

AN ABSTRACT FOR THE THESIS OF

Samuel J. Schneider for the Master of Science Degree in Biological Sciences from Emporia State University presented on November 4, 2019 entitled: Seasonal fish assemblage structure in riffles, wadeable pools and non-wadeable pools of a perennial warmwater river

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Abstract approved:

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(Thesis Advisor Signature)

Abstract

Research on intermittent streams has linked deep pools with successful completion of critical life history requirements; however, few studies have investigated this concept in larger rivers. I compared fish assemblages, including species richness and fish density, in riffles, wadeable pools, and non-wadeable pools of the Neosho River, a 5<sup>th</sup>- order perennial warmwater river in Kansas, USA. Samples were collected by trawl during spawning and post-spawning seasons at eight sites from May to November 2018. I predicted that these mesohabitats would support disparate fish assemblages that changed in structure seasonally. I found that spatial patterns of fish assemblage structure were largely explained by differences between riffle and pool samples, consistent with that prediction. Species composition also varied between wadeable and non-wadeable pools, with Ghost Shiner (*Notropis buchmanii*) abundance greatest in non-wadeable pools and Shortnose Gar (*Lepisosteus platostomus*), Smallmouth Buffalo (*Ictiobus bubalus*), and White Crappie (*Pomoxis annularis*) collected only in this mesohabitat. Temporal patterns

reflected higher species richness and fish density during spawn than post-spawn, with the density of fishes greatest in riffles and wadeable pools during the spawn but greatest in wadeable pools during post-spawn. Results were dependent on whether area- or volume-based densities were analyzed, as more significant non-wadeable pool comparisons, higher riffle densities, and more indicator species were identified using volume-based densities. When sampling a diverse fish assemblage with species associated with surface, benthic, and water column habitats, both metrics and deep pools should be examined.

Keywords: Mesohabitat, Spawn, Refugia, Life History, Spatio-temporal,  
Multivariate Statistics

SEASONAL FISH ASSEMBLAGE STRUCTURE IN RIFFLES,  
WADEABLE POOLS AND NON-WADEABLE POOLS OF A  
PERENNIAL WARMWATER RIVER

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The Department of Biological Sciences  
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In Partial Fulfillment  
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Master of Science

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by  
Samuel J. Schneider  
November 4 2019

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## **PREFACE**

My thesis will be submitted for publication to *Ecology of Freshwater Fish* and is formatted for that journal.

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## 1 | Introduction

Lotic ecosystems with juxtaposed pool–riffle mesohabitats support diverse fish assemblages (Gelwick, 1990; Schlosser, 1982; Taylor, 2000) that vary in their habitat use based on environmental factors that generate patterns of spatio-temporal heterogeneity (Kirsch & Peterson, 2014; Pease, Taylor, Winemiller, & King, 2011; Wolter, Buijse, & Parasiewicz, 2016). Temporal shifts in fish assemblage structure between mesohabitats are driven by many factors, including life history requirements (e.g., spawning, feeding) (Roberts & Angermeier, 2007; Schlosser, 1991), refuge from harsh physicochemical conditions (Jackson, Peres-Neto, & Olden, 2001; Magoulick, 2000), and disturbance (Labbe & Fausch, 2000; Matthews, Marsh-Matthews, Cashner, & Gelwick, 2013). Multiple studies of spatio-temporal patterns have examined fish assemblage structure in riffles and pools of small, wadeable stream reaches (e.g., Gelwick, 1990; Schlosser, 1982; Taylor, 2000); however many larger rivers have areas too deep to wade. Often, non-wadeable pools are not accessed due to the difficulty of sampling them quantitatively (e.g., Matthews, 1986; Tiemann, Gillette, Wildhaber, & Edds, 2004), yet several studies have suggested that they provide refugia for certain fishes (e.g., Hodges & Magoulick, 2011; Labbe & Fausch, 2000; Magoulick & Kobza, 2003), increase persistence during disturbance (Lake, 2003; Sedell, Reeves, Hauer, Stanford, & Hawkins, 1990), and are important for completion of various life history requirements, including spawning (Vokoun, Guerrant, & Rabeni, 2003), feeding (Schlosser, 1991), and growth (Roberts & Angermeier, 2007).

Successful spawning is partly a function of heterogeneous mesohabitat availability, as reproductive behavior reflects the diverse strategies utilized by fishes

(Garcia et al., 2018; Perkin & Gido, 2011), with breeding often occurring in riffles or pools, contingent upon discharge, substrate, depth, and structure (Aadland, 1993). For some fish species, spawning site selection is strongly associated with proximity to deep pools, including Golden Redhorse (*Moxostoma erythrurum*) (Kwak & Skelly, 1992) and Blue Sucker (*Cycleptus elongatus*) (Vokoun et al., 2003) that use deep pools as a resting area before and after spawning; other species, such as Lake Sturgeon (*Acipenser fulvescens*), reproduce in deep pools (Bruch & Binkowski, 2002). During post-spawn, adults of many species occupy habitats that optimize feeding and growth (Schlosser, 1991), and young-of-year (YOY) move into nurseries, augmenting recruitment (King, Humphries, & Lake, 2003). Nursery habitats are particularly important for YOY, as they mitigate predation and harsh abiotic conditions while facilitating growth (King, Humphries, & Lake, 2003). Floodplains and backwaters are often used as nursery habitats due to stable discharge, complex structure, and influxes of trophic resources (King, Humphries, & Lake, 2003; Ross & Baker, 1983), and deep pools and habitat margins also provide abiotic conditions conducive for YOY (Li & Gelwick, 2005).

Climate-induced increases in hydrological disturbance (e.g., droughts and floods) (Jaeger, Olden, & Pelland, 2014), as well as anthropogenic flow alteration (e.g., dams, water abstraction) (Poff, 2018), impair the ability of fishes to complete vital spawn and post-spawn activities (Perkin & Gido, 2011). In the face of disturbance, resistance and resilience of fish assemblages can depend largely on the availability of local refugia, as has been demonstrated in studies of intermittent streams (e.g., Hodges & Magoulick, 2011; Lake, 2003; Sedell et al., 1990), when shallow habitats desiccate and fishes move downstream into deep-pool refugia (Davey & Kelly, 2007; Ross, Matthews, & Echelle,

1985). Discharge affects habitat use (Gillette, Tiemann, Edds, & Wildhaber, 2006), and indirect ramifications of drought, like physicochemical extremes in water temperature and dissolved oxygen, prompt fish to move into deeper pools with more benign conditions (Labbe & Fausch, 2000; Magoulick & Kobza, 2003).

Our knowledge of deep-pool use by fish assemblages stems primarily from studies of intermittent streams (e.g., Hodges & Magoulick, 2011; Roberts & Angermeier, 2007), which generally lack non-wadeable deep-pools, and the importance of non-wadeable mesohabitats to fish assemblage dynamics in larger streams remains poorly understood (Pierce et al., 2014). I studied fish assemblages in a perennial warmwater river in Kansas, USA, to: 1. compare fish assemblage structure at the mesohabitat scale in riffles, wadeable pools, and non-wadeable pools, and 2. examine the relationships of fish density and species richness with depth, water temperature, dissolved oxygen, and season, emphasizing fish use of non-wadeable pools during spawning and post-spawning seasons. I hypothesized that riffles, wadeable pools and non-wadeable pools would support disparate fish assemblages that changed in structure seasonally. Specifically, I predicted that species richness and fish density would vary among mesohabitats and between seasons, with non-wadeable pools and the spawn season having the greatest species richness and fish density.

## **2 | Materials and Methods**

### **2.1 | Study Area**

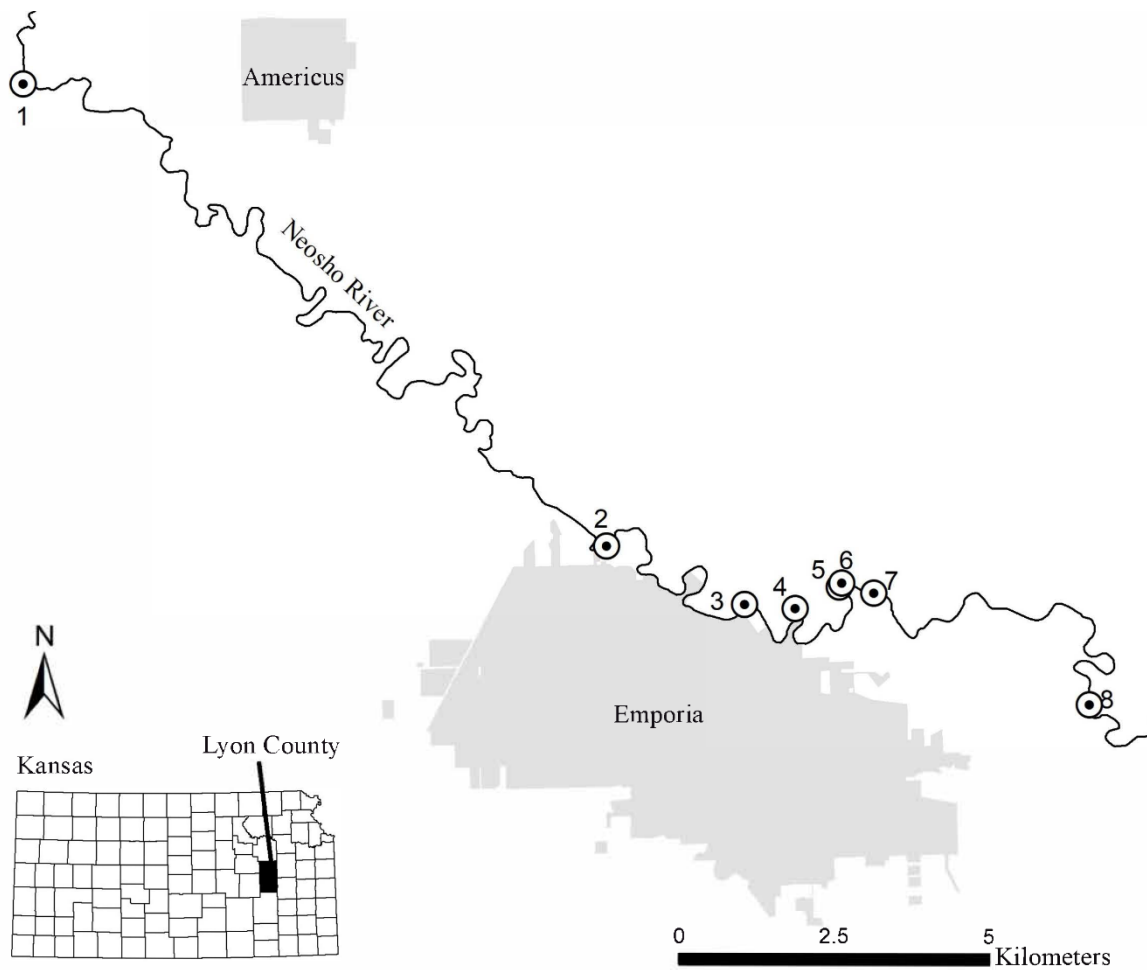
This study was conducted in the Neosho River, part of the Arkansas River drainage in the Prairie Parkland ecoregion (Chapman et al., 2001) in Kansas, USA. Within my study reach, the Neosho is a 5<sup>th</sup>-order stream (Strahler method; Hitchman, Mather, Smith, & Fencel, 2018), flowing southeast through prairie and thin riparian zones (Tiemann et al., 2004). The Neosho River exhibits riffle–pool geomorphology, supports a diverse fish fauna of at least 55 native species (Kansas Fishes Committee, 2014), and has predictably variable water temperature and flow regimes typical of a prairie stream (Dodds, Gido, Whiles, Fritz, & Matthews, 2004). Predominate substrate depends on mesohabitat, with gravel and pebbles typically making up 50–75% of riffles and wadeable pools, and non-wadeable pools having at least 50% silt, sand, and clay.

