Assessing the spawning movement and habitat needs of riverine Neosho Smallmouth Bass

***Shannon K. Brewer*[1]**
***Andrew Miller*[2]**

[1] U.S. Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State University, Stillwater, OK

[2] Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State University, Stillwater, OK

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For additional copies or information, contact:

Shannon Brewer
U.S. Geological Survey
Alabama Cooperative Fish and Wildlife Research Unit
Auburn University
Auburn, Alabama 36849
E-mail: skbrewer@usgs.gov

FINAL REPORT

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Photo credit: *S. Brewer*

Shannon K. Brewer[1], and Andrew Miller[2]

[1] U.S. Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit; [2]Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State University

Principal Investigator

Shannon K. Brewer, Ph.D. – Assistant Unit Leader-Fisheries, U.S. Geological Survey, Oklahoma Cooperative Fish & Wildlife Research Unit, Oklahoma State University, 007 Agriculture Hall, Stillwater, OK 74078
405-744-9841 (P) | 405-744-5006 (F) | shannon.brewer@okstate.edu

Executive Summary

Stream fishes are vulnerable to a variety of natural and anthropogenic stressors. Information on fish movements and habitat use is essential to conserve and manage populations, particularly at the edges of distributions and novel habitats. The Neosho Smallmouth Bass *Micropterus dolomieu velox* is endemic to the southwestern Ozark Highlands ecoregion, where the riverscape is highly dissected by impoundments. Our study objectives were to determine the pre-spawn, spawn, and post-spawn movements of adult, radio-tagged Neosho Smallmouth Bass, and identify the habitat factors at multiple spatial scales related to suitable spawning habitat. Movements by tagged fish in the Elk River of Oklahoma and Missouri and two Oklahoma tributaries draining to lower Elk River and Grand Lake O' the Cherokee were greatest during the spring spawning period and were positively related to discharge and fish size; however, we observed considerable individual and stream-specific variability. Temperature and fish movement rate in the Elk River were positively related in all seasons except for winter, although temperature was less important for Smallmouth Bass movement in the smaller streams. Tagged fish were never detected using active or passive telemetry in the reservoir or reservoir-river interface except during periods of lotic character (i.e., the reservoir was not pooled above the Buffalo Creek-Elk River confluence). Nests were typically located at intermediate depths (mean = 0.8 m; SD = 0.3) and in low velocity habitats (0.0–0.2 m/s). Most of the nests examined comprised gravel substrates; however, 2.5% of the nests observed were located on full or partial bedrock substrate. We also documented nest clustering behavior by Neosho Smallmouth Bass (i.e., adjacent nests within 2 m of each other); 66 nest clusters were identified across 22 stream reaches. Cluster presence was more prevalent in warmer stream reaches with wide, shallow channels, and less likely in groundwater-gaining reaches, whereas overall nest abundance was greater in warmer streams and reaches with deeper pools. We showed the importance of both warmer streams and deep pools of small streams for

Smallmouth Bass rearing (i.e., young-of-year abundance). We found negative relationships between floods and first-year juvenile survival and show the importance of stream network position (i.e., adjacency to larger streams) for mitigating the negative effects of July floods. Our analyses of both nesting and young-of-year habitat use suggest small streams, typically not considered important to many fisheries, are responsible for a proportion of Neosho Smallmouth Bass production. Further, consideration of management actions restricting take during the early spawning season may be warranted due to the unique nesting behavior (i.e., clustering) exhibited by this subspecies.

Background

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 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).

A disproportionately high degree 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). Projected 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).

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). The species is a common target species of recreational anglers (Long et al. 2015), known for strong fighting ability relative to body size (Henshall 1881). Fisheries including combination of Smallmouth Bass 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). The subspecies is a popular angler target 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 distribution 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 subspecies range. Information on seasonal movement patterns, and an improved understanding of the hierarchical influences on nesting and juvenile habitat 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). Therefore, our study objectives were to determine the pre-spawn, spawn, and post-spawn movements of riverine Neosho Smallmouth Bass, and identify the habitat factors at multiple spatial scales related to suitable spawning habitat.

Objective 1. Assess the movements of riverine Neosho Smallmouth Bass before and following the spawning period

Background

Much of what is known about spawning by Smallmouth Bass relates to studies of the northern subspecies (*Micropterus dolomieu dolomieu*). Spawning occurs within the littoral zone of lakes and nearshore habitat of lotic systems from April to mid-July at southern latitudes (e.g., Missouri, Pflieger 1975). Adult Smallmouth Bass migrate to spawning sites in spring when the temperature is approximately 15 ºC (Coble 1975). Larger males spawn first, and repeat nesting may occur if nest failure is perceived by fish due to flooding or weather events (Shuter et al. 1980; Lukas and Orth 1995; Larimore 2002; Orth and Newcomb 2002; Cooke et al. 2006). Larger males account for the highest production of free-swimming larvae and make the most re-nesting attempts (Lukas and Orth 1995; Knotek and Orth 1998). Male Smallmouth Bass guard saucer-shaped nests (depressions in coarse substrates, Pflieger 1966). Many males exhibit nest-site fidelity, nesting within 20 m of their previous year’s nest site (Ridgway et al. 1991; Barthel et al. 2008). Larvae become free-swimming 4-16 days after hatching and are 8.1–10.1 mm total length (Ridgway and Friesen 1992; Warren 2009). Males provide parental care during early ontogeny until juveniles begin to disperse (see Brewer and Orth 2015 for a complete review). The free-swimming larvae are referred to as ‘black fry’ due to their pigmentation. Young-of-year

(YOY) have the body shape and pigmentation of adults at approximately 24 mm total length (TL; Brewer and Orth 2015). The black fry school near the nest and guarding male, slowly expanding their foraging area during the day but remaining near the stream bottom at night (Brewer and Orth 2015). Although research efforts historically tended to focus on the northern subspecies, conservation and management agencies recognize the importance of the subspecies (i.e., Neosho subspecies *M. dolomieu velox*) and much more attention is being paid to this and other endemic bass (Taylor et al. 2019).

Migration patterns 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*, Mallen-Cooper and Stuart 2003; Shoal Bass *M. cataractae*, Sammons 2015). For example, Smallmouth Bass in a connected lotic-lentic system in Ontario, Canada, overwinter in a lake, but spawn in either the lake or 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). Understanding migration patterns between these connected systems would allow for more relevant management actions to be developed (e.g., when to sample and how to define management units and seasons).

Study area

We 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 tributary (Buffalo Creek) that terminates at the confluence of a larger river-transient reservoir interface, and 3) a fifth-order 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 reservoir 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. Groundwater inflows are common but spatially variable (Brewer 2013a; Zhou et al. 2018). Substrates are predominately gravel, pebble, and cobble with some exposed bedrock.

Field collection and tagging

We 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. We used boat and tow-barge (Stealth Mini-Boat; Midwest Lake Management, Polo, Missouri) electrofishing and angling to sample 99 Smallmouth Bass 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 river-reservoir interface (Figure 1). We 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 TL (1 mm), sex (where possible), 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 was continuously flushed across the gills. We 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). Estimated tag life was 723 and 860 days, respectively. We 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). The incision was closed 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.

We 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. We 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 period (n = 62 in Buffalo Creek, n = 50 in Elk River, n = 40 in Sycamore Creek).

Movement and habitat use

Location accuracy associated with tracking tagged fish was determined prior to fish tagging. Tags were hidden in numerous stream reaches and relocated by each team member without prior knowledge of the tag location. Location accuracy was within ~1.5 m based on dummy tag relocations.

We actively tracked radio-tagged Smallmouth Bass in our three tracking reaches from June 2016 to February 2018. Fish tracking did not occur until after a minimum of 48 h post-surgery. We tracked approximately weekly from March–October and monthly from November–February (Appendix A, Table A1). All tracking was conducted during daylight hours (~0700-1900). Manual tracking occurred via foot or from a kayak or on foot using an SRX800 VHF receiver (Lotek Wireless) and a three-element Yagi antenna. We 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, we 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). We were able to visually confirm tagged fish presence for 23% (505/2,233) of relocations.

In addition to tracking our regularly designated stream reaches, we also actively tracked fish into the reservoir on multiple occasions. Each tracking event started at the downstream end of either the Sycamore Creek reach or the Elk River. From Sycamore Creek, we tracked to a location near Council Cove (36.717886, -94.738625). From the Buffalo Creek-Elk River confluence, we also actively tracked downriver into Grand Lake O' the Cherokee at S 678 Road (36.646781, -94.666359).

Tagged fish using coded radio tags can be individually identified and located either actively (with an antenna as described above) or with passive receivers (Kuechle and Kuechle 2012). Both methods of tracking were used in this study with the passive receivers used primarily to determine if tagged fish left the active tracking area and moved into the reservoir. Three receiver stations with fixed-position antennas were used to help monitor tagged fish in the study area. The stations were placed at the confluence of Elk River and Buffalo Creek, the Sycamore Creek-reservoir interface, and the Elk River-reservoir confluence downriver of Buffalo Creek (36.650083, -94.650809). The stations were placed near major confluences or reservoir interfaces to detect fish leaving the rivers or crossing the reservoir interface with Buffalo Creek during the spring when the reservoir backed up. Each receiver station consisted of two, three-element Yagi antennas (i.e., one facing upstream and one downstream) positioned 3–4 m high on the bank (i.e., in a nearby tree) and angled toward the river. The three stations continuously scanned the radio frequencies used and recorded the frequency, identification number, and time stamp of each detection. Each receiver was powered by a marine battery connected to a solar panel. Data collected by the receivers were downloaded approximately every 7-10 days.

We obtained GPS coordinates and recorded habitat characteristics at each fish re-location. We recorded channel unit type as riffle, run, pool, or slackwater based on current velocity, depth, gradient, and substrate (simplified from Rabeni and Jacobson 1993). We 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). We noted the nearest cover type within the channel unit each fish was relocated: 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). We also quantified distance to cover (0.5 m) for each location; fish were considered using cover if cover occurred within 1 m of their location (Probst et al. 1984). We 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), we recorded a waypoint at the initial fish location but did not collect microhabitat information.

