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Disturbance frequency and functional identity mediate ecosystem processes in prairie streams

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A major consequence of climate change will be the alteration of precipitation patterns and concomitant changes in the flood frequencies in streams. Species losses or introductions will accompany these changes, which necessitates understanding the interactions between altered disturbance regimes and consumer functional identity to predict dynamics of streams. We used experimental mesocosms and field enclosures to test the interactive effects of flood frequency and two fishes from distinct consumer groups (benthic grazers and water-column minnows) on recovery of stream ecosystem properties (algal form and biomass, invertebrate densities, metabolism and nutrient uptake rates). Our results generally suggest that periphyton communities under nutrient limitation are likely to recover more quickly when grazing and water-column minnows are present and these effects can diminish or reverse with time since the disturbance. We hypothesized that increased periphyton production and biomass was the result of increased nutrient turnover, but decreased light limitation and indirect effects on other trophic levels are alternative explanations. Recovery of stream ecosystem properties after a natural flood differed from mesocosms (e.g. lower algal biomass and no long algal filaments present) and species manipulations did not explain recovery of ecosystem properties; rather, ecosystem processes varied along a downstream gradient of increasing temperature and nutrient concentrations. Different results between field enclosures and experimental mesocosms are attributable to a number of factors including differences in algal and invertebrate communities in the natural stream and relatively short enclosure lengths (mean area = 35.8 m^2) compared with recirculating water in the experimental mesocosms. These differences may provide insight into conditions necessary to elicit a strong interaction between consumers and ecosystem properties.

Changes in disturbance regimes associated with global climate change may have a strong influence on the functioning of ecosystems, particularly if these changes lead to shifts in species composition or dominance (Chapin et al. 1997, Petchey et al. 1999, Lake et al. 2000, Knapp et al. 2002). Streams may be particularly vulnerable to changes in climate because ecosystem structure and function is greatly influenced by hydrologic disturbance regimes (Fontaine and Bartell 1983, Poff and Allan 1995, Gibson et al. 2005). Species composition of streams also is highly threatened (Jelks et al. 2008) and many stream dwelling organisms can potentially affect stream ecosystem structure and function (Taylor et al. 2006, McIntyre et al. 2007). Predicting the effects of altered hydrology and consumer diversity on stream ecosystems and the services they provide will require a comprehensive understanding of how animals interact with disturbance regimes to regulate ecosystem processes (Power et al. 1988, 2008, Uehlinger 2000).

Because most streams are non-equilibrium systems, consumer effects must be placed in a context of recovery from disturbance. Not only are frequent floods predicted to constrain species composition (Poff and Allan 1995) and mediate interactions of species (Connell 1978), the relative influence of consumers on ecosystem properties is expected to be greatest during successional periods between disturbance events (Biggs et al. 2005). The effects of consumers on the successional trajectory of primary producers during these interim periods can depend on consumer trophic position, consumer density, and periphyton resource limitation (Steinman 1996, Rosemond et al. 2000). Benthic grazing and water-column minnows have different fundamental roles in streams. Grazing minnows interact directly and indirectly with biofilms and affect ecosystem properties by mechanically removing algae, altering nutrient availability, mediating light limitation, and altering food quality (Power et al. 1989, Grimm 1988, Gelwick and Matthews 1992, Bertrand and Gido 2007). Whereas the effects of grazers on ecosystem function and structure are well-studied (reviewed by Hillebrand 2002), less is known about the influences of higher trophic levels (Thébault and Loreau 2006), such as water-column minnows. These fish can expedite succession of algal communities through suppression of grazers (e.g. trophic cascade) or by remineralizing nutrients from autochthonous or allochthonous sources

(Gido and Matthews 2001). Quantifying contributions of dominant functional groups to ecosystem properties in North American prairie streams following disturbance is a critical step in predicting future consequences of altered hydrology and biodiversity.

We measured the recovery of ecosystem properties in experimental mesocosms to test the interactive effects of flood frequency and presence of two fish species that represent grazer and water-column minnow functional groups in North American prairie streams. Experimental mesocosms allowed us to manipulate flood frequencies and consumer presence in a factorial design where the mechanisms underlying ecosystem processes could be disentangled from the inherent variability of natural systems. These experiments were followed by a field experiment that allowed us to characterize recovery of a natural stream in the presence and absence of these two consumer groups but did not allow us to test the interaction with flood frequency.

We hypothesized that effects of fishes will vary with consumer group (Fig. 1). Grazers are not predicted to alter recovery of primary productivity following flood disturbances because consumption of autotrophs would be offset by increased production of remaining algae, through changes in nutrient or light availability (Power 1990, Bertrand and Gido 2007). Grazers are also predicted to negatively affect invertebrate communities through resource competition, substrate disturbance or direct consumption (Steinman et al. 1987). Water-column foragers, like water-column minnows, are predicted to generally increase primary productivity following disturbances by increasing nutrient availability (Gido and Matthews 2001) or by suppressing grazing invertebrates (Dahl 1998).

Because consumer effects are likely to vary with both flood frequency and time between disturbances, we separated our analyses into three time periods, and separately tested early (first 12 days of the experiment), intermediate (13–24 days) and late (>24 days) effects. Although consumptive demand on periphyton and invertebrate communities may be great soon after a scouring flood, the relative effects of consumers may be hard to detect because standing stocks are low. Alternatively, if the community is frequently reset by floods, resources will be too unpredictable to maintain stable populations of consumers, and fish effects will be limited (Lepori and Hjerdt 2006). In the absence of floods, we hypothesize that consumer effects on ecosystem properties will diminish as periphyton and invertebrates establish complex communities that include taxa that are resistant to consumption (Bertrand and Gido 2007, Bengtson et al. 2008). Thus, we predict effects of consumers on ecosystem properties will be greatest soon after disturbances and in streams with intermediate flood frequencies.

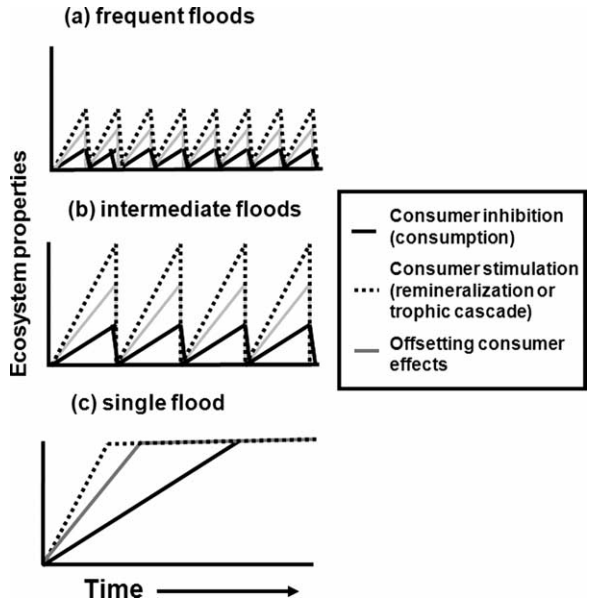

Figure 1. Conceptual diagram of hypothesized ecosystem response to interactive effects of flood frequency and consumers.

Methods

Study organisms

Grazers and water-column minnows are predicted to have different effects on stream ecosystem properties. Diet of southern redbelly dace *Phoxinus erythrogaster* (hereafter referred to as dace) and red shiners *Cyprinella lutrensis* (hereafter referred to as shiners) measured concurrent with these experiments showed that dace almost exclusively fed on filamentous green algae or diatoms, whereas shiner diet consisted primarily of chironomids, chydorids, ostracods and terrestrial invertebrates (Bertrand 2007). Dace are typically most abundant in spring-fed headwaters (Felley and Hill 1983, Franssen et al. 2006). Shiners are more broadly distributed throughout the Great Plains and occur in large to medium-sized rivers (Matthews and Hill 1979, Cross and Collins 1995).

Experimental mesocosms

Twenty-four large experimental stream mesocosms located on the Konza Prairie Biological Station (KPBS) in north central Kansas, USA, were used to test the effects of flood frequency and fish species on ecosystem properties. Each mesocosm is approximately 1800 l and consists of a 2.54 m^2 pool connected to a 0.84 m^2 riffle (Matthews et al. 2006). Water is recirculated through a large pipe beneath the substrata by an electric trolling motor, and propelled downstream through the riffle and pool at a mean discharge of 10.0 l s^{-1}. In addition, low-nutrient groundwater is continuously added from a natural spring at a mean rate of 1.2 l min^{-1}, which allows a complete replacement of water approximately each day. A shade canopy that blocked 57% of incoming solar irradiance was used to simulate riparian cover. Substrata were a mixture of pebble, gravel and fine sediment from a local quarry. Algae and invertebrate taxa with winged adults (e.g. chironomids) readily colonized these systems. In addition, each experimental stream was inoculated one week prior to the experiment with a slurry of benthic material (approximately 100 ml) collected from nearby Kings Creek to enhance development of microbial and invertebrate communities.

We simulated floods by scouring the substrata for 10 min with a pressure sprayer and rapidly exporting material from the stream through a 10 cm diameter drain

pipe. A second trolling motor was run at full speed in the pool to keep dislodged material in suspension while the stream was draining. A 500 ml grab sample was taken while the experimental mesocosm was fully mixed after several rounds of pressure washing (approximately 5 min), but before any water was released, to estimate the amount of exported organic matter. Experimental mesocosms were immediately refilled with spring water.

We tested the interactive effects of flood frequency and dace in summer 2003 and shiners in summer 2004. In 2003, two levels of flood frequency (12- and 24-day return intervals) and a no flood control were crossed with the presence (6.8 fish m^{-2}; 14.9 g m^{-2}) or absence of dace. Our selection of flood frequencies represented typical flood intervals in Kings Creek; 35% of floods >0.5 m^3 s^{-1} (enough to scour substrata, Dodds et al. 1996) occurred within 12 days of each other, and ten percent occurred between 12 and 24 days of each other (USGS gauging station no. 06879650 daily discharge data between 1980–2006). We randomly assigned each of the six treatment combinations to four replicate experimental mesocosms. All 24 experimental mesocosms were flooded on 3 June 2003 to begin the experiment, and the last measurements were recorded on 8 August 2003 (day 65). Water temperature ranged from 13 to 31°C (mean = 22°C). In summer 2004, the same flood treatments were crossed with the presence (8.9 fish m^{-2}; 11.5 g m^{-2}) or absence of shiners. The experiment began on 26 May 2004, and the last measurements were recorded on 14 August 2004 (day 80). Water temperature ranged from 15 to 30°C (mean = 22°C). Fish were stocked at densities typical of dace in Kings Creek (0–9 fish m^{-2}; Bertrand et al. 2006, Franssen et al. 2006).