### **2.2 | Sites and Mesohabitats**

Sampling was conducted at eight sites along a reach of the Neosho River that extends 50 river-km from west of Americus to east of Emporia in Lyon Co., KS (Figure 1; Appendix A). Sample sites were selected based on presence of an upstream riffle, a downstream wadeable pool, a downstream non-wadeable pool, accessibility, and landowner permission. I distinguished riffles by their breaking water at the surface, and pools by their smooth surface flow (Gelwick, 1990). I defined wadeable pools as <1.25 m deep (seivable depth) and non-wadeable pools as  $\geq 1.25$  m deep (i.e., too deep to seine) (Matthews, 1986).



Figure 1 Map of study area, Neosho River, Lyon County, KS, USA, showing eight study sites sampled May–November 2018.



### 2.3 | Fish Sampling

I sampled fishes at each site and in each mesohabitat during daylight hours monthly from May through November 2018, with the exception of October when floods prevented sampling (Appendix B). Site order was randomized each month, and sampling mesohabitats within each site was also randomized. I divided months into two behaviorally-defined seasons: spawn (May, June, July) and post-spawn (August, September, November). Inclusion of months into spawning season was based on known reproductive activity of fishes in Kansas (Kansas Fishes Committee, 2014); months of post-spawn were characterized by non-reproductive behavior, including feeding and growth (Schlosser, 1991).

A hand-drawn Siamese trawl (4.35-m length, 76 cm height, 4 mm mesh size, 2.9-m head rope, 2.4-m foot rope; equipped with otter boards and a tickler chain; Innovative Net Systems, Milton, Louisiana) was used to sample all mesohabitats. This net effectively captures fishes both in wadeable and non-wadeable mesohabitats (Hitchman et al., 2018). Three persons staged the trawl in each mesohabitat and waited 5 minutes before sampling to let fish adjust to any disturbance staging may have caused. The trawl was then pulled by hand a minimum mid-mesohabitat length of 10 m (maximum 32 m) from upstream to downstream at a speed slightly faster than the current velocity in each mesohabitat (Herzog, Ostendorf, Hrabik, & Barko, 2009). Sampling was standardized and quantified by catch per unit effort based on area and volume, with effort ranging 24.3–52.5 m<sup>2</sup> and 1.1–20.44 m<sup>3</sup> in riffles, 26.1–71.5 m<sup>2</sup> and 7.9–46.0 m<sup>3</sup> in wadeable pools, and 29.0–92.8 m<sup>2</sup> and 20.1–64.5 m<sup>3</sup> in non-wadeable pools. After sampling a mesohabitat, collected fish were held in an 18.9-liter bucket until all mesohabitats were

sampled, after which fish were identified, counted, and released. Fish that could not reliably be spot-identified were preserved in 10% formalin and identified in the lab.

## **2.4 | Habitat Variables**

After sampling each mesohabitat at a site, I used a Nikon Aculon range finder (Nikon Americas Inc., Melville, New York) to measure length of the sample area and took geographic coordinates with a Garmin eTrex 10 GPS (Garmin International, Olathe, Kansas) at upstream and downstream boundaries to mark mesohabitats for subsequent sampling at the same location. I used a YSI ODO200 meter (YSI Inc., Yellow Springs, Ohio), calibrated every sampling day, to measure benthic dissolved oxygen and water temperatures approximately 2–5 cm off the river bed at five evenly-spaced points along a mid-mesohabitat transect in each mesohabitat at each site every month. Depths in riffles and wadeable pools were measured with a meter stick at five points along the mid-mesohabitat transect, and depths in non-wadeable pools were measured with a demarcated cable. Dissolved oxygen and water temperature were measured at the surface, 1 m below the surface, and at the deepest point in non-wadeable pools at each site to produce a vertical profile during July, August, September, and November. Measurements in non-wadeable pools were taken from a boat. Discharge data were compiled for 2018 plus from available historical data (2010–2017) from a U.S. Geological Survey stream gage (07179750, Burlingame Road, Emporia, KS) located between sites 7 and 8 (Figure 1).

## **2.5 | Data Analysis**

All analyses were performed with R statistical software (Version 3.5.1) (R Core Team, 2019), and packages used in specific analyses are provided where applicable.

Fish density and environmental variables (depth, water temperature, dissolved oxygen) were compared among mesohabitats and between seasons with mixed model two-factor analysis of variance (ANOVA) using the *lme4* package (Bates, Mäeçhler, Bolker, & Walker, 2015). The random variable was the repeatedly-sampled subject (site) in all models. Density data were  $\log_{10}(x+0.01)^{-2}$  transformed to meet distributional assumptions, and Tukey pairwise comparisons were made when a significant effect was found (*emmeans* package; Lenth, 2019).

Sample-size-based rarefaction was performed (*iNEXT* package; Hsieh, Ma, & Chao, 2019) on abundance data to compare species richness among mesohabitats and between seasons. Rarefaction allows comparison of species richness between samples with different abundances by calculating the expected number of species for each sample from a single reference sample size (Gotelli & Colwell, 2001). A bootstrap procedure with 999 replications was used to calculate 95% confidence intervals for each richness value (Chao et al., 2014). Confidence interval overlap of rarefaction curves was assessed visually to examine differences in species richness among riffle, wadeable pool, and non-wadeable pool mesohabitats and between seasons.

Seasonal species compositions among mesohabitats were compared with three multivariate techniques: non-metric multidimensional scaling (NMDS), permutational multivariate analysis of variance (PERMANOVA), and indicator species analysis. All multivariate tests used fish density data that were fourth-root transformed prior to analysis to reduce the influence of highly abundant species (Clarke, 1993), included rare species (Cao, Larsen, & Thorne, 2001), and were based on Bray–Curtis distance

matrices, which outperforms other matrices when count data are used (Faith, Minchin, & Belbin, 1987).

NMDS was used to visualize the relationship between fish samples and mesohabitat, and between fish samples and season (*vegan* package; Oksanen et al., 2019). NMDS is an ordination method based on rank-ordered distances between sample points in ordination space that does not rely on distributional assumptions, and orders samples in a way that minimizes stress between abundance dissimilarities (Clarke, 1993). Bray–Curtis dissimilarity matrices and 999 randomized starts were used for the ordination.

Multivariate dispersion among mesohabitats and between seasons was evaluated using the *betadisper* function in the *vegan* package to aid interpretation of results (Anderson, 2001). PERMANOVA with 9999 permutations was conducted using the *adonis* function in the *vegan* package to quantify differences in seasonal mesohabitat fish assemblage composition based on the pseudo-F test statistic (Oksanen et al., 2019); a two-step PERMANOVA procedure was used to account for the repeated measures design (J. Stephen Brewer, University of Mississippi, personal communication, April 20, 2019), as implemented by Anderson, Gorley, and Clarke (2008) in PERMANOVA+ for Primer. To test for between-subject effects (mesohabitats), I converted fish assemblage composition data into a Bray–Curtis distance matrix grouped by the repeatedly-measured subject (site). I applied the distance matrix to the *betadisper* function in the *vegan* package (Oksanen et al., 2019), which uses principal coordinate analysis to create centroids for each repeatedly-measured grouping; centroids were used to test between-subject effects. A second PERMANOVA model, which accounted for within-subject effects, included season, season×mesohabitat interaction, and the between-subject effects

term (mesohabitat). Only the within-subject and interaction term results were used (between-subject degrees of freedom accurately accounts for the between-subjects variance, J. Stephen Brewer, University of Mississippi, personal communication, April 20, 2019). When interactions and differences between factors occurred, I used the package *pairwiseAdonis* (Arbizu, 2017) to perform individual pair-wise PERMANOVA tests on each site during all six months to assess which mesohabitat level accounted for the significance, based on Bonferroni-corrected  $p$ -values significant at  $\leq 0.05$ .

Indicator species analysis was performed with 9999 permutations (*labdsv* package; Roberts, 2016) to identify species that contributed most to variation in mesohabitat assemblages (Duf rene & Legendre, 1997). Species were considered significant indicators of mesohabitats at Bonferroni-corrected  $p$ -values  $\leq 0.05$ .

