Riverscape nesting dynamics of Neosho Smallmouth Bass: To cluster or not to cluster?

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Abstract

Aim: Hierarchical stream habitat conditions influence patterns of fish abundance and population dynamics. The spawning period is important for stream fishes but coincides with unpredictable environmental conditions and stressors. Thus, identifying habitats that confer suitable spawning is crucial to managing vulnerable fish populations, including narrow-range endemics. Here, we evaluate reach- and catchment-scale habitat features related to Neosho Smallmouth Bass (Micropterus dolomieu velox) nest presence, abundance and aggregations (clusters) and quantify nest microhabitat.

Location: Ozark Highlands ecoregion, USA.

Methods: We conducted snorkel and habitat surveys from 2016 to 2018 to quantify nest abundance, describe nest cluster characteristics and quantify nest microhabitat. We used field-collected and geospatial variables and developed generalized mixed models to evaluate the influence of multi-scale habitat features on nest cluster presence and nest abundance.

Results: Nest clusters, scarcely known for other Smallmouth Bass populations, contained 25% of all documented nests. Presence of nests was more likely in warmer stream reaches with wide, shallow channels and more pool habitat. Nest cluster presence was more likely with greater nest densities and earlier in the spawning season. The abundance of Smallmouth Bass nests was related to several reach-scale habitat conditions, with greater nest counts in warmer reaches and reaches with deeper pool habitat. Regardless of cluster behaviour, nesting Smallmouth Bass used similar microhabitats, including a range of depths (0.26–1.85 m), low velocities (<0.1 m/s) and typically gravel substrates.

Main conclusions: Our results indicate plasticity in nesting ecology within Neosho Smallmouth Bass populations and highlight the need to consider multiple aspects of stream habitat when developing conservation and management plans. The importance of reach-scale habitat features suggests it may be important to limit landscape and channel alterations. Nest clustering behaviour suggests these populations may be vulnerable to human influence during the nesting season, but also provides management opportunities for protection during critical time periods.
KEYWORDS

Micropterus dolomieu velox, multi-scale habitat, nest habitat, riverscape, Smallmouth Bass, stream fish, stream temperature

1 | INTRODUCTION

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

Spawning is a critical component of the life history of fishes (Schlosser & Angermeier, 1995). Eggs and larval fish are particularly vulnerable to both biotic and abiotic stressors including starvation, predation and physicochemical extremes (e.g., floods, temperatures; Brewer et al., 2019; Jennings & Filip, 1994; Lukas & Orth, 1995). Appropriate habitat mitigates these threats by providing refuge from stream currents and predators (Schlosser, 1987, 1991) and must also provide favourable growing conditions for developing offspring until they are capable of seeking out other profitable locations (Lawrence et al., 2015). These constraints collectively influence stream fish demographic patterns in heterogeneous lotic environments.

There is tremendous diversity in life history traits and behaviours among fishes, and spawning habitat choice and associated species-nesting behaviour may vary along environmental gradients. Life history diversity reflects trade-offs among demographic parameters (e.g., survival, fecundity) and phylogenetic and biogeographic constraints (Mims et al., 2010; Winemiller & Rose, 1992). Intraspecific variation in spawning habitat and behaviour may relate to differences in habitat quality and quantity (Blanc & Lamouroux, 2007; Isaak et al., 2007; Senay et al., 2015). Aggregations form when spawning individuals are mutually attracted to resources such as food or habitat (Freeman & Grossman, 1992; Helfman et al., 2009); this behaviour may confer advantages such as improved mate attraction and protection from predators. Diversity in spawning behaviour and habitat use of fishes can confer population resistance and resilience to disturbance and changing environmental conditions (Schindler et al. 2010; Thorson et al., 2014) and represents an important consideration when developing conservation strategies for freshwater fishes (Fausch et al., 2002; Schindler et al., 2015; White et al., 2014).

Although the general nesting ecology of Smallmouth Bass (*Micropterus dolomieu*, Lacépédé) is well documented, unique genetic lineages occupying the southwest edge of the native range allow the examination of geographic variation in nesting habitat and behaviour. Spawning by the northern subspecies (*M. d. dolomieu*, Hubbs & Bailey) is typically preceded by migrations (Barthel et al., 2008) with nesting occurring from April to mid-July beginning when water temperatures reach ~15°C (Shuter et al., 1980). Males excavate shallow substrate depressions in low-velocity areas near cover (Pfieger, 1966) and vigorously defend eggs and larvae from predators (Scott et al., 1997). Territoriality by male Smallmouth Bass typically leads to ample spacing (i.e., >17 m) between nests in lake and river systems (Scott, 1996; Wiegmann et al., 1992; Winemiller & Taylor, 1982).

In addition to well-studied northern populations, Smallmouth Bass has two known genetic variants at the southwest edge of the native range including the Neosho subspecies (*M. d. velox*, Hubbs & Bailey; Stark & Echelle, 1998; Brewer & Long, 2015). This subspecies (hereafter “Neosho Smallmouth Bass”) occupies a range characterized by impoundments that appear to limit gene mixing among riverine subpopulations (Taylor et al., 2018) and may result in distinct subpopulation habitat use. Our current understanding of Neosho Smallmouth Bass nesting ecology is limited to a study of one river (Dauwalter & Fisher, 2007), but results indicate high nest densities (i.e., 100–147 km⁻²), microhabitat use consistent with the northern subspecies and multiple causes of nest failure (i.e., angling, human physical disturbance and nest predation). Anecdotal reports suggest nest aggregation behaviours by this subspecies that are rarely reported or quantified, though Pfieger (1966) reported relatively lower inter-nest spacing (mean = 4.2 m) and a single instance of nests ~1.2 m apart for the northern subspecies in an interior Ozark Highlands stream.