Field enclosures

Field enclosures were constructed in 20 pools in Kings Creek on the KPBS to characterize the recovery of stream ecosystem properties after a natural flood. Gray et al. (1998) and Gray and Dodds (1998) provide physicochemical and biological descriptions of Kings Creek. The study pools were located in three reaches: a spring-fed headwater reach (HW; n = 8 enclosures), an intermittent middle reach (IM; n = 8), and a perennial downstream reach (PD; n = 4). Distance between pools ranged from 20–500 m within a reach, and all study pools were separated by at least one riffle. A nutrient gradient exists from the upper to the lower reach. The headwater site is fed by low-nutrient groundwater (mean levels during experiment: 41 g l^{-1} DIN (NH_4^+-N and NO_3^--N) and 3 g l^{-1} soluble reactive phosphorus (SRP), whereas downstream sites are more agriculturally influenced, which increases the nutrient content with distance downstream (IM: 84 g l^{-1} DIN and 2 g l^{-1} SRP; PD: 444 g l^{-1} DIN). Temperature also was influenced by groundwater inputs and varied by reach with HW ranging from 15 to 31°C (mean = 22°C), IM ranging from 14 to 24°C (mean = 18°C), and PD ranging from to 16 to 38°C (mean = 19°C). Surface area, depth, and discharge increased from the HW to the PD reach and varied through the sample period. 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^{-1} (mean = 12.4 l s^{-1}). Substrata in the study pools were similar in size and texture to that in the experimental mesocosms and were dominated by gravel (2–16 mm; 59%) and pebble (16–64 mm; 32%). The fish assemblages in Kings Creek are numerically dominated by two grazing minnows, central stoneroller *Campostoma anomalum* and southern redbelly dace, and the orangethroat darter *Etheostoma spectabile* (Franssen et al. 2006). Shiners are regionally abundant, but only occur in the lower reaches of Kings Creek in low abundance. Grazing invertebrates, including numerous insect taxa, crayfish *Orconectes* spp. and snails (*Physa* and *Physella* spp.) are abundant in Kings Creek.

We installed 5-mm mesh hardware cloth barriers (secured to steel poles and buried roughly 20 cm into the streambed) at the upstream and downstream ends of 20 pools (8 in HW, 8 in IM, and 4 in PD) following two successive scouring floods (5.5 m^3 s^{-1} flood on 4 June and 2.1 m^3 s^{-1} flood on 10 June) in spring 2005. Discharge steadily decreased following the second flood and there were no additional precipitation events or increases in discharge. Organic matter was removed from the mesh as needed to maintain natural stream flow through the study pools. Enclosures were assigned one of four treatments: no fish, ambient fish assemblage enclosure, dace enclosure, or shiners enclosure. The experiment started on 15 June 2005 in the HW and approximately a week later at the IM and PD reaches; the experiment ran for eight weeks in all three reaches, ending on 9 August in the HW and approximately a week later in the IM and PD reaches.

To begin the experiment, we removed fishes from field enclosures using multiple passes with a backpack electrofisher and seines. Fish were returned to ambient treatment enclosures, whereas dace and shiner treatment enclosures were restocked with those species at densities of 8 fish m^{-2}, which are typical for Kings Creek fish assemblages. However, densities of dace greater than 6 fish m^{-2} are considered high in Kings Creek. Shiners are generally less common and occurs at lower densities than dace in the long-term monitoring sites on Kings Creek. We were unable to fully prevent movement of fish and other organisms in some field enclosures; young-of-year fishes migrated through the wire mesh, crayfishes and some fishes burrowed under enclosure barriers. Thus, we used a backpack electrofisher to survey fish assemblages and remove invaders on week 2 and 6. In addition, we conducted population censuses at the end of the experiment to evaluate the integrity of each treatment. One enclosure barrier was lost to beaver activity and another study pool dried up in week 6. Thus, data from those time periods were excluded from the analyses.

Data collection

Stream metabolism

Gross primary productivity (GPP) was based on diurnal changes in dissolved oxygen measurements. In the experimental mesocosms, we used a single sonde per experimental mesocosm and the open-system single-station approach (Owens 1974) to estimate production across seven time

periods. During the dace experiment, production was estimated on days 1–4, 8–11, 14–17, 20–23, 29–32, 38–41 and 50–53, whereas during the shiner experiment, production was estimated on days 4–7, 16–19, 30–33, 40–43, 54–57, 65–68 and 77–80. Reaeration was estimated using the surface renewal model (Owens 1974) and was assumed to be the same across all experimental mesocosms. Because GPP for each mesocosm was not measured on the same day, it was necessary to control for variable solar irradiance for dates over which irradiance explained a significant amount of variability in GPP (Bertrand 2007).

In the field enclosures, GPP was estimated from substrata baskets placed in pools at the beginning of the experiment then removed and placed in recirculating chambers. Each pool contained 30 plastic mesh baskets ($10 \times 10 \times 10$ cm) filled with dried pebbles (16–64 mm) from the stream bank. Baskets were arranged into three rows of ten baskets perpendicular to the channel in the downstream half of the enclosure to maximize the influence of nutrient remineralization by fishes. Baskets were buried approximately 10 cm in the streambed so tops were flush with the stream bottom. Three baskets were randomly selected from each enclosure every seven days starting on day 7 and returned to the laboratory in moist, sealed plastic containers within 2 h of collection. Baskets were analyzed for benthic metabolism [respiration and net primary productivity (NPP)] in 22 l recirculating chambers (Dodds and Brock 1998) using stream water collected from the study reach and kept at ambient stream temperature.

The baskets from each enclosure were sealed airtight in a plexiglass chamber fitted with an YSI DO probe, and water circulated at approximately 10 cm s^{-1}. Light was excluded from the chambers and DO decline (i.e. respiration) was measured for 1.5 h. After respiration measurements, chambers were exposed to overhanging fluorescent grow lights (approximately 300 mol quanta m^{-2} s^{-1} PAR) and dissolved oxygen monitored for another 1.5 h. Respiration and NPP were calculated using linear regressions fit to the change in water oxygen concentration over time. GPP was calculated as NPP-respiration.

Nutrient retention and uptake

Nutrient retention was estimated every 6 days starting on day 1 in the experimental mesocosms by sampling inflowing and outflowing water for total nitrogen (TN) and total phosphorus (TP). We collected 125 ml of unfiltered water from the inflow and overflow for each experimental mesocosm. Samples were stored frozen until digestion and nutrient analysis following methods detailed in Dodds (2003).

Ammonium (NH_4^+) uptake rates in Kings Creek field enclosures were measured directly following metabolism measurements using substrata baskets in the recirculating chambers. An NH_4^+ spike was added to raise the water concentration by approximately 40 g l^{-1} and filtered water samples were taken at 0, 15, 30, 45, 60, 90 and 120 min to monitor the decline in water concentration over time. Ammonium uptake rates were calculated as the slope of the natural log transformed NH_4^+ concentration versus time corrected for background concentrations, and adjusted to g NH_4^+-N m^{-2} s^{-1} (Dodds et al. 2002).

Algal filament length

We estimated mean algal filament length in experimental mesocosm pools and riffles every 12 days, right before each repeated experimental mesocosm flood. The length of the longest algal filament was recorded at three points along each of three equally-spaced transects oriented perpendicular to flow in the riffle ($n = 9$), and five points in the pool (four around the outer perimeter and one in the deep center). We did not measure algal filament lengths in Kings Creek field enclosures because there were few, if any, noticeable strands of algae >1 mm in length during the experiment.

Algal biomass

Algal biomass was estimated as the concentration of chlorophyll a extracted from pebbles from pools and riffles of experimental mesocosms or from substrata baskets. Pebbles were collected and frozen within 4 h of collection. Chlorophyll a was extracted by submerging pebbles in a 78°C, 95% EtOH solution for 5 min as described in Sartory and Grobelaar (1984). Extracts were analyzed for chlorophyll a with a fluorometer using an optical configuration optimized for the analysis of chlorophyll a without phaeophyton interference (Welschmeyer 1995). Algal biomass was reported as chlorophyll a per m^2 (cross-sectional area of pebbles, or surface area of the substrata basket opening). In the experimental mesocosms, we estimated biomass on days 1, 6 and every 12 days thereafter, with three pebbles selected without bias along algal filament length transects from the riffle and five from the pool. In the field enclosures, we estimated algal biomass every seven days starting on day 7 from one of the three substrata baskets used for GPP and nutrient uptake measurements.

Benthic particulate organic matter

We used a 0.018 m^2 core sampler fitted with an electric pump (0.1 l s^{-1}) to collect benthic particulate organic matter (POM), invertebrates, and algae from the substrata in both experimental mesocosms and field enclosures. Substrata inside the corer were agitated by hand until 9 l of water were transferred to a bucket. After homogenizing the collected material, we took a 500 ml subsample for POM, and preserved it with formalin. One core sample was taken from the riffle and the pool in each experimental mesocosm on days 1, 6 and every 12 days thereafter. Five replicate core samples were taken weekly from five equally spaced transects in each field enclosure. Dry mass and ash-free dry mass of POM was measured for five size classes: >500 μm, 499–250 μm, 249–180 μm, 179–100 μm and 99–1 μm.

Algal assemblage structure

A 20 ml subsample of the 9 l slurry from the core sample was preserved in formalin for analyzing algal assemblage

structure. We counted algal cells according to functional groups (e.g. filaments, single cells, and colonies) within one of three broad taxonomic classifications (i.e. Chlorophyta, Bacillariophyta or Cyanobacteria).

Invertebrate assemblage structure

The remaining slurry (~8.5 l) from the core sample was passed through a 250 μm mesh sieve to collect invertebrates. We identified and enumerated invertebrates to the lowest possible taxonomic resolution (typically genus, except those of the family Chironomidae, which were typically assigned to tribe) using keys provided in Merritt and Cummins (1996). Large samples were occasionally subsampled down to 1/8 original volume using a Folsom wheel.

Statistical analysis

Mesocosm experiments

Statistical tests were conducted in three separate analyses to account for shifts in species effects with time since disturbance and to balance statistical analyses. Because experimental mesocosms were not flooded before the 12th day of the experiment, we initially only tested main effects of fish and habitat (pool vs riffle) from day 1 through 11 using two-way ANOVA. Between day 12 and 24, experimental mesocosms to be flooded at a 24-day interval were combined with no flood controls and were used to test for main effects of fish, a single flood on day 12, habitat, and their interactions using three-way ANOVA. After day 24, all treatment combinations were tested using repeated-measures ANOVA with presence of fish, flood frequency (every 12 or 24 days), and habitat as the three main effects and sample day as the repeated factor. Algal assemblage structure was only analyzed on two dates from each experiment; we tested for interactive effects of fish, flood frequency, and habitat using three-way ANOVA on each of these dates. Prior to analysis, a likelihood-ratio test of homogeneity of variances was used to evaluate heteroscedasticity in our data, and the best variance-stabilizing transformation was applied wherever necessary (Table 1–3). Where we found significant differences in main effects, we applied Tukey post hoc comparisons to test the relative differences between levels of flood frequency.

Because GPP was dependent on mean daily solar irradiance in the dace experiment, we used repeated measures ANCOVA with GPP as the response variable and irradiance as the covariate to test for differences in metabolism among treatment combinations. Continuous irradiance was measured on the Konza Prairie Biological Station approximately 0.5 km from the experimental stream facility. For the repeated measures ANCOVA, we used the value of Akaike's information criterion (Akaike 1974) to select the most adequate covariance structure from those evaluated (Milliken and Johnson 2002). We then used backward model selection and χ^2-tests to select the best model of our data and the Kenward–Rogers approximation to find approximate degrees of freedom for the F-test.

