

Influence of macroconsumers, stream position, and nutrient gradients on invertebrate assemblage development following flooding in intermittent prairie streams

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Abstract Climate change in the US Great Plains is expected to result in less frequent but more severe floods. This will affect hydrologic cycles, stream organisms, and ultimately ecosystem structure and function. We examined factors influencing invertebrate assemblages following flooding in 3 reaches (20 pools) of Kings Creek, an intermittent prairie stream on the Konza Prairie Biological Station, using replicated macroconsumer enclosures (fishless, dace, shiners, ambient). Invertebrate densities and biomass increased rapidly following scouring, including rapid colonizing taxa and relatively long-lived taxa, but macroconsumers had no significant effects. Rather, distance, which was negatively correlated with the concentration of

dissolved inorganic nitrogen, from the downstream confluence with a larger stream significantly influenced assemblage structure, with higher richness and greater nutrient concentrations closer to the confluence. Results support previous findings that recovery patterns following flooding in this grassland stream are strongly influenced by proximity to refuges. Furthermore, physical rather than biological factors appear more influential in structuring invertebrate assemblages in these frequently disturbed systems. Predicted increases in the intensity and duration of hydrologic disturbances will increase direct impacts on stream communities, relative to indirect effects through potential changes in macroconsumer communities. Human activities that alter refuges may further impede recovery following hydrologic disturbances.

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Introduction

Prairie streams experience regular cycles of drying and rewetting, creating harsh conditions for inhabitants, and repeated recovery sequences (Dodds et al., 2004). Anthropogenic changes that augment terrestrial nutrient subsidies or alter the natural flow regime or species composition might alter these recovery sequences, with important implications for the ecosystem services

that streams provide (Lake et al., 2000; Dodds & Oakes, 2008). Some climate models predict no change in mean annual rainfall amounts in the Great Plains, but the timing and intensity of precipitation events will be altered (Knapp et al., 2002; Solomon et al., 2007). For streams, this will result in longer droughts, punctuated by intense floods. Altered stream connectivity may decouple extinction and colonization dynamics of intermittent stream organisms (Larned et al., 2010), which in turn influence stream structure and function, because many stream organisms recolonize longitudinally from upstream or downstream refuges. Furthermore, nutrient loading from the watershed may disproportionately affect upper and lower trophic levels in the stream food web, causing a mismatch in the recovery rates of producers and consumers (Cushing, 1990).

Disturbance influences macroconsumer identity and abundance in prairie streams, and macroconsumers have the potential to influence recovery of stream function (Stanley et al., 2010). Fish, crayfish, and tadpoles consume detritus, primary producers, and other animals (Power, 1990; Evans-White & Dodds, 2003; Ranvestel et al., 2004), translocate nutrients (Flecker et al., 2002), and alter physical structure including substrata architecture (Creed & Reed, 2004). Macroconsumers also interact with disturbance regimes to influence ecosystem structure and function (Bertrand et al., 2009; Murdock et al., 2010). Some investigations have documented effects of macroconsumers on stream invertebrate assemblages (Rosenfeld, 2000; Peckarsky et al., 2002; Bengtson et al., 2008); others have documented recovery patterns of invertebrates following various types of hydrologic disturbances (e.g., Lake et al., 2000; Fritz & Dodds, 2004; Acuna et al., 2005; Effenberger et al., 2008). However, few have empirically examined the effects of macroconsumers on invertebrate assemblage spatial and temporal recovery patterns following hydrologic disturbance (but see Bertrand et al., 2009; Murdock et al., 2010; Effenberger et al., 2011).

Resistance and resilience are two general strategies for persistence in non-equilibrium systems such as intermittent prairie streams. Resistance is the ability to withstand a disturbance, whereas resilience is the ability to recover following a disturbance (Stanley et al., 1994; Fritz & Dodds, 2004). McMullen & Lytle (2012) estimated that floods reduce invertebrate abundance by at least 50% in a study of 41 streams

on 6 continents. Macroinvertebrates in a desert stream showed both high resistance and resilience over multi-annual hydrologic disturbance cycles (Boulton et al., 1992), and in a tropical stream in Brazil, macroinvertebrate coping strategies were typified by resilience during the variable flows of the wet season and resistance during the dry season (Rocha et al., 2012). Evidence from prairie streams suggests that invertebrates are generally more resilient than resistant (Hax & Golladay, 1998; Fritz & Dodds, 2004), but underlying factors are not well-studied. For example, longitudinal stream position affects ecosystem productivity and invertebrate and fish assemblage structure (Vannote et al., 1980), and continuum patterns can vary with region. Prairie streams typically have open-canopied headwaters and gallery-forested middle reaches, which results in greater algal biomass (net autotrophic) in the headwaters than in the middle reaches (net heterotrophic) (Whiting et al., 2011). However, we are unaware of any studies of the effect of macroconsumers on invertebrate assemblage structure and recovery from disturbance along a continuum from headwaters to confluence with a larger stream. Nutrient concentrations and distance from perennial refuges can be important predictors of invertebrate assemblages; recovery should be most rapid near refuges and in reaches with elevated dissolved inorganic nutrient concentrations. Distance from refuge has a direct effect on the rate of recolonization, whereas nutrient concentrations have an indirect effect on macroinvertebrate densities, mediated by canopy cover and increases in periphyton biomass (Robinson et al., 2011). Furthermore, disturbance-adapted organisms may be more or less successful in their strategies to cope with altered disturbance regimes (Lytle & Poff, 2004).

