A perched culvert and natural obstructions limit fish dispersal in an intermittent prairie stream

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Abstract: Poorly constructed road crossings block upstream movement of fish into stream reaches that provide critical habitat or connect isolated populations. Although removing these barriers is often a conservation priority, quantifying fish passage following removal has not been well studied, particularly in intermittent streams. In this study, we sought to understand how barriers influence the dispersal of fishes in intermittent prairie streams. We used passive integrated transponder tags and antenna stations to quantify fish movement of 3 prairie-stream fishes (Central Stoneroller *Campostoma anomalum* [Rafinesque, 1820], Southern Redbelly Dace *Chrosomus erythrogaster* [Rafinesque, 1820], and Creek Chub *Semotilis atromaculatus* [Mitchill, 1818]) through a road crossing in an intermittent prairie stream for 3 y before and 3 y after removing a perched culvert. We verified that no upstream fish movement occurred through the culvert, despite large aggregations of tagged fish in the intermittent reach below the culvert. In contrast, tagged individuals of all 3 species were detected above the road crossing in each of the 3 y following removal. We also tracked the recovery of these species, plus the Orangethroat Darter *Etheostoma spectabile* (Agassiz, 1854), following a severe drought in 2018 in 2 spring-fed tributary reaches, 1 without a downstream barrier and 1 with the removed downstream culvert. Surveys of the tributary reaches showed rapid recovery of fish densities following drought in the tributary without a downstream barrier. However, recovery at the site above the removed culvert appeared to be limited by a natural waterfall. Our observations suggest barrier removal allowed access to spawning habitat within the intermittent reach immediately upstream of the site, but other obstacles or shear distance to perennial spring-fed tributary reaches also limited recolonization following severe drought. Increased connectivity between perennial and intermittent reaches in prairie streams likely benefits fishes by increasing their resilience following disturbance and providing habitat during critical life stages.
Key words: stream restoration, road crossing, fragmentation, PIT tag, movement, fish passage, stream connectivity, drought, resilience

Barriers that fragment streams have profound consequences for both demographic and genetic viability of fish populations (Fagan 2002, Gido et al. 2016). Streams intersected by road crossings that either completely or partially block fish passage are of particular concern because they are ubiquitous on the landscape (Warren and Pardew 1998, Perkin and Gido 2012, Januchowski-Hartley et al. 2013). In many cases, steel or concrete culverts with undersized openings cause accumulation of bed materials upstream of the road crossing and down-cutting on the downstream side of the crossing, resulting in perched culverts with a waterfall (e.g., Fig. 1A, B). The permeability, or period of time in which

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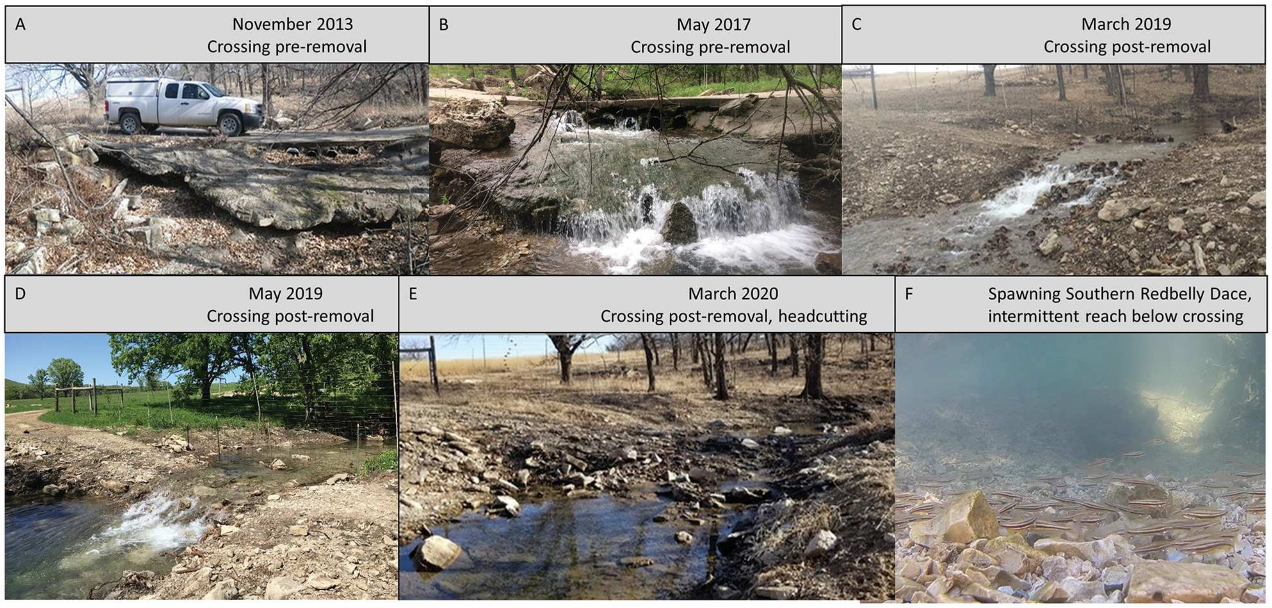

Figure 1. Time series of perched culverts at a road crossing on Kings Creek, Kansas, USA, before removal (A, B), soon after removal but before headcutting (C, D), and 15 mo after removal following headcutting (E). Spawning Southern Redbelly Dace in June 2020 are shown in the intermittent reach downstream of the road crossing depicted in panels A through E (F). Photo credit: KBG.

