COMMUNITY ECOLOGY – ORIGINAL RESEARCH

CrossMark

Fine-scale movement and habitat use of a prairie stream fish assemblage

Casey A. Pennock[1] · C. Nathan Cathcart[1,2] · Skyler C. Hedden[1] · Robert E. Weber[1,3] · Keith B. Gido[1]

Abstract

Measuring an organism's movement and habitat use is highly dependent on the spatial and temporal scale of the study, with most studies measuring distributions once a day or at less frequent intervals. Yet, to fully understand the rates of intra- and interspecific encounters among individuals, observations at finer spatial and temporal scales might be necessary. We used passive integrated transponder tags and antenna arrays to continuously monitor habitat use and vagility of three stream minnows; southern redbelly dace *Chrosomus erythrogaster*, central stoneroller *Campostoma anomalum*, and creek chub *Semotilus atromaculatus*, among and within pools of an intermittent stream. Most fish remained in the pool where they were caught and released, or returned after emigrating from the pool. Despite largely remaining within the release pool, distribution among four microhabitats differed significantly over six, 4-h time periods for all three species. Vagility, the summed distance moved among antennas, differed significantly among species. Individual vagility (m day^{-1}) increased significantly with body length for stoneroller and chub, but not dace. Some individuals moved as much as 110 m day^{-1} within the pool, showcasing extensive movement at fine scales. Finally, we found no evidence that feeding activity changed as a result of differential habitat use over a 24-h period. Our findings indicate considerable variation in habitat use and movement occurs among species over a 24-h period. This suggests ecologists can broaden the interpretation of processes influencing community structure (e.g., resource partitioning, avoidance of predators) by quantifying species distributions across a range of spatial and temporal scales.

Keywords Intermittent streams · Vagility · PIT tags · Minnows · Fine scale

Introduction

Comparing habitat use among species can help identify key resources necessary for population growth and potential interactions among species when those resources are limited. However, interpreting patterns of species overlap

✉ Casey A. Pennock
   pennock@ksu.edu

[1] Division of Biology, Kansas State University, 116 Ackert Hall, Manhattan, KS 66506, USA

[2] Present Address: Oklahoma Cooperative Fish and Wildlife Research Unit, Oklahoma State University, Stillwater, OK 74078, USA

[3] Present Address: Department of Natural Resource Ecology and Management, Iowa State University, Ames, IA 50011, USA

depends upon the spatial and temporal scales of measurement (MacArthur 1958; Baker and Ross 1981; Ross 1986; Horton et al. 2004). Recent review papers (Winemiller et al. 2010; Logue et al. 2011) emphasize that assumptions of habitat use patterns measured at one scale might not apply when measured at a different scale, but understanding when and where assumptions hold is important for furthering concepts of community dynamics. For example, classic research by MacArthur (1958) found overlapping habitat use among warbler species at the scale of a single tree, but species strongly partitioned feeding positions within branches of the tree. Thus, habitat overlap often depends on the dimension (e.g., space or time) where observations are made. Scale-dependent relationships of habitat use are known for a variety of taxonomic groups including birds (MacArthur 1958; Pinaud and Weimerskirch 2005), mammals (Apps et al. 2001; Vernes 2003; Wolf and Trillmich 2007), turtles (Senko et al. 2010), and spiders (Samu et al. 2003). Because of constraints on directly observing aquatic

organisms, such as stream fishes, there is limited information on their distributions at fine spatial and temporal scales.

A number of mechanisms might lead to differential habitat use by stream fishes, including the need to partition limited resources, different predator avoidance strategies, and aggregation around abundant or high-quality food supplies (e.g., drift feeding stations). Gorman (1988) measured habitat use of numerically dominant stream minnows that co-occurred in pools, and found individual habitat use dynamics to be driven by habitat configuration and interspecific interactions. Nakano (1995) identified differential foraging behaviors by two species of salmonids in pool microhabitats, whereby a size-structured dominance hierarchy gave rise to larger individuals maintaining profitable feeding stations at the head of the pool while subordinates were displaced to less-profitable stations. Predator avoidance strategies might preclude use of certain habitats over the course of a day (e.g., avoidance of birds in shallow water during daylight; Power 1987) or fish could form interspecific associations in response to predators (Gorman 1988). The dynamics of habitat use, including movement (or exchange) among habitat types can be complex and difficult to measure, because the scale at which an organism perceives its environment is not always apparent to researchers (Fausch et al. 2002).

A challenge in assessing habitat use is that fish often move among habitat types at varying temporal scales (e.g., hourly, daily, seasonally). For example, fish might overlap in habitat during high flows when resources are not limited, but partition habitat during low flows when resources are scarce (e.g., Zaret and Rand 1971). Fish can move among spatially disjunct habitat types during different life stages to obtain necessary resources (Schlosser and Angermeier 1995), but characterizations of how much fish move are normally assessed at coarse spatial (i.e., reaches 10^1–10^3 m or segments 10^3–10^5 m; Fausch et al. 2002) and temporal scales (i.e., 10^0–10^1 years) (e.g., Albanese et al. 2004; Wells et al. 2017). Less is known about fine-scale (i.e., within a pool) distribution and movements that are just as likely to influence species interactions (Nakano and Furukawa-Tanaka 1994; Fausch et al. 1994; Nakano 1995; Usio and Nakano 1998). For example, the intensive snorkeling observations of two stream salmonid species by Nakano and Furukawa-Tanaka (1994) identified differences in foraging strategies as the mechanism for interspecific food partitioning; where previously, competition was implied from diet analysis, observations of interspecific aggression in aquariums, and removal experiments in the wild.