Our overall goal was to use field manipulations in conjunction with natural hydrologic disturbance events to evaluate drivers of invertebrate assemblage structure following scouring floods in an intermittent prairie stream. Specifically, we addressed two key questions: (1) What are the general recovery patterns of prairie stream invertebrate communities following floods? (2) Do macroconsumers (fish, tadpoles, crayfish), stream position (e.g., distance to refuges), or components of ecosystem structure (e.g., algal biomass) influence invertebrate assemblage recovery patterns? Our prior investigations indicated that ecosystem functioning (e.g., primary productivity) in

prairie streams typically rebounds to pre-disturbance rates within 1 month following a flood (Bertrand et al., 2009) or drought (Murdock et al., 2010). Thus, we predicted that a complex community consisting of more early colonizing taxa (*r* strategists) than longer-lived *K* strategists would develop within that time frame. Furthermore, we expected that community structure could vary as a function of stream permanency, which varies from spring-fed perennial headwaters to intermittent middle reaches to perennial downstream reaches. We predicted that macroconsumer effects on invertebrate recovery following flooding would be greater nearer to the confluence, where macroconsumer density and richness are the highest (Franssen et al., 2006). We also predicted algal biomass would be the greatest nearest to the confluence, resulting from openings in the riparian canopy with wider stream widths and increased terrestrial nutrient loading lower in the watershed (Bertrand et al., 2009).

Methods

Study site

Kings Creek is an intermittent prairie stream draining the Konza Prairie Biological Station (KPBS) in the Flint Hills region of northeastern Kansas, USA. Gray et al. (1998b) and Gray et al. (1998a) provide detailed physicochemical and biological descriptions of Kings Creek. Kings Creek is typical of lower order streams in this region, and is characterized by frequent and sometimes severe floods and droughts (Dodds et al., 2004).

We conducted an experiment to evaluate the effect of macroconsumers on invertebrate structure in three reaches of Kings Creek (Fig. 1): an ephemeral spring-fed headwater reach (SFH; $N = 8$ pool enclosures), an intermittent middle reach (IM; $N = 8$ pool enclosures), and a perennial downstream reach (PD; $N = 4$ pool enclosures). The mouth of Kings Creek forms a confluence with McDowell Creek, from which we measured river km distance to each of our pool enclosures to use as an index of distance from a downstream colonist pool. Upstream colonization is by air along the riparian corridor. Temperature is influenced by groundwater inputs and varied by reach during our study with SFH ranging from 15 to 31°C

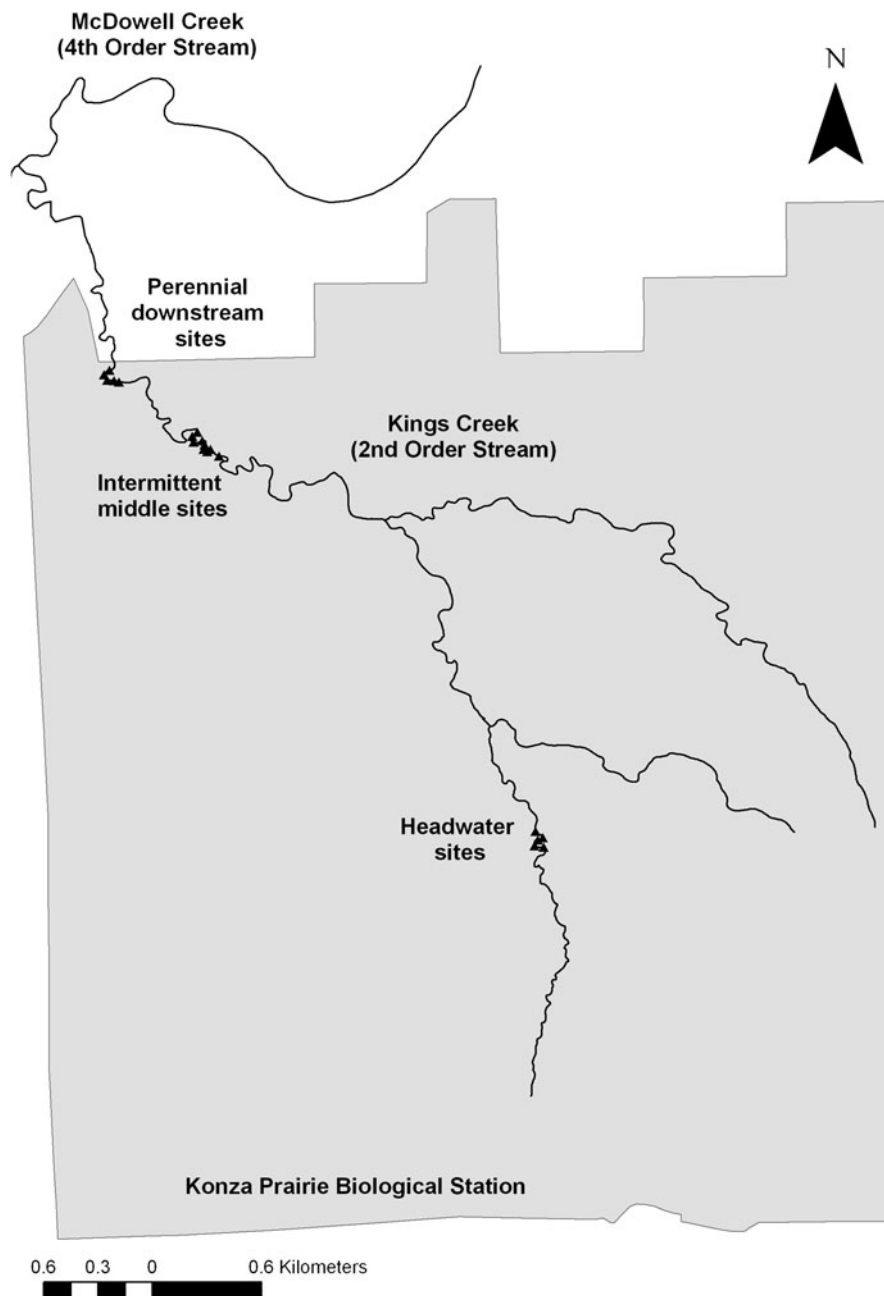
(mean = 22°C), IM from 14 to 24°C (mean = 18°C), and PD from 16 to 38°C (mean = 19°C). Ambient stream nutrient concentrations are influenced by agriculture in the watershed and increase downstream with mean dissolved inorganic nitrogen concentrations of 41 $\mu\text{g l}^{-1}$ in the SFH, 84 $\mu\text{g l}^{-1}$ in the IM, and 444 $\mu\text{g l}^{-1}$ in the PD during the study period. Surface area, depth, and discharge increased from the SFH to the PD reach and varied through the study period.