The effects of fixed environmental variables (site, season, mesohabitat, water temperature, dissolved oxygen, and depth) and a random variable (site) on fish density were evaluated through Generalized Linear Mixed Models (GLMM) (*glmmTMB* package; Brooks et al., 2017). General Linear Models (GLM) (*stats* package; R Core Team, 2019) were used to evaluate rarefied species richness, as variation explained by the random variable (site) approached zero and was eliminated from models (Bolker et al., 2009). Pearson correlations were used to assess collinearity between variables before models were generated (*stats* package; R Core Team, 2019). Because depth and mesohabitat were highly correlated (0.88), as were dissolved oxygen and water temperature (0.82), mesohabitat and water temperature were dropped from model analysis (Zar, 1999). For GLM, only samples with more than 20 individuals collected were used to calculate rarefied species richness (Gotelli & Colwell, 2001). Negative

binomial distributions were assumed for density models to avoid overdispersion, and Poisson distributions were assumed for species richness models (Lindén & Mäntyniemi, 2011). Continuous variables were standardized to improve convergence of the models, and overdispersion tests were applied to confirm model assumptions (Bolker et al., 2009). Overdispersion was assessed visually with residual plots using the *DHARMA* package (Hartig, 2019) and tested using the function *overdisp\_fun* in the *PsychHelperFunctions* package (Huff & Papenmeier, 2017). Collinearity between explanatory variables was measured after model analysis using the variance inflation factor (VIF) (*car* package; Fox & Weisberg, 2011), with models having values less than 3 indicating limited collinearity (Myers, 1990).

Candidate models were generated based on combinations of fixed variables (season, dissolved oxygen, depth, depth×dissolved oxygen) that tested *a priori* hypotheses of mesohabitat use. The random variable *site* was incorporated in all density models, including the null model (intercept only). The best model was selected using the Akaike Information Criterion corrected for small sample size ( $AIC_c$ ) and Akaike weight (wAIC), with the largest indicating the best-ranked model; only models with  $\Delta AIC_c$  values  $\leq 2$  were selected for model averaging (Arnold, 2010). Fit of averaged models was determined based on  $R^2$  and 95% confidence intervals (*sjstats* package; Lüdtke, 2019). The marginal  $R^2$  ( $R^2_m$ ) value explained the variance associated with the fixed variables, and the conditional  $R^2$  ( $R^2_c$ ) value explained the variance associated with the fixed and random variables (Nakagawa & Schielzeth, 2013). Because GLM did not include a random factor,  $R^2$  values were a measure of variance explained by fixed factors.



### 3 | Results

#### 3.1 | Environmental Conditions

Mean daily discharge for 2018 was lower during May, June, and July, similar in August, and higher in September, October, and November than in the 8 years for which historical data were available (Figure 2). Depth varied from 3.9 cm to 234.2 cm among mesohabitats, with non-wadeable pools having the largest range (minimum 77.0 cm, maximum 234.2 cm). Non-wadeable pools were significantly deeper than wadeable pools, whereas riffles were significantly shallower (Table 1). Depths varied seasonally, with post-spawn season being significantly deeper than spawn season; no mesohabitat $\times$ season interaction was observed (Table 1). Dissolved oxygen concentrations and water temperature ranged from 1.1 mg $\cdot$ L<sup>-1</sup> to 15.4 mg $\cdot$ L<sup>-1</sup> and 2.7 °C to 33.1 °C, respectively. The minimum dissolved oxygen concentration occurred in a deep pool in June and corresponded with a water temperature of 24.9 °C, while maximum dissolved oxygen concentrations and lowest water temperatures occurred in November in all mesohabitats. Water temperature and dissolved oxygen varied seasonally, but neither had a significant mesohabitat effect or interaction (Table 1). Vertical profiles in non-wadeable pools identified no significant thermal stratification ( $F_{2,74} = 0.18, p = 0.839$ ). Oxidation stratification was marginally significant ( $F_{3,74} = 2.84, p = 0.065$ ) over all months, and dissolved oxygen was significantly lower at the bottom than at the surface in July if November is excluded from the analysis ( $F_{2,54} = 3.37, p = 0.042$ ; Figure 3).

Figure 2 Mean daily discharge ( $\text{m}^3 \cdot \text{s}^{-1}$ ) for the Neosho River, KS, January–December 2018 and historical data, 2010–2017, from U.S. Geological Survey gaging station 07179750, Neosho River, Burlingame Road, Emporia, KS.

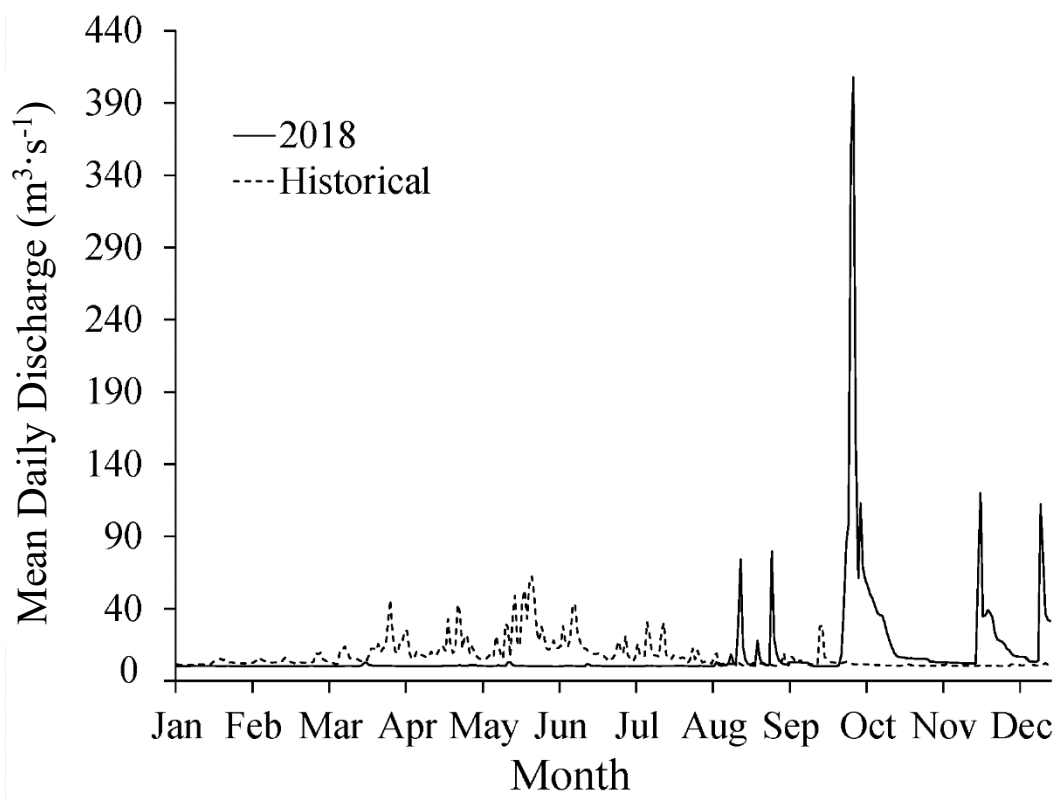
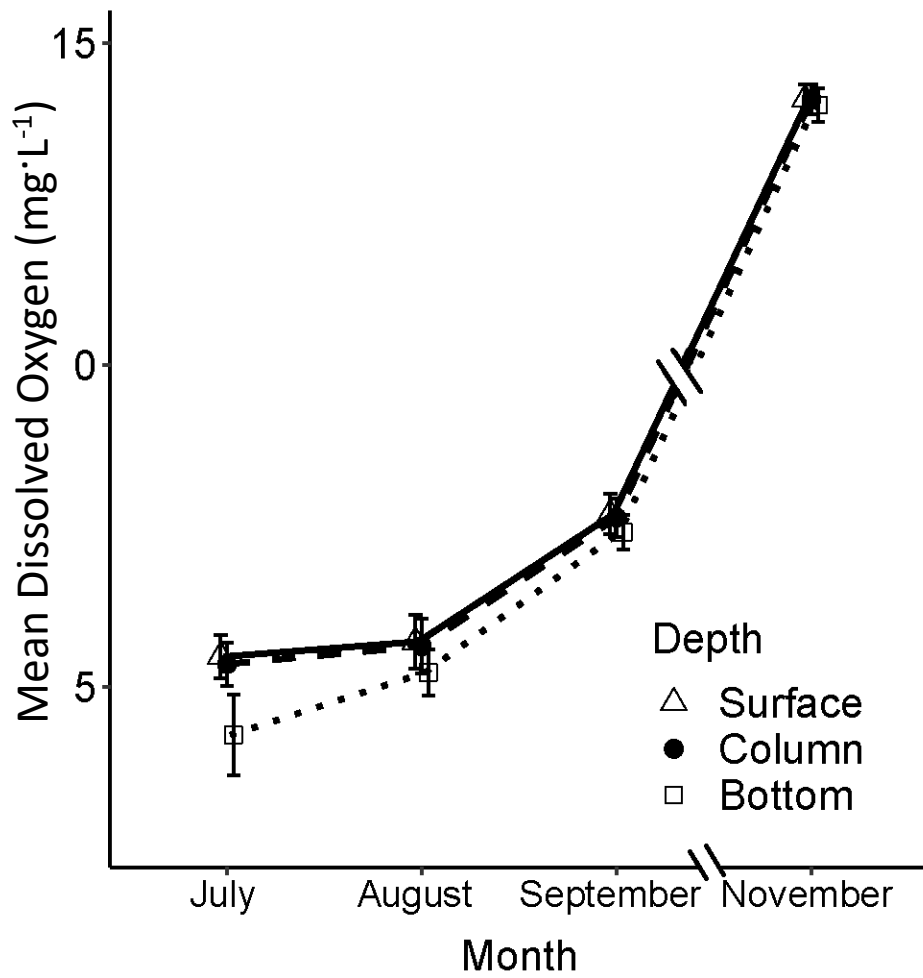


Table 1 Results of a two-way mixed model ANOVA for effects of mesohabitat and season on mean depth, water temperature, dissolved oxygen, and fish density based on area and volume during spawn and post-spawn seasons in the Neosho River, KS, May–November 2018.

