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AGE-SPECIFIC PATTERNS OF OCCURRENCE, DENSITY, AND GROWTH OF TWO CYPRINID FISHES IN HEADWATER PRAIRIE STREAMS

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Abstract—Ontogenetic changes in the ecological requirements of fishes are thought to influence intraspecific patterns of occurrence and abundance, yet patterns of variation in the distribution of different cohorts are unknown for many species. In prairie stream headwaters with variable habitats, we predict cohort occurrences, densities, and juvenile growth rates to vary considerably over both space and time. Specifically, the differences in abiotic factors across sites will likely affect the occurrence and growth of different age classes. To evaluate factors associated with cohort structure, we evaluated population dynamics of two cyprinid species, central stoneroller *Campostoma anomalum* and southern redbelly dace *Chrosomus erythrogaster,* using a long-term monitoring data set that included six sites sampled semiannually for 8 to 14 years. Densities of adult stoneroller were higher in pools while juveniles had higher densities in riffles, leading to within-site spatial differences in the occurrence of each age class. Across-site habitats also varied in the occurrence of different age classes of stonerollers, with sites being either suitable for both adults and juveniles, specialized for one age class, or temporally variable for both age classes. In contrast to stonerollers, all age classes of dace were pool specialists with constantly high occurrences of both age classes during all times of the year. Age-specific growth, for both species, did not vary across sites, but growth was higher for stonerollers during wet years compared with drier years at two sites. Headwater streams provide important habitat for many fishes, but the use of age-specific habitats is variable among species and likely driven by species traits as well as biotic and abiotic characteristics of those habitats.

Resumen—Se cree que los cambios ontogenéticos en los requisitos ecológicos de los peces influyen en los patrones intraespecíficos de ocurrencia y abundancia, pero se desconocen los patrones de variación en la distribución de las diferentes cohortes para muchas especies. En las cabeceras de las corrientes de praderas con hábitats variables, predecimos que las ocurrencias de cohortes, las densidades y las tasas de crecimiento juvenil variaran considerablemente en el espacio y el tiempo. Específicamente, las diferencias en los factores abióticos entre sitios probablemente afectarán la ocurrencia y crecimiento de diferentes clases de edad. Para evaluar los factores asociados con la estructura de la cohorte, evaluamos la dinámica poblacional de dos especies de ciprínidos, rodapiedras del centro *Campostoma anomalum* y la carpita *Chrosomus erythrogaster,* utilizando un conjunto de datos de monitoreo a largo plazo que incluyó seis sitios muestreados semestralmente durante 8 a 14 años. Las densidades de los adultos del rodapiedras del centro fueron mayores en las pozas, mientras que los juveniles tuvieron mayores densidades en las correderas, lo que condujo a diferencias espaciales dentro del sitio en la ocurrencia de cada clase de edad. Los hábitats entre sitios también variaron en la ocurrencia de diferentes clases de edad de rodapiedras del centro, con sitios adecuados tanto para adultos como para juveniles, especializados para una clase de edad o temporalmente variable para ambas clases de edad. A diferencia de los rodapiedras del centro, todas las clases de edad de las carpitas eran especialistas en pozas con constantes altas ocurrencias de ambas clases de edad durante todo el año. El crecimiento específico por edad, para ambas especies, no varió entre los sitios, pero el crecimiento fue mayor para los rodapiedras del centro durante los años húmedos en comparación con los años más secos en dos sitios. Las cabeceras de corrientes proporcionan un hábitat importante para muchos peces, pero el uso de hábitats específicos por edad es variable entre las especies y probablemente se debe a los rasgos de las especies, así como a las características bióticas y abióticas de esos hábitats.

Multiscale approaches are needed to understand habitat requirements of organisms (Wu et al., 2000; Fausch et al., 2002), as habitat patches within a riverscape are exploited by different species and different life stages of those species (Wiens, 2002). Adult and juvenile fish might have different habitat needs and respond differently to environmental conditions (Gillanders et al., 2003). Younger age classes are typically more influenced by stochastic factors than are older age classes, which are more regulated by deterministic factors (Schlosser, 1982; Rahel et al., 1984). If species have variation in habitat needs among age classes, it is necessary to survey at broad spatial and temporal scales to identify the full range of habitats required for species persistence. For example, the "nursery-role" concept postulates that motile fishes with complex life cycles target habitats for juvenile rearing, and these habitats contribute disproportionally to the production of individuals recruiting to adult populations (Beck et al., 2001). Thus, restricted access (e.g., through fragmentation) to these spatially segregated nursery habitats might lead to population declines.