Fish assemblages in Kings Creek are numerically dominated by two grazing minnows (*Camptostoma anomalum* [central stoneroller; natural densities in Kings Creek are highly variable ranging from 0 to 7 fish m^{-2}]) and *Phoxinus erythrogaster* [southern redbelly dace; 0–8 fish m^{-2}]) and the orangethroat darter (*Etheostoma spectabile*; 0–1 fish m^{-2}) (Franssen et al., 2006). Red shiners are regionally abundant, but only occur in the lower reaches of Kings Creek in low abundance (detected at densities less than 1 fish m^{-2} during 18 of 29 sampling events in PD reach; Franssen et al., 2006; Bertrand unpublished data). Grazing invertebrates, including numerous insect taxa, crayfish (*Orconectes* spp.) and snails (*Physa* and *Physella* spp.) also are abundant in Kings Creek (Gray et al., 1998a). The macroinvertebrate assemblage in Kings Creek varies in functional composition from headwaters to downstream areas (Whiting, 2009). Invertebrate production is dominated by collector-gatherers (e.g., Chironomidae and Oligochaeta) in open-canopy reaches and collector-gatherers and shredders (e.g., *Tipula abdominalis* (Say)) in closed-canopy reaches (Stagliano & Whiles, 2002; Whiting, 2009).

Post-flood sampling

Pool enclosures were constructed in 20 pools in Kings Creek to characterize the recovery of stream ecosystem properties after a natural flood. Between 11 and 25 July 2005, pool surface area ranged from 11.2 to 62.5 m^2 (mean = 35.8 m^2), pool depth ranged from 0.13 to 0.31 m (mean = 0.21 m), and discharge ranged from 1.9 to 35.4 l/s (mean = 12.4 l/s). Substrata in the study pools were predominately gravel (2–16 mm; 59%) and pebble (16–64 mm; 32%). We assessed relative substrata disturbance intensity among reaches by monitoring rock movement following a 5 m^3/s flood on 4 June 2005. Rocks with an average length between 3 and 28 cm were removed

Fig. 1 Map of study area showing study pools (triangles) in Kings Creek in 2005



from King's Creek and marked with pink paint. Five size classes (3–5, 6–10, 11–15, 16–20, and 21–28 cm length) were put in the SFH, IM, and PD reaches and the location of each rock recorded. At each site, we put out 15 rocks in each in the smallest 2 size classes, 10 in the middle size class, and 5 in each of the largest size classes. This uneven distribution was due to the likelihood of not recovering smaller rocks. On 7 June,

we located marked rocks and measured the distance moved.

Following 2 consecutive floods (5.5 m³/s flood on 4 June 2005 and 2.1 m³/s flood on 10 June 2005, Fig. 2), we installed 5-mm mesh steel hardware cloth barriers (secured to steel poles and buried 20 cm into the stream bed) at the upstream and downstream ends of each study pool. Each study pool was approximately

12–20 m long. A detailed description of the pool enclosures is available in Bertrand et al. (2009). Discharge steadily decreased following the second flood and there were no additional precipitation events or increases in discharge. Enclosures were installed in the SFH on 14 June and in the IM on 16–17 June and in the PD on 21 June. The staggered start date among reaches was a result of gage height and water velocity levels declining sooner at upstream sites, allowing earlier access to the stream to install enclosures and begin sampling at the upstream reach sites. Pool enclosures were assigned one of four treatments: no fish, ambient fish assemblage enclosure, southern redbelly dace enclosure, or red shiner (*Cyprinella lutrensis*) enclosure. The experiment started on 15 June 2005 in the SFH and ~1 week later at the IM and PD reaches; the experiment ran for 5 weeks in all three reaches, ending on 18 July in the SFH and 25 July in the IM and PD reaches.

We removed fish and crayfish from pool enclosures using multiple passes with a backpack electrofisher and seines at the beginning of the experiment. All fish and crayfish were returned to ambient treatment pool enclosures, whereas dace and shiner treatment enclosures were stocked with only dace or shiner (no crayfish) at densities of 8 fish/m². Crayfish were not returned to no fish enclosures. Typical total fish densities in Kings Creek are approximately 8 fish/m² (Franssen et al., 2006); however, densities of dace

>6 fish/m² are considered high in Kings Creek and red shiners generally occur at lower densities than dace in all three study reaches, but are most abundant in the PD reach (Franssen et al. 2006).

We were unable to fully prevent movement of fish and other organisms in some pool enclosures; young-of-year fishes migrated through the wire mesh, and crayfishes and some fishes burrowed under pool enclosure barriers. Thus, we used a backpack electrofisher to survey fish assemblages and remove invaders on week 2. In addition, we conducted population censuses at the end of the experiment to confirm that each treatment assemblage had been maintained. One pool enclosure barrier was lost to beaver activity and another pool enclosure dried up in week 6; data from these two pool enclosures following these events were excluded from analyses.

Data collection

We used a 0.018 m² core sampler fitted with an electric pump (0.1 l/s) to collect invertebrates from the substrata. Substrata from 0 to 15 cm below the substrata-water interface inside the corer were agitated by hand until 8.5 l of water was pumped to a bucket. Samples were then passed through a 250 μm mesh sieve to retain invertebrates. Five replicate core samples were collected from each pool enclosure along equally spaced transects in weeks 1 and 5.

We identified invertebrates to the lowest practical taxonomic level, typically genus, except for Chironomidae (tribe or subfamily) using keys provided in Merritt & Cummins (1996). Dense samples were occasionally subsampled up to 1/8 original volume using a Folsom wheel. We estimated biomass by measuring individual body lengths and applying published length-mass relationships (Benke et al., 1999) or relationships we developed using methods of Benke et al. (1999). We calculated mean generation time by first summing the biomass of invertebrates in each of four categories (poly-, bi-, uni-, or semivoltine), and then weighting the average of turnover by biomass.

