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Consumer return chronology alters recovery trajectory of stream ecosystem structure and function following drought

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Abstract. Consumers are increasingly being recognized as important drivers of ecological succession, yet it is still hard to predict the nature and direction of consumer effects in nonequilibrium environments. We used stream consumer exclosures and large outdoor mesocosms to study the impact of macroconsumers (i.e., fish and crayfish) on recovery of intermittent prairie streams after drying. In the stream, macroconsumers altered system recovery trajectory by decreasing algal and macroinvertebrate biomass, primary productivity, and benthic nutrient uptake rates. However, macroconsumer influence was transient, and differences between exclosures and controls disappeared after 35 days. Introducing and removing macroconsumers after 28 days resulted mainly in changes to macroinvertebrates. In mesocosms, a dominant consumer (the grazing minnow *Phoxinus erythrogaster*) reduced macroinvertebrate biomass but had little effect on algal assemblage structure and ecosystem rates during recovery. The weak effect of *P. erythrogaster* in mesocosms, in contrast to the strong consumer effect in the natural stream, suggests that both timing and diversity of returning consumers are important to their overall influence on stream recovery patterns. Although we found that consumers significantly altered ecosystem structure and function in a system experiencing rapid changes in abiotic and biotic factors following disturbance, consumer effects diminished over time and trajectories converged to similar states with respect to primary producers, in spite of differences in consumer colonization history. Thus, consumer impacts can be substantial in recovering ecosystems and are likely to be dependent on the disturbance regime and diversity of the consumer community.

Key words: disturbance; functional group; grazer; Konza Prairie Biological Station, Kansas, USA; nonequilibrium; succession.

INTRODUCTION

Characterizing factors that influence ecological succession has long been a focus of ecological studies (e.g., Clements 1916, Gleason 1927, Connell and Slatyer 1977). Primary producers regulate energy flow into the system during succession, and producer assembly patterns often shape ecosystem functional properties (Fisher et al. 1982). Factors that regulate the recovery of primary producers from disturbance include traits of producers (i.e., resistance and resilience to disturbance) and the magnitude and spatial characteristics (heterogeneity and extent) of the disturbance, which regulate the distance from refugia and source pool of potential colonists (Grimm and Fisher 1989, Peterson 1996, Turner et al. 1998). Although patterns of ecosystem recovery from disturbance can be strongly affected by bottom-up processes (Dodds et al. 1996), consumers also can shape system recovery trajectories (Mills 1986, Biggs et al. 1998, Hamilton 2000). Given the context-

dependent nature of consumer effects across ecosystems (e.g., Bertness et al. 2004, Schoener and Spiller 2006, Power et al. 2008), it may be difficult to extrapolate consumer effects observed during equilibrium conditions to predict consumer influence following a disturbance (in a time of rapidly shifting biotic and abiotic conditions).

A main challenge of predicting consumer influence during recovery is that factors dictating consumer impacts (e.g., consumer abundance, resource abundance, and competition) vary with asynchronous temporal recovery patterns of consumers and their resources (Schoener and Spiller 2006, Snyder 2009). Many consumers are larger and more mobile than their resources; grazers in particular tend to be more mobile than their food. Mobility can allow consumers to avoid physical disturbances that reduce abundances of resources, yielding high ratios of consumer to resource biomass immediately following a disturbance. In streams for example, fish can move to low-velocity areas during a flood (Ross and Baker 1983) while sessile algae is scoured. In the surrounding terrestrial portions of the watersheds, large grassland-grazing ungulates can move

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out of the path of wildfire flames that remove grasses. However, if disturbance intensity is such that consumers must rely more on reproduction or immigration from long distances, a longer consumer recolonization time results (Turner et al. 1998, Snyder 2009), decreasing consumer influence on early system recovery (e.g., Schoener and Spiller 2006). Therefore, the timing of consumer return, mediated by the consumer's response to the disturbance, may have substantial impacts on community succession.

Consumer diversity and functional traits are likely to influence succession. In general, consumer groups that are well adapted to use the prevailing resource (i.e., consume the dominant producer) in a given successional series should have a strong impact on succession. For example, herbivores that consume grasses and shrubs can hasten early terrestrial plant succession to persistent trees, whereas grainivores can have a strong impact on late succession when more seed-producing species are present (Davidson 1993). Additionally, benthivores (crabs and snails) can slow, or potentially halt the recovery of mussel beds and seaweed canopies following substrata clearing in marine rocky intertidal zones (Bertness et al. 2002, 2004). The ability of a stream to return to a state similar to the pre-disturbance state should increase when all members of the previously disturbed community are present (Elmquist et al. 2003). Increasing diversity within a functional group should stabilize the effects of that group on succession because it is less likely that all members of the group would be adversely affected by the disturbance (Fargione et al. 2003). However, there is little information on the functional redundancy among species and whether or not functional feeding groups remain constant under nonequilibrium conditions.

Intermittent prairie streams frequently undergo periods of flood and drying, and therefore are almost always in a state of succession (Matthews 1988, Dodds et al. 2004), which proceeds rapidly (weeks to months). Thus, transient effects of consumers are a vital component of these ecosystems, making them a good model system to evaluate the relationships between consumers and their temporal patterns of colonization and recovery. The recovery of structural and functional properties of producers in intermittent streams have been studied in some streams (e.g., Fisher et al. 1982, Dodds et al. 1996, 2004, Boulton 2003, Biggs et al. 2005), but the role of consumers influencing recovery following disturbance in streams is not as well documented (but see Gelwick and Matthews 1992, Pringle and Hamazaki 1997, Bertrand et al. 2009). Consumer effects in streams are generally strong during equilibrium states (Feminella and Hawkins 1995, Steinman 1996, Hillebrand 2002), but disturbances have the potential to change these interactions by altering community structure and producer growth rates (Whittaker 1965, Connell 1978, Huston 1979, Resh et al. 1988, Biggs et al. 2005).

Given the prominence of large consumers (herbivorous fishes, crayfish; hereafter referred to as macroconsumers) in intermittent prairie streams, we predicted that the resistance to disturbance, and thus the chronology of colonization of these animals, would alter their influence on system recovery. We used exclosure cages and a mid-recovery treatment reversal to evaluate the temporal influence of macroconsumers, and scenarios of delayed arrival and emigration of macroconsumers, on stream structure and function following a disturbance. We also isolated the effect of a dominant grazing minnow on ecosystem structure and function following drought in stream mesocosms. Specifically, we hypothesized that influence of macroconsumers on succession would be strongest when macroconsumer biomass and edible producer accumulation rates are high, which is typical of early recovery in prairie streams (Dodds et al. 1996, 2004). Macroconsumers arriving during mid-recovery should change benthic communities relatively fast as consumption should occur faster than algal and macroinvertebrate immigration and growth. Conversely, the effect of macroconsumers leaving mid-recovery should depend on ambient algal growth rates. In general, the magnitude of macroconsumer effects should decrease over time as additional consumer groups (i.e., small macroinvertebrate consumers) colonize and exert additional grazing pressure on primary producers, and as producers switch to slower growing, late recovery species.

METHODS

Stream experiment

Kings Creek is an intermittent prairie stream located on the Konza Prairie Biological Station (KPBS) in the Flint Hills region of northeastern Kansas, USA (see Gray and Dodds 1998 for further description). In March 2006, two exclosure cages were constructed in each of four consecutive pools in a dry, intermittent reach. The reach had been dry for the previous nine months. Pools had an average surface area of ~ 74 m² and average depth of ~ 0.6 m when wetted. The nearest upstream permanent pool with surface water was ~ 3.5 km, and the nearest downstream pool was ~ 100 m. Each cage had a closed side that excluded macroconsumers from baskets, and a control side that allowed macroconsumers access to the baskets from the downstream end. Cages were made of 5-mm mesh hardware cloth secured to steel poles, and buried 20 cm into the streambed. Twenty-one plastic mesh baskets (10 × 10 × 10 cm, 2 × 1.25 cm mesh size) filled with dry rocks from the stream channel were placed in each half of the exclosure and buried so basket tops were flush with the stream bottom.