After evaluating fish location data, we summarized fish movement in two ways and estimated their home range. We 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, we used prior locations and visual confirmations of tagged fish to identify and remove spurious "fish" locations. We 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. We 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). We 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 model assumptions and improve interpretation. The response variable, movement rate, was natural-log transformed to account for skewness; we added a constant (i.e., y + 1) to all values to facilitate the transformation in cases of no apparent movement. We used stream and season as categorical predictors with three and four levels, respectively. Water temperatures were used to define the following seasons as 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). We 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): Buffalo Creek (0.43 m^3/s), Elk River (6.68 m^3/s) and Sycamore Creek (0.38 m^3/s). We 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, we included fish TL as a predictor. We 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).

We built linear mixed models (LMMs) and used a model selection approach to determine the relationship among 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). We 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). We 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. We used the R package 'AICcmodavg' (Mazerolle 2017) to rank our models using Akaike's information criterion adjusted for small sample size (AIC_c, Sugiura 1978). For this and all subsequent model-selection efforts, we 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). We 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, we 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).

We evaluated and summarized habitat use in relation to season, stream, fish sex, and fish TL. Our initial plots suggested depth and velocity related to fish length, whereas cover and substrate plots revealed little association. Based on apparent seasonal, among-stream, and individual differences in depth and velocity use, we modeled predictors of both depth and velocity use via separate candidate LMM sets that differed only in their response term. We natural-log transformed velocity values (i.e., ln (y + 0.001)) to address skewness. Categorical predictors included stream (three levels), season (four levels), and fish sex (three levels, i.e., male, female, unknown). We natural-log transformed and standardized (mean = 0; SD = 1) the continuous predictor, TL. Each candidate model set included all additive combinations of the fixed effect predictors (*n* = 16 models). We 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). We ranked candidate models using AIC_c (Sugiura 1978). We assessed model fit and assumptions of our most supported model 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, we calculated proportional use of cover types and substrate classes for each season and stream.

Objective 2. Determine the habitat factors at multiple spatial scales that relate to suitable spawning habitat, particularly in regions influenced by reservoirs

Background

Rheophilic fishes are managed under a variety of landscape characteristics, many of which have been altered. Some landscape characteristics constrain the ability of populations to succeed under a variety of management scenarios. For example, Smallmouth Bass populations thrive under some natural landscape conditions that vary spatially (Brewer et al. 2007) and are less likely to benefit from improved land-use conditions when natural soil conditions relate to high runoff potential (Brewer and Rabeni 2011). Understanding the constraints imposed by both natural and human-induced landscape changes allows managers to apply more realistic regulations or expectations (e.g., trophy fishery designations in feasible locations) on populations. Without this knowledge, management activities may not be successful, and the observed patterns may not even relate to the designated management activities. Understanding how different life stages benefit (i.e., grow, reproduce, survive) from the use of different ecosystem components would help direct management actions across the landscape.

Little information is available on habitat use by Neosho Smallmouth Bass during the spawning period (Brewer and Long 2015). The only study conducted on the subspecies occurred during a below average discharge year and indicated spawning occurred in low velocity, nearshore habitats located close to adjacent cover (Dauwalter and Fisher 2007). The number of Smallmouth Bass occupying these locations reflected some of the highest nest densities ever reported (i.e., (147 nests/km and 100 nests/km at Baron Fork upstream and downstream reaches, respectively). The cause for these high densities is unknown but two possibilities exist: 1) spawning habitat was limited, and 2) there are factors that interact with these very local combinations of depth, velocity and cover that create suitable conditions for Smallmouth Bass. We anticipate both factors are interactive because other, more coarse-scale variables are likely responsible for the creation of suitable spawning habitat (e.g., groundwater, soils, etc). Other studies on Smallmouth Bass indicate coarse features of the landscape are significantly related to use of local habitat features (Brewer et al. 2007; Brewer 2013b). Unfortunately, studies on Smallmouth Bass nesting have focused primarily on fine-scale habitat conditions and this applies to not only the Neosho subspecies, but also to the nominal species.

Study area

We conducted surveys for Smallmouth Bass nests (Figure 2) and YOY juveniles (Figure 3) in the known range of Neosho Smallmouth Bass in the southwest Ozark Highlands ecoregion. This portion of the ecoregion includes tributaries to several major impoundments, including Grand Lake, Spavinaw Lake, Lake Hudson, Fort Gibson Lake, and Tenkiller Lake. Sampled stream reaches were located within second-to-fifth-order tributaries. Many of these streams, particularly the Elk River, Illinois River, and their tributaries, support popular Smallmouth Bass fisheries.

Nest surveys

The primary targets of our surveys were Smallmouth Bass nests or nest aggregations (hereafter clusters, where at least two actively guarded nests or nests containing eggs or larvae were located within 2 m of one another). We only considered nests that were guarded or that contained eggs or fry, as individual Smallmouth Bass sometimes excavate multiple nests in close proximity before choosing their nesting location (Cleary 1956; Mraz 1964). The minimum nest distance criteria we used to define a cluster was based on the minimum distance observed between lotic Smallmouth Bass nests in some interior Ozark Highland streams (~1.1 m; Pflieger 1966). However, the distances between neighboring nests of spawning bass are usually far greater (e.g., ~78 m, Winemiller and Taylor 1982; Wiegmann et al. 1992). Smallmouth Bass nests are typically defined by depressions made in gravel-cobble substrates in low-velocity areas (Warren 2009). However, anecdotal observations suggest the Neosho subspecies may also spawn on solid bedrock where a depression or fanned area may not be obvious (S. K. Brewer and Brandon Brown, personal communications). Thus, we used multiple characteristics to define nests: the presence of a guarding male, and the presence of eggs or fry.

We surveyed nesting Neosho Smallmouth Bass (i.e., nest and nest clusters) from 120 stream reaches representative of the study area during late spring and early summer (May–early July) of 2016–2018 (Figure 2). Because the majority of properties were owned by private landowners, we could not realistically randomly select our sample locations. Sampling began after water temperatures reached ~15°C (Pflieger 1966; Graham and Orth 1986; 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 and (or) re-nest following flood events (Warren 2009). At least one flood event, for example, prevented our sampling for ~7 d each sampling year and frequent high flows resulted in continued spawning activity by fish into July.

We 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. Snorkelers slowly moved upstream in parallel lanes (e.g., left, middle, right), carefully searching complex habitats for guarding male bass or groups of eggs or fry in small depressions or near cover. Communication between observers was required to prevent double counting nests. We uniquely marked individual nests with numbered flags for later microhabitat measurements (Dunham et al. 2009; Brewer 2011) unless we were planning to conduct a second pass (i.e., for sampling efficiency estimates). We adjusted lane widths to reflect visibility and habitat complexity; in areas with reduced visibility or more-complex habitat, narrower lanes were used, and more snorkelers were used (Hillman et al. 1992; Thurow et al. 2012). After each snorkeling pass, we measured water clarity (0.1 m), as the distance an observer could distinguish a bass-shaped silhouette underwater (Dunham et al. 2009). Observers were trained on models (i.e., cut outs of different sizes that resembled Smallmouth Bass) varying from 150–305 mm to assist with estimating the TL of guarding bass on marked nests.

We conducted a second snorkeling pass at 60 sample reaches to assess nest detection efficiency (i.e., the proportion of nests detected among those present, *sensu* Peterson and Paukert 2009). We allowed a minimum of one hour between the start of passes one and two so the stream could return to a relatively undisturbed state (O'Neal 2007; Thurow et al. 2012). If the same snorkelers surveyed the second pass, each observer switched lanes so there would be no prior information on fish from the previous survey. Count data were not shared between the observers after pass one to prevent biasing counts on the second pass. The second survey was completed using the aforementioned approach and individual nests were marked with numbered flags.

Habitat

We quantified physicochemical conditions associated with nesting habitat at multiple spatial scales. First, we measured focal conditions at each individual nest and cluster within each reach. Then, we quantified reach-scale attributes describing conditions among reaches where fish chose to nest. Because of the inherent nested structure of streams, we also quantified attributes associated with stream segments (i.e., section of stream between tributary confluences) because multiple stream reaches were nested within stream segments (see also analyses). Lastly, we 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).

Microhabitat characteristics were quantified at encountered nest clusters beginning in 2016 (n =120 reaches), whereas individual nest microhabitats were quantified in 2017-2018 (*n* =

88 reaches). For each nest observed, we measured water depth (0.01 m) and velocity at the nest surface (0.1 m/s, focal location at estimated nest center). We also estimated guarding male total length (TL) to the nearest 5-mm increment (i.e., to offset estimated error from our training with bass silhouettes). For each cluster, we counted the number of nests and measured length and width to calculate approximate area of the cluster (0.1 m^2). Lastly, we measured the center-to-center distance of each nest in the cluster to the nearest neighboring nest.

We measured additional physicochemical characteristics to determine the relative importance of reach-scale factors on nest abundance (Table 1). We 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 these data, we converted stream temperature to a factor with two levels (cool: ≤ 19.5°C, warm: > 19.5°C). We 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 units in the main channel, runs were transitional habitats of intermediate depth and velocity, and off-channel habitats were low-velocity and located 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 on sampling efficiency (Schill and Griffith 1984; Hicks and Watson 1985) and its relationship with land use (Clifton 1989). We 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. We quantified high-flow characteristics of channel hydrology by measuring bankfull width-depth ratios (Gordon et al. 2004) and by estimating median substrate size (D50) as a proxy for channel shear stress (Shields 1936). To estimate D50, we measured intermediate diameters (1 mm) of ≥100 substrate particles collected evenly along transects across a run channel unit and the associated floodplain (Wolman 1954; Leopold 1970). We 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; we used the difference in discharge to calculate reach-scale groundwater flow. We 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 flow), neutral streams (no change) and gaining streams (net gain of flow).

We 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]), we 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. We calculated instream 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). We used the instream flow direction raster to calculate two metrics of stream topology: link magnitude (Shreve 1966) and downstream link (Osborne and Wiley 1992). Link magnitude describes stream size, whereas downstream link describes 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).

