

# ***Fragmentation and drying ratchet down Great Plains stream fish diversity***

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## ABSTRACT

1. Stream fragmentation alters the structure of aquatic communities on a global scale, generally through loss of native species. Among riverscapes in the Great Plains of North America, stream fragmentation and hydrologic alteration (flow regulation and dewatering) are implicated in the decline of native fish diversity.

2. This study documents the spatio-temporal distribution of fish reproductive guilds in the fragmented Arkansas and Ninnescah rivers of south-central Kansas using retrospective analyses involving 63 years of fish community data.

3. Pelagic-spawning fishes declined throughout the study area during 1950–2013, including Arkansas River shiner (*Notropis girardi*) last reported in 1983, plains minnow (*Hybognathus placitus*) in 2006, and peppered chub (*Macrhybopsis tetranema*) in 2012. Longitudinal patterns in fish community structure in both rivers consisted of strong breaks associated with dams, and pelagic-spawning fishes were missing from shorter fragments upstream of those barriers. Among downstream and longer fragments, probability of occurrence for pelagic-spawning fishes declined or fell to zero during periods of drought.

4. Based on these data, interactions between fragmentation and drying are hypothesized as operating as an ecological ratchet mechanism in which forward movement toward pelagic-spawning fish extirpation occurs during desiccation, and reciprocated reverse movement toward recolonization following return of flows is blocked by fragmentation.

5. The ratchet mechanism is capable of explaining the long-term 'ratcheting down' of fish diversity in Great Plains rivers and has implications for managing biodiversity in fragmented riverscapes where water is scarce or might become so in the future.

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Received 8 April 2014; Revised 3 July 2014; Accepted 21 July 2014

KEY WORDS: river; stream; biodiversity; reproduction; fish; drought; impoundment

## INTRODUCTION

Habitat fragmentation and loss threaten biodiversity and ecosystem integrity on a global scale (Dudgeon

*et al.*, 2006; Pardini *et al.*, 2010). In streams and rivers, fragmentation and loss are particularly problematic because of the naturally occurring

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hierarchical organization and dendritic (branching) arrangement of habitats, which limit dispersal paths for organisms confined to water (Campbell Grant *et al.*, 2007). In stream and river networks (herein 'riverscapes' *sensu* Fausch *et al.*, 2002), fishes represent a group of organisms confined to within-network movement with increasingly well-documented responses to riverscape fragmentation (Fullerton *et al.*, 2010; Perkin and Gido, 2012). In fragmented riverscapes, there are notable declines in fish biodiversity (Liermann *et al.*, 2012), size and connectivity of populations (Junge *et al.*, 2014), dispersal opportunities (Perkin *et al.*, 2013a; Rolls *et al.*, 2013), and resistance and resilience to stochastic extinctions (Dunham *et al.*, 2004). Consequently, the global pattern of stream fragmentation has led to considerable change to riverine fish faunas (Lehner *et al.*, 2011; Cooke *et al.*, 2012). In particular, habitat fragmentation coupled with naturally occurring or anthropogenically magnified disturbance regimes have contributed to directional and irreversible change to stream fish distributions (Roberts *et al.*, 2013). Changes to stream fish abundances and distributions brought on by interactions between fragmentation and disturbance regimes probably operate through processes similar to those governing organisms in other fragmented ecosystems (e.g. terrestrial or marine systems; Roques and Stoica, 2007), although conceptual frameworks are currently lacking for application to riverscapes (Pringle, 2003; Rolls *et al.*, 2013).

Self-reinforcing processes that degrade populations and disrupt community or ecosystem structuring reflect 'ecological ratchets'. The ecological ratchet concept was originally used to describe dynamics of marine fish stocks (Caddy and Gulland, 1983; Ludwig *et al.*, 1993), but has been applied to coral reef ecology (Birkeland, 2004), marine food webs (Thrush and Dayton, 2010), and terrestrial plant communities (Jackson *et al.*, 2009). The ratchet concept involves forward movement (change) in a given response variable (e.g. species distributions) through space or time in response to natural or human disturbance(s) without reciprocal reverse movement (resetting of change), which is typically blocked through some introduced or derived mechanism(s) and ultimately results in continued or irreversible degradation (Birkeland, 2004). Thus,

ecological ratchets require three key components: some response variable, a form of disturbance (natural or anthropogenic) that elicits change in the response variable, and an introduced or derived mechanism that prohibits resetting of the observed change in the response variable. Ratchets might operate as mechanisms for species expansion and thus new invasions (Jackson *et al.*, 2009) or decline and thus extirpations (Birkeland, 2004); however, an advantage to this conceptual framework is that it might be applied to a variety of organisms occupying diverse ecosystems, including fishes occupying fragmented riverscapes. Fish distributions in riverscapes are changing on a global scale in response to ecosystem variability (a natural change) or degradation (an anthropogenic change) and provide a useful response variable for observing change within stream ecosystems (Simon, 1999). Hydrologic variability is among the strongest drivers of ecological change within riverscapes, and disturbances related to floods and droughts exist within most stream ecosystems on Earth (Poff and Ward, 1989; Matthews and Marsh-Matthews, 2003). In addition, longitudinal connectivity within riverscapes has been fragmented and is implicated in the largely irreversible processes of fish biodiversity loss (Lehner *et al.*, 2011; Liermann *et al.*, 2012). Although the necessary components for ratchet manifestation are documented within riverscapes, the extent to which the global processes of habitat fragmentation and hydrologic disturbance are operating to ratchet-down (species loss) or ratchet-up (species invasions) fish species distribution remains largely unaddressed despite the considerable implications for ecosystem conservation and restoration (Januchowski-Hartley *et al.*, 2013).

Great Plains stream fishes evolved under connected riverscapes characterized by broadly fluctuating environmental conditions including frequent disturbances caused by flooding and drought (Dodds *et al.*, 2004). However, contemporary riverscapes in this region are highly fragmented (>19 000 barriers, Figure S1), characterized by regulated stream flows with dampened flooding (Costigan and Daniels, 2012), and routinely become dewatered because of surface and groundwater depletion (Falke *et al.*, 2011). Associated with these riverscape alterations, broad-scale changes in community composition

have occurred (Gido *et al.*, 2010) and 65% of endemic species have declined because of fragmentation (Hoagstrom *et al.*, 2011). The greatest magnitude of community change is evident among historically abundant and wide-spread small-bodied fishes in the family Cyprinidae ('cyprinids' hereafter), especially for species that belong to the pelagic-spawning reproductive guild (Hoagstrom and Turner, 2013; Perkin *et al.*, 2014). Fishes that broadcast non-adhesive, drifting eggs into the pelagic zones of Great Plains rivers declined massively during the past half century (Dudley and Platania, 2007; Gido *et al.*, 2010), including threshold responses to fragmented riverscapes (Perkin and Gido, 2011; Wilde and Urbanczyk, 2013). In some cases, pelagic-spawning fish extirpations occur when the effects of fragmentation occur in concert with desiccation disturbances, either in the form of water withdrawal by humans (Perkin *et al.*, 2014) or periodic droughts (Kelsch, 1994; Perkin *et al.*, 2013b). These community shifts have persisted through time (40+ years in some rivers; Gido *et al.*, 2002), suggesting a level of reinforcement by current environmental conditions (Luttrell *et al.*, 1999). However, the relationship between disrupted mechanisms of community structuring and extensive fragmentation of Great Plains riverscapes lacks conceptual synthesis capable of explaining the directional and reinforced change in fish communities throughout the region.