On 29–30 April 2006, rainfall recharged groundwater that gradually reintroduced surface flow. Continuous stream discharge measurements were collected from USGS station no. 06879650 located ~ 0.5 km above the study site. Debris that collected on the upstream mesh

was removed as needed to maintain a consistent flow through cages. On day 29, one enclosure in each pool was reversed (i.e., the side open to macroconsumers was closed, and the area that excluded macroconsumers was opened) to assess two scenarios regarding macroconsumer return timing; (1) macroconsumers arriving early, but leaving after the benthic community had developed, and (2) macroconsumers returning late, after the benthic community was already established. This created four macroconsumer treatments from day 29 through 63: macroconsumers always present, never present, only present early, and only present late. Structural and functional response variables in cages were measured on days 7, 14, 21, 28, 35, 49, and 63, and included algal and macroinvertebrate biomass and composition, algal filament length, and benthic metabolism and nutrient uptake. Water nutrient concentrations (total nitrogen [TN], total phosphorus [TP], nitrate [NO_3^-] and soluble reactive phosphorus [SRP]) were measured in each pool at each sampling time.

Mesocosm experiment

Eight large outdoor mesocosms located ~ 200 m from Kings Creek were used to isolate the effect of one of the dominant macroconsumers in the stream, southern redbelly dace (*Phoxinus erythrogaster*), a grazing minnow. Each mesocosm consisted of a 2.54-m^2 pool connected to a 0.84-m^2 riffle. The basic design of these mesocosms is presented in Matthews et al. (2006). Spring water was continuously added to each mesocosm at a rate of ~ 10 L/h to offset evaporation losses and provide some nutrient input. Inflowing nutrient concentrations were low (TN, $133\ \mu\text{g/L}$; TP, $2.85\ \mu\text{g/L}$). Water was recirculated with an electric motor creating a discharge of 4–6 L/s, and riffle current velocity of 6–8 cm/s. Substrata were a mixture of native limestone pebble, gravel, and fine sediment and similar in size and texture to substrata in Kings Creek. An experiment immediately preceding this one inoculated all the mesocosms with a benthic slurry from Kings Creek, which provided a source of microbes and invertebrates typical of Kings Creek for potential colonization. Aquatic insects emerging from Kings Creek also readily colonized mesocosms.

Benthic communities developed in mesocosms for two months. On 20 June 2006, mesocosms were drained and let dry for two weeks with no hyporheic refugia. Rocks were taken from each pool and riffle, homogenized, and redistributed to ensure desiccation resistant taxa were present in all mesocosms. Mesocosms were refilled on 4–5 July 2006, and *P. erythrogaster* were stocked in four mesocosms at a density of 31 individuals per stream (~ 9 individuals/ m^2 ; ~ 4.25 g dry mass (DM)/ m^2 , ~ 9 g wet mass/ m^2), matching typical densities in Kings Creek (Franssen et al. 2006). Dead fish were immediately replaced to maintain initial densities throughout the experiment. The remaining four mesocosms served as a

fishless control. Mesocosms were sampled for the same response variables as in Kings Creek on days 6, 12, 18, 30, 42, 59, and 66.

Functional measurements

Benthic metabolism and nutrient uptake potential in Kings Creek were measured in sequence from rock baskets. Three baskets were randomly selected from each side of each cage, stored in the dark at stream temperature in moist, sealed plastic containers, and returned to the laboratory within two hours of collection. The three baskets from each treatment were sealed in an airtight 22-L recirculating chamber (Dodds and Brock 1998) with a YSI dissolved oxygen (O_2) probe (Yellow Springs Instruments, Yellow Springs, Ohio, USA). Chamber water was circulated at a velocity of ~ 10 cm/s, which was similar to stream velocity. Light was excluded from the chambers and respiration (R) was measured as the decline in O_2 over 1.5 hours. Chambers were then exposed to fluorescent plant grow lights ($\sim 300\ \mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR, photosynthetically active radiation) and O_2 was monitored for 1.5 hours. Respiration and net primary production (NPP) were calculated as the slope of the change of O_2 concentration over time per total surface area of the three baskets (top only, $300\ \text{cm}^2$) (Bott 1996) and adjusted to $\text{mg O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$. Gross primary production (GPP) was calculated as $\text{NPP} + \text{R}$. Biomass specific GPP was calculated by dividing GPP per total chlorophyll of the three baskets (i.e., $\text{mg O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}\cdot\text{mg chl}^{-1}$).

Ammonium (NH_4^+) was used to estimate maximum nutrient uptake rates because primary producers in Kings Creek are typically nitrogen- (N) limited, or co-limited by N and phosphorus (P) (Tank and Dodds 2003). Immediately following metabolism measurements, a NH_4^+ spike was added to raise the water concentration by $\sim 40\ \mu\text{g/L}$. Filtered water samples were taken at 0, 15, 30, 45, 60, and 90 minutes. Samples were analyzed on an OI Analytical Flow Solution IV autoanalyzer using the indophenol blue method (APHA 1998). Ammonium uptake rates were calculated from the slope of the natural log-transformed NH_4^+ concentration vs. time and adjusted to $\mu\text{g NH}_4^+\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ (Dodds et al. 2002, O'Brien and Dodds 2008).

Mesocosm NPP and R were measured using diurnal changes in O_2 concentrations with YSI 600XLM sondes using the open system single-station approach (Owens 1974). Aeration was measured in three mesocosms by the propane injection method (Marzolf et al. 1994, Young and Huryn 1998) and assumed to be the same in all mesocosms. Ammonium uptake was measured similarly as in chambers. A solution containing 0.4 g of NH_4Cl was added at the top of the riffle, and filtered water samples were collected every 15 minutes for 1.5 hours, placed on ice, and frozen within two hours (Tank et al. 2006). A plastic flow diffuser was added below the riffle to increase mixing in the pool. Mean daily solar

irradiance was measured at the Konza meteorological station located ~0.5 km from the mesocosms (data available online).⁶ GPP and NH_4^+ uptake rates were calculated as in the field experiment and adjusted for ambient light intensity to account for variation in cloud cover among sampling days.

Structural measurements

Macroconsumers.—Population densities of macroconsumers (fish, crayfish, and tadpoles) in Kings Creek pools were estimated on days 22 and 64. Single-pass electrofishing was used on day 22 to minimize substrata disturbance in the pools. Three-pass depletion electrofishing was used to estimate population densities on day 64 following the final sampling. Population densities from single-pass collections were adjusted to three-pass estimates using the relationship developed by Bertrand et al. (2006) in Kings Creek pools. Individual lengths were measured and converted to grams DM using equations developed by Kaufman and Beyers (1972) for fish, and Benke et al. (1999) for crayfish and tadpoles. Additionally, small, shallow pools and clear water allowed weekly visual estimates of fish abundance within pools from the bank. The numbers of individuals visually counted in each pool were converted to g DM/m² using mean mass of individuals from day 22 samples and pool area.

Algae and macroinvertebrates.—Kings Creek algae and macroinvertebrates were collected from baskets following chamber measurements. For each three-basket set, one was used for benthic algal biomass (chlorophyll *a*), one for algal composition, and one for macroinvertebrate composition. All rocks from one basket were put in an autoclavable bag and submerged in 95% EtOH. Bags were put in a 78°C water bath for five minutes, and extracted in the dark for 12 hours (Sartory and Grobbelaar 1984). Chlorophyll *a* was measured on a Turner model 112 fluorometer with a filter set and lamp that does not allow interference from phaeophytin (Welschmeyer 1995), and calculated as chlorophyll per surface area of the basket (100 cm²). Three rocks from the second basket were brushed into a beaker and homogenized, and a 20-mL subsample was preserved with 5% formalin for algal identification. Dominant algae were identified to genus, with a minimum of 300 cells counted for each sample. Algae were placed into one of nine functional groups: diatoms (single cell pennate, chain-forming pennate, single cell centric, chain-forming centric), cyanobacteria (filamentous or coccoid), and green (filamentous, single cell, or colonial), as broadly based physical and biological characteristics relating to recovery aspects (e.g., grazer susceptibility and nutrient use) may better reveal algal recovery patterns (Steneck and Dethier 1994). All rocks from the third basket were rinsed in a 250- μm mesh

sieve, and macroinvertebrates (non-crayfish) were preserved with 10% formalin, identified to the family level, and assigned functional feeding groups based on Merritt et al. (2008). Algal filament lengths were measured inside each cage half on days 28 and 63 by measuring the average filament length at five random points in three transects. Algal community composition was assessed for days 7, 21, 35, and 63, and macroinvertebrate composition at days 21, 35, and 63.

