Age-0 Smallmouth Bass abundance depends on physicochemical conditions and stream network position

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Abstract. Stream fish survival and recruitment are products of a physicochemical environment that affects growth and provides refuge; yet, the drivers of spatiotemporal variation in juvenile fish abundance remain unclear. Understanding how physicochemical conditions drive spatial and temporal patterns in fish abundances provides insight into how conditions across stream networks influence fish population success, thereby providing direction to managers about the types and locations of conservation actions that would be most beneficial. Using snorkel and habitat surveys of 120 sites sampled from 2015 to 2017, we evaluated the multiscale relationships among physicochemical features, hydrology, and age-0 Smallmouth Bass (Micropterus dolomieu velox) abundance in relation to network spatial position. Abundance of age-0 bass was spatiotemporally variable in relation to a July streamflow–network position interaction, a pool depth–stream size interaction, and a stream temperature–network position interaction. High flows at the end of the nesting season were related to lower age-0 abundance, but this effect was dampened in stream reaches in close proximity to larger mainstems. In small streams, reaches with deeper pool habitat supported higher age-0 bass abundances, but this trend was not apparent in larger tributaries and mainstem systems. Generally, colder streams had lower age-0 Smallmouth Bass abundance, though this relationship was not apparent in reaches adjacent to larger streams that generally supported higher age-0 bass abundances. Conservation actions that (1) facilitate habitat connectivity within and among streams, (2) limit future anthropogenic practices that alter natural geomorphology by creating shallower stream channels, and (3) maintain adequate flow magnitude and timing to support channel complexity (e.g., deeper pools within smaller catchments) would be most beneficial to supporting rearing habitat for age-0 riverine Smallmouth Bass.

Key words: extreme events; hydrology; rearing habitat; riverscape; Smallmouth Bass (Micropterus dolomieu velox).

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INTRODUCTION

Stream habitats are arranged in a spatially nested hierarchy, wherein coarse-scale landscape features modify finer-scale abiotic and biotic conditions (Frissell et al. 1986, Schlosser 1991) and create habitat heterogeneity (Wiens 1989, Allan et al. 1997). The relationship between local fish assemblages and habitat conditions is related to a variety of coarse-scale factors including climate (Eaton and Scheller 1996, Comte and Grenouillet 2013), geology (Neff and Jackson 2012), soils
(Brewer et al. 2007), and land use (Allan 2004, Brewer and Rabeni 2011). Intermediate-scale patterns in hydrology, water temperature, and groundwater influence are dictated by coarse-scale features and further modify local stream habitat, fish occupancy, and fish abundance (Torgersen et al. 2006, Brewer et al. 2007, Falke et al. 2010). Understanding how physicochemical conditions drive spatial and temporal patterns in fish abundances provides insight about how conditions across stream networks influence fish population success; unfortunately, the multiscale interactions that drive juvenile recruitment are rarely examined despite the importance of spatial proximity to conservation actions across catchments.

The first growing season of life represents a critical population bottleneck for many stream fishes and is influenced by a variety of abiotic factors across the river network. Although both biotic (e.g., predation, starvation, disease) and abiotic (e.g., extreme flows, temperatures) pressures affect juvenile fish survival (Schlosser 1982, Knotek and Orth 1998), abiotic factors across river networks are highly variable and can disproportionately affect fish populations (Hynes 1975, Fausch et al. 2002). For example, seasonal floods influence age-0 fish survival and subsequent recruitment (Smith et al. 2005); however, flood timing, fish size, and the availability of refuge habitats all influence fish susceptibility to flood disturbances (Pearsons et al. 1992, Lobón-Cerviá 1996). The nature of both disturbances and refuges varies with environmental conditions and the degree of local adaptation by fishes (Gelwick 1990, Schlosser and Angermeier 1995), and multiscale habitat features may further influence these relationships (Kennard et al. 2007, Arthington et al. 2010). Because multiscale physicochemical conditions lead to spatiotemporal variability in recruitment and, thus, population dynamics (Elliott 1989, Schlosser 1998), efforts to elucidate these relationships in the context of stream network position (i.e., relative location in a connected network of headwater and mainstem streams) are essential for the effective conservation and management of stream fishes.

Our study objective was to evaluate the multiscale relationships among physicochemical features, hydrology, spatial context, and age-0 Smallmouth Bass (Micropterus dolomieu velox) abundance in the Ozark Highlands ecoregion. Previous research indicates that both fine-scale habitat (see overview by Pert et al. 2002) and coarse-scale features (e.g., land use, soil texture, soil permeability; Dauwalter et al. 2007, Brewer and Rabeni 2011) influence age-0 Smallmouth Bass abundance. Likewise, there is evidence for both microhabitat specialization and plasticity by age-0 Smallmouth Bass (Orth and Newcomb 2015). Because age-0 Smallmouth Bass abundance is frequently used as an index of reproductive success (Pflieger 1975, Smith et al. 2005), we identified factors related to age-0 abundance that correspond to the scale most relevant to fisheries management evaluations (i.e., reach scale; Fausch et al. 2002). Additionally, we examined abiotic factors at coarser spatial scales (i.e., stream segment, catchment) known to constrain finer-scale patterns and processes (see overview by Frissell et al. 1986) and which allowed us to make use of existing geospatial and hydrologic data matching those scales (e.g., multiple stream reaches within the same stream segment are influenced by similar patterns of lithology).

**Materials and Methods**

**Study area**

We sampled 120 stream reaches (20 times average channel width) that were nested within 70 stream segments (i.e., portion of a stream between two tributary junctions; Frissell et al. 1986) across the Neosho subspecies’ range in the southwest Ozark Highlands ecoregion (Fig. 1). Stream reaches comprised multiple channel units representing typical riffle-run-pool morphology.
with occasional slackwater complexes (Rabeni and Jacobson 1993). Average channel width across sampled streams ranged 3.8–21.8 m during the late summer–autumn study period.

