Seasonal Habitat Shifts by Benthic Fishes in Headwater Streams

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Abstract: Fish-habitat associations in streams have been widely studied; however, temporal considerations have been neglected, particularly during the winter. We quantitatively sampled perennial headwater streams in the Missouri Ozarks during the summer ($n = 13$) and winter ($n = 4$) to evaluate possible habitat shifts by three benthic fishes at two spatial scales: channel unit and microhabitat. Density of all three headwater species in streams was generally lower in winter than summer, with some species being ubiquitous in channel units of streams during the summer and almost entirely absent from the same streams during winter. Presence of each of three species during the summer varied by stream and channel unit, but patterns of channel-unit use did not change depending on stream sampled. Ozark sculpin (*Cottus hypselurus*) was more likely to be present (> 50% probability) in riffles and runs, but not pools. Fantail darter (*Etheostoma flabellare*) was much more likely to be found in riffles than other channel units whereas rainbow darter (*Etheostoma caeruleum*) was more likely to occur in runs or pools than riffles. During winter, each of the three species was equally likely to be present or absent from any of the channel units indicating a more general use of channel units. However, each of the three species used deeper microhabitats within pools and slower-velocity areas of riffles during winter compared to summer. Results of this study indicate benthic, headwater species used habitat more generally during cold-water periods compared to warm-water periods, but density estimates indicated changes in channel unit use occurred in some streams and patterns of fine-scale microhabitat shifts did occur.

Key words: channel unit, temperature, *Etheostoma*, *Cottus*

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 65:105–111

Understanding the spatial and temporal extent of habitat use is the basic building block of fish management and conservation strategies. Understanding how a fish uses its immediate environment allows for the development of strategies to maintain, enhance, or restore populations. While our understanding of spatial fish-habitat associations has grown considerably, temporal considerations have often been neglected. Important habitat conditions are those with obvious fitness consequences (Rosenfeld 2003), sometimes referred to as "bottleneck" conditions. Bottleneck conditions are unknown for many stream fishes, but likely encompass both spatial and temporal elements. The vast majority of studies emphasizes the spatial aspect but encompass a limited temporal aspect, i.e., usually daylight hours during warm-water periods. Changes in habitat use from warm to cold-weather periods have been shown for some species and attributed to bioenergetic considerations, a contributor to population success (Cunjak 1996). However contrary results showing no seasonal changes in habitat use (e.g., movement from riffles in Minnesota streams in winter by fantail darter *Etheostoma flabellare*, Coon 1987) indicate winter habitat-use patterns need to be better understood for more species and situations to aid in developing accurate management strategies.

This study examined several small, permanent, streams in the Missouri Ozarks to evaluate channel unit and microhabitat use between warm and cold seasons. We were particularly interested in small, benthic species where there is some evidence of movement to deeper water with slower current velocities in colder-water periods for some species (e.g., *Etheostoma* spp.; Madison 1993, Musselman and Brewer 2009), but not other species (Ross et al. 1992). The objective of this study was to determine seasonal (summer and winter) habitat use by three benthic fishes at multiple spatial scales (channel unit and microhabitat): Ozark sculpin (*Cottus hypselurus*), fantail darter, and rainbow darter (*Etheostoma caeruleum*).

Study Area

Sampling was conducted on 13 streams during the summer and repeated on four of the same streams during the winter. Each stream was located in different catchments of the Ozark Highland Section of Missouri (Nigh and Schroeder 2002) (Figure 1). In Missouri, the Ozark Highland Section is restricted to the southern portion of the state and characterized by extensive geologic erosion, carbonate bedrock, and karst features. Stream segments were further restricted to three subsections within the Ozark Highlands Section: Gascon-