those culverts allow fish passage, depends on the hydrology of the stream as well as the behavior and jumping ability of fish (Bouska and Paukert 2009, Norman et al. 2009, Ficke et al. 2011, Perkin and Gido 2012, Schumann et al. 2019). Perched culverts typically occur in small to medium-sized streams because larger streams have bridges that span the channel, allowing bed material to move freely below the bridge (Perkin and Gido 2012). Although fragmentation of streams is well studied and there are many conservation projects that focus on facilitating fish passage (e.g., McKay et al. 2017), data on fish dispersal before and after barrier removal or construction of fish-passage channels are less common. Studies in perennial streams that evaluated connectivity of fish populations before and after culvert removal suggest restoration efforts can be successful (Evans et al. 2015, Wood et al. 2018), but little is known about fragmentation effects of perched culverts in intermittent streams, which provide important temporary habitats for fishes (Labbe and Fausch 2000, Hooley-Underwood et al. 2019, Hedden and Gido 2020) and many other ecosystem services (Colvin et al. 2019, Stubbington et al. 2020). Because the legal protections for intermittent headwater streams in the United States have oscillated over the past 2 decades along with shifts in political ideologies, more research on the importance of these ecosystems is necessary to inform conservation decisions.

Intermittent prairie streams provide essential habitat to fishes and can act as movement corridors to perennial upstream habitats (Labbe and Fausch 2000, Franssen et al. 2006, Kerezsy et al. 2017). Some networks have intermittent headwaters with perennial reaches downstream, whereas others have intermittent middle reaches that connect perennial habitats upstream, such as headwater springs (Datry et al. 2017). High rates of local extirpation throughout many small stream networks are driven by drought (Magoulick 2000, Whitney et al. 2016, Hopper et al. 2020), and fish assemblage resilience to drought is dependent on connectivity through intermittent reaches (Magoulick and Kobza 2003, Hedden and Gido 2022). Thus, dispersal is necessary to access important intermittent habitats and connect isolated populations (Hodges and Magoulick 2011). In prairie streams, fish commonly disperse into intermittent reaches, particularly during spring and summer when they are in spawning condition (Hedden and Gido 2020). Perkin and Gido (2012) found reduced fish diversity in prairie stream reaches above perched culverts relative to connected reaches and noted species-specific responses to fragmentation. Rosenthal (2007) documented that movement of the Longnose Dace *Rhinichthys cataractae* (Valenciennes in Cuvier and Valenciennes, 1842) was restricted by culverts in prairie streams, but movement of 3 other species was not restricted. Regardless of the presumed importance of intermittent stream habitats, the consequences of blocking access to these habitats are not well understood.

In this paper, we present results from a 6-y experiment that quantified stream fish dispersal and abundance before and after removal of a perched culvert (Fig. 1A–E) from an intermittent stream reach of Kings Creek on the Konza Prairie Biological Station in Kansas, USA. Observations from Kings Creek suggest large numbers of individuals and multiple fish species use loose and clean substrates to spawn in intermittent reaches (Fig. 1F; KBG, personal observation). Spawning in these intermittent reaches presumably confers benefits to offspring through increased resource availability (Labbe and Fausch 2000, Kerezsy et al. 2017). The Kings Creek stream network has middle reaches with intermittent flow separating perennial spring headwaters from a perennial downstream reach (Fig. 2B). A previous study in this system using visual implant elastomer tags reported summer aggregation of fishes below this culvert (Franssen et al. 2006), suggesting the road crossing limited upstream dispersal.

Our main objective was to understand how barriers influence the dispersal of fishes in intermittent prairie streams. We asked: did fish density increase above the road crossing following culvert removal? A secondary objective was to see if removing a barrier from an intermittent reach would allow fish to colonize perennial spring habitats above the barrier. To address this objective, we tested if fish assemblages changed in a perennial headwater reach above the culvert-removal site relative to a site with no downstream culvert. Collectively, these experiments provide critical information regarding the importance of connectivity through understudied intermittent stream systems.

METHODS

To answer our research questions, we first conducted a field study to quantify changes in dispersal of 3 common fish species in response to the culvert removal. We tested if the detection of passive integrated transponder (PIT)-tagged individuals from the perennial downstream reach increased at a stationary antenna above the road crossing following removal. Second, we used long-term fish assemblage sampling data to compare fish densities in 2 perennial headwater reaches: 1 above the road crossing and a control, after removal of the perched culvert. A severe drought that occurred the same year as the culvert removal completely dried both perennial springs, resulting in total mortality of fishes in these tributaries (KBG, personal observation), and the downstream perennial reach served as the only potential source of colonists. Thus, we were able to follow recolonization of the tributary reaches for 3 y following drought, with the expectation that after the end of drought-related drying, when connectivity to the downstream perennial reach was reestablished, the fish assemblages in both reaches would be similarly rescued by recolonization. Alternatively, because of a natural waterfall between the road crossing and the long-term study site (Fig. 2B, C), we might expect limited recolonization, regardless of the culvert removal.