Our objectives were to quantify the multi-scale habitat related to the presence and abundance of Neosho Smallmouth Bass nests, to describe factors related to nest aggregations (hereafter “clusters”), and to quantify nest microhabitat conditions. Multi-scale approaches are increasingly used in warmwater stream-fisheries research (e.g., Dunn & Angermeier, 2019; Wellemeyer et al., 2019). For example, Dunn and Angermeier (2019) show that imperilled Candy Darter (*Etheostoma osburni*) persistence requires refugia conferred by habitat conditions at local (i.e., temperature, sedimentation) and catchment (i.e., land use) spatial scales. However, most efforts to understand hierarchical controls on warmwater stream fish abundance focus on adult fish outside of the reproductive period (but see Peoples et al., 2014). This lack of research belies the importance of the spawning period for population dynamics and the often-narrow environmental tolerances of spawning fish (e.g., temperature; Asch & Erisman, 2018; Grabowski & Isely, 2007). Thus, it is imperative to
evaluate the multi-scale spawning habitat relationships for warmwater stream fish, particularly for populations that occupy novel riverscapes such as those on range boundaries. We considered local habitat characteristics (e.g., temperature, pool availability, pool depth) and catchment attributes (e.g., land use disturbance, soils, network location) including several linked to Neosho and Northern Smallmouth Bass presence and abundance outside of the reproductive period (Brewer et al., 2007; Miller & Brewer, 2020). As nest aggregations are undescribed for Smallmouth Bass, we evaluated features related to nesting aggregations in other species, including aspects of channel morphology, groundwater inputs, landscape disturbance and sample timing (Baxter & Hauer, 2000; Beard & Carline, 1991; Grabowski & Isely, 2007).

2 | METHODS

2.1 | Study area

We sampled 120 stream reaches across the Neosho Smallmouth Bass range within the Ozark Highlands ecoregion (hereafter “Ozarks”) to determine the physicochemical factors associated with nesting (Figure 1). The Neosho Smallmouth Bass range is restricted to the Ozarks of southwest Missouri, northeast Oklahoma, northwest Arkansas and southeast Kansas, USA (Brewer & Long, 2015). The Ozarks receive an average of 108 cm of precipitation annually and hydrographs reflect typical spring floods followed by much lower baseflow conditions in summer and autumn (Nigh & Schroeder, 2002). Lithology of the southwest Ozarks is primarily cherty limestone. The karst topography and associated springs confer spatially variable groundwater inputs (Zhou et al., 2018) and gravel and cobble substrates (Nigh & Schroeder, 2002). Land use is generally forest, with pasture more common in valleys and in the southwest Ozarks (Nigh & Schroeder, 2002). The naturally flashy flow regime (Leasure et al., 2016) and wide and shallow stream channel morphology in this ecoregion have been exacerbated by anthropogenic flow alteration and land use change (Brewer, 2011; Splinter et al., 2010). Streams are generally clear under baseflow conditions, and reach-scale habitat typically comprises pools, riffles, runs and off-channel habitats (simplified from Rabeni & Jacobson, 1993). Our sample reaches (~20x mean wetted stream width, Flosi et al., 1998) were chosen using a combination of criteria: high water clarity, representation of available habitat and access to privately owned lands (Figure 1).

2.2 | Nest surveys

We examined habitat conditions at individual Neosho Smallmouth Bass nests and nest clusters. Smallmouth Bass nests are typically defined by individual depressions made in gravel-cobble substrates in low-velocity areas (Warren, 2009); however, anecdotal observations suggest the Neosho subspecies may also spawn on solid rock where a depression or fanned area is not obvious, and they may nest in aggregated clusters. Thus, we used multiple characteristics to define nests. First, we observed Neosho Smallmouth Bass to identify guarding behaviours such as quick swimming bursts towards perceived threats to the nest (e.g., other fishes and surveyors) and nest circling. In addition, we thoroughly searched substrate depressions for the presence of eggs or larvae. We defined nest clusters as groups of at least two nests within 2 m of one another. The distances between neighbouring nests of spawning riverine Smallmouth Bass are usually greater (e.g., means: 4.2 m; Pflieger, 1966; 54.6 m; Lukas & Orth, 1995; 77.9 m; Winemiller & Taylor, 1982), though a single pair of nests was documented ~1.2 m apart by Pflieger (1966). We only quantified nests that were guarded or contained eggs or fry because Smallmouth Bass may excavate multiple nests in close proximity before choosing their nesting location (Cleary, 1956).