Movement and habitat use are inherently linked as organisms must move among or within habitats to obtain resources (Schlosser 1991), and the coarse scales at which movements have been typically measured create generalities that may mask the underlying mechanisms or patterns at fine scales. For example, stream fish populations have often been viewed to consist of mobile and sedentary individuals (Gerking 1959; Gowan et al. 1994; Rodriguez 2002; Radinger and Wolter 2014). Based on a meta-analysis of fish dispersal patterns, to be considered a mobile individual, a fish must generally move greater than 100 m in an upstream or downstream direction over the course of a study (Radinger and Wolter 2014). However, a potentially important step in understanding habitat use is to understand the home range or boundaries of where a fish travels at fine spatial and temporal scales (i.e., over a 24-h period). Many things influence how much fish move, with body length being one of the best explanatory variables (Skalski and Gilliam 2000; Radinger and Wolter 2014), and this propensity to move could influence species interactions. For instance, larger-bodied species (or individuals) could exhibit more movement even at small scales, creating greater potential for species interactions. If the majority of individuals in fish populations are sedentary (Radinger and Wolter 2014), it is important to understand how movements among habitat types influence fish species interactions and resource partitioning at fine spatial scales (i.e., microhabitats 10^0–10^1 m; Fausch et al. 2002).

In this study, we measured habitat use of a prairie stream fish assemblage consisting of three minnow species at fine spatial and temporal scales. Prairie stream minnows can differ in their morphology and diet, but are generally opportunistic strategists (Winemiller and Rose 1992) in response to the stochastic conditions in these systems. Target species in our study included the southern redbelly dace *Chrosomus erythrogaster* (hereafter dace), central stoneroller *Campostoma anomalum* (hereafter stoneroller), and creek chub *Semotilus atromaculatus* (hereafter chub). Dace are primarily herbivorous in our study system, but feed more in the water column nipping algal filaments or consuming drifting algal particles (Bertrand and Gido 2007). The stoneroller is a benthic herbivore (Fowler and Taber 1985; Power et al. 1988) that uses its cartilaginous lower lip to scrape algae off substrates. Chub are largely a water column insectivore, feeding on aquatic and terrestrial insects, but also consuming fish prey as adults (Eberle 2014). These three species account for > 85% of the total individuals that occur in this reach (K. Gido, unpublished data) and can reach extremely high densities (> 50 fish m^{-2}; Franssen et al. 2006), making species interactions a potentially important aspect of assemblage dynamics.

Our first objective was to compare reach-scale patterns of movement among pools for three minnow species. We hypothesized the majority of fish would exhibit limited movement among pools, but if movement occurred it would be at night to avoid avian predators. Following this, we conducted a pool-scale study to assess habitat use within a pool. We assumed fish would exhibit temporal differences in habitat use among species over a 24-h period due to anti-predator or foraging behaviors that vary among species.

Because body length is a strong predictor of a fish's movement tendencies (Radinger and Wolter 2014), we also predicted greater vagility (i.e., summed distance moved among antennas) would occur for larger-bodied individuals. Lastly, because temporal differences in habitat use might be linked to feeding, we measured gut fullness over a 24-h period for each species to test if periods of higher feeding activity were associated with occurrence in particular habitats.

Methods

Study area and fish tagging

We used passive integrated transponder (PIT) technology to perform a multi-scale comparison of movement and habitat use of a prairie stream fish assemblage. To assess how stream fishes were distributed within and among a 100 m sequence of three pool–riffle habitats, we tagged 30 dace, 37 stoneroller, and 33 chub on 14 March 2014 in Kings Creek on Konza Prairie Biological Station, Kansas (Fig. 1). Our study reach occurred in a third-order stream reach that maintains perennial flow throughout the year. All fish were collected from a central pool with a seine (4.6 × 1.8 m, 3.2 mm mesh; Fig. 1). Fish were anesthetized in a 100 mg L^{-1} concentration of buffered tricaine methanesulfonate (MS-222), and PIT tags (8 mm × 1.44 mm; Oregon RFID, Portland,

Oregon) were injected into all fish following puncture of the peritoneal cavity with the tip of a hypodermic needle (specific methods outlined in Pennock et al. 2016). Tagged fishes ranged in total length from 55 to 75 mm for dace, 66 to 116 mm for stoneroller, and 58 to 104 mm for chub.

A second study began on 20 March 2016 to characterize species distribution within a single pool that was 189 m^2 and 40 m long. Thirty-five individuals of each species were tagged using the methods described above, and tagged individuals ranged in total length from 52 to 72 mm for dace, 66 to 105 mm for stoneroller, and 85 to 180 for chub. In both studies, tagged fishes were held in cages in the release pool for 7 days to assess survival and tag retention before they were released into the pool. We caught, held, released, and monitored fish in the same central pool for both studies.

Antenna placement

To examine patterns of distribution and movement in the first experiment, an array of four stationary antennas (3.05 × 1 m) attached to individual readers (RM310, Biomark Inc., Boise, Idaho) were installed upright in the water column to allow for detection of fishes that swam through antenna loops. Antennas were long enough to cover the entire wetted width of the stream in their respective locations. These antennas and readers were programmed to log unique tag detections at 1 min intervals. One antenna was
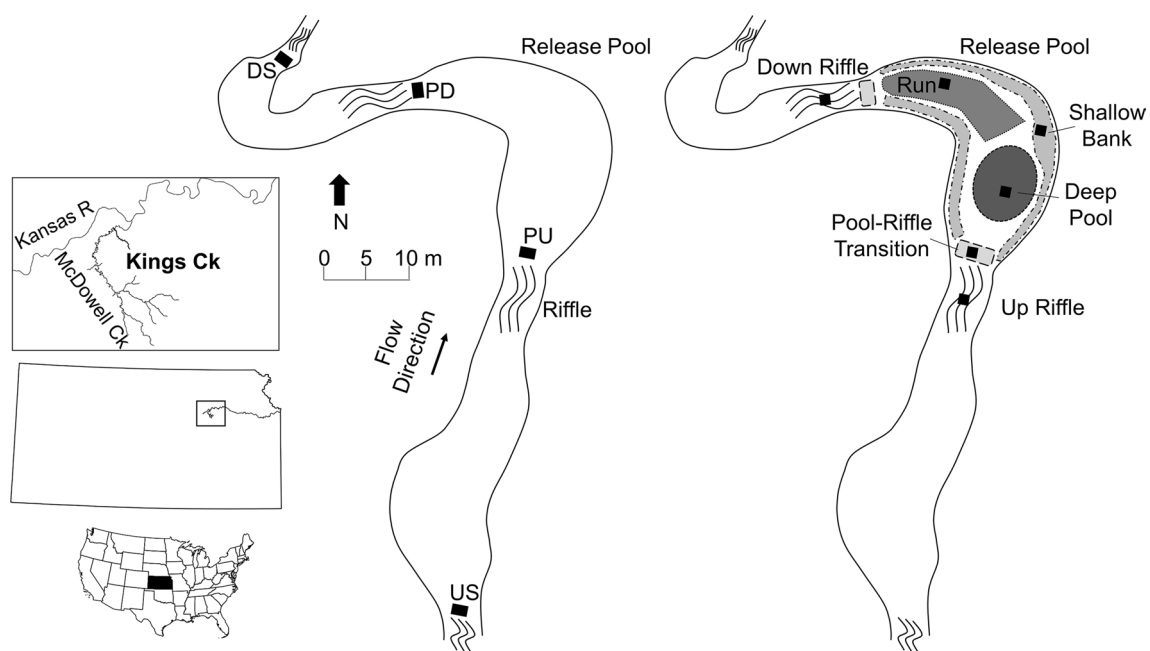