Heterogeneous habitats within stream networks might provide conditions that influence the occurrence of different cohorts, with some reaches offering habitat mosaics suitable for multiple life stages and other reaches being more suitable for specific age classes (Labbe and Fausch, 2000). Distinct patterns in abundance, growth, and survival of different age classes over broad spatial and temporal scales (Labbe and Fausch, 2000; Scheurer et al., 2003; Dexter et al., 2014) suggest that habitats throughout a population's range should have differences in age-specific occurrences. Thus, we developed a conceptual model highlighting how habitats are likely to vary along a gradient of suitability, with some being suitable (ideal for survival, growth, or reproduction) for both juveniles and adults, some that may be unsuitable for both juveniles and adults, and some that may only be favorable for a particular age class (Fig. 1). Evidence from prairie streams (Martin et al., 2013) supports the conceptual model developed by Power (1987) predicting that smaller-bodied fish inhabit shallow waters (<0.3 m) to avoid aquatic predators, while larger-bodied fish inhabit deeper areas (>0.3 m) to avoid terrestrial predators. In addition, the distribution of different age classes may vary temporally, based on the dispersal of specific age classes to different habitats during certain times of year (Schlosser, 1991; Scharbert and Borcherding, 2013; Wolter et al., 2016). Well-studied examples of this temporal dynamic exist in salmonid systems where adults return to juvenile rearing habitats to spawn (Hendry et al., 2004), but few examples of these behaviors are documented for warm-water fish assemblages, especially in spatially and temporally variable habitats such as headwater prairie streams.

Many headwater prairie streams are intermittent, and therefore highly selective for organisms that can withstand or recover from harsh conditions by rapidly colonizing or having high reproductive rates (Matthews and Hill, 1979; Dodds et al., 2004; Whitney et al., 2016; Hopper et al., 2020*a*). Central stoneroller *Campostoma anomalum* and southern redbelly dace *Chrosomus erythrogaster* (hereafter stoneroller and dace) are common in these streams and have relatively short life spans, making them capable of rapid colonization (Hedden and Gido, 2020). Regardless of this temporal variability, prairie headwater streams are critical for sustaining biodiversity and ecosystem services (Meyer et al., 2007; Creed et al., 2017; Datry et al., 2017; Colvin et al., 2019). Thus, quantifying habitat needs of headwater prairie stream fishes will help guide management and conservation efforts attempting to mitigate habitat modification (e.g., through fragmentation) or destruction (e.g., draining or impounding) in these dynamic systems (Hedden et al., 2018; Pennock et al., 2018).

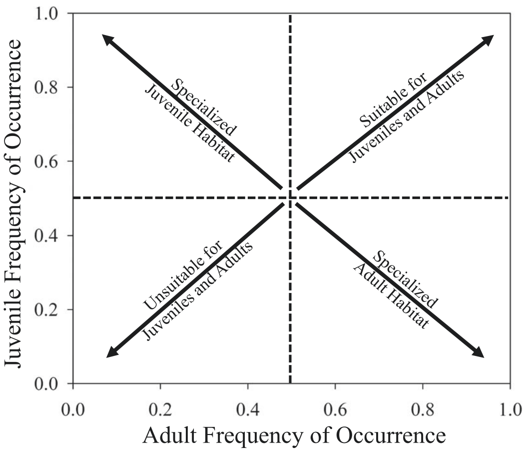

FIG. 1—Conceptual model of how site-specific characteristics can be specialized for adults (lower right) or juveniles (upper left), suitable for both adults and juveniles (upper right), or unsuitable for adults and juveniles (lower left) for a given species. Dotted lines divide habitat types into four quadrants. Arrows represent the gradient of suitable, unsuitable, and specialized habitats.

The objective of this study was to examine spatial and temporal variation in age-specific occurrences, densities, and juvenile growth rates of stoneroller and dace across two prairie stream networks. Specifically, we examined how site-specific differences in abiotic factors might influence age-specific occurrences and if different habitat types were used by differing age classes. Additionally, we assessed if growth rates varied across sites that have differing habitat types and abiotic conditions (e.g., drought). We predicted that the occurrence of juveniles and adults would be variable across space and time, given the frequent fluctuations in local conditions that occur in headwater streams (Hopper et al., 2020*b*). We also predicted juvenile fish would have higher growth rates at sites with shallower habitats because of the higher