We calculated metrics describing landscape disturbance, topography, soils, geology, runoff, and baseflow conditions for each catchment (Table 1). We 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) and Mouser et al. (2019) (Table 2). The lowest index 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 we averaged their coefficients to make them applicable to the NLCD (see Mouser et al. 2019). Then, we calculated an area-weighted average of these coefficients across the upstream contributing area for each stream segment. We characterized topography using an instream measure of stream gradient from the NHDPlus V2 and calculated average slope in the upstream catchment of each stream segment. We calculated percent hydrologic soil group D and percent carbonate lithology for each catchment using existing data (Stoeser et al. 2005). Hydrologic soils groups (A-D) reflect soil permeability characteristics and would be highly correlated among one another (i.e., total 100% across groups). Thus, we quantified soil group D because of previous relationships described with Smallmouth Bass (Brewer et al. 2007). Likewise, lithology data would also be highly correlated, so we chose to quantify carbonate lithology because of its relationship with karst topography and springs. Lastly, we used data from Hill et al. (2016) to summarize variation in average annual runoff and baseflow contributions (i.e., groundwater) across the upstream contributing area for each segment.

Analyses

Nest clusters

We used a mixed-effects logistic regression model to evaluate the multiscale habitat features associated with nest cluster presence. First, we 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 (e.g., habitat limitation, groundwater influence, progression of nesting season; Table 3). We also included late-summer YOY densities collected from the same reach in the same year (See “young-of-year sampling”, this report) as a model predictor to assess whether nest-clustering behavior was related to differences in offspring survival. Because we lack YOY sample data from all stream reaches, we calculated mean values of YOY density in place of missing observations ($n = 71$ sites). We included a sample-area term in the model to account for differences in snorkeling effort among stream reaches. We natural-log (continuous variables) or logit-transformed proportions and standardized predictors to reduce skewness and simplify interpretation of model terms (Warton and Hui 2011). We also included random effects for stream segment and year to account for non-independent observations and address unexplained variability among reaches (Wagner et al. 2006; Gelman and Hill 2007). We used a parametric bootstrapping procedure with 1,000 replications to ensure more robust coefficient estimates. Logistic regression modeling and bootstrapping were implemented in R package ‘lme4’ (Bates et al. 2015). Lastly, we calculated marginal R^2 and conditional R^2 (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 abundances among reaches

First, we evaluated the influence of water clarity, wetted channel width, and thalweg depth on sampling efficiency (p) among sites (Royle 2004) using the ‘unmarked’ package in Program R (Version 3.5.1, R Core Team 2018). We scaled wetted width by the number of observers for each sample reach to account for differences in personnel among sites. We 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). We used the ‘unmarked’ package (Fiske and Chandler 2011) 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 4). We 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). We used model coefficients and empirical Bayes methods to adjust nest abundance estimates for variable detection efficiency among sites (Royle and Dorazio 2008; Fiske et al. 2017) so that these adjusted counts could be evaluated in a mixed-model framework (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).

We evaluated the predictor variable distribution and reasonable generalized linear mixed model (GLMM) forms for comparing adjusted Smallmouth Bass nest abundances and habitat. We first transformed all continuous (natural log) and proportion (logit) variables as needed to reduce skew (Warton and Hui 2011) and then standardized all independent variables (mean = 0 and SD = 1) to improve model convergence and simplify interpretation. We performed all transformations and standardizations with the ‘MuMIn’ (Bartoń 2018) and ‘psych’ (Revelle 2018) packages in R. A natural break in our data led us to convert stream temperature to a factor with two levels (≤ 19.5°C and > 19.5°C). Initial evaluation of our nest count data suggested overdispersion and zero inflation. We 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, ZINB). We included random effects for stream segment and sample year in these models to address unexplained variability among reaches and the non-independence between observations (Wagner et al. 2006; Gelman and Hill 2007). Comparison of model forms revealed that a ZINB model best fit the data (AIC_c weight > 0.99).

We used model ranking to reduce our set of predictor variables. We 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, we retained that model predictor (Burnham and Anderson 2002). We also filtered our 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).

We used the reduced variable set to create a candidate set of nest abundance models. This exploratory approach used AICc 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 × residual pool depth [RPD] and stream temperature × drainage area) were especially important. Using these three terms and an additive combination of the interaction terms, we built a base set of four models. We built our 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, we capped fixed-effect predictors at 11 per model (in addition to one random effect; Peduzzi et al. 1995; Harrell 2001). We 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). We assumed the random effect was normally distributed N(0, τ2), where τ2 represented population variance among levels of a random effect (e.g., among stream segments). We built all ZINB models in the R package ‘glmmTMB’ (Magnusson et al. 2018) and conducted model selection (AICc) using the ‘bbmle’ package (Bolker 2017).

We assessed model fit of our top model by calculating marginal R^2 and conditional R^2 (Vonesh et al. 1996; Nakagawa and Schielzeth 2013). We performed these calculations in the ‘sjstats’ (Lüdecke 2018) package in R.

Young-of-year sampling

We conducted snorkel surveys for YOY Smallmouth Bass in 120 stream reaches (i.e., 20 times average channel width) 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 (Figure 3). Our 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).

At a subset of stream reaches (*n* = 78), we snorkeled a second pass to assess sampling efficiency (i.e., the proportion of individuals detected among those present; Peterson and Paukert 2009) of YOY Smallmouth Bass. Observers did not discuss fish counts between each pass, and observers changed survey lanes in the stream between passes. We 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 and on the same day to avoid changes due to emigration or immigration.

Habitat

We quantified habitat characteristics at each stream reach immediately following our fish survey(s) (Table 5). Discharge (0.01 m^3/s) 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). We 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. We measured water temperature (0.1 °C) at mid-pool depth with a thermometer (Ultrapen PT1, Myron L, Carlsbad, CA). Because we only had a point measure from the time of sampling and these data reflected a natural break in temperature conditions, we converted stream temperature to a categorical variable with two levels (≤ 19.5 °C and > 19.5 °C).

We 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 5). Following the methods of Jenson and Domingue (1988), we 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]). We 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 our instream flow-direction grid, we 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.

We 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, we calculated a disturbance index that was modified from Brown and Vivas (2005) and Mouser et al. (2019) (see complete description under Habitat for Nest Surveys). The resulting coefficients ranged from 1.00 describing relatively undisturbed habitats (e.g., forests, wetlands) to 7.92 for high intensity development. We averaged the coefficients across the upstream contributing area so one value represented each stream segment. We also calculated area-weighted percent impervious cover using 30-m imperviousness data from Xian et al. (2011); we 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). We 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. We 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

We characterized annual hydrology (i.e., 2015–2017) as a proxy for the flow conditions during the spawning and early growth period of Smallmouth Bass. Because many streams we sampled did not have stream gages, we summarized available data using 11 representative stream gages (USGS gages: 07189100, 07188653, 07188838, 07188885, 07189540, 07189542, 07191222, 071912213, 07196000, 07197000, and 07197360; Table A2). Using daily streamflow data, we calculated mean discharge from April–July for each year (2015–2017). We 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 we averaged discharge across all streams in each sample year, we used monthly flow EP due to its relative independence from stream size. Lastly, we calculated the average frequency of higher flow events (> 10 m^3/s) and the average number of days (duration) with mean daily streamflow above this threshold from April–July of each year. We used 10 m^3/s 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, we 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 A3).

Analyses

We used data from 78 sites with two snorkel surveys to assess our sampling efficiency (Royle 2004). Our multiple-survey data showed high concordance at each site (Pearson's *r* = 0.97), suggesting our 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). We, therefore, proceeded with our habitat analyses using unadjusted counts. We used the higher counts at the sites where multiple surveys were conducted.

We assessed the distribution of our predictor variables and compared generalized linear mixed models (GLMMs) with different probability distributions prior to evaluating the relationship between YOY Smallmouth Bass abundance and habitat. To reduce skewness, we 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 our count data suggested both overdispersion and zero inflation. We 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 5). 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, we 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). We retained terms from all models with $\Delta AIC_c < 2$ relative to the null model (Burnham and Anderson 2002). To minimize issues with interpretation, we reduced any remaining covariates with pairwise correlations ≥ |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 5).

Using our reduced variable set, we 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. We used all additive combinations of these terms to build a base set of 17 models. We then added the remaining univariate and two-way interaction terms (Table 5) to this base model set to build our candidate set of 261 models. We 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). We 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 we used the 'bbmle' package (Bolker 2017) to calculate AIC_c for our 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).

We calculated the amount of variation explained by the top model using marginal R^2 and conditional R^2 (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

Objective 1. Assess the movements of riverine Neosho Smallmouth Bass before and following the spawning period

Movement and habitat use

The size of tagged fish varied within and among study systems, with the largest fish were generally tagged in the larger streams (Appendix A, Table A4). 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 in both TL (mean: 322 mm; range: 290–370 mm) and weight (mean: 481 g; range: 376–765 g). Over the duration of the study, we recovered 71 transmitters; we re-implanted 53 into new fish (n = 22 in Buffalo Creek, n = 20 in Elk River, and n = 11 in Sycamore Creek, Appendix A, Tables A5, A6). Tracking efforts from the 21-month study period resulted in n = 2,362 individual locations from n = 130 fish (i.e., includes only tagged fish redetected on more than two occasions).

Discharge conditions and water temperature during the study followed typical seasonal patterns and reflected groundwater variability of these Ozark Highland streams (Figure 4). High flows typically occurred during spring for all three streams. There was one major flood event in late April 2017 representing a substantial deviation (> 10 times) from median flow values and approaching the maximum flow recorded over the period of record at the USGS stream gauges (i.e., 80 years for the Elk River gauge). In late summer and autumn 2016 and 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).

Tagged fish were never detected using either active or passive telemetry in the reservoir or reservoir-river interface except during periods of lotic character (i.e., the reservoir was not pooled above the Buffalo Creek-Elk River confluence). Fish detected via the passive stations were also detected during active tracking efforts and thus, events were not duplicated in the analyses. During our active tracking events into Grand Lake O' the Cherokee from the lower Elk

River and lower extent of Sycamore Creek, we did not detect any of our tagged Smallmouth Bass.

Movements by 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%). We 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 6). 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 5). 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 6). 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, a small but positive relationship between mean temperature and movement rate was observed in all seasons except winter. Across all streams and seasons, larger fish were predicted to display greater movement rates (Figure 7). 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).

Several aspects of habitat use varied among streams and seasons (Table 7). 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 7). 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 indicated proportional use of different substrate and cover types was slightly different among streams and seasons (Figure 8). A greater proportion of tagged Smallmouth Bass in the 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 the 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.