Fig. 1 Study reach illustration with antenna locations depicted for both the reach-scale [left; downstream (DS), pool down (PD), pool up (PU), and upstream (US)] and the pool-scale (right) studies. During the pool-scale study, antennas in the upstream and downstream riffles

were placed to detect any fish leaving the release pool. Antennas were placed in representative positions to cover as much observed habitat heterogeneity as possible (right; outlined and shaded), but only covered a portion of each habitat type within the release pool

placed at the upstream (PU) and downstream (PD) ends of the release pool (Fig. 1). Antennas also were placed at the upstream end of the adjacent upstream pool (US) and at the downstream end of the adjacent downstream pool (DS). This arrangement allowed us to detect fish leaving the release pool in both upstream and downstream directions, while also detecting movement beyond the pools adjacent to the release pool. Antennas were run continuously from 22 March 2014 to 27 April 2014 (37 days). During the morning of 27 April, rainfall increased flow from < 1 to a peak of 27.6 m^3 s^{-1} over a 3-h period and washed all four antennas out of the system, thus ending our first study.

Pool-scale patterns of distribution were investigated with an array of four antennas (1 × 1 m) covering the main habitat heterogeneity within the pool (e.g., depth, substrate, and velocity) (Table 1). Antennas were placed in a run, a shallow bank, a deep pool, and at the upstream pool–riffle transition (Fig. 1). The pool–riffle transition antenna was placed in the same location as the PU antenna in the previous study. We also placed one antenna in the middle of the downstream and upstream riffle to detect any individuals leaving the pool. Antennas were all monitored with a QuBE multiplexer (Biomark, Boise, Idaho) and were running from 31 March 2016 to 4 April 2016 (5 days). This antenna configuration provided a representation of major habitat types within the pool, but because of limited detection range of antennas (approximately 0.2 m) did not completely cover the entire pool area.

Data analysis

Reach-scale study

To compare interspecific differences in distribution, we calculated the daily proportion of individuals detected for each species that occurred in the release pool (PD and PU) and in the adjacent pools (DS and US). We used a one-way repeated measures ANOVA to test for differences ($\alpha = 0.05$) in proportion of individuals detected across antenna locations for each species. Data did not meet the assumption of normality (Shapiro–Wilk test, $P < 0.05$), but did meet the assumption of equal variance (Levene's test, $P > 0.05$). Hence, we ran statistics on raw data because transformation (i.e., arc-sine square root) did not help with meeting the normality assumption, and ANOVA is robust to violations of normality (Schmider et al. 2010). We used the Holm–Šidák stepdown procedure (Holm 1979) to assess pairwise differences. To further identify the patterns of distribution among species, we calculated the total number of detections and the proportion of total detections at each antenna (DS, PD, PU or US) over the duration of the study.

Pool-scale study

To visualize temporal patterns of concordance in species distribution across habitats for species pairs, we used a percent similarity index (PSI):

$$PSI = \text{Sum (minimum proportion detected at antenna}$$
$$i \text{ for each species } j, \ k).$$

This index represented how similar the proportion of detected individuals was across antennas for each species pair during a 4-h time period. Thus, we could evaluate habitat overlap between species across six time periods over a 24-h period. We weighted detections of individuals by the number of antennas that an individual was detected at in a time period to account for movement among habitats during that time period (Fig. 2). For example, if a fish was detected at two antennas in a 4-h period, we assigned a value of 0.5 for each antenna detection. The PSI between species was calculated for each day of the experiment. To test for differences in PSI across time for each species pair, we used a one-way repeated measures ANOVA with time period as a factor and day of detection as a repeated measure. We used the Holm–Šidák stepdown procedure to assess pairwise differences. Data did not meet the assumption of normality (Shapiro–Wilk test, $P < 0.05$), but did meet the assumption of equal variance (Levene's test, $P > 0.05$) so raw data values were used as previously described.

Table 1 Habitat variables at each antenna location used during the pool-scale study

Antenna/pool characteristics	Depth (m)	Dominant substrate (> 50% coverage)	Velocity (m s^{-1})
Run	0.64	Clay	0.01
Shallow bank	0.43	Clay	0
Deep pool	0.88	Silt	0.01
Pool–riffle transition	0.32	Pebble	0.13
Overall pool average	0.34	–	0.02

