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Dispersal drives changes in fish community abundance in intermittent stream networks

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Abstract

Increasing trends in fragmentation and dewatering of streams warrants research on how populations and communities respond to varying water levels and barriers to movement. Although these responses are complicated by many spatial and temporal processes, long-term datasets might help reveal complex patterns and processes driving variability in species abundances. The objective of this study was to develop a predictive framework for fish community and population responses to varying levels of water availability across six sites in two intermittent stream networks sampled >10 years. We predicted that fishes would emigrate into intermittent reaches during wet conditions; thus, overall abundances within perennial source locations will decline. Accordingly, when intermittent reaches dry, fishes will contract to wetted habitats resulting in high abundance. Observed fish community abundances were highly variable within and among study sites, but four of six sites matched our predictions. A tagging study confirmed these results and demonstrated a substantial proportion of individuals moved away from perennial reaches and into newly wetted intermittent reaches. However, site and species-specific relationships were variable and likely depended on the habitat, metacommunity dynamics, and life history strategies. Findings suggest that species dispersal dynamics, in addition to recruitment and mortality, should be carefully considered when interpreting species responses to varying water levels, particularly in intermittent stream networks where access to habitat can change drastically with water availability.

KEYWORDS
abundance, dispersal, fish, stream

1 | INTRODUCTION

A major goal of community ecology is to characterize patterns occurring in natural systems and then attempt to identify processes that drive these patterns (Wiens, 1984). In streams, hydrology plays a fundamental role in many ecological processes (Lytle & Poff, 2004; Poff et al., 1997). Community responses to stream flow have been evaluated across broad spatial (Schlosser, 1987; Stanley, Fisher, & Grimm, 1997) and temporal (Freeman, Bowen, Bovee, & Irwin, 2001; Gido, Propst, Olden, & Bestgen, 2013) scales. Long-term studies that track species abundance at sentinel sites across years with different flow patterns are particularly useful at detecting interannual responses of fishes to flow (Gido & Propst, 2012). However, most of these studies are correlative in nature, and the mechanisms that drive species responses to flows are equivocal. Whereas high or low flows might influence survival or reproductive success, we argue that changes in habitat availability and dispersal might also partially explain the response to variable levels of water availability at the spatial scale at which most sampling occurs. This is particularly true of intermittent streams, which are highly dynamic, and the availability of wetted habitat can vary drastically over time (Datry, Bonada, & Boulton, 2017).

The biota in intermittent prairie streams have adapted to living in these highly dynamic systems (Dodds, Gido, Whiles, Fritz, & Matthews, 2004). Prairie stream networks include a mosaic of reaches that can be classified as perennial or intermittent. Perennial reaches typically contain water year-round and are either lower in the watershed or near groundwater inputs. Intermittent reaches typically lose all water on a yearly basis when local conditions become dry. Thus, the stream network exhibits an expansion–contraction cycle with a fluctuation in available aquatic habitat, and the connectivity of these systems is dependent on seasonal and interannual climate patterns (Datry, Larned, & Tockner, 2014). Because of severe fluctuations in the amount of wetted habitat, fish communities in headwater prairie streams are typically dominated by small bodied (<100 mm) species that can rapidly colonize habitats and withstand harsh conditions (Matthews & Hill, 1979; Whitney, Gido, Martin, & Hase, 2016).

The objective of this study was to develop a predictive framework of the fish community response to varying levels of water availability and test those predictions using a long-term dataset from intermittent stream networks. We predicted that when conditions are wet and intermittent reaches become inundated, the fish community would expand and disperse throughout the stream network, colonizing these intermittent reaches and thus reducing abundances in perennial reaches (Figure 1). When conditions become dry and intermittent reaches lose water, we predicted the fish community would be forced to contract and aggregate in areas of perennial water, increasing fish abundances. We also predicted under extreme drying, when abiotic conditions such as temperature and dissolved oxygen are harsh in

perennial reaches (Hopper et al., 2020), there will be a transitional state where abundances would decline due to mortality. Mortality due to drying should vary spatially as smaller streams that are higher in the watershed are more isolated and hold less water. These smaller streams should dry sooner compared with more stable, larger downstream reaches that are more resilient due to deeper pools. Given the importance of scale when studying ecological processes (Fausch, Torgersen, Baxter, & Li, 2002; Pickett & Cadenasso, 1995; Wiens, 1999), a long-term dataset collected at broad spatial (two stream networks, composed of six total sites varying in stream size) and temporal (sites were sampled three times a year for 10–16 years) scales was used to examine fish community responses to varying levels of wetted habitat and test our predictions. These predictions were further tested by tracking fish movements between perennial and intermittent stream reaches to quantify the proportion of fish within the community dispersing into intermittent reaches once they became inundated. Our study investigates the importance of considering dispersal, an often overlooked dynamic (Roni, 2019), while evaluating long-term fluxes in fish abundance in relation to flow regimes.