Objective 2. Determine the habitat factors at multiple spatial scales that relate to suitable spawning habitat, particularly in regions influenced by reservoirs

Nest surveys

Nest surveys

We observed Smallmouth Bass nests in 77 of 120 stream reaches (64%). An additional 15 reaches were occupied by age-1+ Smallmouth Bass even though no nests were present. Non-zero nest counts ranged from 1 to 79 (mean: 11.5; SD: 13.7), and non-zero nest densities varied from 1.2 to 90.0 ha^{-1} (mean: 19.4 ha^{-1}; SD: 16.3). Nest counts per stream length varied from 2 to 140 km^{-1} (mean = 26.8 km^{-1}; SD = 26.7) at these sites.

Nest clusters and microhabitat

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 but variable among sample reaches (mean = 64%; SD = 17, range: 3–92%). Channel morphology also varied considerably among streams, particularly 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) stream reaches. Coarse-scale habitat reflected a wide range of stream sizes, spatial metrics, and catchment characteristics. Drainage area of our sample sites varied from 18.0 to 886.6 km^2. Downstream link varied from 3 to 874, indicating some reaches were adjacent to larger streams, whereas others were in more isolated, upstream portions of the river network. Catchment slope varied from 1 to 15% and the amount of hydrologic soil group D varied from 6% to 70% across the study area. Disturbance index values were low to moderate (range: 1.5–3.9; mean = 2.3; SD = 0.4).

The model developed describing nest cluster habitat indicated relationships with stream temperature, groundwater flow, sample timing, and channel morphology on cluster presence (Table 3). 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 at the reach scale were not associated with higher or lower offspring densities when compared to non-clustered nest behavior (95% CI: -1.71–4.49). Fixed effects explained 72% of the variability in nest cluster presence (marginal $R^2 = 0.72$), and 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. Male Smallmouth Bass guarding nests varied in size from 130 to 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 were 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 clustered nests, 97% of individual, non-clustered nests), though use of bedrock (2% of clustered nests, 3% of non-clustered nests) and other substrates (i.e., roots, < 1% of clustered nests) was observed.

Nest abundances among reaches

Average sampling efficiency of our nest surveys was relatively high (72%) and varied across sites in response to water clarity, depth, and lane width surveyed per observer (Table 8). 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 surveying wider lanes. Adjusted non-zero nest counts varied from 1 to 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 was similar support for several models (Table 9). 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 depended on stream temperature (Figure 9). 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 the quantity of pool habitat. 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 $R^2 = 0.80$), and the random stream segment effect did not explain any additional variability in nest abundance (conditional $R^2 = 0.80$). There was 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 was 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 had a positive relationship with pool habitat when substrate was small-to-average (i.e., reflecting low-average shear stress), with this relationship changing to slightly negative when substrate was larger than average (i.e., reflecting greater shear stress at higher flow).

Young-of-year sampling

Young-of-year Smallmouth Bass occurrence and abundance varied among study reaches. We observed YOY 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}). YOY Smallmouth Bass were disproportionately absent from streams we classified as cold (≤ 19.5 °C). Stream temperature explained some absences of YOY Smallmouth Bass, with model-predicted zero-inflation probabilities of 29.5% for cold streams and 8.0% for warm streams. We observed YOY Smallmouth Bass in both very small streams and larger rivers within our study area (drainage area range: 16.9–772.7 km^2).

Habitat and annual hydrology

Habitat conditions and hydrology varied considerably among sites and years (Table 5, Appendix A, Table A2). 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 to 694. Thus, some reaches were adjacent to large mainstem rivers, but others were located in upstream, more isolated portions 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 (Appendix A, Tables A2, A3).

YOY Smallmouth Bass abundance

The top model explaining conditional abundance of YOY 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 10). Late-summer abundances of YOY 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 up in the river network (i.e., not adjacent to larger rivers (Figure 10). The influence of residual pool depth on YOY Smallmouth Bass abundance depended on stream size (Figure 11). In smaller streams, deeper pool habitat was associated with greater YOY 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 YOY 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 (Figure 12). Thus, although cold stream reaches generally had lower numbers of YOY Smallmouth Bass, this relationship was less apparent in reaches adjacent to larger streams. Collectively, fixed effects in our model explained 57% of the variability in YOY 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

Fish movement

Neosho Smallmouth Bass exhibit a considerable degree of heterogeneity in seasonal movement behavior. As expected, tagged fish exhibited greater mobility associated with spawning during the spring and reduced movement during winter (Todd and Rabeni 1989; Lyons and Kanehl 2002; Barthel et al. 2008). We 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. We 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.

We did not observe any evidence of fish using Grand Lake or transient river-reservoir interfaces during the study suggesting lentic habitats 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 of the Ozarks of Oklahoma and Missouri including the Elk River basin (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 we 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.

We found movement rates by tagged 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, we found lower movement rates and dampened relationships between environmental 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, we found the relationship between water temperature and 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, high individual variability in movements was observed.

Individual variation and unexplained residual variability in movement rates among tagged Smallmouth Bass were apparent in our 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 we observed via a few tagged individuals. 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).

We observed seasonal and stream-specific patterns in habitat use by Smallmouth Bass. Use of deeper-water habitats during winter, regardless of stream size, 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 we 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 we 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 the Elk River than in the other streams. The 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 we examined. Use of gravel substrates increased in spring, consistent with the reproductive period and known spawning habitat preferences (Dauwalter and Fisher 2007). 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 or perhaps scavenging (e.g., bite and tooth marks). Harvest can greatly reduce numbers of tagged fish (Westhoff et al. 2016) and several of our tagged fish were caught by anglers. We know of one tagged fish that was harvested by anglers because the transmitter was returned. Several catch-and-release anglers we 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, we 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, we 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, we are confident that surgical technique or post-release mortality was not the underlying cause of transmitter loss. Transmitter loss had little 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).

Nest habitat

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 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 behavior may explain why our 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). We 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 (27–28°C, Peek 1965; Coutant and DeAngelis 1983). The greater abundance of nests in warm streams may relate to 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, YOY Smallmouth Bass are typically more abundant but may grow slower in stream segments with high spring-flow influence (Brewer 2013a). 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. We 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 and S. Brewer, 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 been beneficial for nest success in these systems. Future efforts focused on examining survival by clustering versus individual nests would provide insight into the possible mechanisms.

We found nest clusters were 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 we 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). 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 our 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).

Young of year

We found several relationships between YOY Smallmouth Bass abundance and abiotic conditions were modified by stream network position and stream size, indicating 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 YOY 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 YOY Smallmouth Bass use a diverse range of habitats throughout their distribution, 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 do not consider 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 YOY 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 and 28 °C (Peek 1965; Coutant and DeAngelis 1983), though development and growth are possible between 20 and 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 YOY 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, we observed YOY 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 via springs and seeps 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). YOY 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 YOY 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 YOY 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 YOY Smallmouth Bass abundance at the end of the first summer, although we found this relationship was influenced by stream network position. Late-summer abundance of YOY Smallmouth Bass was greater in years where July flow EP was greater (i.e., July flows were more benign). Considerable inter-annual variability in YOY 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 YOY Smallmouth Bass in large Virginia rivers is inversely related to the magnitude of June streamflow (Smith et al. 2005). 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 we observed in 2015, precluded 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 YOY 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 YOY 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). Although our 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, our choice of 10 m^3/s for calculating high-flow frequency and duration metrics likely overlooks stream-size dependent variability in this threshold. We chose this value from observations of

Smallmouth Bass nest failure in similarly sized streams (Lukas and Orth 1995), though many of our study streams were smaller and were likely vulnerable to substrate mobility and nest failure at lower flows (Pflieger 1975). Our use of annual averages across all gaged streams was a conservative approach that we felt best represented the range of study streams given the available data. Future work focusing on finer-scale modeling of streamflow dynamics and developing mechanistic linkages between hydrology and habitat on YOY abundance would be beneficial.

An interactive effect of residual pool depth and drainage area also explained variation in YOY Smallmouth Bass abundance. YOY 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). Our 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). YOY 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 small-bodied fishes such as YOY 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), whereas deeper habitats are less favorable in larger streams due to larger fish predators (Harvey 1991; Steinmetz et al. 2008). Density-dependent effects on YOY 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 YOY and adult Smallmouth Bass (Dauwalter and Fisher 2008a; Hafs et al. 2010).

MANAGEMENT RECOMMENDATIONS

Accounting for fish movements is essential for defining the appropriate scale for effective conservation and management actions. Movement data provide insight on the diversity 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 tagged fish in smaller streams moved primarily during the spawning season and in response to high discharge, efforts to limit flow peaks (i.e., removal to offsite storage) are likely not beneficial to these populations. 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. Limiting the introgression of nonnative Smallmouth Bass genetics into these populations is also important, 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 rare in the smallest stream where we examined fish movement 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 appears to be 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 (i.e., not a human safety concern). 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, protecting or enhancing the physical conditions that allow stream fish movement in response to changing environmental conditions and biological needs may prove beneficial to population persistence.

We suspect angler effort may be substantially higher on the Elk River where we lost more tagged fish when compared to other sample reaches (i.e., Buffalo Creek, Sycamore Creek). We tracked tagged fish to an angler’s stringer on one occasion, and we received multiple, anecdotal angler reports of tagged fish being captured and released (from conversations during our tracking efforts). We also received two reports of tagged fish capture by anglers on Buffalo Creek (one fish was harvested, and the tag returned). Exploitation, as suggested by tag loss due to angling, may be an issue of interest to the management agency.

The unique nest clustering behavior and influence of multi-scale habitat features on Neosho Smallmouth Bass nest abundances create 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, a proportion of 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 nest-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).

Disentangling the multi-scale influences on spawning habitat is important for conserving existing habitat and for guiding stream restoration efforts. 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 YOY Smallmouth Bass (Pert et al. 2002; Fore et al. 2007). With several subpopulations of Neosho Smallmouth Bass that appear isolated due to limited gene mixing (Taylor et al. 2018), observed habitat plasticity may reflect adaptation to specific habitat types among drainages. Our results highlight the unique nesting behavior of Neosho Smallmouth Bass and the myriad of habitat features that influence clustering, presence, and nest abundance during this life-history period.

YOY 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 YOY 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 YOY 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 a changing climate anticipated to increase extreme weather and hydrology patterns (Mulholland et al. 1997; Döll and Zhang 2010; Singh et al. 2013). Our results show 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) although considerable efforts to acquire available resources and avoid conflicts of interest in smaller watersheds may be necessary (i.e., Lake et al. 2007).

