

Effects of floods on fish assemblages in an intermittent prairie stream

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SUMMARY

1. Floods are major disturbances to stream ecosystems that can kill or displace organisms and modify habitats. Many studies have reported changes in fish assemblages after a single flood, but few studies have evaluated the importance of timing and intensity of floods on long-term fish assemblage dynamics.
2. We used a 10-year dataset to evaluate the effects of floods on fishes in Kings Creek, an intermittent prairie stream in north-eastern, Kansas, U.S.A. Samples were collected seasonally at two perennial headwater sites (1995–2005) and one perennial downstream flowing site (1997–2005) allowing us to evaluate the effects of floods at different locations within a watershed. In addition, four surveys during 2003 and 2004 sampled 3–5 km of stream between the long-term study sites to evaluate the use of intermittent reaches of this stream.
3. Because of higher discharge and bed scouring at the downstream site, we predicted that the fish assemblage would have lowered species richness and abundance following floods. In contrast, we expected increased species richness and abundance at headwater sites because floods increase stream connectivity and create the potential for colonisation from downstream reaches.
4. Akaike Information Criteria (AIC) was used to select among candidate regression models that predicted species richness and abundance based on Julian date, time since floods, season and physical habitat at each site. At the downstream site, AIC weightings suggested Julian date was the best predictor of fish assemblage structure, but no model explained >16% of the variation in species richness or community structure. Variation explained by Julian date was primarily attributed to a long-term pattern of declining abundance of common species. At the headwater sites, there was not a single candidate model selected to predict total species abundance and assemblage structure. AIC weightings suggested variation in assemblage structure was associated with either Julian date or local habitat characteristics.

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5. Fishes rapidly colonised isolated or dry habitats following floods. This was evidenced by the occurrence of fishes in intermittent reaches and the positive association between maximum daily discharge and colonisation events at both headwater sites.
6. Our study suggests floods allow dispersal into intermittent habitats with little or no downstream displacement of fishes. Movement of fishes among habitats during flooding highlights the importance of maintaining connectivity of stream networks of low to medium order prairie streams.

Keywords: colonisation, drought, fish dispersal, stream connectivity, temporal variation

Introduction

Both environmental variability (Grossman, Moyle & Whitaker, 1982; Schlosser, 1982; Grossman *et al.*, 1998) and biotic interactions (Harvey, 1991; Gilliam, Fraser & Alkins-Koo, 1993; Harvey, White & Nakamoto, 2004) have been cited as important factors driving stream fish assemblage structure. However, the relative importance of these factors is likely dependent on the disturbance regime of the stream (Poff & Allan, 1995). Because prairie streams are harsh environments with unpredictable and extreme environmental conditions, assemblages are thought to be structured by abiotic factors (Poff & Ward, 1989; Dodds *et al.*, 2004; Fritz & Dodds, 2005). However, many lotic organisms are adapted to harsh conditions (Lytle, 2002; Dodds *et al.*, 2004) and can recover rapidly from disturbances, increasing the potential for biotic interactions between disturbance events. The dynamic nature of streams necessitates the need for long-term data to track the response of assemblages after disturbance events and to understand structuring forces in these systems (Grossman, Dowd & Crawford, 1990; Meador & Matthews, 1992).

Both drought and flooding can affect stream fishes. During periods of drought, biotic interactions (e.g. predation) and abiotic pressures (e.g. temperature extremes) can be intensified, resulting in a change in fish assemblage structure (Magoulick, 2000; Lake, 2003). Floods, which occur over much shorter periods of time than drought, can alter stream channel morphology, kill or displace biota downstream (Harrell, 1978; Matthews, 1986; Fritz, Tripe & Guy, 2002), or remove potential resources (Dodds *et al.*, 1996; Fritz & Dodds, 2004). Floods also can increase abundance and richness of fish assemblages in intermittent prairie streams by temporarily connecting isolated pools and creating potential movement opportunities

previously impeded by barriers (Taylor, 1997; Taylor & Warren, 2001). Although the effects of single floods or droughts have been well studied, few long-term studies have evaluated the effects of multiple floods that vary in intensity on fish assemblage structure. Moreover, because flood intensity varies with catchment area, it is also important to test the effects of flooding at different locations in a watershed.

The effects of flooding and drought should have opposite effects in headwater and downstream reaches. For example, in Midwestern streams, fish species richness should increase from low to high order streams because of increased habitat complexity and lower probability of desiccation in downstream reaches (Schlosser, 1995). Thus, drought or periods of low flow should limit fish assemblages in low order streams by reducing habitat availability. However, smaller order streams should experience fewer scouring floods and displacement of fishes, assuming that exponential increases in stream discharge associated with stream order (Leopold & Miller, 1956) are not offset by reduced gradient or increased channel width in higher order streams (Ritter, Kochel & Miller, 1995). Thus, headwater reaches may provide refugia for fishes during floods, whereas severe flooding downstream should result in a greater likelihood of displacing algae, invertebrates and fishes. Indeed, algal and invertebrate biomass after scouring floods in a prairie stream can be near zero (Dodds *et al.*, 1996; Fritz & Dodds, 2004), but the effect of this reduction in food resource availability on fish assemblage structure will depend on the recovery response of these taxa.

Based on the hydrology of prairie streams and life history of prairie stream fishes (e.g. spawning chronology), we predict the effects of floods will likely vary with intensity and season. There is likely a threshold level of flood intensity that will result in a change to fish assemblages and this threshold should

vary with catchment morphology, spatial location in the watershed and season. In Kings Creek, we predicted the likelihood of crossing such a threshold should increase from headwaters to downstream reaches and that fishes should be most vulnerable to floods in early spring or summer after spawning, as age-0 fishes are more susceptible to downstream displacement (Harvey, 1987).

We used a long-term dataset from an intermittent prairie stream to test the importance of floods on fish assemblage structure in two perennial headwater sites and one perennial downstream site separated by intermittent reaches. We hypothesised that floods should negatively impact fish species richness and abundance in the downstream reach and that floods should have a positive affect on fish abundance and species richness in headwater sites. In addition, we evaluated the effects of flood intensity and season on fish assemblage structure and the longitudinal abundance and species richness of fishes in intermittent reaches between these locations.