Finally, we used two-way ANOVA to test the effects of fish and flood frequency on total nutrient retention, based on the inflow and outflow samples and also used two-way ANOVA to test for effects on organic matter export, based on grab samples taken during simulated floods in the experimental mesocosms flooded on 12-day and 24-day intervals.

We used the Dunn–Sidak method to calculate a more conservative critical value for our hypothesis tests to correct for the large number of response variables (n = 15) and hypothesis tests. We interpreted p-values less than 0.003 as robust patterns and values between 0.05 and 0.003 as potential trends based on this assessment. All analyses were conducted using SAS ver. 9.1.

Field enclosures

To account for the variation in densities of the target species among treatments, we used an information theoretic approach (Burnham and Anderson 1998) to evaluate which manipulations (i.e. fish densities) or field conditions (i.e. days since flood) were significant predictors of measured response variables in the field enclosures. We developed models to predict GPP, NH_4^+ uptake rate, algal biomass, abundance of size fractions of POM, percent composition of four algal taxa groups individually, and density of three dominant (numerically and according to their biomass) invertebrate taxa. We chose a subset of candidate models that included individual predictors or groups of predictor variables that were thought to be important based on our previous experiments in the experimental mesocosms. For each response variable, if the full model (y = intercept + days since flood + shiner density + grazer density + error) explained less than 15% of the variance, we did not compare candidate models. As recommended by Burnham and Anderson (1998), we used the small sample adjustment of AIC (AIC_c; Akaike 1973) to rank candidate models by the difference between the AICc value for each candidate model and the model with the lowest AICc value. We then calculated the Akaike weight (w_i; weight of evidence) for each candidate model, which gives the probability that each model is the best model for the data, relative to the highest ranked model.

Results

Experimental mesocosms (effects of consumers and habitat)

We observed greater effects of dace on ecosystem properties during the first 11 days after flooding than in the shiner experiment (Table 1). Dace significantly reduced algal filament lengths by 60% (Fig. 2a) and the abundance of large and small POM (Fig. 3a, 3c) on day 6 of the experiment (Table 1). In addition, there was a trend of fewer chironomids in the presence of dace (Fig. 4), but this was not significant after controlling for experiment-wise error. There was a highly significant effect of habitat in the dace experiment, but not in the shiner experiment (Table 1). In the dace experiment, algal filament lengths and biomass were generally greater in riffles than pools, but this effect did not interact with the presence of dace.

Between day 12 to 24 dace effects on ecosystem properties also were more pronounced than shiner effects (Table 2). For example, by day 18, dace significantly

Table 1. Results from statistical tests using two-way ANOVAs on data from dace and shiner experiments prior to day 12. Response variables included algal filament length (AFL), algal biomass, large benthic particulate organic matter (large POM; >500 μm), medium particulate organic matter (medium POM; 499–100 μm), small particulate organic matter (small POM; 99–1 μm), chironomid density, microcrustacean density, oligochaete density, and snail density. Boldface indicates tests that were significant at the 0.003 level.

Response variable	Transform	Day of experiment	Effect	Dace experiment			Shiner experiment		
				DF	F	p	DF	F	p
AFL	square-root	11	habitat	1	94.38	**0.000**	1	0.000	1.000
			fish	1	16.70	**0.000**	1	3.177	0.082
			habitat × fish	1	3.64	0.063	1	0.000	1.000
			error	44			44		
Algal biomass	square-root	6	habitat	1	74.71	**0.000**	1	4.686	0.036
			fish	1	0.08	0.778	1	1.265	0.267
			habitat × fish	1	1.08	0.304	1	0.022	0.882
			error	44			43		
Large POM	$\log_{10}(x)$	6	habitat	1	6.57	0.014	1	0.158	0.693
			fish	1	14.03	**0.001**	1	2.356	0.132
			habitat × fish	1	0.07	0.791	1	0.030	0.864
			error	44			44		
Medium POM	$\log_{10}(x)$	6	habitat	1	0.60	0.444	1	0.086	0.770
			fish	1	5.09	0.029	1	3.902	0.055
			habitat × fish	1	1.66	0.205	1	0.070	0.793
			error	43			44		
Small POM	$\log_{10}(x)$	6	habitat	1	11.81	**0.001**	1	0.988	0.326
			fish	1	10.40	**0.002**	1	4.058	0.050
			habitat × fish	1	0.45	0.508	1	0.128	0.722
			error	44			44		
Chironomids	square-root	6	habitat	1	7.45	0.009	1	0.005	0.945
			fish	1	8.55	0.005	1	0.363	0.550
			habitat × fish	1	0.25	0.622	1	0.246	0.623
			error	44			44		
Microcrustacea	square-root	6	habitat	1	5.78	0.020	1	25.217	**0.000**
			fish	1	0.80	0.376	1	1.029	0.316
			habitat × fish	1	1.88	0.177	1	2.329	0.134
			error	44			44		
Oligochaetes	square-root	6	habitat	1	3.67	0.062	1	1.021	0.318
			fish	1	2.42	0.127	1	0.063	0.802
			habitat × fish	1	0.28	0.602	1	0.483	0.491
			error	44			44		
Snails	square-root	6	habitat	1	.	.	1	0.038	0.846
			fish	1	.	.	1	0.090	0.765
			habitat × fish	1	.	.	1	0.406	0.528
			error	44			44		

increased algal biomass by approximately 30% (Fig. 5a). Dace also reduced the amount of large POM, but this effect was only apparent in streams that were flooded on day 12 (i.e. there was a significant fish × flood interaction; Fig. 3a). Both dace and shiners had marginal effects on algal filament lengths (Fig. 2), but these were not significant after controlling for experiment-wise error. As in the first 11 days of the experiment, significant habitat effects were only observed in the dace experiment and did not show a significant interaction with the presence of fish (Table 2).

After day 24, both dace and shiners significantly affected ecosystem properties (Table 3). Dace effects on algal filament lengths became positive (Fig. 2a) and algal biomass was greater in their presence (Fig. 5a). Shiners increased algal filament lengths (Fig. 2b), increased large and medium POM (Fig. 6a–b) and reduced small POM (Fig. 6c). Finally, the effect of shiners on invertebrate densities was most pronounced around day 30 and 42, when microcrustacean density was generally 50% higher in experimental mesocosms with shiners than in experimental mesocosms without shiners (Fig. 7). Main effects of habitat on algal filament lengths and biomass were highly significant in the dace experiment, and there were some higher order interactions between habitat, day of experiment and flood frequency in the shiner experiment (Table 3). Similar to earlier time periods, there appeared to be minimal interactions between habitat and consumer effects.

Effects of flood frequency and interactions with consumer functional identity

Experimental flooding generally reduced algal biomass, abundance of POM and invertebrate densities (Table 3). Mesocoms flooded every 12 days generally had the lowest algal biomass and experimental mesocosms that were not flooded had the highest (Fig. 5). Increasing flood frequency decreased GPP after day 29 in the shiner experiment (Fig. 8b), but flooding did not affect nutrient retention. Green filaments were the most abundant type of algae present in both the dace and shiner experiments (mean = 65% (SD = 26.9%) and 48% (SD = 29.5%)) of the assemblage, respectively). Green filamentous and unicellular green algae comprised a greater fraction of the assemblage in flooded than in unflooded experimental mesocosms, whereas cyanobacteria initially were relatively more abundant in experimental mesocosms that were not flooded but later

Table 2. Results from statistical tests using three-way ANOVAs on data from dace and shiner experiments between day 12 and 24. Response variables included algal filament length (AFL), algal biomass, large benthic particulate organic matter (large POM; >500 μm), medium particulate organic matter (medium POM; 499–100 μm), small particulate organic matter (small POM; 99–1 μm), chironomid density, microcrustacean density, oligochaete density, snail density, abundance of unicellular green algae (green), abundance of filamentous green algae (filaments), abundance of cyanobacteria (cyanobacteria), and abundance of diatoms (diatom). Boldface indicates tests that were significant at the 0.003 level.

Response variable	Transform	Day of experiment	Effect	Dace experiment			Shiner experiment		
				DF	F	p	DF	F	p
AFL	square-root	23	habitat	1	119.10	**0.000**	1	0.00	1.000
			fish	1	6.71	0.013	1	8.93	0.005
			flood	1	2.10	0.156	1	1.41	0.243
			habitat × fish	1	4.64	0.037	1	0.00	1.000
			habitat × flood	1	1.13	0.294	1	0.00	1.000
			fish × flood	1	0.61	0.439	1	3.64	0.064
			habitat × fish × flood	1	0.28	0.601	1	0.00	1.000
			error	40			40		
Algal biomass	square-root	18	habitat	1	76.34	**0.000**	1	1.67	0.203
			fish	1	13.51	**0.001**	1	0.02	0.879
			flood	1	0.28	0.600	1	3.54	0.067
			habitat × fish	1	1.08	0.305	1	0.01	0.912
			habitat × flood	1	0.02	0.898	1	1.66	0.205
			fish × flood	1	0.03	0.870	1	0.48	0.491
			habitat × fish × flood	1	0.86	0.360	1	0.62	0.437
			error	40			40		
Large POM	$\log_{10}(x)$	18	habitat	1	2.28	0.139	1	0.99	0.325
			fish	1	10.31	**0.003**	1	1.69	0.201
			flood	1	29.92	0.000	1	6.55	0.014
			habitat × fish	1	2.26	0.140	1	0.18	0.675
			habitat × flood	1	4.12	0.049	1	0.00	0.976
			fish × flood	1	22.15	**0.000**	1	5.20	0.028
			habitat × fish × flood	1	4.57	0.039	1	0.14	0.715
			error	40			40		
Medium POM	$\log_{10}(x)$	18	habitat	1	0.10	0.752	1	4.42	0.042
			fish	1	0.57	0.456	1	2.06	0.159
			flood	1	4.28	0.045	1	5.80	0.021
			habitat × fish	1	0.01	0.937	1	0.04	0.841
			habitat × flood	1	0.97	0.331	1	3.96	0.053
			fish × flood	1	3.85	0.057	1	1.16	0.288
			habitat × fish × flood	1	0.49	0.489	1	0.95	0.336
			error	39			40		
Small POM	$\log_{10}(x)$	18	habitat	1	0.01	0.932	1	0.04	0.838
			fish	1	0.02	0.891	1	4.64	0.037
			flood	1	28.60	**0.000**	1	33.13	**0.000**
			habitat × fish	1	0.10	0.752	1	0.26	0.616
			habitat × flood	1	1.07	0.306	1	0.41	0.527
			fish × flood	1	5.17	0.028	1	1.99	0.166
			habitat × fish × flood	1	0.08	0.782	1	0.75	0.392
			error	40			40		
Chironomids	square-root	18	habitat	1	0.52	0.474			
			fish	1	5.89	0.020			
			flood	1	5.34	0.026			
			habitat × fish	1	0.80	0.376			
			habitat × flood	1	0.11	0.737			
			fish × flood	1	1.22	0.276			
			habitat × fish × flood	1	0.26	0.616			
			error	39					
Microcrustacea	square-root	18	habitat	1	0.15	0.697			
			fish	1	0.30	0.586			
			flood	1	12.16	**0.001**			
			habitat × fish	1	0.25	0.620			
			habitat × flood	1	0.46	0.503			
			fish × flood	1	0.04	0.840			
			habitat × fish × flood	1	0.23	0.637			
			error	39					
Oligochaetes	square-root	18	habitat	1	1.95	0.170			
			fish	1	0.02	0.896			
			flood	1	7.41	0.010			
			habitat × fish	1	0.51	0.478			
			habitat × flood	1	0.99	0.326			
			fish × flood	1	1.54	0.222			
			habitat × fish × flood	1	0.07	0.796			
			error	39					

Table 2 (*Continued*)

Response variable	Transform	Day of experiment	Effect	Dace experiment			Shiner experiment		
				DF	F	p	DF	F	p
Snails	square-root	18	habitat	1	1.72	0.198			
			fish	1	1.15	0.290			
			flood	1	0.49	0.487			
			habitat × fish	1	0.56	0.459			
			habitat × flood	1	0.14	0.707			
			fish × flood	1	3.65	0.063			
			habitat × fish × flood	1	0.88	0.353			
			error	39					

more abundant at a 24-day flood frequency. During the dace experiment, experimental mesocosms that were flooded on day 12 had four times more unicellular green algae than those experimental mesocosms that were not flooded ($F_{1,40} = 20.69$, $p < 0.0001$; mean fraction = 0.10 (SE = 0.001) vs 0.02 (SE = 0.0004)).