Variable	Mesohabitat		Season		Mesohabitat×Season	
	F <sub>2,131</sub>	<i>p</i>	F <sub>1,131</sub>	<i>p</i>	F <sub>2,131</sub>	<i>p</i>
<b>Environmental</b>						
Depth	<b>400.13</b>	<b>&lt; 0.001</b>	<b>9.82</b>	<b>0.002</b>	2.64	0.075
Water temperature	0.04	0.962	<b>60.09</b>	<b>0.001</b>	0.06	0.942
Dissolved oxygen	1.34	0.264	<b>36.47</b>	<b>0.001</b>	0.63	0.535
<b>Fish Density</b>						
Area (m <sup>2</sup> )	<b>15.62</b>	<b>&lt; 0.001</b>	<b>27.42</b>	<b>0.001</b>	1.01	0.364
Volume (m <sup>3</sup> )	<b>17.12</b>	<b>&lt; 0.001</b>	<b>31.71</b>	<b>0.001</b>	<b>3.85</b>	<b>0.024</b>

Note: Results in boldface significant at  $p \leq 0.05$

Figure 3 Vertical profile of mean ( $\pm$ SEM) dissolved oxygen concentration in non-wadeable pools during July, August, September, and November 2018 at the eight sample sites along the Neosho River, KS. Dissolved oxygen was measured at the surface, 1 m below the surface, and just above the stream bed.



### 3.2 | Fish Species Richness and Density

I collected 11,319 fish representing nine families and 36 species (Table 2). Cyprinids comprised 85% of the individuals collected, with four species, Red Shiner (*Cyprinella lutrensis*), Bullhead Minnow (*Pimephales vigilax*), Ghost Shiner (*Notropis buchanani*), and Bluntnose Minnow (*Pimephales notatus*), predominating collections in both seasons and all mesohabitats (Table 2). The most abundant species varied by mesohabitat during spawning season: Red Shiner in riffles (62%), Bullhead Minnow in wadeable pools (30%), and Ghost Shiner in non-wadeable pools (45%). During post-spawning season, Red Shiner predominated in riffles (56%) and wadeable pools (28%) whereas Ghost Shiner was the most abundant species in non-wadeable pools (22%) (Table 2).

Wadeable and non-wadeable pools yielded 30 fish species, whereas riffles had 28, with 5,029 individuals collected in wadeable pools, 2,641 in non-wadeable pools, and 3,649 in riffles. No difference in mesohabitat species richness was observed based on overlap in 95% confidence intervals of rarefaction curves (Figure 4a). Fishes unique to riffles were Cardinal Shiner (*Luxilus cardinalis*), Stonecat (*Noturus flavus*), and Freckled Madtom (*Noturus nocturnus*); species unique to wadeable pools were Grass Carp (*Ctenopharyngodon idella*) and Redfin Shiner (*Lythrurus umbratilis*); fishes collected only in non-wadeable pools were Shortnose Gar (*Lepisosteus platostomus*), Smallmouth Buffalo (*Ictiobus bubalus*), and White Crappie (*Pomoxis annularis*) (Table 2). Rarefaction curves were also constructed for richness in spawning and post-spawning seasons, with 7,965 individuals and 35 species during spawning season and 3,354 individuals and 27 species during post-spawn (Figure 4b).

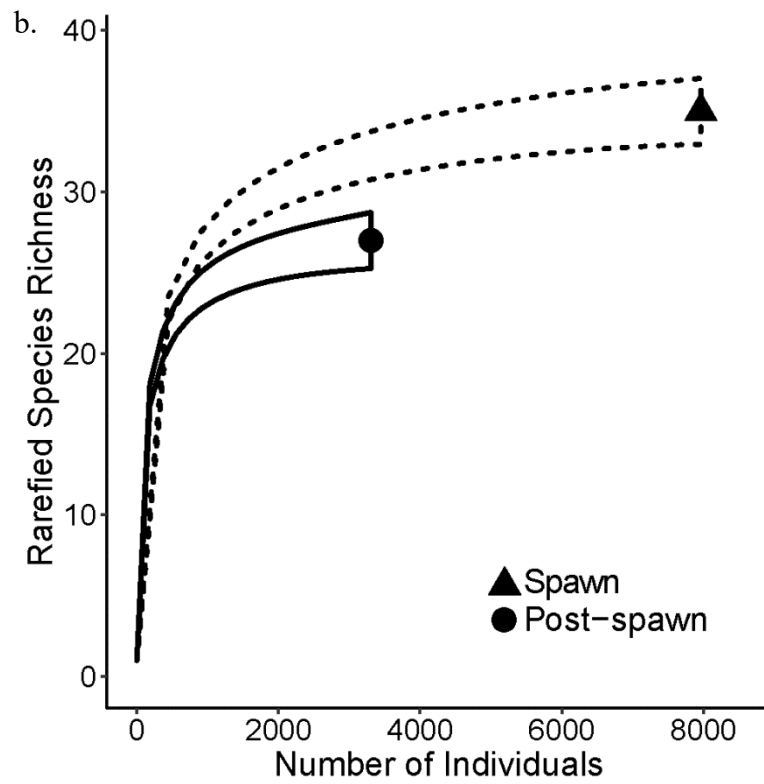
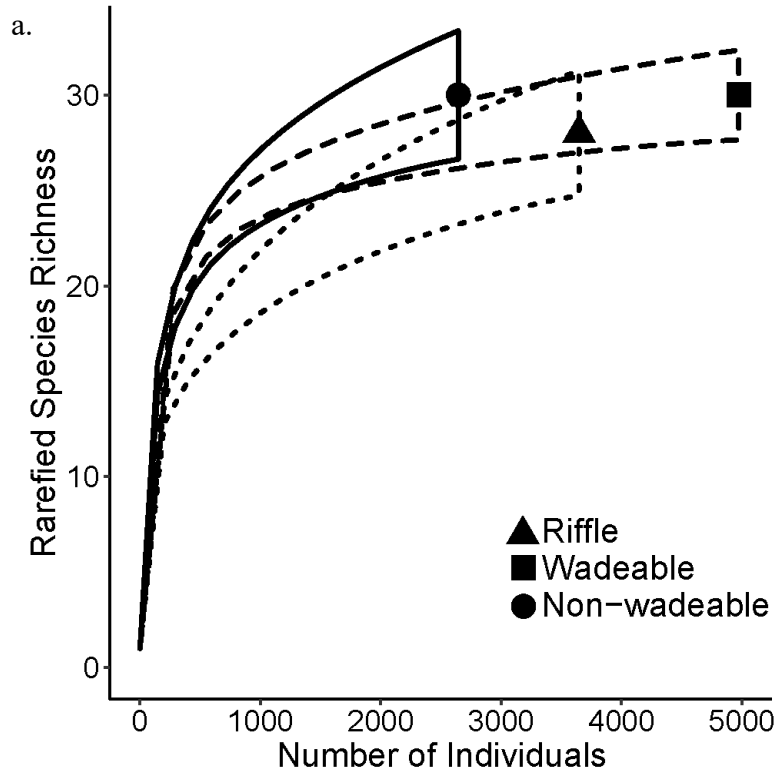
Table 2 Number of individuals collected in riffles, wadeable pools, and non-wadeable pools during spawning and post-spawning seasons at eight sites in the Neosho River, KS, May–November 2018.

Species	Spawn			Post-spawn			Total
	Riffle	Wadeable pool	Non-wadeable pool	Riffle	Wadeable pool	Non-wadeable pool	
<b>Lepisosteidae</b>							
<i>Lepisosteus osseus</i>	0	1	1	0	0	0	2
<i>L. platostomus</i>	0	0	3	0	0	1	4
<b>Cyprinidae</b>							
<i>Campostoma anomalum</i>	181	10	2	46	13	0	252
<i>Ctenopharyngodon idella</i>	0	1	0	0	0	0	1
<i>Cyprinella camura</i>	7	1	1	13	1	0	23
<i>C. lutrensis</i>	1771	518	245	456	534	39	3563
<i>Luxilus cardinalis</i>	1	0	0	0	0	0	1
<i>Lythrurus umbratilis</i>	0	2	0	0	14	0	16
<i>Notropis buchmanii</i>	28	546	911	15	213	135	1848
<i>N. percobromus</i>	2	4	1	0	0	0	7
<i>N. stramineus</i>	9	90	136	42	118	38	433
<i>N. volucellus</i>	1	13	16	0	0	0	30
<i>Phenacobius mirabilis</i>	14	12	0	6	4	0	36
<i>Pimephales notatus</i>	138	544	82	48	410	65	1287
<i>P. tenellus</i>	1	21	7	5	35	3	72
<i>P. vigilax</i>	216	916	434	24	379	118	2087
<b>Catostomidae</b>							
<i>Ictiobus bubalus</i>	0	0	5	0	0	0	5
<b>Ictaluridae</b>							



<i>Ictalurus punctatus</i>	1	23	29	1	2	10	66
<i>Noturus flavus</i>	42	0	0	9	0	1	52
<i>N. nocturnus</i>	2	0	0	0	0	0	2
<i>N. placidus</i>	5	2	1	1	0	0	9
<i>Pylodictis olivaris</i>	1	1	7	1	0	2	12
<b>Atherinopsidae</b>							
<i>Labidesthes sicculus</i>	1	37	1	0	0	0	39
<b>Poeciliidae</b>							
<i>Gambusia affinis</i>	231	44	10	57	23	4	369
<b>Centrarchidae</b>							
<i>Lepomis cyanellus</i>	4	5	16	0	4	1	30
<i>L. humilis</i>	7	57	61	1	80	77	283
<i>L. macrochirus</i>	0	20	14	1	22	22	79
<i>L. megalotis</i>	1	62	16	0	19	4	102
<i>Micropterus salmoides</i>	1	18	2	0	0	0	21
<i>M. punctulatus</i>	0	2	1	0	5	1	9
<i>Pomoxis annularis</i>	0	0	0	0	0	3	3
<b>Percidae</b>							
<i>Etheostoma spectabile</i>	130	48	0	68	46	9	301
<i>Percina caprodes</i>	4	27	5	2	6	6	50
<i>P. copelandi</i>	2	8	4	0	0	2	16
<i>P. phoxocephala</i>	37	57	18	15	9	3	139
<b>Sciaenidae</b>							
<i>Aplodinotus grunniens</i>	0	2	6	0	0	62	70
Total	2838	3092	2035	811	1937	606	11319

Figure 4 Rarefaction curves with 95% confidence intervals for species richness among mesohabitats and between seasons in the Neosho River, KS, May–November 2018: (a) species richness in riffle, wadeable pool, and non-wadeable pool mesohabitats; (b) species richness in spawning and post-spawning seasons.