The results of both our nesting and juvenile habitat analyses suggest small streams, typically not considered important to many fisheries, are responsible for a proportion of Smallmouth Bass end-of-summer abundance. This is especially interesting to the Neosho subspecies as these populations appear to be somewhat insulated from hybridization resulting from historic or unknown stockings (Taylor et al. 2018). We found that nest abundance was positively related to deeper pools of smaller streams and low-velocity habitat was more important in streams with smaller than average substrates. Both findings have implications for both habitat protection and restoration. For example, protecting deeper pool morphology (i.e., fencing cattle from smaller streams or other activities that result in widening and shallowing of stream channels) is more important in smaller streams compared to larger stream systems. We also highlight the importance of smaller, cool-water tributaries located close in proximity to larger streams. These streams are important juvenile rearing habitat and their stream morphology is also an important element to quality habitat for Neosho Smallmouth Bass.

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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. We 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). We 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]

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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. 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	3.09
Cultivated crops	82	4.54
Woody wetlands	90	1.00
Emergent herbaceous wetlands	95	1.00

Table 3. 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 provided. 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 was warm (> 19.5°C) and the reference condition for groundwater flow was losing (i.e., longitudinal decrease in stream discharge). Area sampled was 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 4. Coefficient estimates, standard errors (SE) and 95% confidence intervals (CI) for the model of Smallmouth Bass nest detection efficiency in Ozark streams. We 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) were 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 5. Predictor variables used for modeling YOY 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). We 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. We 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. We 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/s)[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			
Drainage area (km^2)[a]	171.8 ± 165.9	16.9 – 772.7	USGS NED[c]
Link magnitude	26.2 ± 34.3	1 – 215	USGS NHD[d]
Downstream link[a]	73.3 ± 127.0	4 – 694	USGS NHD[d]
Disturbance index	2.21 ± 0.32	1.48 – 2.90	NLCD 2011[e]

Impervious cover (%)	0.93 ± 0.64	0.17 – 3.64	NLCD 2011[f]
Catchment slope (%)	7.33 ± 3.31	2.59 – 18.02	USGS NED[c]
Hydro soil group D (%)	33.04 ± 14.60	5.93 – 72.49	SSURGO 2.2[g]
Carbonate geology (%)	94.45 ± 11.07	43.76 – 100	USGS, USDA NRCS[h]
Baseflow/total flow (%)	44.58 ± 5.13	31.43 – 53.26	USEPA StreamCat[i]
Runoff (mm)	345.8 ± 21.3	316.0 – 383.7	USEPA StreamCat[i]
Soil permeability (cm/hour)[a]	4.08 ± 0.31	3.08 – 4.90	USEPA StreamCat[i]
Precipitation and streamflow metrics			
April-July precip (mm)[a]	646.4 ± 179.2	417.6 – 1069.6	Oklahoma Mesonet[j]
Mean April-July flow (m^3/s)[a]	8.5 ± 6.2	3.0 – 11.7	USGS NWIS[k]
Mean April flow EP (%)	3.76 ± 3.06	0.04 – 6.43	USGS NWIS[k]
Mean May flow EP (%)	2.90 ± 2.93	0.32 – 6.23	USGS NWIS[k]
Mean June flow EP (%)	14.13 ± 9.00	0.84 – 23.86	USGS NWIS[k]
Mean July flow EP (%)[a]	13.43 ± 7.75	0.34 – 21.79	USGS NWIS[k]
Mean flood frequency	3.32 ± 1.33	1.82 – 4.73	USGS NWIS[k]
Mean flood duration (d)	17.13 ± 10.93	5.27 – 33.00	USGS NWIS[k]

a: Predictors (*n* = 11) used in evaluation of model distribution.
b: Ancillary variables (*n* = 3) measured only to evaluate sampling efficiency. Stream temperature and wetted width were considered for modeling both sampling efficiency and fish abundance.
c: http://ned.usgs.gov/
d: http://nhd.usgs.gov/
e: Homer et al. 2015, https://www.mrlc.gov/nlcd11_data.php
f: Xian et al. 2011, https://www.mrlc.gov/nlcd11_data.php
g: https://nrcs.app.box.com/v/soils
h: Stoeser et al. 2005, https://datagateway.nrcs.usda.gov/
i: Hill et al. 2016, https://www.epa.gov/national-aquatic-resource-surveys/streamcat
j: https://www.mesonet.org/
k: https://nwis.waterdata.usgs.gov/nwis/sw

Table 6. 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 were included in respective models but are not shown below 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 ΔAIC$_c$ 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$_c$	ΔAIC$_c$	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 7. 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 Highland 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

Table 8. Coefficient estimates, standard errors (SE) and 95% confidence intervals (CI) for the model of Smallmouth Bass nest detection efficiency in Ozark Highland streams. We 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 9. Rankings of top (i.e., within 2 AIC$_c$) candidate linear mixed models of Smallmouth Bass nest abundance in Ozark Highland 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 10. Coefficient estimates and 95% confidence intervals (CI) from the top-ranked candidate model of YOY 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

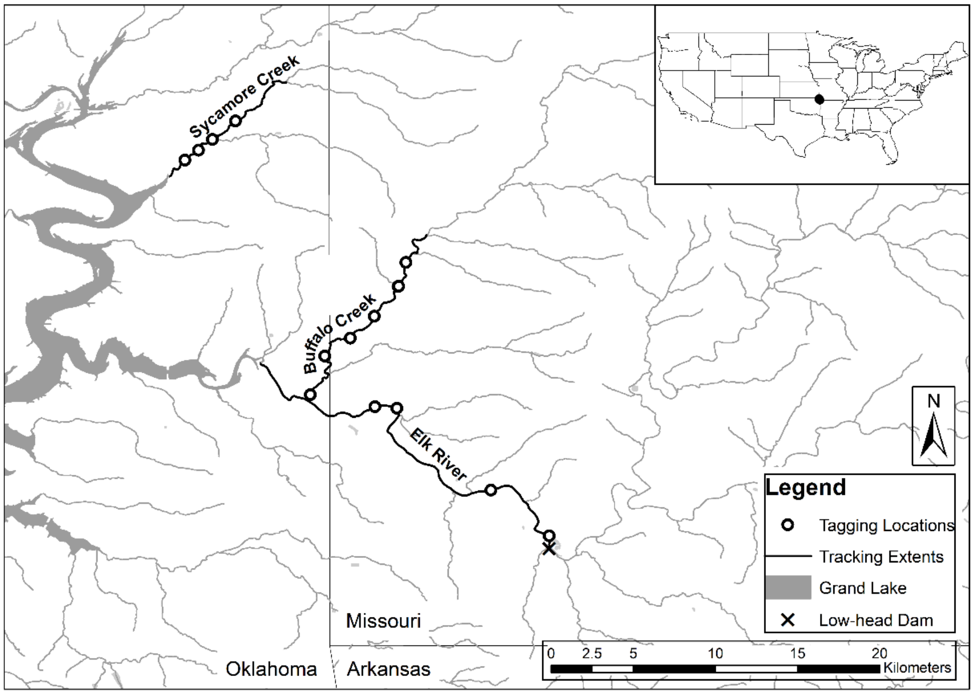

Figure 1. Tagging locations and tracking extents (bolded) for three Ozark streams where we evaluated movement and habitat use by adult Smallmouth Bass.

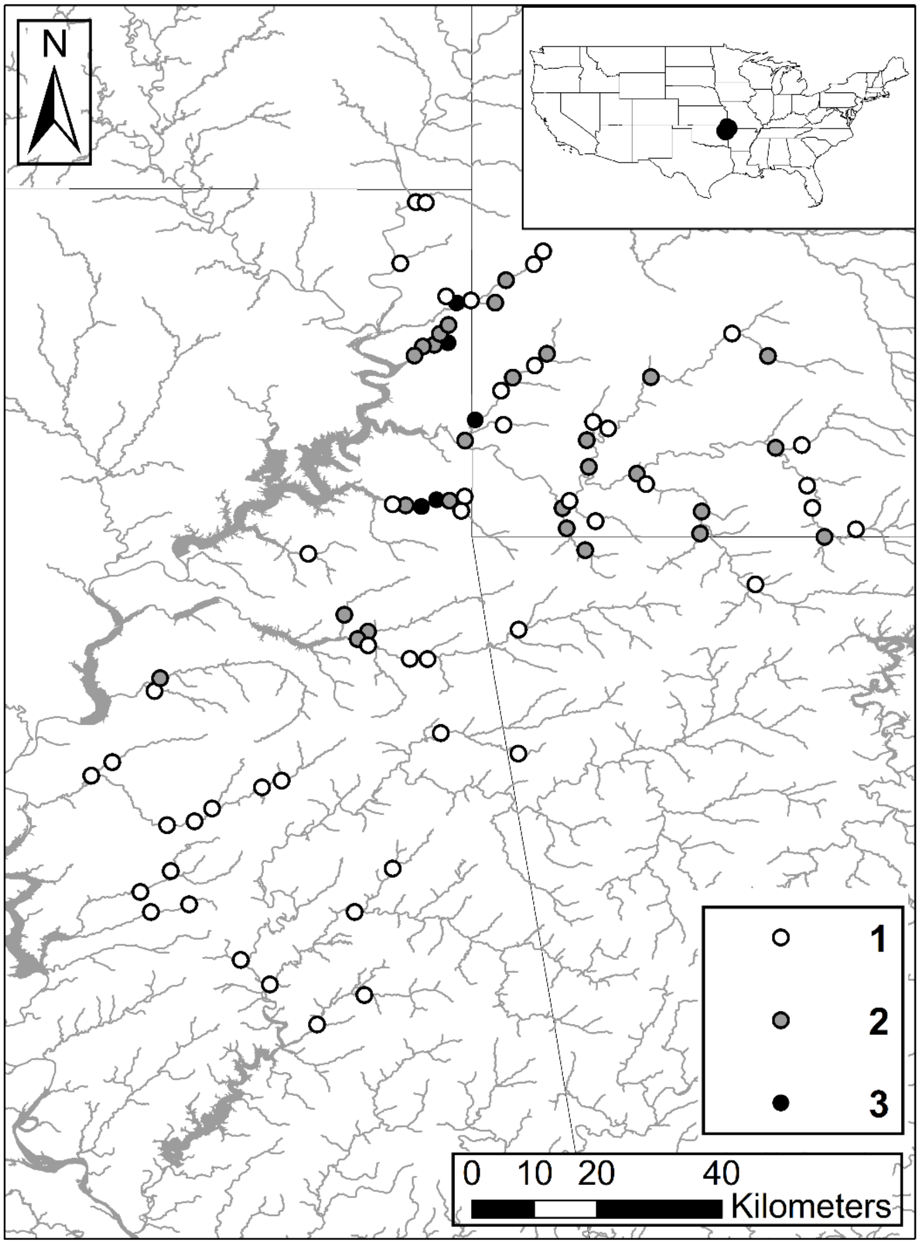

Figure 2. Map of stream reaches (*n* = 120) surveyed for Neosho Smallmouth Bass nests. Number of years (from 2016-2018) each reach was sampled is indicated by dot color. Reaches were sampled only once within a given year, and thus were treated as unique sites across years.