This study applies an ecological ratcheting framework to changes in fish community structure brought on by habitat fragmentation and hydrologic disturbance in the Great Plains, USA. The goal of this novel approach is to shed light on the mechanism(s) responsible for broad-scale and long-term declines among native and endemic Great Plains fishes as documented in other recent works (Perkin *et al.*, 2014; Worthington *et al.*, 2014). Specific objectives include: (i) testing for long-term (1950–2013) change in the probability of occurrence for cyprinid fishes belonging to common reproductive guilds in the central Great Plains, USA; (ii) assessing change in fish community structure upstream and downstream of barriers that potentially fragment longitudinal connectivity; and (iii) evaluating fish response to hydrologic desiccation during drought disturbances. The objectives of the current study are related to each

of the three key components of ecological ratcheting, including change in fish distributions (i.e. response variable), fish sensitivity to droughts (i.e. disturbance), and reinforcement of observed change by fragmentation of riverscapes (i.e. human-induced mechanism that blocks resetting).

## MATERIALS AND METHODS

### Study area

The Arkansas River and its tributary the Ninnescah River in south-central Kansas are representative Great Plains streams that have experienced groundwater depletion (i.e. extraction > recharge) and surface water diversion and retention. Both are sand-bed rivers characterized by braided, shallow, and wide channels with sediment transport at most stages (Costigan *et al.*, 2014). The Arkansas River is dry nearly year-round upstream of Great Bend, KS because of depletion of the High Plains Aquifer (Steward *et al.*, 2013), and many fish species that historically inhabited the river are now extirpated between this point and the Colorado–Kansas border (Gido *et al.*, 2010). Surface water alterations include Cheney Reservoir (constructed in 1969) on the North Fork Ninnescah River and Kaw Reservoir (constructed in 1975) on the Arkansas River just downstream of the Kansas–Oklahoma border (Figure 1). Longitudinal fragmentation occurs in the form of multiple small dams, located in the cities of Wichita, KS on the Arkansas River (two dams, built *c.* 1975) and Kingman, KS on the Ninnescah River (one dam, Figure S2). These structures are run-of-the-river dams that do not retain water for long-term storage. The downstream dam near Wichita, KS underwent reconstruction during the period of study and is now fitted with a fish passage channel (Figure S3), although this channel remained dry or closed during the extent of the study because of drought and structural failures.

### Fish community data and reproductive guilds

Historical and contemporary fish collection data were obtained for the Arkansas River between Great Bend, KS and Kaw Reservoir and the Ninnescah River between Pratt, KS and the confluence with the Arkansas River for the period

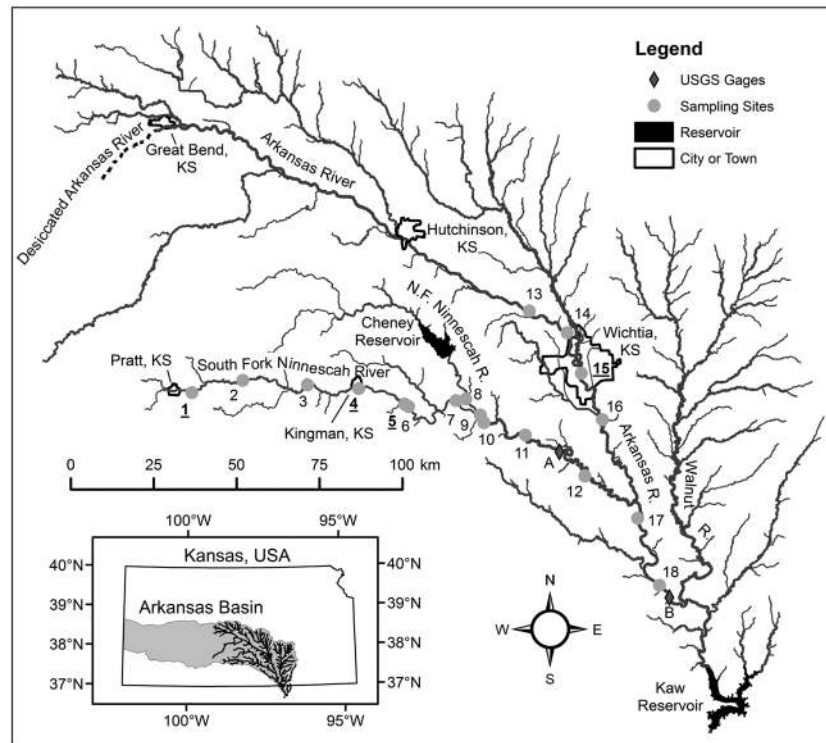


Figure 1. Locations of the Arkansas and Ninnescah rivers of south-central Kansas. Sites for 2011–2013 sampling are shown; those immediately downstream of low-head dams are labelled with bold and underlined numbers (see Figure S2 for pictures of dams). Locations of US Geological Survey streamflow gages are shown as lettered diamonds.

1950–2013. Fish community collections for these rivers were extracted from the Kansas Aquatic Gap Program as described by Gido *et al.* (2010) and supplemented by two additional datasets. The first dataset was collected by the City of Wichita during 2000–2008 as a part of standardized monitoring of the Arkansas River, including two sites upstream and five sites downstream of the series of dams in the city (Vaughn Weaver, unpublished data). These data were collected using a combination of seining and electrofishing during summer months in which entire communities and all available habitats were targeted. The second dataset consisted of collections made by the authors during 2011–2013 among 18 sites distributed along the Arkansas ( $n=6$ ) and Ninnescah ( $n=12$ ) rivers. Sampling sites were visited fortnightly during 2011 and 2012 summers (May–August) and fish communities were sampled from all available habitats using a seine ( $4.6 \times 1.8$  m, 3.2 mm mesh) for a period of at least 1 h. The area ( $m^2$ ) of each seine haul was recorded

to allow calculation of fish density (number of fish/area sampled). Monitoring was continued for a subset of these sites (three at the downstream extent of each river) using the same methods during the summer of 2013.

Cyprinid fishes reported in these databases were classified into four reproductive guilds based on spawning behaviour, habitat, and egg characteristics (Table 1). Guilds were based on Balon (1975) and described and reviewed in detail by Simon (1999). Pelagic spawners (pelagophilic) release non-adhesive, drifting eggs within the pelagic zone (open water) of the stream without regard to substrate; pelagic substrate-spawners (lithopelagophilic) have non-adhesive, demersal (sinking) eggs released within the pelagic zone and over sand or gravel substrate; substrate spawners (lithophilic) have adhesive, demersal eggs released over sand or gravel substrate; crevice spawners (speleophilic) have adhesive, demersal eggs deposited over nests or within cracks or crevices of the benthos. Existing literature sources were used for all guild classifications (Table 1).