Methods

Study area

Kings Creek drains 3487 ha of native tallgrass prairie on the Konza Prairie Biological Station (KPBS), located in the Flint Hills region of Kansas. Long-term ecological experiments on the KPBS include a variety of fire burn regimes and stocking of American bison (*Bos bison*) in the headwaters of Kings Creek (Knapp & Seastedt, 1999). The geomorphology of the watershed is primarily limestone and shale bedrock (Oviatt, 1999). Discharge in Kings Creek is highly variable, but tends to peak during April, May and June. Intermittent reaches of Kings Creek are typically dry from late summer through winter leaving only perennial reaches as refugia for fishes (Fig. 1). Riparian vegetation is dominated by prairie grasses and shrubs in the headwaters and gallery forest in the downstream reaches. However, shrub densities have steadily increased at headwater reaches over the past 50 years (Briggs *et al.*, 2005). Long-term monitoring occurred at sites located below two perennial headwater springs and in a downstream perennial reach. One headwater site was relatively shallow (mean depth = 0.17, range 0.07–0.48 m) compared with the other (mean depth = 0.18, range 0.07–0.32 m), and both were upstream of

intermittent reaches that were typically disconnected from the lower perennial reach, with the exception of a small (<0.5 km) spring-fed perennial reach just below the deep headwater site (Fig. 1). We typically sampled two pools at the shallow headwater site (total surface area ranged from 60 to 120 m²) and three pools at the deep headwater site (total surface area ranged from 65 to 106 m²). The downstream site typically included three pools and varied considerably more in sample area than upstream sites (110–1110 m²) during this study. Catchment area of the downstream site was 13.05 km², compared with 1.35 and 1.20 km² at the two headwater sites. Although channel slope was higher at headwater sites than the downstream site (20–30 m km⁻¹ versus 5 m km⁻¹), because the downstream site was constrained by an incised channel (mean bank full height 0.54 m, range 0.4–1.5 m; and mean incised height 2.3 m, range 1.2–4.25 m), we assumed the downstream site was subjected to greater substrate scour during periods of increased discharge.

Field and habitat sampling

Fishes were sampled from pools using a single pass with a backpack electrofisher and two netters. Data from these samples are presented as density (number of individuals per square metre). The same sample reaches and pools within those reaches were visited seasonally (i.e. May, August, November and February) from 1995 to 2005 at the two headwater sites (shallow headwater visited 37 times, deep headwater 37 times) and from 1997 to 2005 at the downstream site (29 visits). Fishes were identified, counted and measured (TL to the nearest mm) on site and released. Because of the narrow width of the stream channel at the sample sites our electrofishing efficiency was likely high (e.g. Kruse, Hubert & Rahel, 1998). In Kings Creek, Bertrand, Gido & Guy (2006) found that fish densities from a first pass backpack electrofishing sample were highly correlated ($r > 0.78$, $n = 31$) with densities from second or third passes. They also found that cumulate species richness did not increase after the first pass electrofishing in pools with fewer than six species (i.e. headwaters) and increased by no more than two species in pools with six or more species. Thus our effort was considered to be an effective estimate of population trends and species richness.

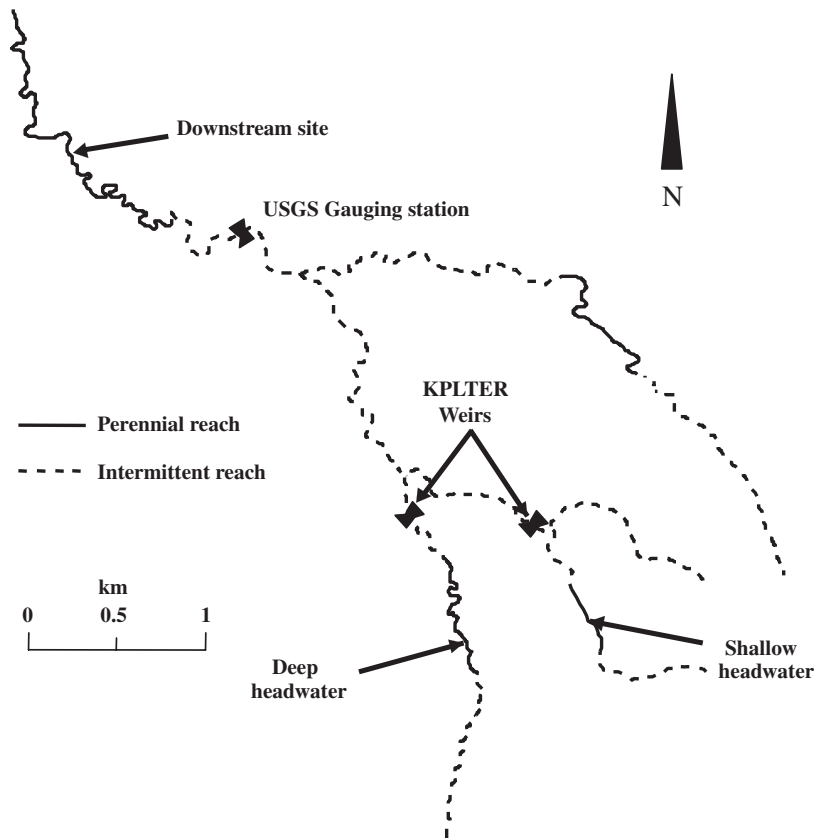


Fig. 1 Fish assemblage and discharge monitoring sites on Kings Creek, Riley County, KS, U.S.A.

Following fish collections, current velocity ($\pm 0.1 \text{ cm s}^{-1}$ at 60% water depth; FLO-MATE, Model 2000, Marsh-McBirney, Fredrick, MD, U.S.A.), depth ($\pm 1 \text{ cm}$), and substrate size [according to modified Wentworth scale (Cummins, 1962)] were recorded at five equally spaced points along three equally spaced transects in each pool to characterise physical habitat. Fish abundance (number of individuals m^{-2}), velocity, dominant substrate size, and depth were averaged across all pools for each site and date. Seasonal samples were missing at all three sites for Fall 2000, Winter 2001, Spring 2001 and Summer 2001.

To evaluate the longitudinal distribution of fishes between the three long-term sampling sites, the entire creek was sampled using single-pass electrofishing from the downstream site to the deep headwater site in 2003. A reach starting 2.0 km upstream of the downstream site to both the shallow and deep headwater sites was sampled three times in 2004. In 2003, we began sampling the day after a $2.0 \text{ m}^3 \text{ s}^{-1}$ daily maximum discharge event, and the 2004 sampling occurred 24, 5 and 13 days following 0.1, 0.2 and

$165.0 \text{ m}^3 \text{ s}^{-1}$ daily maximum discharge events [United States Geological Survey (USGS) gauging station], respectively. Fishes were identified, counted and released at approximately 100 m intervals along this reach. Catch rates were expressed as catch per unit effort (CPUE; number of individuals collected per second electrofishing).