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

We surveyed each sample reach with a crew of 2–5 snorkellers (depending on wetted width and habitat complexity) during daytime (09:00–17:00 hr) to maximize visibility. Narrower snorkelling lane widths were used in areas with reduced visibility or more-complex habitat (Dunham et al., 2009; Thurow et al., 2012). Snorkellers moved upstream in parallel lanes, carefully searching for guarding male bass or groups of eggs or fry in small depressions or near cover. When a guarding male bass was observed, the surveyor slowly approached the area to determine the exact nest location. If a potential guarding bass was spooked, the observer moved away from the location and waited for the fish to return to determine if the fish was guarding a nest and to estimate fish size (5.0 mm increments, total length [TL]). Snorkellers were trained to estimate fish lengths using a bass model (i.e., Smallmouth Bass silhouette of different sizes, 150–305 mm TL; Dunham et al., 2009). Visibility during all snorkel surveys was at least 1.5 m and could distinguish a bass-shaped silhouette underwater (Dunham et al., 2009). We adjusted nest abundance estimates for variable detection among sample sites in relation to water clarity, size and segment location within the stream network (e.g., gravel, bedrock). For clusters, we counted the number of nests and measured length and width to calculate cluster area (0.1 m²). Lastly, we measured the centre-to-centre distance of each nest in the cluster to the nearest neighbouring nest.

We measured additional physicochemical characteristics to determine the relative importance of reach-scale habitat on nest abundance (Table 1). We used a thermometer (Ultrapen PT1; Myron L) to measure water temperature (0.1°C) at mid-pool depth. Because water temperature represented only a point measure at the sampling event and there was a natural break in the data, we converted temperature to a factor with two levels (cool: ≤19.5°C, warm: >19.5°C). Of our 120 sample reaches, 85 were classified as warm and 35 were classified as cool. We classified channel units using a simplified version of Rabeni and Jacobson (1993) and calculated per cent 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, and off-channel habitats were low-velocity and adjacent to the main channel (i.e., backwaters and forewaters). We measured residual pool depth (RPD; 0.01 m) as the difference between maximum pool depth and the downstream riffle crest (Lisle, 1987). We quantified high-flow characteristics of channel hydrology by measuring bankfull width-to-depth ratios (Gordon et al., 2004) and by estimating median substrate size (D50) as a proxy for channel shear stress (Wilcock & Southard, 1988). 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 (Leopold, 1970). We also conducted seepage runs (Harvey & Wagner, 2000) using an acoustic Doppler current profiler (RiverSurveyor M9; SonTek) to quantify discharge (0.01 m³/s) at the upstream and downstream ends of each reach. We categorized this reach-scale groundwater flow into three categories based on longitudinal gain or loss of streamflow relative to discharge measurement uncertainty (0.03 m³/s; Zhou et al., 2018): losing streams (net loss of flow; n = 48), neutral streams (no change; n = 33) and gaining streams (net gain of flow; n = 39). In order to model variable detection of nests among sample sites, we calculated mean wetted channel width (0.1 m) and mean thalweg depth (0.01 m) from measurements taken every ~50 m along each reach.

We used terrain analysis and existing geospatial data in ArcMap 10.3.1 (ESRI) to calculate stream segment attributes (Table 1). Using a 30-m resolution raster digital elevation model (USGS National Elevation Dataset [NED]), we defined overland flow direction pathways and upstream catchment areas for each stream segment (Jenson & Domingue, 1988; O’Callaghan & Mark, 1984). We calculated in-stream flow direction using rasterized 1:100,000 flowlines (USGS National Hydrography Dataset [NHD]) to ensure that flow pathways agreed with mapped streams (Betz et al., 2010). We used the in-stream flow direction raster to calculate two metrics of stream topology: link magnitude (Shreve, 1966) and downstream link (Osborne & Wiley, 1992). These metrics describe both stream size and segment location within the stream network (e.g., a similar-sized stream may be located in the headwaters or adjacent to a large mainstem river). We considered spatial location because it describes...
proximity to different habitats or resources that might influence nesting location.

We quantified 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 & Vivas, 2005; Mouser et al., 2019; Table S1). Because the land use types used by Brown and Vivas (2005) are finer resolution than NLCD categories, we

| Variable                        | Mean ± SD  | Range     | Data source                  |
|---------------------------------|------------|-----------|------------------------------|
| Reach scale                     |            |           |                              |
| Sampling date (day of year)     | 155.5 ± 19.2| 122-190   | Field-collected              |
| Stream temperature (°C)         | 19.7 ± 2.4 | 15.1-24.6 | Field-collected              |
| Residual pool depth (m)         | 1.03 ± 0.53| 0.35-3.14 | Field-collected              |
| Pool habitat (%)                | 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)      | 25.1 ± 5.3 | 10.0-40.0 | Field-collected              |
| Bankfull width-to-depth ratio   | 42.0 ± 21.8| 7.9-122.7 | Field-collected              |
| Groundwater flow (m³/s)         | −0.01 ± 0.24| −0.70-1.13| Field-collected              |
| Area sampled (m²)               | 4,771.9 ± 3,887.6| 565.9-20,127.3| Field-collected |

Segment scale

| Variable                        | Mean ± SD  | Range     | Data source                  |
|---------------------------------|------------|-----------|------------------------------|
| Link magnitude                  | 23.5 ± 37.9| 1-264     | USGS NHD^c                   |
| Downstream link                 | 69.2 ± 132.5| 3-874     | USGS NHD^c                   |
| Stream gradient (%)             | 0.34 ± 0.16| 0.03-0.73 | NHD Plus Version 2^d         |
| Drainage area (km²)             | 172.2 ± 176.0| 18.0-886.6| USGS NED^e,f                  |
| Catchment slope (%)             | 7.2 ± 3.3  | 1.4-15.4  | USGS NED^e,f                  |
| Disturbance index^e             | 2.3 ± 0.4  | 1.5-3.9   | NLCD, 2011^g                  |
| Hydro soil group D (%)          | 33.5 ± 14.4| 5.9-70.3  | USDA NRCS SSURGO 2.2^e,h      |
| Carbonate geology (%)           | 96.8 ± 8.9 | 17.3-100.0| USGS, USDA NRCS^i            |
| Base flow/total flow (%)        | 46.0 ± 4.1 | 34.4-53.3 | USEPA StreamCat^j            |
| Runoff (mm)                     | 350.4 ± 17.8| 316.0-381.6| USEPA StreamCat^j            |

Notes: 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). Main effects retained following variable reduction for the nest density model are bolded (n = 3), while interaction terms (n = 4, all with stream temperature) are italicized. SD is standard deviation.

