FISHES AND FLOODS: STREAM ECOSYSTEM DRIVERS IN THE GREAT PLAINS

by

KATIE NICOLE BERTRAND

B.A., Gustavus Adolphus College, 2002

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2007

Abstract

Global climate change could lead to less frequent but more severe precipitation events in the Great Plains, altering the hydrologic regimes of streams. It is important to quantify species roles in these dynamic systems, because changes in stream communities are likely to accompany predicted changes in hydrology. The effects of species on ecosystem processes also are limited by the frequency of disturbance, because prairie streams are harsh, nonequilibrium systems characterized by a wide range of disturbances. In particular, frequent floods that reset the ecosystem to an early successional state can override the influence of consumer populations because the availability of resources is too unpredictable to maintain stable populations of those species or because species are absent following the flood. As flood frequency decreases, potential consumer effects may intensify. Using a combination of field and experimental stream mesocosm experiments, I (1) characterized the ecosystem effects of southern redbelly dace (*Phoxinus erythrogaster*), a grazing minnow, (2) tested the interactive effects of flood frequency and the presence of water column (red shiner; *Cyprinella lutrensis*) or grazing minnows (*Phoxinus*) on ecosystem processes, and (3) tested the effects of species loss from the grazer functional feeding group on stream ecosystem structure and function. I found that dace affected some aspects of ecosystem structure but not function, which suggested that grazer effects in prairie streams may not be consistent across taxa. In the context of flood frequency, both the water column omnivore and dace affected recovery of prairie stream primary producers following flooding disturbance by stimulating production, presumably through nutrient remineralization. However, some of these effects were transient or dependent on flood frequency, and my results indicate that consumer effects depend not only on environmental venue but also on the balance between consumptive losses and nutrient stimulation. In a comparison of the effects of removing different taxa from a grazer assemblage, the loss of crayfish, snails, or dace from a grazer assemblage did not differentially affect ecosystem processes, suggesting overlap in the ecosystem roles of these species in the context of this experiment.

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CHAPTER 1 - OVERVIEW OF DIVERSITY, DISTURBANCE, AND ECOSYSTEM FUNCTION IN PRAIRIE STREAMS

Globally, freshwater ecosystems are among the systems most impacted by human activities and, as such, experience some of the highest rates of species loss. Maintaining ecosystem function in prairie streams is particularly critical because nearly 30% of all global runoff is carried by grassland streams (Dodds 1997). In Great Plains streams, organisms are adapted to the harsh conditions, but drainage networks are oriented along an East to West axis, thus there is great potential for species loss under regional climate change scenarios, especially for fishes unable to migrate North or South to escape intolerable conditions (Matthews and Zimmerman 1990). In light of potential species extirpations and extinctions, it is critical to understand the role of species in Great Plains streams in order to prevent and mitigate the effects of potentially altered ecosystem function.

The consequences of species loss on ecosystem productivity are understood according to three main hypotheses. The idiosyncratic hypothesis (Lawton 1994) suggests that ecosystem function changes when diversity increases or decreases, but the change in function has no particular direction and is unpredictable. The rivet hypothesis (Erlich and Erlich 1981) contends that each species in a community makes a contribution to ecosystem function, but there is some minimum level of species diversity required to maintain function. The drivers and passengers hypothesis (Walker 1992) suggests that there are critical species in the community that maintain ecosystem function (i.e., drivers), and there are also non-critical species (i.e., passengers) whose loss would not alter ecosystem function. These views provide a framework against which to

evaluate the effects of species loss in a system and contribute to a greater understanding of the role of biodiversity in ecosystem functioning.

It is not biodiversity per se that mediates ecosystem function but rather the density and functional diversity of the organisms present in a system. However, species loss does limit the number of ways in which a system can reorganize following disturbance (Peterson et al. 1998). Several freshwater and marine studies demonstrated that changes in the structure of higher trophic levels are reflected in changes in the structure and productivity of lower trophic levels, likely because higher trophic levels are less diverse and have inherently fewer redundant species (Hooper et al. 2005). In general, the effects of benthic biodiversity depend on nutrient concentrations, temperature, water flow, and frequency of disturbance, but lower trophic levels in freshwater systems, especially those in streams, are poorly understood with regard to the effects of consumer diversity on ecosystem function (Covich et al. 2004).