Mesocosm algal biomass (mg chlorophyll *a*/m²) was measured in each mesocosm riffle and pool by collecting three and five random rocks, respectively. Rocks were placed on ice and frozen within four hours of collection. Chlorophyll *a* was extracted as described earlier. Rock area was measured by tracing the top surface of the rock on paper, digitizing the image, and determining the area of the tracing with SigmaScan 5 (Systat Software, San Jose, California, USA). Algal filament length was measured at three points along three equally-spaced transects in the riffle, and at five equally-spaced points in the pool.

Mesocosm algal and macroinvertebrate composition samples were collected with a core sampler consisting of a 0.018-m² tin pipe with an electric pump (0.1 L/s) attached through the side. Substrata inside the corer were agitated by hand while 9 L of water were pumped into a bucket. Bucket contents were homogenized, and a 20-mL subsample (preserved with 5% formalin) was collected for algal identification. The remaining material was passed through a 250- μm mesh sieve and macroinvertebrates preserved with 10% formalin. One core sample was taken from the riffle and one from the pool in each mesocosm. Composition was assessed on days 18 and 42.

Algal desiccation resistance was assessed to identify the initial algal pool present upon rewetting. The day prior to rewetting, 10 rocks containing dried biofilm were taken from each riffle, placed in a bucket, and mixed. Eight rocks were put into each of three autoclaved 1-L Erlenmeyer flasks, filled with 500 mL of deionized water, capped with cotton, and placed under a fluorescent light (300 $\mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR). Additional rocks from the bucket were sterilized by autoclaving for one hour and put into three flasks in identical conditions as a control. After three weeks, rocks were brushed, and algae were preserved with 5% formalin and identified to genus.

DATA ANALYSIS

Kings Creek.—A repeated-measures analysis of variance (RM ANOVA), blocked by cage, was used to test treatment differences and treatment by time interactions for each response variable (chlorophyll *a*, filament length, macroinvertebrate biomass, area, and biomass specific GPP, NPP, R, and NH_4^+ uptake). We used the PROC Mixed command in SAS to model the covariance structure of untransformed data and used AIC_c (Akaike information criterion adjusted for small sample sizes)

⁶ <http://www.konza.ksu.edu/konza/datasets>

values to pick the covariate matrix model that best fit the data (Milliken and Johnson 2002), and used Kenward-Rogers approximations to find F test approximate degrees of freedom.

Differences in algal (proportion of total biovolume) and macroinvertebrate (arcsine square-root-transformations of biomass) functional group composition were quantified with Bray-Curtis similarity matrices, and treatment differences were assessed with analysis of similarity (ANOSIM). Repeated-measures ANOVA was then used to test for differences in individual algal and macroinvertebrate functional groups that composed >10% of total biomass.

Reversing half of the cages created four macro-consumer treatments after day 28: macroconsumers always present, never present, only present early, and only present late. Repeated-measures ANOVA on response variables during days 35–63 with a priori planned contrasts was used to test the effect of macroconsumers (1) arriving early in recovery, but leaving mid-recovery (i.e., always present vs. only present early), and (2) arriving later in recovery (i.e., never present vs. only present late) on the measured response variables.

Mesocosms.—Repeated-measures ANOVA was used to detect treatment differences in all structural and functional response variables in mesocosms. Pool and riffle structural variables were analyzed separately. Area- and biomass-specific GPP were significantly correlated to mean daily solar irradiance measurements ($r^2 = 0.18$, $P < 0.001$ and $r^2 = 0.28$, $P < 0.001$ for area and biomass GPP, respectively), so light was used as a covariate for these variables in the RM ANOVA. Repeated-measures ANOVA also was used to test compositional differences between individual algal and macroinvertebrate functional groups that made >10% of total biomass on days 18 and 42.

We used the Dunn-Sidak method to calculate a conservative critical value for all RM ANOVA hypothesis tests because of the large number of response variables. Adjusted critical values were calculated for each data set analyzed with RM ANOVAs (stream cages, $n = 16$, $\alpha = 0.003$; cage reversals, $n = 16$, $\alpha = 0.003$; mesocosms, $n = 13$, $\alpha = 0.004$). We interpreted P values less than the adjusted critical value as robust patterns, and P values between 0.05 and the adjusted critical value as trends. Treatment-induced differences in response variables among days were analyzed with Tukey post hoc comparisons. Repeated-measures ANOVAs were performed using SAS version 9.2 (SAS Institute, Cary, North Carolina, USA), and ANOSIMs were conducted with PRIMER version 5 (PRIMER-E, Ivybridge, UK).

RESULTS

Stream study

Discharge peaked at $0.07 \text{ m}^3/\text{s}$ immediately following channel rewetting, stabilized at $0.04 \text{ m}^3/\text{s}$ after two days, and then gradually decreased (Fig. 1A). Resumption of discharge was not strong enough to be considered a

flood, and there was no major visible loss of organic matter (leaves and wood) from the streambed. Historical mean discharge (1979–2007) at the nearby upstream gauging station was $0.18 \text{ m}^3/\text{s}$ for May and the mean consecutive flow was 24 weeks (SD 19, USGS station no. 06879650). Channel flow continued in the study reach until day 63 and then pools became disconnected. Total N and TP dropped by 45% and 38%, respectively, by day 14, and gradually increased back to initial concentrations by day 35 (Fig. 1B). Nitrate followed the same pattern as TN, but SRP steadily decreased by half from day 7 to day 63. Stream water TN:TP ratios following channel rewetting were <16 (in regard to Redfield ratio), suggesting possible algal N limitation.

Macroconsumer colonization.—Large schools of fishes were observed in pools three days after rewetting, with maximum observed densities during days 14 to 21, and few fish visible after day 35 (Table 1). Plains leopard frog (*Rana blairi*) tadpoles were observed in the downstream pool throughout the experiment. Adult crayfish (*Orconectes* spp.) were observed seven days after rewetting through day 63. Electrofishing samples on day 21 were dominated by *P. erythrogaster* and central stoneroller (*Camptostoma anomalum*) (Table 2). Other fish species collected were orangethroat darter (*Etheostoma spectabile*), a benthic invertivore, in three pools and creek chub (*Semotilus atromaculatus*), a water column/benthic omnivore, in the downstream pool. No fish were collected on day 63. Tadpole biomass increased fourfold and crayfish biomass 12-fold from day 21 to 63 (Table 2).

Structural recovery.—Macroconsumer effects of algal biomass varied temporally during recovery as there was a marginally significant macroconsumer-by-time interaction (RM ANOVA, $F_{6,14,6} = 3.33$, $P = 0.028$; Fig. 1C; also see Plate 1). Where macroconsumers were excluded, algal biomass increased faster during the first 35 days, acquiring 113% and 70% higher mean biomass at days 14 (post hoc comparisons, $P = 0.002$) and 28 ($P = 0.017$), respectively. Biomass peaked on day 35 ($227 \pm 187 \text{ mg chl}/\text{m}^2$, mean \pm SD), with algal filaments in visibly different stages of senescence among cages, as noted by heterogeneous yellowing and detachment of filaments. Algal biomass decreased substantially by day 35 and then was not significantly different from substrata exposed to macroconsumers through day 63. With macroconsumers present, algal biomass recovery was less variable, steadily increasing and peaking on day 63 at $153 \pm 26 \text{ mg chl}/\text{m}^2$.