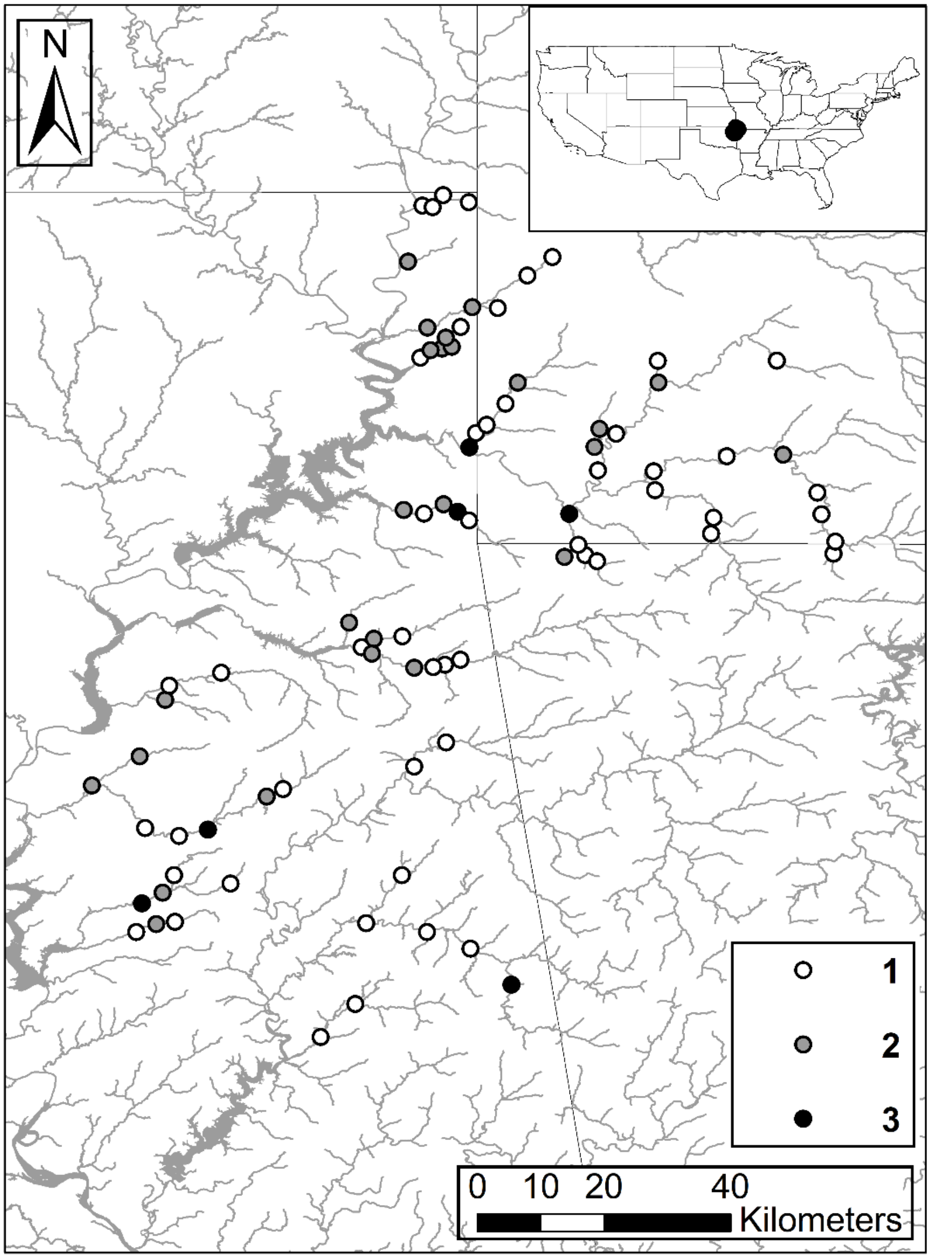

Figure 3. Location of stream reaches surveyed for YOY Smallmouth Bass. Dot color represents the number of years a reach was sampled (from 2015-2017). We did not sample reaches twice within a given year and reaches sampled in different years were treated as unique sites.

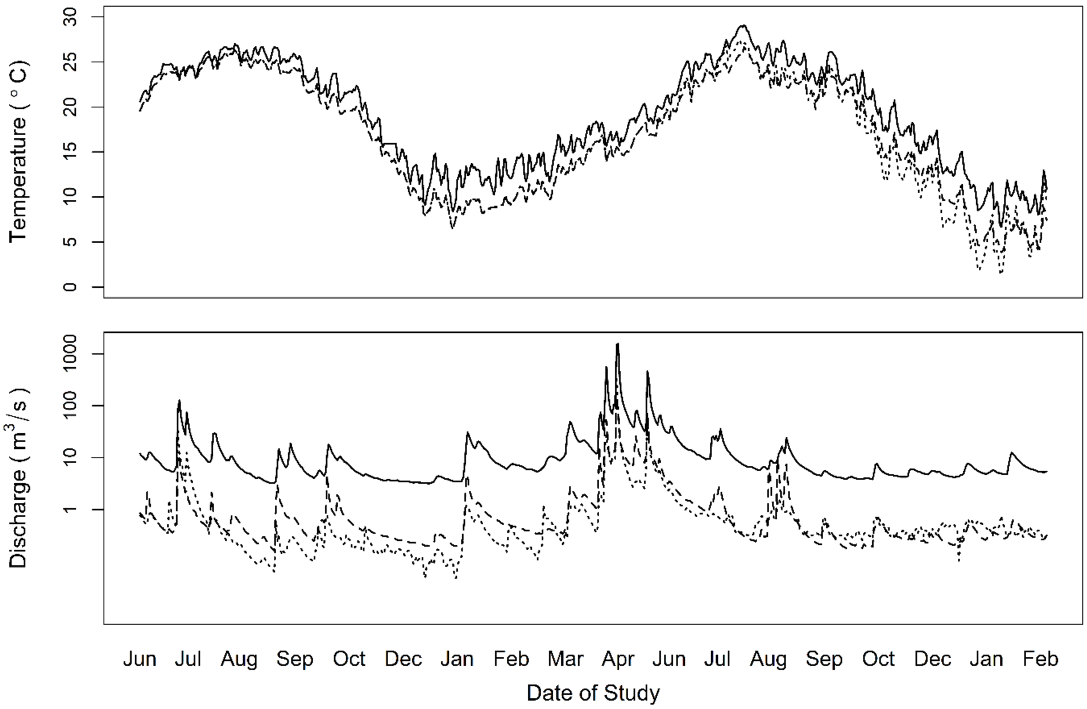

Figure 4. Daily mean water temperature (top) and discharge (bottom) conditions for Elk River (solid line), Buffalo Creek (dashed) and Sycamore Creek (dotted) during the June 2016–February 2018 study of adult Smallmouth Bass movement and habitat use. For reference, 1.0 m^3/s equals 35.3 ft^3/s. Note that 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 the Elk River).

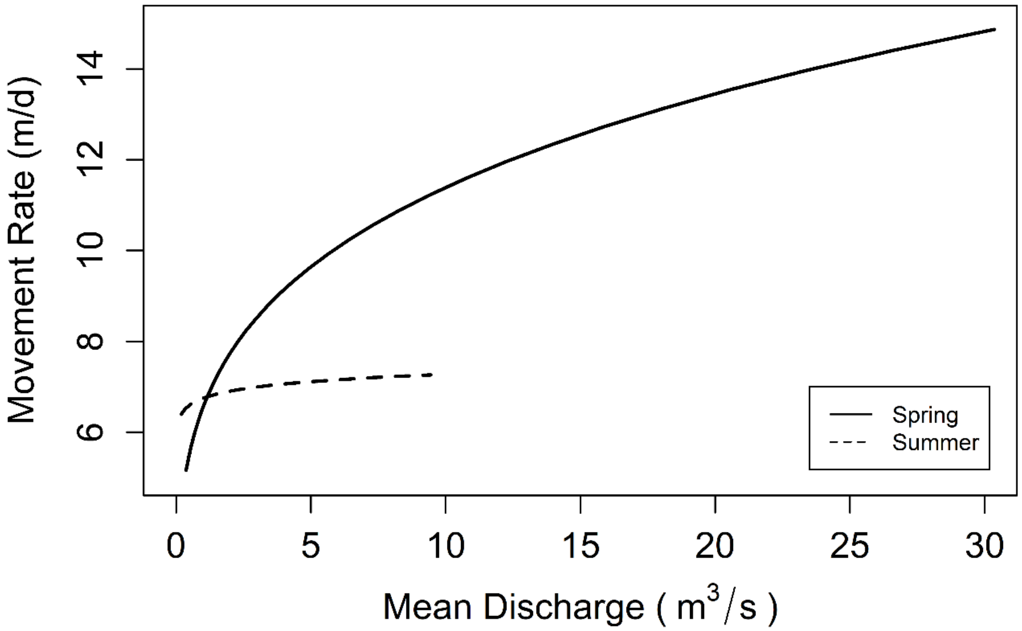

Figure 5. Predicted relationship between Smallmouth Bass movement rate (m/d) and mean discharge (m^3/s) in spring and summer. Predicted movement rates are not pictured for autumn (mean: 3.4 m/d) or winter (mean: < 0.1 m/d) as these predictions do not vary over the small range of discharge values (0.29–0.92 m^3/s) observed in the field. Predicted movement rates represent back-transformed mean discharge values in Buffalo Creek with all other continuous predictors held constant at mean levels.