^a Subset of variables (n = 9) evaluated for nest presence model.

^b Converted to categorical variables, with reference conditions of warm (for stream temperature) and losing streams (for groundwater flow).

^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/data?f%5B0%5D=category%3ALand%20Cover.

^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.
averaged multiple coefficient values from Brown and Vivas (2005) if an NLCD category comprised more than one land use type (e.g., Mouser et al., 2019). For example, we used a coefficient for the NLCD "pasture/hay" category (2.99) that reflected the average of woodland pasture (2.02), improved pasture without livestock (2.77), improved pasture low-intensity with livestock (3.41) and improved pasture high-intensity with livestock (3.74) land use types from Brown and Vivas (2005). The lowest coefficient (1.00) described undisturbed habitats (e.g., forests, wetlands), whereas habitats subject to greater disturbance were assigned larger coefficients (e.g., 7.92, high-intensity development). We then calculated the area-weighted average of disturbance coefficients across the catchment of each stream segment. We characterized topography using stream gradient from the NHDPplus V2 and calculated average catchment slope. We calculated per cent hydrologic soil group D (i.e., indicative of high runoff potential) and per cent carbonate lithology for each catchment using existing data (NRCS, 2017; Stoeser et al., 2005). Hydrologic soil groups (A-D) describe soil permeability and are correlated with one another (i.e., total 100% across groups). Thus, we quantified soil group D because it negatively influences Smallmouth Bass presence and relative abundance in Ozark streams (Brewer et al., 2007). Likewise, lithology data are highly correlated, so we quantified carbonate lithology because of its association with karst topography and springs. Lastly, we used data from the StreamCat database (Hill et al., 2016) to summarize variation in mean annual runoff and relative baseflow contribution (i.e., per cent of total flow attributable to groundwater) for each catchment.

### 2.4 Nest presence and cluster presence analyses

We used mixed-effects logistic regression models to evaluate the multi-scale habitat features associated with nest presence. First, we modelled the presence of nests at \( n = 120 \) stream reaches in relation to a subset of predictors at the reach and segment scales (Table 1). We added a fixed effect for area sampled to the model to account for differences in snorkelling effort among stream reaches. To reduce skewness, we natural log-transformed continuous variables and logit-transformed proportions (after adding a constant of 0.001 to channel unit proportions to facilitate transformation when raw values were zero; Warton & Hui, 2011). We then standardized all predictors to a mean of 0 and standard deviation (SD) = 1 to simplify model interpretation. In this and subsequent models, we used “warm” and “losing streams” as the reference conditions for the categorical stream temperature and groundwater flow predictors. We included random effects of stream segment and year in this and all subsequent mixed models to account for non-independent observations and address unexplained variability among reaches (Gelman & Hill, 2007; Wagner et al., 2006). We conducted all-subsets model selection (\( n = 511 \) models) with a limit of eight fixed terms to maintain appropriate degrees of freedom (Harrell, 2015). Models were ranked based on AICc (Hurvich & Tsai, 1989; Sugiura, 1978) and relative model support was calculated using Akaike weights (\( w \)), which give the conditional probability for each model (Burnham & Anderson, 2002). When interpreting ranked models, we considered only the most parsimonious model within 2 AICc of the top model to avoid inclusion of uninformative parameters (Arnold, 2010). Lastly, we calculated two types of pseudo \( R^2 \); marginal \( R^2 \) (i.e., amount of variance explained by fixed effects) and conditional \( R^2 \) (i.e., amount of variance explained by both fixed and random effects, Nakagawa et al., 2017; Vonesh et al., 1996) to evaluate model fit.

We repeated this process with a few modifications to model nest cluster presence across the \( n = 77 \) reaches which contained nests. Model predictors were based on hypothesized explanations for clustering behaviour (i.e., habitat limitation, groundwater, disturbance, progression of spawning season; Table 2). Such conditions influence aggregations and behaviour of spawning fish in streams (e.g., Baxter & Hauer, 2000; Beard & Carline, 1991; Grabowski & Isely, 2007). We conducted all-subsets model selection with a limit of five fixed terms (\( n = 638 \) models). Logistic regression modelling and \( R^2 \) calculations were implemented in the statistical software R (version 3.5.1; R Core Team, 2018) using packages "lme4" (Bates et al., 2015) and “MuMIn” (Bartoń, 2018).

### 2.5 Nest abundance modelling

Prior to modelling nest abundance, we used an N-mixture model (Royle, 2004) and the R package "unmarked" (Fiske & Chandler, 2011) to evaluate the influence of water clarity, thalweg depth and wetted channel width on nest detection variability among sites (Brewer & Miller, in press). These models allow estimation of population sizes while accounting for variable detection probability and have been used to assess adult Smallmouth Bass populations in Ozark streams (e.g., Mollenhauer & Brewer, 2017). Briefly, we used model coefficients and empirical Bayes methods to adjust raw nest counts for variable detection among sites (Royle & Dorazio, 2008) so that these adjusted counts could be evaluated in a mixed-model framework, which is not currently possible in "unmarked."