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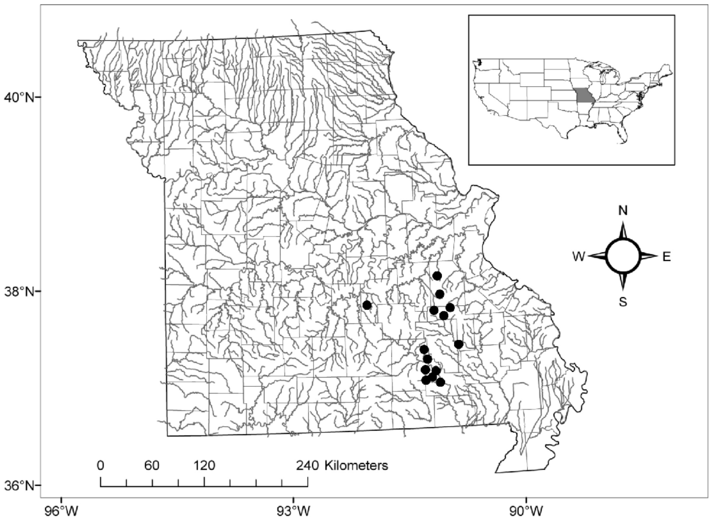

Figure 1. Map of Missouri showing the distribution of sampling sites.

ade River Hills, Meramec River Hills, and Current River Hills (Nigh and Schroeder 2002). These subsections are hilly to deeply dissected lands and range in characteristics from shallow to moderately deep soils of varying lithology to rocky soils composed primarily of carbonate and sandstone bedrock and chert. Catchment areas ranged from 6 to14 km^2. Study streams were perennial, gaining, second-to third-order warmwater streams, all within 70-yr median discharge levels at the time of sampling (U.S. Geological Survey gage data, summarized in Rettig 2003). Water temperatures in 12 of the streams sampled during the summer were 19–31 C. Three streams that were sampled during both seasons had water temperatures between 19 and 23 C during the summer and 2–6 C during winter (Rettig, unpublished data). The temperature logger placed in Kaintuck Creek malfunctioned so temperatures were unavailable for that stream.

Methods

Each sample site was 150 to 200 m in length and located at the outlet of each catchment. Samples were collected from each stream once in June or July 2001 (hereafter referred to as summer) and January 2002 (hereafter referred to as winter) using a 1-m^2 quadrat sampler (Peterson and Rabeni 2001) paired with backpack electrofisher. The quadrat sampler consisted of two 1-m^2 frames attached 0.5 m apart, with 0.25-m long legs at the bottom. A net wall surrounded each side and a 0.75-m-deep collection bag with 3.175-mm mesh was attached to the downstream end of the sampler. The efficiency of this gear was found to be >50% when used to estimate densities of Cottidae and Percidae in riffles (Peterson and Rabeni 2001). However, a pilot study indicated that combining backpack electrofishing with the quadrat sampler increased efficiency to approximately 80% for both families in riffles, runs, and pools (Rettig 2003). Peterson and Rabeni (2001) indicated sampling efficiency for Cottidae and Percidae was not influenced by water temperature.

Channel Unit Habitat Use

Channel units (relatively discrete morphological features—e.g., riffles, formed by interactions between the stream and surrounding landscape at high discharges; Leopold et al. 1995) at each site were systematically sampled for benthic fishes. Channel units sampled were riffles, runs, and pools. Channel units were classified according to depth and velocity characteristics after Rabeni and Jacobson (1993). Channel units were sampled beginning at the most downstream location of each study site. Each subsample (individual quadrat) was randomly placed within the channel unit and each successive subsample was taken ≥2 m away to maintain independence between subsamples, but still allow adequate representation of available habitat conditions.

We completed a pilot study in spring 2001 to determine the number of each channel unit type to sample and the number of quadrats (subsamples) to take from each channel unit. Results indicated variation in benthic fish densities was greater in riffles and runs when compared to pools (Rettig 2003) so we took more samples from riffles and runs in an effort to reduce the variation. The number of samples taken from each stream depended on the availability and condition (e.g., thick ice cover) of channel units. During the summer, we sampled 2 to 5 pools, 8 to15 riffles, and 8 to 15 runs in each stream. During the winter, we sampled 3 to 5 pools, 3 to 5 riffles, and 5 runs in each stream. Additionally, we subsampled each channel unit (2 to 5 subsamples per channel unit depending on channel unit area). Each subsample was taken ≥2 m away from the previous sample to allow for independence between subsamples. Regardless of season, the quadrat sampler could effectively sample pools ≤0.5-m deep so no areas deeper were sampled. Depths >0.5 m represented a small proportion of the study streams (1%–2%).

