 m) and water-column velocity (±0.01 m/s) across the six grid cells. Velocity was measured at 60% of depth using an electromagnetic flow meter (Marsh-McBirney Model 2000; Hach Flow, Loveland, Colorado). I also estimated the proportional coverage of both instream wood (diameter > 1 cm; Stevenson and Bain 1999) and vegetation (emergent and submerged). I estimated median substrate size (D_{50}) at each habitat patch using pebble counts (Gordon et al. 2004), wherein I measured the intermediate diameters (±1.0 mm) of 60 total particles collected equally across all grid cells. Lastly, I measured the distance from the center of the grid to the nearest bank (±0.5 m) to estimate space use within each occupied channel unit.

I used my fish movement data to calculate three metrics of displacement to assess relationships with water temperature and fish size. I imported fish locations into ArcMap 10.3.1

(ESRI, Redlands, California), and I measured the distance (±1 m) along the stream between relocations using the Locate Features Along Routes tool. I quantified movement three ways. First, incremental displacement was calculated as the distance moved between two consecutive relocations regardless of the time elapsed between them. Second, I summed incremental movements for each fish and scaled by the number of days over which each individual was relocated to calculate mean daily displacement. Third, net displacement was the difference between the maximum upstream and downstream positions of a fish relative to its initial release point, where positive values represent overall upstream-movement patterns and negative values denote downstream patterns. I modeled incremental movement magnitude in relation to water temperature and fish size, and summarized mean daily and net movements for each tagged fish.

Movement analysis

I evaluated the relationship between water temperature, fish length and the magnitude and direction of juvenile Smallmouth Bass movement using a model-selection approach. Residuals displayed a normal distribution and error variance was homoscedastic. I created a candidate set of four linear mixed models (LMM) to examine the relationship between incremental movement magnitude (response variable), water temperature, and fish TL (Table 2). Water temperature was averaged over the period between consecutive relocations for each individual. Stream discharge was not included as a predictor due to its lack of variation during the study period. All models included a random individual fish effect to account for unequal sample sizes, unexplained variability among individuals, and the lack of independence among observations on the same fish (Otis and White 1999; Wagner et al. 2006). The random effects were assumed normally distributed as $N(0, \tau^2)$, where τ^2 is the population variance among levels of a random effect (i.e., among individual fish). Both water temperature and fish size were standardized (mean = 0, SD = 1) to simplify interpretation of model coefficients. I selected the top-ranked model for movement using Akaike's information criterion adjusted for small sample size (AIC_c; Sugiura 1978). I calculated R^2 as described by Nakagawa and Schielzeth (2013) to assess the amount of variance explained by my top-ranked models by both fixed and random effects. The marginal R^2 represents the amount of variance explained by the fixed effects, whereas the conditional R^2 quantifies the amount of variance explained by both fixed and random effects (Vonesh et al. 1996). I used model averaging for all models with $\Delta\mathrm{AIC}_c < 2$ to calculate unconditional coefficients and standard errors, and relative variable importance (RVI) values. In model averaging, parameter estimates are calculated using a weighted average of the models based on relative model support (e.g., AIC_c; Burnham and Anderson 2002; Johnson and Omland 2004). In cases of model selection uncertainty, model averaging provides more robust estimates of fixed effects that account for uncertainty in the top models (Johnson and Omland 2004; Bolker et al. 2009). I report unconditional model-averaged estimates, which account for the number of models in the averaged set that lack a given predictor and thereby penalize variables with weak relationships (Grueber et al. 2011; Bartoń 2018). The RVI of an explanatory variable is the sum of the Akaike weights for all models in the averaged set that include that variable (Burnham and Anderson 2002; Bartoń 2018).

Habitat use analysis

Initially, I visually assessed the habitat-use data (i.e., notched boxplots) across different time blocks to identify diel differences in habitat use by tagged juvenile Smallmouth Bass. With notched boxplots, notch width approximates a 95% confidence interval (CI) for each median, and the lack of notch overlap between two distributions suggests that medians are different (Chambers et al. 1983). There was very little variation in use of cover or distance to bank (Figure 3). Preliminary assessments suggested diel differences in both depth and velocity use (Figure 3) and weak correlation ($r = 0.02$) between these two variables, so I evaluated these patterns further using a model-selection approach.

I used a model-selection approach to determine the predictor variables that explained diel shifts in depth and velocity use by tagged juvenile Smallmouth Bass. Plots indicated that residuals were normally distributed with constant variance. I developed 16 candidate LMMs where depth and velocity were response variables in eight models each (Table 3). I added 0.001 to my velocity data to accommodate a natural log-transformation to reduce skewness. Each candidate model set included all possible combinations of the predictor variables date, time, and fish length. Date was day of the study (1–26), time was a binary variable that reflected tracking time (0 = night: 1900–0659 hours, 1 = day: 0700–1859 hours), and fish length was TL of the tagged fish. I also included a random individual fish effect in all of the models, with the same distributional assumptions, for the reasons described in the above movement modeling section. I standardized both date and fish length (mean = 0, SD = 1) and selected the top-ranked model for each response variable using AIC_c (Sugiura 1978). To describe the amount of variation explained by each model, I calculated marginal and conditional R^2 (Vonesh et al. 1996; Nakagawa and Schielzeth 2013). I calculated unconditional coefficients and standard errors, and RVI using model-averaging of all models with $\Delta AIC_c < 2$. All analyses were performed in R version 3.4.2 (R Core Team 2017) using the 'lme4' (Bates et al. 2015) and 'AICcmodavg' (Mazerolle 2017), and 'MuMIn' (Bartoń 2018) packages.