We evaluated several potential generalized linear mixed model (GLMM) forms for comparing adjusted Smallmouth Bass nest abundances and habitat. Initial evaluation of the adjusted nest count data suggested overdispersion and zero inflation, so we modelled nest abundance (scaled by area sampled; i.e., nest density) without ecological predictors using several candidate model forms (i.e., Poisson, negative binomial, zero-inflated Poisson, zero-inflated negative binomial [ZINB]; Table S2). We also included ZIP and ZINB models with single covariates for the binomial (i.e., zero inflation) component of the model; these covariates (i.e., stream temperature, per cent pool habitat, bankfull width-to-depth ratio and sampling date) were chosen based on their importance in our logistic model of nest presence. All models included random effects for stream segment and year to account for non-independence among observations (Gelman & Hill, 2007; Wagner et al., 2006). Comparison of model forms...
revealed that a ZINB model with zero inflation related to stream temperature best fits the data ($w_\text{r} = 0.98$; Table S2).

To reduce our set of predictor variables, we compared a set of ZINB GLMMs with each main effect predictor ($n = 19$) and ecologically sensible two-way interaction term ($n = 20$) to an ecological null model containing only random intercepts for segment and year, an offset (coefficient = 1) for area sampled, and a zero inflation term related to stream temperature (Table S3). If the candidate model $AIC_c$ was sufficiently less than the intercept-only model $AIC_c$ (i.e., $AIC_c$ reduction of $\geq 2$ for each additional degree of freedom; Arnold, 2010), we retained that model predictor (Burnham & Anderson, 2002). The retained continuous variables had a pairwise correlation $r = 0.16$, so no additional predictors were excluded on the basis of collinearity (Dormann et al., 2013). The reduced variable set consisted of $n = 3$ main effect predictors and $n = 4$ two-way interaction terms (Table 1).

We used all-subsets model selection with the retained predictors to evaluate and rank models of nest abundance ($n = 148$ models). To ensure appropriate degrees of freedom for model performance and avoid overfitting, we limited fixed-effect predictors to 8 per model. We included a random effect for stream segment and year, an offset (coefficient = 1) for area sampled, and a zero inflation term related to stream temperature in all models, and assumed that random effects were normally distributed $N(0, \tau^2)$, where $\tau^2$ represented population variance among levels of the random effect (e.g., among stream segments). We used $AIC_c$ and Akaike weights ($w_\text{r}$) to determine the set of predictors with the most support from an ecologically sensible candidate model set (Grueber et al., 2011). Model parsimony was used to decide between multiple competing models, wherein candidate models within 2 $AIC_c$ of the top model were only considered to have support if they contained an equal or lower number of parameters than the top model (Arnold, 2010). We built all ZINB models in the R package “glmmTMB” (Magnusson et al., 2018) and conducted model selection ($AIC_c$) using the “bbmle” package (Bolker, 2017). We assessed model fit of our top ZINB model by calculating marginal and conditional $R^2$ (Nakagawa et al., 2017; Vonesh et al., 1996) in the R package “sjstats” (Lüdecke, 2018).

### RESULTS

#### 3.1 Nest surveys

We observed Neosho Smallmouth Bass nests in 77 of 120 sampled reaches (64%). An additional 15 reaches were occupied by age-1 Smallmouth Bass even though no nests were present. In reaches with nests, unadjusted nest counts ranged from 1 to 79 (mean = 11.5; SD = 13.7) and nest densities ranged from 1.2 to 90.0 ha$^{-1}$ (mean = 19.4 ha$^{-1}$; SD = 16.3). Average detection efficiency was 72%, with variation among reaches related to water clarity, average depth and wetted width (scaled by the number of observers). After adjusting for heterogeneous detection probability at these sites, we saw modest increases in nest count (mean = 14.3; SD = 15.8) and nest density (mean = 23.6 ha$^{-1}$; SD = 17.7). Nest clusters were observed in $n = 28$ stream reaches.

#### 3.2 Nest presence, cluster presence and nest microhabitat

The presence of nests was positively related to sampled area, bankfull width-to-depth ratio and per cent of pool habitat. Nests were less likely to be found in reaches that were cool or that were surveyed

### TABLE 2 Coefficients, standard errors (SE) and 95% confidence intervals (CI) for mixed-effects logistic regression describing presence of Smallmouth Bass nest clusters in $n = 77$ Ozark Highlands stream reaches sampled from 2016 to 2018

| Predictor variable         | Coefficient ± SE | 95% CI         | Hypotheses               |
|----------------------------|------------------|----------------|--------------------------|
| Intercept                  | −0.96 ± 0.39     | −1.72, −0.20   | Habitat limitation       |
| Stream temperature         | NA               | NA             | Habitat limitation       |
| Pool habitat               | NA               | NA             | Habitat limitation       |
| Off-channel habitat        | NA               | NA             | Habitat limitation       |
| Stream gradient            | NA               | NA             | Habitat limitation       |
| Nest density               | 1.51 ± 0.47      | 0.59, 2.42     | Habitat limitation       |
| Bankfull width-to-depth    | NA               | NA             | Habitat limitation, Disturbance |
| Disturbance index          | NA               | NA             | Disturbance              |
| Neutral groundwater flow   | NA               | NA             | Groundwater              |
| Gaining groundwater flow   | NA               | NA             | Groundwater              |
| Sampling date              | −1.07 ± 0.43     | −1.90, −0.23   | Progression of spawning season |
| Area sampled               | 0.99 ± 0.38      | 0.25, 1.73     | Sampling effort          |