Microhabitat Use

Directly upstream (<0.25 m) of each fish sample, microhabitat measures were taken. We assumed habitat availability would be adequately represented using this technique because of our stratified sampling design. Water depth (cm) and mean water column velocity (0.6 times depth, m/sec) were measured at the upstream center of each quadrat using a meter stick and Marsh McBirney flow meter. We assumed these measures would represent average conditions within each quadrat. Substrate characteristics were determined by sieving two shovels of the top layer of substrate (approximately 7.5 cm) upstream of each quadrat sample after Grost et al. (1991). Substrate samples had to be taken outside the quadrat because of the altered conditions following fish sampling. Substrate samples were sieved into size classes: large cobble (>128 mm), small cobble (64–128 mm), pebble (16–64 mm), gravel (2–16 mm), and sand (<2 mm). Substrate samples were weighed to determine proportions of each size class.

Fish Sampling

Fishes were collected in the quadrat sampler by trapping, subduing, and moving them into the downstream collection bag. The sampler was quickly placed at the area to be sampled and secured to the streambed. A backpack electrofishing unit was used to immobilize fish within the secured area of the sampler for 120 seconds. The sampler was then cleared of all rocks and debris while sweeping stunned fish into the collection net. Finally, the area within the quadrat was electrofished again for approximately 30 sec while the substrate was vigorously agitated, to sweep any remaining fishes into the collection bag. Captured fish were stored in 10% formalin and later identified in the laboratory.

Analyses

Young-of-year fishes were removed from the dataset prior to analyses. The mesh size used on the quadrat sampler allowed some juveniles to pass through, limiting capture efficiency and comparison. The minimum size used to eliminate young-of-year from the dataset was determined by creating length-frequency histograms from all 13 streams sampled during the summer (Rettig, unpublished data).

Density of fish in each channel unit was calculated using our subsamples. First, the density of each species in each channel unit sampled was calculated using the subsamples as pseudoreplicates (quadrat samples taken inside each channel unit). Density of fish (fish per m^2) occupying riffles, runs, and pools was then calculated by taking the mean across each channel unit type for each stream.

Generalized linear models (SAS Institute 2000) were created to determine the likelihood fish would be present (binomial distribution) in particular streams, channel units, or channel units depending on stream sample ($\alpha < 0.05$). Likelihood ratio statistics were calculated for each treatment (stream, channel unit, and interaction between the main effects). Likelihood ratio statistics test the null hypothesis that all coefficients in the data set are equal to zero (Allison 1999). The antilog of each logit estimate was used to calculate the odds of fish being present ($P_p / 1 - P_p$), where P_p is the probability of fish being present. An odds ratio [($P_x / 1 - P_x$) / ($P_y / 1 - P_y$)] where x and y are different treatments (e.g., different channel units) and *P* is the probability of residing in that treatment, was used to determine the likelihood of each species presence in one treatment versus another (e.g., more likely to be present in pools versus runs).

Microhabitat use was determined for each species by calculating means and ranges of each microhabitat variable within the respective channel unit. Microhabitat data were pooled across streams to show use patterns because the available conditions within channel units were similar among streams. Additionally, there was not enough microhabitat data to create multivariate models within a hierarchical framework (i.e., model microhabitat conditions used within specific channel units). Microhabitat use was reported for summer and winter.

Results

Stream and Channel Unit Habitat Use

Density Estimates Variation in density of each species occupying any particular channel unit was high; however, several patterns still emerged (Table 1). During the summer, Ozark sculpins had the highest densities in riffles and runs in all the streams where the species was present. Fantail darters had the highest densities in riffles and runs in all but one instance (Little Creek). Rainbow darter densities were more variable than other species, but densities were higher in runs and pools than riffles in 62% of streams (8 of 13 streams).

In several streams (e.g., Town Branch), densities of fishes were similar across channel units during the winter supporting a general-use pattern during this period. However, there were exceptions that suggest a move to deeper, slower-velocity areas. Contrary to the summer period, Ozark sculpins had higher densities in pools during winter when compared to other channel units (though these differences were not significant due to the variation in our density estimates). Raindow darters used runs and pools during summer in Kaintuck Creek but exclusively used pools during winter. Rainbow darter densities increased substantially in pools of Middle Fork Black River during winter when compared to summer. Further, rainbow darters used riffles of the Middle Fork Black River and Town Branch during summer, but were never sampled there during winter.