Algal filament lengths and POM were affected by consumer functional identity and scouring floods of different frequencies (Table 3). On day 35, mean algal filament lengths were greatest in experimental mesocosms with shiners, and this effect was greatest in mesocosms that were not flooded (Fig. 2b). After day 56, mean algal filament lengths were generally greatest in unflooded mesocosms and smallest in mesocosms flooded every 12 days. In addition, shiners had a positive effect on algal filaments, but this effect was only apparent in mesocosms flooded every 24 days (Fig. 2b).

An analysis of the three dominant invertebrate groups including microcrustaceans (calanoid and cyclopoid copepods, Chydoridae, Ostracoda, and Isopoda), oligochaetes, and chironomids (Chironomini, Tanytarsini, Tanypodinae, and Orthocladiinae) indicated that streams that were flooded more frequently had reduced densities of these taxa (Table 2, 3). Floods on day 12 and 48 reduced densities of these taxa in experimental mesocosms subjected to 12-day and 24-day flood frequencies (e.g. chironomids by 60% after the day 48 flood in the dace experiment, Fig. 4). The only notable interaction with invertebrate density and fish was a marginally significant interaction effect between flood frequency and shiners for microcrustaceans (Table 3). This trend was most apparent in the experimental mesocosms that were flooded every 24 days, where microcrustaceans were more abundant in the presence of shiners (Fig. 7).

The presence of dace also seemed to influence nutrient retention measured on day 18. In the presence of dace, the concentration of total nitrogen was 50 g l^{-1} less in the outflow than the inflow on day 42 of the experiment ($F_{1,12} = 5.60$, $p = 0.04$; Fig. 10).

Field enclosures

There was a strong temporal trend of increasing GPP and algal biomass that was dependent on study reach (Fig. 10) but not fish functional identity treatments following a scouring flood in 2005. Time since flood was closely linked with ecosystem response variables in Kings Creek study pools based on our model ranking criteria (Table 4). Variance in GPP, NH_4^+ uptake rate and invertebrate densities was best predicted with a model that only included days since flood disturbance. The Akaike weights from these models suggest other candidate models, which included consumer densities, were almost two times less likely to be the best model. The only exception was algal biomass, which was best predicted with a model including days since flood, but the Akaike weight ($w_i = 0.40$) of this model suggests that it was only 30% more likely to be the best approximating model than the next highest ranked candidate model which included grazer density ($w_i = 0.31$).

Discussion

Our results from experimental mesocosms indicate that fishes from two dominant functional groups can influence the successional trajectory of stream ecosystem structure and function following scouring floods. Simulated floods in mesocosms differed physically from those in natural streams, but led to significant export of organic matter and alterations in benthic communities in both systems. Interestingly, there was little evidence of a legacy effect of flood treatment in mesocosms, as ecosystem properties were generally reset to similar levels after floods in both 12- and 24-day flood treatments. For example, benthic particulate organic matter (POM) was reduced to less than 275 mg m^{-2} after each flood, regardless of how many times that treatment had previously been flooded. We only found evidence of a flood legacy effect when shiners were present, as GPP and algal biomass recovered more rapidly in the 24-day than in 12-day flood treatments, but these trends were only marginally significant.

Two interactive effects during the shiner experiment provided support for our hypothesis that flood frequency can mediate fish effects on ecosystem processes. Experimental mesocosms with shiners had longer algal filaments, but around day 42, this effect was strongest in the unflooded mesocosms and on day 60 and 72, this effect was strongest in the mesocosms flooded every 24 days. Furthermore, increased density of microcrustaceans in mesocosms with shiners was most notable in the 24-day flood treatment, perhaps a result of increased habitat provided by long algal filaments. We also hypothesized that the intermediate flood frequency created conditions where nutrient mineralization by shiners would have the greatest effects. Specifically, increased rates of biomass accrual were slow enough that frequent flooding limited

Table 3. Results from statistical tests using repeated-measures ANOVA on data from dace and shiner experiments. Response variables included algal filament length (AFL), algal biomass, large benthic particulate organic matter (large POM; >500 μm), medium particulate organic matter (medium POM; 499–100 μm), small particulate organic matter (small POM; 99–1 μm), chironomid density, microcrustacean density, oligochaete density, and snail density. Boldface indicates tests that were significant at the 0.003 level.

Response variable	Transform	Day of experiment	Effect	Dace experiment				Shiner experiment			
				nDF	dDF	F	p	nDF	dDF	F	p
AFL	square-root	29–65	habitat	1	40.9	105.18	<**0.0001**	1	36	0.00	1.000
			day	2	54.1	11.90	<**0.0001**	3	34	5.28	0.004
			habitat × day	2	54.1	1.16	0.321	3	34	0.00	1.000
			fish	1	40.9	15.78	**0.000**	1	36	13.75	**0.001**
			habitat × fish	1	40.9	1.53	0.223	1	36	0.00	1.000
			day × fish	2	54.1	7.14	**0.002**	3	34	1.32	0.284
			habitat × day × fish	2	54.1	3.84	0.028	3	34	0.00	1.000
			flood	2	40.9	1.28	0.288	2	36	5.37	0.009
			habitat × flood	2	40.9	0.50	0.612	2	36	0.00	1.000
			day × flood	4	60.2	3.36	0.015	6	43.9	11.45	<**0.0001**
			habitat × day × flood	4	60.2	0.32	0.864	6	43.9	0.00	1.000
			fish × flood	2	40.9	1.35	0.270	2	36	2.10	0.137
			habitat × fish × flood	2	40.9	0.33	0.722	2	36	0.00	1.000
			day × fish × flood	4	60.2	2.73	0.037	6	43.9	7.49	<**0.0001**
			habitat × day × fish × flood	4	60.2	1.48	0.221	6	43.9	0.00	1.000
Algal biomass	square-root	29–65	habitat	1	52.4	31.09	<**0.0001**	1	36	0.69	0.413
			day	3	99.8	20.07	<**0.0001**	4	144	8.16	<**0.0001**
			habitat × day	3	99.8	3.28	0.024	4	144	4.89	**0.001**
			fish	1	52.4	19.24	<**0.0001**	1	36	4.35	0.044
			habitat × fish	1	52.4	2.10	0.154	1	36	0.04	0.842
			day × fish	3	99.8	1.09	0.358	4	144	1.55	0.192
			habitat × day × fish	3	99.8	0.17	0.918	4	144	3.24	0.014
			flood	2	52.3	29.32	<**0.0001**	2	36	12.96	<**0.0001**
			habitat × flood	2	52.3	0.98	0.381	2	36	9.32	**0.001**
			day × flood	6	105	1.91	0.086	8	144	1.75	0.093
			habitat × day × flood	6	105	0.70	0.653	8	144	4.73	<**0.0001**
			fish × flood	2	52.3	0.58	0.566	2	36	1.53	0.231
			habitat × fish × flood	2	52.3	0.67	0.515	2	36	2.54	0.093
			day × fish × flood	6	105	1.21	0.305	8	144	1.28	0.260
			habitat × day × fish × flood	6	105	0.75	0.614	8	144	1.17	0.319
Large POM	$\log_{10}(x)$	29–65	habitat	1	35.6	0.51	0.482	1	36	2.77	0.105
			day	3	61.5	16.19	<**0.0001**	4	144	0.38	0.819
			habitat × day	3	61.5	2.49	0.069	4	144	0.98	0.420
			fish	1	35.6	0.34	0.565	1	36	21.59	<**0.0001**
			habitat × fish	1	35.6	3.60	0.066	1	36	0.26	0.615
			day × fish	3	61.5	4.23	0.009	4	144	1.08	0.367
			habitat × day × fish	3	61.5	0.09	0.966	4	144	0.35	0.843
			flood	2	35.5	41.71	<**0.0001**	2	36	34.71	<**0.0001**
			habitat × flood	2	35.5	0.78	0.468	2	36	0.70	0.501
			day × flood	6	70.2	1.37	0.239	8	144	5.36	<**0.0001**
			habitat × day × flood	6	70.2	1.28	0.277	8	144	0.40	0.921
			fish × flood	2	35.5	1.74	0.190	2	36	3.87	0.030
			habitat × fish × flood	2	35.5	0.66	0.524	2	36	0.58	0.564
			day × fish × flood	6	70.2	1.46	0.205	8	144	0.96	0.468
			habitat × day × fish × flood	6	70.2	0.35	0.908	8	144	0.67	0.719
Medium POM	$\log_{10}(x)$	29–65	habitat	1	50.6	3.03	0.088	1	38	2.68	0.110
			day	3	106	82.06	<**0.0001**	4	78.3	6.27	**0.000**
			habitat × day	3	106	0.33	0.807	4	78.3	0.59	0.670
			fish	1	50.6	0.01	0.931	1	38	10.52	**0.003**
			habitat × fish	1	50.6	0.16	0.690	1	38	0.42	0.520
			day × fish	3	106	1.02	0.387	4	78.3	0.71	0.588
			habitat × day × fish	3	106	0.15	0.928	4	78.3	1.71	0.155
			flood	2	50.6	40.88	<**0.0001**	2	38	14.58	<**0.0001**
			habitat × flood	2	50.6	0.51	0.602	2	38	1.60	0.216
			day × flood	6	110	4.81	**0.000**	8	93.4	2.52	0.016
			habitat × day × flood	6	110	1.04	0.403	8	93.4	0.76	0.642
			fish × flood	2	50.6	0.30	0.742	2	38	0.83	0.445
			habitat × fish × flood	2	50.6	0.00	0.998	2	38	0.13	0.880
			day × fish × flood	6	110	1.87	0.093	8	93.4	1.88	0.072
			habitat × day × fish × flood	6	110	1.40	0.223	8	93.4	0.43	0.901
Small POM	$\log_{10}(x)$	29–65	habitat	1	51.5	2.01	0.163	1	46	20.24	<**0.0001**
			day	3	107	25.75	<**0.0001**	4	53.1	13.26	<**0.0001**
			habitat × day	3	107	1.76	0.160	4	53.1	0.22	0.927
			fish	1	51.5	1.18	0.283	1	46	39.05	<**0.0001**
			habitat × fish	1	51.5	0.54	0.467	1	46	0.07	0.799
			day × fish	3	107	2.61	0.055	4	53.1	1.88	0.128
			habitat × day × fish	3	107	0.16	0.926	4	53.1	1.40	0.246