Hydrologic data

Hydrologic data were collected from the USGS Hydrologic Station (06879650) located 4.0 km upstream of the downstream site and the Konza Prairie Long-Term Ecological Research (KPLTER) weirs 1.1 km and 1.5 km downstream of the shallow and deep headwater sites, respectively (<http://www.konza.ksu.edu>). Because of their physical design, KPLTER weirs and the USGS gauging station did not impede fish movement, (KPLTER weirs are v-notched flumes and USGS gauging station is in an open channel). The shallow headwater weir drains 1.18 km^2 , the deep headwater weir drains 1.34 km^2

and the USGS gauging station drains 10.59 km². Discharge at the USGS station and KPLTER weirs was assumed to be proportional to discharge at the sample sites because of their close proximity; however the USGS station and KPLTER weirs are in ephemeral reaches of Kings Creek. The occurrence of zero discharge at the headwater sites only reflected a lack of connectivity with downstream perennial reaches. Thus, low flow at the headwater sites that did not reach the KPLTER weirs may not have been documented and was assumed to be zero discharge. Inasmuch, zero discharge at the USGS station upstream of the perennial downstream site did not represent zero flow at the downstream reach, only low flow. During periods of flow, the daily maximum discharge at the shallow and deep headwater weirs were 47% and 77% of daily maximum discharge measured at the downstream USGS gauging station, respectively.

Data analysis

A principle components analysis (PCA) was used to capture changes in fish assemblage structure and summarise variation in species densities at the downstream site and the deep headwater site. Only species that comprised >5% of the total number of individuals collected during each sampling period were included in the analysis. Species densities were $\log_{10}(x + 1)$ transformed, centred and standardised prior to analysis. Eigenvalues and eigenvectors were based on covariance matrices of transformed species densities because variations in species abundance were similar (Grossman, Nickerson & Freeman, 1991). Too few species at the shallow headwater site precluded PCA.

To evaluate the importance of flood intensity, we tested relationships between fish assemblage structure and the number of days since four different levels of daily maximum discharge, 0.1, 0.2, 0.4 and 0.6 m³ s⁻¹. Because we predicted a threshold effect on connectivity, a range of discharge values were tested. We began with a discharge of 0.1 m³ s⁻¹ because these events displace substrates typically found in the headwater reaches of Kings Creek (Dodds *et al.*, 1996).

We created 12 candidate multiple linear regression models from environmental variables that were suspected to influence fish assemblages in Kings Creek. Models were used to predict total fish abundance,

species richness and assemblage structure. Julian date (i) was used to assess long-term trends in assemblage structure. Season (ii) was used to evaluate the effect of intra-annual change in assemblage structure associated with reproduction and growth. Time since four levels of flooding (days since a 0.1, 0.2, 0.4 and 0.6 m³ s⁻¹ flood) were included in separate models (iii–vi) to assess the influence of flooding and to identify a potential threshold effect. Because we expected flood effects to vary with size classes of fishes, we tested the interaction of time since the various levels of flooding and season in separate models (vii–x). The association of fish assemblage structure with habitat availability was tested with a model (xi) that included local habitat variables depth, velocity and substrate. The final model (xii) included all of the measured variables with the exception of time since the different flood intensities. Because of the correlation ($r > 0.70$) among these variables, only days as a 0.2 m³ s⁻¹ flood was included in this model. Other variables were not highly correlated ($r < 0.60$). The best models were selected using Akaike Information Criterion (AIC) rankings by comparing all candidate models simultaneously (Burnham & Anderson, 1998). The AIC scores were adjusted for bias because of small sample size (AIC_c) and Akaike weights (w_i) were calculated to rank the candidate models. Therefore, models with the lowest AIC_c and the highest w_i were considered the best models. Additionally, only models that had w_i values <10% of the model with the maximum w_i were interpreted (Burnham & Anderson, 1998). Only species that comprised >5% of the total number of individuals collected during each sampling period were included in total fish density calculations. Species densities were log transformed [$\log_{10}(x + 1)$] to stabilise the variance.

To test the hypothesis that high discharge increased colonisation at the headwater reaches, differences in maximum daily discharge [$\log_{10}(x + 1)$] between known colonisation events (i.e. when new species were collected at a site), and non-colonisation events were tested with *t*-tests. All analyses were conducted in SPSS 11.0 (SPSS Inc., 2001) and SAS 8.01 (SAS Institute, 2000).

Results

High flow events were more sustained (Fig. 2) and more frequent (Figs 3–5) at the downstream site than

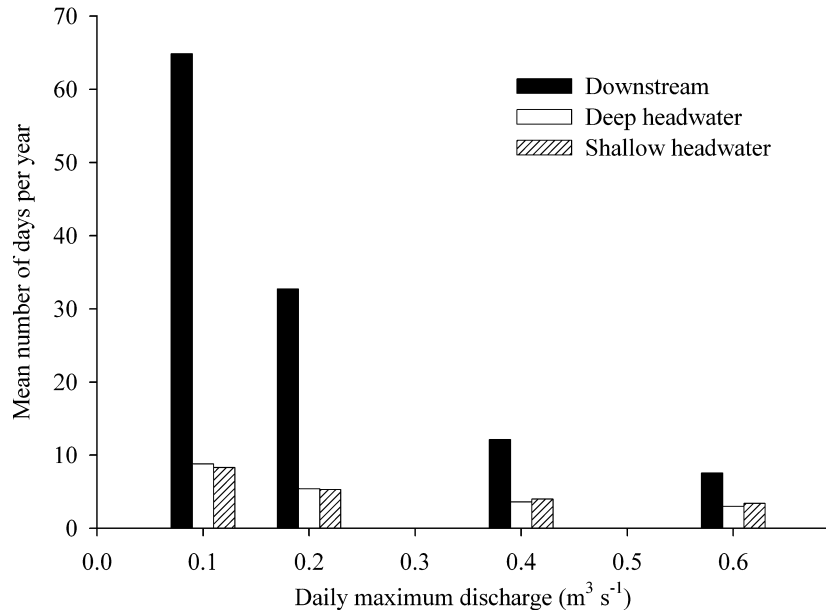


Fig. 2 Mean number of days discharge per year above four flood levels used to evaluate the response of fish assemblages for a downstream site (1997–2005) and two headwater sites (1995–2005) on Kings Creek, Riley County, KS, U.S.A.

headwater sites. In addition, 18 fish species were collected at the downstream site between 1995 and 2005 compared with five species collected at each of the headwater sites between 1997 and 2005 (Table 1). Densities of the most common species [i.e. *Semotilus atromaculatus* (Mitchell), *Campostoma anomalum* (Rafinesque), *Etheostoma spectabile* (Agassiz) and *Phoxinus erythrogaster* (Rafinesque)] were highly variable at all sites (coefficient of variation (CV) ranged between 62% and 583%; Figs 3–5). *Campostoma anomalum* was the only species consistently collected at the shallow headwater site (Fig. 4) and collections at the deep headwater site always included *C. anomalum*, *E. spectabile* and *P. erythrogaster* (Fig. 5).