Species Presence During the summer, some fish species were absent from particular streams but were common in others. Rainbow darters were present in all 13 streams sampled (Table 1). Fantail darters and Ozark sculpins were absent from two streams (Middle Fork Black and Mill Creek, and Rocky Creek and Rogers Creek, respectively). Fantail darters and Ozark sculpins were present in all channel units of Little Creek. Fantail darters were also ubiquitous in channel units of Town Branch, and Ozark sculpins were found in all channel units of Middle Fork Black River. These aforementioned streams were excluded from the channel unit analyses because the algorithm will not converge when zeros exist in an entire unit (i.e., an entire stream or channel unit type in any stream). This also created difficulty in analyzing channel unit data where species found in a stream, were either entirely present or absent from all of a particular channel unit type (i.e., riffle, run, or pool). The channel unit type where this occurred varied for Ozark sculpins and rainbow darters, but included only one riffle for fantail darters. Because the algorithm would not converge with zeros in an entire channel unit type, we added one presence or absence response to these channel units (10 of 313) to complete our analyses.

Presence of each of the three species varied by stream and channel unit, but patterns of channel-unit use did not change depending on stream sampled during the summer. Ozark sculpins were more likely to be present in some streams than others (Chi-square = 18.00, df = 9, P = 0.03) and were twice as likely to be found in riffles or runs but there was an equal probability of finding them in pools (Table 2; Chi-square = 10.10, df = 2, P < 0.01). However, channel unit use did not change depending on the stream sampled (stream * channel unit interaction, Chi-square = 8.36, df = 18, P = 0.97). Fantail darters were more likely to be present in some streams than others (Chi-square = 41.34, df = 8, P < 0.01) and were much more likely to be found in riffles than other channel units (Table 2; Chi-square = 6.45, df = 2, P = 0.04). Similar to Ozark sculpins, channel unit use by fantail darters did not change depending on the stream sampled (Chi-square = 6.72, df = 16, P = 0.97). Rainbow darters were more likely to be present in some streams than others (Chi-square = 55.14, df = 11, P < 0.01) and were more likely to occur in runs or pools than riffles (Table 2, Chi-square = 8.67, df = 2, P = 0.01), but like the other species, channel unit use did not change depending on stream sampled (Chi-square = 13.62, df = 22, P = 0.91).

A few streams were excluded from the winter model because certain species were not present in any samples from an entire stream or were extremely rare. Similar to the summer period, fantail darters were absent from Middle Fork Black River during winter. However, Ozark sculpins were only found in one riffle of Little Creek during the winter, whereas this species was nearly ubiquitous in riffles and runs of this stream during the summer. Thus, the Middle Fork Black River and Little Creek were excluded from analyses for each of the aforementioned species. Also, of the 52 channel units sampled during the winter, 4 had fish present or absent in all the samples (e.g., fish were present in all four pool samples taken), and thus changes had to be made to the data to allow the model algorithm to converge as described above. This was done for Ozark sculpin in one pool (added a presence) and one riffle (added a presence) in Little Creek, and fantail darter in two pools (one was present and one was absent), of Little Creek and Town Branch.

Presence or absence of each of the benthic species during winter

Table 1. Density (number of fish per m^2) of benthic fishes in different channel units (CU) of headwater Ozark streams during summer and winter. Confidence interval (+/– 95%) is indicated in parentheses.