A point measurement for each variable was taken at the midpoint of each antenna. The substrate was defined by grain size (Wentworth 1922). Pool averages for depth and velocity were calculated from ten evenly spaced transects with five point measurements per transect
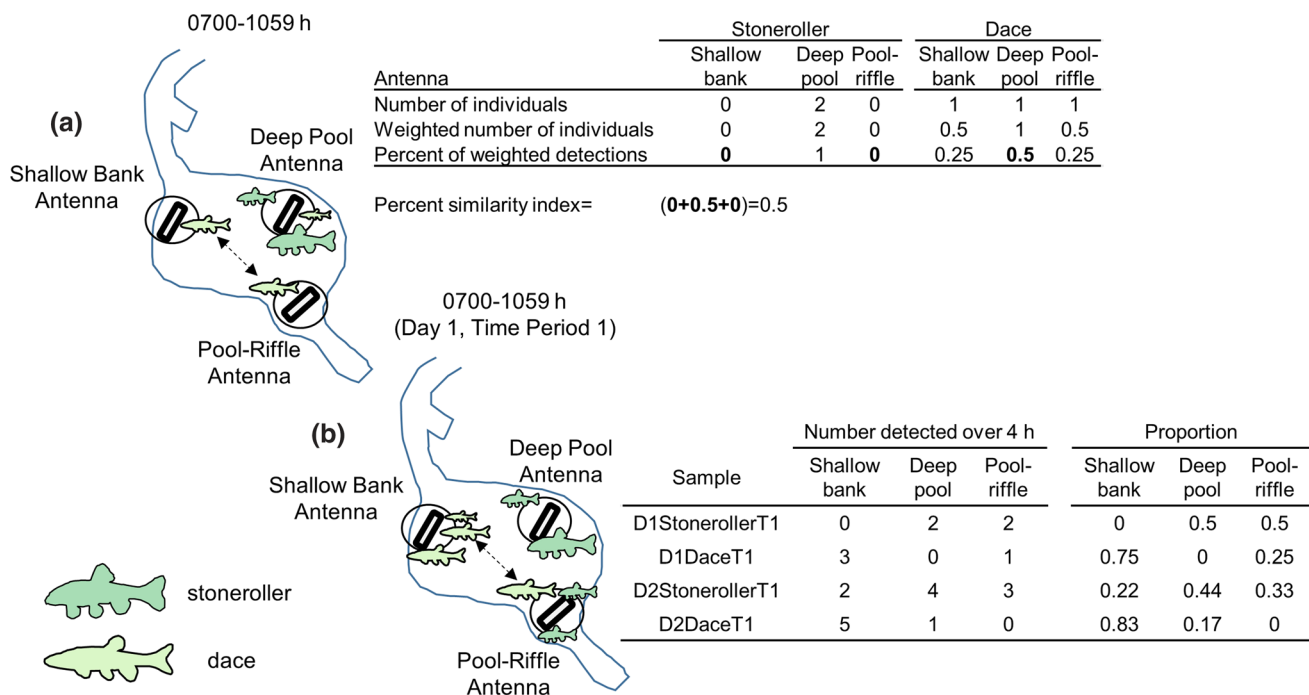
	Stoneroller			Dace		
Antenna	Shallow bank	Deep pool	Pool-riffle	Shallow bank	Deep pool	Pool-riffle
Number of individuals	0	2	0	1	1	1
Weighted number of individuals	0	2	0	0.5	1	0.5
Percent of weighted detections	**0**	1	**0**	0.25	**0.5**	0.25

Percent similarity index= **(0+0.5+0)**=0.5

	Number detected over 4 h			Proportion		
Sample	Shallow bank	Deep pool	Pool-riffle	Shallow bank	Deep pool	Pool-riffle
D1StonerollerT1	0	2	2	0	0.5	0.5
D1DaceT1	3	0	1	0.75	0	0.25
D2StonerollerT1	2	4	3	0.22	0.44	0.33
D2DaceT1	5	1	0	0.83	0.17	0

Fig. 2 Conceptual diagram of how we summarized tag detections at antennas placed throughout a single pool to calculate the **a** percent similarity index (PSI) of species overlap at different times and **b** proportion of individuals detected at an antenna over 4-h time periods to test for differential habitat use. We weighted the number of individuals detected by the number of antennas each individual was detected at when calculating PSI. This allowed us to account for indi- viduals using multiple habitats (dashed arrow in **a**) during a given time period, since the calculation of PSI did not discriminate among habitat types (antennas). We used the maximum number of individu- als detected at an antenna over a 4-h period for a test of differential habitat use so we would not inflate our detection values with indi- viduals detected multiple times while still maintaining habitat identity (dashed arrow in **b**)

To visualize how species were distributed over time and space, we calculated the proportion of detected individuals across habitat types during 4-h time periods. We used the maximum number of detected individuals for each species within a time period at each habitat type to avoid inflat- ing the number of detections at an antenna with individu- als detected over multiple hours (Fig. 2). For each species, the maximum number of detected individuals per habitat type was divided by the total number of detected individu- als across all habitat types in each time period to obtain the proportion of detected individuals per habitat type. To test if a species' proportional distribution among habitat types differed across time, we used a two-way repeated measures ANOVA with time period and habitat type as factors and day as a repeated measure. Again, we used the Holm–Šidák step down procedure to assess pairwise differences. Data were not transformed because the assumption of equal vari- ances were met (Leven's test, $P > 0.05$), but as with PSI the normality assumption was violated (Shapiro–Wilk test, $P < 0.05$).

Species-specific vagility

To quantify movement among habitat types within a single pool (vagility), we summed the distances between antenna detections for tagged individuals and divided these by the number of days the individual was detected. Vagility data did not meet parametric-model assumptions of normality (Shapiro–Wilk test, $P < 0.05$) or equal variance (Levene's test, $P < 0.05$), so differences in vagility among species were tested with a Kruskal–Wallis one-way ANOVA on ranks and pairwise comparisons assessed with a Dunn's test. Because the length distribution of tagged fish was variable among species and we predicted larger-bodied individuals would move longer distances, we tested if individual vagil- ity increased with increasing total length for all three spe- cies using linear regression. Normality and equal variance assumptions were met for all regression analyses.

Fish gut fullness

Because foraging activity could determine the patterns of habitat use, we assessed gut fullness over a 24-h period. On 2 May 2017, we collected 9–13 individuals of each species with a seine every 4 h from habitats within 1 km of the study

reaches used above. Collections occurred at approximately 0600, 1000, 1400, 1800, 2200, and 0200 hours. All fish were euthanized with an overdose of MS-222 and preserved in 10% formalin. In the laboratory, fish were measured for total length and the entire alimentary canal was removed. The entire intestinal tract plus contents were dried at 55 °C for 24 h and weighed to the nearest 0.01 g. For each species, we used a single-factor ANCOVA to test for differences in log-transformed (log + 0.1) dry gut weight using time as a fixed factor and total length as the covariate. Data met assumptions of normality for dace and chub, but not stoneroller (Shapiro–Wilk test, $P < 0.05$), and satisfied assumptions of equal variance (Fligner-Killeen test, $P > 0.05$). The ANCOVA and model checking were performed using the car package, version 2.1-4 (Fox and Weisberg 2011) and stats package in R, version 3.4.0 (R Core Team 2017).