Principle components analysis of the downstream site and the deep headwater site explained a large portion of assemblage variation. At the downstream site, 54.4% of the variation was explained on the first two axes (PCA axis I = 38.2%, axis II = 16.2%). PCA axis I was associated with high densities of the most common species (*S. atromaculatus*, *C. anomalum*, *E. spectabile* and *P. erythrogaster*) and axis II was associated with high densities of the less common species [e.g. *Cyprinella lutrensis* (Baird and Girard), *Lepomis cyanellus* Rafinesque and *Luxilus cornutus* (Mitchell)]. At the deep headwater site, 83% of the variation was explained with two axes (PCA axis I = 56.6%, axis II = 26.4%), where positive axis I scores were associated with high densities of *C. anomalum*, *E. spectabile* and *P. erythrogaster*, and positive

axis II scores were associated with high density of *S. atromaculatus*.

Variation in total fish abundance, fish species richness and assemblage structure was evaluated with a series of regression models ranked by AIC_c and w_i . At the downstream site, the only interpretable models predicting total fish density, PCA axis I and PCA axis II scores included Julian date. However, these models explained <16% of the variation in metrics of assemblage structure (Table 2). The association between assemblage structure and Julian data reflected a general decline in density of the most common species (PCA axis I scores), and a general increase in less common species (PCA axis II scores) through time (Fig. 6). Whereas the highest ranked models to predict species richness at the downstream site included effects of days as four different levels of floods and Julian date, these models explained <1% of the variation in the dependent variable.

At the deep headwater site, the top ranked model predicting total fish density included only the global model and explained 74% of the variation (Table 2). Top ranked models predicting PCA axis I scores included the global model (adjusted $R^2 = 0.73$), and the top ranked model predicting PCA axis II scores included Julian date (adjusted $R^2 = 0.21$). At the shallow headwater site, the candidate model that included local habitat variables (i.e. depth, velocity and substrate) was ranked highest and explained 37% of the variation in total fish density (Table 2).

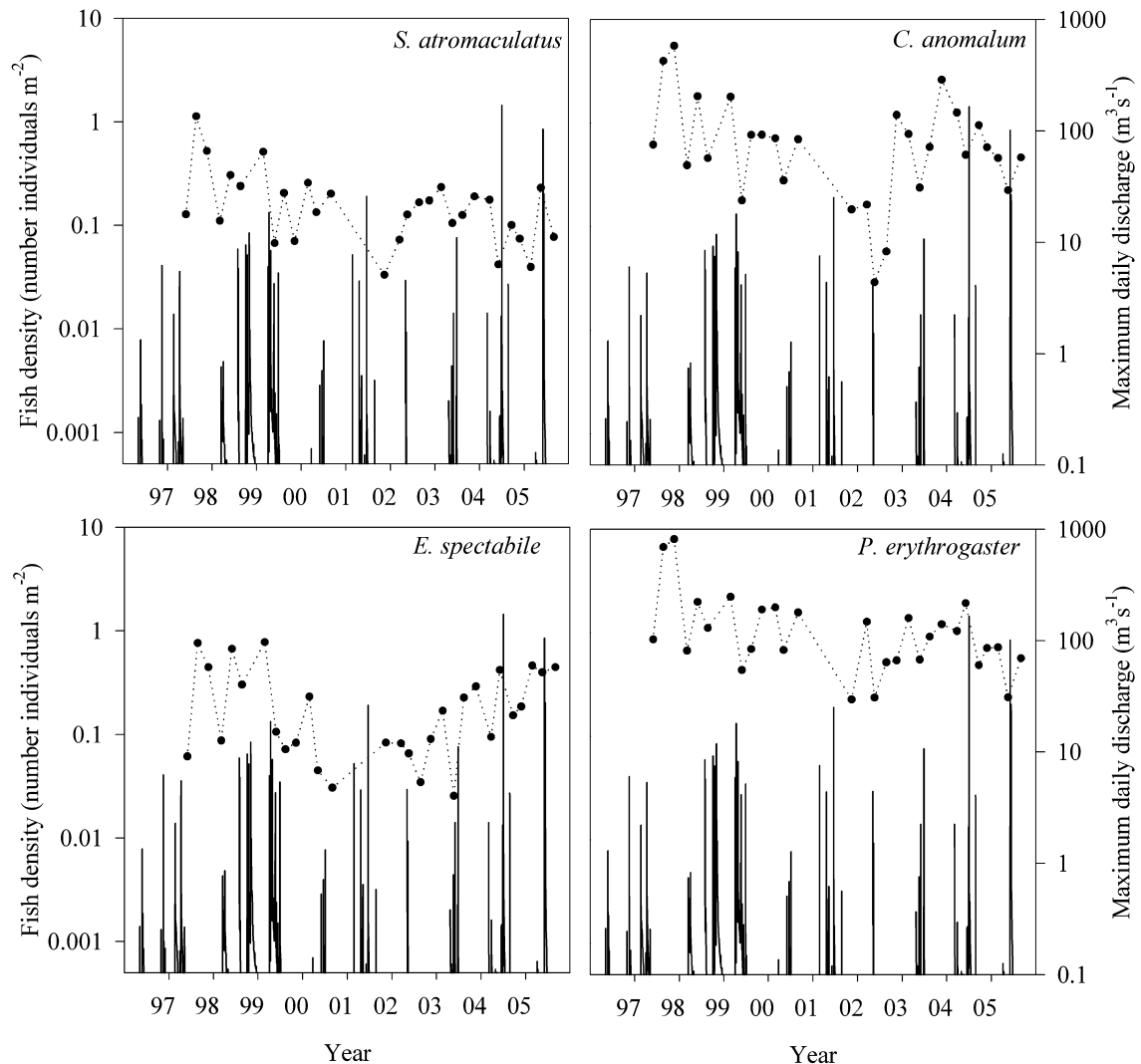


Fig. 3 Fish density (number of individuals m^{-2} ; left axis and dashed line) and maximum daily discharge ($\text{m}^3 \text{s}^{-1}$; right axis and solid line) from a downstream site 1997–2005 on Kings Creek, Riley County, KS, U.S.A. Stream discharge has had 0.001 added to facilitate plotting on a log plot.

Longitudinal sampling in 2003 and 2004 showed fishes present in varying abundances (CPUE, number of individuals collected per second electrofishing) throughout the intermittent reach in both years (Fig. 7). Total fish CPUE in some areas was comparable with catch rates in the downstream perennial reach sampled in 2003. Variability in catch rates along this reach appeared to be associated with favourable habitat (e.g. deep pools) and barriers to migration (e.g. culverts and waterfalls). Shifts in longitudinal abundances in response to flooding were evident, as catch rates were lower following floods (23 June and 16 July 2004) compared with before a flood (2 June 2004).