Prairie streams are ideal systems for evaluating the effects of species loss, because they play critical roles in global water quality and their biota are among the most threatened. In contrast to forested streams, autotrophy and heterotrophy are typically more balanced (P:R $\approx$ 1) in prairie streams, because the riparian canopy bordering the stream is open, increasing solar irradiance reaching the stream (Webster et al. 2003). Consumer assemblages in many prairie streams are dominated by grazers, which could be considered functionally redundant (*sensu* Lawton 1994) based on trophic position. The grazer functional feeding group directly consumes primary producers, and relative to densely canopied stream systems, grazers can have potentially strong effects on ecosystem structure and function in prairie streams (Matthews 1998, Evans-White and Dodds 2003). Ecosystem effects of the grazer functional feeding group have been well-studied in streams, but most of these studies have focused on the effects of one grazing

minnow, the central stoneroller (*Campostoma anomalum*). The generality of grazer effects based on studies of this single species is still largely unknown. Furthermore, the effects of stream organisms have not previously been studied in the context of disturbance.

Water column omnivores also have strong effects in prairie streams by consuming terrestrial invertebrates. In contrast with benthic invertivores, which consume primarily aquatic invertebrates, water column omnivores provide an allochthonous source of remineralized nutrients to the stream ecosystem (Gido and Matthews 2001). The activities of benthic grazers and water column omnivores determine in part the capacity for processing of labile nutrients and organic matter within the reach, thus mediating downstream water quality.

Given the potential for global change to alter disturbance regimes in streams, there is a need for information on the relevance of species in ecosystem recovery under varied flood frequencies. The relationship between biodiversity and ecosystem function has been well-studied in terrestrial plant communities (Tilman et al. 2001) and in fine-scale short-term aquatic experiments with microconsumers (Naeem and Baker 2005), but little work has been done to identify the role of biodiversity within the macroconsumer grazer functional group in streams. Given the threatened status of prairie stream biota (e.g., Haslouer et al. 2005), it seems prudent to investigate the effects of species loss from this group on ecosystem structure and function.

To address these research needs, this dissertation consists of three research-based chapters. In chapter two, I characterized the effects of a grazing minnow, southern redbelly dace (*Phoxinus erythrogaster*), on ecosystem structure and function to examine whether the strong effects of other grazing fishes (e.g., *Campostoma*) could be generalized to a co-occuring grazing minnow. This study consisted of two investigations in experimental streams as well as a field experiment in nearby Kings Creek. Chapter 3 examined the interactive effects of two fishes (a

grazer and a water column omnivore) and flood frequency on ecosystem structure and function with two studies in the experimental streams and a field experiment in Kings Creek. In chapter 4, I describe manipulations of species composition of grazer assemblages in the experimental streams to test the hypothesis of functional redundancy of a grazing fish, crayfish, and snail.

CHAPTER 2 - EFFECTS OF THE HERBIVOROUS MINNOW, SOUTHERN REDBELLY DACE (*PHOXINUS ERYTHROGASTER*), ON STREAM PRODUCTIVITY AND ECOSYSTEM STRUCTURE

Katie N. Bertrand and Keith B. Gido

ABSTRACT

We used field and mesocosm experiments to measure effects of southern redbelly dace (*Phoxinus erythrogaster*), a grazing minnow, on stream ecosystem structure and function. Ecosystem structure was quantified as algal filament length, algal biomass, size distribution of particulate organic matter, algal assemblage structure, and invertebrate assemblage structure, whereas ecosystem function was based on gross and net primary productivity. Our experiments showed that moderate densities of *Phoxinus* temporarily reduced mean algal filament length and mean size of particulate organic matter relative to fishless controls. However, there was no detectable effect on algal biomass or ecosystem primary productivity. Several factors could explain the lack of effect of *Phoxinus* on primary productivity including increased algal production efficiency in grazed treatments or increased grazing by other organisms in fishless treatments. The inability of *Phoxinus* to reduce algal biomass and system productivity contrasts experimental results based on other grazing minnows, such as the central stoneroller (*Campostoma anomalum*), and questions the generality of grazer effects in stream ecosystems. However, environmental venue and the spatial and temporal scale of ecosystem measurements can greatly influence the outcome of these experiments.