Results

Fish tagging and total detections

Tag loss and mortality was negligible. Tag retention in the reach-scale study was 100% and post-tagging survival was 96%. Depending on species, 85–92% of released individuals were detected during this study (Table 2). During the pool-scale study, 11 fish were unaccounted for in holding cages after the 7 days assessment of survival and tag retention. We recorded no detections of these individuals; thus, they were excluded from all analyses. Of the fish remaining in cages, post-tagging survival was 99% and tag retention was 97%.

Reach-scale patterns of detection

Movement between antennas was largely restricted to antennas located within the release pool for all three species, as predicted. Most detections (99% of total detections) occurred at the PD and PU antennas (Table 2), and of these only 3–26% of individuals were detected outside the release pool at the DS or US antenna. All detections of fish at the DS and US antenna (54 total; Table 2), with the exception of two dace detections, occurred during nighttime (2000–0459 hours). The proportion of individuals
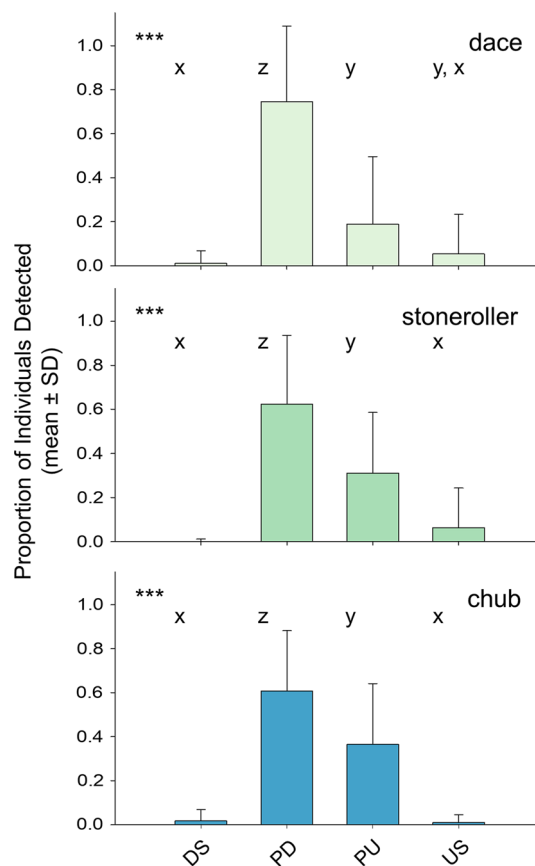

Fig. 3 Proportion of individuals detected across antennas during the reach-scale study. Abbreviations for antenna locations follow those in Fig. 1. We tested for differences in the proportion of individuals detected across antennas for southern redbelly dace *Chrosomus erythrogaster* ($n = 34$ days), central stoneroller *Campostoma anomalum* ($n = 37$ days), and creek chub *Semotilus atromaculatus* ($n = 35$ days) using a repeated measures ANOVA with antenna as a factor and day of detection as the repeated measure. The proportion of individuals detected was significantly different across antennas for all species (***, $P < 0.001$). Pairwise differences were tested with the Holm–Sidak stepdown procedure. Antennas sharing the same letter did not differ significantly ($P > 0.05$)

detected differed significantly among antenna locations for dace (ANOVA: $F_{3,99} = 45.9$, $P < 0.001$), stoneroller (ANOVA: $F_{3,108} = 42.0$, $P < 0.001$), and chub (ANOVA: $F_{3,102} = 55.6$, $P < 0.001$) (Fig. 3). The PD antenna had the highest proportion of individuals detected for all three

Table 2 The proportion of total detections and total number of detections for each of the three species at each antenna during the reach-scale study

Species	Number detected/ released	Proportion of total detections				Total number of detections			
		DS	PD	PU	US	DS	PD	PU	US
Southern redbelly dace	27/30	0.01	0.76	0.22	< 0.01	15	984	288	11
Central stoneroller	34/37	< 0.01	0.24	0.75	< 0.01	3	1646	5193	14
Creek chub	28/33	< 0.01	0.24	0.75	< 0.01	7	510	1646	4

The proportion of detections was calculated from the total number of detections across antennas for each species separately

species ($P < 0.05$). The PU antenna had a higher proportion of individuals detected than the DS antenna for dace ($P < 0.05$), but did not differ from the US antenna. The PU antenna had an intermediate proportion of individuals detected for both stoneroller and chub ($P < 0.05$), and for both species there was no difference between the DS and US antenna.

Pool-scale patterns of detection

Generally, overlap in distribution across habitats was temporally variable for each species pair with the most overlap for the assemblage occurring in the afternoon (Fig. 4). Average PSI dropped considerably during the 2300- to 0259-hour period for comparisons involving stoneroller, and was largely driven by the absence of stoneroller detections during this time. Similar to the inter-pool study, 99% of detections occurred within the release pool, but varied among antenna locations (Table 3). All three species had their highest proportion of total detections (> 1/3 total detections) at the run antenna. The pool–riffle transition was the second most shared habitat with greater than 20% (range 20–32%) of detections for all species. Despite these general patterns across species, combinations of habitats used based on the proportion of total detections were variable among species. Dace were primarily detected at the run and shallow bank antennas (73%), but also had relatively high detections (20%) at the pool–riffle transition antenna. Stoneroller used the run most followed by the pool–riffle transition and lastly the deep pool antenna locations, respectively. Sixty-seven percent of chub detections were at the run and deep pool antennas. Despite a low overall proportion of detections at riffle-located antenna for the entire assemblage, 50% of stonerollers were detected at the down riffle antenna over the course of the study.