Notes: Hypothesized explanations for including each predictor variable are also included. Model coefficients from the top model (Table S5) are presented on a logit scale, and continuous predictors were standardized to mean = 0 and standard deviation = 1 prior to model specification. The reference condition for stream temperature is warm (>19.5°C), and the reference condition for groundwater flow is losing (i.e., longitudinal decrease in stream discharge). Area sampled is included to account for differences in sampling effort among stream reaches. NA is used for terms that were not retained in the final model.
later in the spawning season. All continuous predictors had effects similar in magnitude (range: [0.70–0.79] on a logit scale; Table S4). Akaike weight for this model was 0.05, as it was one of several (n = 9) competitive models with similar predictors (Table S4). The fixed effects collectively explained 54% of the variation in nest presence (marginal $R^2 = 0.54$), and the addition of segment and year random effects resulted in a conditional $R^2 = 0.56$.

After accounting for nest presence, nest cluster presence was positively related to nest density and area sampled and negatively related to spawning season progression (Table 2). Clusters were more likely to be present in reaches with higher nest densities and earlier in the sampling period. Increased sampling effort also predicted increased likelihood of nest cluster presence. Model support was divided among several competing models with similar model terms (n = 9; Table S5), and model weight for the top model was 0.07. For this model, fixed effects explained 49% of the variability in nest cluster presence (marginal $R^2 = 0.49$), whereas the random stream segment and year effects did not explain any additional variability (conditional $R^2 = 0.49$).

Nest cluster characteristics were measured for $n = 66$ clusters in $n = 22$ stream reaches. Nest clusters contained 2–6 nests (mean = 2.4; SD = 0.8). Centre-to-centre spacing between clustered nests ranged from 0.5 to 2.0 m (mean = 1.5 m; SD = 0.3). Average area of nest clusters was 2.4 m² (SD = 2.6, range = 0.5–14.0 m²).

Nest microhabitat measures ($n = 646$ nests in $n = 55$ reaches) were similar for nests regardless of cluster behaviour, and reflected variability in nesting Smallmouth Bass size, a range of nesting depths and predominate use of low-velocity areas with gravel substrates. We found 25% (160 of 646) of nests were associated with clusters. Guarding male Smallmouth Bass ranged from 130 to 400 mm TL. Average TL of male fish belonging to clusters or single nests were 269 mm (SD = 45) and 253 mm (SD = 46), respectively. Nests were constructed at depths of 0.26–1.85 m; average water depths of nests in clusters and of single nests were 0.84 m (SD = 0.29) and 0.83 m (SD = 0.31), respectively. Nest surface water velocities ranged from 0.0 to 0.2 m/s, though most cluster nests (96%) and regular nests (96%) occurred in calm water (i.e., zero velocity). Nest substrate was predominately gravel (98% of cluster nests, 97% of regular nests), though use of bedrock (2% of cluster nests, 3% of regular nests) and other substrates (i.e., roots, <1% of cluster nests) was observed.

3.3 | Nest abundance

The top-ranked model for adjusted Smallmouth Bass nest abundance (scaled by area sampled) indicated the importance of multiple reach-scale habitat features; however, there was support for several similar models ($n = 4$; Table 3). Zero inflation in the top model suggests that zero nest counts were expected in 16% of warm stream reaches and 56% of cool stream reaches. Nest abundances were generally much greater in warmer streams, and nest abundance was also positively related to residual pool depth across all reaches (Figure 2). Model support was split among four competitive models, and support for the most parsimonious model was modest ($w_1 = 0.12$), but all competitive models contained main effect or interaction terms for temperature and residual pool depth (Table 3). Fixed effects in the top model (Table S6) explained 67% of the variability in nest abundance (marginal $R^2 = 0.67$), whereas the random stream segment and year effects explained some additional variability (conditional $R^2 = 0.69$).

4 | DISCUSSION

Nest clustering by Neosho Smallmouth Bass reflects intraspecific variation in spawning behaviour within and among these range-edge populations. Variation in reproductive traits is common among fish populations across large spatial extents (Blanck & Lamouroux, 2007; Winemiller & Rose, 1992). Behavioural differences such as spawning aggregations may reflect adaptations to novel environmental conditions, such as those found at range boundaries (Winemiller & Rose, 1992). The use of multiple nesting strategies within and among these subpopulations may be important given the varying