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Table 1. Species reproductive guilds, abundance rank (total individuals collected) for 2011–2012 sampling by authors, reproductive season, and conservation status of fishes included in this study

Reproductive guild <sup>1</sup>	Rank (number collected)	Reproductive season <sup>2</sup>	Conservation status <sup>3</sup>
<b>Pelagic (Pelagophilic)</b>			
PM Plains minnow <i>Hybognathus placitus</i>	0 (0)	April – August	Vulnerable
PC Peppered chub <i>Macrhybopsis tetranema</i>	10 (47)	May – August	Endangered
ARS Arkansas River shiner <i>Notropis girardi</i>	0 (0)	June – August	Endangered
<b>Pelagic-Substrate (Lithopelagophilic)</b>			
SC Silver chub <i>Macrhybopsis storeriana</i>	7 (447)	April – July	No listing
ES Emerald shiner <i>Notropis atherinoides</i>	2 (44,799)	May – July	No listing
<b>Substrate (Lithophilic)</b>			
CSR Central stoneroller <i>Campostoma anomalum</i>	6 (893)	March – May	No listing
SS Sand shiner <i>Notropis stramineus</i>	3 (36,783)	April – August	No listing
SMM Suckermouth minnow <i>Phenacobius mirabilis</i>	5 (1,506)	April – August	No listing
<b>Crevice (Speleophilic)</b>			
RS Red shiner <i>Cyprinella lutrensis</i>	1 (83,721)	May – September	No listing
FHM Fathead minnow <i>Pimephales promelas</i>	9 (87)	April – August	No listing
BNM Bluntnose minnow <i>Pimephales notatus</i>	8 (405)	May – August	No listing
BHM Bullhead minnow <i>Pimephales vigilax</i>	4 (4,444)	June – July	No listing

<sup>1</sup>Simon (1999).

<sup>2</sup>Cross and Collins (1995).

<sup>3</sup>Jelks *et al.* (2008).

### Data analyses

The first objective was to test for long-term changes in the probability of occurrence for fishes during 1950–2013. Data from the multiple sources were combined and abundances transformed to presence–absence (Gido *et al.*, 2010). Occurrence data for the 12 most common cyprinid fishes over the course of the 63-year period were extracted and grouped according to their reproductive mechanism. Long-term trends in the probability of occurrence (0 = absent, 1 = present) for each species were tested using a generalized estimation equation to account for autocorrelation among samples taken close together in time. Binomial logistic equations were fitted assuming an auto-regressive correlation structure in the data (Zuur *et al.*, 2009) using the *geepack* Package in Program R (Halekoh *et al.*, 2006). The modelled mean and 95% confidence intervals, slope of the regression, Wald test statistic, and *P*-value for probability of occurrence of each species were then plotted through time to illustrate temporal changes in fish distributions.

The second objective was to assess the effects of small barriers on fish community structure in each river. Longitudinal changes in fish community structure were assessed in each river using data collected during the summers of 2011 and 2012 from river fragments upstream and downstream of

the small dams in each river. This analysis process began with construction of a Bray–Curtis distance matrix (Bray and Curtis, 1957) based on fish densities from the 18 sampling sites across the 2 years of intense sampling. Occurrence of longitudinal breaks in community structure caused by fragmentation was tested in the Arkansas and Ninescah rivers separately. Sites were systematically grouped beginning with the most upstream site versus all remaining sites, then the first two upstream sites versus all remaining sites, and so on until a theoretical community break was inserted between all possible longitudinal groups of sites in each river. Significant clustering among groups was tested using a permutational multivariate analysis of variance (pMANOVA) on the Bray–Curtis distance matrix, which allowed for calculating a coefficient of determination ( $r^2$ ) value for each theoretical community break. Location of the strongest community break in each river was assessed using pMANOVA  $r^2$  results and compared with barrier locations to evaluate agreement between breaks in community structure and stream fragmentation. Differences between the groups upstream and downstream of the strongest break in community structure were illustrated using non-metric multi-dimensional scaling (NMDS) bi-plots. All statistics were conducted in Program R using the *vegdist* (Bray–Curtis), *adonis* (pMANOVA) and

*nmds* (NMDS) functions in the *Vegan* Package (Oksanen *et al.*, 2007).

The third objective was to evaluate fish reproductive guild responses to drought. This objective was developed in part because of the fortuitous timing of a major drought during 2011 and 2012 sampling years (Figure S4). Since preliminary results suggested that fish community structure did vary longitudinally, further testing was used to assess changes in fish distributions upstream and downstream of barriers as well as during periods of drought. Occurrences (presence or absence) were analysed using a random sub-sampling approach as outlined in Gido *et al.* (2010) to avoid potential bias caused by non-independence of samples either in space or time. In particular, 80% of the minimum number of samples taken upstream or downstream of barriers across years was randomly sub-sampled without replacement 1000 times and the mean ( $\pm 95\%$  confidence interval) probability of occurrence calculated. For temporal patterns, a similar approach involving sub-sampling 80% of the minimum number of collections across years was used only for the downstream communities since preliminary results suggested that some reproductive guilds did not occur in the upstream portions of each river. Differences across space and time were considered significant if 95% confidence intervals did not overlap (Gido *et al.*, 2010). Spatio-temporal patterns in probability of occurrence were plotted for the 2000–2008 and 2011–2013 periods separately to control for differences in collection gears and efforts.

Drought and streamflow data were compared with fish occurrence probabilities to illustrate responses to desiccation disturbance. Palmer Drought Severity Index values from the National Climate Data Center operated by the National Oceanic and Atmospheric Administration (<http://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers.php>, last accessed 1 February 2014) were used to quantify annual variation in drought. Historical records (1950–2013) were downloaded for the climatological division covering the extent of the study area in south-central Kansas (Division # 14-08). Historical streamflow data (1950–2013) were extracted from two USGS gauges located at the downstream extent of the Arkansas River (gauge # 07146500) and the Ninescah River (gauge # 07145500). Streamflow

data were analyzed using Indicators of Hydrologic Alteration (IHA; Richter *et al.*, 1996) to determine mean annual stream flow during cyprinid reproductive seasons (March–September) as well as long-term mean ( $\pm 95\%$  confidence interval) streamflow for the Arkansas and Ninescah rivers. Palmer Drought Severity Index values  $< -2$  were considered moderate drought and values  $< -3$  were considered severe drought. Mean annual streamflow magnitudes below the lower 95% confidence level (i.e. non-overlapping confidence intervals) of average flows were considered exceptionally dry years. Continuous occurrence data for fish collections taken during the two most recent datasets (City of Wichita and the authors) were then compared with desiccation disturbance periods to assess responses to drought.