Study area

Kings Creek drains 35 km^2 of native tallgrass prairie on the Konza Prairie Biological Station in the Flint Hills region of Kansas (Fig. 2A). Grasses and shrubs dominate the landcover in the basin and are maintained through grazing by American Bison (*Bison bison*) and fire management. Most stream reaches contain a forest buffer, with minimal row-crop agriculture in lower reaches of the catchment. Streamflow, monitored at a United States Geological Survey gauging station (no. 06879650; 0.75 km downstream of the culvert removal site) during the 6 y of this study, was highly variable (Fig. 3). Discharge at the gauging station was intermittent,

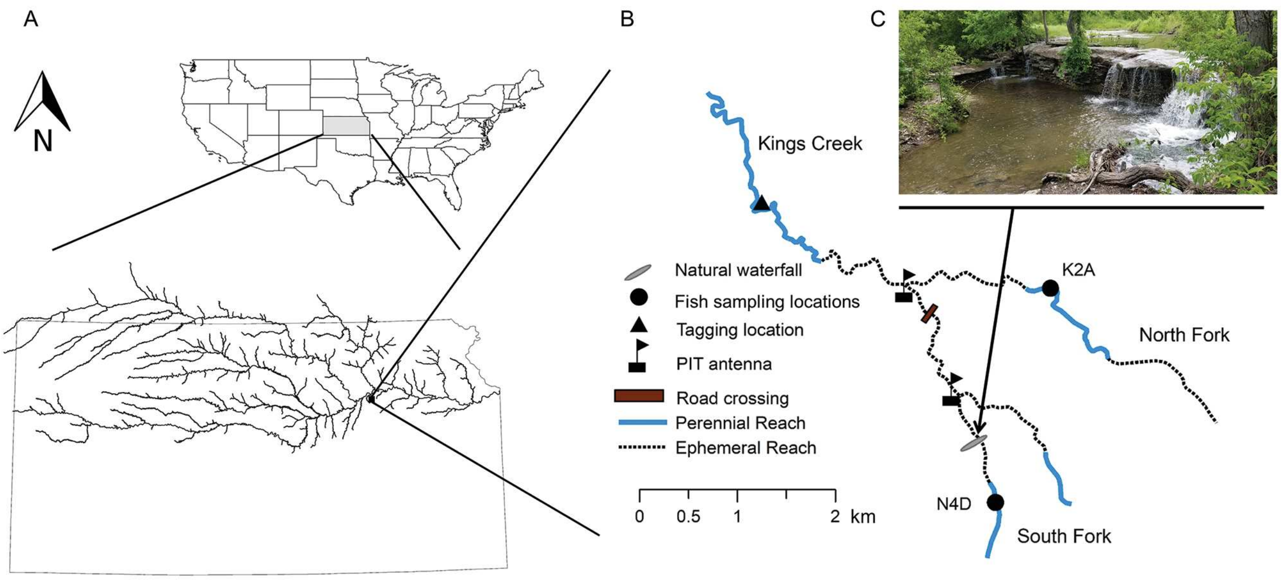

Figure 2. Location of Kings Creek, Kansas, USA, within the Kansas River basin represented by major streams and tributaries (A). Map of Kings Creek with the location of a culvert that was removed in November 2018, fish sampling locations, passive integrated transponder (PIT)-tagging location, stationary PIT-tag antenna locations, and a natural waterfall between the road crossing and N4D sampling location (B). The natural waterfall is a potential barrier to movement upstream (C). Photo credit: KBG.

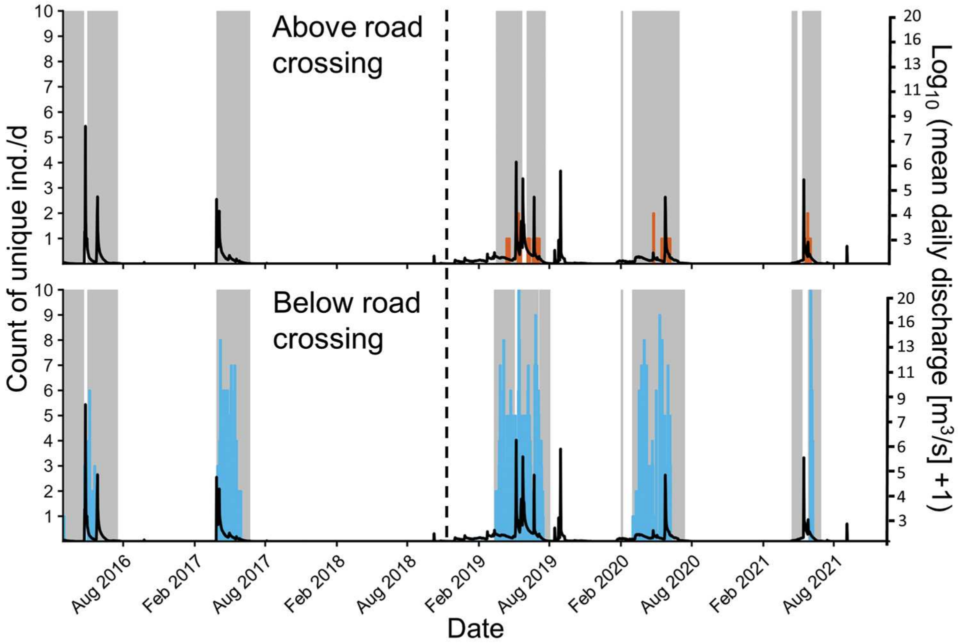

Figure 3. Hydrograph (black lines), dates of antenna deployment (gray shading), and detections at passive integrated transponder antennas located above (orange bars, top panel) and below (blue bars, bottom panel) the road crossing on Kings Creek, Kansas, USA. Dashed vertical lines represent when the barrier was removed. Discharge is the same in both panels and was obtained from United States Geological Survey gauging station #06879650 (0.75 km distance from the road crossing). Detections represent the number of individuals (species combined) with unique passive integrated transponder tags detected each day.