Limited overlap between the two rarefaction curves indicates spawning season had greater species richness than post-spawning season. Fishes unique to spawning season were Longnose Gar (*Lepisosteus osseus*), Grass Carp, Carmine Shiner (*Notropis percobromus*), Cardinal Shiner, Smallmouth Buffalo, Freckled Madtom, Brook Silverside (*Labidesthes sicculus*), and Largemouth Bass (*Micropterus salmoides*), while White Crappie was specific to the post-spawn. Fish species unique to mesohabitats and seasons occurred in less than 5% of all samples.

Fish density based on area and volume differed significantly among mesohabitats and between seasons, with volume-based density showing a significant mesohabitat×season interaction (Table 1). Area-based and volume-based densities were significantly higher in spawning season than in post-spawning season (Table 1) and were higher in wadeable pools than in non-wadeable pools but varied seasonally in riffles (Figure 5). Area-based density in riffles was similar to that in wadeable and non-wadeable pools during spawning season but significantly less than in wadeable pools during post-spawn (Figure 5a). Volume-based density in riffles and wadeable pools was significantly higher than in non-wadeable pools during spawning season, but density in riffles was significantly less than in wadeable pools during post-spawn (Figure 5b). The significant interaction in volume-based density reflected the decrease in riffles from spawn to post-spawn (Figure 5b).

### **3.3 | Fish Assemblage Structure**

Assemblage data were represented with two dimensions of a three-dimensional solution, both for area-based (stress = 0.153; Figure 6a,b) and volume-based densities

Figure 5 Fish density based on (a) area and (b) volume (mean±SEM) among riffles, wadeable pools, and non-wadeable pools during spawn and post-spawn in the Neosho River, KS, May through November 2018. Bars with different letters within a season indicate a significant difference between mesohabitat type ( $p \leq 0.05$ ) based on two-way mixed model ANOVA.

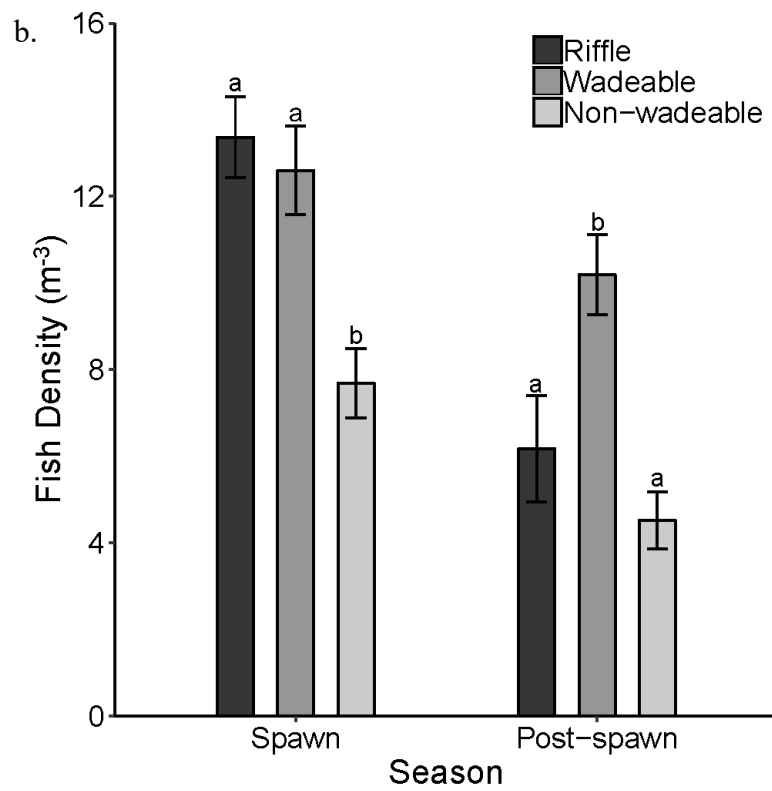
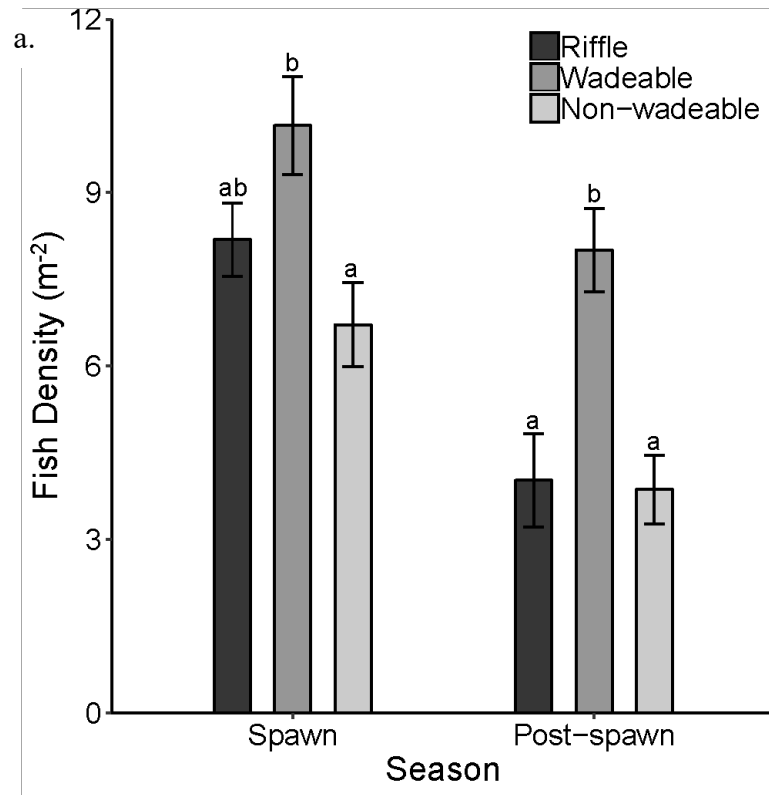
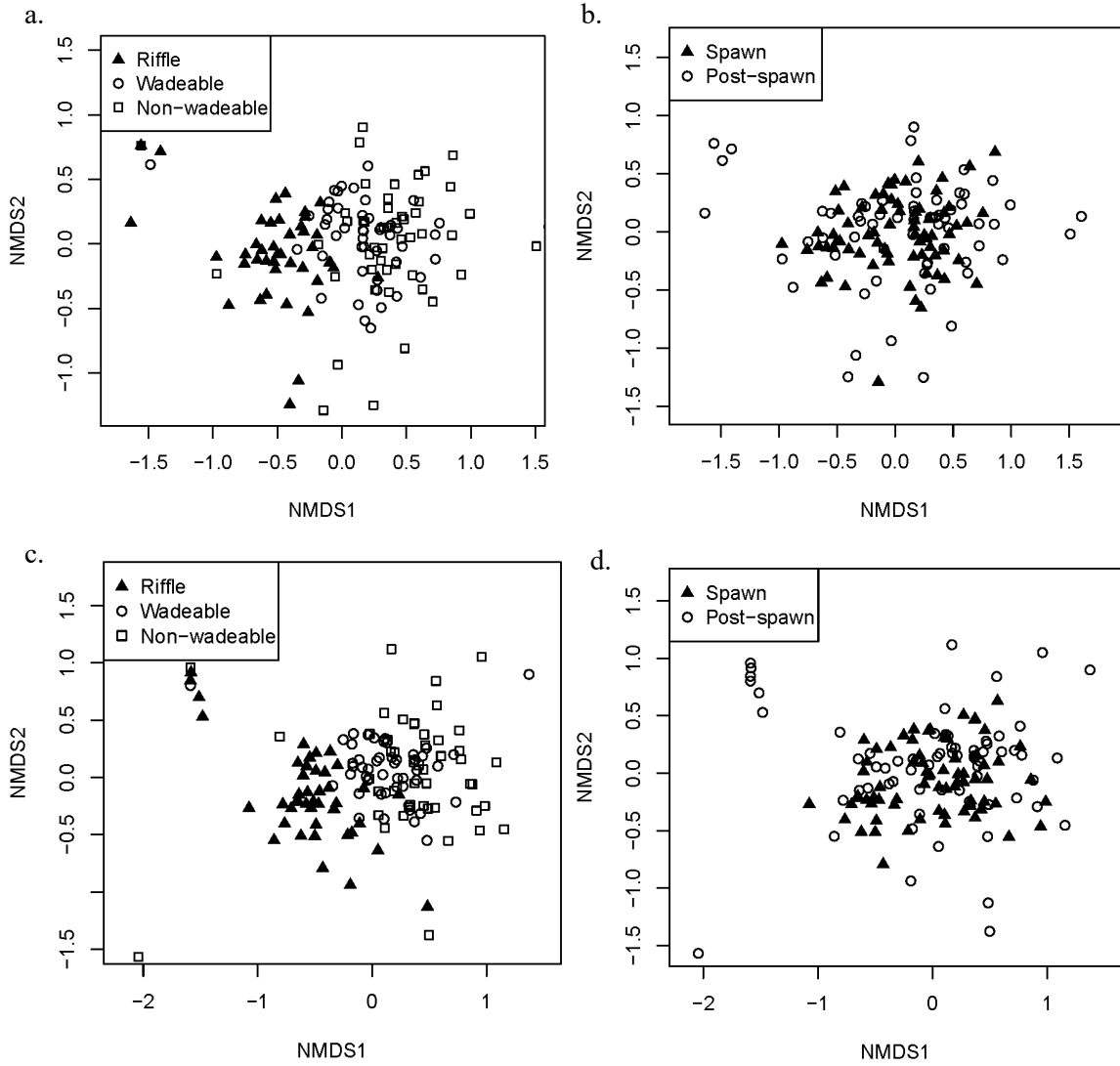


Figure 6 Non-metric multidimensional scaling (NMDS) ordination plots of Bray-Curtis distances for spatial and temporal comparisons of area- (a and b) and volume-based fish densities (c and d) in the Neosho River, May to November 2018. Points represent 139 samples from three mesohabitats at each of eight sites across two seasons, fourth-root transformed for riffle, wadeable pool, and non-wadeable pool mesohabitats (a and c) and spawning and post-spawning seasons (b and d). Data are represented in two dimensions of the three-dimensional solution, with final stress values of 0.153 (a and b) and 0.148 (c and d).