Table 3 (*Continued*)

Response variable	Transform	Day of experiment	Effect	Dace experiment				Shiner experiment			
				nDF	dDF	F	p	nDF	dDF	F	p
			flood	2	51.4	211.54	<**0.0001**	2	46	39.64	<**0.0001**
			habitat × flood	2	51.4	0.02	0.979	2	46	3.50	0.038
			day × flood	6	110	11.94	<**0.0001**	8	69.3	7.54	<**0.0001**
			habitat × day × flood	6	110	1.21	0.309	8	69.3	0.68	0.711
			fish × flood	2	51.4	2.71	0.076	2	46	5.09	0.010
			habitat × fish × flood	2	51.4	0.61	0.547	2	46	0.13	0.878
			day × fish × flood	6	110	2.71	0.017	8	69.3	1.27	0.272
			habitat × day × fish × flood	6	110	0.58	0.745	8	69.3	1.19	0.320
Chironomids	square-root	29–65	habitat	1	39.3	5.17	0.029	1	36	0.07	0.787
			day	2	39.1	1.78	0.182	2	72	0.28	0.755
			habitat × day	2	39.1	1.50	0.235	2	72	2.23	0.115
			fish	1	39.3	0.80	0.377	1	36	0.98	0.329
			habitat × fish	1	39.3	0.04	0.835	1	36	1.87	0.180
			day × fish	2	39.1	0.20	0.823	2	72	2.74	0.072
			habitat × day × fish	2	39.1	1.39	0.262	2	72	0.09	0.918
			flood	2	39	12.69	<**0.0001**	2	36	24.61	<**0.0001**
			habitat × flood	2	39	0.40	0.672	2	36	0.31	0.733
			day × flood	4	45.5	10.50	<**0.0001**	4	72	9.06	<**0.0001**
			habitat × day × flood	4	45.5	0.88	0.482	4	72	1.08	0.371
			fish × flood	2	39	0.41	0.668	2	36	0.77	0.469
			habitat × fish × flood	2	39	0.27	0.767	2	36	0.27	0.762
			day × fish × flood	4	45.5	0.41	0.800	4	72	0.25	0.911
			habitat × day × fish × flood	4	45.5	1.74	0.159	4	72	1.10	0.365
Microcrustacea	square-root	29–65	habitat	1	36.1	1.47	0.233	1	38.9	6.81	0.013
			day	2	35.8	10.46	**0.000**	2	42.2	25.38	<**0.0001**
			habitat × day	2	35.8	3.07	0.059	2	42.2	0.18	0.836
			fish	1	36.1	3.69	0.063	1	38.9	18.15	0.000
			habitat*fish	1	36.1	1.43	0.239	1	38.9	2.73	0.106
			day × fish	2	35.8	1.66	0.204	2	42.2	10.25	0.000
			habitat × day × fish	2	35.8	0.70	0.501	2	42.2	0.27	0.767
			flood	2	36.1	10.59	**0.000**	2	38.9	46.20	<**0.0001**
			habitat × flood	2	36.1	0.34	0.716	2	38.9	0.29	0.747
			day × flood	4	41.7	4.48	0.004	4	49.5	3.58	0.012
			habitat × day × flood	4	41.7	2.11	0.096	4	49.5	0.57	0.688
			fish × flood	2	36.1	2.61	0.087	2	38.9	5.27	0.009
			habitat × fish × flood	2	36.1	0.85	0.436	2	38.9	1.60	0.214
			day × fish × flood	4	41.7	2.85	0.035	4	49.5	2.09	0.096
			habitat × day × fish × flood	4	41.7	0.44	0.779	4	49.5	0.47	0.757
Oligochaetes	square-root	29–65	habitat	1	32.8	0.04	0.843	1	36	0.01	0.915
			day	2	40.3	0.03	0.966	2	36.1	2.49	0.097
			habitat × day	2	40.3	3.33	0.046	2	36.1	2.99	0.063
			fish	1	32.8	3.43	0.073	1	36	1.71	0.199
			habitat × fish	1	32.8	0.04	0.850	1	36	0.04	0.834
			day × fish	2	40.3	0.53	0.593	2	36.1	1.81	0.178
			habitat × day × fish	2	40.3	1.65	0.205	2	36.1	0.90	0.415
			flood	2	32.7	80.07	<**0.0001**	2	36	1.81	0.179
			habitat × flood	2	32.7	2.14	0.134	2	36	0.01	0.987
			day × flood	4	47.2	3.35	0.017	4	42.4	1.04	0.396
			habitat × day × flood	4	47.2	0.64	0.640	4	42.4	0.68	0.607
			fish × flood	2	32.7	3.36	0.047	2	36	0.94	0.400
			habitat × fish × flood	2	32.7	1.67	0.204	2	36	0.24	0.784
			day × fish × flood	4	47.2	0.76	0.555	4	42.4	0.79	0.537
			habitat × day × fish × flood	4	47.2	1.17	0.336	4	42.4	0.36	0.833
Snails	square-root	29–65	habitat	1	37.4	0.03	0.867	1	36	0.27	0.604
			day	2	50.4	2.48	0.094	2	35	37.49	<**0.0001**
			habitat × day	2	50.4	1.66	0.201	2	35	1.64	0.209
			fish	1	37.4	0.12	0.733	1	36	0.12	0.733
			habitat × fish	1	37.4	0.02	0.896	1	36	0.13	0.723
			day × fish	2	50.4	0.54	0.587	2	35	0.13	0.878
			habitat × day × fish	2	50.4	0.11	0.895	2	35	0.51	0.605
			flood	2	37.3	1.74	0.189	2	36	1.48	0.241
			habitat × flood	2	37.3	0.07	0.933	2	36	0.41	0.666
			day × flood	4	54.6	1.46	0.228	4	41.2	3.37	0.018
			habitat × day × flood	4	54.6	0.23	0.918	4	41.2	0.31	0.871
			fish × flood	2	37.3	0.09	0.915	2	36	1.83	0.175
			habitat × fish × flood	2	37.3	0.12	0.890	2	36	0.25	0.778
			day × fish × flood	4	54.6	1.39	0.250	4	41.2	0.37	0.827
			habitat × day × fish × flood	4	54.6	0.61	0.656	4	41.2	0.74	0.567

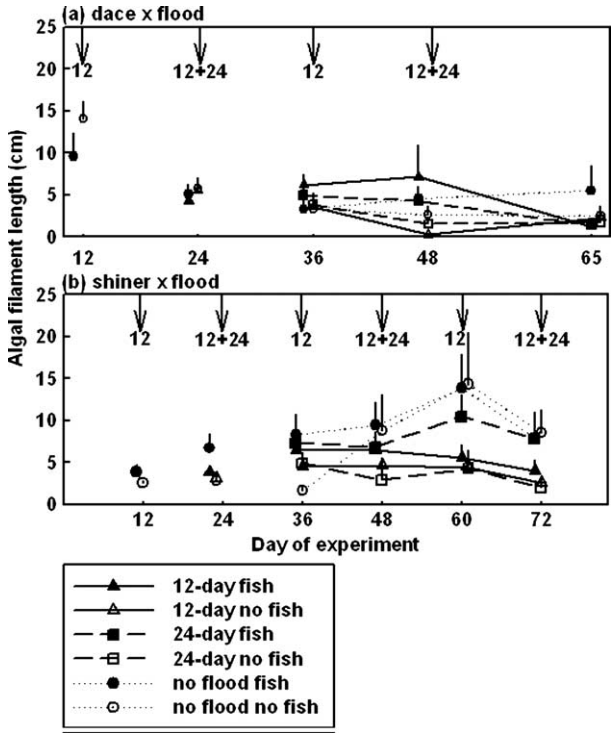

Figure 2. Mean algal filament length (+ SE) in dace (a) and shiner (b) experimental mesocosms. Control (no fish; open symbols) data points are offset one day later to prevent overlap. Arrows indicate floods.

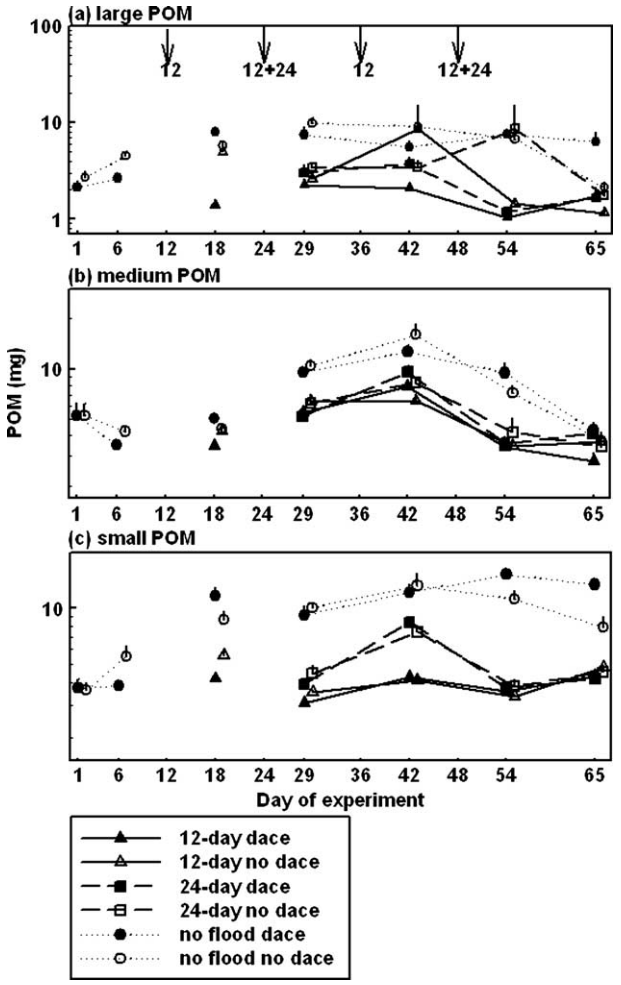

Figure 3. Mean mass (+ SE) of total fine particulate organic matter (FPOM) in experimental mesocosms with (filled symbols) and without (open symbols; offset 1 day later) dace in the >500 μm (a), 499–100 μm (b), and 99–1 μm (c) size classes during the dace experiment. Arrows indicate floods.

detection of this effect, and in the absence of flooding, greater accrual of periphyton resulted in a decline in biomass-specific productivity. After day 40 of the mesocosm experiments, the ratio of GPP to total POM, averaged across fish treatments, was approximately twice as high in mesocosms flooded every 12 days than in unflooded units (data not shown). Higher per capita rates of production support our predictions that primary producers become self-limited in the absence of floods and that the ability of fish to stimulate primary producers by releasing nutrients is likely greatest in more frequently floods streams. Moreover, the stronger effect of shiners under the intermediate disturbance frequency is consistent with other research that suggests the influence of biota on ecosystem recovery depends on disturbance frequency and disturbance legacy (Parsons et al. 2006), as well as the potential for these fishes to alleviate constraints on primary productivity (e.g. by increasing availability of nutrients).