Recovery time had a strong effect on algal functional group composition producing three distinct assemblages at early (day 7), mid- (days 21 and 35), and late (day 63) recovery (ANOSIM, $R = 0.40$, $P = 0.001$). Macroconsumers altered algal recovery dynamics by reducing green filaments (*Ulothrix* spp.) (RM ANOVA, $F_{1,12,5} = 10.81$, $P = 0.006$) and increasing chain-forming pennate diatoms (*Meridon* sp.) during mid-recovery only (significant macroconsumer by time interaction $F_{3,23,9} =$

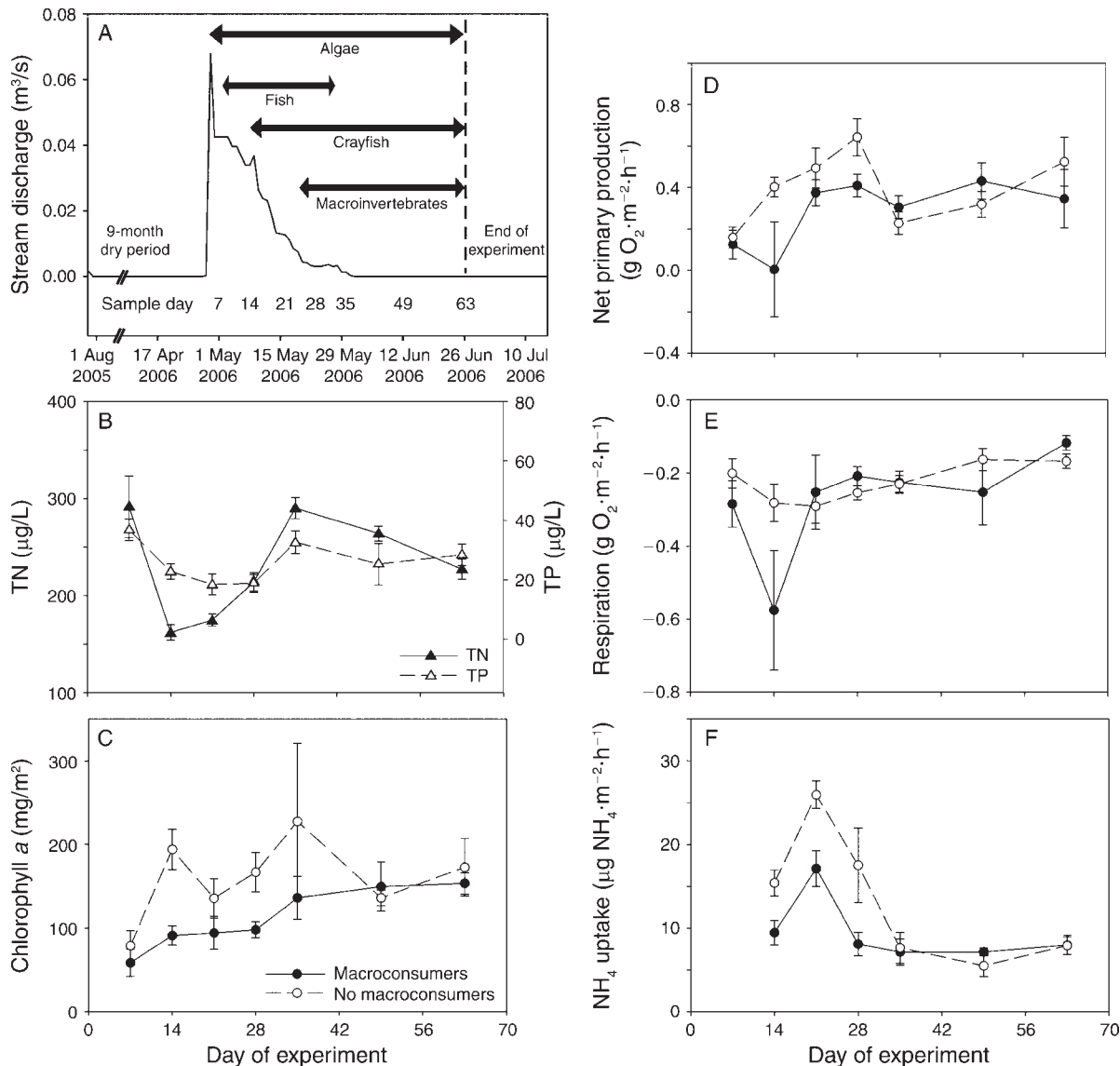


FIG. 1. Structural and functional responses following rewetting in Kings Creek, Konza Prairie Biological Station, northeastern Kansas, USA. (A) Stream discharge after drought and experiment timeline (August 2005; April–July 2006). Arrows show timing of returns of various groups of organisms. Fish returned within days, but large schools were absent following day 35. (B) Water nutrient concentrations: total nitrogen (TN) and total phosphorus (TP). (C) Algal biomass, measured as mass of chlorophyll *a*. (D) Net primary productivity. (E) Benthic respiration. (F) Ammonium uptake potential. In panels C–F, open circles indicate macroconsumers absent, and solid circles indicate macroconsumers present. Day zero was 29 April 2006. Values are expressed as mean \pm SE.

5.00, $P = 0.007$, Fig. 2). Macroconsumer effect was greatest during mid-recovery (day 21; ANOSIM, $R = 0.53$, $P = 0.006$), when green filament biovolume was 4.4 times higher, and chain-forming pennate diatoms biovolume was 2.2 times lower without macroconsumers (post hoc, $P = 0.001$ and $P = 0.016$, respectively). Filament senescence between days 21 and 28 caused an abrupt change in assemblages without macroconsumers, and there was no difference in algal composition between macroconsumer treatments by day 35. By day 63, filaments had increased in both treatments, but were

more grazing-resistant forms (i.e., *Stigeoclonium* sp. and the cyanobacterium *Oscillatoria* sp.), and diatoms had become dominated by larger species (i.e., *Gomphonema*, *Synedra*, and *Pinnularia* spp.) and chain-forming cells (i.e., *Meridon* and *Fragilaria* spp.). Patterns of filament lengths matched algal counts. Cyanobacteria filaments made up $<15\%$ of total algal biomass but were marginally increased by the presence of macroconsumers ($F_{1,17} = 6.61$, $P = 0.020$, Fig. 2). Although macroconsumers altered algal functional group proportions, both treatments contained the same species.

TABLE 1. Visual estimates of total fish densities in each pool in Kings Creek, on the Konza Prairie Biological Station, Kansas, USA, converted to g DM/m².

Day	Pool 1	Pool 2	Pool 3	Pool 4	Average
1	0.0	0	0	0	0
3	0.7	0.3	0	0.5	0.4
4	1.1	1.0	0.9	1.9	1.2
10	1.4	0.8	0.6	1.4	1.0
11	1.4	0.8	0.6	1.4	1.0
17	1.4	0.8	0.6	1.4	1.0
24	1.4	0.6	0	1.4	0.9
35	0	0	0	0	0
61	0	0	0	0	0

Note: Day zero was 29 April 2006.

Small macroinvertebrate (non-crayfish) composition changed during recovery (ANOSIM, $R = 0.19$, $P = 0.028$). Total macroinvertebrate biomass was low until day 35, when collector-gatherers (dominated by Chironomidae) became abundant. Concurrently, macroconsumers had the strongest effect on macroinvertebrates on day 35 ($R = 0.73$, $P = 0.001$) as substrata without macroconsumers had sixfold higher collector-gatherer biomass than with macroconsumers (RM ANOVA, $F_{1,6.79} = 6.50$, $P = 0.039$; post hoc, $P = 0.039$; Fig. 3). By day 63, scrapers (mainly *Stenonema* spp., mayflies) colonized both treatments equally, resulting in no significant macroconsumer effect. Predator biomass was consistently lower in the presence of macroconsumers, but this trend was not significant and total predator biomass remained relatively low (>10%) throughout the experiment.

Functional recovery.—NPP increased faster in the absence of macroconsumers ($F_{1,41} = 7.23$, $P = 0.010$), becoming 64% higher by day 28 ($P = 0.043$; Fig. 1D). However, on day 35, NPP dropped 65% in macroconsumer-excluded treatments and was not significantly different from substrata exposed to macroconsumers through day 63. Benthic respiration was marginally increased by macroconsumers ($F_{1,41} = 7.23$, $P = 0.010$), with the highest differences on day 14 where respiration was twice as high with macroconsumers ($P = 0.064$; Fig. 1E). Area-specific GPP followed a similar trend as NPP reaching 48% higher without macroconsumers on day 28, but the overall trend was not significant. Biomass-specific GPP did not differ between treatments. Macroconsumers decreased ammonium uptake potential ($F_{1,21.6} = 13.83$, $P = 0.001$) with a marginal interaction with time ($F_{5,18.5} = 4.11$, $P = 0.011$). Ammonium uptake was 1.6 ($P = 0.015$), 1.5 ($P = 0.006$), and 2.2 ($P = 0.064$) times higher without macroconsumers on days 14, 21, and 28, respectively, but uptake rates fell below rates of substrata exposed to macroconsumers on day 35 (Fig. 1F).