| TABLE 3 | Rankings of top (i.e., within 2 AICc) candidate linear mixed models of Smallmouth Bass nest abundance in n = 120 Ozark Highlands stream reaches sampled from 2016 to 2018 |
|----------|----------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Model    | K      | LL              | AICc | ΔAICc | $w_1$ | $R^2_{\text{c}}$ | $R^2_{\text{e}}$ |
| $Y_{\text{i,j}} = \beta_0 + \gamma_i + \delta_1 + \beta_1 \times \text{Temp}_i \times \text{RPD}_i + \beta_2 \times \text{Pool}_i$ | 10 | -290.2 | 602.5 | 0.0 | 0.12 | 0.75 | 0.77 |
| $Y_{\text{i,j}} = \beta_3 + \gamma_i + \delta_1 + \beta_1 \times \text{Temp}_i \times \text{RPD}_i + \beta_4 \times \text{Pool}_i$ | 8 | -292.6 | 602.5 | 0.0 | 0.12 | 0.67 | 0.69 |
| $Y_{\text{i,j}} = \beta_5 + \gamma_i + \delta_1 + \beta_1 \times \text{Temp}_i \times \text{RPD}_i + \beta_3 \times \text{Pool}_i + \beta_4 \times \text{RPD}_i$ | 9 | -291.6 | 602.8 | 0.3 | 0.10 | 0.68 | 0.70 |
| $Y_{\text{i,j}} = \beta_6 + \gamma_i + \delta_1 + \beta_1 \times \text{Temp}_i \times \text{RPD}_i + \beta_3 \times \text{Pool}_i + \beta_4 \times \text{RPD}_i$ | 9 | -291.7 | 602.9 | 0.4 | 0.10 | 0.75 | 0.77 |
| $Y_{\text{i,j}} = \beta_7 + \gamma_i + \delta_1 + \beta_1 \times \text{Temp}_i + \beta_3 \times \text{Pool}_i + \beta_4 \times \text{RPD}_i$ | 5 | -309.5 | 631.0 | 28.5 | <0.01 | 0.00 | 0.24 |

Notes: $Y_{\text{i,j}}$ is nest abundance of reach $i$ in stream segment $j$ in year $l$, $\beta_0$ is the grand intercept, $\gamma_i$ is the random stream segment intercept, and $\delta_1$ is the random year intercept. All models include a scaling term for area sampled (coefficient = 1) and account for zero inflation due to water temperature. Temp is water temperature class, where warm (>19.5°C) is the reference condition. RPD is residual pool depth (m). Pool is per cent pool habitat, BF is bankfull width-to-depth ratio, and $D_{\text{mm}}$ is median substrate size (mm). $K$ is the number of model parameters, LL is log-likelihood, AICc is Akaike’s information criterion adjusted for small sample size, and ΔAICc is the difference in AICc score between the given model and the top model. Akaike weight ($w_1$) indicates the relative support for the given model. Marginal $R^2 (R^2_{\text{c}})$ and conditional $R^2 (R^2_{\text{e}})$ 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. We include the null (random effect only) model for reference.
quality and predictability of stream habitats over time (Schindler et al., 2010). Several endemic congeners of Neosho Smallmouth Bass show partial use of spawning aggregations including Guadalupe Bass (M. treculii; Enríquez et al., 2016) and Shoal Bass (M. cataractae; Taylor, 2012; Cottrell, 2018). Other riverine fishes, including Sauger (Sander canadensis) and Blue Sucker (Cycleptus elongatus), demonstrate similar behaviours due to habitat limitation from anthropogenic modifications and suboptimal habitat at range peripheries (Jaeger et al., 2005; Vokoun et al., 2003).

Several physicochemical factors were associated with the occurrence of Smallmouth Bass nests. Nests were more likely to occur in warmer stream reaches (>19.5°C), possibly reflecting favourable growing conditions for offspring (Coutant & DeAngelis, 1983; Peek, 1965). Likelihood of nest presence also increased with the availability of low-velocity pool habitat and wide, shallow channels. Low-velocity areas (e.g., pools) require less energy expenditure by guarding males and confer greater retention of eggs and larvae in nest substrates (Copp et al., 2002; Harvey, 1987). Use of low-velocity habitats by nesting Smallmouth Bass has been documented in many populations (e.g., Dauwalter & Fisher, 2007; Pfieger, 1966; Winemiller & Taylor, 1982), and juvenile Smallmouth Bass show similar habitat-use patterns (Brewer, 2011; Miller et al., 2019). Wide, shallow stream reaches receive more solar radiation due to relatively less riparian overhang, which may benefit adult fish and especially developing offspring via increased water temperatures and primary productivity (Coutant & DeAngelis, 1983; Vannote et al., 1980; Whitlege et al., 2006). Nest presence was more likely early in the spawning season. This may reflect coincident nesting efforts following delays in spawning due to high flows (i.e., 2016–2017) or cool temperatures (i.e., 2018). Similar spawning delays have been observed elsewhere by Smallmouth Bass (e.g., Pfieger, 1966; Sabo & Orth, 1994). Furthermore, many bass build new nests if earlier broods are destroyed (e.g., flooding or predation) or disperse, but not all bass make multiple nesting attempts (Lukas & Orth, 1995; Orth & Newcomb, 2002), such that nests are less likely to be present later in the spawning season following nest failures. Lastly, nest presence was more common in reaches for which a larger wetted area was surveyed, underscoring the need to account for area surveyed (i.e., effort) in models of nest abundance and cluster presence (Thurow et al., 2012).

Nest clustering was more common when nest densities were relatively high and early in the spawning season. Greater nest densities may require aggregated nesting to overcome spawning habitat limitation, which in many riverine systems limits the total number of nests (e.g., Baxter & Hauer, 2000; Beard & Carline, 1991; Grabowski & Isely, 2007). Nest clusters may be less common later in the spawning season because not all individuals make multiple nesting attempts as the season progresses (Lukas & Orth, 1995; Orth & Newcomb, 2002; Pfieger, 1966), potentially alleviating habitat limitations that may lead to nest clustering. In one lacustrine population of Smallmouth Bass, proximity of nesting Smallmouth Bass inhibited mate acquisition and nest success of nearby conspecifics, though this relationship was substrate dependent (Wiegmann et al., 1992).