The proportion of individuals detected differed significantly among habitat types, but was dependent on time period for each species (Fig. 5). A significant two-way interaction was found between habitat type and time period for dace (ANOVA: $F_{15,60} = 3.17$, $P < 0.001$), stoneroller (ANOVA: $F_{15,60} = 5.61$, $P < 0.001$), and chub (ANOVA: $F_{15,60} = 3.59$, $P < 0.001$). A consistently high proportion of dace used the shallow bank and run habitats throughout the diel period, but appeared to be more general in their habitat use during daylight hours. Stoneroller used the deep pool habitat almost exclusively during the hours of 0700–1059, before switching to more general habitat use from 1100 to 1859 hours and using the pool–riffle transition and run habitats from 1900 to 2259 h. There were limited detections of stoneroller from 2300 to 0259 h. Patterns of chub detections were similar to stoneroller during daylight hours, but chub remained active during the night, showcasing more general habitat use patterns from 2300 to 0659 h.
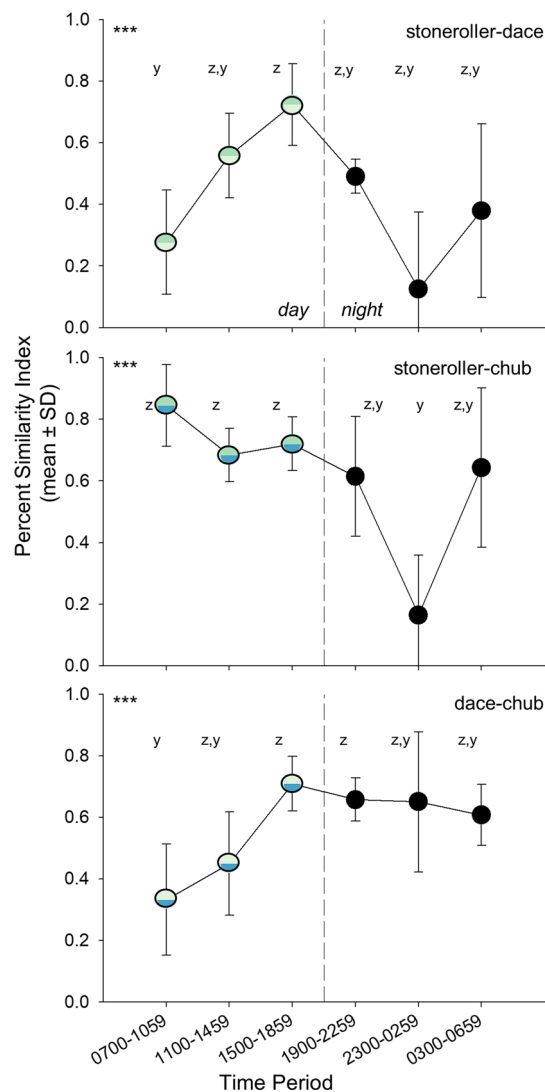

Fig. 4 Percent similarity index (PSI; mean ± SD) of the proportion of individuals detected across habitats for all species combinations of southern redbelly dace, central stoneroller, and creek chub over six, 4-h time periods. To test for differences in PSI across time for each species pair, we used a one-way repeated measures ANOVA with time period as a factor and day of detection ($n = 5$) as the repeated measure. A significant (***, $P < 0.01$) difference in PSI was found for each species pair across time. Pairwise comparisons among time periods were conducted using the Holm–Sidak step down procedure. Time periods sharing the same letter in each panel did not differ significantly ($P > 0.05$). Black circles represent time periods after sunset and before sunrise

Species-specific vagility

Despite largely remaining in the release pool, all three fish species showed high amounts of exchange among habitat types with some individuals moving over 100 m day^{-1} (range across species: 2–112 m day^{-1}), equivalent to 2.5 × the length of the pool per day. Species differed in mean vagility (summed distance, m day^{-1}; ANOVA: $F_{2,68} = 4.99$,

Table 3 Pool-scale study detections by antenna for each species

Species	Number detected/released	Proportion of total detections						Total number of detections					
		Down riffle	Run	Shallow bank	Deep pool	Pool–riffle transition	Up riffle	Down riffle	Run	Shallow bank	Deep pool	Pool–riffle transition	Up riffle
Southern redbelly dace	24/28	0.00	0.43	0.30	0.06	0.20	0.01	4	538	369	77	245	7
Central stoneroller	22/31	0.01	0.39	0.04	0.24	0.32	0.00	16	709	78	440	589	9
Creek chub	25/27	0.00	0.38	0.09	0.29	0.24	0.00	0	715	163	551	456	3

The proportion of detections was calculated from the total number of detections across antennas for each species separately

$P = 0.01$) based on total distances moved among habitat types (antennas). Dace and chub vagility was not significantly different, but stoneroller vagility was significantly higher than that of chub and dace ($P < 0.05$; inset Fig. 6). Dace showed no relationship between vagility and length (slope = 0.007, $r^2 = 0.00$, $df = 23$, $P = 0.989$), but this species also had the smallest size range among individuals. The vagility of stoneroller and chub increased significantly with total length (stoneroller: slope = 1.21, $r^2 = 0.18$, $df = 21$, $P = 0.049$; chub: slope = 0.68, $r^2 = 0.47$, $df = 24$, $P < 0.001$) (Fig. 6).

Fish gut fullness

We found no evidence of diel variation in feeding despite the differences we found in habitat use for all three species. Dry gut weight increased significantly with total length (ANCOVA: $P < 0.001$), and the interaction between time and total length was not significant ($P > 0.05$) for all three species. There was no significant difference across time periods for dace (ANCOVA: $F_{1,59} = 0.999$, $P = 0.322$), stoneroller (ANCOVA: $F_{1,58} = 2.38$, $P = 0.128$), or chub (ANCOVA: $F_{1,57} = 1.51$, $P = 0.225$).