Cage reversals.—Reversing cages in mid-recovery had a strong impact on macroinvertebrates. The main effect of macroconsumers returning in mid-succession vs. where macroconsumers were never present was a decrease in collector-gatherer biomass (RM ANOVA,

$F_{3,12.3} = 4.24$, $P = 0.029$), with a 91% reduction on day 35 (post hoc, $P = 0.034$; Fig. 3). From day 35 to 63, scrapers colonized both treatments equally, leading to similar total macroinvertebrate biomass by day 63. The effects of macroconsumers leaving during mid-recovery were not immediate. On day 35, macroinvertebrate assemblages exposed to macroconsumers leaving in mid-recovery were similar to where macroconsumers were always present. However, macroconsumers leaving eventually led to increased algal biomass ($F_{1,10.9} = 12.83$, $P = 0.004$), with a 37% increase by day 63 ($P = 0.008$). Scrapers were also marginally reduced ($F_{1,11} = 5.75$, $P = 0.035$), with a 55% reduction by day 63 ($P = 0.034$).

Mesocosm study

Phoxinus erythrogaster did not significantly alter algal biomass in pools or riffles. Green filamentous algae dominated early assemblages in both treatments, averaging 84% of the total algal biomass. Fish had no effect on pool filament length (Fig. 4B), but riffle filament length was 9.4 cm (230%) longer with fish by day 30 ($F_{1,5.9} = 8.97$, $P = 0.024$, post hoc, $P = 0.011$; Fig. 4C). Maximum filament lengths occurred on day 18 in pools (7.8 cm) and day 30 in riffles (12.1 cm), and decreased through day 66. Filaments senesced at roughly the same time in mesocosms as in Kings Creek, starting at day 30.

Desiccation-resilient species dominated early algal assemblages in mesocosms. In the laboratory rewetting experiment, only green algae and cyanobacteria species (mostly filamentous forms) were observed. The green algal species pool was comprised of the green filaments *Ulothrix* sp., *Spirogyra* sp., *Microspora* sp., *Cylindrocapsa geminella*, and a green colonial coccoid algae. Initial cyanobacteria available were filamentous *Oscillatoria* spp., *Dichothrix* sp., *Anabeana* sp., and *Nostoc* sp., with the coccoid colonial *Aphanothece* sp. also common. Fish had no significant effect on algal compositional recovery

TABLE 2. Density estimates of macroconsumers in stream pools with enclosure cages.

Species	Macroconsumer density (g DM/m ²)	
	Day 21	Day 63
Fish		
<i>Phoxinus erythrogaster</i>	1.21 (1.70)	0
<i>Camptostoma anomalum</i>	2.20 (1.33)	0
<i>Etheostoma spectabile</i>	0.19 (0.07)	0
<i>Semotilus atromaculatus</i>	0.18	0
Crayfish		
<i>Orconectes nais</i> , <i>O. neglectus</i>	0.42 (0.11)	4.97 (3.51)
Tadpole†		
<i>Rana pipiens</i>	0.04	1.74

Notes: Single-pass electrofishing was used on day 21 to minimize substrata disturbance, and three-pass depletion sampling was used to estimate population densities on day 63. Densities are given as means, with SD in parentheses.

† Tadpole biomass is in grams ash-free dry mass/m².

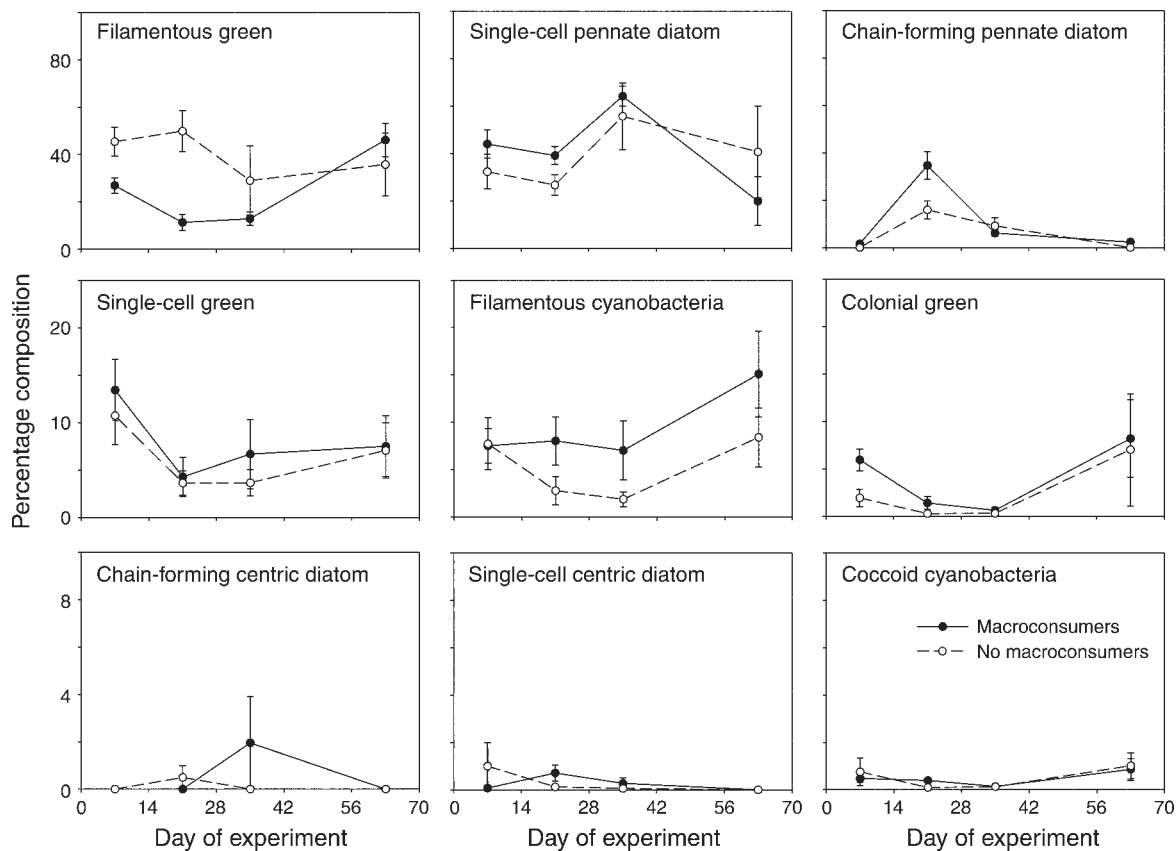


FIG. 2. Kings Creek algal functional group composition. Solid circles indicate macroconsumers present, and open circles indicate macroconsumers absent. Day zero was 29 April 2006. Note the different y-axis scales on each row. Values are expressed as mean \pm SE.

in mesocosms (Table 3). Similar to Kings Creek, the green filamentous algae *Ulothrix* sp. became the dominant species after six days in both treatments and continued to dominate through day 66. However, in mesocosms, senescing *Ulothrix* was replaced by shorter *Ulothrix* and *Spirogyra* filaments. Diatoms (mainly *Navicula* and *Synedra* spp.) and cyanobacteria (mainly *Oscillatoria* sp.) made up <10% of total biomass through day 66.

Fish marginally reduced total macroinvertebrate biomass in mesocosms ($F_{1,10.4} = 6.13$, $P = 0.027$). Fishless control treatments had 129% more invertebrate biomass on day 18 and 55% more on day 42 ($P = 0.024$, Table 3) than fish treatments. On day 18, biomass was predominantly Chironomidae (78%) without fish, and Chironomidae (42%) and Ostracoda (48%) with fish. By day 42, both treatments were codominated by Chironomidae and Ostracoda, with slight increases in libellulid dragonfly nymphs (predator), Cladocerans (collector-filterer), snails, and baetid mayflies (scrapers).

Fish effects on stream function were weak in mesocosms. Metabolic activity recovered quickly upon rewetting. The highest rates of productivity and nutrient uptake occurred during the first week and decreased

with time (Fig. 4). There were no significant effects of *P. erythrogaster* on functional recovery in mesocosms.