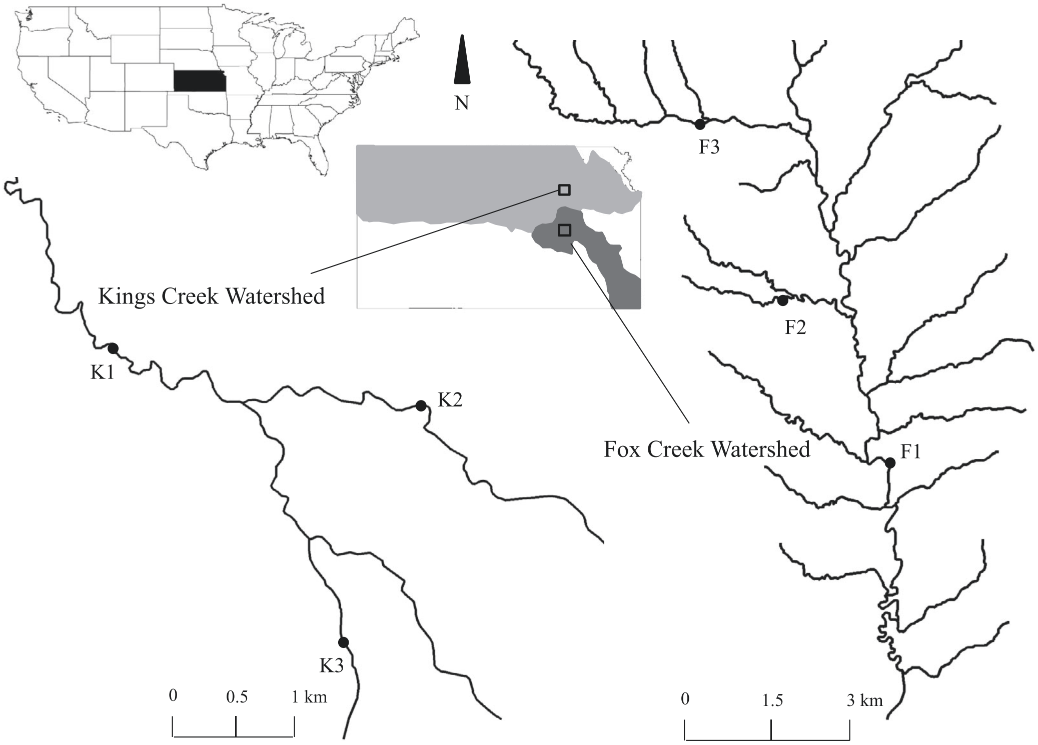

FIG. 2—Sample sites located on Kings Creek (Kansas River Basin = light grey shading) and Fox Creek (Neosho River Basin = dark grey shading) watersheds, Kansas. Sites were sampled in August and November from 2002 to 2015 (K1 and K3), 2006 to 2015 (K2), and 2008 to 2015 (F1, F2, and F3).

temperatures, reduced predation risks, and greater rates of primary production (Spranza and Stanley, 2000).

METHODS—*Study Area and Data Collection*—Sampling occurred in the Kings Creek watershed at three sites (K1, K2, and K3) from 2002 to 2015 (site K2 was only sampled between 2006 and 2015) and in the Fox Creek watershed at three sites (F1, F2, and F3) from 2008 to 2015. Both watersheds are within the Flint Hills, Kansas (Fig. 2). Kings Creek is located on the Konza Prairie Biological Station and has a drainage area 17.5 km^2 above the lowermost site. Fox Creek is located on the Tallgrass Prairie National Preserve and has a drainage area 88.4 km^2 above the lowermost site. Both watersheds are owned by The Nature Conservancy. The Konza Prairie Biological Station is managed by Kansas State University and the Tallgrass Prairie National Preserve by the National Park Service with a combination of fire and grazing to maintain native tallgrass prairie. Given that stonerollers and dace are capable of moving large distances (Walker et al., 2013; Hedden and Gido, 2020), dispersal ability likely did not limit these species occurrences within these watersheds.

Sites were a minimum of 20 times the average stream width, encompassing 1–3 pool-riffle reaches (except K2 and K3, which only contained pools). Site length varied from 55 to 130 m and, within each site, we sampled pools and riffles separately. We sampled fish communities in August and November with single pass electrofishing (Smith-Root model 20B, Vancouver, Washington) or a combination of electrofishing and seining (4.6 × 1.2 m with 3.2-mm mesh). We conducted electrofishing in all habitats, while seining only occurred in pools with widths greater than the width of the seine. We identified fish, measured them to total length, and released them back to the habitat (pool or riffle) from which they were sampled. We measured length of each habitat and the average width and depth three to five equally spaced points along three to six transects in each habitat, depending on stream length and width. We measured all habitat characteristics immediately following fish sampling.

Data Analysis—Prior to examining spatial and temporal variation in occurrences, densities, and growth rates of species, we used modal progression analysis to classify individuals into age classes based on length frequencies. Length-frequency analysis can reliably separate early age classes of fish and is useful for short-lived species (Isely and Grabowski, 2007). Thus, we were able to calculate the number of individuals in each age class for each species captured at each site for all sample periods. We performed analyses on stoneroller populations at all sites, whereas dace populations only occurred at the three sites within the Kings Creek watershed. We conducted analyses using the software Food and Agriculture Organization–International Center for Living Aquatic Resources Management Stock Assessment Tools II (FiSAT; http://www.fao.org/fishery/topic/16072/en). We categorized fish total lengths into 5-mm bins to delineate cohorts at each site in August and November of each year. We used Bhattacharya's method to separate cohorts by identifying slopes using the equation $\ln(N_{i+1}) - \ln(N_i)$, where N_i and N_{i+1} are the successive frequencies of size bins in a sample (Bhattacharya, 1967). From this we computed a mean of the normal distribution and its standard deviation. We used maximum likelihood to separate the normally distributed components of a size-frequency sample using the estimates from Bhattacharya's method. We examined the number of cohorts for each species (Gayanilo et al., 2005); this analysis also produced a mean total length and population size for each age class collected at a site.

Across sites, age-0 and age-1 fish dominated the population by contributing to more than 90% of all individuals captured for stonerollers and more than 95% for dace. Also, both species have short life spans and reach sexual maturity quickly; thus, age-0 fish were considered as juveniles and age-1 fish were considered as adults. We calculated frequency of occurrence for juveniles and adults by dividing the number of sampling events during which an age class was present by the total number of sampling events; we calculated this for each species in August and November at all sites. We used the Wilson interval (Brown et al., 2001) to estimate 95% confidence intervals around the frequency of occurrence observed at each site. To examine variation in the occurrence of juvenile and adults across sites, we compared the 95% confidence intervals for juveniles and adults to the four quadrants outlined in our conceptual model (Fig. 1). A site could be assigned into one or more quadrants based on its juvenile and adult frequency of occurrence and associated 95% confidence interval. If the confidence intervals overlapped multiple quadrants, the site was assigned to those multiple quadrants.