The landscape of the Ozark Highlands is characterized by cherty limestone lithology, karst topography, and numerous springs, resulting in variable groundwater inputs within and among streams (Zhou et al. 2018), low suspended sediment loads under baseflow conditions, and predominately gravel-cobble substrates (Nigh and Schroeder 2002). The climate is relatively humid (average annual rainfall: 106–110 cm), and stream flow regimes range from flashy to stable with some streams displaying seasonal intermittency (e.g., disconnected surface flows; Hafs et al. 2010, Leasure et al. 2016). Predominant land uses in this region are forest and pasture,
though ongoing watershed development has resulted in more frequent high-magnitude flows and reduced baseflows (Nigh and Schroeder 2002, TNC 2003, Lynch et al. 2019). Impoundments across the catchments create a number of river–reservoir complexes and river fragments.

Fish surveys
We surveyed age-0 Smallmouth Bass using snorkel surveys that were conducted in late summer and early autumn 2015–2017. We timed our sampling efforts 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 (Dunham et al. 2009), water temperature, and fish activity (Oliver et al. 1979). All surveys were conducted during daylight 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). Lanes were defined by both visibility and habitat complexity where areas of lower visibility and highly complex habitat resulted in much narrower sample lanes (Thurow et al. 2012). Age-0 Smallmouth Bass were distinguished from other sympatric basses (Spotted Bass M. punctulatus and Largemouth Bass M. salmoides) via the lack of horizontal black bars and the presence of a tri-colored tail.

Habitat
We quantified habitat characteristics at each stream reach immediately following our fish survey(s) (Table 1). Discharge (0.01 m³/s) was measured at each site using the velocity–area method (Gordon et al. 2004). Channel units were classified as riffles, runs, pools, or slackwaters following a simplified version of Rabeni and Jacobson (1993). We quantified the percent area of different channel unit types in each reach. 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), representative of channel depth independent of stream stage height, following the methods of Lisle (1987). We measured water temperature (0.1°C) at mid-pool depth with a thermometer (Ultrapen PT1, Myron L, Carlsbad, California, USA). Because we only had a point measure from the time of sampling and these data showed a distinct break between cooler and warmer streams (i.e., bimodal distribution), 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, USA) to summarize habitat attributes for each stream segment (Table 1). Following the methods of Jenson and Domingue (1988), we delineated overland flow-direction pathways (O’Callaghan and Mark 1984) and upstream contributing areas (i.e., catchments; 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]). Using our in-stream flow-direction grid, we calculated two topology metrics: link magnitude (Shreve 1966) and downstream link (Osborne and Wiley 1992). Link magnitude reflects stream size and is calculated as the number of unique sources contributing to a given stream segment. Downstream link describes spatial position within the stream network (i.e., the size of the stream receiving a segment). For example, stream segments located in the headwaters of a catchment have small downstream link magnitudes, while those located lower in the drainage network (e.g., connected to large, main-channel rivers) have larger downstream link values. 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 an index following Mouser et al. (2019); modified from Brown and Vivas (2005). The coefficients (possible range 1.00–8.32) reflected the hypothesized severity of particular land cover on aquatic biota (2011 National Land Cover Dataset, Appendix S1: Table S1). The lowest coefficient (1.00) represented undisturbed habitats (e.g., forests, wetlands), whereas more disturbed habitats had higher values (e.g., 7.92 for high-intensity development). Undisturbed habitat included several land use categories: open water, barren land, deciduous forest, evergreen forest, mixed forest, shrub/scrub, herbaceous, woody wetlands, and emergent
Table 1. Summary statistics and data sources associated with the predictor variables used for modeling age-0 Smallmouth Bass abundance–habitat relationships.

| Scale         | Variable                                | Mean ± SD      | Range          | Data source          |
|---------------|-----------------------------------------|----------------|----------------|----------------------|
| Reach         | Sampling date (day of year)†            | 258.4 ± 19.1   | 215–312        | F†                   |
|               | Stream temperature (°C)†,§              | 21.6 ± 2.7     | 15.1–27.5      | F                    |
|               | Wetted width (m)†                       | 9.9 ± 4.0      | 3.8–21.8       | F                    |
|               | Residual pool depth (m)†                | 0.92 ± 0.40    | 0.20–2.37      | F                    |
|               | Pool habitat (%)†,§                     | 73.7 ± 15.8    | 9.9–100        | F                    |
|               | Riffle habitat (%)§                     | 9.4 ± 7.8      | 0.0–35.3       | F                    |
|               | Wetted area sampled (m²)†               | 4046.5 ± 4195.7| 295.2–28415.1  | F                    |
| Segment       | Link magnitude                          | 26.2 ± 34.3    | 1–215          | USGS§                |
|               | Downstream link†,§                      | 73.3 ± 127.0   | 4–694          | USGS§                |
|               | Drainage area (km²)†,§                  | 171.8 ± 165.9  | 16.9–772.7     | USGS§                |
|               | Catchment slope (%)                     | 7.33 ± 3.31    | 2.59–18.02     | USGS§                |
|               | Disturbance index                       | 2.21 ± 0.32    | 1.48–2.90      | NLCD†                 |
|               | Impervious cover (%)                    | 0.93 ± 0.64    | 0.17–3.64      | NLCD†                 |
|               | Hydro soil group D (%)                  | 33.04 ± 14.60  | 5.93–72.49     | USDA§§               |
|               | Carbonate geology (%)                   | 94.45 ± 11.07  | 43.76–100      | USGS, USDA#          |
|               | Baseflow/total flow (%)§                | 44.58 ± 5.13   | 31.43–53.26    | USEPA#               |
|               | Runoff (mm)§                            | 345.8 ± 21.3   | 316.0–383.7    | USEPA#               |
|               | Soil permeability (cm/hour)†,§          | 4.08 ± 0.31    | 3.08–4.90      | USEPA#               |
|               | April–July precip (mm)†,§               | 646.4 ± 179.2  | 417.6–1069.6   | OK Mesonet|||
|               | Mean April–July flow (m³/s)†            | 8.5 ± 6.2      | 3.0–11.7       | USGS††               |
|               | Mean April FE (%)                       | 3.76 ± 3.06    | 0.04–6.43      | USGS††               |
|               | Mean May FE (%)                         | 2.90 ± 2.93    | 0.32–6.23      | USGS††               |
|               | Mean June FE (%)                        | 14.13 ± 9.00   | 0.84–23.86     | USGS††               |
|               | Mean July FE (%)‡,§                     | 13.43 ± 7.75   | 0.34–21.79     | USGS††               |
|               | Mean flood frequency                    | 3.32 ± 1.33    | 1.82–4.73      | USGS††               |
|               | Mean flood duration                     | 17.13 ± 10.93  | 5.27–33.00     | USGS††               |