### Conceptualizing the ratchet

A conceptual model detailing the three components of an ecological ratchet at the sub-basin scale (i.e. both Arkansas and Ninescah rivers) was used to synthesize findings. Fish distribution data were used to assign an approximate last year of collection for pelagic-spawning fishes throughout the sub-basin. Drought disturbance for the region and flow data for the downstream extent of both rivers were combined to identify exceptionally low streamflow throughout the sub-basin. A measure of long-term habitat connectivity for the sub-basin was obtained from Perkin *et al.* (2014); this measure of connectivity was the potadromous component of the Dendritic Connectivity Index (DCI) developed by Cote *et al.* (2009). A DCI value of 100 indicates complete natural connectivity among all habitats in a network, and this value declines toward zero with increased fragmentation caused by artificial barriers (Cote *et al.*, 2009; Perkin *et al.*, 2014). The ratchet mechanism was conceptualized by simultaneously illustrating estimated last occurrences of fishes, drought disturbances, and longitudinal habitat connectivity through time (1950–2013) for the entire sub-basin. Insights gained from this approach were further illustrated as a conceptual diagram that demonstrated how changes in fish distributions might be ratcheted by the interaction between fragmentation and drought disturbance.

RESULTS

Review of historical fish data resulted in 274 collections included in the long-term analysis of occurrence probabilities. Sixty-four collections were obtained from the Kansas Aquatic Gap Database, 67 from the City of Wichita, and 143 by the authors during 2011–2013. Probability of occurrence changed through time for eight of the 12 species (Figure 2). Logistic regression indicated a significant decline through time for pelagic-spawning Arkansas River shiner (*Notropis girardi*) and plains minnow (*Hybognathus placitus*) but no change for peppered chub (*Macrhybopsis tetranema*). All of these pelagic-spawning fishes were missing from collections during 2013 and a review of historical

data indicated that the last reports were in 1983 for Arkansas River shiner, in 2006 for plains minnow, and in 2012 for peppered chub. Pelagic substrate-spawning fishes increased through time, including silver chub (*Macrhybopsis storeriana*) and emerald shiner (*Notropis atherinoides*). Substrate-spawning fishes generally increased, including sand shiner (*Notropis stramineus*) and suckermouth minnow (*Phenacobius mirabilis*), but no change for central stoneroller (*Campostoma anomalum*). Crevice-spawning red shiner (*Cyprinella lutrensis*) and bullhead minnow (*Pimephales vigilax*) increased, but there was no change for fathead minnow (*Pimephales promelas*) or bluntnose minnow (*Pimephales notatus*).

Longitudinal variability in cyprinid community structure based on 2 years of intensive sampling

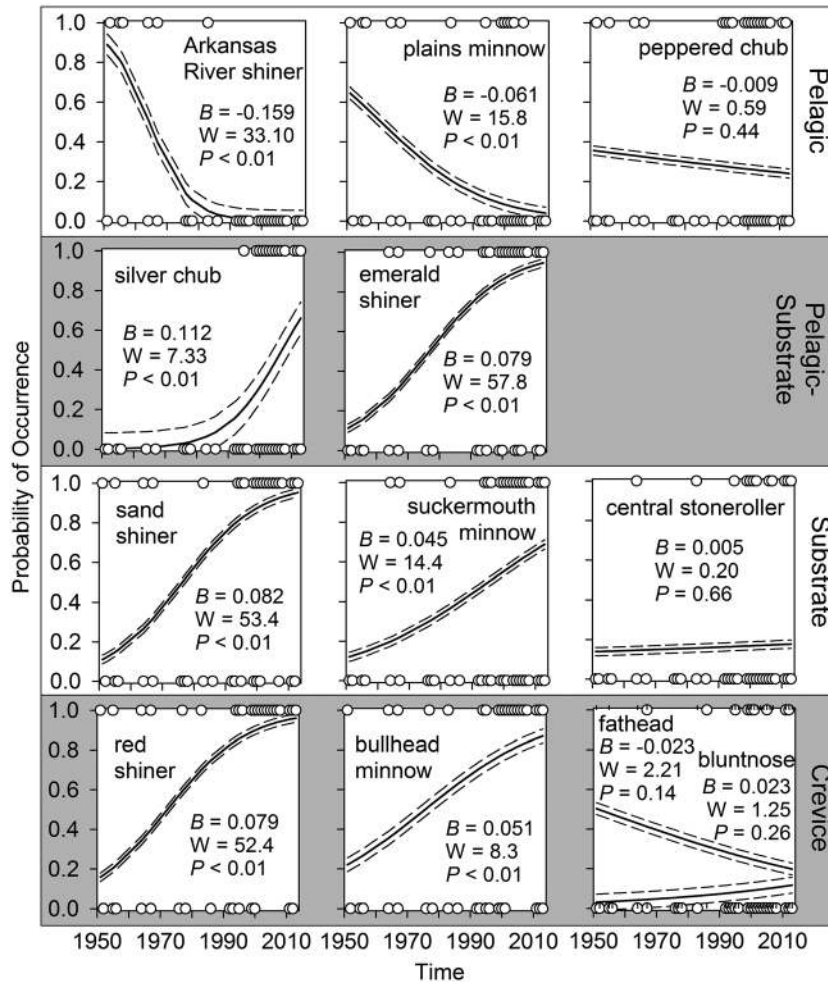


Figure 2. Long-term (1950–2013) trends in the probability of occurrence for cyprinid fishes in the Arkansas and Ninescah rivers of south-central Kansas. Logistic generalized equation estimations (solid lines), 95% confidence intervals (dashed lines), and statistics ( $B$  = slope,  $W$  = Wald value,  $P$ -value) are shown for collections (white points) in which each species was present (occurrence = 1) or absent (occurrence = 0).

revealed strong breaks in the Arkansas and Ninnescah rivers. Theoretical community breaks iteratively inserted between sites in the Arkansas River produced significant models in all cases (pMANOVA  $P < 0.05$ ;  $r^2 = 0.08$ – $0.19$ ), and the strongest model (Pseudo  $F_{1,80} = 18.3$ ;  $r^2 = 0.19$ ,  $P < 0.001$ ) corresponded with the barriers between sites 14 and 15 (Figure 3(A)). Theoretical community breaks in the Ninnescah River produced significant models in all cases (pMANOVA  $P < 0.05$ ;  $r^2 = 0.02$ – $0.22$ ), and the strongest break (Pseudo  $F_{1,206} = 59.0$ ;  $r^2 = 0.22$ ,  $P < 0.001$ ) corresponded with the permanent barrier location upstream of Site 4 (Figure 3(B)). Two-dimensional NMDS plots were characterized by low stress values ( $< 0.15$ ) and strong clustering of community samples taken upstream and downstream of barriers in the Arkansas (Figure 3(C)) and Ninnescah (Figure 3(D)) rivers. Separation of sites in NMDS plots was driven in part by absence of fish species among upstream sites in both rivers

(Table 2), including pelagic-spawning peppered chub as well as pelagic substrate-spawning emerald shiner and silver chub.