INTRODUCTION

Accelerated rates of species extinctions (Lawton and May 1995; Pimm et al. 1995; Vitousek et al. 1997; Rosenzweig 1999; Sala et al. 2000) are forcing ecologists to consider the consequences of diversity losses on ecosystems. Whereas the loss of entire functional groups is likely to alter ecosystem processes (Ghilarov 2000; Schwartz et al. 2000; Rosenfeld 2002), recent studies indicate that even individual species can make unique contributions to an ecosystem (e.g., Cardinale et al. 2002). In particular, grazing animals are tightly coupled with primary production and can affect both structural (e.g., species composition, standing stock) and functional (e.g., productivity) components of ecosystems. Although grazers ingest producer biomass (Krebs 2001), they also remineralize nutrients, which may stimulate production and decrease turnover time of remaining cells (Cooper 1973; Hill et al. 1992). Grazing also can increase biomass-specific productivity by altering the availability of limiting resources such as light and nutrients (e.g., by decreasing shading and increasing the rate of delivery of nutrients across the boundary layer; Newbold et al. 1982; Power et al. 1988a). The trade-off between biomass loss and increased photosynthetic efficiency of residual algae will dictate the rate of ecosystem primary productivity (Carpenter and Kitchell 1984).

Effects of grazers on ecosystem structure and function in streams have been reported for a variety of organisms including insects (e.g., Wallace and Webster 1996), snails (e.g., Hill et al. 1992; Sarnelle et al. 1993; Vaughn et al. 1993; Turner 1997), crayfishes (e.g., Gelwick 2000; Evans-White and Dodds 2003), tadpoles (e.g., Nystrom and Abjornsson 2000), and fishes (e.g., Cooper 1973; Power 1990; Matthews 1998; Flecker et al. 2002). In prairie streams, which are typically more net autotrophic (i.e., Production/Respiration ≈ 1) relative to densely canopied streams (Webster et al. 2003), we might expect grazing organisms to have a stronger influence

on ecosystem structure and function than in more heterotrophic systems because they interact directly with autotrophs (e.g., ingesting them) but only indirectly with heterotrophs. Studies of *Campostoma anomalum* (central stoneroller) demonstrate the potentially strong effects of grazing minnows in prairie streams (Matthews 1998; Evans-White and Dodds 2003), but it is not clear if these results can be generalized to other grazing fishes.

Our study tested for structural and functional effects of the herbivorous minnow, *Phoxinus erythrogaster*, which can occur in sympatry with *Campostoma* in prairie streams. Both of these species prefer streambeds dominated by pebble, gravel, or sand and avoid reaches with greater proportions of silt or clay (Lennon and Parker 1960; McKee and Parker 1982; Slack et al. 1997). *Phoxinus* are abundant in springfed headwater reaches, whereas *Campostoma* are typically found downstream from these habitats (Hill and Jenssen 1968; Settles and Hoyt 1976; Felley and Hill 1983). *Campostoma* appear to be selective feeders preferring diatoms to other forms of algae (Stewart 1987; Power et al. 1988a; Napolitano et al. 1996), whereas *Phoxinus* are more generalist omnivores, feeding on algae and invertebrates when they are available (Phillips 1969; Settles and Hoyt 1976; Felley and Hill 1983). Whereas *Phoxinus* can only bite algae (Forbes and Richardson 1920), *Campostoma* uses a cartilaginous ridge on its lower jaw (McKee and Parker 1982; Miller and Robinson 2004) to swipe, shovel, or bite attached algae from the substrate (Matthews et al. 1986). Although these fishes can use similar habitat and overlap in diet, it is unknown if the effects of *Phoxinus* are redundant (*sensu* Lawton 1994) with those of *Campostoma* in prairie streams.

To test the structural and functional effects of *Phoxinus* in prairie streams, we used field and mesocosm experiments. Mesocosm experiments allowed us to replicate treatments, control effects of heterogeneous discharge, and improve the precision of our whole stream productivity

measurements. Measurements of structural components from field experiments allowed us to extrapolate our experimental stream results to local natural streams. Based on studies of *Campostoma* (Gelwick and Matthews 1992), we predicted that structural effects of *Phoxinus* would include reduced algal filament length, reduced algal biomass, altered algal assemblage structure, and reduced mean particle size of particulate organic matter. Moreover, these structural changes should result in functional changes (i.e., reduced primary productivity) and bottom up effects on invertebrate assemblage structure.