Algal biomass was estimated as the concentration of chlorophyll *a* extracted from substrata baskets. Each pool contained 30 plastic mesh baskets (10 cm × 10 cm × 10 cm) filled with dried pebbles (16–64 mm) from the stream bank. Baskets were arranged into three rows of ten baskets perpendicular

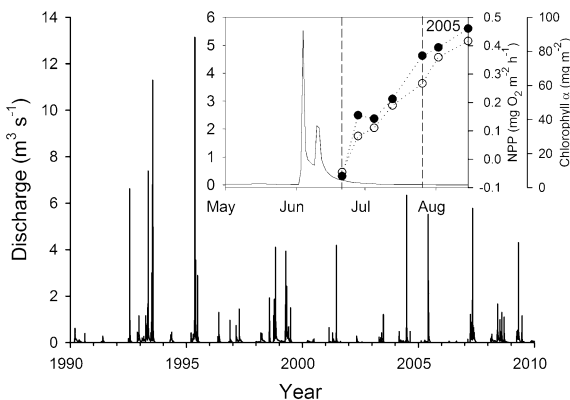


Fig. 2 Twenty-year Kings Creek hydrograph highlighting the two consecutive scouring events (5.5 and 2.1 m³ s⁻¹) that initiated the post-flood study in 2005 (*inset*). The *inset* panel also illustrates the trajectories of benthic net primary productivity (*closed circles*) and benthic chlorophyll *a* (*open circles*), and the *vertical dashed lines* indicate the invertebrate sampling intervals

to the channel in the downstream half of the enclosure to maximize the influence of nutrient remineralization by fishes. Baskets were buried ~ 10 cm in the streambed so tops were flush with the stream bottom. Three baskets were randomly selected from each enclosure in week 1 and 5 and returned to the laboratory in sealed plastic containers within 2 h of collection. Chlorophyll *a* was extracted by submerging baskets in a 78°C, 95% EtOH solution for 5 min as described in Sartory & Grobbelaar (1984). Extracts were analyzed for chlorophyll *a* with a Turner Model 112 fluorometer (Turner Designs Inc., Sunnyvale, CA, USA) using an optical configuration optimized for the analysis of chlorophyll *a* without phaeophyton interference (Welschmeyer, 1995). Algal biomass was reported as chlorophyll *a* per m² (surface area of the substrata basket opening).

Statistical analyses

We simultaneously examined the development of invertebrate assemblages 1 and 5 weeks post-flood, spatial location of study pools, and the effect of macroconsumers using a permutational multiple analysis of variance (MANOVA) (Anderson, 2001). This allowed us to partition Bray–Curtis distance matrices among interactions and main effects of time since disturbance, distance from confluence, and macroconsumer treatment, using permuted pseudo-*F* ratios. Experimental units for evaluating effects of macroconsumers were pools, and experimental units for evaluating effects of flood were core samples. Pseudo-*F* ratios with $\alpha = 0.05$ were based on 1000 permutations and run using the *vegan* (*adonis*) package in software R (version 2.9.1). Before performing the permutational MANOVA on invertebrate densities, we removed taxa with total abundance less than two individuals across all samples (Marchant, 1999) and then log-transformed data to correct for heteroscedasticity. We examined patterns in the multivariate data with a distance-based ordination principle coordinates analysis (PCoA).

We further examined the effect of time since flood using paired sample *t*-tests on invertebrate mean generation time, richness, evenness, and total biomass. We used linear regression to evaluate the influence of distance from confluence on invertebrate richness, evenness, and total biomass, and to test the association between total invertebrate biomass and algal biomass.

Finally, difference in substrata disturbance were only analyzed for the larger three size classes as low recovery of the smaller rocks precluded statistical test on the smaller two groups. We used the non-parametric Wilcoxon multiple comparison method to compare rock movement among sites.

Results

Following the flood, macroconsumer treatments did not explain a significant portion of the variation in invertebrate assemblages for any of the pool enclosure treatments (density: pseudo- $F_{1,106} = 1.27$, $P = 0.25$; biomass: pseudo- $F_{1,106} = 1.42$, $P = 0.20$). Bray–Curtis distances between invertebrate assemblages were as great as or greater within macroconsumer treatments than among macroconsumer treatments, and we were unable to discern treatment patterns in the ordinations of density or biomass data with Principle Coordinates Analysis. Rather, there was a strong interaction between reach and week of experiment for invertebrate density (pseudo- $F_{1,106} = 3.12$, $P < 0.01$; Fig. 3) and significant main effects of reach and week on biomass (reach pseudo- $F_{1,103} = 9.43$, $P < 0.01$; week pseudo- $F_{1,103} = 14.47$, $P < 0.01$; Fig. 4). For invertebrate density, the first ordination axis distinguished samples by location and time; more upstream samples (spring-fed headwaters; SFH) and first week samples generally had more negative scores (Fig. 3). Variation along both axes corresponded with time; samples taken in the first week of the experiment were, on average, slightly nearer the left and top of the ordination plot than those taken in the fifth week of the experiment. On axis 1, assemblages in the SFH in week 5 were similar to IM and PD sites in week 1. For biomass, the first axis corresponded with time and reach, with samples on the left side from week 1 and samples on the right side generally from week 5, and with SFH sites with more negative scores than IM sites (Fig. 4). The second axis corresponded with reach, with upstream samples near the top and downstream samples (perennial downstream; PD) near the bottom of the ordination.