During 2000–2013, temporal patterns in probability of occurrence for fishes downstream of barriers in the Arkansas and Ninnescah rivers were consistent among river systems and reproductive guilds. Arkansas River shiner was not collected during 2000–2008, nor was the species observed during 2011–2013. Similarly, although plains minnow was captured during 2000–2008, the species was not observed during 2011–2013. Downstream of the dams on the Arkansas River, the probability of occurrence for pelagic-spawning plains minnow and peppered chub declined during 2001–2003 and then again during 2006–2008 (Figure 4). During the second decline, probability of occurrence for both pelagic-spawning fishes declined to zero. Fishes belonging to the remaining reproductive guilds persisted through time. In the Arkansas and Ninnescah rivers during 2011–2013, the probability

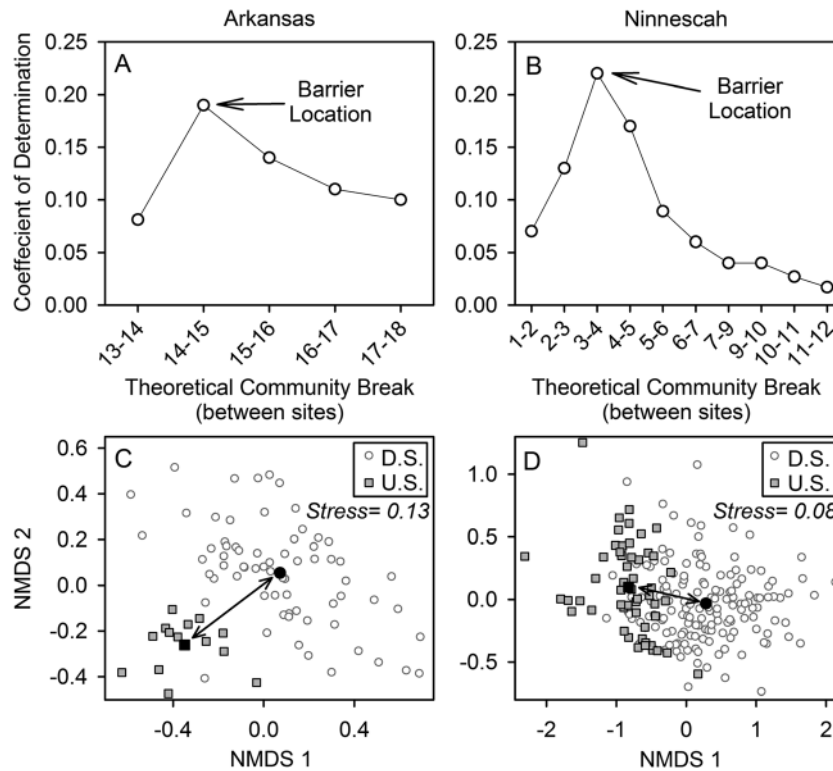


Figure 3. Spatial variability in cyprinid community structure for streams in south-central Kansas. The most variation (maximum coefficient of determination) corresponded with barriers in the (A) Arkansas and (B) Ninnescah rivers and was associated with strong clustering of collections upstream (U.S., white symbols) and downstream (D.S., grey symbols) of barriers as illustrated by non-metric multi-dimensional scaling (NMDS) bi-plots for the (C) Arkansas and (D) Ninnescah rivers (black symbols connected by arrows are means).



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Table 2. Mean probability of occurrence (95% confidence interval) for cyprinid fishes upstream and downstream of barriers in the Arkansas and Ninescah rivers of south-central, Kansas. Fishes that were historically present but not collected during sampling are indicated (-)

Reproductive guild	Arkansas (2000–2008)		Arkansas (2011–2013)		Ninescah (2011–2013)	
	Upstream	Downstream	Upstream	Downstream	Upstream	Downstream
<b>Pelagic</b>						
Plains minnow <i>Hybognathus placitus</i>	0.00 (0.00)	0.09 (0.08)	-	-	-	-
Peppered chub <i>Macrhybopsis tetranema</i>	0.00 (0.00)	0.38 (0.15)	0.00 (0.00)	0.06 (0.03)	0.00 (0.00)	0.15 (0.02)
Arkansas River shiner <i>Notropis girardi</i>	-	-	-	-	-	-
<b>Pelagic-Substrate</b>						
Silver chub <i>Macrhybopsis storeriana</i>	0.00 (0.00)	0.68 (0.14)	0.00 (0.00)	0.44 (0.06)	0.00 (0.00)	0.25 (0.02)
Emerald shiner <i>Notropis atherinoides</i>	0.00 (0.00)	0.85 (0.11)	0.00 (0.00)	1.00 (0.00)	0.00 (0.00)	1.00 (0.00)
<b>Substrate</b>						
Central stoneroller <i>Camptostoma anomalum</i>	0.00 (0.00)	0.07 (0.08)	0.00 (0.00)	0.06 (0.03)	0.68 (0.01)	0.28 (0.02)
Sand shiner <i>Notropis stramineus</i>	1.00 (0.00)	0.98 (0.01)	0.93 (0.02)	1.00 (0.00)	0.80 (0.01)	1.00 (0.00)
Suckermouth minnow <i>Phenacobius mirabilis</i>	0.87 (0.06)	0.79 (0.13)	0.43 (0.03)	0.42 (0.06)	0.32 (0.01)	0.75 (0.02)
<b>Crevice</b>						
Red shiner <i>Cyprinella lutrensis</i>	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
Fathead minnow <i>Pimephales promelas</i>	1.00 (0.00)	0.38 (0.15)	0.14 (0.02)	0.15 (0.04)	0.02 (0.01)	0.01 (0.01)
Bluntnose minnow <i>Pimephales notatus</i>	0.00 (0.00)	0.02 (0.04)	0.00 (0.00)	0.02 (0.02)	0.22 (0.01)	0.36 (0.02)
Bullhead minnow <i>Pimephales vigilax</i>	1.00 (0.00)	0.98 (0.04)	0.50 (0.03)	0.82 (0.05)	0.83 (0.01)	0.93 (0.01)

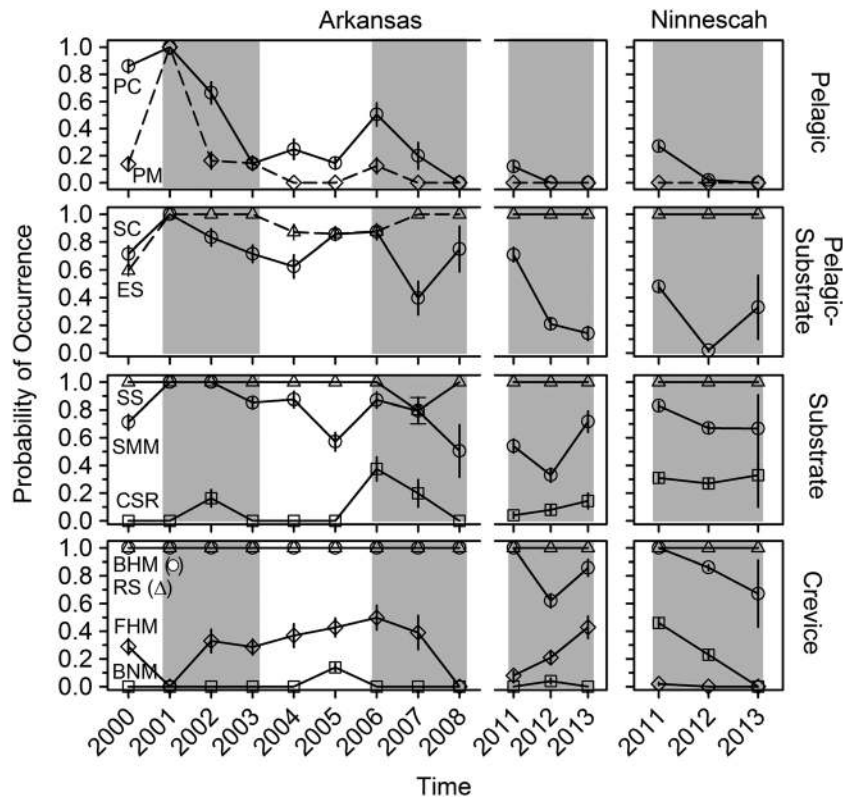


Figure 4. Temporal variability in mean ( $\pm 95\%$  confidence interval) probability of occurrence for fishes belonging to four reproductive guilds downstream of dams on the Arkansas and Ninescah rivers in south-central Kansas. Species are labelled using two- or three-letter codes (see Table 1) and drought cycles are shaded grey.