but the stream is perennial ~1.5 km downstream of the gauge as well as in various springs above the gauge. Discharge in Kings Creek varies annually but tends to peak during April, May, and June (Dodds et al. 2004). During mid- to late-summer (July–September), a lack of precipitation typically leads to drying of middle reaches, whereas downstream reaches continue to flow and upstream reaches become isolated pools fed by groundwater springs. Long-term reductions in discharge coupled with severe drought in 2018 resulted in complete stream drying throughout the catchment upstream of the perennial reach. During this year, middle reaches dried first, followed by headwater springs, and downstream reaches that historically flowed year-round dried or became isolated pools (Hopper et al. 2020).

The perched culvert road crossing was a cement structure with three ~30-cm-diameter corrugated-steel culvert tubes imbedded in concrete to pass water through the crossing structure (Fig. 1A, B). This structure included a concrete apron downstream of the crossing, presumably to reduce erosion of the stream bed. Scouring below the apron created an extensive drop of >1 m. On 30 November 2018, the cement structure and culverts were removed, and the channel was sculpted to create a road crossing over natural bed materials (Fig. 1C, D). In the 3 y following the removal of the culvert, several large floods resulted in headcutting into the streambed materials that accumulated over time above the road crossing (Fig. 1E), but there were no obvious restrictions to fish movement following culvert removal.

Changes in dispersal in response to culvert removal

To test if fish dispersal upstream of the road culvert changed following its removal, we tracked the occurrence of PIT-tagged fish at stationary antennas upstream and downstream of the road crossing for 3 y before and 3 y after culvert removal. The stationary antenna placed below this road crossing served as a control to compare differences in movement into the intermittent reach connected to the downstream perennial reach. Annually in November, from 2015 through 2020, we captured 3 fish species (Central Stoneroller *Campostoma anomalum* [Rafinesque, 1820], Southern Redbelly Dace *Chrosomus erythrogaster* [Rafinesque, 1820], and Creek Chub *Semotilis atromaculatus* [Mitchill, 1818]) at a fixed site in the perennial downstream reach of Kings Creek that was ~3.0 km downstream of the road crossing (Fig. 2B). We implanted individuals with 8-mm HPT8 MiniChip PIT tags (full duplex; BioMark®, Boise, Idaho) following the procedures of Pennock et al. (2016). We captured fish with a combination of backpack electrofishing and seining from 2 adjacent pools, tagged the fish, and released them back into capture pools within 30 min. Our goal was to tag ~100 individuals of each species annually, but numbers varied depending on abundance at the time of sampling. Although we detected tagged fish across multiple years, in any given year we only considered fish tagged in November of the previous year in our analysis to control for unknown mortality rates or tag loss across multiple years.

To quantify dispersal from the perennial reach into the intermittent reach below and above the road crossing, we used the 2 stationary PIT-tag antennas to track fish tagged in November the following spring and summer when flow resumed in those reaches (Fig. 2B). The amount of time antennas were active depended on discharge at each location (Fig. 3). We placed 1 antenna at the confluence of the north and south forks of Kings Creek, 0.52 km below the road crossing. We placed a 2nd antenna 1.25 km upstream of the road crossing, below the confluence of 2 tributary branches. Antennas were anchored to the substrate in pools and were either a 1.3×0.8-m rectangle or a 0.91-m diameter hoop. Detections were primarily based on fish passing over the antennas. Rectangular antennas were connected to a BioMark RM310 reader powered by a 12V battery connected to a solar panel, whereas hoop (submersible) antennas were connected to a BioMark IS1001 reader powered by a 12V battery pack. Read ranges, checked at least monthly, ranged from 5 to 20 cm.

Because of the dynamic hydrology, the stationary antennas did not always function or did not span the entire stream, thus detection of fish moving into or upstream of reaches with antennas was not assumed to be perfect. Moreover, we did not estimate mortality of tagged fish between tagging and detection on PIT antennas the following spring and summer. Reported fish detections at these antennas are, therefore, likely underestimates of the proportions of PIT-tagged fish released in the downstream reach that were moving into or through reaches with PIT antennas. To partially address this issue, we fit a Cormack–Jolly–Seber model to estimate detection probability of the antennas and apparent success of upstream movement (Appendix S1). For the statistical analyses described below, we assumed detections at these antennas reflected the timing of dispersal for each species as well as the relative densities of tagged fish, inferred by the number of detections upstream and downstream of the barrier.

Data analysis: Fish dispersal following culvert removal
To evaluate changes in the number of PIT-tagged fish detected above and below the road crossing before and after culvert removal, we used multivariate generalized linear models (GLM) assuming a negative binomial distribution with individual counts of each species detected at the PIT antennas as the dependent variable. Because we ran tests for multiple species, we used a manyGLM approach to fit individual GLMs with the same set of predictor variables for each species while adjusting p-values for multiple tests with the Holms step-down procedure (Wang et al. 2012). Likelihood ratios (LR) of each model were summed together (i.e., sum of LR) and used to perform an assemblage-level test with p-values estimated with resampling. We then obtained p-values of individual species GLMs with permutation-based analysis of variance (permutations = 9999). We estimated individual species contributions to the overall assemblage-level effect by dividing the LR of species-specific models by the sum of LR, which estimates individual species contributions to the overall assemblage-level effect for variables and interaction terms that were important for explaining variation in fish detections at the $\alpha = 0.05$ level. We included an additive effect of the number of fish tagged the previous year for each species to account for tagging effort. We also included the additive and interactive effects of location (above or below the road crossing) and time (before or after culvert removal). We ran the models in the *mvabund* package (version 4.1.3; Wang et al. 2020) in R (version 4.1.2; R Project for Statistical Computing, Vienna, Austria).