† Predictors (n = 11) used in evaluation of model distribution.
‡ F = Variable was measured in the field.
§ Univariate predictors (n = 10) retained following variable reduction along with two way interactions (n = 11; all combinations of drainage area, mean July flow exceedance (FE, a probability converted to percentile), downstream link, and stream temperature, and drainage area × residual pool depth, drainage area × April–July precip, drainage area × pool habitat, mean July FE × soil permeability, and stream temperature × April–July precip).
¶ Wetted area sampled was used to scale abundance values and was included in all models as an offset term.
# http://nhd.usgs.gov/ || http://ned.usgs.gov/ †† http://mrlc.gov/ncld11_data.php †‡ Xian et al. (2011), https://www.mrlc.gov/ncld11_data.php §§ NRCS (2017), https://websoilsurvey.sc.egov.usda.gov |||| Stoeser et al. (2005), https://datagateway.nrcs.usda.gov/ # Hill et al. 2016, https://www.epa.gov/national-aquatic-resource-surveys/streamcat |||| https://www.mesonet.org/ ††† https://nwis.waterdata.usgs.gov/nwis/sw

Herbaceous wetlands. The coefficient was multiplied by the proportion of that land cover category within the catchment of each stream segment. The resulting values were summed across all land-use categories to obtain a final disturbance index for 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). 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 hydrology (2015–2017) during the perceived spawning and early growing period of Smallmouth Bass (April–July depending on flow conditions; Brewer et al. 2019, Brewer and Miller 2019). Because many of the streams we sampled did not have stream gages, we summarized available data using 11 representative U.S. Geological Survey stream gages: 07189100, 07188653, 07188838, 07188885, 07189540, 07189542, 07191222, 071912213, 07196000, 07197000, and 07197360 (Appendix S1: Table S2). Using daily streamflow data, we calculated mean and maximum discharge from April to July for each year. We also calculated corresponding minimum monthly flow exceedance probabilities. Flow exceedance probabilities quantify the relative frequency of a given streamflow magnitude based on historical discharge data, typically from at least 10 yr of record (Gordon et al. 2004). For example, if a given daily discharge occurs or is exceeded, on average, once every 20 d, it would have an exceedance probability or percentage of 0.05% or 5%, respectively. Thus, smaller flow exceedance percentages correspond to higher discharge values for a given stream. Lastly, we calculated the average frequency and duration of higher flow events (>10 m$^3$/s, associated with Smallmouth Bass nest failure; Lukas and Orth 1995) and summarized precipitation trends across the study area for April–July of each year (https://www.mesonet.org/, accessed April 2018; Appendix S1: Table S3).

**Analyses**

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 age-0 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 (Bartoci 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. A comparison of GLMM forms (i.e., Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial [ZINB]) using 11 fixed-effect predictors (Table 1) and random effects for stream segment and sample year indicated that a ZINB model with zero inflation modeled in relation to stream temperature provided the best model fit (AIC$_c$ weight > 0.99).

We used model selection to reduce the number of possible explanatory variables in our final analysis. We developed 47 ZINB models, each containing one univariate predictor variable ($n$ = 25; Table 1) or two-way interactions of a priori interest ($n$ = 22; Appendix S1: Table S4) and compared them to a random-intercept only (null) model. We used Akaike’s information criterion adjusted for small sample size (AIC$_c$, Sugita 1978, Hurvich and Tsai 1989) to rank our models. We retained predictor variables from all models with AAIC$_c$ < 2 relative to the null model (Burnham and Anderson 2002). To minimize issues with interpretation, we reduced any remaining covariates with pairwise correlations ≥0.6 by retaining the predictor variable with better model fit (Dormann et al. 2013; Appendix S1: Table S5). The reduced variable set contained 10 univariate predictors and 11 two-way interaction terms (Table 1).

Using our reduced variable set, we developed a set of 261 candidate models. Initial model comparisons suggested July flow exceedance (FE, expressed as a percentage) and several two-way interaction terms (i.e., July FE × drainage area, July FE × downstream link, July FE × stream temperature, and drainage area × residual pool depth) were particularly influential predictors (i.e., AIC$_c$ weight ≥ 0.11). We used all additive combinations of these five terms to build a base set of 17 models. We then added the remaining univariate and two-way interaction terms (Table 1) to this base model set to build our candidate set of 261 models. Models that included interaction terms also contained the univariate terms for each predictor involved in the interaction. 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 1996).
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 $\tau^2$ 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 AICc for our candidate set to determine the variable set that had the most support. This approach was intended to be somewhat exploratory but also 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 $R^2$ (amount of variance explained by the fixed effects) and conditional $R^2$ (amount of variance explained by both fixed and random effects; Vonesh et al. 2006, Nakagawa and Schielzeth 2013). For zero-inflated mixed models, marginal $R^2$ and conditional $R^2$ calculations do not consider the zero-inflation model. These calculations were performed using the sjstats package (Lüdecke 2018) in R.