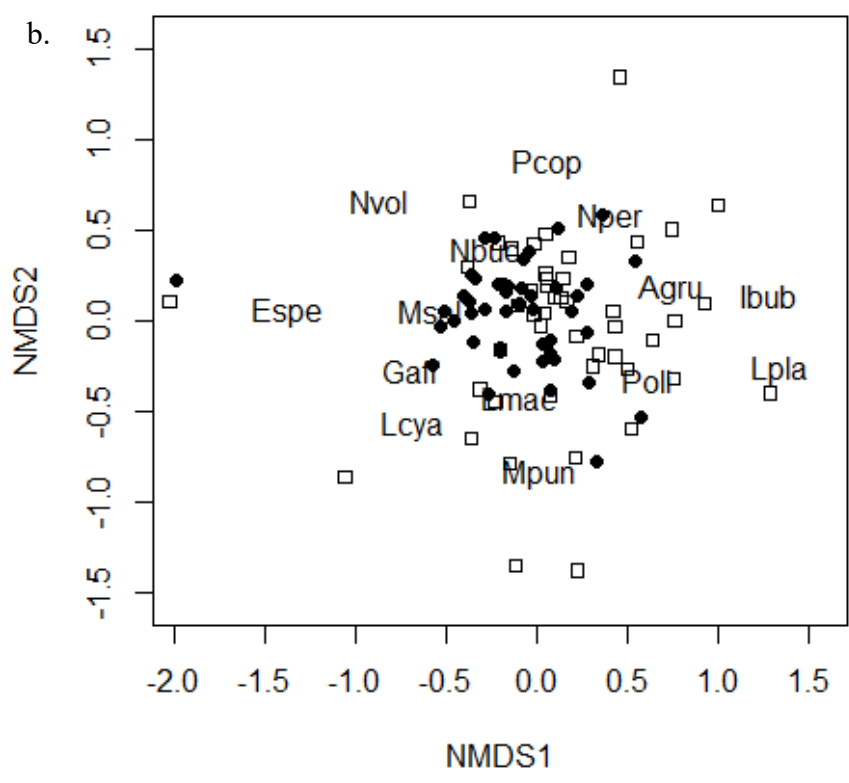
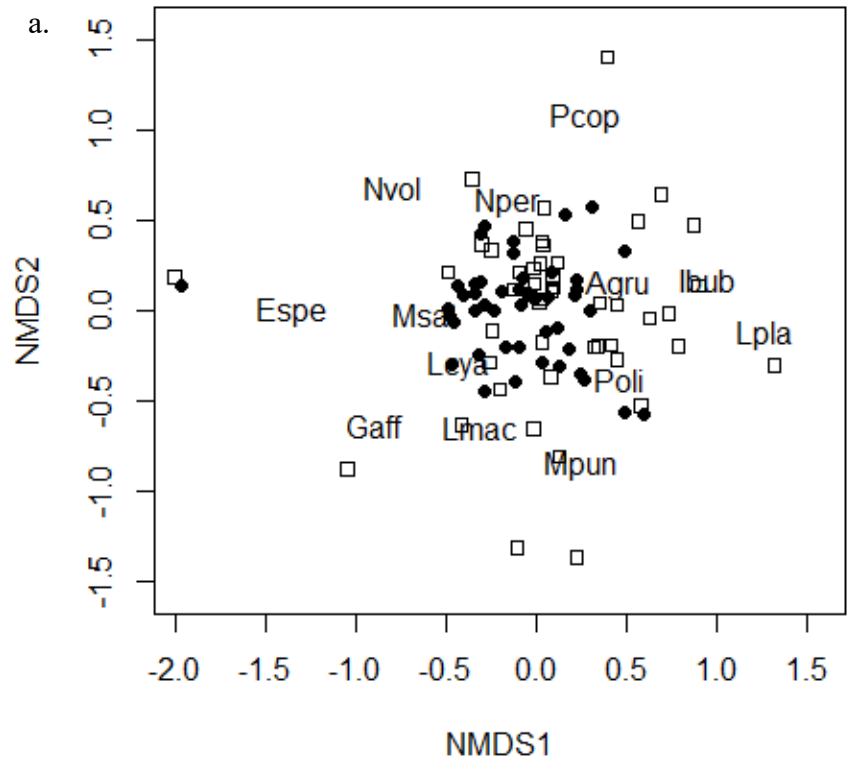


(stress = 0.148; Figure 6c,d); stress values < 0.2 are typically interpreted with limited caution (Clarke, 1993). Visually, the NMDS ordination for both area and volume densities showed no distinction between seasons but revealed two distinct mesohabitat clusters corresponding to riffles and pools, with wadeable and non-wadeable pools clustering in close proximity (Figure 6). Visual assessment of ordination results and a multivariate dispersion test indicated significant dispersion for area-based and volume-based densities, respectively, between seasons ( $F_{1,137} = 14.36, p < 0.001$ ;  $F_{1,137} = 13.55, p < 0.001$ ) and among mesohabitats ( $F_{2,136} = 8.99, p < 0.001$ ;  $F_{2,136} = 8.09, p < 0.001$ ), with post-spawning season having greater dispersion than spawning season and non-wadeable pools having greater dispersion than riffles and wadeable pools (Figure 6).

To more critically examine differences between wadeable and non-wadeable pools, I excluded disparate riffle samples in a secondary NMDS analysis. Species associated with non-wadeable pools were Shortnose Gar (*Lpla*), Smallmouth Buffalo (*Ibub*), Flathead Catfish (*Pylodictis olivaris*, *Poli*), and Freshwater Drum (*Aplodinotus grunniens*, *Agru*), while species found more in wadeable pools were Largemouth Bass (*Msal*) and Orangethroat Darter (*Etheostoma spectabile*, *Espe*) (Figure 7).

PERMANOVA and pairwise comparisons addressing mesohabitat effects were consistent with ordination results for both fish density measures—fish assemblage structure among mesohabitats was significantly different based on area ( $F_{2,14} = 8.01, p = 0.0001$ ) and volume ( $F_{2,14} = 8.96, p = 0.0001$ ). For area-based densities, pairwise comparisons of mesohabitat assemblages at seven of the eight sites showed significant differences between riffles and wadeable pools, and riffles and non-wadeable pools were significantly different at four sites; two sites were significantly different between

Figure 7 Non-metric multidimensional scaling (NMDS) ordination plot of Bray-Curtis distances for spatial comparisons of area- (a) and volume-based fish densities (b) in the Neosho River, May–November 2018. Points represent 95 samples from two mesohabitats at each of eight sites across two seasons, fourth-root transformed for wadeable pool and non-wadeable pool mesohabitats. Data are represented in two dimensions of the three-dimensional solution, with a final stress values of 0.165 (a) and 0.163 (b). Species with low correlations to ordination axes were removed to clarify illustration. Species names are abbreviated from Table 2 with the first letter of the genus and the first three letters of the specific epithet.



wadeable pools and non-wadeable pools (Table 3). Volume-based densities were significantly different at seven sites between riffles and wadeable pools, five sites between riffles and non-wadeable pools, and three sites between wadeable and non-wadeable pools (Table 3). Season had a significant effect on fish assemblage structure for both area-based ( $F_{1,112} = 5.61, p = 0.0001$ ) and volume-based densities ( $F_{1,112} = 5.82, p = 0.0001$ ), with no significant interaction between season and mesohabitat ( $F_{2,112} = 1.28, p = 0.1952$ ;  $F_{2,112} = 1.59, p = 0.055$  for area-based and volume-based densities, respectively). The significant effect of season on fish assemblage structure was not consistent, with large overlap between seasonal samples in the ordination diagram, and was likely a result of higher multivariate dispersion in the post-spawning season than during the spawn (Figure 6). Heterogeneous dispersion can identify significant differences within factors in addition to between factors, thus can provide additional information about the fish assemblage but should be interpreted with caution (Anderson & Walsh, 2013).

Indicator species analysis identified seven significant indicators for area-based densities and 10 for volume-based densities in two mesohabitats (Table 4). For area-based densities, three species were identified in riffles, with Orangethroat Darter having the highest indicator value, followed by Central Stoneroller (*Campostoma anomalum*) and Stonecat (*Noturus flavus*). Volume-based densities identified six indicator species in riffles, with Red Shiner, Suckermouth Minnow (*Phenacobius mirabilis*), and Western Mosquitofish (*Gambusia affinis*) added. Area-based densities in wadeable pools had four

Table 3 Results of pairwise comparisons of area-based and volume-based fish densities among mesohabitats at eight sites in the Neosho River, KS, May through November 2018.