RESULTS

Fish tracking

I used tracking data from twelve juvenile Smallmouth Bass in my analyses. Seven of these fish were tracked throughout the 26-d duration of the study. Of the remaining five individuals, I tracked two fish for approximately 75% of the study, one fish for 50% of the study, and two fish for nearly 25% of the study (Table 1). One fish was lost via predation within the first 36 h of the study and therefore, could not be included in my analyses.

Movement

I observed substantial individual variation in fish movement distance and direction (Table 1). Incremental movements ranged from 0–297 m (mean = 20 m; SD = 33). After accounting for differences in the period of time individual fish were tracked, mean daily movements ranged from 7–52 m (mean = 27 m; SD = 15). Net movements by tagged Smallmouth Bass ranged from 12–1,046 m (mean = 277 m; SD = 317). Four tagged fish moved a net minimum of 400-m longitudinally, whereas five fish moved < 100 m. The three remaining individuals moved a net distance ranging from 100–400 m. Seven fish (58%) displayed greater net movement in the upstream direction, whereas five fish (42%) had downstream movement tendencies.

The modeled relationship between juvenile Smallmouth Bass movement patterns, water temperature, and individual fish length suggests that movement magnitude is marginally related to both water temperature and fish size. Incremental displacement had a weak ($R^2 = 0.04$) but positive relationship with both fish size and water temperature, and the inclusion of the random individual fish effect improved the variability explained ($R^2 = 0.11$). As there was similar support for the top three models of movement (i.e., $\Delta AIC_c < 2$, Table 2), I used model averaging to generate coefficient and standard errors for these effects (Table 4). Modeled incremental movements increased an average of 1.3 m for each 1.0 °C increase in temperature. Incremental movements also increased by an average of 1.1 m for each 1.0 mm increase in fish TL. Water temperature and fish size each occurred in two of the three averaged models, and had RVIs of 0.77 and 0.72, respectively.

Habitat use

I observed some diel variation in channel unit use by my tagged fish, though patterns of cover, substrate, and spatial proximity within the channel varied minimally (Figure 3). Tagged fish used low-velocity pool (66% of all observations) and slackwater (16%) habitats consistently throughout the diel period. They also used run habitats 15% of the time overall, but use of these habitats was greater during the day (22%) than at night (8%). The percentage of relocated fish using cover was not related to time of day, and the percent of cover in each occupied patch was generally low (wood: mean = 2.4%; SD = 7.4; vegetation: mean = 3.1%; SD = 11.9). The substrate size (D_{50}) of occupied patches was most frequently pebble (> 16-64 mm, 43%) or bedrock (> 4000 mm, 32%). Tagged fish maintained similar positions in the channel relative to the streambank throughout the diel period (mean = 3.4 m; SD = 1.8).

I found fish use of both depth and velocity was related to diel and seasonal period, and reflected fish size. The top two depth-use models had similar model support, and included the observation-level variables time and date and the individual-level variable fish size (Table 3). These relationships explained a limited amount of variation in my data ($R^2 = 0.14$), and the addition of the random individual fish effect explained additional variability ($R^2 = 0.25$). Averaging these models produced coefficient and standard error estimates that indicate use of deeper habitats during the day and by larger fish (Table 5). Modeled depth use increased roughly 0.08 m during the day, as well as an average of 0.01 m for each additional 1.0 mm in fish TL. While date was included in the averaged model, its effect on depth use by juvenile Smallmouth Bass was marginal and its importance in the averaged model was low relative to time of day and fish size (Table 5). There was similar support for my top three velocity-use models, which included the observation-level variables time and date and the individual-level variable fish size (Table 3). These fixed effects explained a small amount of variation in my data ($R^2 = 0.08$), and the random individual fish effect explained additional variation ($R^2 = 0.18$). Coefficient and standard error estimates derived from the average of these models show the use of faster habitats diurnally (0.04 m/s faster) and later in the season, though the latter effect is very small (Table 5). Fish size was retained in the averaged model, though its relationship with velocity use was unclear and its relative importance as a predictor was low (Table 5).