2 | METHODS

2.1 | Study area and data collection

Kings Creek and Fox Creek watersheds are located within the Flint Hills region of Kansas, USA (Figure 2). Both properties are owned by
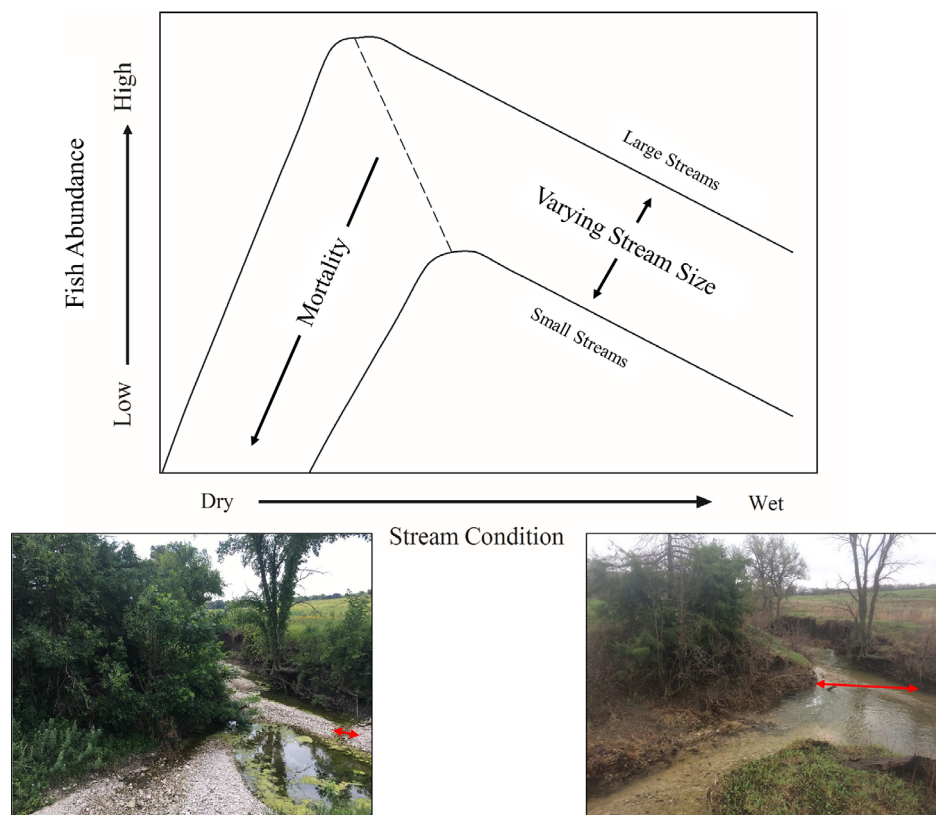
FIGURE 1 Conceptual figure predicting how fish community abundance fluctuates along a gradient of stream wetted habitat and the potential differences with varying stream sizes due to dispersal and mortality. Photos show varying degrees of water levels at the same location in Kings Creek, Kansas, USA. Red arrows in the pictures highlight differences in riffle widths
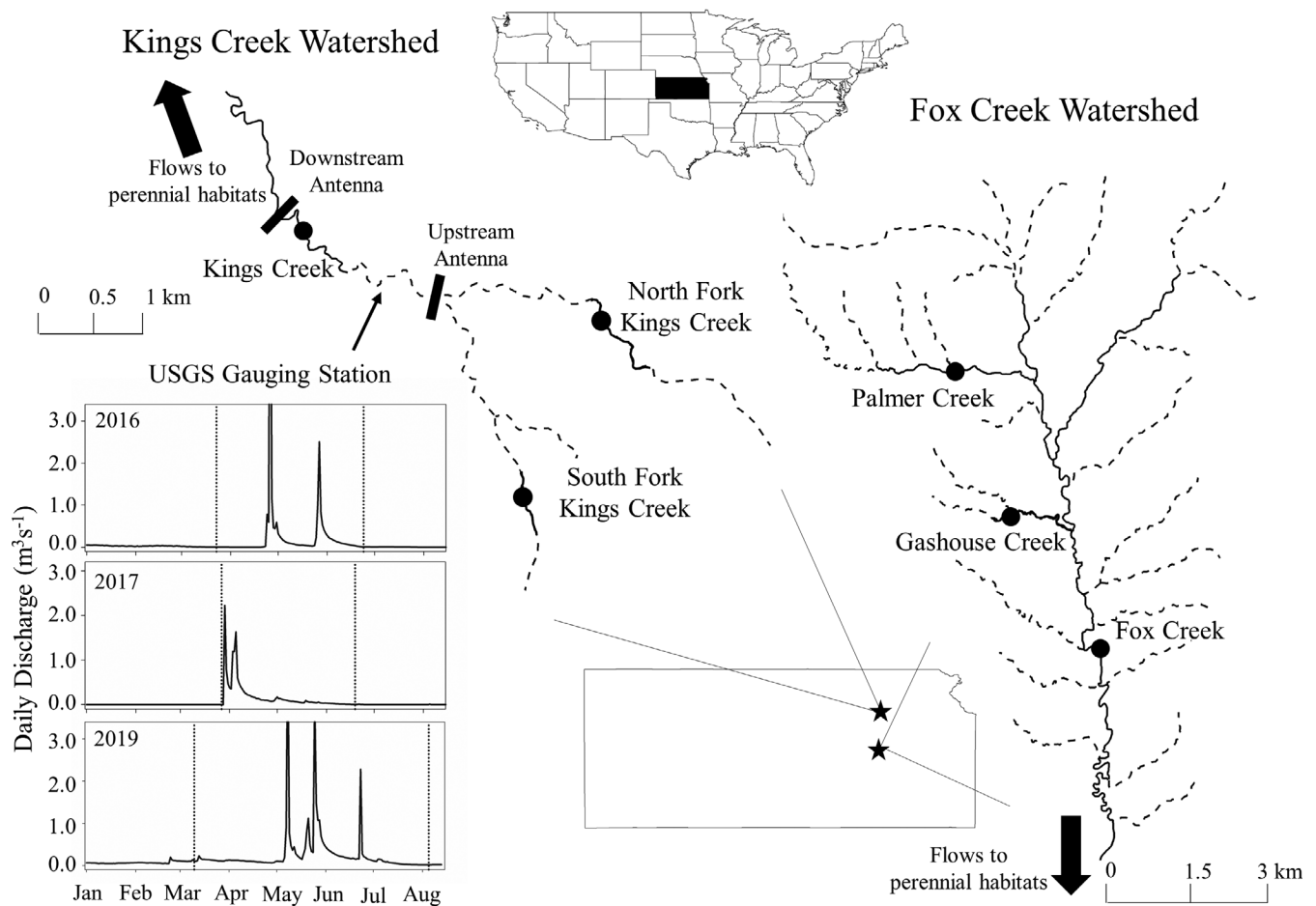
FIGURE 2 Six sites located in the Kings Creek and Fox Creek watersheds in Kansas, USA. Dotted lines represent intermittent reaches, and solid lines represent perennial reaches. Location of upstream and downstream PIT antennas are marked with black bars, and inset hydrograph is from U.S. Geological Survey gauging station 06879650 in Kings Creek from 2016, 2017, and 2019; time between the dotted vertical lines in the hydrograph represents when intermittent reaches were inundated with water and antenna were deployed