Tributary fish assemblage response to culvert removal

To evaluate if the culvert removal influenced upstream fish assemblage structure, we compared fish densities at 2 spring-fed tributary sites that are part of a long-term monitoring program, with annual and seasonal sampling occurring between 2008 and 2021; however, we only used data from 2016 through 2021 to have the same number of samples before and after barrier removal. The treatment site was upstream of the road crossing (N4D) on the south fork of Kings Creek, and the other site was located on the north fork of Kings Creek (K2A) without a barrier impeding access to fishes downstream (Fig. 2B). The long-term fish assemblage sampling at K2A was used as a control because this tributary reach was not blocked by a barrier but also had an intermittent reach separating this site from the downstream perennial reach. It is important to note that a natural waterfall occurs between the road crossing and N4D (Fig. 2B, C), with a previously unknown influence on colonization because of the perched culvert downstream.

We used a single pass with a backpack electrofisher and 2 netters to sample the fish assemblage in pools. We recorded area sampled to account for differences in sampling effort over time and between sample sites. The same pools within these sites were sampled annually in May, August, and November. All fishes were identified, counted, and measured on site and released, but we focused on the 3 species included in the tagging study plus the Orangethroat Darter *Etheostoma spectabile* (Agassiz, 1854), which were generally too small to PIT tag but were abundant in the system. Other species were rarely observed at these sites.

Data analysis: Tributary site fish assemblages To test if species abundances increased at the upstream, spring-fed tributary sites following culvert removal, we used a manyGLM model, as described above, with counts of individuals of each species captured during long-term sampling at treatment and control sites as the dependent variable. We included an additive effect of the area of habitat sampled to account for differences in sampling effort across years and plotted data as densities (no. of fish/m^2 + 0.01) to control for sampling effort. We also included additive and interactive effects of site (control or treatment) and time (before or after barrier removal).

RESULTS

Changes in dispersal in response to culvert removal

During spring and summer periods with flow, all 3 species of tagged fishes moved into the intermittent reach below the barrier with a proportion of these fish moving into the upstream reach following culvert removal. Prior to the removal of the perched culvert in 2016 and 2017, no fish were detected at the antenna above the road crossing, whereas individuals of all 3 species were detected below the road crossing (Table 1). Following the barrier removal, all 3 species were detected above the road crossing, albeit the total number of individuals detected was still 9× higher below than above the road crossing ($LR_{1,6} = 19.28$, $p = 0.04$; Table 2, Fig. 3). Greater differences in detections before and after culvert removal at the PIT antenna above the road crossing, in contrast with those differences at the antenna below the crossing, contributed to the weak interactive effect of location and time in our statistical model ($LR_{1,5} = 8.01$, $p = 0.07$) (Fig. 4A–H). All 3 species were detected above the road crossing in 2019 and 2021, but only Southern Redbelly Dace were detected above the crossing in 2020. Notably, however, only 3 Creek Chub were tagged in November 2019, which were also not detected below the crossing in 2020 (Table 1). Variation in detections over time were largely attributed to Southern Redbelly Dace, which increased following barrier removal both above and below the road crossing. Both Southern Redbelly Dace ($LR_{1,5} = 8.73$, $p = 0.04$) and Central Stoneroller ($LR_{1,5} = 8.77$, $p = 0.04$) had more detections below compared with above the road crossing (Table 2).

The Cormack–Jolly–Seber model results confirmed that although our rate of fish detection likely underestimated the proportion of tagged fishes moving past our PIT antennas, our detection probability was sufficiently high to detect the effects of culvert removal. Cormack–Jolly–Seber models estimated detection probability of antennas to be 0.63 (95% CI = 0.40–0.81) for all species combined (Table S1). Apparent success of upstream movement from the tagging location to the reach below the road crossing was similar before (0.27; 95% CI = 0.17–0.39) and after culvert removal (0.37; 95% CI = 0.25–0.50). Estimated success of movement above the road crossing was 0.12 (95% CI = 0.07–0.18) following culvert removal and virtually 0 before removal.

Table 1. Number of fish detected (% of number tagged in parentheses) at passive integrated transponder antennas below and above the road crossing for years before (2016–2018) and years after (2019–2021) culvert removal. The number of tagged fish represented those tagged in November the previous year (e.g., 30 Central Stoneroller were tagged in November 2015, but detections of those fish occurred in 2016). No fish were detected in 2018 (indicated by –) because of drought that resulted in no flow at sites below or above the road crossing.