Context dependency of fish effects

Variation in the effects of flood frequency and the presence of fish over the course of the experiments resulted in several complex interactions. Although we predicted that fish effects would be greatest soon after flooding, several surprising effects were only evident during later successional stages. In both mesocosm experiments, nutrient remineralization apparently became more important to ecosystem processes as time since disturbance increased. For example, dace had a negative effect on algal filament length before day 30, but had a positive effect on algal filament length after day 30. Moreover, shiners stimulated algal biomass and filament length, but this effect was most pronounced after day 30 of the experiment. These temporally variable responses of periphyton to dace and shiners were related to the gradual accrual of nutrients by periphyton (as indicated by the continuous retention of nutrients in fish treatments, Fig. 10). Measurements of the effects of consumers on stream ecosystem processes typically are constrained by relatively short time scales (<1 month), whereas this study examined these effects over longer periods and captured the dynamic recovery patterns of ecosystem processes, which seems particularly relevant in non-equilibrium systems, such as prairie streams.

We also predicted that the magnitude of fish effects would depend on the balance between consumptive losses and algal production stimulation through nutrient remineralization and/or mediation of light limitation. Our results support this prediction; however, rather than finding that grazers and water-column minnows had different effects on primary production, these groups each stimulated some aspects of primary producer communities. We assumed nutrients were limiting in mesocosms because

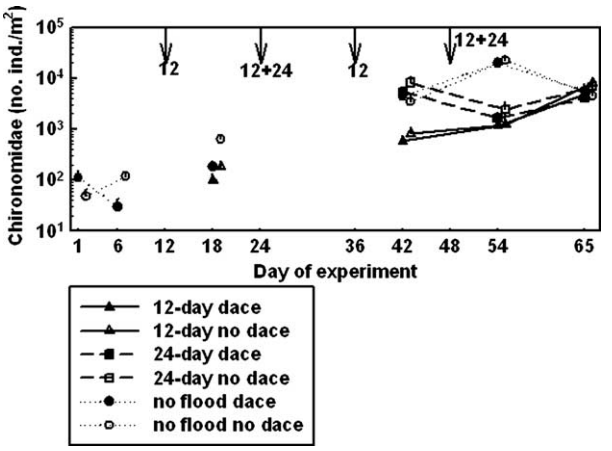

Figure 4. Mean densities (+ SE) of chironomids in experimental mesocosms during the dace experiment. Closed symbols are treatments with dace and open symbols (offset 1 day later) are without dace. Arrows indicate floods.

the water source has low concentrations of total nitrogen and phosphorus (<100 μg l^{-1} and <5 μg l^{-1}, respectively) and water is recirculated repeatedly before exiting the experimental mesocosms. Because terrestrial invertebrates were almost half of shiner diets (Bertrand 2007), we presumed those invertebrates were converted to soluble nutrients that facilitated nutrient-limited primary producers. Positive effects of dace on benthic algae could have resulted from either selective grazing or remineralization of nutrients from algae. However, in contrast to shiners, dace could only increase turnover rates of nutrients

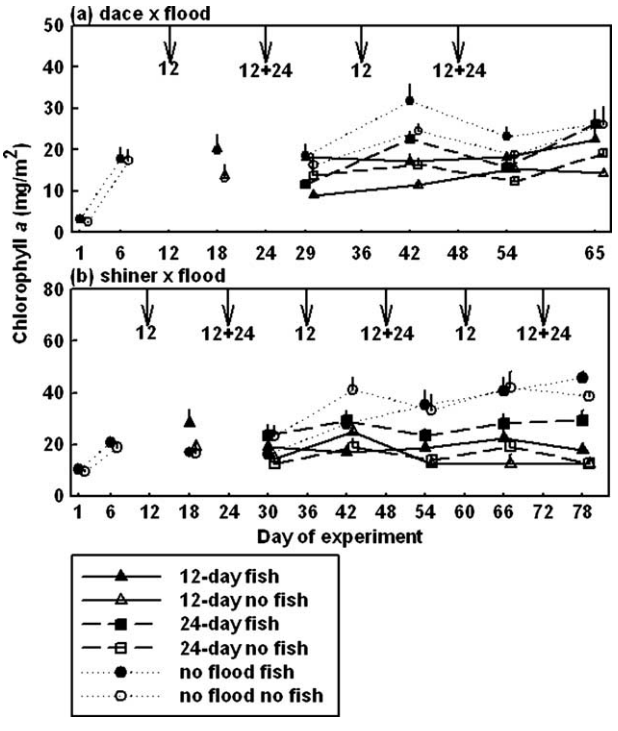

Figure 5. Algal biomass (chlorophyll a; + SE) in dace (a) and in shiner (b) experimental mesocosms. Control (no fish; open symbols) data points are offset one day later to prevent overlap. Arrows indicate floods.

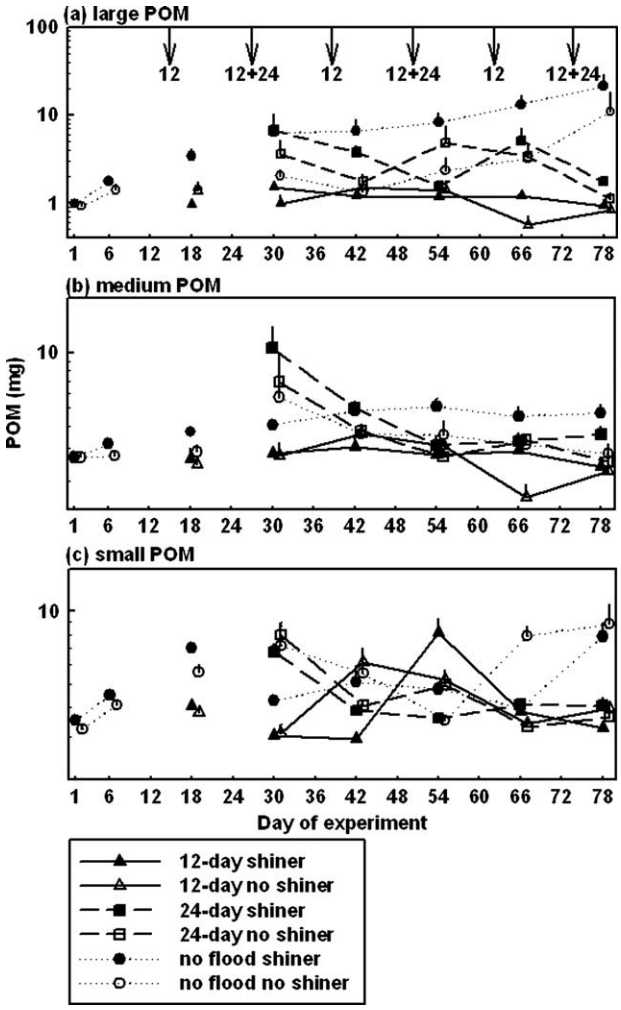

Figure 6. Mean mass (+ SE) of total benthic particulate organic matter (POM) in experimental mesocosms with (filled symbols) and without (open symbols; offset 1 day later) shiners in the > 500 μm (a), 499–100 μm (b), and 99–1 μm (c) size classes during the shiner experiment. Arrows indicate floods.

because they did not consume allocthonous material (Bertrand 2007). Data from this experiment corroborates the potential effect of fish stimulating primary production through nutrient remineralization, as treatments with dace tended to retain total nitrogen (Fig. 10). Whereas increased turnover of nutrients can stimulate primary production when nutrients are limiting (DeAngelis 1992), dace also reduced algal filament lengths and may have alleviated potential light limitation or shifted algal community structure to species that are more efficient primary producers (e.g. Cyanobacteria), thus increasing productivity (Dodds et al. 1999). Because we did not find a significant effect of dace on relative proportions of major algal taxa, changes at finer scales of taxonomic resolution would need to be tested to establish this as a potential mechanism.

Another complex interaction was detected in the post-flood succession of the invertebrate assemblage. The main effect of flood frequency on invertebrate assemblages was reduced densities. However, some invertebrate groups did respond to fish treatments, the most notable of which were marginal decreases in chironomids and in the presence of

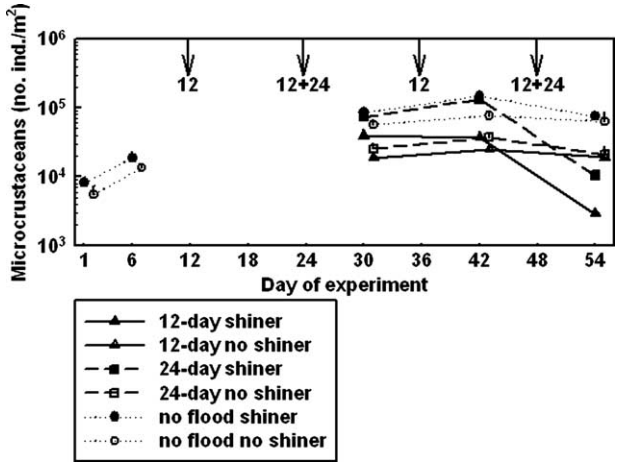

Figure 7. Mean densities (+ SE) of microcrustaceans in experimental mesocosms during the shiner experiment. Closed symbols are treatments with shiners and open symbols (offset 1 day later) are without shiners. Arrows indicate floods.

dace and significant increases in microcrustaceans in the presence of shiners. Relatively high abundances of small-bodied invertebrates with rapid life cycles such as crustaceans are typical of recently disturbed streams that are in an early state of succession (Lugthart and Wallace 1992, Mackay 1992). Increased habitat and food resources for microcrustaceans were related to fish increasing algal production, algal filament length, and POM and explain the positive relationship between fish and microcrustaceans. We think it is important to note that dace negatively affected chironomid densities, although those effects were only marginally significant. Diet analyses indicated that these taxa were not commonly consumed by dace: only 3% of dace examined from field enclosures and 26% from experimental mesocosms had these invertebrates in their guts, and when present only represented a minor fraction of the total gut contents (Bertrand 2007). We hypothesize decreasing chironomid densities were more likely related to structural habitat change than to consumption. Lower chironomid densities in riffles of dace treatments were primarily a result of smaller numbers of *Rheotanytarus*. Increased algal cover and filament lengths benefitted microcrustaceans but may have inhibited *Rheotanytarsus* by interfering with their tube building and filter feeding activities (Dudley et al. 1986). Hence, fish elicited mostly indirect responses in invertebrates, by altering habitat and food availability. Although Schmitz et al. (1997) documented a behaviorally-mediated trophic cascade in terrestrial experimental mesocosms, we did not observe a trophic cascade as a result of the indirect effects of fish on invertebrates.