The Nature Conservancy and managed with a combination of fire and grazing to maintain native tallgrass prairie. Stream discharge in both systems is highly variable but typically exhibits peak flows in the spring (March–June). These stream networks are classified as intermittent (a stream that flows only when it receives rainfall run-off or spring input, or from some surface source; U.S. Geological Survey, 2013) and are composed of perennial and intermittent reaches. Perennial reaches are those that typically retain water year-round, whereas intermittent reaches typically dry every year. All sample sites were located on perennial reaches, and long-term monitoring occurred from 2002–2017 (Kings Creek and South Fork Kings Creek) and 2006–2017 (North Fork Kings Creek) in the Kings Creek watershed and 2008–2017 at all sites in the Fox Creek watershed. Sampling occurred at each site in May, August, and November of every year. We standardized our sampling of the fish communities by sampling the same reach each sampling event and using the same gear, backpack electrofisher, or a combination of electrofishing and a 4.6 m × 1.2 m, 3.2-mm mesh seine if deep pools were present. Fish were identified, measured, and released after each sampling event. Habitat measurements were taken following each fish sampling bout.

Given that sampling efficiency can differ based on species and environmental conditions (Gwinn, Beesley, Close, Gawne, & Davies, 2016; Mollenhauer, Logue, & Brewer, 2018), we examined how pool and riffle depths differed across sampling events to ensure sampling efficiency did not confound results. Because sampling only occurred during base-flow conditions, we found that mean pool and riffle depths were relatively constant at these sites (Figure S1) with mean depths typically within 0.1 m in pools and 0.05 m in riffles for most of the sampling events, never differing more than 0.5 m across sampling events. In addition, efficiency in sampling these fish communities is typically constant (Bertrand, Gido, & Guy, 2006), and given that mean depths varied only slightly across sampling events at a site, capture probabilities of small (<100 mm) fish likely did not differ through time (Dauwalter & Fisher, 2007). Because we standardized our sampling effort and habitats were relatively stable, we assumed that differences in capture probability associated with discharge at the time of sampling were minimal.

To reduce bias associated with different spawning times among species and highly variable abundances of young-of-the-year fish, small (TL < 40 mm) individuals were removed from the community

dataset. Long-term length data from these sites suggest that 40 mm is typical growth after the first summer/fall for most species in the system (K. Gido, unpublished data). To evaluate the fish community response to varying degrees of stream wetted habitat, the total fish abundance was compared with the mean riffle width for each sampling occasion. Mean riffle width within our study reaches was calculated from multiple transects along each riffle at a site; if multiple riffles were sampled, then the area-weighted width was computed. Riffle widths were used because they are the most stable habitat within a stream (Rosgen, 1996) and represent an index of the total wetted habitat and connectivity within the intermittent stream network adjacent to our stream reach. This was confirmed by the positive association between average discharge for each sampling, obtained from habitat transect data, and area-weighted riffle width (Figure S2). Because two sampling sites (North Fork and South Fork Kings Creek) did not include riffles, riffle widths from the nearby Kings Creek site were used as a substitute for stream water level at these sites. We believe this was appropriate given that sites close in proximity to one another have highly correlated changes in riffle widths (Figure S3).