DISCUSSION

My findings indicate that movement of juvenile Smallmouth Bass varies with water temperature and fish size, with additional variability among individual fish. Juvenile Smallmouth Bass typically use warmer temperatures than adults (Armour 1993; Brewer 2013), with optimum growth at 28 °C (Peek 1965). Unsurprisingly, I observed increased movement by tagged individuals when water temperatures were greater. Temperature is particularly important for age-0 Smallmouth Bass growth prior to the overwinter period (i.e., < 10 °C), when fish are generally inactive must subsist on accumulated energy reserves (Oliver et al. 1979; Shuter et al. 1980).Thermal cues for long-distance movements are unknown for juvenile Smallmouth Bass, though adult spawning movements and dispersal to overwinter refuge areas typically occur around 15–16 °C in the spring and fall, respectively (Munther 1970; Langhurst and Schoenike 1990). Water temperature displayed an expected seasonal decline during my study, but only reached 15 °C near the end of the study. One previous study demonstrated the potential for tributary-mainstem movements by juvenile Smallmouth Bass on the order of several kilometers (Humston et al. 2010). These movements, characterized using otolith microchemistry of 135 age-1 bass, occur between the age-0 and age-1 periods, and predominate in the downstream direction. The timing of these movements is unclear, and it is possible that my some of my mobile individuals had already undertaken substantial movements or were in the process of such movements when my study concluded. However, tag life limited the temporal scope of my study, hindering my ability to infer coarse-scale movements. Fish size was also an important predictor of movement, with larger individuals moving greater distances. Juvenile Smallmouth Bass of intermediate age (i.e., 2–4) are considered the most mobile (Funk 1957; Ridgway et al. 2002). Younger, smaller Smallmouth Bass (e.g., age-0 and age-1), like those tagged in this study, are capable of considerable movements in riverine environments (Humston et al. 2010). Throughout the juvenile period, many riverine Smallmouth Bass undertake substantial migrations between different habitats, with evidence suggesting that much of this dispersal occurs very early in life (Humston et al. 2017). Lastly, there was evidence of variation in movement behavior among individual tagged fish in my study. Some of my tagged fish displayed strong directionality (i.e., upstream or downstream) in their movements, while others moved in a more restricted fashion (i.e., remained within an individual channel unit). The movement patterns I observed are consistent with the broader literature on lotic fish dispersal, as mobile and non-mobile subsets of individuals have been observed in many juvenile (Kahler et al. 2001; Roy et al. 2013; Myrvold and Kennedy 2016) and adult (Schmetterling and Adams 2004; Booth et al. 2013; Mollenhauer et al. 2013) stream fish populations. Similar patterns have been observed for adult Smallmouth Bass (Funk 1957; Gunderson VanArnum et al. 2001; Westhoff et al. 2016), as have highly individualized patterns of diel movement (Ettinger-Dietzel 2016). These patterns of individuality could reflect factors that were not measured, such as fish sex, foraging or predator-avoidance behavior, or biological interactions (Fraser et al. 2001).

Limited variability in discharge during my study precluded any meaningful analysis of its relationship with fish movement. Increased discharge affects Smallmouth Bass fry via downstream displacement (Winemiller and Taylor 1982; Harvey 1987), though susceptibility of larger age-0 fish is reduced (Harvey 1987). Though movement was not explicitly measured by the authors, Brewer et al. (2019) observed apparent movements between different channel unit types in response to changing streamflow during surveys of age-0 Smallmouth Bass in Ozark streams. In adult Smallmouth Bass, higher flows promote longitudinal movements and refuge use (Todd and Rabeni 1989). During my study, discharge was relatively stable and remained below 20-year median flows for all but two days of the study.

My modeling results demonstrate how variation in depth and velocity use among juvenile Smallmouth Bass is influenced by time of day, fish size (depth only), and date (velocity only). Fish were associated with relatively deeper, though still intermediate, habitats during the day, which may reflect the use of runs for feeding (Sabo et al. 1996). Such a pattern may also reflect the avoidance of visual predators at depth extremes, particularly in clear water such as my study stream (Helfrich et al. 1991; Orth and Newcomb 2002; Kadye and Booth 2014). I also observed a positive relationship between fish size and depth use. Larger individual Smallmouth Bass are typically found in deeper water, though there is some variation in this trend, particularly for juveniles (Orth and Newcomb 2002; Fore et al. 2007; Dauwalter and Fisher 2008). Sabo and Orth (1994) monitored age-0 Smallmouth Bass microhabitat use over the first growing season (May-August), and observed a positive relationship between fish size and depth use, though this relationship was not consistent across the study period. Age-0 Smallmouth Bass generally use shallower microhabitats as the growing season progresses (Sabo and Orth 1994), though there is considerable plasticity in depths used by age-0 individuals (Pert et al. 2002; Brewer 2011). This flexibility may explain the small and inconclusive relationship between depth use and study date in my averaged model. Tagged fish were associated with higher-velocity habitats during the day, although daytime velocities were still relatively low (≤ 0.10 m/s). This is consistent with my observations of more frequent use of run habitats during the day. Other juvenile Smallmouth Bass studies have also reported an affinity for run habitats. Age-0 and juvenile Smallmouth Bass have been classified in ‘run guilds’ based on use of relatively shallower and faster habitats than other stream fish, including conspecific adults (Leonard and Orth 1988). Foraging rates of age-0 Smallmouth Bass increase in faster habitats (Sabo et al. 1996), where most of their prey is more abundant (Aadland et al. 1991). Further, juveniles have been documented drift feeding in higher-velocity habitats (Simonson and Swenson 1990). Use of low-velocity habitats by juvenile Smallmouth Bass has been observed frequently in the lab (Sechnick et al. 1986) and the field (Aadland 1993; Sabo and Orth 1994; Newcomb et al. 1995; Fore et al. 2007; Brewer 2011). The use of faster velocities later in the study period may reflect ontogenetic habitat shifts, as age-0 Smallmouth Bass have been shown to use faster habitats later in the growing season (Sabo and Orth 1994). The negligible relationship between velocity use and fish size in the averaged model is consistent with plastic habitat use patterns documented in other lotic systems (Sabo and Orth 1994; Fore et al. 2007). Unexplained individual variability in depth use and velocity use may reflect characteristics that were not measured, such as foraging behavior or biotic interactions (Power et al. 1985). Individual variability may also reflect fidelity to specific habitat patches, such as shallow vegetated margins or deep pockets behind boulders, by non-mobile individuals (Clough and Ladle 1997; Steingrímsson and Grant 2003).