DISCUSSION

Macroconsumers in this intermittent stream had significant, but transient effects during recovery from drying. Results were consistent with our prediction that consumer biomass and algal growth rates determine macroconsumer influence. Macroconsumer structural and functional influence was initially weak (measured as the difference between treatments; Fig. 1). However, fish effects on algae increased markedly from days 7 to 14 as fish reduced algal biomass by roughly 70%. After crayfish returned, no net algal accrual occurred until fish began to leave the reach. Algae in this system typically take one to two weeks to reach exponential growth following a large disturbance and reach peak biomass after one to two months (Dodds et al. 1996, Murdock and Dodds 2007). Algal assemblages without macroconsumers were less stable, undergoing oscillations of rapid growth and decline, with fast shifts in dominant algal forms. Productivity and nutrient uptake rates mimicked algal biomass, and following an algal transition due to senescing filaments, algal structure and

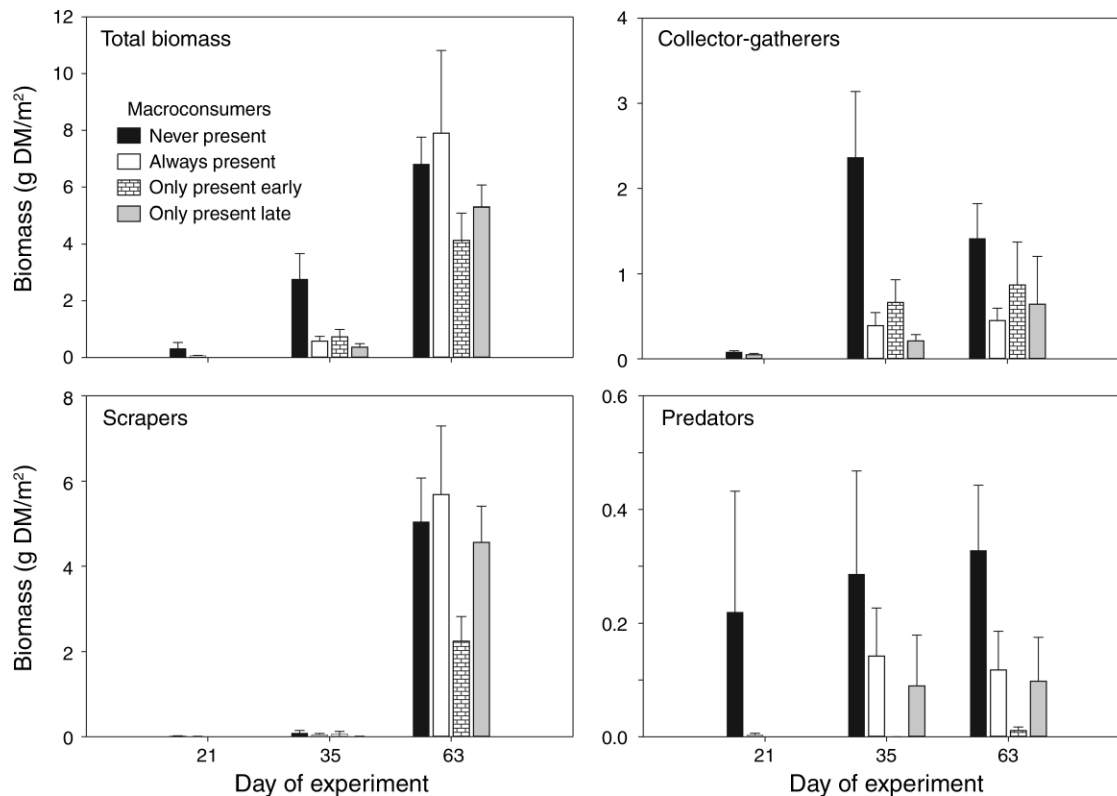


FIG. 3. Stream macroinvertebrate (non-crayfish) functional group composition by dry mass (DM) biomass. Prior to day 28, macroconsumers were either always present or never present in each cage half. On day 29, half the cages were reversed (i.e., consumer-excluded areas were opened, and open areas were closed to consumers), creating two additional treatments (macroconsumers present only early in recovery, and macroconsumers present only late in recovery) through day 63. Values are expressed as mean + SE.

function in control and enclosure cages were similar (i.e., there was an eventual weakening of macroconsumer impact). Algal recovery in cages open to macroconsumers was more similar to typical algal recovery in Kings Creek (e.g., Dodds et al. 1996, 2004, Bertrand et al. 2009). Therefore, a surprising result was a convergence of treatment trajectories in late succession with benthic communities reaching a similar state regardless of macroconsumer presence.

Our hypothesis that small consumers would reduce the impact of macroconsumers was supported by algal structure and function becoming similar between treatments with the colonization of invertebrates too small to be excluded by the cages (hereafter referred to as microconsumers). Microconsumers became abundant in mid-recovery, and colonization coincided with a leveling off of algal accumulation and a precipitous drop in abundant, small diatoms in both treatments. Also as predicted, macroconsumers arriving in mid-recovery had a relatively fast impact on benthic communities, while the effect of macroconsumers leaving in mid-recovery was delayed. However, the movement of macroconsumers in and out of areas altering macroinvertebrates more than algae was unexpected.

Context-dependent effects

The changing macroconsumer effect during recovery was strongly influenced by the shifting biotic and abiotic conditions (e.g., consumer return time, producer accumulation rates, and macroconsumer functional roles). Our results suggest a strong context-dependent recovery process as biotic interactions changed with shifting environmental conditions, and support the dynamic equilibrium model of Huston (1979). Seasonal variability in consumer influence has been observed with grazing fish on benthic organic matter accumulation in a South American floodplain river with changing water level (Winemiller et al. 2006), over several years in a prairie grassland entering a dry period (Suttle et al. 2007), and in a rocky intertidal community during El Niño years (Vinueza et al. 2006). Our data show that consumer influence can also change over days to weeks in response to local environmental shifts. Quick temporal shifts in consumer impact can lead to substantial changes in community structure and function, due to the changing nature and degree of interspecific interactions during succession (Lake 2003, Cardinale et al. 2005).

Drought recovery was not regulated strictly by top-down or bottom-up processes. The earliest macro-