2.2 | Long-term community data

Regression analysis was used to examine the relationship between fish community abundance and the wetted habitat (riffle widths). For sites in the Fox Creek watershed that experienced wet and extreme dry (area-weighted riffle width was zero) conditions over the 10-year sampling period, polynomial regression (quadratic) was used to test the hypothesized "hump-shaped" association between abundance and wetted habitat in perennial streams. For sites in the Kings Creek watershed, linear regression was used because these perennial streams did not experience extreme drying over the 16-year sampling period; thus, we expected a linear decline in abundance as wetted habitat increased. Two sampling events from one site in the Fox Creek watershed (Gashouse Creek) were removed from the regression analysis because fish were temporality extirpated after the site completely dried and they had yet to colonize after the stream rewetted. To assess how stream size influenced any potential relationships between fish abundance and wetted habitat, the effect size (adjusted R^2), calculated from the relationship between total fish abundance and riffle width, was related to $\log_{10}$ transformed watershed catchment area (km^2) for the six sites using linear regression.

If communities were determined to respond to temporal variation in water levels, individual species responses at each site were tested using a model-based approach employing simultaneous generalized linear models of multivariate data (ManyGLM) using the MVabund package (Wang, Naumann, Wright, Edelbuettel, & Warton, 2017) in the R statistical environment (R Core Team, 2018). This procedure fits a GLM to each species, and the log-likelihood ratios for each species are summed and then used as a test statistic via randomization (Warton, Foster, De'ath, Stoklosa, & Dunstan, 2015). Using the anova.ManyGLM procedure, univariate test statistics and accompanying p values, corrected for multiple

testing, were generated using a bootstrap approach with 999 iterations. Given the variable abundances of species across sites and through time, results from this analysis were examined at both the α levels of .10 and .05. Rare species (composition less than 1% at a site) were not examined for this analysis.

2.3 | Passive integrated transponder tagging experiment

To better understand the processes driving patterns of association between discharge and fish abundance, the dispersal of fishes from perennial habitats into recently wetted intermittent habitats was quantified with a tagging study. Individuals at the Kings Creek site were tagged with an 8-mm passive integrated transponder (PIT) tag following the procedures by Pennock, Frenette, Waters, and Gido (2016), and dispersal was monitored with stationary antennas. Three dominate species at this site (central stoneroller *Campostoma anomalum*, southern redbelly dace *Chrosomus erythrogaster*, and creek chub *Semotilus atromaculatus*) were implanted with tags in November of 2015 (88 total individuals: 30 central stoneroller, 29 southern redbelly dace, and 29 creek chub), 2016 (266 total individuals: 115 central stoneroller, 122 southern redbelly dace, and 29 creek chub), and 2018 (266 individuals: 124 central stoneroller, 131 southern redbelly dace, and 11 creek chub). To examine if tagged fishes moved either upstream into intermittent habitats or downstream into more perennial habitats, PIT antennas upstream (2.0 km) and downstream (0.53 km) of the sampled site (Figure 2) were deployed. The number of tagged fish that moved into the intermittent (upstream) or more perennial (downstream) reach was calculated during the dates in which the intermittent reaches were inundated with water and antennas were deployed (March 23 to June 24, 2016; March 31 to June 19, 2017; and March 10 to August 5, 2019; Figure 1). Pearson's chi-square test was used to evaluate if mobile individuals moved in different proportions towards intermittent or perennial reaches. Species and yearly differences were visualized by dividing the number of individuals that moved upstream (intermittent) or downstream (perennial) by the total number of individuals tagged in the previous year. To test if fishes "contracted" back to perennial reaches after intermittent reaches began to dry, we examined if fishes that were detected in the intermittent reach were recaptured during the long-term monitoring at the Kings Creek site.