Other habitat-use patterns of my tagged fish were mostly consistent with studies of Smallmouth Bass. I found tagged juvenile Smallmouth Bass were associated with low percentages of cover throughout the day, with woody cover used more frequently than vegetation. The amount of cover in occupied patches was sparse, possibly to reduce predation risk. Use of wood and vegetative cover has been observed in many populations of age-0 Smallmouth Bass (Pert et al. 2002; Fore et al. 2007; Brown and Bozek 2010), though a shift to coarse substrates is sometimes observed in late summer to improve feeding opportunities and avoid predation risk associated with other cover types (Olson et al. 2003; Brown and Bozek 2010). Substrate use by tagged fish was consistent throughout the day, with pebble and bedrock substrates used most often. Visual observations indicated that these two substrate sizes accounted for the majority of available substrate. Similarly, Brewer (2011) found that substrate use by juvenile Smallmouth Bass in the Ozark region depended on availability (Brewer 2011). Bedrock and other coarse substrates are used by all stages of riverine Smallmouth Bass (Leonard and Orth 1988). The use of certain substrates is further modified by land use (Brewer 2011), instream cover (Livingstone and Rabeni 1991) and predation risk (Olson et al. 2003; Brown and Bozek 2010). Tagged Smallmouth Bass were consistent in their proximity to the stream bank. The average habitat patch used by tagged individuals was several meters from the streambank, and could reflect predator avoidance or habitat quality (Olson et al. 2003, Brown and Bozek 2010).

Radio telemetry is a promising technique for evaluating movement and habitat-use patterns of juvenile and other small-bodied stream fish, though there are some issues related to applying this technique in the field. Telemetry techniques allow continuous assessment of fish movement and habitat use, though transmitter cost often limits sample size. Despite this, telemetry studies with modest sample sizes still provide valuable information for conserving and managing fisheries (e.g., D'Amelio et al. 2008; Goclowski et al. 2013; Shipley et al. 2018). Other problems may arise due to the species or size of fish being tagged. For example, I experienced issues of premature tag failure (*n*=2), predation (*n*=1), and possible transmitter loss or mortality (*n*=1). Lastly, although current transmitter technology allows very small tags, there is a clear tradeoff with battery life that limits the study duration. As these technologies continue to improve, so too will the quality of information for juvenile fishes.

Based on my findings, there are several potential avenues for future research involving juvenile Smallmouth Bass ecology in streams. Increasing the spatiotemporal scope of this work would allow the study of movement and habitat needs across seasons, ontogeny, and under more heterogeneous environmental conditions. Such a study could highlight differences in populations within and among streams and their underlying causes, potentially helping to explain recruitment variability. Additionally, such work may elucidate the full scope of movement behavior, use of refuge habitats (e.g., springs), directional contributions (e.g., tributary-mainstem), and possible relationships with impoundments. Such longer-term studies with less invasive tagging but more labor- or cost-intensive sampling methods have demonstrated substantial movement of juvenile Smallmouth Bass and other diminutive stream fishes (Humston et al. 2010; Schumann et al. 2015). However, my study demonstrates the utility of a radio-tagging approach for studying juvenile warmwater fish. With present transmitter battery limitations, a longer-term study on age-0 Smallmouth Bass would be limited to mark-recapture methods or otolith microchemistry, though telemetry could still be used for shorter-duration studies at other critical times of the year (e.g., overwinter periods).

Table 1. Characteristics and movement summaries of 13 radio-tagged juvenile Smallmouth Bass. Individual fish attributes are: tag ID (tag number associated with each fish), total length (TL), and wet weight (Weight). Movement is described by net movement distance (Net), direction of net movement (Dir), and mean daily displacement (MDD). Net measures the difference between the maximum upstream and downstream locations of a fish relative to its initial release point, with Dir indicating the direction of net movement ('+' is upstream, '-' is downstream). MDD represents the total distance moved by an individual over the study period, scaled by the number of days over which the fish was located. I also report the number of relocations (RL), and period of observation (Days) for each tagged fish. I also report means and standard deviations (SD) for each variable.

Tag ID	TL (mm)	Weight (g)	Net (m)	Dir	MDD (m)	RL	Days
10	106	14.0	666	-	52	23	22
11	97	9.8	85	-	26	41	26
12	97	10.4	106	+	27	26	18
13	97	9.8	176	+	24	41	26
14	82	6.5	119	-	15	41	26
15	83	6.5	38	-	14	41	26
16	96	10.2	473	+	44	39	26
17	91	8.9	12	+	7	7	5
18	81	5.7	79	+	20	9	8
19[a]	98	11.5	NA	NA	NA	1	1
20	85	6.6	91	+	13	16	12
21	79	6.3	427	-	30	41	26
22	83	5.9	1046	+	50	40	26
Mean	90	8.4	277		602	30	21
SD	9	2.5	317		420	14	8

a: Smallmouth Bass with Tag ID 19 was lost in the first 36 h of the study and was excluded from analyses.