MATERIALS AND METHODS

Field experiment

Study site—The field experiment was conducted in four pools in Kings Creek, Riley County, Kansas (USA), from August to October 2002. Kings Creek drains 1059 ha of tallgrass prairie on the Konza Prairie Biological Station (KPBS). Physicochemical and biological descriptions of this stream are in Gray et al. (1998) and Gray and Dodds (1998). The four study pools were located in a forested stream reach with perennial flow. Pool surface area ranged from 23 to 84 m^2 (mean = 59 m^2), and substrate typically was cobble, pebble, and gravel, according to the Wentworth scale (Cummins 1962). Dominant fishes in the study reach included three minnows [*Campostoma anomalum*, *Phoxinus erythrogaster*, and *Semotilis atromaculatus* (creek chub)] and the orangethroat darter (*Etheostoma spectabile*). Grazing invertebrates such as crayfish (*Orconectes* spp.) and snails (*Physa* and *Physella* spp.) also were present.

Experimental design—Wire screen (5-mm mesh) was used to block the upstream and downstream ends of four study pools (fishless exclosures and fish enclosures). Wire mesh was secured to steel poles and buried roughly 20 cm into the streambed to prevent the escape or

entrance of fishes. Leaf litter was removed from the wire mesh as needed to maintain natural stream flow through the study pools. On 15 August 2002 (day 0) of the experiment, three-pass electrofishing depletion samples were conducted in each study pool. In two randomly selected exclosure pools, all captured *Phoxinus*, other fish species and crayfishes were removed. Fishes collected from the other two enclosure pools were counted, measured (total length) and returned to the pools. Another depletion sample was conducted in each pool during the sixth week of the experiment to quantify the immigration of young-of-the-year fishes into exclosures. *Phoxinus* densities in each study pool were based on maximum-likelihood population estimates (Van Deventer and Platts 1989) from the three-pass electrofishing depletion samples. Because we did not initially remove all fish from the exclosures, we estimated the density of fish remaining as the difference between the maximum-likelihood population estimate and the total number of fish removed after three passes.

Mesocosm experiments

Study system—The second phase of this study was conducted in nine experimental streams at the KPBS. Experimental streams were similar to those used by Gido and Matthews (2001), and each stream consisted of a 2.54 m^2 pool connected to a 0.84 m^2 riffle. Recirculating flow was powered by an electric trolling motor with a mean discharge of 10.8 L / s, and water was supplied by a natural spring that also supplies nearby Kings Creek. Substrate was a mixture of gravel, pebble, and fines from a local quarry. Although algae and winged invertebrates (e.g., chironomids) readily colonized these systems, each stream was inoculated one week prior to the beginning of the experiment with an algal slurry obtained from Kings Creek to stimulate algal growth.

Experimental design—In Fall 2002, two *Phoxinus* treatments [small *Phoxinus* (30 – 50 mm TL, 28.3 fish / m^2) and large *Phoxinus* (> 60 mm TL, 5.7 fish / m^2)] and a fishless control were randomly assigned to stream units with three replicates each. The different stocking densities were intended to equalize biomass and isolate the effect of body size; however, biomass in the small fish treatment (26.1 g / m^2) was slightly greater than that in the large fish treatment (22.4 g / m^2). The experiment began on 17 October 2002 (day 0) and concluded on 26 November 2002 (day 40). Mean water temperature was 7°C (range: 2 - 13°C). Fish that were lost to natural mortality during this experiment were replaced within one week.

This experiment was repeated in the summer of 2003 with eight experimental stream units. However, we only compared a fishless control to a fish treatment [24 *Phoxinus* (mean TL = 56 mm, range TL: 40 - 78 mm, 6.8 fish / m^2, 14.9 g / m^2)] because we found no significant differences between large and small *Phoxinus* treatments in 2002 (see Results). This experiment began on 5 June 2003 (day 0) and concluded on 8 August 2003 (day 65). Mean water temperature was 22°C (range: 13 - 31°C).