3 | RESULTS

3.1 | Long-term community data

Fish abundances were highly variable within and across sites during the study period with no clear patterns of increasing or decreasing abundances over the duration of the study (Figure 3). When comparing fish abundance to stream mean riffle width, four sites, Kings Creek, $F(1, 47) = 3.87$, $p = .055$, $r^2 = .08$, Gashouse Creek, $F(1, 27) = 4.20$,
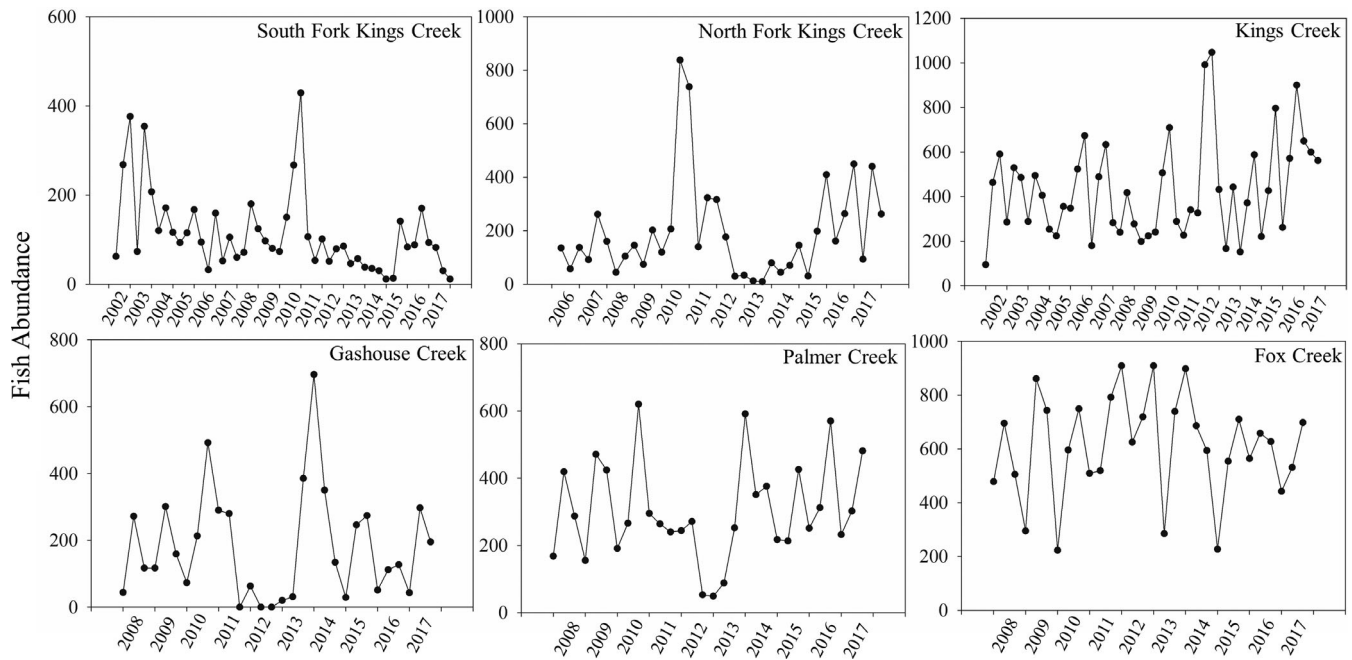
FIGURE 3 Total fish abundance (>40 mm) across six sites sampled in May, August, and November from 2002–2017 (Kings Creek and South Fork Kings Creek), 2006–2017 (North Fork Kings Creek), and 2008–2017 (Fox Creek, Palmer Creek, and Gashouse Creek) in Kansas, USA
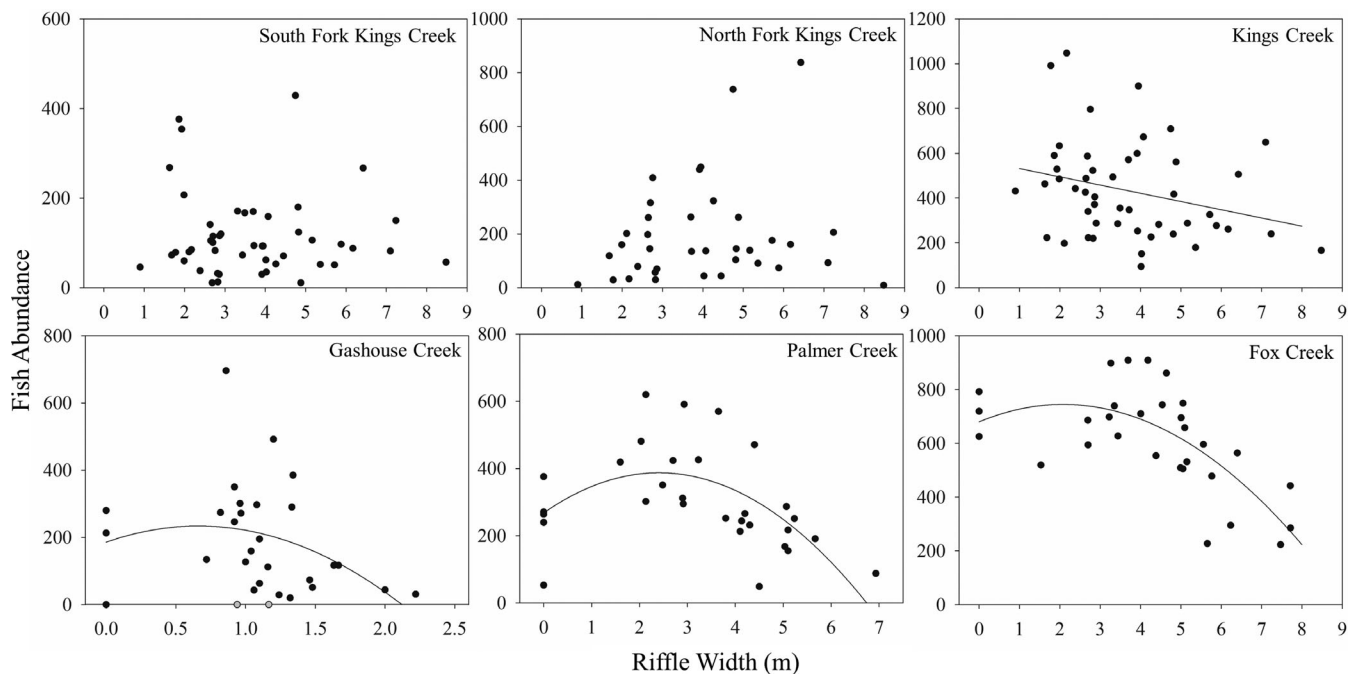