Site	Mesohabitat comparisons					
	Riffle vs. Wadeable		Riffle vs. Non-wadeable		Wadeable vs. Non-wadeable	
	F <sub>1,16</sub>	<i>p</i>	F <sub>1,16</sub>	<i>p</i>	F <sub>1,16</sub>	<i>p</i>
<b>Area</b>						
1	<b>2.81</b>	<b>0.021</b>	2.97	0.069	<b>2.35</b>	<b>0.031</b>
2	<b>2.97</b>	<b>0.015</b>	<b>3.56</b>	<b>0.006</b>	1.07	1.000
3	<b>4.32</b>	<b>0.005</b>	<b>3.43</b>	<b>0.008</b>	2.04	0.195
4	<b>4.01</b>	<b>0.019</b>	<b>4.25</b>	<b>0.007</b>	1.66	0.390
5	1.86	0.267	2.10	0.119	0.62	1.000
6	<b>1.98</b>	<b>0.039</b>	1.57	0.416	1.23	1.000
7	<b>4.68</b>	<b>0.005</b>	1.92	0.158	<b>1.73</b>	<b>0.049</b>
8	<b>3.77</b>	<b>0.041</b>	<b>6.78</b>	<b>0.008</b>	2.03	0.077
<b>Volume</b>						
1	<b>2.64</b>	<b>0.018</b>	<b>3.09</b>	<b>0.042</b>	<b>2.45</b>	<b>0.035</b>
2	<b>3.04</b>	<b>0.007</b>	<b>3.71</b>	<b>0.010</b>	1.08	1.000
3	<b>4.06</b>	<b>0.006</b>	<b>3.96</b>	<b>0.010</b>	<b>2.72</b>	<b>0.017</b>
4	<b>4.20</b>	<b>0.010</b>	<b>4.89</b>	<b>0.003</b>	1.71	0.327
5	1.67	0.365	<b>2.85</b>	<b>0.029</b>	1.36	0.659
6	<b>2.10</b>	<b>0.050</b>	1.97	0.140	1.55	0.454
7	<b>3.88</b>	<b>0.004</b>	2.11	0.069	<b>1.92</b>	<b>0.041</b>
8	<b>4.12</b>	<b>0.022</b>	7.56	0.063	2.08	0.084

Note: Results in boldface significant at Bonferroni-adjusted  $p \leq 0.05$

Table 4 Results from indicator species analysis of area-based and volume-based fish densities among mesohabitats at eight sites in the Neosho River, KS, May–November 2018. No indicator species were represented in non-wadeable pools.

Mesohabitat	Species	Indicator Value	<i>p</i>
<b>Area-based</b>			
Riffle	<i>Campostoma anomalum</i>	0.447	0.0001
	<i>Noturus flavus</i>	0.357	0.0001
	<i>Etheostoma spectabile</i>	0.555	0.0001
Wadeable pool	<i>Pimephales notatus</i>	0.490	0.0001
	<i>Pimephales vigilax</i>	0.430	0.0001
	<i>Lepomis humilis</i>	0.307	0.0005
	<i>Lepomis megalotis</i>	0.401	0.0001
<b>Volume-based</b>			
Riffle	<i>Campostoma anomalum</i>	0.476	0.0001
	<i>Cyprinella lutrensis</i>	0.452	0.0001
	<i>Phenacobius mirabilis</i>	0.203	0.0012
	<i>Noturus flavus</i>	0.362	0.0001
	<i>Gambusia affinis</i>	0.284	0.0013
	<i>Etheostoma spectabile</i>	0.609	0.0001
Wadeable pool	<i>Pimephales notatus</i>	0.456	0.0001
	<i>Pimephales vigilax</i>	0.406	0.0002
	<i>Lepomis humilis</i>	0.314	0.0008
	<i>Lepomis megalotis</i>	0.408	0.0001

Note: Bonferroni-adjusted *p*-values

indicator species: Bluntnose Minnow, Bullhead Minnow, Orangespotted Sunfish (*Lepomis humilis*), and Longear Sunfish (*Lepomis megalotis*). Analysis of volume-based densities in wadeable pools provided the same indicator species as area-based densities. No significant indicator species were demonstrated for non-wadeable pools.

### 3.4 | Fish Assemblage/Habitat Relationships

Six candidate GLM were analyzed for rarefied species richness, with three retained as best predictors. The null model had the lowest  $\Delta AIC_c$  value and carried the most Akaike weight (wAIC), thus was considered the best model, while the second best included only season, and the third only depth (Table 5), having less than half the support of the null model. Based on 95% confidence intervals, no environmental variables were significant predictors of species richness. No model explained  $>2\%$  of the variation in species richness (Table 5).

Six candidate GLMM were analyzed for fish density based on area and volume. Two were retained as the best models for area-based densities, and one was retained for volume-based density, with  $\Delta AIC_c$  values  $< 2$  (Table 5). Depth, season, and dissolved oxygen were retained in at least one model, while depth and season were retained in all models. The 95% confidence interval for depth and season did not include zero, indicating a significant effect on area-based densities, while volume-based density was significantly related to depth, season, and dissolved oxygen (Table 5). As a general pattern, density decreased with increasing depth, and from spawn to post-spawn season, as well as from low to high dissolved oxygen concentration, with high dissolved oxygen concentrations and low fish densities during November influencing this relationship.

Table 5 Top GLM for predicting fish species richness based on samples with more than 20 individuals, and GLMM for density based on area and volume using Akaike Information Criterion correct for small sample size AICc.  $\Delta AICc$  values  $< 2$  are shown as they indicate highly ranked models. Akaike weights (wAIC) sum to one, with the largest indicating the best ranked model. Marginal  $R^2$  ( $R^2m$ ) is the variation explained by the fixed factors, and conditional  $R^2$  ( $R^2c$ ) is variation explained by the random factor and fixed factors. 95% confidence intervals for significant predictors are given, with significance indicated by the exclusion of zero.

Dependent Variable	Model	AICc	$\Delta AICc$	wAIC	$R^2m$	$R^2c$	Significant Predictor	95% CI
Richness	Null	381.70	0.00	0.54	0.00			
Richness	Season	383.22	1.52	0.25	0.02			
Richness	Depth	383.64	1.94	0.21	$< 0.01$			
Density ( $m^{-2}$ )	Depth + Season + DO	499.10	0.00	0.53	0.36	0.41	Depth	(-0.64, -0.23)
Density ( $m^{-2}$ )	Depth + Season	499.38	0.27	0.47	0.34	0.39	Season	(-1.14, -0.35)
Density ( $m^{-3}$ )	Depth + Season + DO	767.61	0.00	0.92	0.73	0.73	Depth Season DO	(-1.39, -0.97) (-0.82, -0.27) (-0.53, -0.09)



Models based on area explained a small portion of the overall variance in fish density, with the best model having an  $R^2_m$  value of 0.36 and an  $R^2_c$  value of 0.41. Models based on volume explained more variation, with the highest-ranked model having an  $R^2_m$  value of 0.73 and an  $R^2_c$  value of 0.73 (Table 5).

#### **4 | Discussion**

As hypothesized, comparisons among three mesohabitats and between two seasons in this perennial warmwater river indicated a significant spatio-temporal effect on the fish assemblage. Mesohabitat accounted for more variation than season. Spatial patterns of relative abundance in multivariate space reflected distinctions between riffle and pool assemblages (Figure 6a,c). Indicator species identified in riffles and wadeable pools, including Central Stoneroller, Orangethroat Darter, Bullhead Minnow, and Bluntnose Minnow, likely played a role in compositional differences between riffle and pool mesohabitats (Table 4). Similarly, previous work sampling warmwater fish assemblages within reach types (i.e., within headwater, midstream, or downstream reaches), attributed spatial variation to dissimilarities between riffle and pool mesohabitats (Fuselier & Edds, 1996; Taylor, 2000). Conversely, fish assemblages of warmwater streams varied spatially and temporally in riffles and pools, but when compared among reach types they demonstrated patterns of longitudinal zonation (Gelwick, 1990; Schlosser, 1982). Spatial variation reflects the scale of observation, with larger study areas likely to encompass a wider range of environmental conditions and, thus, more spatial variation among fish assemblages (Camana, Dala-Corte, & Becker, 2016; Chea, Lek, Ngor, & Grenouillet, 2017; Pease et al., 2011). The small scale and homogenous reach type in my study could partially explain why no significant predictors were identified for species richness.

Secondary ordination examining the two types of pool mesohabitats identified species, including Shortnose Gar, Smallmouth Buffalo, Flathead Catfish, and Freshwater Drum, as distinguishing of non-wadeable pool samples (Figure 7a,b). Multivariate pairwise comparisons of wadeable and non-wadeable pool fish assemblages showed differences at only two of eight sites for area-based density and three of eight sites for volume-based density (Table 3). Although significant differences between wadeable and non-wadeable pool assemblages were limited, studies of fish assemblages that do not include samples from non-wadeable pools likely underestimate abundance of fish like Ghost Shiners, which predominated in that mesohabitat during spawning and post-spawning seasons, as well as pool species like Shortnose Gar, Smallmouth Buffalo, and White Crappie, which were collected only there. The low collection frequency of these fishes could have been a function of sampling gear limitations, as I avoided structure to improve sample efficiency in non-wadeable pools, pulling the trawl manually, or perhaps because seven of the eight sites had non-wadeable pools that were relatively shallow (< 3 m) compared to those in larger rivers.