			Antenna location	
Species	Year	No. tagged	No. below (% of tagged)	No. above (% of tagged)
Central Stoneroller	2016	30	5 (16.7)	0
	2017	148	20 (13.5)	0
	2018	76	–	–
	2019	124	47 (37.9)	4 (3.2)
	2020	158	19 (12.0)	0
	2021	62	3 (4.8)	1 (1.6)
Creek Chub	2016	29	0	0
	2017	63	3 (4.8)	0
	2018	43	–	–
	2019	11	4 (36.3)	2 (18.2)
	2020	3	0	0
	2021	45	2 (4.4)	1 (2.2)
Southern Redbelly Dace	2016	29	2 (6.9)	0
	2017	223	23 (10.3)	0
	2018	90	–	–
	2019	131	59 (45.0)	4 (3.1)
	2020	123	39 (31.7)	4 (3.3)
	2021	56	8 (14.3)	1 (1.8)

Table 2. Model output from manyGLM models assessing fish counts as a function of number tagged, location (above or below the road crossing), time (before or after culvert removal), and the interactive effect of location and time. *P*-values for individual species models were corrected for multiple testing by the Holms step-down procedure. LR = likelihood ratio, % sum of LR estimates individual species contributions to the overall assemblage-level effect for variables and interaction terms that were important for explaining variation in fish abundances at the $\alpha = 0.05$ level, – indicates not applicable.

Species	Term	LR	p	% sum of LR
Assemblage	No. tagged	3.14	0.40	–
	Location	19.24	0.02	–
	Time	19.28	0.04	–
	Location × Time	8.01	0.07	–
Central Stoneroller	No. tagged	0.95	0.54	–
	Location	8.77	0.04	46
	Time	3.48	0.29	–
	Location × Time	2.54	0.25	–
Creek Chub	No. tagged	0.62	0.55	–
	Location	1.74	0.24	–
	Time	2.17	0.29	–
	Location × Time	1.87	0.25	–
Southern Redbelly Dace	No. tagged	1.58	0.45	–
	Location	8.73	0.04	45
	Time	13.63	0.03	71
	Location × Time	3.60	0.17	–

Tributary fish assemblage response to culvert removal

Long-term assemblage monitoring showed that fish densities were more resilient to drought at K2A without a barrier downstream than N4D above the road crossing and natural waterfall (Fig. 5A–J). Assemblages at both sites had an apparent 100% mortality rate in August 2018 when these sites dried completely, and the only source of recolonization was from downstream. Densities of all 4 species rebounded at K2A in 2019 and reached pre-2018 values by 2020. In contrast, densities at N4D failed to recover following the drought of 2018. The interactive effect of site and time on fish abundance ($LR_{1,29} = 59.81$, $p = 0.02$; Table 3) was driven mainly by Southern Redbelly Dace, Orangethroat Darter, and Central Stoneroller (all $p = 0.02$; Table 3). The only fish captured at N4D following the drought was a single Creek Chub caught in August and November 2020, which was most likely the same individual.

DISCUSSION

This study sought to understand how barriers influence the dispersal of fishes in intermittent prairie streams. The large proportion of fish moving from downstream perennial reaches into our intermittent study reach during periods of flow illustrates the potential importance of these dynamic habitats for fish assemblages in prairie streams. Our results show that both human-engineered and natural barriers can limit access to intermittent reaches. Below, we discuss the evidence that barriers limit dispersal through intermittent reaches and the implications of barrier removal for conservation of prairie stream fishes.

Changes in dispersal in response to culvert removal

The perched culvert in the intermittent reach of Kings Creek was a barrier to fish movement, as indicated by the lack of PIT-tagged fish detected upstream of the crossing in 2016 and 2017 and detections of all 3 species at the upstream PIT-tag antenna after culvert removal in 2019 and 2021. Although movement of fishes into and through the intermittent reach above the road crossing was constrained by precipitation and subsequent flow events, we do not believe this obscured our interpretation that the culvert removal improved fish passage. Specifically, despite a lack of flow in this reach in 2018, there were opportunities for movement above the road crossing in 2016 and 2017 (Fig. 2A–C), and large numbers of fish were observed at our antenna just downstream of the road crossing. It is notable that the highest number of detections occurred in 2019, which was an exceptionally high flow year coinciding with culvert removal. Thus, movement of fish into intermittent reaches was likely foremost driven by hydrology, but the perched culvert blocked these potentially important dispersal events during years prior to its removal.

Of the 3 PIT-tagged species, there were no obvious differences in proportion of tagged fish detected or the timing of those detections in the intermittent reach. This finding indicates that regardless of individual species abundances