Twelve colonisation events were observed at the two headwater sites. Slightly fewer colonisation events were observed at the shallow headwater ($n = 5$; Fig. 4) than the deep headwater ($n = 7$; Fig. 5); however, more species were observed colonising the shallow headwater site: only *S. atromaculatus* was observed colonising the deep headwater site. Colonisation events occurred in the spring or summer for *S. atromaculatus*, *E. spectabile* and *L. cyanellus* at the shallow headwater site and *S. atromaculatus* colonised the deep headwater site once in spring, twice in winter, and four times during summer. As predicted, $\log_{10}(x + 1)$ maximum daily discharge between

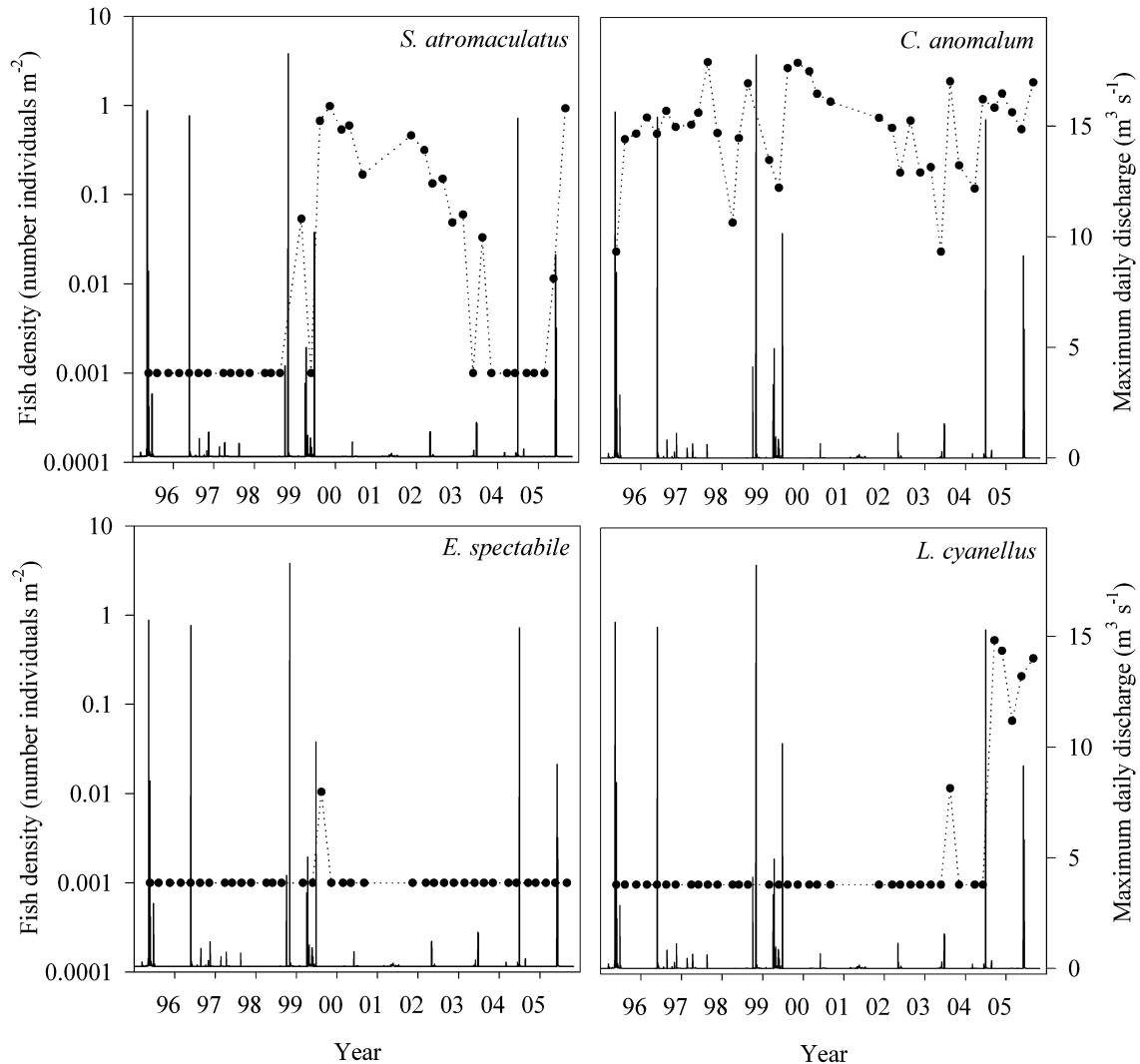


Fig. 4 Fish density (number of individuals m^{-2} ; left axis and dashed line) and maximum daily discharge ($\text{m}^3 \text{s}^{-1}$; right axis and solid line) from a shallow headwater site 1995–2005 on Kings Creek, Riley County, KS, U.S.A. Fish densities have had 0.001 added to facilitate plotting on a log plot.

sample dates was significantly higher between sample dates in which a colonisation event occurred than between samples in which no colonisation event occurred at the shallow headwater site ($t = 3.65$, d.f. = 34, $P < 0.001$) and the deep headwater site ($t = 2.33$, d.f. = 34, $P = 0.026$; Fig. 8).

Discussion

Our data did not support the hypotheses that floods would negatively affect fish species richness at the downstream site. Whereas multiple regression

models that used days since a flood to predict species richness were ranked highly using AIC, they explained very little variation in this variable (adjusted $R^2 < 0.02$). There also was no evidence to suggest total fish density or assemblage structure was associated with time since flooding. Rather, Julian date explained the majority of the variation in these variables. In general, total densities of fishes, primarily common species, have declined during the study period. In addition, as inferred from PCA scores, densities of several less common species increased (Fig. 6). Although our sampling spanned 9 years, we