To understand if differences in age-specific occupancy across sites were attributed to interannual environmental variability observed in headwater streams, we tested if regional water availability between January and July, based on the Palmer Drought Severity Index (PDSI), predicted the occupancy of certain habitats by different age-classes. This time frame encompasses critical periods of reproduction and growth leading up to our sampling in August and November. The PDSI reflects regional water availability based on the balance between water supply and environmental demand with negative values indicating dry conditions, values close to zero indicating normal conditions, and positive values indicating wet conditions (Heddinghaus and Sabol, 1991). PDSI is commonly used to understand fish responses to abiotic conditions (Grossman et al., 2010; Gido et al. 2019). We obtained monthly PDSI values from the National Oceanic and Atmospheric Administration website (station USC00144972 for Kings Creek watershed and USC00141858 for Fox Creek watershed). Each weather station is <15 km from all study sites and represents the local water availability. We used generalized linear models (function "glm") with a binomial distribution in the R statistical environment (R Core Team, 2015) to evaluate the effects of average monthly PDSI (January–July), month, cohort, and their interactive effects ability to predict occurrences of fishes. We ran models separately for each species and site. We included cohort in the model to assess if the effects of PDSI and month were dependent on age class. To examine if differences in juvenile and adult fish densities occurred between specific habitats (pool or riffle) within sites, we used t tests on $\log(x + 1)$ transformed density data. Two sites (K2 and K3) lacked riffles and thus were not used in this analysis.

For this study, we did not have access to direct measurements of individual growth rates; rather, we refer to growth as the difference in mean total lengths of an age class between August and November of the same year. We only tested the variability in growth between age classes and sites when the specific age class was present in both months of the same year. To test for differences in growth across sites while also examining the effects of PDSI, we used linear models (function "glm") of PDSI, site, cohort, and their interactive effects on growth in the R statistical environment (R Core Team, 2015).

RESULTS—Spatial and temporal variation in age-specific occurrence was dependent on the species and site. For stonerollers, sites fell into all four of the quadrants of our conceptual model. Two sites (K1 and F3) always had high occurrences of juvenile and adult stonerollers, thus appearing suitable for both age classes. Two sites (F1 and F2) were variable across years, with confidence intervals spanning two quadrants, indicating a mix between high occurrence of both age classes and a higher occurrence of a specific age-class. The two remaining sites (K2 and K3) had intermediate occurrences of both juveniles and adults, with confidence intervals overlapping all four quadrants (Fig. 3). Lastly, one site (F2) showed a shift in age class dominance, with confidence intervals spanning between the upper right and lower right quadrants in August but the upper right and upper left quadrants in November, highlighting a decline in the occurrence of adult stonerollers between the two sampling periods.

The spatial and temporal variation in age-specific frequency of occurrence for dace was less variable than it was for stonerollers. Adult and juvenile dace frequency of occurrence was high at all sites for each month. These frequent occurrences led to sites being assigned either as suitable for both juvenile and adult dace (K1) or showing patterns of a mix between high occurrence of both age classes and a higher occurrence of adults over juveniles, given that the confidence intervals overlapped these two quadrants (K2 and K3). Adult dace occurrences always remained high between months, but juvenile dace occurrence increased into November at all sites.

PDSI was highly variable across years, consisting of normal years and abnormally dry and wet years (PDSI range, −3.3 to 3.2). However, PDSI alone did not predict either juvenile or adult occurrences for stonerollers or dace across sites, except at one site (K2) in which both stoneroller and dace had a lower probability of occurring during dry periods and a higher probability of occurring during wet periods (Table 1). Results from the generalized linear models gave support for variable occurrences of different cohorts across sites. For stonerollers, there was a significant interaction between cohort and PDSI at the F1 site, where adults were almost always present at the site but juveniles were absent during wet years. A significant interaction between cohort and month was observed at the F2 site, where juveniles were more likely to occur than adults in November. For dace, juveniles occurred less frequently than adults at the K2 and K3 sites (Table 1).

At sites with both pool and riffle habitats, juvenile stonerollers had significantly higher densities in riffles than in pools ($P = 0.045$; $t = 2.02$; $df = 2, 138$), whereas adult stonerollers had marginally significant higher densities in pools than in riffles ($P = 0.080$; $t = 1.76$; df