of occurrence for peppered chub, the only remaining pelagic-spawning fish, declined over the course of 3 years in both rivers so that no individuals were collected during summer 2013 in either river system following severe drought. The remaining reproductive guilds generally persisted through time with only silver chub indicating consistent declines in both rivers.

The timing of declines and last reports for pelagic-spawning fishes occurred after fragmentation of the Arkansas River basin and correlated with drought periods when stream flows were below

average. Construction of Keystone Reservoir (downstream of Kaw Reservoir in Oklahoma) in 1964 reduced the amount of longitudinal connectivity by half, followed by additional fragmentation by Cheney Reservoir in 1969 and construction of Kaw Reservoir and the dams near Wichita in 1975 (Figure 5). There was no additional fragmentation in the basin after 1975. Although severe drought occurred throughout the study area during 1953–1956 (Figure 5(A)), the first moderate drought following basin-wide fragmentation occurred during 1981. Normal or wetter-than-normal years occurred after

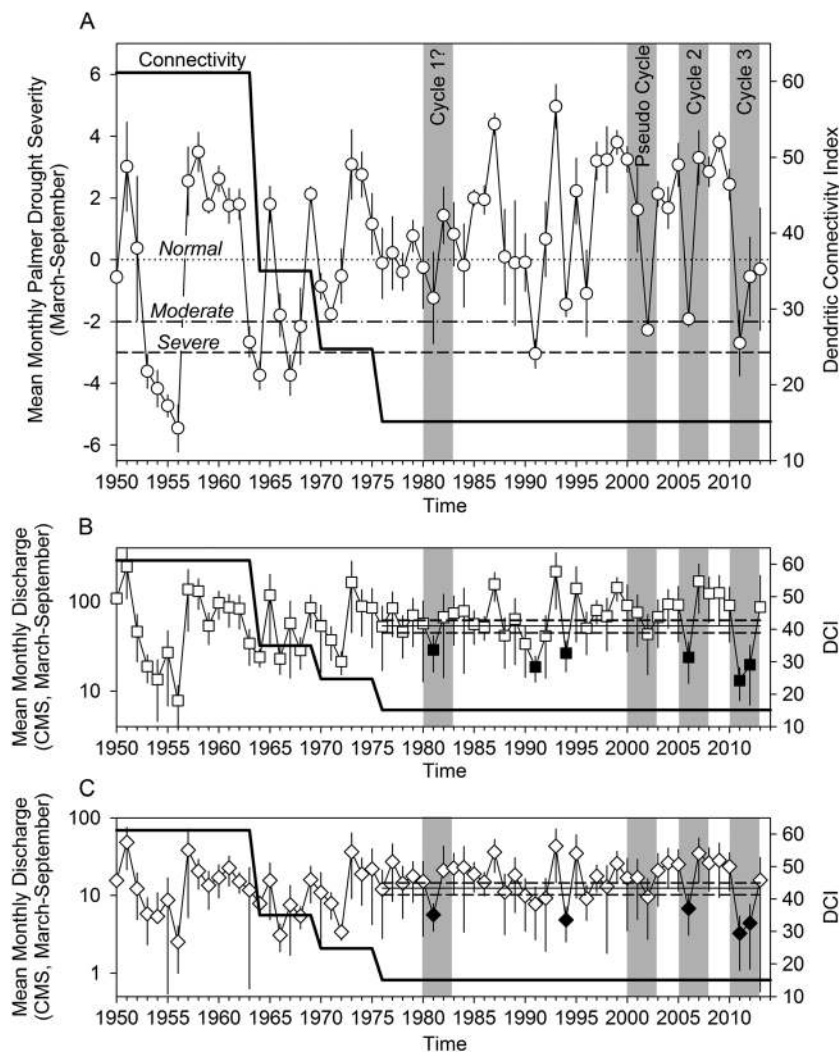


Figure 5. (A) Drought records for south-central Kansas illustrating mean ( $\pm 95\%$  confidence interval) Palmer Drought Severity Index (white circles) across cyprinid reproductive months (March–September). The solid black line illustrates change in habitat connectivity through time (see text), grey shades represent cycles of an ecological ratchet mechanism. (B) Mean streamflow ( $\pm 95\%$  CI) for the Arkansas River (US Geological Survey gauge 07146500; squares) and long-term mean ( $\pm 95\%$  CI) across years (solid and dashed black lines) illustrated for the period following fragmentation; exceptionally dry years are shown in black. (C) Streamflow data for the Ninnescah River (gauge 07145500); symbols are as in panel B.

this period with a punctuated moderate drought in 1989, a severe drought in 1991, moderate droughts during 1996, 2002, and 2006, and a severe drought during 2011. Within these drought periods, streamflow in the Arkansas River was exceptionally low during 1981, 1991, 1994, 2006, and 2011–2012 (Figure 5(B)). Similarly, streamflow in the Ninnescah River was exceptionally low during 1981, 1994, 2006, and 2011–2012 (Figure 5(C)). The last reported records of Arkansas River shiner (1983), plains minnow (2006), and peppered chub (2012) each occurred during or shortly after (within 2 years) droughts that caused low flow conditions in both rivers (i.e., throughout the sub-basin).

## DISCUSSION

Stream fish communities in the Great Plains of North America changed considerably during the past half century owing to the effects of fragmentation and dewatering (Gido *et al.*, 2010; Hoagstrom *et al.*, 2011). Although the individual effects of dewatering (Cross *et al.*, 1985; Durham and Wilde, 2009) and fragmentation (Perkin and Gido, 2011; Wilde and Urbanczyk, 2013) have been evaluated, recent broad-scale analyses suggest that these processes act in concert to cause declines among some fishes, especially pelagic-spawning species (Perkin *et al.*, 2014). The current study builds upon existing knowledge in at least three ways. First, results suggest that long-term declines among multiple pelagic-spawning fish species are driven by similar processes and have occurred during a period of increases for most other fishes, highlighting the utility of approaches that target ecotypes or guilds in restoration (Dudley and Platania, 2007; Worthington *et al.*, 2014). Second, data collected in this study indicate that even small dams (<5 m height) are capable of causing longitudinal fragmentation of Great Plains fish communities in a manner consistent with much larger structures (Winston *et al.*, 1991; Luttrell *et al.*, 1999). Perhaps most significantly, this study provides a mechanistic underpinning for the correlative relationship between stream fragmentation and the disappearance of pelagic-spawning fishes throughout the Great Plains (Perkin *et al.*, 2014).