FIGURE 4 Total fish abundance (TL > 40 mm) and mean riffle width (stream water level) across six sites in Kansas, USA. Sites were sampled in May, August, and November from 2002–2017 (Kings Creek and South Fork Kings Creek), 2006–2017 (North Fork Kings Creek), and 2008–2017 (Fox Creek, Palmer Creek, and Gashouse Creek). Grey dots in Gashouse Creek plot represent drought years when fish abundance was zero and thus were not included in regression analysis. Riffle habitat did not occur at North or South Fork Kings Creek, so Kings Creek width was substituted

$p = .045$, $R^2 = .13$, Palmer Creek, $F(1, 29) = 7.77$, $p = .010$, $R^2 = .37$, and Fox Creek, $F(1, 29) = 12.55$, $p < .001$, $R^2 = .48$, matched the predictions and showed significant or marginally significant relationship of

decreasing fish abundances with increasing wetted habitat (Figure 4). The two smallest streams, South Fork Kings Creek $F(1, 47) = 0.02$, $p = .686$, $r^2 = .00$, and North Fork Kings Creek, $F(1, 35) = 0.91$, $p = .347$,
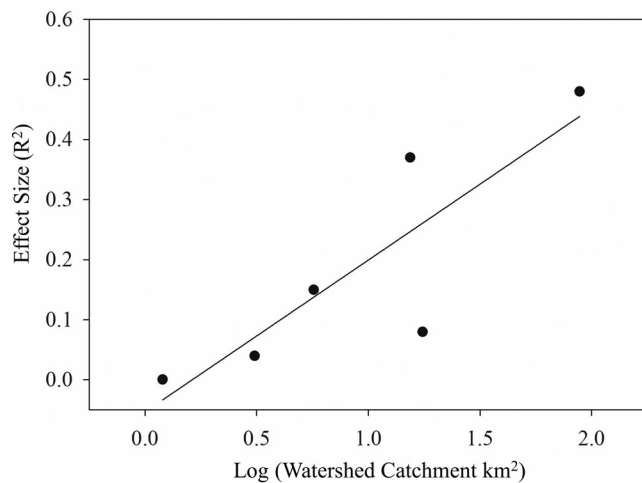
FIGURE 5 Relationship between the effect size (R^2) and $\log_{10}$ transformed watershed catchment (km^2) from six sites in Kansas, USA. Effect size was calculated from the relationship between total fish abundance and stream water level (see Figure 4)

r^2 = .03, did not show a relationship between fish abundance and wetted habitat. Consistent with our predictions, larger, more downstream sites were found to show stronger patterns of fish community expansion and contraction (Figure 5), $F(1, 5)$ = 10.73, p = .031, r^2 = .73.

Individual species responses to fluctuating water levels were variable (Table 1). Of the 16 species analysed, six showed a response to differences in wetted habitat. All six species matched the community response of higher abundances when conditions were dry and lower when wet, whereas no species yielded significant results of the opposite response. The central stoneroller was the only species to show a significant response of higher abundances when conditions were dry and lower abundances when they were wet across multiple sites, whereas the remaining five species showed a response at only one site. Further, only sites in the Fox Creek watershed showed significant species responses with Fox and Gashouse Creek each having three species responding (change in abundance) to differences in wetted habitat, whereas Palmer Creek only had one species responding.

3.2 | PIT-tagging experiment

In the PIT tag experiment, a greater proportion of tagged individuals were found moving upstream into the intermittent reach (25.0%) than downstream within the perennial reach (4.7%; χ^2 = 86.3, p < .001), and this upstream bias in movement was observed for all three fish species (Figure 6). Of the 155 individuals that dispersed upstream (i.e., detected at the upstream antenna) during these wet periods, 17 individuals (11%) were recaptured or detected back downstream at the Kings Creek site (Figure 2) after the intermittent reach had dried.