Discussion

Our findings suggest that quantifying patterns of habitat overlap at multiple spatial and temporal scales can have important implications regarding species interactions, such as resource competition or predation. Our use of PIT tagging to continuously monitor fish distribution across different stream habitats identified a more detailed view of habitat use and movement than was previously available for most fish assemblages. To us, a surprising result was that more inter-specific differences in habitat use were observed than expected based on habitat associations quantified with traditional capture techniques in Kings Creek (Martin et al. 2013).

Beginning with the reach scale, patterns of detection within the duration of our study (i.e., 37 days) illustrated that most fish remained within a single pool with a limited number of individuals showing directional inter-pool movements and most of the individuals dispersing from the central release pool returning at some point. Clough and Ladle (1997) documented a similar homing behavior in Eurasian dace *Leuciscus leuciscus* where individuals would make diel movements between discrete day time and night time habitats, returning to the same general area in each habitat. The significant statistical interaction between species habitat use and time period during the pool-scale study suggests that species overlap changed over a 24-h period. Intra-pool
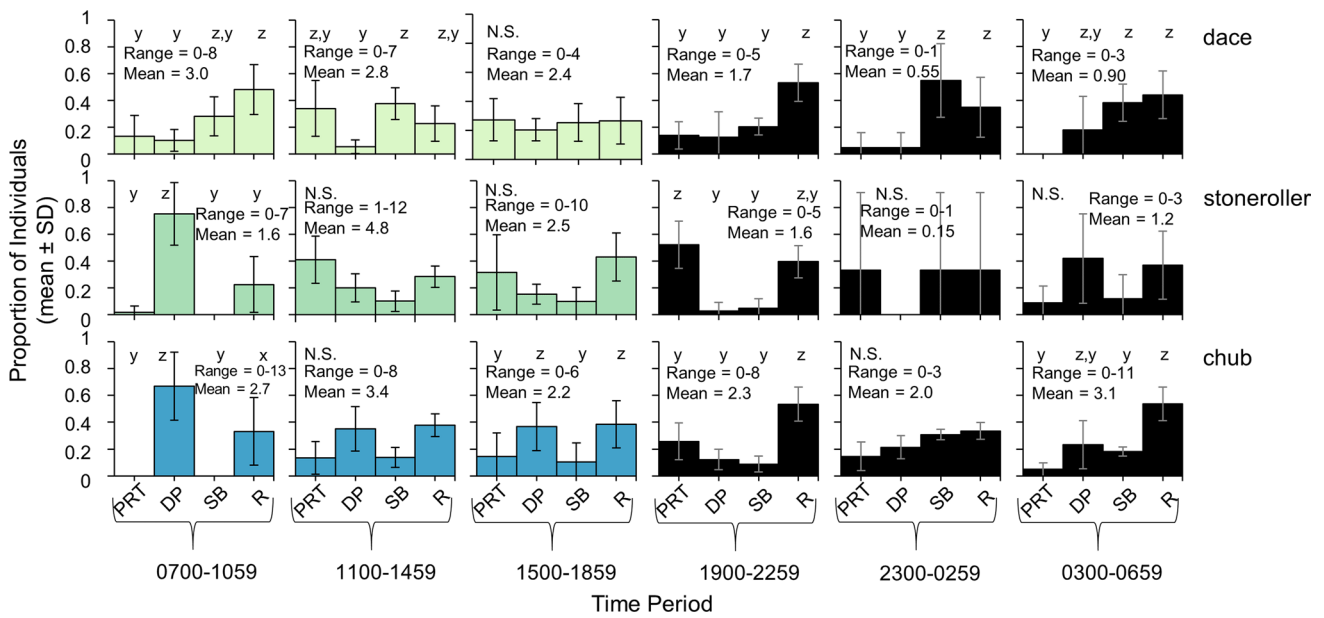
Fig. 5 Proportion of individuals (mean ± SD) detected at four habitat types of southern redbelly dace (top), central stoneroller (middle), and creek chub (bottom) across the diel period during the pool-scale study. Habitat types are abbreviated as PRT (pool–riffle transition), DP (deep pool), SB (shallow bank), and R (run). Differential habitat use for each species was tested with a two-way repeated measures ANOVA with time period and habitat type as factors and day of detection ($n = 5$) as the repeated measure. Pairwise comparisons were conducted using the Holm–Sidak step down procedure. Habitat types sharing the same letter within each panel did not differ significantly ($P > 0.05$). The number of individuals (range and mean) detected across days during each time period are presented in each panel
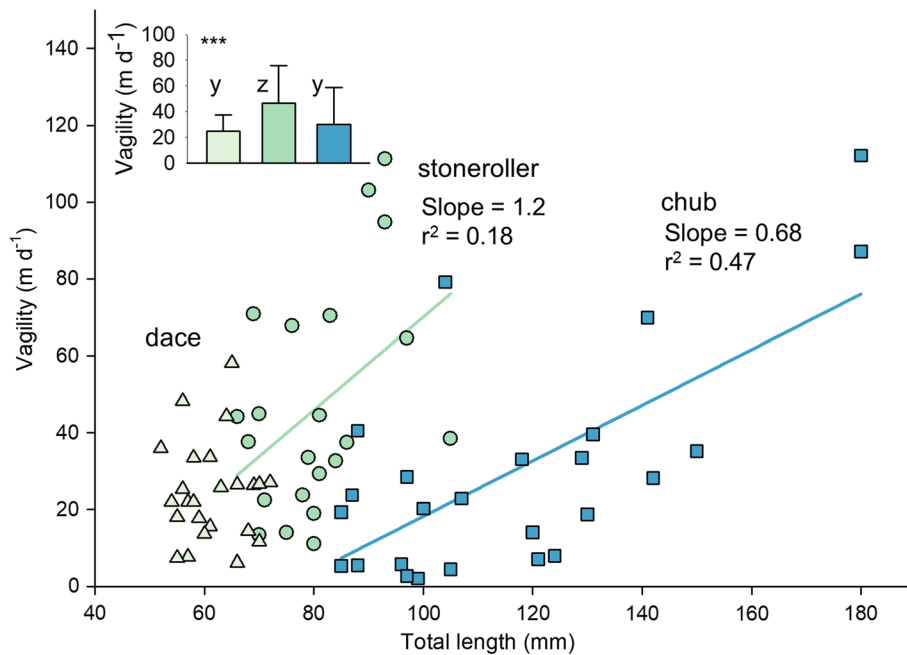
Fig. 6 Regression plot of the vagility (summed distance per day) for each detected individual as a function of their total body length (mm) of southern redbelly dace (triangles, $n = 24$), central stoneroller (circles, $n = 22$), and creek chub (squares, $n = 25$). Summed distance was divided by the number of days each individual was detected during the pool-scale habitat use study to account for days when fish were not detected. The relationship between total length and vagility was significant for stoneroller ($P = 0.049$) and chub ($P < 0.001$). Dace showed no significant relationship ($P = 0.989$). Inset is median vagility for the three species. Species sharing the same letter did not differ significantly ($P > 0.05$). Error bars represent the 75th percentile. Colors of bars and order of bars match those within the regression plot in regard to species