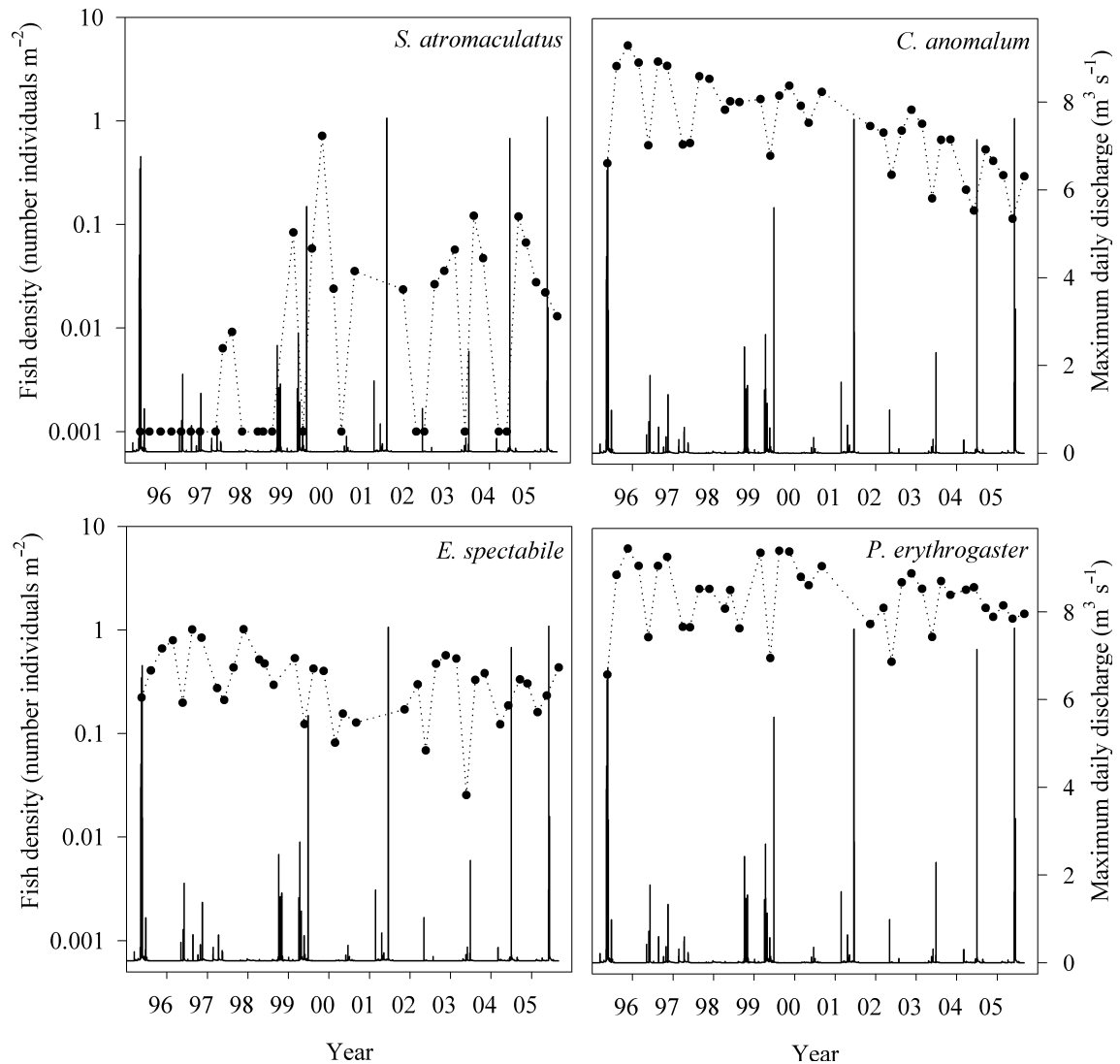


Fig. 5 Fish density (number of individuals m^{-2} ; left axis and dashed line) and maximum daily discharge ($\text{m}^3 \text{s}^{-1}$; right axis and solid line) from a deep headwater site 1995–2005 on Kings Creek, Riley County, KS, U.S.A. Fish densities have had 0.001 added to facilitate plotting on a log plot.

can only speculate on the causes of these relatively long-term changes. The sampling period (1997 to 2005) did coincide with several years of high discharge just prior to the initiation of sampling followed by several years of below mean annual discharge. More specifically, the two largest floods in the 25-year record occurred in 1993 and 1995. Both events altered stream channel morphology (e.g. elimination of a side channel) at this site and elsewhere in the basin (W. Dodds, pers. comm.). Reproductive success of common species (*S. atromaculatus*, *C. anomalum*, *E. spectabile* and *P. erythrogaster*)

may have increased during or just after these high water years because of increased habitat availability in Kings Creek. In addition, the last 6 years of sampling (2000–2005) coincided with below average annual discharge, which likely reduced habitat availability. In the absence of major floods, it is also possible these conditions favoured colonisation of some species (e.g. *C. lutrensis* and *L. cyanellus*) from downstream habitats. Hopefully, continued monitoring will allow us to rigorously test the association between climatic cycles, habitat availability and fish assemblage structure.

Table 1 Species name and number of times collected at the downstream site from 1997 to 2005 and from the headwater sites 1995–2005

Species	Downstream site ($n = 29$)	Deep headwater ($n = 37$)	Shallow headwater ($n = 37$)
<i>Campostoma anomalum</i> (Rafinesque)	29	37	37
<i>Etheostoma spectabile</i> (Agassiz)	29	37	1
<i>Phoxinus erythrogaster</i> (Rafinesque)	29	37	0
<i>Semotilus atromaculatus</i> (Mitchell)	29	18	15
<i>Catostomus commersoni</i> (Lacepede)	29	–	–
<i>Etheostoma nigrum</i> (Rafinesque)	22	–	–
<i>Cyprinella lutrensis</i> (Baird & Girard)	18	–	–
<i>Luxilus cornutus</i> (Mitchell)	12	–	–
<i>Pimephales notatus</i> (Rafinesque)	8	–	–
<i>Noturus exilis</i> Nelson	8	–	–
<i>Notropis stramineus</i> (Cope)	6	–	–
<i>Pimephales promelas</i> (Rafinesque)	6	–	–
<i>Lepomis cyanellus</i> Rafinesque	5	–	6
<i>Gambusia affinis</i> (Baird & Girard)	5	–	–
<i>Lepomis megalotis</i> (Rafinesque)	3	–	–
<i>Lepomis macrochirus</i> Rafinesque	2	–	–
<i>Lepomis humilis</i> (Girard)	2	–	–
<i>Phenacobius mirabilis</i> (Girard)	1	–	–

Table 2 Top linear models for predicting total fish density (number of individuals m^{-2}), PCA axis I and II scores and species richness at the downstream site; total fish density, PCA axis I and II scores at the deep headwater site; and total fish density at the shallow headwater site on Kings Creek as determined by Akaike Information Criterion (AIC). AIC_c is AIC values corrected for small sample size, ΔAIC_c is the difference between the highest ranked model and the candidate model, Akaike weights (w_i) sum to 1.

Dependant	Model	AIC_c	ΔAIC	w_i	Adjusted R^2
Downstream					
Density	Julian date	–59.83	0.00	0.41	0.09
Richness	0.1 $m^3 s^{-1}$ daily max	43.62	0.00	0.20	0.01
Richness	Julian date	43.68	0.05	0.20	0.01
Richness	0.2 $m^3 s^{-1}$ daily max	43.97	0.35	0.17	0.00
Richness	0.4 $m^3 s^{-1}$ daily max	44.08	0.46	0.16	0.00
Richness	0.6 $m^3 s^{-1}$ daily max	44.26	0.63	0.15	0.00
PCA axis I	Julian date	1.46	0.00	0.61	0.12
PCA axis II	Julian date	0.19	0.00	0.80	0.16
Deep headwater					
Density	Global	–103.95	0.00	0.99	0.74
PCA axis I	Global	–4.75	0.00	0.56	0.73
PCA axis II	Julian date	–3.86	0.00	0.93	0.21
Shallow headwater					
Density	Habitat	–59.37	0.00	0.97	0.37

We propose several explanations for the apparent resistance of fishes in Kings Creek to flooding at the downstream site. First, in contrast to the hypothesis that floods would cause downstream displacement, increased discharge resulted in the upstream dispersal of fish into the intermittent reaches of the stream, as seen in our sampling of the intermittent reaches. Regardless of highly incised banks at the downstream site, we believe the presence of slackwater habitats on the inside bends and backwaters at virtually all flood

stages and flooded riparian areas provide refugia for fishes during flooding (e.g. Matheney & Rabeni, 1995; David & Closs, 2002). This is supported by high densities of common species soon after floods and the presence of fish in the intermittent reach shortly after moderate and extreme (i.e. 165.0 $m^3 s^{-1}$ daily maximum discharge) floods. Whereas less common species such as sunfish (*Lepomis* spp.) may be displaced by floods, the majority of the assemblage resists displacement.