4 | DISCUSSION

Prairie stream fish communities generally (four of the six sites) responded to varying stream water levels by having lower abundances when conditions were wet and higher abundances when conditions were dry (Figure 4). We predicted this response to be partially driven by the dispersal of individuals away from perennial reaches and into intermittent reaches when conditions were wet and the dispersal back to perennial reaches with the highest abundances at a site (transitional state) occurring when intermittent reaches began to dry. Although fish might move laterally into off-channel habitats during wet periods (Ross & Baker, 1983), dispersal in intermittent stream networks is likely longitudinal (e.g., upstream or downstream) because of the small size of these streams and limited off-channel habitats. In addition to abundance data from long-term fish community monitoring matching our predictions, the community response was tested by tagging individual fish and reencountering fish in intermittent reaches once conditions became wet and back in perennial reaches when conditions were dry. It is important to note that estimates on the proportion of fish dispersing into intermittent reaches and back down to perennial reaches are likely quite conservative given detection probabilities are imperfect for PIT antennas and the antennas only occupied a small proportion of intermittent stream habitat. Thus, the tagging study contributed to the prediction of fish expansion and contraction but underestimates the actual proportions of fish exhibiting this behaviour.

The pattern of organismal expansion and contraction of abundance following fluctuations between wet and dry conditions, as examined for these fish communities, has been observed for several other terrestrial and aquatic communities (Boulton, 2003; Knapp & Smith, 2001; Redfern, Grant, Biggs, & Getz, 2003; Stanley et al., 1997). The main drivers of this expansion–contraction behaviour are typically related to dispersal associated with resource availability or spawning habitat. The importance of dispersal into intermittent reaches has been largely speculative because of the difficulty in studying these systems (Datry et al., 2014). One possible explanation is that dispersal away from areas of high concentrations of individuals may relieve potential density dependent factors (Grossman, Ratajczak, Crawford, & Freeman, 1998; Pennock & Gido, 2017). Other uses of intermittent habitats might be for spawning behaviours or finding habitats more suitable for juvenile growth and survival (Labbe & Fausch, 2000). Additionally, intermittent reaches could be used as important stepping stones between two distant perennial reaches and play important roles in metapopulation dynamics. Collectively, these results suggest that fish frequently use intermittent stream habitats, yet the benefit of intermittent reaches to stream fish growth and survival still requires more research.

Although the predictions were tested with both long-term fish community sampling and the movement of tagged fish as conditions became wet in these intermittent systems, the ability to obtain reliable estimates of the amount of fish that return to perennial reaches from intermittent reaches as the stream began to dry was lacking. A main limitation in detecting returning fish was the inability to maintain

TABLE 1 Analysis of deviance table generated from ManyGLM procedure testing individual species response to varying levels of wetted habitat at Fox Creek (FC), Gashouse Creek (GC), Palmer Creek (PC), and Kings Creek (KC) in Kansas, USA

Species	Site	Deviance	p value	Composition (%)
Central stoneroller *Campostoma anomalum*	FC	14.13	.076*	26.6
	GC	4.89	.200	75.9
	PC	15.84	.007**	49.6
	KC	5.38	.123	28.8
Orangethroat darter *Etheostoma spectabile*	FC	14.73	.063*	13.0
	GC	3.36	.308	6.1
	PC	4.67	.345	9.0
	KC	0.00	.958	16.0
Green sunfish *Lepomis cyanellus*	FC	2.72	.788	3.3
	GC	16.02	.003**	4.6
	PC	0.38	.782	22.8
Cardinal shiner *Luxilus cardinalis*	FC	6.20	.516	14.2
	GC	2.27	.308	6.8
	PC	7.07	.234	9.3
Creek chub *Semotilus atromaculatus*	GC	11.38	.016**	4.0
	PC	7.26	.234	1.3
	KC	1.89	.558	10.2
Bluntnose minnow *Pimephales notatus*	FC	4.70	.646	9.9
	GC	10.71	.025**	1.2
Longear sunfish *Lepomis megalotis*	FC	4.81	.646	5.6
	PC	5.32	.345	2.1
Orangespotted sunfish *Lepomis humilis*	FC	6.58	.516	3.5
	PC	1.71	.646	1.6
Golden redhorse *Moxostoma erythrurum*	FC	18.72	.022**	2.8
	PC	2.59	.613	1.0
Redfin shiner *Lythurus umbratilis*	FC	1.34	.788	7.8
Red shiner *Cyprinella lutrensis*	FC	2.67	.788	6.1
Bluegill *Lepomis macrochirus*	FC	11.32	.140	1.0
Brook silverside *Labidesthes sicculus*	FC	8.65	.295	1.5
Sand shiner *Notropis stramineus*	FC	3.37	.788	1.0
Southern redbelly dace *Chrosomus erythrogaster*	KC	0.26	.873	43.1
White sucker *Catostomus commersonii*	KC	1.52	.558	1.1

Note: Percent composition refers to each species relative abundance at a site, and species with a composition of less than 1% were not tested.
*Significant results at an α = .10.
**Significant results at an α = .05.

year-around PIT antenna arrays in the perennial reach. Thus, the proportion of fish that disperse back to the same stream reach, disperse to distant stream reaches, or that die due to intermittent reaches drying is unknown. Mark and recapture studies though have been conducted on these species (Belica & Rahel, 2008; Walker, Adams, & Adams, 2013) and provide information on species-specific behaviours and potential estimates of movement into different stream reaches. But tracking individual fish movements back to perennial reaches from intermittent reaches could provide insight into the benefits of intermittent reaches to stream fish growth and survival. Lastly, quantifying the number of fish that move to intermittent reaches and die could contribute to the understanding of the risks associated with

movement and the potential subsidies stream fish contribute to terrestrial systems (Gende, Edwards, Willson, & Wipfli, 2002), which likely occurs because PIT tags from previously tagged individuals have been found in dried reaches in the Kings Creek watershed (G. W. Hopper, Kansas State University, personal communication).