Some relatively long-lived taxa colonized rapidly and were abundant components of the post-flood assemblage. However, mean generation time of all macroinvertebrates from all sites generally increased from week 1 to week 5 (Fig. 5). Non-Tanypodinae

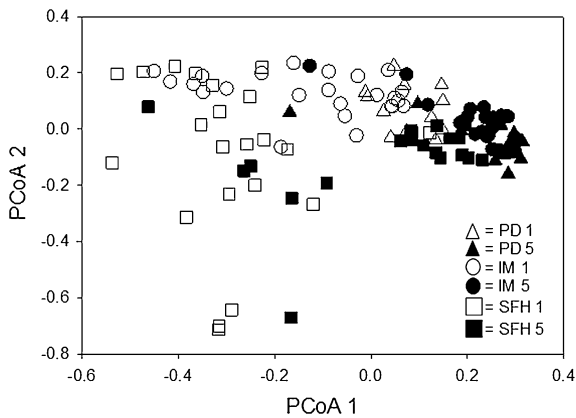


Fig. 3 Ordination of invertebrate assemblages (densities) in samples collected during June and July 2005 from Kings Creek on the Konza Prairie following a scouring flood. The ordination is from principle coordinates analysis (PCoA) of sample distances based on Bray–Curtis dissimilarity. Samples are from weeks one (*open symbols*) and five (*filled symbols*) of the experiment and were collected in three reaches of the stream: perennial downstream (PD), intermittent middle (IM), and spring-fed headwaters (SFH)

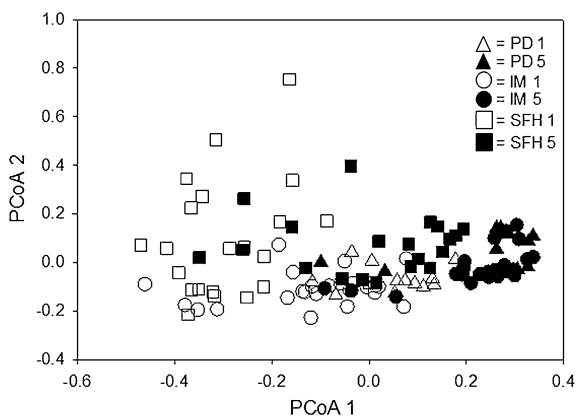


Fig. 4 Ordination of invertebrate assemblages (biomass) in samples collected during June and July 2005 from Kings Creek on the Konza Prairie following a scouring flood. The ordination is from principle coordinates analysis (PCoA) of sample distances based on Bray–Curtis dissimilarity. Samples are from weeks one (*open symbols*) and five (*filled symbols*) of the experiment and were collected in three reaches of the stream: perennial downstream (PD), intermittent middle (IM), and spring-fed headwaters (SFH)

chironomids (Diptera) comprised the greatest percentage of total density during weeks 1 and 5 post-flood (Fig. 6), and in each of the three reaches their density decreased from week 1 to week 5. Overall, density of non-Tanypodinae Chironomidae decreased as distance from the confluence increased. Elmidae larvae

(Coleoptera) and Oligochaeta were abundant in weeks 1 and 5 in the spring-fed headwater reach, but not downstream near the confluence (Fig. 6). Cyclopoid copepods increased in density from week 1 to week 5 in the intermittent middle reach, but comprised <5% of the assemblage in the other two reaches. Cambaridae crayfish had the greatest overall biomass, but trends in their biomass varied by reach (Fig. 6). Week 1 crayfish biomass was similar in the intermittent middle and perennial downstream reaches; crayfish biomass in both of these reaches increased from week 1 to week 5, with the greatest overall crayfish biomass in the intermittent middle reach. In contrast, crayfish biomass in the spring-fed headwater reach decreased from week 1 to week 5. Dytiscidae adults (Coleoptera) were one of the top 3 contributors to total biomass during week 1 in the spring-fed headwaters and the perennial downstream reaches, but their larvae, and not the adults, were among the top 5 contributors to biomass during week 1 in the intermittent middle reach (Fig. 6).

Assemblage richness decreased with distance from the confluence and Shannon diversity was similar among reaches. Assemblages located 2.7 to 3.6 km (PD and IM reaches) from the confluence averaged 5 more species than assemblages that were more than 7.5 km (SFH reach) from the confluence in the first week post-flood (Fig. 7a; $r^2 = 0.65$, $df = 19$, $P < 0.01$), and in the fifth week post-flood the closer sites still averaged 4 more species than more distant assemblages ($r^2 = 0.47$, $df = 18$, $P < 0.01$). Shannon

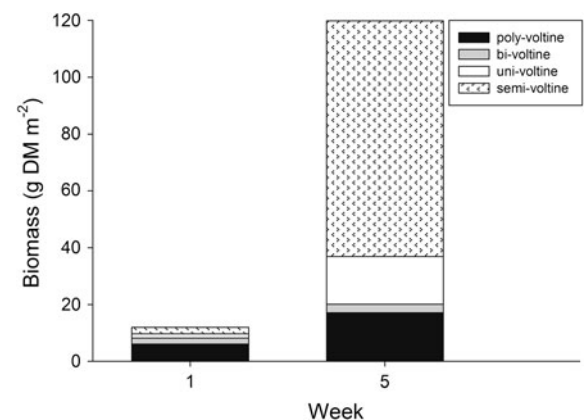


Fig. 5 Biomass of invertebrate taxa collected during June and July 2005 from Kings Creek on the Konza Prairie following a scouring flood. Plotted data include taxa that comprised at least 5% of the total assemblage and represented 4 different life histories: poly-voltine, bi-voltine, uni-voltine, and semi-voltine