RESULTS

Snorkel surveys

Smallmouth Bass abundance varied among the study reaches sampled. We observed age-0 Smallmouth Bass in 103 of 120 surveyed stream reaches (drainage area range: 16.9–772.7 km²), with an average of 181.3 ± 182.5 ha⁻¹ (mean ± SD) at occupied sites (range: 1–1347 ha⁻¹). Stream temperature explained some absences of age-0 Smallmouth Bass, with model-predicted zero-inflation of 30% for cold streams (≤19.5°C) and 8% for warm streams.

Habitat and annual hydrology

Habitat conditions and hydrology varied among sites and years (Table 1; Appendix S1: Table S2). 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 in their spatial position relative to larger streams, with downstream link values ranging from 4 to 694 (i.e., some reaches were located in the headwaters, whereas others were adjacent to large main-channel rivers). Flows during the nesting and early growing 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 S1: Tables S2, S3).

Fish–habitat relations

The top model explaining conditional abundance of age-0 Neosho Smallmouth Bass (i.e., after accounting for zero inflation in cold study reaches) contained several interaction terms for reach and segment-scale predictors and hydrology (Table 2). Late-summer abundances of age-0 Smallmouth Bass were positively associated with higher July FE (i.e., more benign July flows), though this relationship was more pronounced in upstream reaches of the catchment (Fig. 2). The association between residual pool depth and age-0 Smallmouth Bass abundance was dependent on stream size (Fig. 3). In smaller streams, greater age-0 Smallmouth Bass abundance was associated with channels with deeper pools. There was no clear relationship between abundance and pool depth in average-size streams (drainage area: ~117.0 km²), whereas abundance and pool depth were slightly inversely related in larger streams. The relationship between age-0 Smallmouth Bass abundance and downstream link magnitude was minimal in warm (>19.5°C) stream reaches, but a positive trend was observed for cold streams (Fig. 4). Collectively, the fixed effects in our model explained 57% of the variability in age-0 Smallmouth Bass abundance (marginal $R^2 = 0.57$). No additional variability was explained by our 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

We found several relationships between age-0 Smallmouth Bass abundance and abiotic conditions that were modified by stream network position and stream size. This suggests that large and small streams serve as complementary...
refuge habitats under different abiotic scenarios. The relative influences of water temperature, July flow magnitude, and pool depth on age-0 abundance were variable across the stream network. We speculate that these findings reflect the importance of habitat connectivity within and among stream systems to allow fish to seek refuge from natural disturbances and environmental variability. Although age-0 Smallmouth Bass use a variety of habitats throughout their
range (Pert et al. 2002, Dauwalter et al. 2007, Brewer 2013), current conservation and management efforts often fail to support instream habitat complexity. Efforts to preserve and improve habitat diversity across riverscapes would be beneficial for the persistence of this genetically distinct Smallmouth Bass under varying environmental conditions.

Both warm- and cold-water habitats are important to age-0 Smallmouth Bass across large spatial extents. In particular, the juxtaposition of colder tributary stream reaches with warmer main-channel habitats may benefit young fish by providing heterogeneous habitat with both favorable growth conditions (i.e., warmer streams) and lower predation risk (i.e., colder streams). Young Smallmouth Bass grow better in warmer streams, with optimum growth occurring between 25° and 28°C (Peek 1965, Coutant and DeAngelis 1983). Faster growth in turn confers added resistance against predation and environmental disturbance (e.g., displacement during floods; Harvey 1987). Growth of age-0 Smallmouth Bass also creates an important buffer against starvation during the overwinter period, which often serves as a recruitment bottleneck (Oliver et al. 1979, Shuter et al. 1980). However, juvenile development and growth of Smallmouth Bass are possible at temperatures from 20° to 32°C (Wrenn 1980). We observed varying abundances of age-0 Smallmouth Bass in 58% of cold stream reaches, suggesting that these habitats may serve important functions for overall recruitment and merit further study. Cold streams may offer additional foraging opportunities and reduced intraspecific competition. Similarly, predation risk may be lower in colder systems due to fewer large piscivores using these thermally unfavorable environments. Small, groundwater-dominated streams may also provide refuge from highly variable temperature conditions in larger reaches (Peterson and Rabeni 1996). Warm- and cold-water habitats provide conditions favorable for age-0 Smallmouth Bass under varying abiotic and biotic pressures, and the close proximity of these habitats creates heterogeneity that appears to be particularly beneficial for survival.

Flood magnitude and timing during the spawning and post-nesting period were important predictors of age-0 Smallmouth Bass abundance at the end of the first summer, though we found this relationship was influenced by stream network position. Late-summer abundance of
age-0 Smallmouth Bass was greater in years where July flow EP was greater (i.e., July flows were more benign). Considerable inter-annual variability in age-0 stream fish abundance and recruitment is common and often reflects the timing of high flows, with floods that occur during nesting and larval development being particularly detrimental (Smith et al. 2005, Blum et al. 2018). In streams throughout their range, floods destroy and displace Smallmouth Bass eggs and larvae (Larimore 1975, Winemiller and Taylor 1982, Lukas and Orth 1995). That flood timing was important in our study likely reflects the protracted nature of Smallmouth Bass spawning, which can occur from April to July depending on flow and temperature conditions (Brewer and Orth 2015, Brewer and Miller 2019). Early spring flooding destroys nests but allows for re-nesting opportunities over the following months (Lukas and Orth 1995). Conversely, large floods later in the spawning period preclude re-nesting attempts as stream temperatures become too warm (i.e., >25°C; Robbins and MaCrimmon 1977, Graham and Orth 1986). We observed the highest abundances of age-0 Smallmouth Bass in 2017, when early spring flooding was severe but July flows were benign. When July floods were larger, as in 2015, observed abundances of age-0 Smallmouth Bass were notably lower. 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., slackwaters) by age-0 Smallmouth Bass increases under elevated flows (Brewer et al. 2019). The abundance-flow relationship was more pronounced (i.e., higher flows were associated with greater reductions in abundance) in more isolated streams (i.e., those located upstream), suggesting that these streams serve as important habitats for age-0 Smallmouth Bass but are more susceptible to variable flow conditions. 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. Future work focusing on finer-scale modeling of streamflow dynamics and developing mechanistic linkages between hydrology, habitat, and age-0 abundance would be beneficial.
An interactive effect of residual pool depth and drainage area also explained variation in age-0 Smallmouth Bass abundance. Age-0 Smallmouth Bass are often associated with intermediate depths, but deep habitats can also contain high fish densities (Sabo and Orth 1994, Dauwalter et al. 2007) and considerable plasticity in depth use has been observed (Pert et al. 2002, Brewer 2011). The modeled relationship between depth and abundance was positive in smaller streams and negative in larger streams, and may reflect varying degrees of habitat limitation or flexibility in individual habitat use among streams (Pert et al. 2002). Deeper habitats may be favorable in small streams where avian predators predominate (Power et al. 1989), whereas deeper habitats are less favorable in larger streams due to larger fish predators (Steinmetz et al. 2008). Greater habitat area, whether conferred by deeper pools (e.g., in small streams) or wider channels (e.g., in large streams), provides habitat heterogeneity and associated thermal variability (Arrigoni et al. 2008, Westhoff and Paukert 2014), diverse foraging opportunities (Sabo et al. 1996), and refuge from disturbance, predation, and density-dependent effects (Lukas and Orth 1995, Nislow et al. 2004).