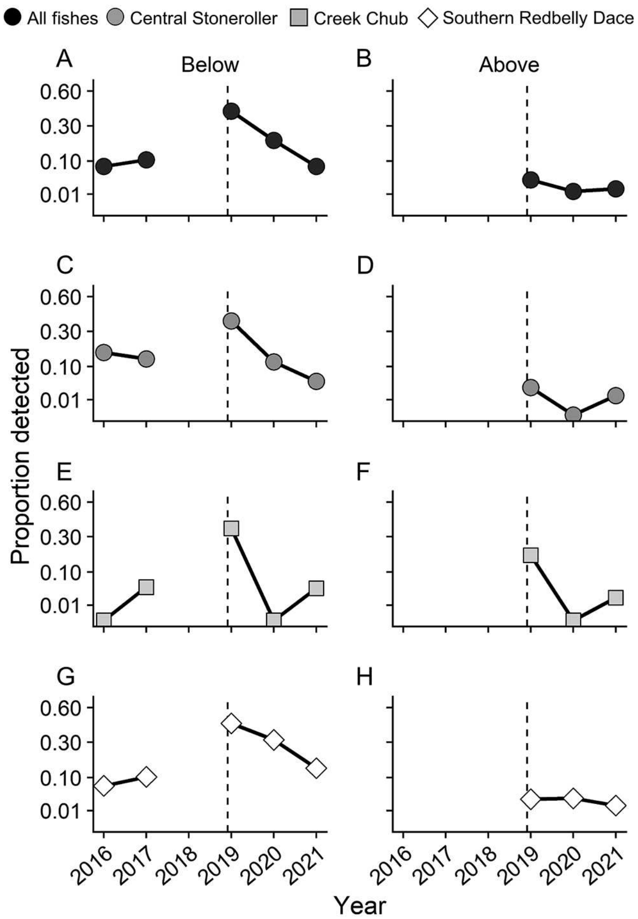

Figure 4. Proportion of individuals detected at passive integrated transponder antennas above and below the road crossing on Kings Creek, Kansas, USA, before (2016–2018) and after (2019–2021) perched culvert removal for all fishes (A, B), Central Stoneroller (C, D), Creek Chub (E, F), and Southern Redbelly Dace (G, H). No data were collected in 2018 because the stream reach was dry. Dashed vertical lines represent when the barrier was removed. Labels on the y-axes are on a square-root scale to better show small proportions.

in the downstream perennial stream, similar proportions of tagged fish moved into the intermittent reach below the road crossing when flow was available. For example, in the wettest year, 2019, the proportion of tagged fish at the antenna downstream of the road crossing ranged from 0.36 for Creek Chub to 0.45 for Southern Redbelly Dace (Fig. 4A). Although there was more variation among species in other years, there also were fewer detections, limiting our ability to draw inference from those interannual differences. Moreover, there were no obvious differences in the timing of occurrence across species (Fig. 3). These observations contrast other studies that reported interspecific differences in fish movement dynamics in response to stream drying (e.g., Albanese et al. 2004, Roberts and Angermeier 2007, Hodges and Magoulick 2011). However, because flow in the intermittent reach in Kings Creek typically occurs for only a few months, it seems reasonable that all species using these habitats are adapted to move synchronously during the initial flow event that wets the channel. This observation is consistent with Albanese et al. (2004), who found that upstream movement of tagged fish species was generally associated with flow increases. Continued monitoring of Kings Creek with larger sample sizes of tagged individuals might help quantify interspecific variation among migrating adults and their offspring into and out of these intermittent reaches.

Tributary fish assemblage response to culvert removal

The severe drought in 2018 coupled with long-term monitoring at both tributary sites provided a unique opportunity to test the importance of barriers to dispersal in intermittent reaches that connect perennial habitats. This drought caused both tributary sites to dry in August for the first time in >25 y of observations, with water returning by November 2018. Despite our success in improving fish passage to reaches immediately above the crossing, these efforts did not facilitate recovery of the fish assemblage at the tributary site (N4D), other than a single Creek Chub that arrived in 2020.

It was only through the culvert removal that we were able to evaluate the role of the natural waterfall as a barrier to fish dispersal into N4D. The lack of recolonization after culvert removal indicates that factors other than the perched culvert limited dispersal of fishes into N4D and that this site was likely more isolated and possibly had lower resilience following drought prior to the construction of the road crossing. The natural waterfall that drops ~1 m over a limestone formation (Fig. 2C) 1 km downstream of N4D was the most likely impediment to upstream dispersal. This structure is passable at high flows when water flows around the structure but might limit dispersal during base flows, minimizing the time at which passage can occur. In contrast, recovery at K2A occurred through fish dispersal from the downstream perennial reach, which could be attributable to several differences between the tributary sites. In addition to not having a similar barrier to dispersal, K2A also is closer (<2.0 km) than N4D (3.0 km) to the downstream perennial reach where source populations of fishes occur (Fig. 2B). K2A also has a larger wetted area and deeper pools than N4D. Finally, there is a tributary branch on the south fork of Kings Creek below N4D providing an alternate path for dispersal. Collectively, there were factors other than the perched culvert limiting recolonization of the headwater spring above the road crossing that appear to inhibit recovery of the fish assemblage following drought.

Broader implications

Why is it important to restore fish passage in intermittent streams? Many Great Plains fish species are known to quickly colonize and use intermittent reaches for spawning (Falke et al. 2012) and restoring flow to intermittent