Table 2. Rankings of four candidate linear mixed models of movement by juvenile Smallmouth Bass in Honey Creek, Oklahoma in autumn 2016. Y is incremental movement distance at location *i* for fish *j*, β_0 is the grand intercept, γ is the random fish intercept, X_1 is the mean water temperature (°C) between location events, X_2 is fish TL (mm), and *K* is the number of model parameters. AIC_c is Akaike's information criterion adjusted for small sample size, and ΔAIC_c is the difference in AIC_c score between the given model and the top model. The Akaike weight (w_i) indicates relative support for each model. I also include marginal (R^2_m) and conditional (R^2_c) variance explained; R^2_m describes variance explained by fixed effects, and R^2_c describes variance explained by both fixed and random effects.

Model	*K*	Log-likelihood	AIC_c	ΔAIC_c	w_i	R^2_m	R^2_c
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2j}$	5	-1726.52	3463.21	0.00	0.45	0.04	0.11
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i}$	4	-1728.14	3464.40	1.18	0.25	0.01	0.10
$Y_{ij} = \beta_0 + \gamma_j + \beta_2 X_{2j}$	4	-1728.34	3464.80	1.59	0.20	0.03	0.10
$Y_{ij} = \beta_0 + \gamma_j$	3	-1730.05	3466.18	2.96	0.10		

Table 3. Results from eight candidate linear mixed models that examined depth and velocity use by juvenile Smallmouth Bass in Honey Creek, Oklahoma in autumn 2016, where Y is the average depth of location *i* for fish *j*, β_0 is the grand intercept, γ is the random fish intercept, X_1 is the day of the location, X_2 is a binary variable for time of day (day: 0700–1859 hours, or night: 1900–0659 hours), X_3 is fish TL, and *K* is the number of model parameters. AIC_c is Akaike's information criterion adjusted for small sample size, and ΔAIC_c is the difference in AIC_c score between the given model and the top model. The Akaike weight (w_i) indicates the relative support for the given model. Marginal and conditional R^2 values represent the amount of variance explained by fixed effects only and by both fixed and random effects, respectively.

Model	*K*	Log-likelihood	AIC_c	ΔAIC_c	w_i	R^2_m	R^2_c
Depth							
$Y_{ij} = \beta_0 + \gamma_j + \beta_2 X_{2i} + \beta_3 X_{3j}$	5	197.25	-384.32	0.00	0.51	0.13	0.25
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3j}$	6	197.72	-383.20	1.11	0.29	0.14	0.25
$Y_{ij} = \beta_0 + \gamma_j + \beta_2 X_{2i}$	4	194.82	-381.53	2.79	0.13		
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2i}$	5	195.37	-380.56	3.76	0.08		
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_3 X_{3j}$	5	185.38	-360.58	23.74	0.00		
$Y_{ij} = \beta_0 + \gamma_j + \beta_3 X_{3j}$	4	183.64	-359.16	25.16	0.00		
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i}$	4	183.07	-358.03	26.28	0.00		
$Y_{ij} = \beta_0 + \gamma_j$	3	181.23	-356.39	27.92	0.00		
Velocity							
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2i}$	5	428.70	-847.22	0.00	0.46	0.07	0.18
$Y_{ij} = \beta_0 + \gamma_j + \beta_2 X_{2i}$	4	426.95	-845.78	1.44	0.22	0.06	0.18
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3j}$	6	429.00	-845.75	1.47	0.22	0.08	0.18
$Y_{ij} = \beta_0 + \gamma_j + \beta_2 X_{2i} + \beta_3 X_{3j}$	5	427.16	-844.15	3.07	0.10		
$Y_{ij} = \beta_0 + \gamma_j$	3	414.06	-822.06	25.17	0.00		
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i}$	4	414.45	-820.79	26.43	0.00		
$Y_{ij} = \beta_0 + \gamma_j + \beta_3 X_{3j}$	4	414.31	-820.51	26.71	0.00		
$Y_{ij} = \beta_0 + \gamma_j + \beta_1 X_{1i} + \beta_3 X_{3j}$	5	414.75	-819.32	27.90	0.00		

Table 4. Unconditional model-averaged coefficients, standard errors, and relative variable importance (RVI) for parameters describing incremental movements by juvenile Smallmouth Bass. Three models with $\Delta AIC_c < 2$ were averaged; N is the number of models included in the average that contain the parameter. Coefficient estimates are in meters, while unit increments (i.e., standard deviations) for predictors are 2.0 °C for water temperature and 3.9 mm for fish TL.

	Estimate	SE	RVI	N
Intercept	20.296	3.217		3
Water temperature	2.572	2.053	0.77	2
Fish TL	4.261	3.700	0.72	2

Table 5. Coefficients, standard errors, and relative variable importance (RVI) for parameters describing depth and velocity use by juvenile Smallmouth Bass, based on unconditional model averaging. Two models with $\Delta AIC_c < 2$ were averaged for depth use and three models having $\Delta AIC_c < 2$ were averaged for velocity use; N is the number of models included in the average that contain each parameter. Coefficient estimate units are meters (depth) and m/s (velocity), while unit increments (i.e., standard deviations) are 3.9 mm for fish TL and 7.9 d for date. Time of day is a factor, with coefficients given for daytime relative to the reference condition (nighttime).