Our analysis of juvenile first-summer survival underscores the importance of diverse habitats and their connectivity across the riverscape, thereby indicating the value of conditions that allow fish movement within and among streams. Age-0 Smallmouth Bass are capable of fine-scale movements between habitats in search of refuge (Brewer et al. 2019, Miller et al. 2019) and larger migrations of age-0 individuals among tributaries occur elsewhere in their range (Humston et al. 2010, 2017). Short-term movements to exploit favorable foraging conditions in warmer, more productive habitats may explain how network position mitigates the influence of colder streams on age-0 Smallmouth Bass abundance. Access to larger, more productive streams may benefit growth (Vannote et al. 1980, Gorman 1986) and in turn confer resistance to size-dependent displacement and mortality during floods (Larimore 1975, Jager et al. 1993).

Age-0 Smallmouth Bass survival is influenced by habitat characteristics that operate at different spatiotemporal scales, and our data suggest habitat connectivity is important for the conservation and management of these populations. Although our disturbance index containing land-use metrics was not related to current juvenile abundances, our results showing the importance of deeper-water habitats of small streams to juvenile rearing could be maintained over time by limiting anthropogenic activities that degrade stream channels and exacerbate extreme flows (e.g., deforestation, urbanization, groundwater pumping; Poff et al. 1997, Paul and Meyer 2001). Gravel-bed streams are frequently reorganized during high, flashy flows (Rabeni and Jacobson 1993, Leasure et al. 2016), and these geomorphic changes (e.g., bed-form change, sedimentation, channel shallowing, and widening) can lead to decreases in age-0 stream fish survival and abundance (Nislow et al. 2004, Harvey et al. 2009). The removal of riparian buffers and gravel mining exacerbate the geomorphic consequences of high and low flows (Rabeni and Jacobson 1993, Naiman and Decamps 1997) and would be expected to negatively affect rearing habitat. Ongoing watershed development and urbanization in the Ozark Highlands ecoregion result in more frequent and higher-magnitude floods and reduced baseflows that decrease habitat connectivity and affect biota (Poff et al. 1997, TNC 2003, Lynch et al. 2019). Maintaining existing stream connectivity patterns is important for permitting fish to access refuge and foraging habitats and may mitigate negative influences on survival across catchments (Peterson and Rabeni 1996, Labbe and Fausch 2000). These efforts will be especially important in light of a changing climate that is expected to result in more extreme weather and hydrology patterns (Mulholland et al. 1997, Doß and Zhang 2010, Singh et al. 2013). Our work shows how consideration of network position is important when examining multiscale approaches to stream management (Rabeni and Sowa 2002) or restoration (Roni et al. 2002) particularly if focused on improving juvenile fish rearing habitat.

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LITERATURE CITED

Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology 37:149–161.

Allan, J. D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35:257–284.

Arrigoni, A. S., G. C. Poole, L. A. K. Mertes, S. J. O’Daniel, W. W. Woessner, and S. A. Thomas. 2008. Buffered, lagged, or cooled? Disentangling hyporheic influences on temperature cycles in stream channels. Water Resources Research 44:09418.

Arthington, A. H., J. D. Olden, S. R. Balcombe, and M. C. Thoms. 2010. Multi-scale environmental factors explain fish losses and refuge quality in drying waterholes of Cooper Creek, an Australian arid-zone river. Marine and Freshwater Research 61:842–856.

Bartoń, K. 2018. MuMIn: multi-model inference. R package version 1.40.4. https://cran.r-project.org/package=MuMIn

Betz, R., N. P. Hitt, R. L. Dymond, and C. D. Heatwole. 2010. A method for quantifying stream network topology over large geographic extents. Journal of Spatial Hydrology 10:15–29.

Blum, A. G., Y. Kanno, and B. H. Letcher. 2018. Seasonal streamflow extremes are key drivers of Brook Trout young-of-the-year abundance. Ecosphere 9:02356.

Bolker, B. 2017. bbmle: tools for general maximum likelihood estimation. R Package Version 1:20. https://cran.r-project.org/package=bbmle

Brewer, S. K. 2011. Patterns in young-of-year Smallmouth Bass microhabitat use in multiple stream segments with contrasting land uses. Fisheries Management and Ecology 18:506–512.

Brewer, S. K. 2013. Groundwater influences on the distribution and abundance of riverine Smallmouth Bass, Micropterus dolomieui, in pasture landscapes of the midwestern USA. River Research and Applications 29:269–278.

Brewer, S. K., B. Brown, T. A. Worthington, R. Mollenhauer, A. Rodger, M. Skoog, and J. Burroughs. 2019. First summer survival and channel-unit habitat use by the Neosho subspecies of Smallmouth Bass (Micropterus dolomieui velox). Pages 21–37 in M. Siepker and J. W. Quinn, editors. Managing centrarchid fisheries in rivers and streams. American Fisheries Society, Bethesda, Maryland, USA.