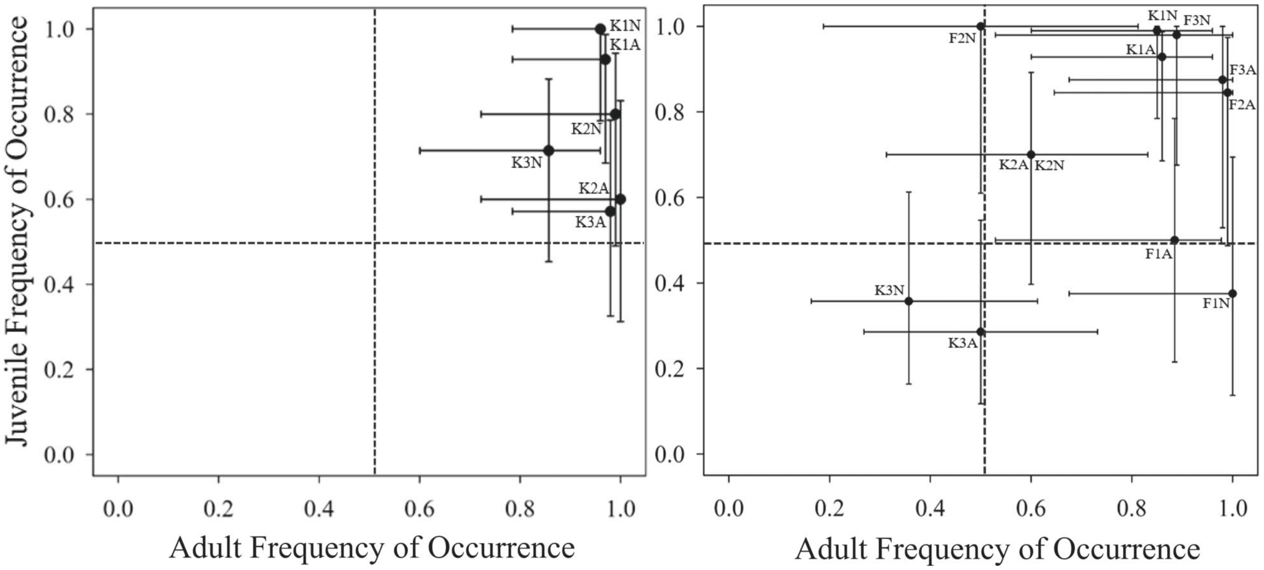

FIG. 3—Juvenile and adult frequency of occurrence (southern redbelly dace = left, central stoneroller = right) across sites sampled in August (A) and November (N) located in the Kings Creek and Fox Creek watersheds, Kansas. Error bars represent 95% confidence intervals.

= 2, 138; Fig. 4). Of the three sites where dace occurred, only one site (K1) had riffle habitat. At K1, dace had almost four times higher densities in pools compared with riffles for juveniles ($P < 0.001$, $t = 3.98$, $df = 2, 54$) and almost seven times higher densities in pools compared with riffles for adults ($P < 0.001$; $t = 5.85$; $df = 2, 54$).

Growth rates were also highly variable between species and across sites (Table 2). On average, age-0 stonerollers grew 6.9 mm (range, 5.2–7.7 mm) from August to November while age-1 stonerollers grew 5.7 mm (range, 4.7–7.7 mm). There was a significant interaction between PDSI and site ($P = 0.012$; likelihood ratio (LR) = 14.73; $df = 5, 62$), with stoneroller growth being higher during wet periods and lower during dry periods at sites F1 and F2. These were also sites with differences in cohort occurrences. Growth rates were less variable across sites for juvenile and adult dace relative to stonerollers and, on average, juvenile dace grew 5.4 mm (range, 4.8–5.9 mm) from August to November while adult dace grew 3.0 mm (range, 2.6–3.3 mm). There was no difference in growth rates across sites for dace ($P = 0.705$; $LR = 0.69$; $df = 2, 51$) and, additionally, there was no relationship between growth and PDSI across sites. There were clear differences in growth between cohorts ($P = 0.009$; $LR = 6.76$; $df = 1, 51$).

DISCUSSION—Long-term variation in juvenile and adult occurrences of stonerollers and dace was driven by site-specific habitat suitability (Franssen et al., 2006). Some

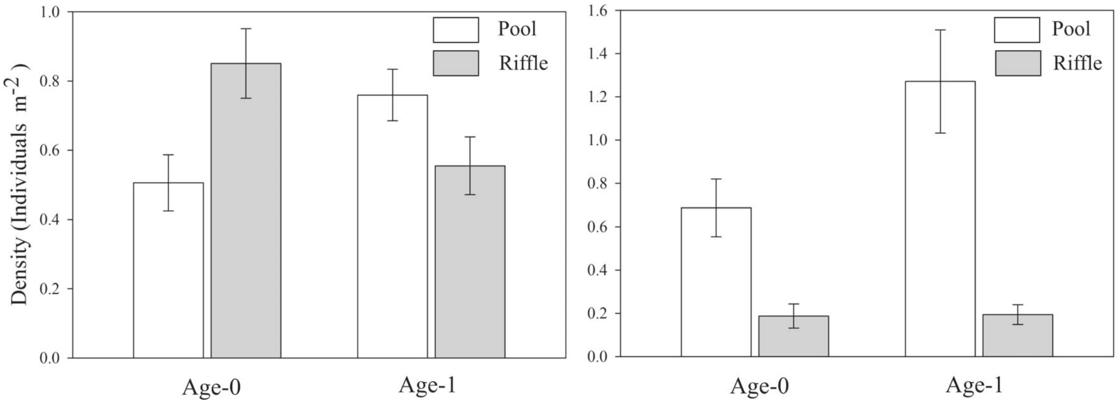

FIG. 4—Density of age-0 and age-1 central stoneroller (left) and southern redbelly dace (right) in pools (white) and riffles (grey) from sites in Kings Creek and Fox Creek watersheds in August and November from 2002 to 2015. Sites with no riffles are not included. Error bars represent standard errors. Log($x + 1$) transformed data revealed stoneroller age-0 densities were significantly higher in riffles than in pools ($P = 0.045$), whereas stoneroller age-1 densities were marginally significant higher in pools than in riffles ($P = 0.080$), while both age-0 ($P < 0.001$) and age-1 ($P < 0.001$) dace had higher densities in pools compared with riffles.