Data collection

Ecosystem function—Gross primary productivity (GPP) and net primary productivity (NPP) in experimental streams were based on diurnal changes in dissolved oxygen measurements from YSI 600XLM sondes (Yellow Springs Instruments, Inc.). We used the open-system single-station approach to estimate productivity (Bott 1996). Water was recirculated at the same velocity and the bed-form was similar in all experimental units so turbulence-induced aeration was similar across experimental stream channels. Reareation was estimated using the surface renewal model, which is calculated from velocity (V, in cm / s) and mean depth (H, in cm) using the formula

$$f(20°C) = 50.8\ V^{0.67}\ H^{-0.85} \quad (1)$$

(Owens 1974). The flow-through rates were the same for all experimental units leading to an approximate turnover time of 13 hrs (i.e., effective channel length ~ 1700 m). The prolonged exposure to stream biota assured that diurnal changes in water oxygen concentration reflected biotic processes in these stream units. We estimated NPP as the mean rate of change per hour in oxygen concentration during daylight and darkness, whereas GPP was estimated by subtracting the mean hourly rate of oxygen uptake during darkness from the mean hourly rate of oxygen productivity during daylight. During the first experimental stream study (Fall 2002), sondes were deployed in three streams for 24h then transferred to another stream, such that metabolism in all nine experimental streams was measured over a period of three days. GPP was estimated for each stream twice: once between day 7 and 27 and again between day 31 and 40. On 14 of 25 sample days, we only recovered oxygen curves during the night and part of the day (before 1300). However, on the other 11 days we recovered complete 24-hour curves, and we found productivity between 0900 and 1300 to be a significant predictor of productivity between 0900 and 1700 ($r^2 = 0.48$, $P < 0.01$). Thus, for the 2002 experiment we used this relationship to predict daytime productivity rates for days without complete data. In Summer 2003, GPP was measured in each stream during eight, 4-day periods beginning on days 1, 8, 14, 20, 29, 38, 50, and 65.

Ecosystem structure—Algal biomass was estimated as the concentration of chlorophyll *a* extracted from pebbles taken from study pools or experimental streams. Pebbles were collected on site and frozen within four hours of collection. Chlorophyll was extracted by submerging pebbles in a 78˚C, 95% EtOH solution as described in Sartory and Grobelaar (1984). Concentration of chlorophyll *a* was corrected for cross-sectional area of pebbles and algal

biomass was reported per unit area. During the field experiment in Kings Creek 2002, we removed three pebbles along ten equally spaced transects perpendicular to the direction of flow from each pool on days 4 and 32. In Fall 2002, chlorophyll *a* samples from pools were lost, but we present data from riffles that were collected across each of three equally spaced transects perpendicular to the direction of flow in the riffles of experimental streams on day 40; chlorophyll *a* in riffles was significantly correlated with that in pools during Summer 2003 (r = 0.65, $P < 0.01$). In Summer 2003, we collected four pebbles from the edges of the pools and one from the deep center of the pools on days 1, 6, 18, 29, 42, 54, and 65.

In the field experiment, algal height was measured on day 39 along the same ten transects used for collecting algal biomass samples. We measured the vertical height of the algae over the substratum at ten points along each transect (100 points per stream pool). The length of the longest filament (vertical or horizontal) was measured in experimental streams because filaments typically were much longer. In Fall 2002, we measured three filaments along each of the same three transects used for collecting algal biomass (9 points per stream riffle) on day 45. In Summer 2003, we measured filaments at the same sampling points used for collecting algal biomass samples (5 points per pool) on days 12, 23, 35, and 47.

Invertebrate samples from Kings Creek were a composite of four replicate Hess samples (500-μm mesh bag) that were combined and subsampled (30-40 % of total sample). Because these samples were only taken on day 4, these data only were used as a reference for assemblage structure comparison between experimental streams and the natural stream because the invertebrate assemblages likely did not have time to respond to treatments. In the experimental stream studies we used a modified core sampler that consisted of a 0.018 m^2 corer with an electric pump (0.1 L / s) to collect invertebrates, particulate organic matter (POM), and algae