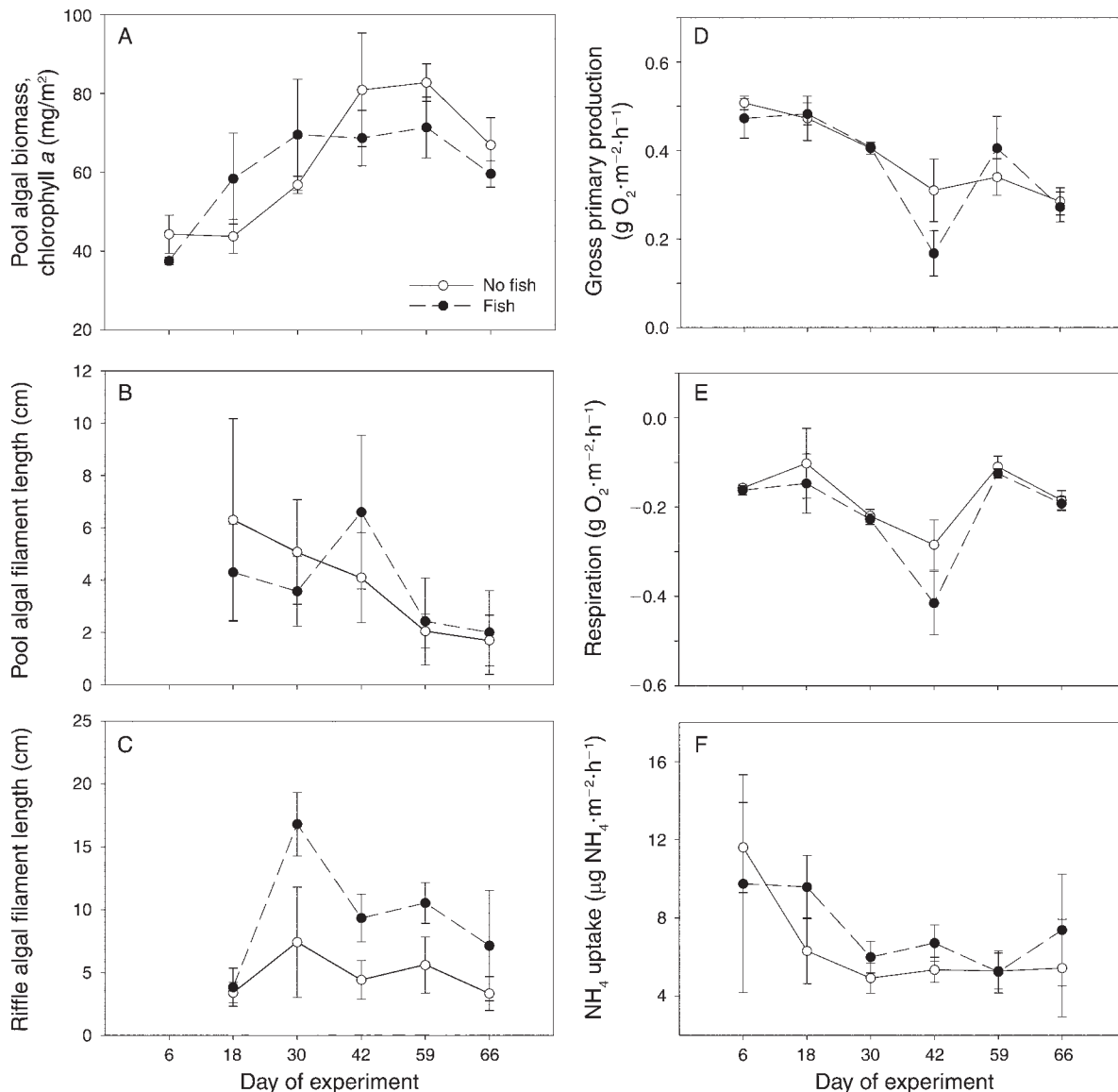


FIG. 4. Mesocosm (A–C) structural and (D–F) functional response variables. Open circles indicate fish absent, and solid circles indicate fish present. Values are expressed as mean ± SE.

consumer alteration of successional trajectories was through a direct reduction of a developing producer (i.e., filamentous green algae). However, fish influence was initially weak, despite relatively high fish biomass. It was not until algae began exponential growth typical of early succession that fish influence became evident. Additionally, filament death (which was not likely due to macroconsumer activity) midway through recovery marked a substantial reduction in macroconsumer (crayfish) influence. This suggests that overall impact of macroconsumers was in part regulated by algal productivity (Whittaker 1965, Roll et al. 2005, Hillebrand et al. 2007), and that diversity of colonizers and system function are closely linked during recovery in this system (Cardinale et al. 2009). Macroconsumer

impact during succession increased as both macroconsumer consumption rates (governed by return timing) and producer growth rates (governed by nutrient and space availability and by competition) increased, which was consistent with our hypotheses. Disturbance history also played a role in macroconsumer effect (Power et al. 2008). Interestingly, a single species (desiccation resistant filamentous algae, *Ulothrix*) played a major role in defining the altered successional trajectory imposed by macroconsumers. *Ulothrix* presence was based on disturbance characteristics as it is easily removed during floods, and would likely not have been abundant if water returned to the dry channel with a scouring flow.

TABLE 3. Average algal and macroinvertebrate functional group composition in mesocosms with and without fish during early and late recovery.

Functional group	Day 18		Day 42	
	No fish	Fish	No fish	Fish
Algae (% composition)				
Single-cell pennate diatoms	22.75 (27.92)	11.59 (15.46)	3.45 (1.95)	5.2 (4.81)
Filamentous cyanobacteria	1.62 (1.95)	0.11 (0.09)	0.18 (0.18)	0.51 (0.69)
Cocoid cyanobacteria	0.17 (0.20)	0.06 (0.07)	0.17 (0.16)	0.04 (0.06)
Filamentous green	70.79 (25.98)	86.03 (14.83)	88.45 (5.16)	89.57 (6.01)
Colonial cocoid green	1.45 (2.64)	0.84 (0.95)	0.31 (0.28)	0.24 (0.24)
Single-cell green	3.22 (3.88)	1.36 (0.75)	7.45 (3.93)	4.44 (2.22)
Macroinvertebrates (g dry mass/m ²)				
Scrapers	0.04 (0.08)	0.03 (0.06)	0.03 (0.05)	0.08 (0.15)
Predators	0.03 (0.05)	0.01 (0.01)	0.13 (0.19)	0.06 (0.07)
Collector-gatherers	1.05 (0.45)	0.45 (0.26)	1.68 (0.64)	1.03 (0.44)
Collector-filterers	0.04 (0.03)	0.02 (0.03)	0.03 (0.01)	0.04 (0.02)
Total biomass	1.17 (0.49)	0.51 (0.29)	1.87 (0.79)	1.20 (0.33)

Note: Values are means, with SD in parentheses.

Macroconsumers (fish and crayfish) slowed recolonization of microconsumers (primarily chironomids) by roughly 14 days in the field experiment, but it was not clear if this was through direct or indirect effects. Mesocosm results from this and previous studies suggest macroconsumer effects occur through physical disturbance of the substrata rather than through direct consumption. For example, Bertrand et al. (2009) and Bengtson et al. (2008) found very low numbers of chironomids in diets of *P. erythrogaster* kept in these same mesocosms, suggesting these fish do not rely on them as a food source. It is possible that macroconsumers may be inadvertently consuming chironomid eggs or early instars during grazing, or the physical disruption of the substrata may be interfering with egg or early instar development. Ostracod abundance was greater early in mesocosms with fish than in fishless controls, and bioturbation can cause increased ostracod abundance (Benzie 1989). Despite a significant effect on chironomids, macroconsumers had less effect on mayfly return, which colonized during mid- to late recovery. These results suggest that the macroconsumer effects on microconsumers were mostly mediated by traits of the microconsumers.

Reversing cages in mid-recovery altered benthic successional trajectories. We predicted a reduction in algal biomass with the addition of macroconsumers in mid-recovery; however allowing access to macroconsumers mid-experiment caused an immediate reduction in chironomids, but not in algal biomass. Crayfish, the major macroconsumer at this time, are omnivorous, and will consume invertebrates as well as algae (Evans-White et al. 2001). Consumption of small invertebrates may have increased as algae shifted from preferred filamentous forms to less preferred diatoms (Evans-White et al. 2003). Removing macroconsumer influence had no initial impact, but led to a later increase in algal biomass and reduction in mayfly colonization. Removing macroconsumers that keep filamentous algae in check may

impede colonization of consumers that utilize smaller algae (Vaughn et al. 1993), and supports the idea of increasing microconsumer impact as recovery proceeds.

Our reversal data suggest that adding a consumer to a system does not necessarily produce the opposite result of removing a consumer. For example, adding crayfish reduced chironomids, but removing crayfish did not increase chironomids. Changing resources may contribute to temporal variability in macroconsumer influence, as macroconsumers diverge in resource use, i.e., shift from consuming algae to invertebrates.

As the importance of context-dependent relationships during recovery unfolds, an obvious question is what controls the initial biotic and abiotic starting conditions? Initial species pools and distributions, and consumer resources are directly related to disturbance type and intensity (Poff and Ward 1989, Turner et al. 1997, Biggs et al. 1998). Moreover, the spatial heterogeneity of the disturbance can regulate successional processes (Turner et al. 1997, 1998, Schoener and Spiller 2006), sometimes leading to altered equilibrium states (Holling 1973, Scheffer et al. 1993, Gunderson 2000). Power et al. (2008) demonstrated that biotic interactions in mediterranean-climate streams during baseflow conditions can depend on previous disturbance history (i.e., flood vs. drought), which dictates the species pool, food web interactions, and structural trajectory. Power et al. (2008) found that filamentous algae were dominant during summer following rainy season scouring floods, but not after drought. This dominance of filaments was due to a reduction in predator-resistant caddisfly grazers by floods but not drying. Our results show that altered successional trajectories can also occur with a single colonizer pool by changing the sequence of species return after a disturbance.