TABLE 1—Generalized linear model (binomial distribution) results predicting the occurrence of central stoneroller (*Campostoma anomalum*) and southern redbelly dace (*Chrosomus erythrogaster*) from six sites sampled in August and November in Kings Creek and Fox Creek watersheds, Kansas. An asterisk (*) highlights *P* values <0.05. *LR* = likelihood ratio.

Site	No. of years sampled	Species	Model	*LR*	*P* value
K1	14	Stoneroller	PDSI	3.76	0.052
			Cohort	0.25	0.617
			Month	2.30	0.130
			PDSI:Cohort	0.04	0.833
			PDSI:Month	1.14	0.285
			Cohort:Month	1.35	0.245
			PDSI:Cohort:Month	0.00	1.000
		Dace	PDSI	0.38	0.536
			Cohort	1.44	0.230
			Month	1.44	0.230
			PDSI:Cohort	0.00	1.000
			PDSI:Month	0.00	1.000
			Cohort:Month	0.00	1.000
			PDSI:Cohort:Month	0.00	1.000
K2	10	Stoneroller	PDSI	8.77	0.003*
			Cohort	0.56	0.456
			Month	0.00	1.000
			PDSI:Cohort	2.91	0.088
			PDSI:Month	0.00	1.000
			Cohort:Month	0.00	1.000
			PDSI:Cohort:Month	0.00	1.000
		Dace	PDSI	4.31	0.038*
			Cohort	10.77	0.001*
			Month	1.22	0.270
			PDSI:Cohort	0.00	1.000
			PDSI:Month	0.89	0.346
			Cohort:Month	0.00	1.000
			PDSI:Cohort:Month	0.00	1.000
K3	14	Stoneroller	PDSI	0.43	0.514
			Cohort	0.70	0.404
			Month	0.08	0.779
			PDSI:Cohort	1.02	0.313
			PDSI:Month	0.33	0.566
			Cohort:Month	0.75	0.387
			PDSI:Cohort:Month	2.42	0.120
		Dace	PDSI	0.01	0.904
			Cohort	10.41	0.001*
			Month	0.14	0.713
			PDSI:Cohort	0.02	0.887
			PDSI:Month	0.09	0.764
			Cohort:Month	1.87	0.172
			PDSI:Cohort:Month	0.00	1.000
F1	8	Stoneroller	PDSI	1.31	0.253
			Cohort	11.06	<0.001*
			Month	0.00	1.000
			PDSI:Cohort	7.86	0.005*
			PDSI:Month	4.29	0.038*
			Cohort:Month	4.38	0.036*
			PDSI:Cohort:Month	0.00	1.000
F2	8	Stoneroller	PDSI	0.57	0.452
			Cohort	1.01	0.315
			Month	3.83	0.051
			PDSI:Cohort	1.08	0.298
			PDSI:Month	2.49	0.115
			Cohort:Month	4.65	0.031*
			PDSI:Cohort:Month	0.00	1.000

TABLE 1—Continued.

Site	No. of years sampled	Species	Model	*LR*	*P* value
F3	8	Stoneroller	PDSI	0.07	0.787
			Cohort	0.00	1.000
			Month	0.00	1.000
			PDSI:Cohort	0.00	1.000
			PDSI:Month	0.00	1.000
			Cohort:Month	1.87	0.172
			PDSI:Cohort:Month	0.00	1.000

sites had habitats in which both age classes occurred commonly, other sites appeared to have habitats favoring a particular age class, and some sites had lower occurrences of both age classes, indicating less suitable habitats for both age classes at the site. For stonerollers, water availability (PDSI) interacted with habitat suitability to predict occurrences at some sites. While stonerollers have been reported to be common in both riffle and pool habitats (Quist et al., 2005; Peoples et al., 2016), we show that occurrences are age-specific, with juveniles favoring riffles and adults favoring pools (Fig. 4). The two sites (K1 and F3) that were suitable for both age classes of stoneroller were the only sites that had both shallow riffle habitat and moderately deep pools (Appendix). The presence of these complementary habitats might allow partitioning of habitats among multiple age classes, thus stabilizing both the competitive interactions as well as relieving predatory threats (Diehl, 1992). For example, Matthews and Hill (1979) present evidence for within-site habitat complementarity for red shiners *Cyprinella lutrensis* in prairie streams, where juveniles selected higher temperatures and shallower water depths relative to adults. Our findings complement this work and suggest similar processes occur across sites and species within a riverscape.