from the substrate. Substrata inside the corer were agitated by hand for either 1 min (Fall 2002) or 1.5 min (Summer 2003) while materials were pumped through a 250 μm sieve. In the Fall 2002 experiment, we took one invertebrate sample from the approximate center of each riffle on day 16, and on day 40 we took two core samples from each riffle and each pool. The invertebrates were preserved in formalin and later identified to order or family. We took four additional replicate core samples on day 40 (two from the riffle and two from the pool) to estimate size distribution of fine particulate organic matter (FPOM). Particulate organic matter samples were preserved in formalin, and dry as well as ash-free dry mass (AFDM) was measured for six size classes: >1 μm, 1000-500 μm, 500-250 μm, 250-180 μm, 180-98 μm, and 98-0.45 μm. In Summer 2003, we took separate core samples from both the riffle and the pool on days 1, 6, 18, 29, 42, 54, and 65. In Summer 2003, the material pumped from each riffle or pool was homogenized in a bucket and subsampled for fine particulate organic matter (FPOM; 500 mL) and algal assemblage structure (AAS; 50 mL). The remaining invertebrates and detritus were concentrated on a 250 μm sieve and preserved in formalin. Dry and AFDM of FPOM was measured for five size classes: >500 μm, 500-250 μm, 250-180 μm, 180-98 μm and 98-1 μm. Algal assemblage structure samples also were preserved in formalin and later categorized into four general taxonomic groups (unicellular green, filamentous green, diatom, or cyanobacteria). The first 100 algal cells that intersected the ocular transect were placed in these categories.

At the conclusion of the Fall 2002 experiment and twice during the Summer 2003 experimental stream study (days 54 and 78), we collected two *Phoxinus* from each experimental stream to characterize diet. Diet items in the foregut were identified and enumerated using a transect method similar to the procedure for quantifying algal assemblage structure; we categorized the first 100 algal cells as filamentous green algae or diatoms (unicellular green and

cyanobacteria were absent or in very low abundance), and noted the occurrence of invertebrate animal matter.

Statistical analysis

Data from Kings Creek 2002 were not statistically analyzed because each treatment was only replicated twice. Thus, we were limited to qualitative comparisons between results from these experiments and those from experimental stream studies. In Fall 2002, ANOVA was used to test for differences among treatments in the concentration of chlorophyll *a* on pebbles and algal filament length in the experimental streams. In 2003, we used repeated-measures ANOVA with sample date (day) as the repeated factor to test for fish effects on ecosystem function and structure variables over time in the experimental streams. If the variance-covariance matrices of the repeated measures failed Mauchly's sphericity test, we referred to the Huyhn-Feldt adjusted *P*-value for tests of within-subjects effects. Because we found a significant correlation between GPP and mean daily solar irradiance (see Results), we used repeated-measures ANCOVA with GPP as the response variable, day as the repeated factor, and irradiance as the covariate to test for differences in metabolism among treatments (SAS 2003). 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). The covariance structure that best fit our data was first-order autoregressive. We then used backward model selection and chi-square tests, which compared reduced and full model –2 residual log likelihood values, to select the best model of our data (gpp = day + fish + day*fish + irradiance*day*fish). In a repeated measures design such as this, with different sized experimental units, the denominator degrees of freedom must be computed from a linear combination of mean squares, and the denominator is not chi-squared. Thus, we used the Kenward-Rogers approximation to find approximate degrees of freedom for

the F-test, which produced fractional denominator degrees of freedom. Where we found significant differences in main effects, we applied Tukey *post hoc* comparisons to test the relative differences between the fish treatment and the control. Oxygen sonde dysfunction in Summer 2003 resulted in unequal replication between the fish treatment and the control on days 65 – 68 and analysis was limited to three replicates each for the fish treatment and the control on day 29 – 32. Thus, we excluded measurements from days 65 – 68 and used linear trend at point estimates (SPSS 2001) to replace the missing observations from days 29 – 32. Differences in proportional abundance of four major algal groups were tested with repeated-measures ANOVA. Proportions were arcsine square-root transformed prior to this analysis. In Summer 2003, we used a paired t-test to evaluate differences in the ratios of filamentous green algae and diatoms between the diet and core samples. Ratios were square-root transformed prior to analysis to reduce inequality of variances among samples. We tested for differences in invertebrate assemblage structure in Fall 2002 using a partial redundancy analysis (pRDA). This analysis tested the significance of the association between invertebrate assemblage structure and the presence of *Phoxinus* after controlling for effects of sample date. In Summer 2003, we used principal response curve (PRC) analysis, which is an extension of a partial redundancy analysis that considers repeated measures designs (pRDA, ter Braak and Smilauer 2002), to test the effects of fish and a time x fish interaction on invertebrate assemblage structure. Both pRDA and PRC used a Monte Carlo randomization procedure to test the significance of the first axis of the ordination. Monte Carlo simulations were based on 500 permutations and run using CANOCO (ter Braak and Smilauer 2002). Ordinations were based on square-root transformed densities of each taxa (i.e., number of individuals per core), but an analysis based on proportional abundance yielded similar results.