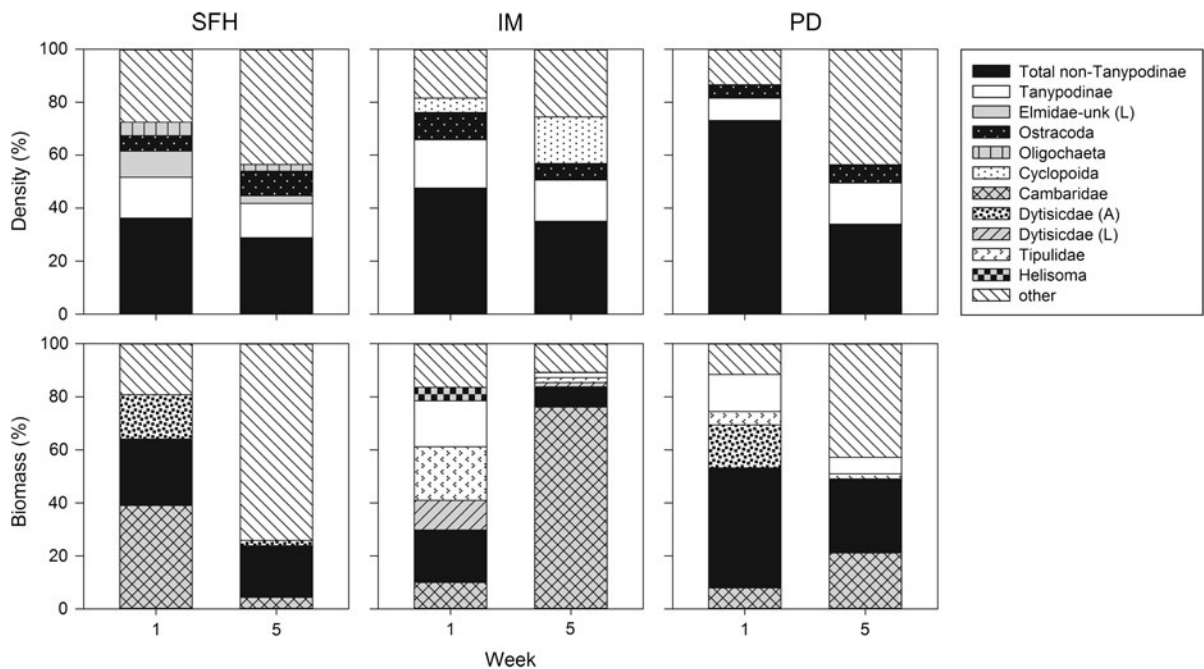


Fig. 6 Percent contribution to density (*upper panels*) and biomass (*lower panels*) of the taxa representing at least 5% of the assemblage in weeks 1 and/or 5 post-flood in Kings Creek in 2005. *Left column panels* illustrate data from the spring-fed headwater reach (SFH), *middle column panels* illustrate data from the intermittent middle reach (IM), and *right column panels* illustrate data from the perennial downstream reach (PD). Dytiscid (A) refers to adults, whereas dytiscid (L) refers to larvae. Note that fill patterns and legend apply to all panels of the figure. Other taxa, which each comprised less than 5% of the

assemblage in weeks 1 and/or 5, included Isopoda, *Baetis*, Leptophlebiidae, *Stenonema*, Amphipoda, Polycentropodidae, *Physa*, Ceratopogoninae, Chironomidae (pupa), Tabanidae, Hydracarina, Baetidae (unk), Hydroptilidae, Hydropsychidae, Hypogastruridae, Calanoida, Harpacticoida, Hydrobiidae, Elmidae (unk-A), Leuctridae, *Sphaerium*, *Sialis*, *Placobdella*, Nematoda, Circulionidae (L), *Lymnaea*, *Caenis*, *Callibaetis*, Calopterygidae, Chydoridae, Corixidae, Culicidae, Gomphidae, Hydrophilidae (A), *Peltodytes* (L), Planaria, Saldidae, *Stenelmis* (L), and *Trepobates*

diversity was greater at all sites in week 5 than in week 1 (mean difference = -0.34 ; $t_{18} = -4.54$; $P < 0.01$) and tended to increase with distance from the confluence (Fig. 7b), but there was no significant effect of distance on Shannon diversity ($r^2 = 0.32$, $df = 18$, $P = 0.91$). The decrease in invertebrate biomass with distance from the confluence was not significant (Fig. 7c). Total invertebrate biomass across all sites was 10 times higher in week 5 than in week 1 ($t_{18} = -2.42$; $P = 0.03$).

Streambed scour increased from the SFH to PD reach, with IM and PD having similar substrata movement intensity. Rocks in the largest size class moved an average distance of 9.5 m (SD = 8.9), 34.4 m (SD = 32.7), and 47.8 m (SD = 6.9) in the SFH, IM, and PD reaches, respectively. There was a significant difference in large rock movement between the SFH and PD reaches ($Z = 2.09$, $P = 0.037$), but not between SFH and IM ($Z = 1.59$, $P = 0.113$), or

IM and PD ($Z = 0.09$, $P = 0.376$). The same trend was observed for the 11–15 cm class [SFH and IM ($Z = 2.96$, $P = 0.003$) and IM and PD ($Z = 2.81$, $P = 0.005$)], but differences were only marginally significant for the 16–20 cm size class between the SFH and IM ($Z = 1.74$, $P = 0.08$) and IM and PD ($Z = 1.74$, $P = 0.08$) reaches.

Overall, net primary productivity and algal biomass estimated in the same pools during the same period increased rapidly in the first 2 weeks after the flood, then slowed 3–5 weeks post-flood (Fig. 2; Bertrand et al., 2009). Total invertebrate biomass was predicted by algal biomass (chlorophyll *a*) in week 1 ($r^2 = 0.30$; $P = 0.01$) but not in week 5 ($r^2 < 0.01$; $P = 0.92$), and the gradient in algal biomass tracked patterns of dissolved inorganic nitrogen concentrations in both weeks. By week 5, mean algal biomass increased almost $\times 4$ from the SFH through the IM to the PD reaches (from 34 to 58 to 115 mg m^{-2} chlorophyll α),