Deep-pool mesohabitats can be important to the overall health of fish assemblages, specifically as refugia during harsh seasonal conditions, and research needs to focus on understanding the seasonal dynamics of fish assemblage structure in non-wadeable areas of larger streams. Fish density, based on area and volume, was higher in wadeable pools than in non-wadeable pools (Figure 5). These results may reflect a lack of refugium use during a summer in which stream fragmentation did not occur. Similarly, Dekar and Magoulick (2007) found a negative relationship between fish density and maximum depth in three northwest Arkansas streams when the impacts of drought (e.g.,

stream drying) were minimal. Converse patterns have been observed in intermittent streams during drought, with deep pools commonly used as refugia (Hodges & Magoulick, 2011; Magoulick & Kobza, 2003). Drought impacts, such as complete drying, stream fragmentation, and lethal physicochemical conditions, are often intensified in smaller, intermittent streams, leading to a more dramatic shift in mesohabitat use by the fish assemblage (Lake, 2003; Magoulick, 2000). Perennial streams, like the reach investigated in this study, may not show such shifts in mesohabitat use in response to drought, and lack of robust differences between wadeable and non-wadeable pool fish assemblages could be attributed, in part, to the resistance of perennial reaches to impacts of drought (Davey & Kelly, 2007; Ross et al., 1985). Deep-pool refugia use has also been observed during winter, as fish species including Flathead Catfish have been observed congregating in deep pools at this time (Hawkinson & Grunwald, 1979; Vokoun & Rabeni, 2005). I was unable to sample in winter because of high flows; however, future studies should investigate deep-pool refugia use by large-river fish assemblages during this season.

Both pool mesohabitats supported a similar number of fish species (Figure 4a), yet lower area-based and volume-based densities in non-wadeable pools (Figure 5) suggest the presence of environmental constraints. Spatio-temporal fluctuations in physicochemical conditions, specifically dissolved oxygen and its correlate, water temperature, weakly influenced area- and volume-based fish densities and species richness (Table 5). Although dissolved oxygen was a significant predictor for volume-based density, it explained only a small portion of the variation and was likely driven by seasonally high dissolved oxygen concentrations and concurrent low volume-based

densities in the post-spawn season following floods in September and October. The limited influence of water temperature and dissolved oxygen on fish density and species richness might be attributed to the physicochemical tolerance of warmwater fish assemblages, with hyperthermia and hypoxia thresholds ranging 34.9–38.8°C and 0.49–1.59 mg·L<sup>-1</sup>, respectively (Smale & Rabeni, 1995). During my study in the Neosho River, water temperature reached a maximum of 33°C and dissolved oxygen concentrations fell to 1.13 mg·L<sup>-1</sup>. In the absence of limiting abiotic conditions, biotic factors, including predation, can be more important than abiotic factors in structuring fish assemblages (Jackson et al., 2001) and can result in size-selective depth distribution in pools, with large predatory fish restricting smaller fish to shallow habitats and terrestrial predators limiting large fish to deep habitats (Harvey & Stewart, 1991; Schlosser, 1987). I did not regularly collect large predatory fish at my sample sites, and to test this predation hypothesis would require detailing size and trophic behavior of all fish collected in wadeable and non-wadeable pools.

While there were seasonal effects on the fish assemblage, distinction between seasonal samples in multivariate space was negligible (Figures 6b,d). Many studies have analyzed juvenile fish species as separate taxa (e.g., Gelwick, 1990; Gillette, Tiemann, Edds, & Wildhaber, 2005), which was beyond the scope of my study and could account for the limited temporal variation I observed. Gelwick (1990) found that temporal patterns were associated with species richness and abundance of juvenile taxa in a small Oklahoma stream, and Gillette et al. (2005) found that temporal variation in Neosho River fish assemblage composition was driven by influxes of juvenile Orangethroat

Darters, Slenderhead Darters (*Percina phoxocephala*), Suckermouth Minnows (*Phenacobius mirabilis*), Logperch (*Percina caprodes*), and Central Stonerollers.

Significant differences in multivariate dispersion indicates seasonal effects were, in part, a result of fish assemblage differences within the post-spawning season. High multivariate dispersion of samples during the post-spawn was likely associated with a flood that occurred between September samples (Figure 2), resulting in one sample taken before the flood and several after (Appendix B). Another flood occurred in October, with high flows persisting until mid-November (Figure 2). Both floods likely contributed to the decrease in area-based and volume-based fish densities from spawn to post-spawn and were associated with decreases in riffle and non-wadeable pool fish densities (Figure 5). Specifically, decreases in Red Shiner abundance in riffles occurred, as fish moved into wadeable pools (Table 2). Floods also had immediate impacts on fish density in northern Oregon streams where pre-flood densities were higher than those immediate post-flood (Pearsons et al., 1992). Relatively consistent fish densities in wadeable pools (Figure 5) suggest they were used by fishes during high flow conditions, concordant with Ross and Baker's (1983) observation that fishes moved from main channel to marginal habitats during floods in southeastern Mississippi. Low fish densities during post-spawn could also be related to poor recruitment, as timing and duration of flooding might not have been conducive for survival of YOY fishes. Flooding before the spawn can stimulate reproductive behavior and inundate important floodplain nurseries (Garcia et al., 2018); however, floods after the spawn can displace adults and YOY (Dodds et al., 2004), which could have occurred in my study. Floods can have important short-term impacts on fish assemblage dynamics, including spawn and post-spawn behavior (Garcia et al., 2018).

Conversely, Franssen et al. (2006) found that fish assemblages in a Kansas prairie stream were resilient to long-term effects of floods, which explained only a small portion of variation in density and species richness.

Higher area- and volume-based fish densities in riffles and wadeable pools during the spawn may indicate that these areas were more important for reproduction than non-wadeable pools; fish densities in riffles decreased more than those in wadeable and non-wadeable pools from spawn to post-spawn. Although decreases in fish density in all mesohabitats from spawn to post-spawn season make it difficult to discern the relative importance of wadeable pools and non-wadeable pools for fish recruitment (Figure 5), I commonly collected YOY fishes in wadeable pools and non-wadeable pools. My study did not quantify recruitment, as length of individuals was not measured, and seasonal patterns could have reflected higher adult mortality than YOY recruitment. Future studies should investigate recruitment to better understand post-spawn fish life history.

Rarefied species richness during spawning season was higher than during post-spawning season (Figure 4b), which could be related to spawning migrations, as some fishes move upstream and congregate in shallower habitats and return downstream post-spawn, including Smallmouth Buffalo (Adams & Parsons, 1998) and Longnose Gar (Johnson & Noltie, 1996). However, it should be noted that all eight species unique to spawning season were rare, occurring in < 5% of the samples. Depth, season, and dissolved oxygen were not significant predictors of species richness, with top models explaining only a small amount of variation (Table 5). Instead, habitat complexity, in relation to area, volume, and structure, may be a better predictor for richness, as

complexity typically supports more habitat configurations and food resources (Angermeier & Schlosser, 1989).

Spatial variation in fish assemblage structure among mesohabitats emphasizes the importance of habitat heterogeneity at the local scale, as assemblage differences reflect contrasts between riffles and pools. Non-wadeable pools are often not sampled; however, my study demonstrates that they can differ from wadeable pools in fish density and species composition and should be sampled to accurately characterize fish assemblages. Local water quality variables, specifically water temperature and dissolved oxygen, were only weakly correlated with fish density and species richness, even during a drought summer, which is testament to the abiotic stability of large, perennial rivers, and suggests that: 1. this fish assemblage is well adapted to high water temperatures and low dissolved oxygen, or 2. biotic factors may be more important when structuring this fish assemblage. Higher fish densities in riffles and wadeable pools compared to non-wadeable pools during spawning season may indicate that these two mesohabitats were more important for reproduction; however, observations of YOY and less seasonal change in fish densities in wadeable and non-wadeable pools suggest they were important for recruitment. Results of multivariate pairwise comparisons and mixed model ANOVAs were dependent on area-based or volume-based fish density. Area is related to surface (e.g., gas exchange) and benthic (e.g., trophic resources) phenomena, whereas volume is an indicator of habitat complexity and vertical segregation (Matthews, 1998), and use of area-based or volume-based density as a metric should depend on habitat preference of target species. When attempting to characterize a diverse fish assemblage of species

associated with surface, benthic, and water column habitats, an effort should be made to analyze both metrics and to include sampling of deep pools.



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## **Appendices**

Appendix A. Location of sites on the Neosho River from Americus to Emporia in Lyon Co., KS, sampled May–November 2018.

Site	North Latitude	West Longitude	Landowner, phone number
1	38.50573	-96.31167	Mr. Larry Grimsley, (620) 443-5121
2	38.43644	-96.20654	Mr. Phillip Miller, (620) 342-0982
3	38.42746	-96.18137	Mr. Mike Vangundy, (620) 443-5321
4	38.42661	-96.17208	Emporia State Univ., (620) 341-5465
5	38.43016	-96.16330	Mr. Larry White, (620) 443-5400
6	38.42958	-96.16382	Mr. Larry White, (620) 443-5400
7	38.42855	-96.15752	Mr. Conway Brown, (620) 341-1599
8	38.41146	-96.11834	Mr. Earl Gunkel, (209) 477-3089

Appendix B. Dates each site was sampled, May–November 2018. Floods prevented sampling in October.

Site	Date	Site	Date
1	May 10th	1	Aug 11th
2	May 10th	2	Aug 9th
3	May 9th	3	Aug 10th
4	May 9th	4	Aug 9th
5	May 8th	5	Aug 10th
6	May 8th	6	Aug 10th
7	May 8th	7	Aug 10th
8	May 9th	8	Aug 9th
1	Jun 8th	1	Sep 25th
2	Jun 9th	2	Sep 12th
3	Jun 9th	3	Sep 5th
4	Jun 9th	4	Sep 18th
5	Jun 8th	5	Sep 12th
6	Jun 9th	6	Sep 13th
7	Jun 8th	7	Sep 13th
8	Jun 9th	8	Sep 21st
1	Jul 4th	1	Nov 29th
2	Jul 4th	2	Nov 26th
3	Jul 5th	3	Nov 30th
4	Jul 5th	4	Nov 29th
5	Jul 4th	5	Nov 26th
6	Jul 4th	6	Nov 26th
7	Jul 5th	7	Nov 26th
8	Jul 5th	8	Nov 27th

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Signature of Author

November 4th, 2019

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Date

Seasonal fish assemblage structure in riffles,  
wadeable pools and non-wadeable pools of a  
perennial warmwater river

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Title of Thesis

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Signature of Graduate School Staff