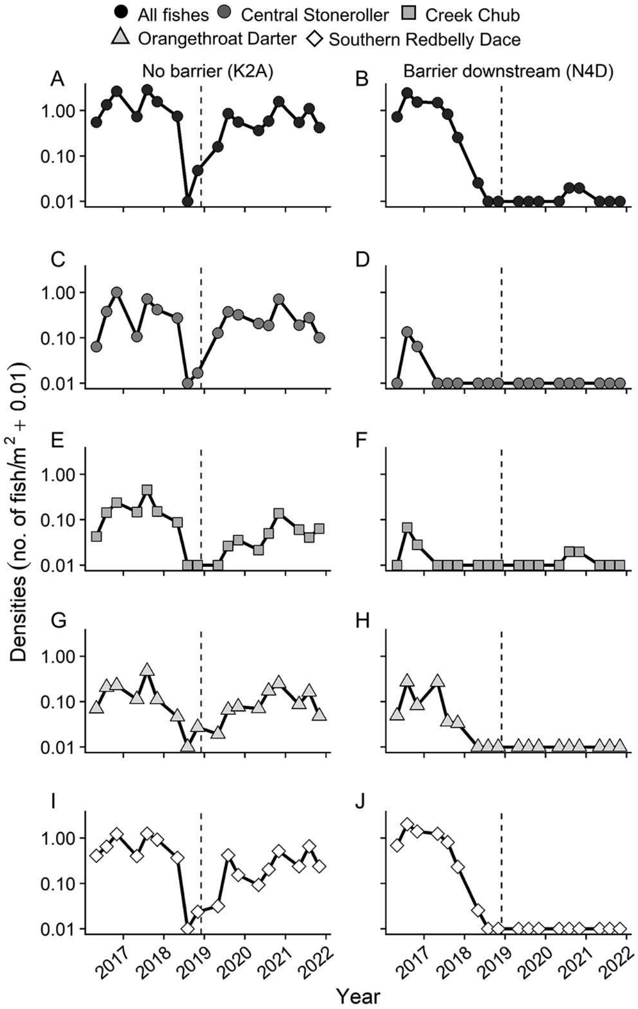

Figure 5. Densities (no. fish/m^2 + 0.01) of all fishes (A, B), Central Stoneroller (C, D), Creek Chub (E, F), Orangethroat Darter (G, H), and Southern Redbelly Dace (I, J) at a reference site without a barrier (K2A) and a site above the road crossing where a perched culvert was removed in November 2018 (N4D) at Kings Creek, Kansas, USA. Dashed vertical lines represent when the barrier was removed. See Fig. 2B for site locations. Values on y-axes are on a $\log_{10}$ scale. Note: A drought occurred in August 2018, resulting in the complete extirpation of fishes from both sites.

streams generally allows fish to expand into new habitats (Rayner et al. 2009). Based on our observations over the past 6 y, thousands of fishes have moved into, or possibly through, the intermittent reach at Kings Creek to gain access to spawning habitats and other resources. In an intermittent stream in Arkansas, USA, Walker et al. (2013) reported that upstream movement of Southern Redbelly Dace occurred in May and July, and Walker and Adams (2016) reported upstream movement of Creek Chub through this same reach in May. Similar to our observations at Kings Creek, the timing of these movements coincided with known spawning periods of these fishes. After flow is restored to intermittent reaches following rain events, these habitats have an abundance of clean pebbles and cobbles where fish have been observed spawning in the interstitial spaces of the substrate at the downstream end of pools (Fig. 1F). Similar-sized substrates are available downstream but are more likely to be embedded or covered in fine sediments, forcing fish to clear areas for spawning (KBG, personal observation). Although the intermittent reach in Kings Creek typically dries within a month or 2 following initial flow events (Fig. 3), larvae produced from spawning there might drift or swim downstream as flows recede (Scheurer et al. 2003, Dexter et al. 2014). We did not quantify larval fish growth rates, but previous studies have indicated that juveniles occupying intermittent reaches grow faster than in downstream, perennial habitats (Labbe and Fausch 2000, Spranza and Stanley 2000), presumably because of relaxed density dependence and warmer water temperatures. We also know that shallow, and presumably warmer, habitats in prairie streams can be dominated by juvenile fish, relative to deeper and cooler downstream habitats where these fish might be exposed to predators or competitors (Martin et al. 2013, Hedden and Gido 2022).

The probability of finding perched culverts at road crossings increases with decreasing stream size (Perkin and Gido 2012). As in other regions (e.g., Maitland and Poesch 2016), there are numerous road crossings of intermittent prairie streams that could be restored to allow fish passage. Our results suggest large proportions of fish from perennial stream reaches disperse into these intermittent reaches during the spawning season. Thus, not only do these habitats provide critical ecosystem services (e.g., Colvin et al. 2019), but there are clear benefits to restoring passage in intermittent streams and allowing fish access to spawning and potentially rearing habitats (e.g., Hooley-Underwood et al. 2019). Moreover, restoration work in small, intermittent streams can be conducted during the dry season, presumably reducing project costs (e.g., Maitland and Poesch 2016). Future efforts that optimize conservation efforts should broadly consider how renovating barriers across a range of perennial and intermittent streams might benefit a wide range of stream fishes.

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Table 3. Model output from manyGLM models assessing fish counts as a function of area sampled, site, time, and the interactive effect of site and time. *P*-values for individual species models were corrected for multiple testing by the Holms step-down procedure. LR = likelihood ratio, % sum of LR estimates individual species contributions to the overall assemblage-level effect for variables and interaction terms that were important for explaining variation in fish abundances at the $\alpha = 0.05$ level, – indicates not applicable.

Species	Term	LR	p	% sum of LR
Assemblage	Area	33.48	<0.001	–
	Site	42.96	<0.001	–
	Time	34.98	0.002	–
	Site × Time	59.81	0.02	–
Central Stoneroller	Area	12.66	<0.001	38
	Site	18.42	<0.001	43
	Time	4.48	0.10	–
	Site × Time	10.21	0.02	17
Creek Chub	Area	12.13	<0.001	36
	Site	14.60	0.001	34
	Time	6.77	0.05	–
	Site × Time	0.01	0.93	–
Orangethroat Darter	Area	6.64	0.002	20
	Site	8.08	0.004	19
	Time	9.91	0.02	28
	Site × Time	19.76	0.02	33
Southern Redbelly Dace	Area	2.05	0.03	6
	Site	1.86	0.13	–
	Time	13.82	0.002	39
	Site × Time	29.83	0.02	50

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