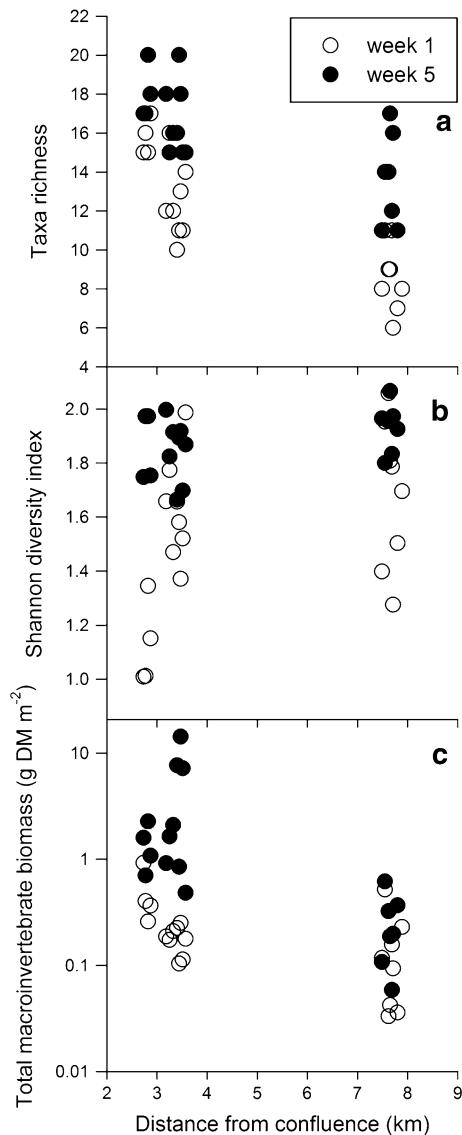


Fig. 7 Scatterplot of taxa richness (a), Shannon diversity (b), and total invertebrate biomass (c) versus distance upstream from the confluence of Kings Creek and McDowell Creek in 2005

and dissolved inorganic nitrogen increased an order of magnitude over the same distance during the same period (from 41 to 84 to 444 $\mu\text{g l}^{-1}$).

Discussion

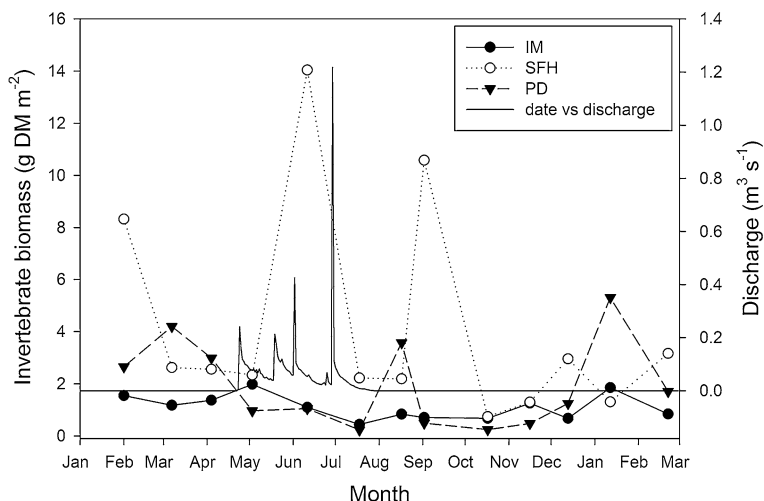
Recovery patterns

Community response varies according to the intensity and/or duration of a disturbance event (Kennen et al.,

2010) and is a function of organismal survival strategies and recovery times (Wallace, 1990; Stanley et al., 1994; Swanson et al., 1998; Effenberger et al., 2008). Although floods have a relatively short duration in these systems, scouring by floods can be extreme (Dodds et al., 2004), resulting in removal of most organisms from a given stream reach and eventual recolonization following flooding (Fritz & Dodds, 2004). Once discharge begins to decline, stream organisms that persist in the reach can make relatively short lateral migrations (meters) or vertical migrations from the hyporheic (Stubbington, 2012) back toward the main channel, which increases community resistance to floods relative to droughts (Mackay, 1992; Matthaei et al., 1996). Our data suggest that distance from the confluence was an important driver of invertebrate assemblage structure, so in prairie streams such as Kings Creek, longitudinal movements (in this case aerial dispersal by adults upstream) may be more important than lateral movements for recolonization. For example, both the PD and IM reaches have similar substrata scour, but total invertebrate biomass was higher in the PD reach than in the IM or SFH reaches during the first week of this study (Fig. 7), and during a $1.2 \text{ m}^3 \text{ s}^{-1}$ flood in this system in July of 2003, biomass also was the highest in the PD reach (Fig. 8).

Community response to disturbance often relates to pre-disturbance conditions. Our study was not designed to evaluate this factor, and thus, we did not collect invertebrate data pre-flood in 2005. However, Whiting et al. (2011) provided data, which we used to indirectly address the effect of pre-flood conditions on invertebrate recovery (Fig. 8). Monthly invertebrate samples were collected from February 2003 through February 2004 in the same three reaches of Kings Creek. In only 4 of the 13 months, biomass was higher in the downstream reach than in the other two upper reaches, and overall maximum biomass was actually collected from the most upstream reach ($\geq 0.85 \text{ mg DM cm}^{-2}$), which was approximately twice as high as maximum biomass recorded over the same period from the most downstream reach ($\sim 0.45 \text{ mg DM cm}^{-2}$). Taxa richness in the Whiting et al. (2011) study was greater in the SFH and PD reaches than in the IM reaches in all but one of the months studied. The PD reach had only marginally greater taxa richness in February, March, and April of 2003, with 1 (out of 39 total), 1 (out of 38), and 2 (out of 37) more taxa than

Fig. 8 Biomass of invertebrates collected monthly from three reaches of Kings Creek during 2003–2004 (Whiting et al., 2011), relative to daily mean discharge during the same period. The intermittent middle reach (IM; closed circles; solid line), the headwater reach (HW; open circles; dotted line), and the perennial downstream reach (PD; closed triangles; dashed line) were the same as those sampled in 2005



the other reaches, respectively. There were 4 spikes in discharge over the 14 month study, and all four spikes occurred in April through July of 2003 (Fig. 8). In 2005, pre-flood richness was not meaningfully higher in the lowest reach, and thus, it does not appear that pre-flood richness is a more important driver of post-flood richness than longitudinal stream position.