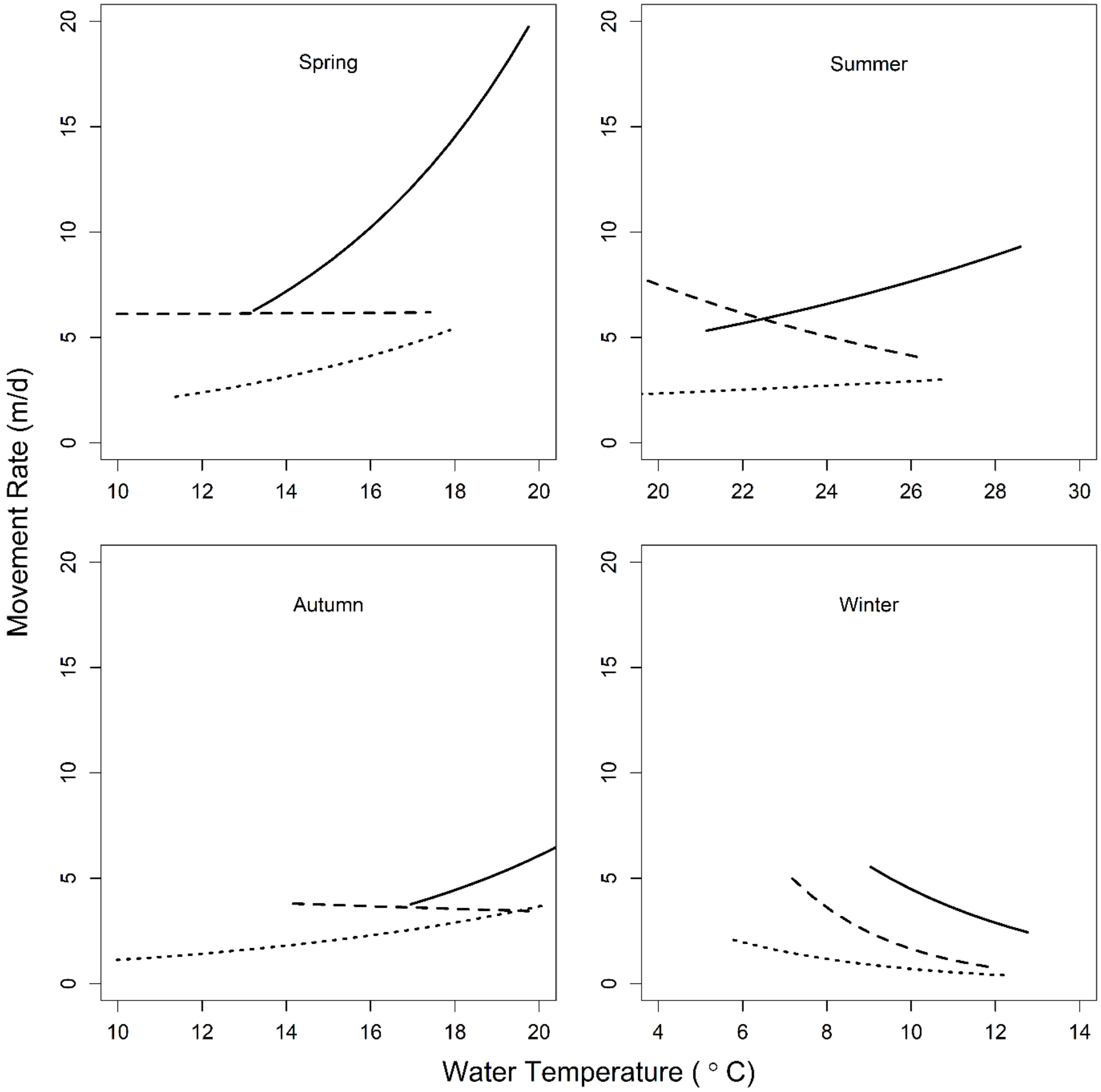

Figure 6. Modeled relationship between movement rate (m/d) of Smallmouth Bass and mean water temperature (°C) across three study streams and four seasons. The study streams are Elk River (solid line), Buffalo Creek (dashed), and Sycamore Creek (dotted). Predictions represent changes in water temperature with all other continuous model predictors held constant at their mean values.

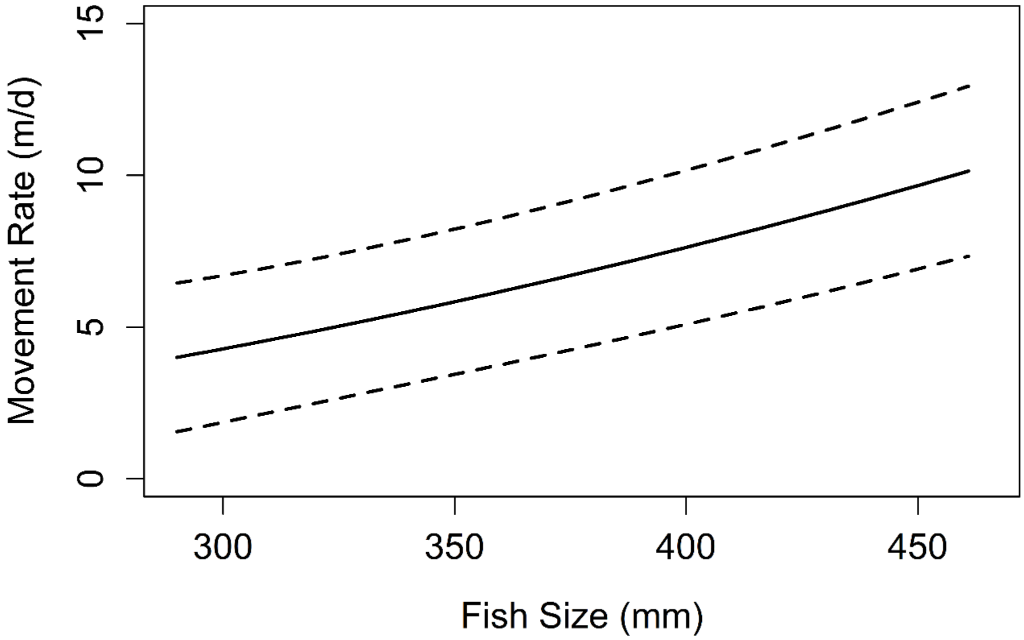

Figure 7. Relationship between movement rate (m/d) and fish size (TL, mm) from the top-ranked model of movement rate. Dashed lines indicate 95% confidence intervals. Predictions are made with all other continuous predictors at mean levels and with Elk River as the reference stream and summer as the reference season.

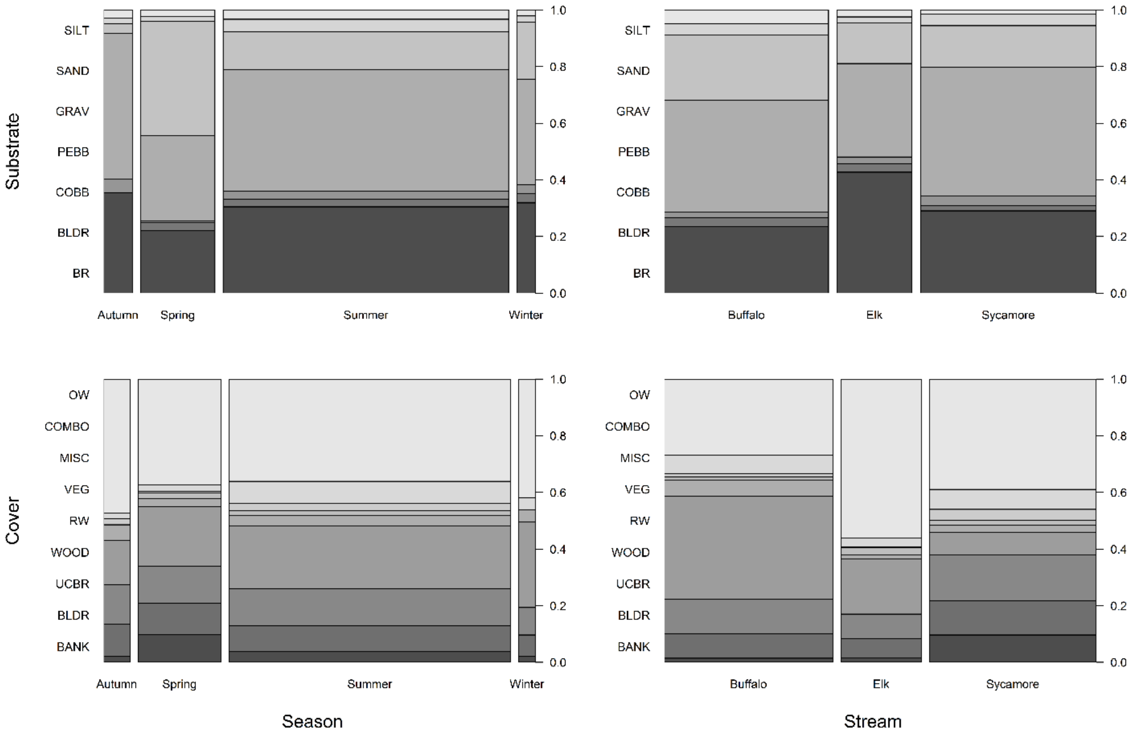

Figure 8. Summaries of proportional substrate and cover use across seasons and streams based on $n = 2{,}362$ observations of radio-tagged Smallmouth Bass. Column widths are proportional to sample size. Substrate types include silt (< 0.06 mm), sand (> 0.06–2 mm), gravel (> 2–16 mm; GRAV), pebble (> 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 and broken concrete.