Brewer, S. K., and J. M. Long. 2015. Biology and ecology of genetically-distinct Neosho and Ouachita Smallmouth Bass. Pages 281–296 in M. D. Tringali, M. S. Allen, T. W. Birdsong, and J. M. Long, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Bethesda, Maryland, USA.

Brewer, S., and A. Miller. 2019. Assessing the spawning movement and habitat needs of riverine Neosho Smallmouth Bass. 2018 Interim Performance Report to the Oklahoma Department of Wildlife Conservation, Oklahoma City, Oklahoma, USA.

Brewer, S. K., and D. J. Orth. 2015. Smallmouth Bass Micropterus dolomieui Lacepède, 1802. Pages 9–26 in M. D. Tringali, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Bethesda, Maryland, USA.

Brewer, S. K., and C. F. Rabeni. 2011. Interactions between natural-occurring landscape conditions and land use influencing the abundance of riverine smallmouth bass, Micropterus dolomieui. Canadian Journal of Fisheries and Aquatic Sciences 68:1922–1933.

Brewer, S. K., C. F. Rabeni, S. P. Sowa, and G. Annis. 2007. Natural landscape and stream segment attributes influencing the distribution and relative abundance of riverine smallmouth bass in Missouri. North American Journal of Fisheries Management 27:326–341.

Brown, M. T., and M. B. Vivas. 2005. Landscape development intensity index. Environmental Monitoring and Assessment 101:289–309.
Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretical approach. Second edition. Springer-Verlag, New York, New York, USA.

Comte, L., and G. Grenouillet. 2013. Do stream fish track climate change? Assessing distribution shifts in recent decades. Ecography 36:1236–1246.

Coutant, C. C., and D. L. DeAngelis. 1983. Comparative temperature-dependent growth rates of Largemouth and Smallmouth Bass fry. Transactions of the American Fisheries Society 112:416–423.

Dauwalter, D. C., D. K. Splinter, W. L. Fisher, and R. A. Marston. 2007. Geomorphology and stream habitat relationships with Smallmouth Bass (Micropterus dolomieu) abundance at multiple spatial scales in eastern Oklahoma. Canadian Journal of Fisheries and Aquatic Sciences 64:1116–1129.

Dochtermann, N. A., and S. H. Jenkins. 2011. Multivariate methods and small sample sizes. Ethology 117:95–101.

Döll, P., and J. Zhang. 2010. Impact of climate change on freshwater ecosystems: a global-scale analysis of ecologically relevant river flow alterations. Hydrology and Earth System Sciences 14:783–799.

Dormann, C. F., et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Dunham, J. B., A. E. Rosenberger, R. F. Thurow, C. A. Dolloff, and P. J. Howell. 2009. Coldwater fish in wadeable streams. Pages 119–138 in S. A. Bonar, W. A. Hubert, and D. W. Willis, editors. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland, USA.

Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnology and Oceanography 41:1109–1115.

Elliott, J. M. 1989. The natural regulation of numbers and growth in contrasting populations of Brown Trout, Salmo trutta, in two Lake District streams. Freshwater Biology 21:7–19.

Falke, J. A., K. R. Bestgen, and K. D. Fauch. 2010. Streamflow reductions and habitat drying affect growth, survival, and recruitment of Brassy Minnow across a Great Plains riverscape. Transactions of the American Fisheries Society 139:1566–1583.

Fausch, K. D., C. E. Torgerson, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483–498.

Frisell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK.

Gelwick, F. P. 1990. Longitudinal and temporal comparisons of riffle and pool fish assemblages in a Northeastern Oklahoma Ozark Stream. Copeia 1990:1072–1082.

Gordon, N. D., T. A. McMahon, B. L. Finlayson, C. J. Gippel, and R. J. Nathan. 2004. Stream hydrology: an introduction for ecologists. Second edition. John Wiley & Sons Ltd, Chichester, UK.

Gorman, O. T. 1986. Assemblage organization of stream fishes: the effect of rivers on adventitious streams. American Naturalist 128:611–616.

Graham, R. J., and D. J. Orth. 1986. Effects of temperature and streamflow on time and duration of spawning by Smallmouth Bass. Transactions of the American Fisheries Society 115:693–702.

Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699–711.

Hafs, A. W., C. J. Gagen, and J. K. Whalen. 2010. Smallmouth Bass summer habitat use, movement, and survival in response to low flow in the Illinois Bayou, Arkansas. North American Journal of Fisheries Management 30:604–612.

Harrell, F. E. Jr. 2001. Regression modeling strategies. Springer-Verlag, New York, New York, USA.

Harvey, B. C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. Transactions of the American Fisheries Society 116:851–855.

Harvey, B. C., J. L. White, and R. J. Nakamoto. 2009. The effect of deposited fine sediment on summer survival and growth of Rainbow Trout in riffles of a small stream. North American Journal of Fisheries Management 29:434–440.

Hill, R. A., M. H. Weber, S. G. Leibowitz, A. R. Olsen, and D. J. Thornbrugh. 2016. The stream-catchment (StreamCat) dataset: a database of watershed metrics for the coterminous United States. Journal of the American Water Resources Association 52:120–128.

Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the coterminous United States – representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81:345–354.

Humston, R., S. S. Doss, C. Wass, C. Hollenbeck, S. R. Thorrold, S. Smith, and C. P. Bataille. 2017. Isotope geochemistry reveals ontogeny of dispersal and exchange between main-river and tributary...
habitats in smallmouth bass *Micropterus dolomieu*. Journal of Fish Biology 90:528–548.

Humston, R. B., M. Priest, W. C. Hamilton, and P. E. Jr Bugas. 2010. Dispersal between tributary and main-stem rivers by juvenile smallmouth bass evaluated using otolith microchemistry. Transactions of the American Fisheries Society 139:171–184.