exchange among habitat types was common throughout the day, indicating fish can transition among habitats at a scale finer than measured by most studies (e.g., Young 1996; Albanese et al. 2004; Wells et al. 2017).

Our fine-scale assessment of habitat use also allowed us to test for differences in vagility among species at a spatial scale that is also not generally considered (i.e., within stream pools). This analysis suggested stonerollers were more vagile than dace and chub, potentially reflecting differences in feeding strategies or behaviors. Stonerollers feed largely at lower trophic levels and might get the lowest energy return out of forage, compared to chub which feed at higher trophic levels (Ahlgren 1990, Evans-White et al. 2003) and dace which feed on algae in the water column but also feed on macroinvertebrates (Phillips 1969; Settles and Hoyt 1976; Felley and Hill 1983). This low energy return means stoneroller might need to feed more continuously, which could explain why they displayed more general habitat use patterns. Indeed, stonerollers are known to feed continuously throughout pools in small mid-western streams (Matthews 1998), and this observation is supported by our gut fullness analysis. However, dace and chub also showed consistent gut fullness across the diel period, suggesting feeding was not diminished by differential habitat use. Predation risk can influence foraging behavior and choices of habitat use (Brown et al. 1988; Hughes et al. 1994; Brown and Kotler 2004). The smaller size of dace might cause them to avoid larger piscivorous fishes (like creek chub), restricting them to shallower habitats (e.g., Power 1987; Schlosser 1987), as evidenced by their lower vagility and fewer number of total detections than larger stoneroller. Chub also exhibited lower average vagility compared to stoneroller. Because the chub we tagged were larger, they might be more susceptible to terrestrial predators than smaller dace and stoneroller. It is possible that terrestrial predator (e.g., birds) avoidance precludes movement into shallower habitats during daylight hours (Power 1987), resulting in more detections of chub in deeper habitats during the day. Despite the relatively small number of detections of all three species during the reach-scale study occurring at the DS and US antennas, 96% occurred during nighttime hours, which suggests avian predators might limit inter-pool movement of the entire assemblage during the day.

Organisms are faced with decisions on when to stay in or leave a habitat type based on benefits (e.g., resource availability) and costs (e.g., predation threat, travel costs) (Brown 1988; Kotler 1997; Petty and Grossman 2010). Resource availability, growth potential, or predation risk might explain species distribution within certain areas of stream pools or among pools (e.g., directly downstream of riffles; Hayes et al. 2007; Weber et al. 2014). For example, incidence of drifting insects increases in higher velocity habitats, and drifting insects are at their highest

abundances between sunset and sunrise (Waters 1962). Our analysis identified the highest spatial overlap at the run antenna and highest temporal overlap (based on PSI for the entire assemblage) occurred during the afternoon. Although our gut analysis suggested continuous feeding over a 24-h period, the run habitat and afternoon time period might provide a high-quality foraging area that concentrates the entire assemblage, despite differences in food preferences and feeding behaviors of these species.

There were several potential limitations and trade-offs associated with data-logging PIT antenna studies that should be considered while interpreting our data. First, PIT antennas only covered a portion of the described microhabitats and did not cover the entire pool. Thus, habitat partitioning could occur at finer spatial scales that we were not able to measure (e.g., vertical position in the water column; Baker and Ross 1981; Gorman 1988). For instance, water column position could potentially be an important difference between stoneroller that feed by grazing the benthos and dace which feed more in the water column. Second, we only conducted this study in spring, and patterns of habitat use and partitioning could change among seasons depending on resource availability and current velocity within habitats (e.g., Matthews and Hill 1980). Third, we only conducted this study in a single reach in a single stream, and conclusions might differ across habitats varying in physicochemical conditions, population densities, community structure (including predator presence/absence), and resource availability. Despite the limitations of this study, the use of PIT technology allowed us to record continuous habitat use and movement at baseflows over multiple 24-h periods on fish smaller than traditional telemetry techniques (e.g., radio telemetry) currently allow (Greenberg and Giller 2000). Moreover, we were able to continuously account for diel differences in intra-pool habitat use of a prairie stream fish assemblage that are difficult to detect with traditional seining or snorkeling methods, which are logistically more difficult to run over a 24-h period.

Our study measured habitat use and movement at fine spatial and temporal scales, while gaining a more comprehensive understanding of multiple species' behavior and potential community interactions. We show that activity in different habitats, as measured by the number of detections and proportion of individuals detected, is highly variable across species over a 24-h period. Based on these findings, we suggest that, depending on scale, ecological studies might either over- or underestimate the extent of habitat overlap relevant to species interactions. Moreover, we captured habitat use and activity patterns at times of day and night that are not typically measured because light and other factors constrain continuous observation. Although the mechanisms responsible for the patterns of habitat use are

still elusive, future researchers might develop methods that combine fine-scale measures of habitat use with measures of food acquisition and resource availability to further advance understanding of species abilities to coexist.

Author contribution statement CAP led writing the manuscript. REW, CNC, and KBG conceived and designed the first study. CAP and KBG conceived and designed the follow-up study. CAP, REW, CNC, SCH, and KBG conducted fieldwork. CAP, REW, and SCH analyzed the data. All authors contributed to the writing of the manuscript.

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