## Disappearance of pelagic-spawning fishes

Long-term patterns in the probability of occurrence for fishes in the Arkansas and Ninnescah rivers were characterized by declines among pelagic-spawning fishes and increases or no change among fishes in remaining reproductive guilds. The first species to disappear was the now federally ‘Threatened’ Arkansas River shiner (missing from 80% of historic range; Wilde, 2002) during the 1980s. Despite more than 230 Arkansas River shiner and 220 peppered chub being collected in the Ninnescah River during the late 1970s (KFGC, 1978), visits to the same area as well as the Arkansas River proper following the drought of 1981 by Cross *et al.* (1985) produced no Arkansas River shiner and no peppered chub. Although peppered chub was encountered among collections following the work of Cross *et al.* (1985), Arkansas River shiner was never collected again after a single report by Cross in 1983 (Kansas Aquatic Gap Program; Cross’s Notes: C-11-83). Based on the effects of fragmentation and dewatering on the timing of disappearance and vulnerability of Arkansas River shiner (Worthington *et al.*, 2014), we hypothesize that disappearance of the species was related to the effects of the first moderate drought in the extensively fragmented riverscape. Similarly, plains minnow was last reported in the vicinity of Wichita, KS during the midst of a moderate drought in 2006, but 152 collections taken from the area since did not produce a single specimen. Although the data on peppered chub did not indicate long-term declines during 1950–2013, contemporary and intensive surveys documented the decline and eventual disappearance of the species in the Arkansas and Ninnescah rivers during the drought cycle of 2010–2013. Peppered chub is missing from 90% of its historical range because of the effects of fragmentation (Luttrell *et al.*, 1999) and stream desiccation (Wilde and Durham, 2008), and data presented in this study indicate substantial decline of this last remaining pelagic-spawning species in the riverscape. Continued sampling in the area is urgently necessary to determine if peppered chub numbers have declined to zero or simply below the point of detection. The latter was probably the case during work by Cross *et al.* (1985) and the species

did eventually recover to detectable abundances. Regardless, long-term fish occurrences suggest that pelagic-spawning fishes responded similarly to the two major forms of landscape alteration in the Great Plains – fragmentation and desiccation (Hoagstrom *et al.*, 2011) – and that conservation approaches that benefit one member of this reproductive guild are likely to benefit the others. Acknowledging that sampling gears and efforts changed during 1950–2013, we believe the long-term changes reported here are accurate given similarities to other reported trends for the region (Gido *et al.*, 2010) and the fact that species disappeared in spite of the potential for increased gear efficiency through time (Patton *et al.*, 1998).

### Fragmentation by small dams

Spatial variability in species occurrences suggest that pelagic-spawning and pelagic substrate-spawning fishes were sensitive to the effects of fragmentation caused by small dams. Dam locations corresponded to strong breaks in community structure in both the Arkansas and Ninescah river systems. These breaks in community structure were driven in part by the absence of pelagic-spawning and pelagic substrate-spawning fishes upstream of the barriers. During 2000–2008 in the Arkansas River, no members of either guild were recorded upstream of the series of dams in Wichita, KS. This pattern continued for collections made during 2011–2012 for the Arkansas River as well as the Ninescah River and all remaining pelagic and pelagic substrate-spawning fishes in the riverscape were missing upstream of small dams in Wichita and Kingman, KS. Although documented occurrences indicate that fishes belonging to these guilds once occupied the now fragmented upstream portions of both rivers (Cross, 1967), small dams have apparently truncated longitudinal distributions. All pelagic-spawning and pelagic substrate-spawning fishes included in this study have experienced range reductions caused by fragmentation throughout the Great Plains (Perkin and Gido, 2011; Perkin *et al.*, 2014), but the results presented here extend the known effects of fragmentation beyond mostly large structures to include even small diversion dams (Winston *et al.*, 1991; Luttrell *et al.*, 1999).

### Ratcheting-down Great Plains fish diversity

Both the Arkansas and Ninescah rivers have surface water retention structures (large reservoirs) and extraction structures (small dams) that fragment longitudinal connectivity, and reduce streamflow (Costigan and Daniels, 2012). In addition to continuing groundwater extraction in the area (Steward *et al.*, 2013), these activities create flow regimes that select for fish species resistant to the effects of stochastic stream desiccation (i.e. drought) by the very nature of removal of water that would otherwise remain instream (Vörösmarty *et al.*, 2010). Indeed, the study area has a long history of drought, including record drought during the 1950s through which pelagic-spawning fishes persisted. However, following fragmentation and consequently dewatering, the effects of drought became increasingly effective at causing declines among pelagic-spawning fishes even in the largest of the remaining stream fragments, as illustrated here on at least three occasions. First, the drought cycle of 2001–2003 caused punctuated decline, but not extirpation, of plains minnow and peppered chub in the Arkansas River. Second, following the 2001–2003 drought cycle, occurrences of both species remained low until the next drought cycle of 2005–2007, during which plains minnow occurrence declined to zero. Third, during the drought cycle of 2010–2013, the probability of occurrence for peppered chub closely followed the pattern of plains minnow during the previous drought cycle, including declining to zero occurrence. It is interesting that only one other drought period (i.e. 1994) caused exceptionally low flows in both the Arkansas and Ninescah rivers, and plains minnow and peppered chub both persisted, although we hypothesize that declines similar to 2001–2003 probably occurred during 1993–1995. Additional historical data are necessary to test this hypothesis; however, it could be that the exceptionally high flow years (1993 and 1995) that bound the low flow year of 1994 buffered populations against the effects of punctuated drought. Thus, antecedent flows combined with stochastic drought affecting broad spatial extents (i.e. the entire sub-basin) contributed to punctuated disappearance of pelagic-spawning fishes.

We hypothesize that loss of pelagic-spawning fishes from the Arkansas and Ninescah rivers

represents an ecological ratchet mechanism in motion. Ratcheting begins when the longitudinal connectivity of a stream is fragmented by barriers (Figure 6(A)). Communities within longitudinal zones of the river are effectively isolated and the effects of local community structuring become decoupled from regional immigration (Angermeier and Winston, 1998). Species that require habitat connectivity at broad spatial scales are lost from short stream fragments even in the absence of stochastic disturbance (Perkin and Guido, 2011; Wilde and Urbanczyk, 2013). Communities in upstream portions of riverscapes are most vulnerable to environmental variability (Schlosser, 1990) and the effects of ratcheting are first evident in these habitats at relatively minor disturbances (Figure 6(B)). During minor drought, pelagic-spawning fishes that depend on broad levels of riverscape connectivity or greater discharge magnitudes decline but are not lost from the riverscape (Wilde and Durham, 2008). At this stage, if the drought cycle subsides and flows return to normal, a ratchet cycle may be averted (i.e. a 'pseudo' ratchet cycle). The ratchet manifests itself when stochastic disturbances such as drought or anthropogenic dewatering induce stream contraction and drying (Figure 6(C)). Pelagic-spawning fishes that were extirpated from small fragments upstream of dams now decline and are eventually lost from large

downstream fragments (Worthington *et al.*, 2014). At this stage, availability and suitability of refuge habitats such as downstream impoundments select for persistence of species based on reproductive mechanisms, and non-pelagic-spawning fishes are at an advantage (Sedell *et al.*, 1990; Dudley and Platania, 2007). Ratcheting inflicts legacy effects when portions of the riverscape are re-wetted and artefacts of the disturbance persist because species diversity is now lower (Figure 6(D)). Each turn of the ratchet represents the loss of a single species; thus, we hypothesize that the ratchet has made up to three turns in the study system: the first affecting Arkansas River shiner, the second plains minnow, and the third and most recent peppered chub. In this context, contemporary community composition reflects current levels of fragmentation together with legacies of historical disturbances, and these 'ghosts of riverscapes past' probably haunt other stream networks in the Great Plains (Kelsch, 1994; Perkin *et al.*, 2013b).