		Summer density			Winter density		
Stream	CU	Ozark sculpin	Fantail darter	Rainbow darter	Ozark sculpin	Fantail darter	Rainbow darter
Chilton Creek	pool	0.50 (0.47)	0.50 (0.26)	0.83 (0.27)			
	riffle	1.15 (0.67)	1.25 (0.69)	0.00 (0.00)			
	run	1.40 (0.61)	1.48 (1.00)	0.30 (0.23)			
Funks Branch	pool	0.00 (0.00)	0.67 (0.49)	6.95 (4.26)			
	riffle	1.00 (0.64)	2.25 (0.94)	3.25 (1.10)			
	run	0.80 (0.40)	2.15 (1.32)	4.80 (2.10)			
Indian Creek	pool	0.52(0.27)	0.68 (0.27)	0.75 (0.97)			
	riffle	0.83 (0.39)	2.89 (0.61)	0.26 (0.19)			
	run	1.48 (0.55)	1.42 (0.75)	0.79 (0.26)			
Jims Creek	pool	0.54 (0.34)	0.50 (0.24)	1.54 (0.93)			
	riffle	3.70 (0.72)	1.00 (0.58)	1.80 (0.66)			
	run	2.50 (0.97)	0.56 (0.53)	4.50 (1.53)			
Kaintuck	pool	0.90 (0.54)	0.50 (0.41)	0.40 (0.65)	0.20 (0.32)	0.80 (0.95)	0.20 (0.32)
	riffle	3.68 (1.36)	1.71 (0.94)	0.00 (0.00)	2.33 (1.25)	2.67 (1.51)	0.00 (0.00)
	run	1.76 (0.50)	2.13 (1.49)	0.22 (0.16)	0.50 (0.42)	1.00 (0.84)	0.00 (0.00)
Little Creek	pool	0.00 (0.00)	3.00 (2.02)	1.22 (0.18)	0.00 (0.00)	1.33 (0.54)	1.00 (0.94)
	riffle	0.50 (0.34)	2.00 (0.41)	3.31 (1.04)	0.20 (0.32)	1.00 (1.04)	1.40 (1.23)
	run	0.24 (0.20)	2.98 (1.06)	3.90 (1.34)	0.00 (0.00)	1.60 (0.83)	1.20 (0.36)
Lower Rocky Creek	pool	0.60 (0.98)	0.21 (0.24)	1.20 (0.32)			
	riffle	15.61 (3.61)	0.61 (0.40)	1.67 (0.65)			
	run	6.29 (2.17)	0.21 (0.46)	4.08 (1.39)			
Middle Fork Black	pool	0.41 (0.13)	0.00 (0.00)	0.67 (0.54)	2.00 (2.68)	0.00 (0.00)	4.00 (2.68)
	riffle	6.84 (2.33)	0.00 (0.00)	1.15 (0.71)	0.60 (0.65)	0.00 (0.00)	0.00 (0.00)
	run	4.06 (0.87)	0.00 (0.00)	1.80 (0.60)	0.80 (0.61)	0.00 (0.00)	1.60 (0.41)
Mill Creek	pool	0.60 (0.65)	0.00 (0.00)	1.86 (1.18)			
	riffle	6.68 (3.71)	0.00 (0.00)	3.33 (1.36)			
	run	2.5 (1.01)	0.00 (0.00)	4.1 (1.97)			
Rocky Creek	pool	0.00 (0.00)	0.00 (0.00)	1.00 (0.52)			
	riffle	0.00 (0.00)	0.40 (0.31)	3.20 (1.17)			
	run	0.00 (0.00)	0.15 (0.23)	3.80 (0.79)			
Rogers Creek	pool	0.00 (0.00)	1.21 (0.42)	1.71 (0.75)			
	riffle	0.00 (0.00)	3.70 (1.34)	1.10 (0.51)			
	run	0.00 (0.00)	1.62 (1.33)	2.75 (0.97)			
Shawnee Creek	pool	0.00 (0.00)	0.00 (0.00)	0.56 (0.91			
	riffle	12.16 (4.11)	0.64 (0.27)	4.66 (3.40)			
	run	1.40 (0.48)	0.17 (0.27)	4.95 (1.66)			
Town Branch	pool	1.00 (0.84)	1.50 (0.84)	0.83 (0.66)	1.33 (0.57)	0.00 (0.00)	1.00 (0.94)
	riffle	1.98 (0.68)	7.49 (3.20)	0.32 (0.20)	2.40 (1.81)	4.00 (1.64)	0.00 (0.00)
	run	5.05 (1.07)	5.33 (1.36)	3.05 (1.46)	2.00 (2.44)	1.00 (0.73)	1.80 (0.80)

Table 2. Generalized linear model results for three benthic headwater fishes during summer. Asterisks identify significant logit values (P < 0.05) indicating an unequal probability of presence versus absence. Positive values indicate fish were more likely to be present than absent (>50% probability of occurrence). The likelihood of being present versus absent (odds) is given in parentheses.