Habitat features appear to be a major component in understanding differences in the occurrence of juveniles and adults across sites. At two sites (F1 and F2), patterns of occurrence differed between juvenile and adult stonerollers. The site (F1) with deep riffles and deep pools was more frequently occupied by adults than juveniles, whereas juveniles more frequently occurred than adults at the site (F2) with shallow riffles and shallow pools (Appendix). Although this pattern was only replicated across time, rather than across multiple sample sites, our observations from other sampling efforts in this region lead us to believe this is a general pattern. Potential explanations for the dominance of a specific age class might be driven by habitat depth. Juvenile stonerollers might avoid deeper sites because of more-diverse and

TABLE 2—Mean total length (mm), range, and growth of age-0 and age-1 central stoneroller (*Campostoma anomalum*) and southern redbelly dace (*Chrosomus erythrogaster*) from six sites sampled in August and November from 2002 to 2015 (K1 and K3), 2006 to 2015 (K2), and 2008 to 2015 (F1, F2, and F3) in Kings Creek and Fox Creek watersheds, Kansas. Mean growth was calculated only when a cohort was present in both August and November in the same year, depicted by the "years present" column.

			August		November				
Species	Age class	Site	Mean (mm)	Range (mm)	Mean (mm)	Range (mm)	Growth (mm)	*SE*	Years present
Stoneroller	0	K1	42.4	34.7–49.6	47.1	39.7–57.9	5.9	1.16	12/14
Stoneroller	0	K2	37.9	29.3–45.7	46.1	33.5–61.3	8.1	2.53	7/10
Stoneroller	0	K3	41.2	37.9–46.7	47.0	40.5–54.4	7.3	3.40	3/14
Stoneroller	0	F1	42.6	34.5–45.7	52.7	51.4–53.5	7.1	0.61	2/8
Stoneroller	0	F2	37.1	30.2–51.6	43.6	34.7–52.7	5.2	1.79	5/8
Stoneroller	0	F3	37.4	31.1–41.9	45.1	37.3–59.5	7.7	2.15	7/8
Stoneroller	1	K1	70.3	49.3–85.0	77.4	67.6–90.3	6.2	2.10	12/14
Stoneroller	1	K2	67.5	57.1–73.8	72.2	58.5–79.6	5.3	1.36	6/10
Stoneroller	1	K3	63.9	54.8–74.0	68.9	54.4–77.8	4.7	1.43	6/14
Stoneroller	1	F1	62.9	50.9–73.0	66.7	52.0–73.7	5.7	2.58	7/8
Stoneroller	1	F2	60.4	49.0–79.3	65.0	57.0–77.4	4.7	4.14	3/8
Stoneroller	1	F3	63.4	51.4–75.8	71.0	54.1–78.7	7.7	3.11	7/8
Dace	0	K1	27.9	22.8–35.7	32.4	28.2–38.4	4.8	0.71	13/14
Dace	0	K2	25.4	21.2–29.1	30.5	25.8–36.1	5.9	1.62	6/10
Dace	0	K3	24.8	19.2–30.9	29.0	25.2–35.3	5.6	0.87	7/14
Dace	1	K1	56.7	46.5–69.0	59.0	50.3–69.1	2.6	0.56	14/14
Dace	1	K2	50.8	39.6–57.8	52.6	40.7–62.6	3.1	1.30	10/10
Dace	1	K3	49.7	38.7–64.6	50.7	42.9–56.5	3.3	1.29	13/14

abundant predator assemblages (Ictalurid and Centrarchid) that are more likely to occur lower in the watershed (Whitney et al., 2016). Although adult stonerollers can persist in habitats with piscivorous fish (Power et al., 1985; Quist et al., 2005; Whitney et al., 2016), younger age classes might need shallow habitat to avoid large fish predators, thus only occurring if a mosaic of habitats is present. This conclusion is consistent with studies showing high juvenile mortality driven by predation at sites lacking habitat complexity or when juveniles disperse away from shallower habitats (Savino and Stein, 1982; Quinn and Peterson, 1996; Willette et al., 2001).

The two remaining sites (K2 and K3) had highly variable stoneroller occurrences for both juveniles and adults. Locations within the watershed and flow intermittency might explain this high variability in occurrences for both age classes. These two sites are surrounded by intermittent reaches and mainly consist of isolated pools which restrict dispersal opportunities. Thus, isolation might cause intermediate occurrences of juveniles and adults if stoneroller populations undergo local extinctions and are dependent on recolonization. In fact, our generalized linear models examining the effects of environmental variability on fish occurrences demonstrated that both stoneroller and dace were more likely to occur at the K2 site during wet years (positive PDSI values) compared with dry years. Further, Whitney et al. (2016) found that intermittent stream fish often recolonized isolated pools after sufficient flows connected those habitats with source populations. Given that these sites are higher in the watershed and surrounded by intermittent reaches, habitat conditions (available water) are likely to depend on season and year, potentially explaining why one age class did not clearly dominate the frequency of occurrence.