#### Evidence for ratchets

Riverscapes throughout the Great Plains now resemble a mosaic of stream fragments isolated by agents of fragmentation such as road crossings, small dams, large impoundments, and desiccated stream segments (Matthews and Marsh-Matthews,

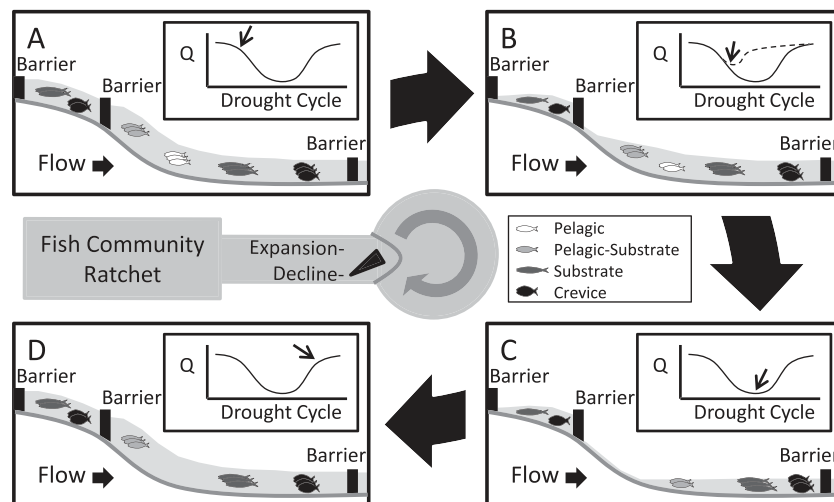


Figure 6. Conceptual diagram of the ecological ratchet mechanism caused by interactions between habitat fragmentation and drought. Ratchets can operate as mechanisms for population expansion or decline (shown here) and involve forward movement without reciprocated reverse movement through four stages in a fragmented riverscape: (A) before drought; (B) onset of drought; (C) height of drought; and (D) following drought. Fish abundance is equal to the number of symbols; if a drought subsides (dashed line of insert in B) then a 'pseudo ratchet cycle' ensues.

2007; Perkin *et al.*, 2014). Within the fragments of stream between these barriers, natural and human disturbances act upon smaller and isolated populations of stream organisms characterized by an impaired ability to resist and subsequently recover from stochastic disturbances (Sedell *et al.*, 1990). This process is probably magnified by alteration of natural gradients along the river continuum (Ward and Stanford, 1983). In theory, stochastic and deterministic disturbances brought on by human activities involve water pollution, introduction of non-native species, regulated streamflow regimes, and artificial dewatering caused by water diversion and withdrawal (Hoagstrom *et al.*, 2011). The unifying theme among these examples involves community change driven by disturbance and in the absence of colonization from outside sources. Legacies or historical contingencies arising from such disturbances leave lasting effects on the isolated fish communities within stream fragments and have undoubtedly contributed to the strong relationship between fragment length and the persistence of some fishes (Perkin and Gido, 2011; Wilde and Urbanczyk, 2013). Application of the ecological ratcheting framework to fragmented riverscapes constitutes the testing of general ecological and landscape theory with potential to enhance conservation of biodiversity in fragmented stream ecosystems on a global scale (Bain and Wine, 2010; Liermann *et al.*, 2012).

### Implications for conservation

Conservation actions can counter the effects of the described ecological ratchet involving fragmentation and desiccation in at least four ways to benefit fishes in fragmented rivers on a global scale (Liermann *et al.*, 2012). First, longitudinal connectivity might be improved through documentation and prioritized removal of barriers (Fullerton *et al.*, 2010; Januchowski-Hartley *et al.*, 2013). This process has already helped to improve the distribution and abundance of pelagic-spawning cyprinids (Archdeacon and Remshardt, 2012) as well as other stream species (Catalano *et al.*, 2007; Hitt *et al.*, 2012). Second, flow regimes might be manipulated to enhance recruitment and persistence of a variety of stream organisms (Propst and Gido, 2004; Konrad

*et al.*, 2011; Kiernan *et al.*, 2012). Third, in the absence of capacity to regulate streamflow, rescuing individuals from drying stream fragments and holding them in captivity until flows recover is one option recently used for pelagic-spawning fishes in the upper Brazos River of Texas (Kevin Mayes, Texas Parks and Wildlife Department, personal communication). However, such reactive approaches will not be effective in perpetuity and require significant resources first to rescue and then to hold species until drought conditions subside. Forth, for stream fragments in which species are now extirpated but environmental conditions have improved following disturbance, repatriation of fishes obtained from genetic reservoirs is an emerging technique that might allow for the re-establishment of self-sustaining populations (Osborne *et al.*, 2013). However, the long-term outlook for re-establishing populations will depend entirely on slowing down ratcheting so that genetic reservoirs for declining species persist. As slowing ratcheting will become increasingly challenging under the expected warmer and drier climatic conditions of the future (Milly *et al.*, 2005), implementing sustainable water management approaches aimed at conserving freshwater resources is crucial (Vörösmarty *et al.*, 2010; Steward *et al.*, 2013).

### ACKNOWLEDGEMENTS

This work was funded by the Kansas Department of Wildlife, Parks and Tourism (KDWPT) and the Great Plains Landscape Conservation Cooperative. Fishes were collected with permission from the KDWPT (permits SC-051-2011 and SC-057-2012 issued to KBG) as well as the Institutional Animal Care and Use Committee at Kansas State University (permit 2996). J. Edmonds, D. Shaw, and T. Starks provided extensive field assistance during long, hot summer days. We thank N. Cathcart, J. Fischer, S. Hedden, K. Kirkbride, E. Martin, B. Scharping, M. Troia, and J. Whitney for occasional sampling trips. Valuable logistical support was provided by A. Austin, J. Conley, A. Lollar, J. Luginbill, and R. Waters with the KDWPT. We are grateful to numerous private land owners as well as Wichita State University for granting access to the Ninnescah River. Data for the Arkansas River

near the City of Wichita were graciously provided by V. Weaver. Finally, L. Fallis, M. Troia, D. Larson, and A. Veach provided helpful comments on earlier versions of the manuscript.

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