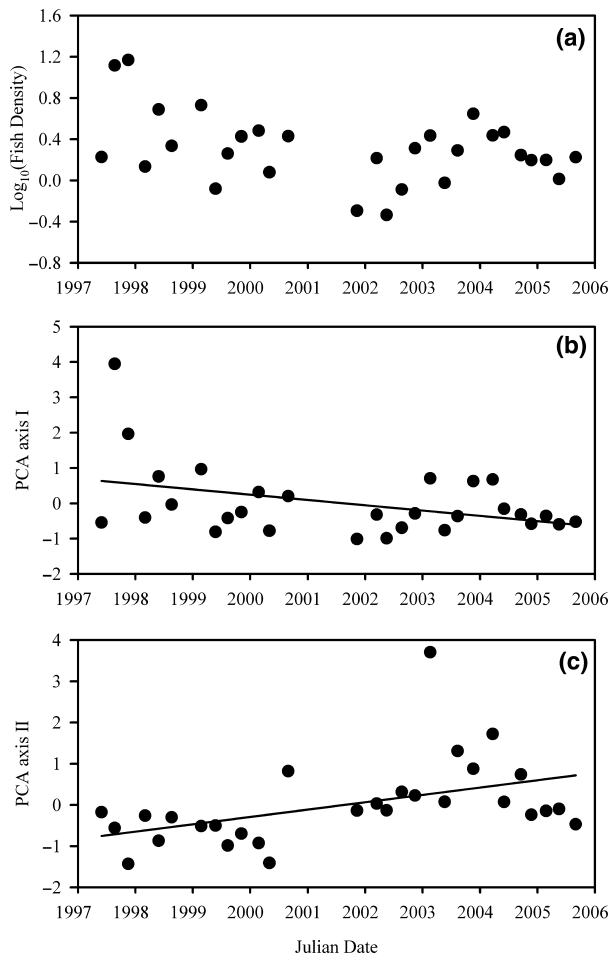


Fig. 6 Relationship between Julian date and total fish density (number of individuals m^{-2}) (a), PCA axis I scores (b), and PCA axis II scores (c) at the downstream site. Significant relationships ($\alpha = 0.05$) are represented with solid lines. PCA axis I scores were associated with the abundance of the more common species (i.e. *C. anomalum*, *P. erythrogaster*, *S. atomaculatus* and *E. spectabile*) and PCA axis II scores were associated with the less common species (e.g. *C. lutrensis*, *L. cyanellus* and *L. cornutus*).

The only evidence that floods affect assemblage structure was at the deep headwater site where the global models predicting PCA I axis scores and total fish density were ranked the highest. In general, PCA axis I scores and total fish density declined as days since flooding increased, which suggested a decline in abundance of the three common species with time since a flood. This is consistent with our prediction that floods would have a positive effect on fish density in headwater reaches.

Scouring floods alter resource availability by removing algae and macroinvertebrates (Dodds *et al.*, 1996; Fritz & Dodds, 2004), which can also influence

fish assemblages. However, these effects would be more subtle, such as a reduction in condition or reduced reproductive output and were not quantified in our study. The relative importance of resource availability will depend on the recovery rates of basal food sources in the stream after flooding. Fortunately, the recovery of algal and invertebrate communities has been well documented in Kings Creek. Dodds *et al.* (1996) monitored the recovery of algal productivity and biomass following an erosive flood and found that primary productivity returned to pre-flood rates within 20 days, but pre-flood biomass did not recover until 50 days following the flood. Fritz & Dodds (2004) showed macroinvertebrates returned to pre-flood richness and abundance 40 days following a flood in 1995. Based on these studies, it appears the availability of autochthonous resources is low for several weeks following a flood. We do not know how important this time period is to the survival of fishes, but the effect of resource depletion is presumably more stressful for smaller individuals with lower energy reserves. Several factors may alleviate these disadvantages during flooding, including dispersal into ephemeral habitats and potentially increased input of allochthonous food items (e.g. winged insects) following a flood.

It was clear that colonisation was associated with floods that connected headwater sites with perennial reaches. Whereas the deep headwater site had perennial habitat immediately below the study reach, the shallow headwater was completely isolated by a dry stream channel most of the time. Thus, colonisation of the shallow headwater site must have occurred from the downstream perennial reach, approximately 5 km downstream. Colonisation of the deep headwater might have been from either immediately below the site or from the perennial downstream reach. In either case, colonisation events were more likely when floods of relatively large magnitude occurred between sampling dates. The probability of colonisation was greatest during spring and summer but colonisation occurred in all seasons. Colonisation of upstream habitat during flooding likely benefits fishes by providing newly inundated habitat for spawning and a higher abundance of resources relative to downstream reaches that experience greater scour and potentially higher competition for resources. Tracking movements of fishes in the entire watershed may be necessary to evaluate the importance of