Hurwich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Hynes, H. B. N. 1975. The stream and its valley. Internationale Vereinigung für Theoretische Und Angewandte Limnologie: Verhandlungen 19:1–15.

Jager, H. I., D. L. DeAngelis, M. J. Sale, W. Van Winkle, D. D. Schmoyer, M. J. Sabo, D. J. Orth, and J. A. Lukas. 1993. An individual-based model for Smallmouth Bass reproduction and young-of-year dynamics in streams. Rivers 4:91–113.

Jenson, S. K., and J. O. Domingue. 1988. Extracting topographic structure from digital elevation data for Geographic Information System analysis. Photogrammetric Engineering and Remote Sensing 54:1593–1600.

Jowett, I. G., J. Richardson, and R. M. McDowall. 1996. Relative effects of in-stream habitat and land use on fish distribution and abundance in tributaries of the Grey River, New Zealand. New Zealand Journal of Marine and Freshwater Research 30:463–475.

Kennard, M. J., J. D. Olden, A. H. Arthington, B. J. Pusey, and N. L. Poft. 2007. Multiscale effects of flow regime and habitat and their interaction of fish assemblage structure in eastern Australia. Canadian Journal of Fisheries and Aquatic Sciences 64:1346–1359.

Knotek, W. L., and D. J. Orth. 1998. Survival for specific life intervals of smallmouth bass, *Micropterus dolomieu*, during parental care. Environmental Biology of Fishes 51:285–296.

Labbe, T. R., and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774–1791.

Larimore, R. W. 1975. Visual and tactile orientation of Smallmouth Bass fry under floodwater conditions. Pages 323–332 in H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C., USA.

Leisure, D. R., D. D. Magoullick, and S. D. Longing. 2016. Natural flow regimes of the Ozark-Ouachita Interior Highlands region. River Research and Applications 32:18–35.

Lisle, T. E. 1987. Using “residual depths” to monitor pool depths independently of discharge. PSW-RN-394. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.

Lobón-Cerviá, J. 1996. Response of a stream fish assemblage to a severe spate in northern Spain. Transactions of the American Fisheries Society 125:913–919.

Lüdecke, D. 2018. sjstats: collection of convenient functions for common statistical computations. R package version 0.17.2. https://cran.r-project.org/package=sjstats

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

Lynch, D. T., D. R. Leasure, and D. D. Magoullick. 2019. Flow alteration-ecology relationships in Ozark Highland streams: consequences for fish, crayfish and macroinvertebrate assemblages. Science of the Total Environment 672:680–697.

Magnusson, A., H. Skauk, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Bentham, B. Bolker, and M. Brooks. 2018. glmTMB: generalized linear mixed models using template model builder. R package version 0.2.2.0. https://cran.r-project.org/package=glmTMB

Miller, A. D., R. Mollenhauer, and S. K. Brewer. 2019. Movement and diel habitat use of juvenile Neosho Smallmouth Bass in an Ozark stream. North American Journal of Fisheries Management 39:240–253.

Mouser, J. B., R. Mollenhauer, and S. K. Brewer. 2019. Relationships between landscape constraints and a crayfish assemblage with consideration of competitor presence. Diversity and Distributions 25:61–73.

Mulholland, P. J., G. R. Best, C. C. Coutant, G. M. Hornberger, J. L. Meyer, P. J. Robinson, J. R. Stenberg, R. E. Turner, F. Vera-Herrera, and R. G. Wetzel. 1997. Effects of climate change on freshwater ecosystems of the South-eastern United States and the Gulf Coast of Mexico. Hydrological Processes 11:949–970.

Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621–658.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Neff, M. R., and D. A. Jackson. 2012. Geology as a structuring mechanism of stream fish communities. Transactions of the American Fisheries Society 141:962–974.

Nigh, T. A., and W. A. Schroeder. 2002. Atlas of Missouri ecoregions. Missouri Department of Conservation, Jefferson City, Missouri, USA.
Nislow, K. H., A. J. Sepulveda, and C. L. Folt. 2004. Mechanistic linkage of hydrologic regime to summer growth of age-0 Atlantic Salmon. Transactions of the American Fisheries Society 133:79–88.

NRCS Soil Survey Staff. 2017. Soil Survey Geographic (SSURGO) Database for Lake O’ the Cherokees Subbasin. Natural Resources Conservation Service, US Department of Agriculture. https://websoilsurvey.sc.egov.usda.gov

O’Callaghan, J. F., and D. M. Mark. 1984. The extraction of drainage networks from digital elevation data. Computer Vision, Graphics, and Image Processing 28:323–344.

Oliver, J. D., G. F. Holeton, and K. E. Chua. 1979. Overwinter mortality of fingerling Smallmouth Bass in relation to size, relative energy stores, and environmental temperature. Transactions of the American Fisheries Society 108:130–136.

Orth, D. J., and T. J. Newcomb. 2002. Certainties and uncertainties in defining essential habitats for riverine Smallmouth Bass. Pages 251–264 in D. P. Philipp and M. S. Ridgway, editors. Black bass ecology, conservation and management. American Fisheries Society, Bethesda, Maryland, USA.

Osborne, L. L., and M. J. Wiley. 1992. Influence of tributary spatial position on the structure of warmwater fish communities. Canadian Journal of Fisheries and Aquatic Sciences 49:671–681.

Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32:333–365.

Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resiliency of stream fish assemblages. Transactions of the American Fisheries Society 121:427–436.

Peduzzi, P., J. Concato, A. R. Feinstein, and T. R. Holford. 1995. Importance of events per independent variable in proportional hazards regression analysis II. Accuracy and precision of regression estimates. Journal of Clinical Epidemiology 48:1503–1510.

Peek, F. 1965. Age and growth of the Smallmouth Bass Micropterus dolomieui Lacepede in Arkansas. Proceedings of the Nineteenth Annual Conference of the Southeastern Association of Game and Fish Commissioners 19:422–431.