The spatial relationship observed across these sites showed that upstream, smaller sites did not fit the expansion and contractions predictions (Figure 5), suggesting that upstream sites have limited dispersal opportunities compared with downstream sites. This supports previous work by Schlosser (1982) that showed greater temporal variation in habitat diversity and habitat volume at upstream headwater sites and suggested that reproductive success is an important driver
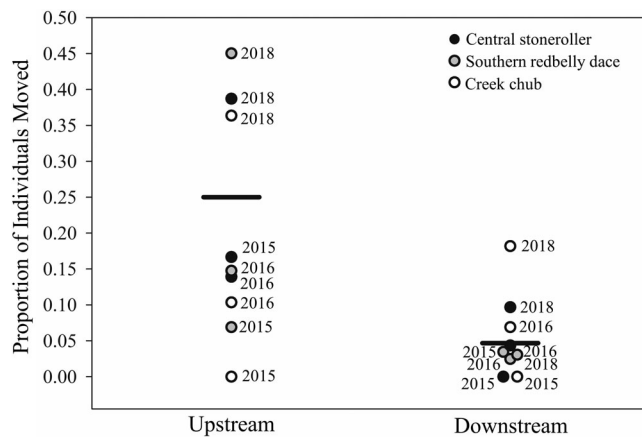
FIGURE 6 Proportion of tagged fish in Kings Creek, Kansas, USA, that were detected upstream in an intermittent reach or downstream in more perennial reaches. Fish were tagged in November of 2015, 2016, and 2018 and detected in the following year. Dots represent each species and the year in which individuals were tagged. Black bar represents the total proportion of fish moving upstream or downstream

of headwater fish community abundances. If upstream reaches are more isolated, they are more likely structured by local influences compared with more downstream reaches that are structured by both local and regional processes (Brown & Swan, 2010). Given that metapopulation and metacommunity dynamics vary spatially, a species desire or opportunity to disperse will vary between upstream and downstream sites (Falke & Fausch, 2010). Lastly, not only may dispersal be limited at upstream sites, the number of species occupying these reaches, compared with downstream reaches, is 2–3 times lower in these systems (Whitney et al., 2016), potentially leading to these weaker relationships.

Along with the observed spatial differences with fish community abundance and stream water level, individual species responses to drying stream conditions were variable. Differences in response to drying conditions likely varied depending on species life history strategies, habitat requirements, dispersal abilities, and spatial variation in stream reach conditions. Six species showed significant responses to differences in wetted habitat, with all of them matching the community response. Central stoneroller was the only species to show a pattern across multiple sites. Central stonerollers are one of the most common species in upland streams (Jenkins & Burkhead, 1994; Pflieger, Sullivan, & Taylor, 1975), and their success is potentially contributed to a life history strategy and behaviour in which the species uses harsh, variable habitats. Of the remaining five species that showed a similar response, all five had a significant response at one of the sites (Table 1), and it is likely that spatial factors are potentially driving this pattern. For instance, species responding to water levels that are more abundant in downstream perennial habitats might exhibit different patterns if expansion and contraction are driven by conditions and populations further downstream.

Fish communities disperse into intermittent reaches as they become inundated, and fluctuations in abundance are partly due to

dispersal, in addition to mortality and recruitment. Currently, fish inhabiting intermittent stream networks are threatened by several modifications to these systems (Ligon, Dietrich, & Trush, 1995; Graf, 1999; Perkin, Troia, Shaw, Gerken, & Gido 2016). Major threats include the construction of impoundments and impassable road crossings that both reduce access to upstream reaches and alteration of those habitats. Restricting access into intermittent habitats disrupts the life history of many stream fish and leads to declines in species richness and densities (Hedden, Renner, Gido, & Hase, 2018). Also, negative impacts occurring in headwater intermittent streams are not only a local issue, as alterations in headwater streams can have broad, cascading ecological influences (Freeman, Pringle, & Jackson, 2007). Thus, measures are needed to protect intermittent streams and ensure fish have access to these reaches as they become inundated (Colvin et al., 2019). Understanding how aquatic organisms respond to varying water levels will become even more important as demand for water supply continues to increase worldwide (Gleick, 2018). Intermittent streams are model systems towards understanding how communities respond to varying degrees of water availability and as demand for water increases, how organisms will be forced to adapt to changing systems. Another consequence of increased water demand is that perennial stream networks will become more intermittent (Perkin et al., 2017). Thus, understanding the response of organisms adapted to intermittent streams can help predict future responses of species and communities in other systems.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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