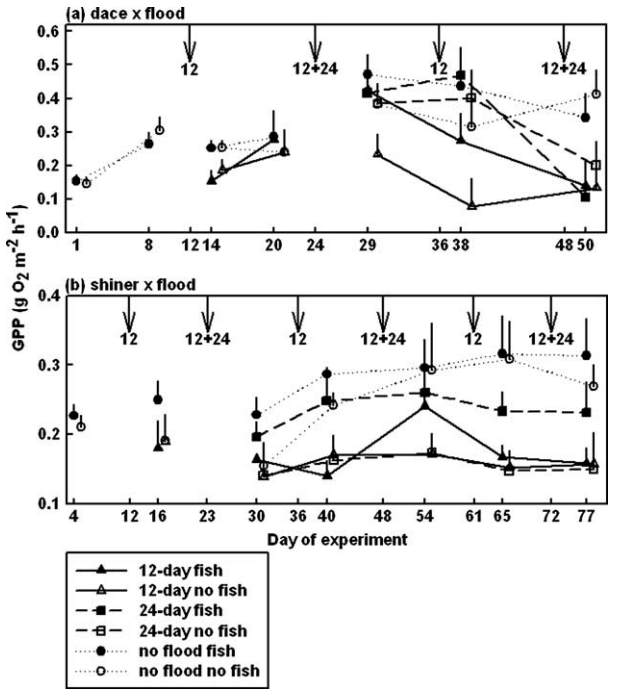

Figure 8. Gross primary production (GPP + SE) in experimental mesocosms in the presence of dace (a) and shiners (b). Control (no fish; open symbols) data points are offset one day later to prevent overlap. Arrows indicate floods.

Evaluation of experimental mesocosm results in field enclosures

Recovery of ecosystem function and structure in experimental mesocosms that were not flooded partially matched results from field enclosures in the intermittent and headwater reaches even though consumer treatments did not affect recovery of ecosystem processes in field enclosures. Response variables in the experimental mesocosms generally followed an asymptotic recovery trajectory, which was similar to results from enclosures in the headwater reaches, and for some response variables, intermittent reaches. This pattern was also reported for a desert stream following flooding (Fisher et al. 1982). Whereas algal biomass in the experimental mesocosms typically stabilized within 30 days to pre-flood levels (30–50 mg m^{-2}), algal biomass continued to increase through the 8th week of the experiment and reached values around 50 mg m^{-2} in the headwater reach and over 150 mg m^{-2} in the downstream reach. Similarly, GPP in the experimental mesocosms appeared to have peaked by 30 days after disturbance (Fig. 8), but in field enclosures, GPP continued to increase through the end of the experiment in the downstream and middle reaches (Fig. 9). In the headwater reach, GPP appeared to stabilize after the second week. An important difference between experimental mesocosms and field enclosures was the absence of long algal filaments within the 8-week experiment. This was possibly due to differences between the intensity of natural and simulated floods and more complex interactions throughout the assemblage of invertebrate and vertebrate grazers that quickly re-colonized Kings Creek after the flood. For example, long-term data on fish assemblage structure, sampled quarterly since 1995, indicated that fish rapidly return to pre-flood densities, days since flood is not a strong predictor of fish assemblage structure (Franssen et al. 2006). Furthermore, in a natural stream, flood-mediated fish effects might be more likely to affect the benthic community during a trophic cascade initiated by fish (Power et al. 2008).

Table 4. Best approximating linear models for predicting ecosystem structure and function variables in Kings Creek study pools during summer 2005 as determined by Akaike information criterion (AIC) values.

Response variable	Model and parameters	Adjusted r^2	AIC_c	K	Δ_i	w_i
GPP	day	0.10	−88.88	3	0.00	0.38
GPP	day, shiner	0.11	−87.71	4	1.18	0.21
GPP	day, grazer	0.10	−87.50	4	1.38	0.19
GPP	day, shiner, grazer	0.11	−86.22	5	2.67	0.10
GPP	shiner	0.01	−85.09	3	3.79	0.06
GPP	grazer	0.00	−84.95	3	3.93	0.05
NH_4^+ uptake	day	0.28	147.57	3	0.00	0.59
NH_4^+ uptake	day, grazer	0.31	149.84	4	2.27	0.19
NH_4^+ uptake	day, shiner	0.26	150.14	4	2.57	0.16
algal biomass	day	0.32	290.57	3	0.00	0.40
algal biomass	day, grazer	0.33	291.07	4	0.49	0.31
algal biomass	day, shiner	0.31	292.34	4	1.76	0.17
algal biomass	day, shiner, grazer	0.33	292.92	5	2.35	0.12
Chironomidae density	day	0.30	–55.60	3	0.00	0.60
Chironomidae density	day, shiner	0.28	–53.11	4	2.48	0.17
Chironomidae density	day, grazer	0.28	–53.11	4	2.49	0.17
Chironomidae density	day, shiner, grazer	0.32	–50.48	5	5.12	0.05
Ephemeroptera density	day	0.55	–34.57	3	0.00	0.53
Ephemeroptera density	day, grazer	0.55	–32.89	4	1.68	0.23
Ephemeroptera density	day, shiner	0.54	–32.34	4	2.23	0.17
Ephemeroptera density	day, grazer, shiner	0.54	–30.52	5	4.06	0.07

Notes: AIC_c is the AIC corrected for small sample size; K is the number of parameters in the fitted model including the intercept and error term; Δ_i is the difference between the candidate model and the model with the lowest ranking AIC_c; the Akaike weights (w_i) sum to zero.

Comparisons between field enclosures and experimental mesocosms allowed us to test the effects of fishes under different levels of complexity and experimental venue. One hypothesis for a difference in consumer effects between the field and mesocosms is due to differences in advective forces. Whereas we were more apt to detect direct effects of fish (e.g. consumption of algae or invertebrates) in the relatively small field enclosures (10–20 m), we were less apt to detect effects of nutrient remineralization because of dilution from groundwater and potentially long nutrient uptake lengths (>100 m, O'Brien and Dodds 2007). Thus, consumers may not have increased nutrient levels enough to elicit a change in periphyton growth on substrata baskets at the downstream end of a field enclosure. Second, the magnitude of the flood and complexity of invertebrate and algal assemblages might also have limited consumer effects on ecosystem recovery. Further experiments that explicitly test nutrient limitation and the role of other consumers are necessary to evaluate the role of grazing and water-column minnows in regulating the recovery of ecosystem processes after natural floods.

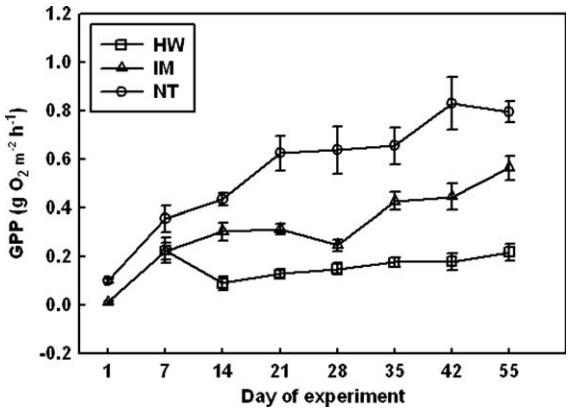

Figure 9. GPP measured in recirculating chambers on substrate baskets incubated during the field experiment in 20 Kings Creek field enclosures. Enclosures were located in three reaches of Kings Creek: headwaters (HW; squares), intermittent middle (IM; triangles), perennial downstream near nature trail bridge (NT; circles).

Ecosystem services provided by stream fishes

Quantifying effects of fishes on ecosystem rates allowed us to speculate about their potential to alter ecosystem services at a coarser scale, such as downstream water quality and export of organic matter (Taylor et al. 2006). In particular, fish might influence basin-wide nutrient dynamics during base-flow conditions by altering nutrient retention of streams (McIntyre et al. 2007). We cannot make a definitive conclusion about the effect of nutrient remineralization by fishes in streams because we were unable to detect effects on nutrient uptake in our field enclosures. However, in recirculating experimental mesocosms we found that in the presence of dace, the concentration of total nitrogen was 50 g l^{-1} less in the outflow than the inflow on day 42 of the experiment (Fig. 10). This concentration difference corresponds to 86 mg of TN per day and demonstrates that consumers have the potential to alter the flux of nutrients from small streams. It is important to note that we could not discern the fate of the 'retained' nutrients because our nitrogen retention estimates in the experimental mesocosms were calculated as a budget of concentration in the inflow versus concentration in the outflow over the course of the experiments. These nutrients could have been denitrified

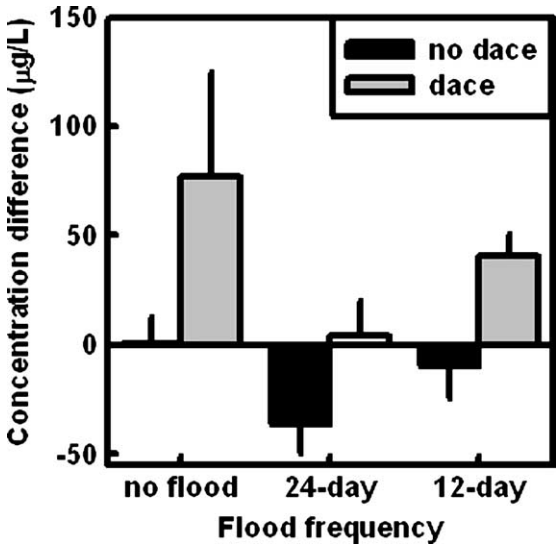

Figure 10. Mean concentration (+SE) of total nitrogen retained in experimental mesocosms with (gray bars) and without (black bars) dace on day 42. Values of bars were calculated by subtracting the concentration of total nitrogen measured in the outflow from that measured in the inflow of each mesocosm.

or could have been stored in the biota, particulate detritus, or hyporheic zones.

Fish might also influence the export of organic matter from streams. In the experimental mesocosms that were flooded every 12 and 24 days, we found that dace slightly decreased the amount of POM export during experimental flooding (range: 9–12%), whereas shiners increased the amount of POM exported up to a maximum of 29% in experimental mesocosms flooded every 24 days, which is consistent with the accumulation of long filaments and algal biomass in those treatments. Differences in export are likely a function of functional identity and a shift between consumptive losses by grazers and an increased supply of limiting nutrients by water-column minnows. These differences, summed across many small grassland streams occupied by these species could be important to downstream water quality (Whiles and Dodds 2002, Dodds et al. 2004), because local nutrient retention or loss depends in part on whether organic matter is retained in fish tissue or transported downstream.