	Estimate	SE	RVI	N
Depth				
Intercept	0.369	0.019		2
Time of day	0.076	0.015	1.00	2
Fish size	0.041	0.017	1.00	2
Date	-0.003	0.006	0.36	1
Velocity				
Intercept	0.040	0.009		3
Time of day	0.041	0.008	1.00	3
Date	0.006	0.005	0.75	2
Fish size	0.002	0.005	0.24	1

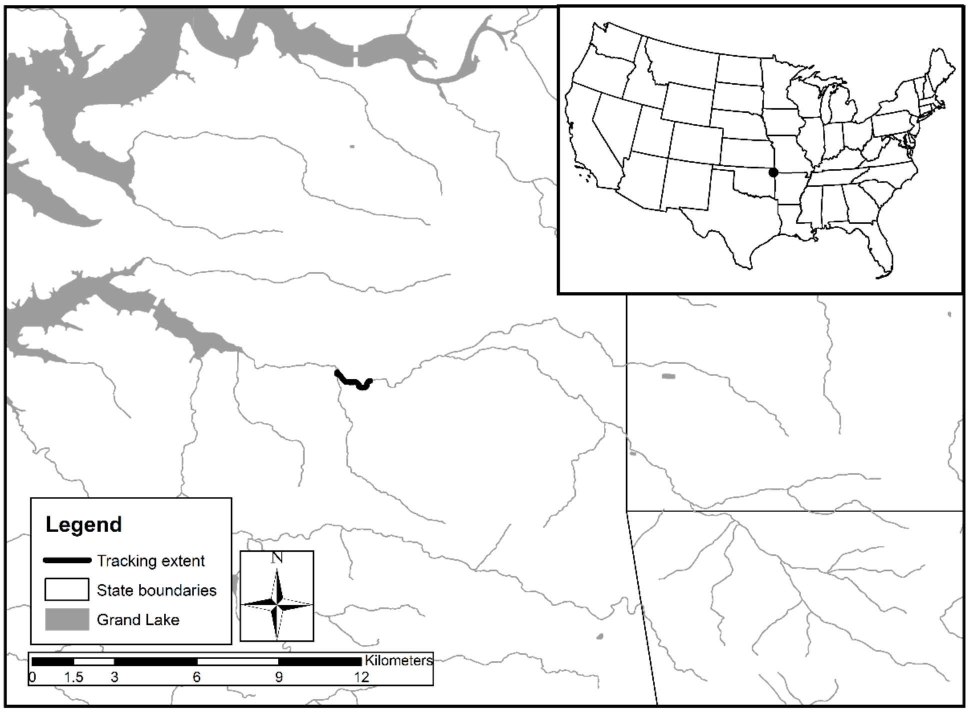


Figure 1. The location of my 1.5-km study reach (bold) in Honey Creek, Oklahoma. I tagged 13 juvenile Smallmouth Bass and tracked them throughout the diel cycle for 26 d in autumn 2016 (October 19–November 13).

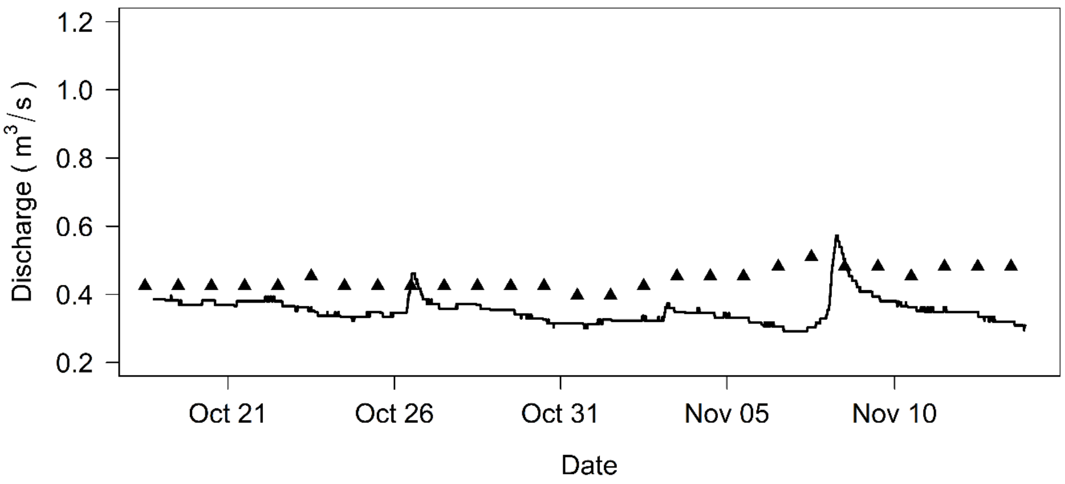


Figure 2. Instantaneous (solid line) and 20-year median daily (triangles) stream flow during my study of juvenile Smallmouth Bass movement in autumn 2016. Y-axis is scaled to mean annual discharge (1.16 m^3/s). For reference, 1.0 m^3/s is 35.3 ft^3/s. Discharge data were obtained from a U.S. Geological Survey stream gauge (07189542) located 2.45 km upstream of my study area.