Peterson, J. T., and C. F. Rabeni. 1996. Natural thermal refugia for temperate warmwater stream fishes. North American Journal of Fisheries Management 16:738–746.

Pflieger, W. L. 1975. Reproduction and survival of the smallmouth bass in Courtois Creek. Pages 231–239 in H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C., USA.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. BioScience 47:769–784.

Power, M. E., T. L. Dudley, and S. D. Cooper. 1989. Grazing catfish, fishing birds, and attached algae in a Panamanian stream. Environmental Biology of Fishes 26:285–294.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabeni, C. F., and R. B. Jacobson. 1993. The importance of fluvial hydraulics to fish-habitat restoration in low-gradient alluvial streams. Freshwater Biology 29:211–220.

Rabeni, C. F., and S. P. Sowa. 2002. A landscape approach to managing the biota of streams. Pages 114–143 in J. Liu and W. W. Taylor, editors. Integrating landscape ecology into natural resources management. Cambridge University Press, Cambridge, UK.

Revelle, W. 2018. psych: procedures for psychological, psychometric, and personality research. R package version. https://cran.r-project.org/package=psych

Ronn, W. H., and H. R. MacCrimmon. 1977. Vital statistics and migratory patterns of a potamodromous stock of Smallmouth Bass, Micropterus dolomieui. Journal of the Fisheries Research Board of Canada 34:142–147.

Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. M. Pollock, and G. R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. North American Journal of Fisheries Management 22:1–20.

Rosenfeld, J., M. Porter, and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile Cutthroat Trout (Oncorhynchus clarki) and Coho Salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences 57:766–774.

Sabo, M. J., and D. J. Orth. 1994. Temporal variation in microhabitat use by age-0 Smallmouth Bass in the North Anna River, Virginia. Transactions of the American Fisheries Society 123:733–746.
Sabo, M. J., D. J. Orth, and E. J. Pert. 1996. Effect of stream microhabitat characteristics on rate of net energy gain by juvenile Smallmouth Bass, *Micropterus dolomieu*. Environmental Biology of Fishes 46:393–403.

Schlosser, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs 52:395–414.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. BioScience 41:704–712.

Schlosser, I. J. 1998. Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. Oecologia 113:260–268.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 in J. L. Nielsen and D. A. Powers, editors. Evolution and the aquatic ecosystem. American Fisheries Society, Bethesda, Maryland, USA.

Shreve, R. L. 1966. Statistical law of stream numbers. Journal of Geology 74:17–38.

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

Singh, D., M. Tsiang, B. Rajaratnam, and N. S. Diffenbaugh. 2013. Precipitation extremes over the continental United States in a transient, high-resolution, ensemble climate model experiment. Journal of Geophysical Research: Atmospheres 118:7063–7086.

Smith, S. M., J. S. Odenkirk, and S. J. Reeser. 2005. Smallmouth Bass recruitment variability and its relation to stream discharge in three Virginia rivers. North American Journal of Fisheries Management 25:1112–1121.

Steinmetz, J., D. A. Soluk, and S. L. Kohler. 2008. Facilitation between herons and Smallmouth Bass foraging on common prey. Environmental Biology of Fishes 81:51–61.

Stoeber, D. B., G. N. Green, L. C. Morath, W. D. Heran, A. B. Wilson, D. W. Moore, and B. S. Van Gosen. 2005. Preliminary integrated geologic map databases for the united states: central states: Montana, Wyoming, Colorado, New Mexico, North Dakota, South Dakota. https://datagateway.nrcs.usda.gov/Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Communications in Statistics, Theory and Methods 7:13–26.

Thurow, R. F., C. A. Dollof, and J. E. Marsden. 2012. Visual observation of fishes and aquatic habitat. Pages 781–817 in A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques. Third edition. American Fisheries Society, Bethesda, Maryland, USA.

TNC (The Nature Conservancy), Ozarks Ecoregional Assessment Team. 2003. Ozarks ecoregional conservation assessment. The Nature Conservancy Midwestern Resource Office, Minneapolis, Minnesota, USA.

Todd, B. L., and C. F. Rabeni. 1989. Movement and habitat use by stream-dwelling Smallmouth Bass. Transactions of the American Fisheries Society 118:229–242.

Torgersen, C. E., C. V. Baxter, H. W. Li, and B. A. McIn- tosh. 2006. Landscape influences on longitudinal patterns of river fishes: spatially continuous analysis of fish-habitat relationships. Pages 473–492 in R. M. Hughes, L. Wang and P. Seelbach, editors. Landscape influences on stream habitats and biological assemblages. American Fisheries Society, Bethesda, Maryland, USA.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Vonesh, E. F., V. P. Chinchilli, and K. W. Pu. 2006. Goodness-of-fit in generalized nonlinear mixed-effects models. Biometrics 52:572–587.

Wagner, T., D. B. Hayes, and M. T. Bremigan. 2006. Accounting for multilevel data structures in fisheries data using mixed models. Fisheries 31:180–187.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10.

Westhoff, J. T., and C. P. Paukert. 2014. Climate change simulations predict altered biotic response in a thermally heterogeneous stream system. PLOS ONE 9:e11438.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Winemiller, K. O., and D. H. Taylor. 1982. Smallmouth Bass nesting behavior and nest site selection in a small Ohio Stream. Ohio Journal of Science 82:266–273.

Wrenn, W. B. 1980. Effects of elevated temperature on growth and survival of Smallmouth Bass. Transactions of the American Fisheries Society 109:617–625.

Xian, G., C. Homer, J. Dewitz, J. Fry, N. Hossain, and J. Wickham. 2011. Change in impervious surface area between 2001 and 2006 in the coterminous United States. Photogrammetric Engineering and Remote Sensing 77:758–762.
Zhou, Y., G. A. Fox, R. B. Miller, R. Mollenhauer, and S. Brewer. 2018. Groundwater flux estimation in streams: a thermal equilibrium approach. Journal of Hydrology 561:822–832.

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Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3245/full