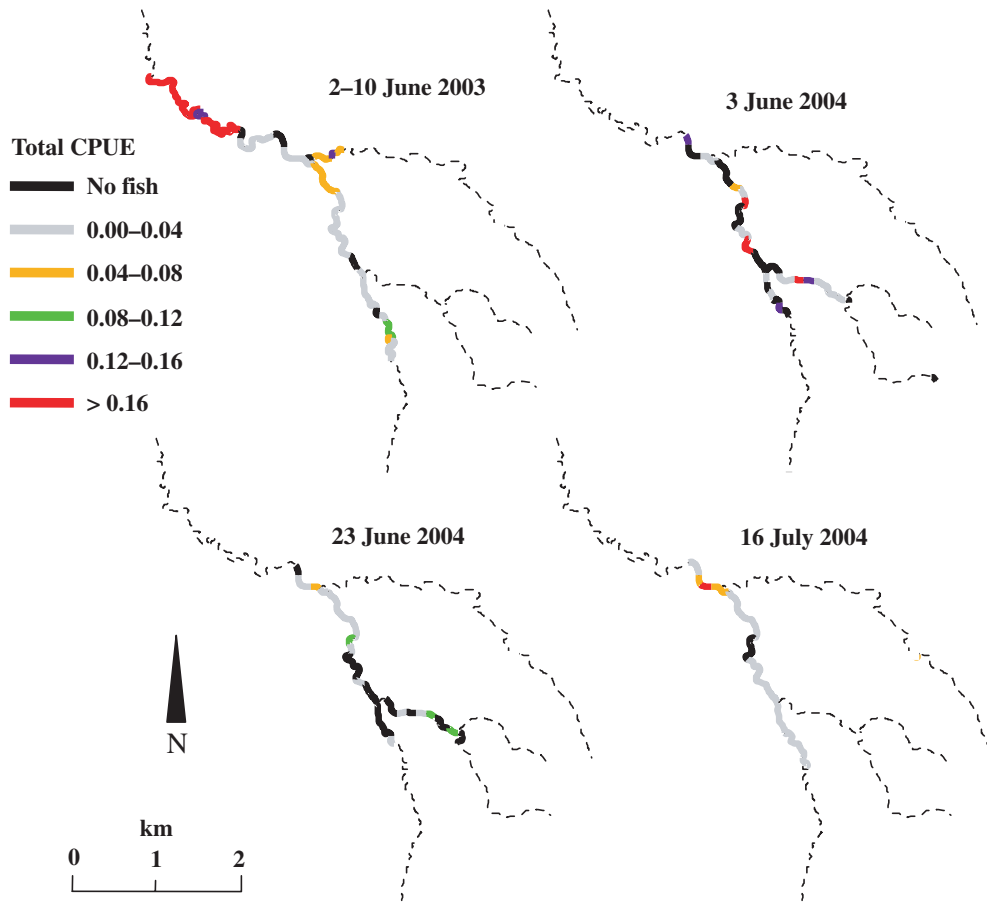


Fig. 7 Total CPUE (number of individuals s^{-1} electrofishing) longitudinally in Kings Creek, Riley County, KS, U.S.A. in 2003 and 2004. Dotted lines indicate reaches not sampled and colour of solid lines indicates abundance. The 2003 sampling began 1 day following a $2.0\text{ m}^3\text{ s}^{-1}$ daily maximum discharge, and the 2004 sampling occurred 24, 5 and 13 days following 0.1 , 0.2 and $165.0\text{ m}^3\text{ s}^{-1}$ daily maximum discharge (USGS gauging station), respectively.

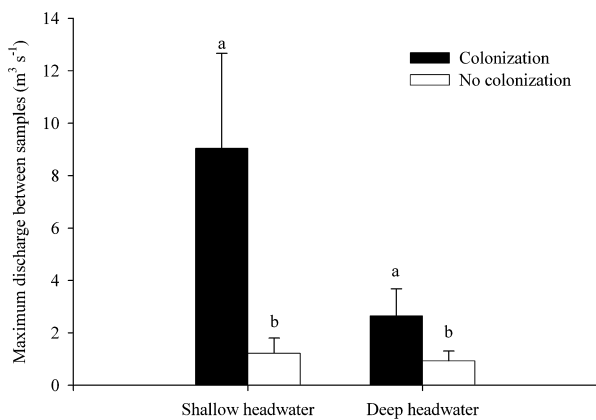


Fig. 8 Maximum daily discharge ($\text{m}^3\text{ s}^{-1}$) between samples with known colonisation and non-colonisation events in the shallow and deep headwater sites. Letters indicate significant difference ($P < 0.05$) in discharge between periods with known colonisation and no known colonisation events. Error bars represent 1 SE.

headwater reaches towards maintenance of fish populations across these habitats.

Although we could explain some of the variability in assemblage structure based on hydrology and physical habitat, a large fraction of this variability was not explained by abiotic factors. Biotic interactions also can be a major influence on prairie stream assemblage structure (e.g. Matthews, Harvey & Power, 1994), and may account for some of the variability we measured. However, no large piscivores were consistently present at our study sites. The two potential piscivores, *L. cyanellus* and *S. atromaculatus* were relatively small (*L. cyanellus* $<75\text{ mm TL}$) or are known to be primarily invertivorous in Kings Creek (C. Guy, unpubl. data). Competitive interaction among species also may explain some of the unexplained variation in assemblage structure, but

competition is rarely a dominant factor in streams (Jackson *et al.*, 2001, Grossman *et al.*, 1998) and was not quantified in our observations.

Fish assemblage structure in the headwater reaches was more closely linked to physical habitat than at the downstream site. Weak links between habitat and assemblage structure at the downstream site were likely because individual pools were highly connected with both up- and down-stream habitats, which allowed movement of fishes across pools. At the headwater sites, upstream refugia was non-existent or very limited and pools were more isolated restricting fishes to those habitats. Thus, although surface area at these headwater reaches was relatively stable because they were spring fed, they were isolated habitats and minor fluctuations in depth and surface area might have greater consequences for population stability. For example, fishes may use shallow pools in downstream reaches, but they may need deeper pools nearby to escape avian predators (Power, 1984). At the headwater sites, no such refugia existed. Moreover, substrates at headwater sites often accumulated heavy loads of sediments because of American bison activity that reduced pool depth and may have negatively affected fish densities. In general, it appeared that fish assemblages in small, isolated headwater pools were more sensitive to changes in physical habitat because they were restricted to those habitats.

The influence of floods on fish assemblage structure showed weak relationships at all levels of floods. This could potentially be attributed to our sampling dates being set by season and not sampling pre- and post-flood. Moreover, we investigated a coarse grain scale of assemblage structure (total fish density and PCA axes scores) over large time scales (months and years), perhaps losing important short-term (weeks) variation in assemblage structure. Future research should focus on the short-term response of individual species to floods in this system.

Hydrologic disturbance is likely important in structuring fish assemblages in prairie streams. However, disturbance effects will vary across streams of different size and position in the catchments. Intense floods that create harsh conditions downstream by scouring substrates may be benign in headwaters. Fishes that migrate to upstream reaches to avoid high current velocities can later colonise downstream habitats. Similarly, drought may stress or kill fishes in headwaters, but once

reconnected, fishes from downstream reaches can later colonise those habitats. Our data are consistent with this view and suggest persistence of fishes in prairie streams is dependent on their ability to disperse among habitats to avoid disturbances. Conservation of prairie stream fishes should aim to maintain connectivity of habitats and minimise the effects of human alterations such as impoundments and road culverts that fragment stream networks (Dynesius & Nilsson, 1994; Schaefer *et al.*, 2003). It also will be important to continue long-term monitoring of these assemblages across the scale of entire catchments to capture critical dynamics across space and time that influence populations throughout their life cycle (Fausch *et al.*, 2002).

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