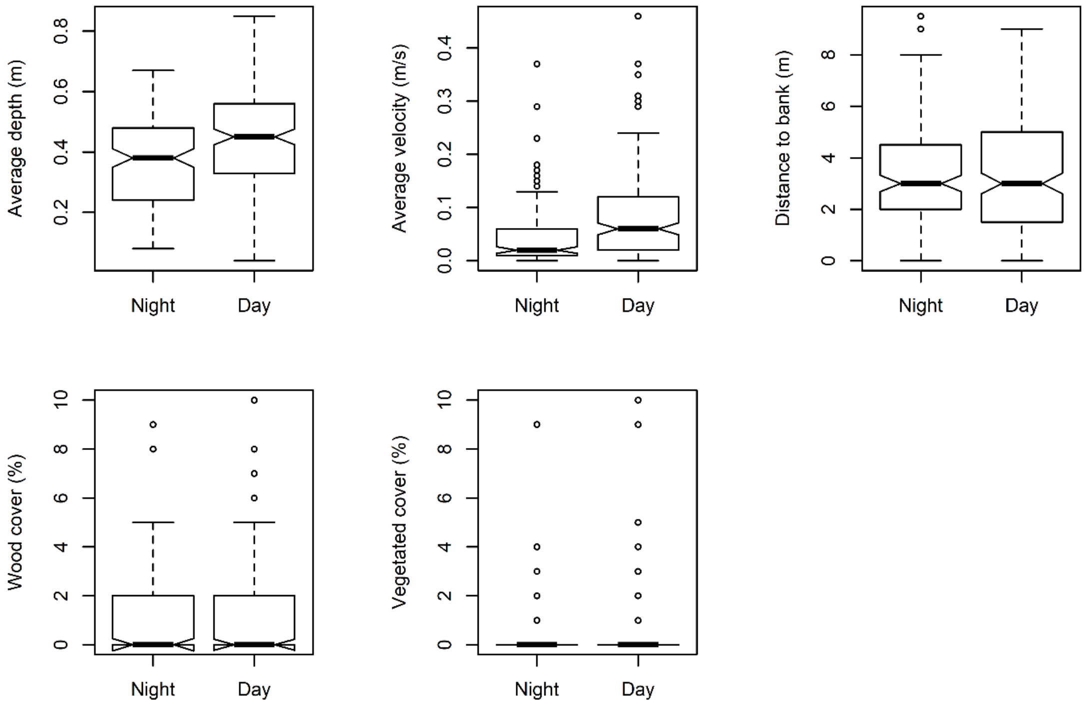


Figure 3. Boxplots of habitat use during both the day and night tracking periods (*n* = 349 observations). Day and night periods are: 0700–1859 and 1900–0659, respectively. Boxes represent the interquartile range (IQR) of the data, while whiskers depict 1.5·IQR. Notch width provides roughly a 95% confidence interval for each median.

CHAPTER VII

MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

I documented multiple pathways by which hierarchical habitat conditions affect Neosho Smallmouth Bass, suggesting several opportunities to improve management of these populations. The presence and abundance of nests and age-0 individuals varied in relation to reach-scale habitat conditions, and these relationships were in some cases modified by stream size and stream network position. The hierarchical structure of stream habitat explains how coarse-scale conditions influence habitats and biota at increasingly finer scales (Frissell et al. 1986), and examples of such pathways exist for other Smallmouth Bass populations (e.g., Brewer et al. 2007; Dauwalter et al. 2007). Most studies of Smallmouth Bass have focused on larger streams and rivers that support fisheries, but my results suggest that small streams are important for Smallmouth Bass fisheries and that habitats used in these systems differ from those used in larger systems. Management efforts should incorporate small streams in routine monitoring of Neosho Smallmouth Bass spawning and rearing and also maintain habitats important for spawning and rearing bass in small streams (e.g., deeper pools). Maintaining natural pool-riffle geomorphology of these systems may require protections against landscape disturbances that alter hydrology (e.g., land conversions) or sediment supply (e.g., gravel mining). Although management and restoration at the landscape scale are challenging, finer-scale projects aimed at solving specific problems in smaller streams and their catchments (e.g., riparian reforestation, cattle fencing) are more cost-effective relative to large-scale projects (Lake et al. 2007).

The spatial context of a stream reach influences local abiotic and biotic conditions and the relationships between them (Vannote et al. 1980; Torgersen et al. 2006). Confluences in a river network alter expected longitudinal gradients in physicochemical conditions, and the resulting heterogeneity affects biological productivity and diversity (Osborne and Wiley 1992; Benda et al. 2004). The importance of spatial context and tributary influences is rarely considered in studies of warmwater stream fish life history (but see Humston et al. 2010), though my findings suggest that these tributary habitats are important for rearing age-0 Smallmouth Bass. Efforts focused on preserving the integrity of confluence habitats via targeted land management or stream restoration of small tributaries and their catchments would benefit rearing conditions for this subspecies. Conserving relatively undisturbed small streams (i.e., those with natural pool-riffle geomorphology) adjacent to large mainstem systems would combine both of the above approaches to benefit nesting and rearing Neosho Smallmouth Bass by providing deeper habitats and spatial proximity to larger, more productive systems.