Whereas occurrence of stonerollers across most sites exhibited low temporal shifts from August to November, at one site (F2) adult fish were present every August but absent half the time in November. Occurrence for juveniles at this site also increased slightly from August (86%) to November (100%). This site can range from being completely dry (in 2012) to having pools >0.40 m deep that are completely connected by shallow riffles in wet years. Thus, shifts in cohort occurrences might be explained by movements associated with spawning, as documented in some minnow species (Franssen et al., 2006; Walker et al., 2013; Perkin et al. 2019). Adult stonerollers might target shallow, isolated reaches for spawning early in the summer and thus are still detected in August. However, adults either die or emigrate from these sites into more-stable reaches before winter. It is not uncommon for adult fish to migrate and reproduce in habitats that favor juvenile survival and growth. For example, Labbe and Fausch (2000) found that some stream habitats were more suitable for the spawning and recruiting of the Arkansas darter *Etheostoma cragini*, which led to rapid first-year growth in habitat more suited for juveniles. Adult Arkansas darters also exhibited apparent post spawn movements that likely reduced intraspecific competition for young of year fish (Labbe and Fausch, 2000). Unfortunately, our generalized linear models, which tested if environmental variables predicted juvenile or adult occurrences, showed no patterns at this site, so further work understanding factors driving interannual variation in occurrence are needed.

In contrast to stonerollers, both age classes of dace appear to be pool specialists and, given the greater consistency of pool habitats across space and time, it was not surprising populations were less responsive to habitat heterogeneity. We observed high overall probabilities of occurrence for both age classes of dace on all sampling occasions across the three sites where dace occurred. Adult dace occupied sites at a higher frequency than did juveniles, but juvenile frequency of occurrence, which ranged from 57 to 100%, tended to increase as juveniles became more frequent at sites later in the year. This could potentially be explained by the extended spawning season (March through July) of dace (Cross, 1967; Becker, 1983; Etnier and Starnes, 1993), thus late-spawned juvenile fish might not recruit to our sampling gear until later in the year. Given that dace only occurred in the Kings Creek watershed, our inference is reduced due to the lower spatial replication for this species relative to stonerollers, especially when comparing the densities in pools vs. riffles, as only one site that had dace present in our study contained both pool and riffle habitats.

Contrary to our prediction, variation in growth was minimal across sites (Table 2). Spranza and Stanley (2000) found that condition factors for juvenile stream fish were higher in streams located higher in the watershed. They hypothesized this was associated with a behavioral, anatomical, or physiological adaptation, or potentially greater resources, perhaps through increased solar radiation that might stimulate algal growth. However, given that growth rates of stonerollers and other cyprinids can be highly variable (Quist and Guy, 2001; Haworth and Bestgen, 2016), it is possible that spatial variation in growth might be driven by other factors rather than location in the watershed alone. For instance, stoneroller growth increased in wet years at two sites (F1 and F2), both of which had differences in age-specific occurrences. Stonerollers can exhibit density-dependent growth, as demonstrated in a mesocosm study showing decreasing growth rates across a likely range of densities from Kings Creek (Pennock and Gido, 2016). During wet periods, more habitat and food resources may be available, potentially alleviating density-dependent effects and leading to higher growth at these two sites. It is important to note that we did not measure growth directly; rather, we estimated growth by calculating the difference in total lengths of specific age classes for each species from August to November, and so we were only able to estimate growth in years when the cohort was present in both months of the same year. Thus, we recognize some potential bias that could occur if death rates or immigration-emigration rates were high or if multiple spawns occurred for a species.

Headwater streams represent the majority of total length of streams in river networks and are important for the maintenance of fish populations (Freeman et al., 2007). These systems are highly threatened and face continual negative pressures with habitats being modified and fragmented (Perkin et al., 2015; Colvin et al., 2019). Quantifying intraspecific variation in habitat use should provide useful information about the sensitivity of prairie headwater species to habitat changes (Falke and Fausch, 2010). Our results show that intermittent stream reaches with different complements of habitats are differentially used by species and age classes of prairie stream fishes. At least for stonerollers, the presence of complementary habitats (both within and across sites) might be beneficial for the success of this species. Thus, information on the variation in age-specific occurrences of stream fishes could help identify factors structuring a species distribution and abundance. Moreover, conservation and restoration of stream ecosystems (i.e., reducing the number of impoundments, removing barriers fragmenting stream networks) will benefit from an improved understanding of how heterogeneous habitats are critical to different age classes of fish.

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Appendix—Mean depth (m) and velocity (m/s) and associated *SD* from six sites sampled in August and November from 2002 to 2015 (K1 and K3), 2006 to 2015 (K2), and 2008 to 2015 (F1, F2, and F3) in Kings Creek and Fox Creek watersheds, Kansas.

		Depth (m)		Velocity (m/s)	
Site	Habitat	Mean	*SD*	Mean	*SD*
F1	Pool	0.51	0.30	0.05	0.09
F1	Riffle	0.13	0.12	0.24	0.24
F2	Pool	0.18	0.11	0.02	0.03
F2	Riffle	0.06	0.05	0.04	0.06
F3	Pool	0.30	0.22	0.01	0.03
F3	Riffle	0.08	0.08	0.07	0.10
K1	Pool	0.28	0.14	0.02	0.04
K1	Riffle	0.06	0.05	0.10	0.13
K2	Pool	0.13	0.08	0.02	0.03
K3	Pool	0.13	0.10	0.01	0.02