Predation threats by Longear Sunfish (Lepomis megalotis), a common nest predator in Ozark streams (Dauwalter & Fisher, 2007), appear common early in the Smallmouth Bass nesting season until sunfish begin their own spawning activities in late May (Warren, 2009). Aggregations of nest-guarding fish help deter potential predators (Dominey, 1981), and thus may be used by Smallmouth Bass early in the spawning season. In summary, clustering behaviour by Neosho Smallmouth Bass seems to reflect a need to overcome habitat limitation and may be a response to abundant nest predators. Density-dependent effects such as predation are particularly detrimental to nest success and offspring survival under benign physicochemical conditions (e.g., stable flows; Dauwalter & Fisher, 2007; Jennings & Philipp, 1994); thus, the benefit of clustering behaviour may vary across streams and years. Accounting for sampling effort in our model was important, as area sampled influenced the likelihood of cluster presence. An explicit comparison of nesting behaviour, reproductive investment (e.g., fecundity, egg size), nest predation and nest success could provide clarity into the mechanisms underlying this reproductive tactic and its importance in Smallmouth Bass population dynamics.

Regardless of clustering behaviour, Neosho Smallmouth Bass nest microhabitat was similar to other Smallmouth Bass populations. Cluster and non-cluster nests did not differ in habitat characteristics or guarding male TL, suggesting that size-based dominance hierarchies and territoriality did not influence nesting behaviour or habitat use as they do in many other stream fish populations (e.g., Petty & Grossman, 2004; Winemiller & Taylor, 1982). Nesting microhabitat (e.g., depth, velocity, substrate) use was consistent with that reported for populations elsewhere in the species range (e.g., Lukas & Orth, 1995; Pfieger, 1966; Winemiller & Taylor, 1982).

Multiple reach-scale habitat factors influenced the abundance of Neosho Smallmouth Bass nests in Ozark streams. Nest absences

**Figure 2** Influence of residual pool depth (m) on Smallmouth Bass nest density in Ozark Highlands stream reaches 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. Stream surveys were conducted from 2016 to 2018.
were expected for 16% of warm stream reaches and 56% of cool reaches. After accounting for this zero inflation, nest abundance increased with residual pool depth in both warm and cool reaches, and nest abundances, on average, were greater in warm reaches. This relationship may reflect reduced vulnerability of nest-guarding males to terrestrial predators (Orth & Newcomb, 2002) or nest scour during high flows (Lukas & Orth, 1995). The positive relationship between nest abundance and stream temperature may reflect better growing conditions for developing larvae and fry (Coutant & DeAngelis, 1983; Peek, 1965).

Disentangling the multi-scale influences on spawning habitat is important for guiding effective conservation and stream restoration efforts (Lawrence et al., 2012). Although cooler water temperatures broadly restrict nesting habitat potential of Neosho Smallmouth Bass, cooler streams, especially those with deeper pools, provide additional spawning habitat. As deeper pools benefit nest abundance regardless of stream temperature, efforts to limit landscape and channel modifications that alter natural geomorphology (e.g., bedform, sedimentation, channel dimensions) would be constructive (Leasure et al., 2016; Rabeni & Jacobson, 1993). Plastic use of velocity refugia by nesting Neosho Smallmouth Bass may explain their presence across streams with varied geomorphology and pool habitat. Habitat plasticity insulates organisms from the effects of environmental change (Beever et al., 2017; Goniea et al., 2006) and has been observed for age-0, juvenile, and adult Smallmouth Bass (Brewer et al., 2019; Fore et al., 2007; Pert et al., 2002). As several subpopulations of Neosho Smallmouth Bass appear isolated due to limited gene mixing (Taylor et al., 2018), observed habitat plasticity may further reflect adaptations to specific habitat types among drainages.

As an endemic sportfish, Neosho Smallmouth Bass present an interesting scenario for fisheries management, particularly given their nest clustering behaviour. In fluvial systems, sportfish management and biodiversity conservation typically represent different goals that require making trade-offs (Clarkson et al., 2005). Given the endemic status of Neosho Smallmouth Bass and their importance both ecologically and economically, these streams provide an opportunity to manage the fishery while simultaneously benefiting life history diversity. For example, approaches combining ideas from traditional fisheries management and conservation biology (e.g., protected areas) may provide disproportionate benefits when focused on spawning aggregations (Erisman et al., 2017). The role of angling on nesting bass has not been studied in these systems, but nest clusters may be especially susceptible to anglers given the aggressiveness of nest-guarding Smallmouth Bass (Philipp et al., 1997; Steinhart et al., 2004). Even catch-and-release angling frequently results in nest predation and nest failure in other systems (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 include the nesting season in all streams or specifically applied to areas that support nesting aggregations to alleviate angling vulnerability (Suski & Cooke, 2007; Suski et al., 2002). Further work to understand the potential role of angling on nest success and the role of nest clusters in population dynamics would be informative for guiding management of these unique populations.

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CONFLICTS OF INTEREST

The authors report no conflicts of interest.

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DATA AVAILABILITY STATEMENT

All data from this study are publicly available via the Environmental Data Initiative at https://doi.org/10.6073/pasta/b65c7e52638d87d7ebd68ac57ca4d938.

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**BIOSKETCH**

Both authors are broadly interested in improving the ecological understanding of stream ecosystems. They conduct research related to a variety of stream topics including freshwater fish and invertebrate demographics, distributions, ecology, and population dynamics, with the aim of informing conservation and management efforts.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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