Understanding movement patterns of fish is necessary to delineate population(s) of management interest and define the appropriate scale for effective management (Cooke et al. 2016). I found movement behavior of adult and juvenile Smallmouth Bass varied spatiotemporally and among individuals, with heterogeneity in movement magnitudes and environmental cues across the riverscape. Movement magnitudes were greatest during the spring season and in larger systems, but considerable individual heterogeneity was apparent. Connectivity appears to be important for these populations on a variety of spatiotemporal scales. I observed routine movements by age-0 and adult Smallmouth Bass between mesohabitats, suggesting the importance of connectivity across channel units for meeting changing habitat needs throughout the life cycle. Because seasonal low-flow conditions in small streams appear to limit movement between mesohabitats, management efforts on small streams should emphasize minimum flows that confer mesohabitat connectivity while balancing human demand (e.g., groundwater pumping, agricultural diversions; Bradford and Heinonen 2008). When confluence conditions were riverine (i.e., at low reservoir pool levels), I observed movement of Smallmouth Bass between Buffalo Creek and Elk River. Such movements allow stream fish to respond to coarse-scale environmental conditions and have important consequences for persistence in light of climate change (Pringle 2003; Pörtner and Peck 2010) and for metapopulation dynamics (Ying et al. 2011). Keeping pool levels in Grand Lake low during the winter and spring, when possible, would improve connectivity between the Buffalo Creek and Elk River populations of Neosho Smallmouth Bass, thereby providing access to more diverse refuge and spawning habitats and potentially allowing gene mixing. Although I evaluated movement patterns of age-0 fish and adults, spatial patterns of other subadult life stages remain unclear for Smallmouth Bass populations. Further insight into the riverscape-scale movement dynamics of Neosho Smallmouth Bass throughout their lifetimes could be gained using techniques such as otolith microchemistry (e.g., Humston et al. 2010) and would benefit from a quantitative assessment of connectivity patterns across their native riverscape (Fullerton et al. 2010).

I observed seasonal and individual variation in habitat use behavior by Neosho Smallmouth Bass across the range of study streams. Stream fish require a variety of habitats throughout their lives for reproduction, growth, and refuge (Schlosser 1991). Ozark streams are naturally flashy and thermally heterogeneous (Brewer 2013; Leasure et al. 2016), creating a mosaic of habitat conditions across the riverscape. My work demonstrated flexibility in the use of thermal habitats by age-0 bass, plastic spawning behavior and hatch timing, and variability in depths and velocities used variability by radio-tagged juveniles and adults. As these characteristics help populations cope with the naturally dynamic and heterogeneous conditions of Ozark streams, it is imperative to preserve the individual- and population-level diversity of the subspecies (Begg et al. 1999). This diversity confers greater resilience to the unpredictable environmental conditions that will occur more frequently due to climate change (Healey 2009).

Introgressive hybridization with nonnative Tennessee strain Smallmouth Bass has been documented in several regional populations of Smallmouth Bass, including those in Elk River and Buffalo Creek (Taylor et al. 2018). This hybridization poses a threat to the persistence of locally-adapted native genotypes (Koppelman 2015), and it is therefore important to educate stakeholders to reduce the potential for future unauthorized introductions (e.g., Cambray 2003).

I observed successful spawning and relatively high autumn densities of age-0 bass even in years where high discharge events delayed reproduction or destroyed earlier broods, but the implications of delayed hatch timing, subsequent growth, and habitat use for age-0 Neosho Smallmouth Bass survival over the first winter of life merits further study. Although favorable conditions during the growing season may allow late-hatched fish to persist, shorter growing periods may reduce accumulated energy reserves prior to more stressful periods (e.g., overwinter), thereby reducing individual survival and recruitment (Oliver et al. 1979). Thus, an evaluation of overwinter survival and recruitment in relation to pre-winter fish size, habitat use (e.g., groundwater), and physicochemical conditions would build on my findings and help predict expected year-class strength following variable spawning and rearing conditions.

Lastly, the clustering behavior observed for some nesting Neosho Smallmouth Bass presents a potential risk for nest failure and high mortality of spawning individuals. Guarding male Smallmouth Bass are highly vulnerable to angling and removal from the nest, which often results in nest predation, brood loss, and overall decreases in fry production (Philipp et al. 1997; Steinhart et al. 2004). Oklahoma does not currently have a closed season for targeting Smallmouth Bass, and the timing of peak angler effort in the state (i.e., June–September; Martin and Fisher 2008) coincides with the latter part of the spawning window in Ozark streams (i.e., April–July). I observed considerable spawning during this period, particularly following high flows that reduced the success of earlier nests. Seasonally closing or otherwise protecting habitats used by spawning aggregations is one possible management approach (Suski and Cooke 2007) that has benefitted population-level reproductive success in some areas (e.g., Suski et al. 2002). A compromise approach could involve closing only small streams to angling during the spawning period (i.e., April–mid-July), as these systems are essential to maintaining both the genetic diversity of Smallmouth Bass populations and the overall fishery.

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