Life histories also provide explanations for post-flood invertebrate assemblage composition. Resilient taxa need to respond quickly to a changing environment, and many of the taxa that dominated in the weeks following the flood disturbance were characterized by rapid development times that are typical of resilient taxa. Others have life history characteristics that facilitate resistance (e.g., burrowers), and some have life history attributes that make them both resistant and resilient. Univoltine and semivoltine invertebrates were largely responsible for the increase in biomass between weeks 1 and 5 of our study (Fig. 5). Midges, including the non-Tanytopodinae chironomids that colonized our study sites rapidly, include many taxa with short, overlapping generations, and adult colonists are readily available following disturbance (Armitage, 1995). Similarly, dytiscid beetles have long-lived adult stages capable of flying considerable distances, which explains their high adult biomass in the upstream (SFH) and downstream (PD) refuges and high larval biomass in the IM reaches following the floods. Crayfish, which were dominant contributors to biomass during recovery, migrate or burrow into sediments and streambanks, rendering them relatively resistant to flood disturbances (Maude & Williams, 1983). Multivoltine cyclopoid copepods

have relatively short life cycles, particularly in warm temperatures; many can reach maturity within 2 weeks of hatching and some can complete their life cycle from egg to egg within a week (Smith, 2001; Thorp et al., 2006). Short generation times of this group may explain their relatively high densities in the IM reach.

Flow dampens macroconsumer effects

Predicting invertebrate assemblage structure following a flood depended more on time since flood and distance from refuges (i.e., the confluence), than the effect of macroconsumers. Although fishes can have strong impacts on stream invertebrates in some situations (Gilliam et al., 1989; Power, 1990; Power et al., 2008; Herrmann et al., 2012), our experiments align with studies suggesting that fishes have only weak effects on invertebrates in streams (Allen, 1951; Reice & Edwards, 1986; Ruetz et al., 2004). This is likely because refuges are more abundant and prey exchange rates among neighboring reaches are enhanced with increasing flow, diminishing the effect of macroconsumers (Cooper et al., 1990). Furthermore, a substantial temperature and nutrient gradient characterizes Kings Creek; both increase from the headwaters to the confluence (Bertrand et al., 2009). Bottom-up effects of temperature and nutrients appeared linked to algal biomass and may explain the gradient of invertebrate biomass from headwaters to the confluence. Furthermore, the gradient of nutrient concentrations would have overpowered any indirect effects of fish nutrient remineralization on

invertebrate recovery patterns. Another potential explanation is that invertebrates typically distribute themselves in response to fish predation risk; both perceived risk assessed with chemical cues and actual risk assessed with rates of invertebrate consumption by fish (Abjornsson et al., 2002). This also may have contributed to the lack of fish effects we observed in these assemblages, which are numerically dominated by small-bodied taxa that can occupy interstitial spaces to avoid predation.

Drivers of invertebrate assemblage structure

In contrast to our findings, Fritz & Dodds (2004) concluded that invertebrate recolonization of four intermittent stream reaches on KPBS was primarily accomplished by drift from upstream refuges. Our study included 20 pools in three reaches across a longer gradient that included sites further downstream (although our reaches were the same, their lowermost site was near our intermittent middle reach), and our results (i.e., Fig. 7) suggested that downstream reaches recover more quickly than middle reaches, even though they are obviously further from upstream refuges and receive greater substrata scouring. This suggests that although upstream refuges may be important source pools for intermittent middle reaches. Especially during short re-wetting periods, recolonization probably happens simultaneously from permanent refuges located both upstream and downstream (Dodds et al., 2004).

Distance from the downstream confluence also represents a gradient of habitat area (small headwaters versus larger downstream reaches) and nutrient concentrations, which can be drivers of invertebrate assemblage structure (Stanley et al., 1994; Fritz & Dodds, 2004). Stream reaches that are nearer to the confluence are more likely to be aerially recolonized from downstream refuges, and downstream reaches are wider, deeper, and more productive, providing more available habitat and resources for colonists. Landuse and nutrient enrichment also may shift the taxonomic structure of macroinvertebrate communities to greater abundance of tolerant taxa (Mesa, 2010). Nutrient concentrations and algal biomass were greatest near the downstream confluence during this study and may have contributed to the rapid recovery and the higher invertebrate biomass at the study pools lower in the catchment. Row crop agriculture in the

lower part of the catchment, including the application of nitrogen fertilizers, drives up the dissolved inorganic nitrogen concentration in the PD reach. Both longitudinal stream position and catchment landuse may influence stream biota and recovery patterns following disturbance.

Although total invertebrate biomass estimates in our study were similar to those of Whiting et al. (2011), algal biomass and invertebrate biomass were greatest in the PD reach during our study, which contrasts with their findings (Fig. 8). The difference in our results is likely related to the timing of each study in relation to the hydrologic disturbance history preceding each study. We examined invertebrate assemblages recovering from a harsh scouring flood, whereas Whiting et al. (2011) studied Kings Creek during a relatively mild year in terms of hydrologic disturbance (February 2003–February 2004; see Figs. 2, 8). Thus, it is possible that lower water levels and more concentrated macroconsumers during the Whiting et al. (2011) experiment limited macroinvertebrate biomass. Whiting et al. (2011) acknowledged that “the dynamic nature of prairie streams cannot be accounted for in 1 year,” and thus, our results complement their study, increasing our understanding of factors driving assemblage structure.

Conclusions

Understanding factors that influence recovery of stream communities following hydrologic disturbance is important, particularly in light of predictions that hydrologic extremes will increase in frequency and magnitude in this region. Stream invertebrates are important regulators of ecosystem processes such as primary production and decomposition (Wallace & Webster, 1996), and thus their recovery following disturbance is linked to recovery of system function. Combining our results with previous work on Kings Creek, a general pattern of the effects of hydrologic disturbance on invertebrate assemblages has emerged. That is, hydrologic disturbance drastically reduces invertebrate taxonomic richness and biomass. Following disturbance, longitudinal gradients can form and are influenced jointly by nutrient gradients and distance to refuges. Although our study did not find an effect of macroconsumers, within a different context (e.g., a year with a milder hydrologic regime

and higher densities of macroconsumers), macroconsumers could possibly interact with the longitudinal gradients of nutrients and distance to refuges. It follows that anthropogenic reduction of refuges in streams (e.g., dewatering) will alter the resistance and resilience of stream communities to increasingly frequent and severe hydrologic disturbances.

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