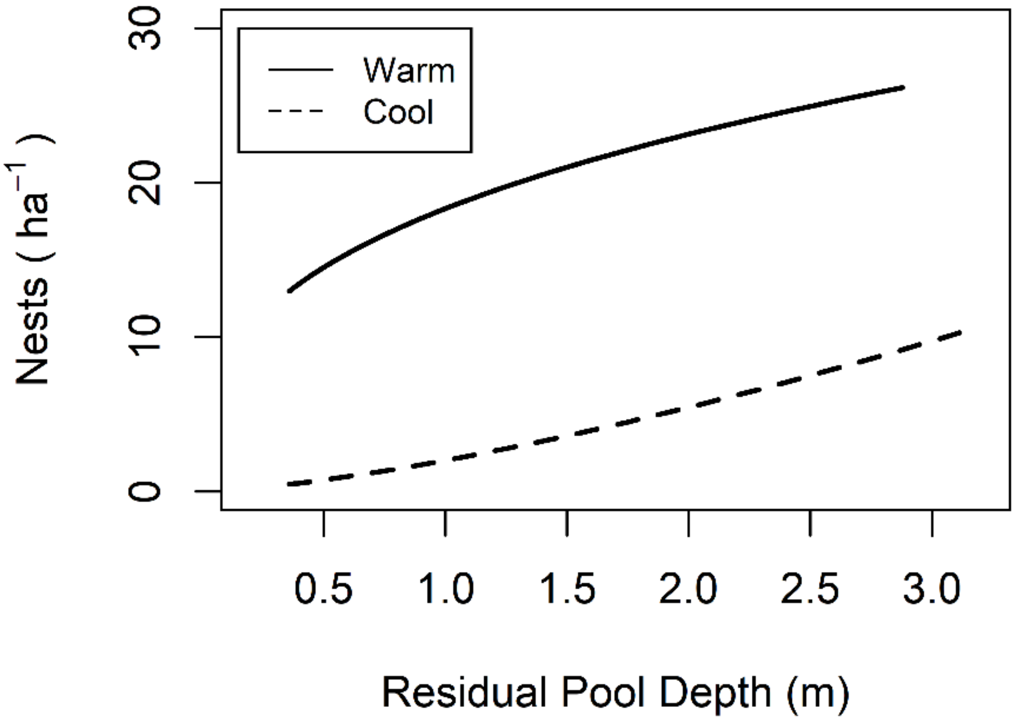

Figure 9. Relationship between residual pool depth (m) and Smallmouth Bass nest density in streams of two temperature classes: warm (> 19.5°C midday) and cool (≤ 19.5°C). Cool streams include those with relatively higher groundwater influence and those sampled earlier in the May–July study period.

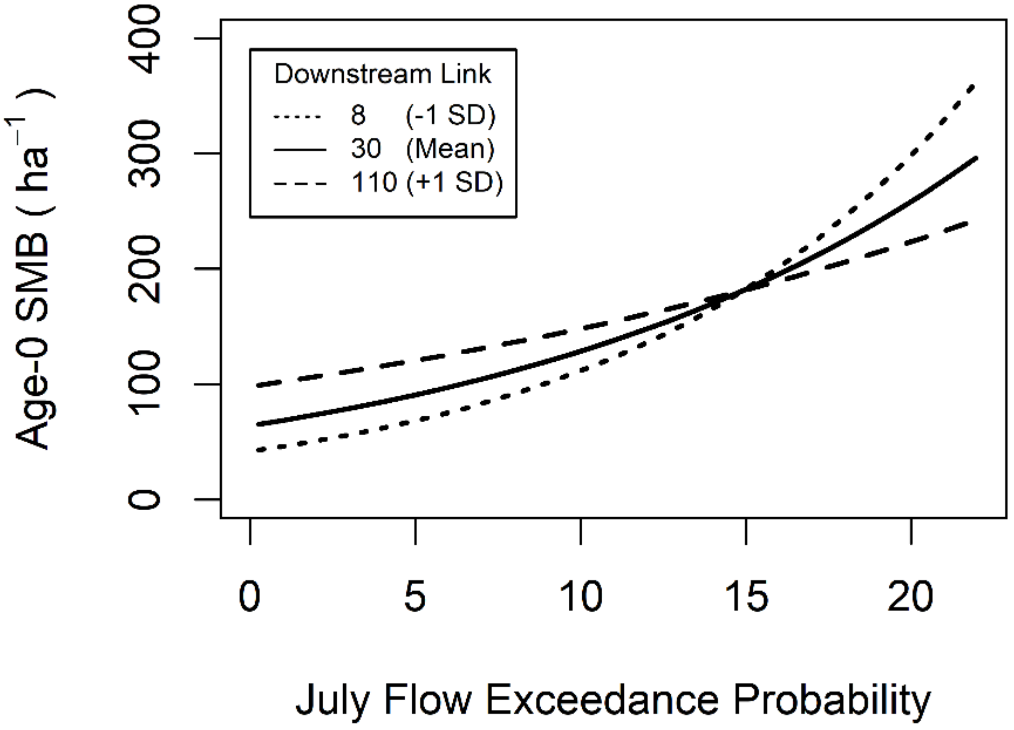

Figure 10. Model-predicted relationship between July flow exceedance probability and YOY Smallmouth Bass abundance in stream reaches with varying downstream link magnitudes. Modeled relationships are at mean values of other continuous predictors and at the reference stream temperature (i.e., warm; > 19.5 °C).

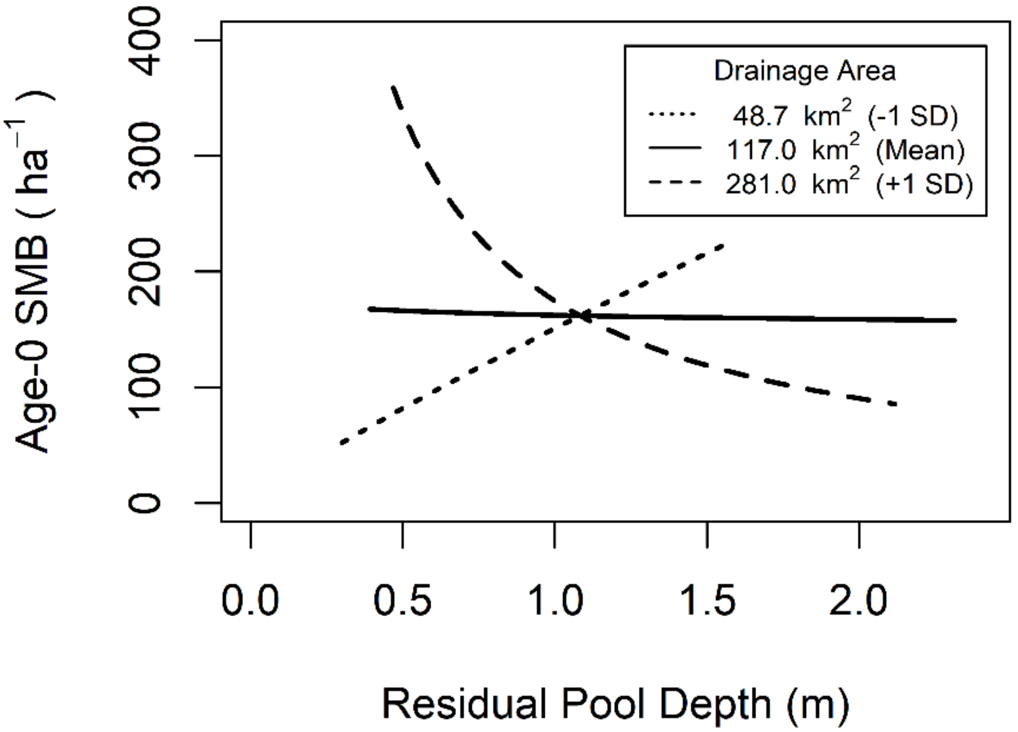

Figure 11. Model-predicted effect of residual pool depth (m) on YOY Smallmouth Bass abundance across three representative stream sizes (drainage areas [km^2]). Predictions are only included for combinations of residual pool depth and drainage area that co-occurred in the field. Relationships are modeled with other continuous predictors held at mean levels and for the reference stream temperature (i.e., warm; > 19.5 °C).

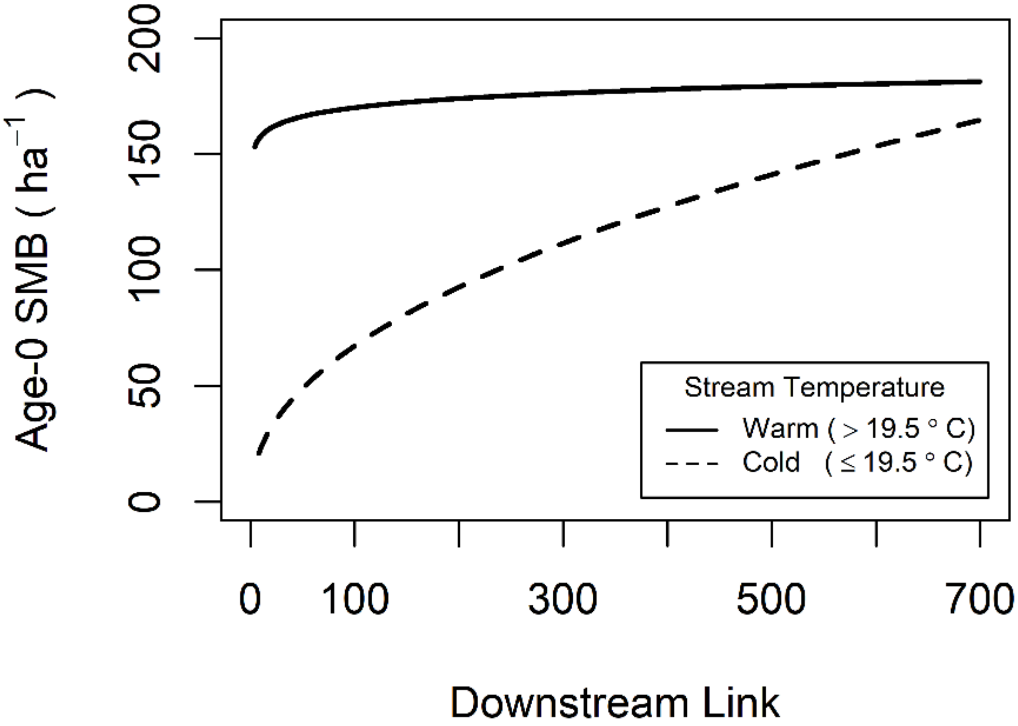

Figure 12. Relationship between downstream link magnitude and YOY Smallmouth Bass abundance in relation to stream temperature based on our top model. Stream temperature consists of two levels, cold (≤ 19.5 °C) and warm (> 19.5 °C), based on a natural break in our data.

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