	Channel unit		
Species	Riffle	Run	Pool
Ozark sculpin	*0.78 (2.18)	*0.80 (2.23)	0.50 (1.63)
Fantail darter	*0.74 (2.09)	0.57 (1.76)	0.49 (1.63)
Rainbow darter	0.22 (1.24)	*0.81 (2.25)	*0.64 (1.90)

did not depend on stream or channel unit sampled. Ozark sculpin (Chi-square = 5.50, df = 3, P = 0.14), fantail darter (Chi-square = 0.14, df = 2, P = 0.93), and rainbow darter (Chi-square = 3.18, df = 3, P = 0.36) were all equally likely to be present or absent in any of the streams sampled. Similarly, all of these species were equally likely to be found in any of the channel units within the streams (Chi-square ≤ 1.84, df = 2, P ≥ 0.39).

Microhabitat Use

Benthic species examined in this study used a broad range of microhabitat conditions within each channel unit type during the summer (Table 3). Rainbow darters used the broadest range of microhabitat conditions within pools when compared to the other species. Range of microhabitat conditions used by all three species in riffles and runs was similar. Microhabitat conditions used during the winter were similar to the summer, except that each of the three species used deeper water in pools with the lower limit being truncated by approximately 20 cm compared to the summer period (Table 4). Additionally, in riffles and runs, the upper limit of velocity conditions used was truncated substantially.

Table 3. Mean microhabitat conditions (range in parentheses) used by three benthic fishes during summer. Microhabitat conditions were pooled among 13 streams and reported within the channel units (CU) used by each species.

		Microhabitat variables		
Species	**CU**	**Depth (cm)**	**Velocity (m/sec)**	**Dominant substrate**
Ozark sculpin	pool	25 (7–39)	0.05 (0.00–0.05)	pebble
	riffle	9 (2–20)	0.43 (0.10–1.15)	small cobble
	run	12 (5–34)	0.25 (0.00–0.90)	pebble
Fantail darter	pool	25 (7–39)	0.01 (0.00–0.10)	pebble
	riffle	9 (3–18)	0.44 (0.14–1.15)	pebble
	run	13 (5–34)	0.24 (0.05–0.90)	pebble
Rainbow darter	pool	27 (7–53)	0.04 (0.00–0.50)	pebble
	riffle	9 (3–20)	0.44 (0.10–0.91)	pebble
	run	14 (5–29)	0.24 (0.00–0.88)	pebble

Table 4. Mean microhabitat conditions (range in parentheses) used by three benthic fishes during winter. Microhabitat conditions were pooled among four streams and reported within the channel units (CU) used by each species.

		Microhabitat variables		
Species	**CU**	**Depth (cm)**	**Velocity (m/s)**	**Dominant substrate**
Ozark sculpin	pool	42 (28–52)	0.02 (0.00–0.07)	pebble
	riffle	10 (5–14)	0.39 (0.12–0.70)	small cobble
	run	17(12–27)	0.16 (0.10–0.33)	pebble
Fantail darter	pool	36 (31–42)	0.03 (0.01–0.06)	pebble
	riffle	10 (5–14)	0.33 (0.12–0.52)	pebble
	run	15 (10–27)	0.13 (0.10–0.20)	pebble
Rainbow darter	pool	39 (33–43)	0.03 (0.00–0.07)	pebble
	riffle	11 (9–12)	0.22 (0.14–0.29)	pebble
	run	16 (10–27)	0.16 (0.09–0.33)	pebble

Discussion

Our results suggest two general trends in habitat use between warm- and cold-water periods. The species presence data indicated a shift from using particular channel units in the summer to a more general-use pattern during the winter. Secondly, nested within the channel unit use was evidence for finer-scale alterations in depth and velocity selection.