Distinct trajectories in Kings Creek driven by the presence of macroconsumers eventually merged, supporting the concept that there is a producer species pool adapted to more stable conditions that will come to

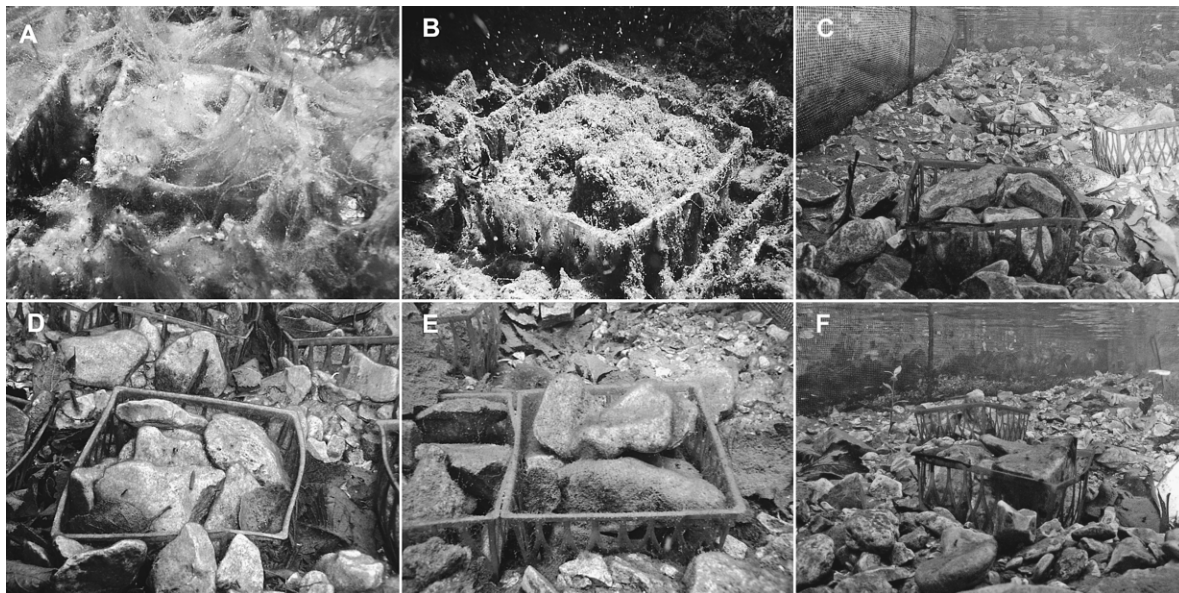


PLATE 1. Rock baskets in exclusion cages in Kings Creek (Kansas, USA). Panels A, B, and C are in the macroconsumer exclusion side on days 14, 28, and 63, respectively. Panels D, E, and F are on sides accessible to macroconsumers on days 14, 28, and 63, respectively. Differences between exclusion and open treatments on day 14 (A vs. D) and the lack of differences on day 63 (C vs. F) illustrate the temporal shifts in macroconsumer effects on stream ecosystem structure. Photo credits: J. N. Murdock.

dominate regardless of macroconsumer presence. However, in frequently disturbed systems, such as intermittent prairie streams, where there is often no “steady state” community, the pathway of succession and community organizational history becomes more important in defining overall system structure and function. For example, succession in this particular prairie stream is frequently reset. Scouring floods ($>0.5 \text{ m}^3/\text{s}$) have a reoccurrence interval of ~ 1.2 years (Dodds et al. 1996, Bertrand et al. 2009), and an average duration between drying of ~ 69 days (USGS station no. 06879650). The effect of large consumers on early succession could be a common feature, ultimately leading to altered system productivity and structure.

Macroconsumer functional role

The functional role of macroconsumers was important in shaping recovery. Fish and crayfish in Kings Creek acted predominantly as grazers, and thus could use the desiccation resilient filamentous algae efficiently soon after flow resumed, exerting a strong top-down control of early recovery. Later in recovery, with the death of filaments, recolonization of microconsumers, and more stable conditions, macroconsumer effect was less noticeable. A strong consumer effect is common during baseflow conditions in many streams (Power 1990, Flecker 1992, Taylor et al. 2006, Winemiller et al. 2006, Bertrand and Gido 2007), and also during mid- and late recovery from flood (Gelwick and Matthews 1992, Pringle and Hamazaki 1997, Bertrand et al. 2009). Why then did we not observe a continued strengthening of macroconsumer effect?

A standard view of successional changes in producer susceptibility to grazing (e.g., small, edible algae early, and more grazer-resistant algae in later recovery) is too simplistic in this system because of a transient grazer assemblage. The two major functional groups in this stream feed in different ways and can use different forms of algae. Macroconsumers that remove filamentous algae came and went quickly; as the stream network resumes flow, they move from high density refugia in permanent downstream reaches up into the network, passing through the pools with the exclusion cages. Microconsumers that eat mainly small diatoms needed time to colonize and establish large enough populations to influence benthic producers. The dominant filamentous alga early in succession (the drought-resistant *Ulothrix*), was easily consumed by early arriving macroconsumers. Therefore initial conditions (filaments present, microconsumers absent) were right for macroconsumers to change the early successional trajectory. The loss of *Ulothrix* filaments, subsequent dominance of small diatoms, and increasing macroinvertebrate abundance led to greater grazing pressure by microconsumers, and a decrease in the importance of macroconsumers in regulating algal assemblage composition. The remaining macroconsumers (primarily crayfish), however, still influenced structural aspects of stream algae later in succession by increasing cyanobacterial abundance, which is consistent with other stream macroconsumer studies (Power et al. 1988, Pringle and Hamazaki 1997). Additionally, macroconsumers continued to eat nonfilamentous algae, and with increasing

microconsumer abundance, overall grazing pressure remained high through late recovery.

Grazing minnows and crayfish are often considered to occupy similar niche space in prairie streams, with overlapping but slightly different diets (Vaughn et al. 1993, Evans-White et al. 2001, Bengtson et al. 2008). Following drought both groups consistently decreased algal biomass, but a greater suppression of algal accumulation occurred when both were present than when either was alone. It is not clear if increased algal reduction with multiple species was due to increased diversity or simply increased consumer biomass. Despite strong fish effect on algae in the stream, a weak effect of *P. erythrogaster* alone in mesocosms suggests either *C. anomalum* are more efficient grazers or distribution and behavior among fish and crayfish may have also factored into their overall effect (Bengtson et al. 2008). Although fish were stocked in mesocosms at average densities found in pools in Kings Creek (Franssen et al. 2006), we noted that after stream rewetting, fish clustered into schools containing hundreds of individuals that concentrated feeding in relatively small areas within pools. This clustering may have led to brief, but intense grazing pressure in specific areas, whereas mesocosms were exposed to constant, but less intense grazing pressure, resulting in an overgrowth of *Ulothrix* filaments.

Conclusions: consumer roles in nonequilibrium systems

One of the most evocative results from our study was that the consumer identity altered the trajectory but not the final state of succession. Macroconsumers had substantial effects early in succession both with respect to ecosystem structure (algal species identity and biomass) and function (primary production rates). Eventually, the more slowly colonizing smaller invertebrates had a similar effect. In many systems, this temporal effect of consumers may not be important at an ecosystem scale. However, in systems that experience frequent disturbances relative to their successional pace, such as streams (Fisher et al. 1982, Dodds et al. 2004, Murdock et al. 2004, Bertrand et al. 2009), consumer role change may be important.

Macroconsumers did not change the species pool set by the disturbance, only the proportion of each at any given point in time. Macroconsumers also stabilized system recovery, producing an algal successional pattern from disturbance more typical of other reports (e.g., Fisher et al. 1982, Grimm and Fisher 1989, Peterson 1996). Stabilization of producer succession by consumers has been observed in tropical streams (Pringle and Hamazaki 1997) and prairie grasslands (Suttle et al. 2007). Consumer influence early in succession can be strong when producer biomass is low and primary productivity increases rapidly. Conversely, in late recovery or equilibrium conditions, consumer impact can be strong when introduced to previously established communities (as is commonly done in consumer cage experiments), which are likely to have a slow replacement

of consumed biomass. Consumer effects are also influenced by bottom-up factors such as primary production rates, colonization rates, and competition within and among functional groups. Our study emphasizes the context-dependent nature of consumer effects during recovery from a physical disturbance, building on previous work (e.g., Power et al. 1988, 2008, Elmquist et al. 2003), and stresses the interactive role of biotic and abiotic regulation of stream communities, and the importance of biotic roles at times other than steady state.

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