General considerations

Streams are dynamic systems with temporally variable abiotic drivers, which is why recovery of stream ecosystem processes is often difficult to quantify (Steinman et al. 1987). Measures of standing stocks to indicate ecosystem function and biodiversity, as commonly used in terrestrial studies (Tilman et al. 2001), are not appropriate in streams and many other aquatic habitats because microbial producers turn over rapidly. With measures of whole ecosystem rates, however, we were able to incorporate changes in the accrual and senescence in benthic communities and better quantify successional processes in streams. We directly address how flood regime, and thus, climate change and consumer functional identity affect rates of ecosystem recovery by explicitly focusing on ecosystem metabolism and nutrient retention. Natural ecosystem functioning of aquatic systems is already jeopardized by changes in land-use, increased nutrient inputs, and changes in biodiversity (Vitousek 1994, Palmer et al. 1997, Covich et al. 1999, Cross et al. 2007). Global climate change could intensify these problems. In the Great Plains, general circulation models predict more frequent and intense precipitation events and longer periods between precipitation events (Knapp et al. 2002). Our experimental flood frequency manipulations directly tested the influence of decreasing frequency of intense scouring floods crossed with different species functional identity on stream structure and function in the Great Plains of North America. Results from experimental mesocosms identified mechanisms that allow consumer groups to interact with microbial communities in streams, but an experiment in field enclosures highlighted limitations to integrating this knowledge over larger, more complex scopes. Nevertheless, because species effects can be offsetting and vary with time since disturbance, predicting those effects will require a comprehensive understanding of the functional roles of species in these aquatic systems and the spatial and temporal scaling of those processes.

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References

Akaike, H. 1973. Information theory and an extension of the maximum-likelihood principle. – In: Petrov, B. N. and Csaki, F. (eds), 2nd Int. Symp. on Information Theory. Akademiai Kiado, pp. 267–281.

Akaike, H. 1974. A new look at the statistical model identification. – IEEE T Automat. Contr. 19: 716–723.

Bengtson, J. R. et al. 2008. Effects of grazing minnows and crayfish on stream ecosystem structure and function. – J. N. Am. Benthol. Soc. 27: 772–782.

Bertrand, K. N. 2007. Fishes and floods: stream ecosystem drivers in the Great Plains. PhD thesis. – Kansas State Univ.

Bertrand, K. N. and Gido, K. B. 2007. Effects of the herbivorous minnow, southern redbelly dace (*Phoxinus erythrogaster*), on stream productivity and ecosystem structure. – Oecologia 151: 69–81.

Bertrand, K. N. et al. 2006. An evaluation of single-pass versus multiple-pass backpack electrofishing to estimate trends in species abundance and richness in prairie streams. – Trans. Kans. Acad. Sci. 109: 131–138.

Biggs, B. J. F. et al. 2005. Linking scales of flow variability to lotic ecosystem structure and function. – River Res. Appl. 21: 283–298.

Burnham, K. P. and Anderson, D. R. 1998. Model selection and inference: a practical information-theoretic approach. – Springer.

Chapin, F. S. et al. 1997. Biotic control over the functioning of ecosystems. – Science 277: 500–504.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – Science 199: 1302–1310.
Covich, A. P. et al. 1999. The role of benthic invertebrate species in freshwater ecosystems. – BioScience 49: 119–127.
Cross, F. B. and Collins, J. T. 1995. Fishes in Kansas. – Univ. Kans. Nat. Hist. Mus.
Cross, W. F. et al. 2007. Nutrient enrichment reduces constraints on material flows in a detritus-based food web. – Ecology 88: 2563–2575.
DeAngelis, D. L. 1992. Dynamics of nutrient cycling and food webs. – Chapman and Hall.
Dahl, J. 1998. Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. – Oecologia 116: 426–432.
Dodds, W. K. 2003. Misuse of inorganic N and soluble reactive P concentrations to indicate nutrient status of surface waters. – J. N. Am. Benthol. Soc. 22: 171–181.
Dodds, W. K. and Brock, J. 1998. A portable chamber for *in situ* determination of benthic metabolism. – Freshwater Biol. 39: 49–59.
Dodds, W. K. et al. 1996. The relationship of floods, drying, flow and light to primary production and producer biomass in a prairie stream. – Hydrobiologia 333: 151–169.
Dodds, W. K. et al. 1999. Photosynthesis-irradiance patterns in benthic algae: variations as a function of assemblage thickness and community structure. – J. Phycol. 35: 42–53.
Dodds, W. K. et al. 2002. N uptake as a function of concentration in streams. – J. N. Am. Benthol. Soc. 21: 206–220.
Dodds, W. K. et al. 2004. Carbon and nitrogen stoichiometry and nitrogen cycling rates in streams. – Oecologia 140: 458–467.
Dudley, T. L. et al. 1986. Effects of macroalgae on a stream invertebrate community. – J. N. Am. Benthol. Soc. 5: 93–106.
Felley, J. D. and Hill, L. G. 1983. Multivariate assessment of environmental preferences of cyprinid fishes of the Illinois River, Oklahoma. – Am. Midl. Nat. 109: 209–221.
Fisher, S. G. et al. 1982. Temporal succession in a desert stream following flash flooding. – Ecol. Monogr. 52: 93–110.
Fontaine, T. D., III and Bartell, S. M. (eds) 1983. Dynamics of lotic ecosystems. – Ann Arbor Press.
Franssen, N. R. et al. 2006. Effects of floods on fish assemblages in an intermittent prairie stream. – Freshwater Biol. 51: 2072–2086.
Gelwick, F. P. and Matthews, W. J. 1992. Effects of an algivorous minnow on temperate stream ecosystem properties. – Ecology 73: 1630–1645.
Gibson, C. A. et al. 2005. Flow regime alterations under changing climate in two river basins: implications for freshwater ecosystems. – River Res. Appl. 21: 849–864.
Gido, K. B. and Matthews, W. J. 2001. Ecosystem effects of water-column minnows in experimental streams. – Oecologia 126: 247–253.
Gray, L. J. and Dodds, W. K. 1998. Structure and dynamics of aquatic communities. – In: Knapp, A. K. et al. (eds), Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford Univ. Press. pp. 177–189.
Gray, L. J. et al. 1998. Hydrology and aquatic chemistry. – In: Knapp, A. K. et al. (eds), Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford Univ Press. pp. 159–176.
Grimm, N. B. 1988. Feeding dynamics, nitrogen budgets, and ecosystem role of a desert stream omnivore, *Agosia chrysogaster* (Pisces: Cyprinidae). – Environ. Biol. Fish. 21: 143–152.
Hillebrand, H. 2002. Top-down versus bottom-up control of autotrophic biomass – a meta-analysis on experiments with periphyton. – J. N. Am. Benthol. Soc. 21: 349–369.
Jelks, H. L. et al. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. – Fisheries 33: 372–407.
Knapp, A. K. et al. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. – Science 298: 2202–2205.
Lake, P. S. et al. 2000. Global change and the biodiversity of freshwater ecosystems: impacts on linkages between above-sediment and sediment biota. – BioScience 50: 1099–1107.
Lepori, F. and Hjerdt, N. 2006. Disturbance and aquatic biodiversity: reconciling contrasting views. – BioScience 56: 809–818.
Lugthart, G. J. and Wallace, J. B. 1992. Effects of disturbance on benthic functional structure and production in mountain streams. – J. N. Am. Benthol. Soc. 11: 138–164.
McIntyre, P. B. et al. 2007. Fish extinctions alter nutrient recycling in tropical freshwaters. – Proc. Natl Acad. Sci. USA 104: 4461–4466.
Mackay, R. J. 1992. Colonization by lotic macroinvertebrates: a review of process and patterns. – Can. J. Fish. Aquat. Sci. 49: 617–628.
Matthews W. J. and Hill, L. G. 1979. Influence of physico-chemical factors on habitat selection by red shiners (*Notropis lutrensis*) (Pisces: Cyprinidae). – Copeia 1979: 70–81.
Matthews, W. J. et al. 2006. Modular experimental riffle-pool stream system. – Trans. Am. Fish. Soc. 135: 1559–1566.
Merritt, R. W. and Cummins, K. W. 1996. An introduction to the aquatic insects of North America. – Kendall/Hunt.
Milliken, G. A. and Johnson, D. E. 2002. Analysis of messy data, Vol. III: analysis of covariance. – Chapman and Hall.
O'Brien, J. M. and Dodds, W. K. 2007. Ammonium uptake and mineralization in prairie streams: chamber incubation and short-term nutrient addition experiments. – Freshwater Biol. 53: 102–112.
Owens, M. 1974. Measurements on non-isolated natural communities in running waters. – In: Vollenweider, R. A. (ed.), A manual on methods for measuring primary production in aquatic environments. Blackwell, pp. 111–119.
Palmer, M. A. et al. 1997. Biodiversity and ecosystem function in freshwater sediments. – Ambio 26: 571–577.
Parsons, M. et al. 2006. The biotic and abiotic legacy of a large infrequent flood disturbance in the Sabie River, South Africa. – River Res. Appl. 22: 187–201.
Petchey, O. L. et al. 1999. Environmental warming alters food-web structure and ecosystem function. – Nature 402: 69–72.
Poff, N. L. and Allan, J. D. 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. – Ecology 76: 606–627.
Power, M. E. 1990. Effects of fish in river food webs. – Science 250: 811–814.
Power, M. E. et al. 1988. Biotic and abiotic controls in river and stream communities. – J. N. Am. Benthol. Soc. 7: 456–479.
Power, M. E. et al. 1989. Grazing catfish, fishing birds, and attached algae in a Panamanian stream. – Environ. Biol. Fish. 26: 285–295.
Power, M. E. et al. 2008. Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. – Ecol. Monogr. 78: 263–282.
Rosemond, A. D. et al. 2000. Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and productivity to variation in light, nutrients, and herbivores. – Can. J. Fish. Aquat. Sci. 57: 66–75.
Sartory, D. P. and Grobbelaar, J. E. 1984. Extraction of chlorophyll a from freshwater phytoplankton for spectrophotometric analysis. – Hydrobiologia 114: 177–187.
Schmitz, O. J. et al. 1997. Behviorally mediated trophic cascades: effects of predation risk on food web interactions. – Ecology 78: 1388–1399.
Steinman, A. D. 1996. Effects of grazers on freshwater benthic algae. – In: Stevenson, R. J. et al. (eds), Algal ecology: freshwater benthic ecosystems. Academic Press. pp. 341–373.

Steinman, A. D. et al. 1987. Effects of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. – J. N. Am. Benthol. Soc. 6: 175–188.
Taylor, B. W. et al. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. – Science 313: 833–836.
Thébault, E. and Loreau, M. 2006. The relationship between biodiversity and ecosystem functioning in food webs. – Ecol. Res. 21: 17–25.
Tilman, D. et al. 2001. Diversity and productivity in a long-term grassland experiment. – Science 294: 843–845.
Uehlinger, U. 2000. Periphyton biomass in an unpredictable environment: exploring the temporal variability with a dynamic model. – Verh. Int. Ver. Theor. Angew. Limnol. 27: 3162–3165.
Vitousek, P. M. 1994. Beyond global warming: ecology and global change. – Ecology 75: 1861–1876.
Welschmeyer, N. A. 1995. Flourometric analysis of chlorophyll a in the presence of chlorophyll b and phaeopigments. – Limnol. Oceanogr. 39: 1985–1992.
Whiles, M. R. and Dodds, W. K. 2002. Relationships between stream size, suspended particles, and filter-feeding macroinvertebrates in a Great Plains drainage network. – J. Environ. Qual. 31: 1589–1600.