The shift to use of multiple channel units (i.e., likely to be present in any channel unit) during the cold-weather period may be related to feeding during harsh conditions and ontogeny. Gillette et al. (2006) suggested that feeding by darters may be more advantageous in shallower, higher velocity habitats during warm periods, but less important as metabolism slows during the winter. An alternative explanation is that darters may move between channel units, using deeper channel units as refugia, and then feeding in the more advantageous habitat when necessary. We would expect feeding to be reduced during winter so fish densities would be lower in the feeding habitats compared to refuge habitats. Alternatively, some studies have indicated ontogeny is related to differential use of habitats (Schlosser 1982, Gelwick 1990, Musselman and Brewer 2009). We omitted young-of-year fishes from our dataset but size-related differentiation of habitat use may still occur within the larger-sized fishes. Unfortunately, we did not measure length of all fish collected during both seasons to test this theory.

Benthic stream fishes have been observed to move to alternative habitats, particularly deeper water, during times of harsh environmental conditions (Matthews 1998, Peterson and Rabeni 1996, Helfman et al. 1997, Musselman and Brewer 2009). Low-flow conditions are an obvious motivator (Schlosser and Toth 1984). However, the discharge conditions under which we sampled were well within the range of conditions normally experienced by species in our study streams during the both seasons. Some fishes may migrate long distances or from adjacent streams during extreme hot or cold periods to take advantage of refugia provided by groundwater inputs (Peterson and Rabeni 1996, Power et al. 1999). Most of the streams sampled in this study had lower fish densities during the winter suggesting that at least a proportion of the populations may move downstream, where conditions of a larger stream provide a more stable winter environment (Helfman et al. 1997). However, some of these small, headwater streams may have substantial groundwater influences (relative to surface water) thereby creating thermal refugia without the need for fish migration. Unfortunately, the contributions from smaller springs have not been quantified in Missouri (but see Vineyard and Feder 1982). Town Branch likely had significant groundwater influence (19 C during summer) and maintained relatively high densities of fishes during the winter compared to other streams.

Whereas our results indicated substantial variation between streams in how some benthic headwater species use channel unit habitat during the cold-weather season, there were fine adjustments made to microhabitat use likely in response to bioenergetic considerations. All species examined in this study truncated use of depth and velocity within the channel units they occupied during the winter. Fish using pools began using deeper available areas and fish using riffles and runs used the slower-velocity areas of the channel units. The use of channel units providing deeper water and slower velocities in specific streams by rainbow darters during winter as compared to summer, is similar to other studies of this species showing overwintering in pools in larger Minnesota (Coon 1987) and Kentucky streams (Madison 1993).

Water temperatures experienced during the two sample seasons likely influenced habitat-use patterns at fine spatial scales. Ross et al. (1992) indicated constraints on habitat selection of bayou darter *E. rubrum* were related to temperature-induced swimming limitations and speculated that these limitations would be most pronounced during cold-water periods for temperate stream fishes. Results from our study corroborated this hypothesis, as all three species used lower available velocities in shallow channel units during the winter and shifted depth use in pools to exclude very shallow areas. Our microhabitat results agree with some studies on small-bodies fishes where use of habitat at larger spatial scales remained unchanged between seasons, but habitat shifts occurred at finer spatial scales (e.g., microhabitat) (Stiles 1972, Mundahl and Ingersoll 1983). Benthic fishes have morphological features that reduce the energy expended to maintain their stream position (Bisson et al. 1988, Facey and Grossman 1990), though they are still thought to select local velocity refugia (e.g., rainbow darter, Harding et al. 1998).

The spatial and temporal changes in fish habitat use observed during this and other studies suggest the importance of certain habitats varies among seasons for some species, but not others. Unfortunately, few fish-habitat studies investigate habitat use across seasons, an omission that makes attempts to protect, enhance, or restore fish populations difficult or impossible. This study indicates management objectives based on summer sampling would suffice for some species but not for others. We suggest additional studies should be conducted to better understand why shifts are made among channel units in some streams but not others.

Acknowledgments

This research is a contribution of the Oklahoma Cooperative Fish and Wildlife Research Unit (U.S. Geological Survey, Oklahoma Department of Wildlife Conservation, Oklahoma State University, and Wildlife Management Institute cooperating) and University of Missouri, Department of Fisheries and Wildlife Sciences. Funding was provided by the Missouri Department of Conservation. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The manuscript was improved by comments from Scott Stephens and two anonymous reviewers.

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