RESULTS

Fish density and biomass in stream enclosures

Our removal efforts in field exclosures only initially affected total numbers and biomass of fishes. Immigration and rapid growth of juvenile fishes resulted in similar fish assemblage structure between enclosures and exclosures by the sixth week of the experiment. After the initial removal, *Phoxinus* densities were estimated at 0.4 and 0.5 fish / m^2 in exclosures as compared to densities of 3.1 and 1.4 fish / m^2 in enclosures. In the same study pools, the density of *Campostoma* was 1.5 and 1.0 fish / m^2 in exclosures and 1.6 and 0.5 fish / m^2 in enclosures. By the sixth week of the experiment, *Phoxinus* densities in the exclosures were 4.6 and 18.3 fish / m^2 (1.8 and 7.9 g / m^2) compared to 5.5 and 5.6 fish / m^2 (8.0 and 10.3 g / m^2) in enclosures. Although densities and biomass were similar, mean length of *Phoxinus* was much smaller in exclosures (31.2 mm and 32.6 mm TL) than in enclosures (44.5 mm and 47.3 mm TL). Density of *Campostoma* was similar between exclosures [8.2 and 10.5 fish / m^2 (10.3 and 10.9 g / m^2)] and enclosures [9.4 and 9.2 fish / m^2 (16.7 and 12.4 g / m^2)], but biomass was less in exclosures by the sixth week. Mean length of *Campostoma* was slightly smaller in exclosures (45.6 mm and 43.1 mm TL) than in enclosures (49.7 mm and 46.8 mm TL).

Ecosystem function

Primary productivity—There was no significant effect of the presence of *Phoxinus* on GPP in the experimental streams during Fall 2002 (all $F \leq 0.44$ and all *P*-values ≥ 0.66, Fig. 2.1a). In 2003, we found a significant correlation between GPP and mean daily solar irradiance ($r = 0.57$, $P < 0.01$; Fig. 2.2), but no effect of *Phoxinus* on GPP after controlling for the effects of irradiance ($F_{1,23.2} = 2.38$, $P = 0.14$, Fig. 2.1b). As with GPP, the presence of *Phoxinus* did not affect NPP in experimental streams (all $F \leq 2.62$ and all *P*-values ≥ 0.15).

Ecosystem structure

Algal biomass—In Kings Creek, the concentration of chlorophyll *a* on pebbles was slightly higher (from 13 to 38%, on days 4 and 32 respectively) in the exclosures than enclosures on days 4 and 32, but there was high variability among pools (Fig. 2.3a). Similarly, in the experimental streams, algal biomass was not significantly affected by the presence of *Phoxinus* during Fall 2002 ($F_{2,6} = 1.09$, $P = 0.40$; Fig. 2.3b) or Summer 2003 ($F_{1,6} = 1.98$, $P = 0.21$; Fig. 2.3c).

Algal assemblage structure —In Summer 2003, filamentous green algae dominated the assemblage (65%) followed by diatoms (17%), unicellular green algae (11%), and cyanobacteria (7%). We found a temporal pattern of increasing relative abundance of unicellular green algae ($F_{6,36} = 13.49$, $P < 0.01$) and a subsequent decline in filamentous green algae ($F_{6,36} = 6.99$, $P < 0.01$), but no effect of grazing by *Phoxinus* on the relative abundance of the four algal taxa (all $F \leq 4.43$ and all P-values ≥ 0.08).

Algal Filament Length—In Kings Creek, algal filaments were 0.2 to 1.6 cm shorter in enclosures than in the exclosures on day 39 (Fig. 2.4a). In the experimental streams during Fall 2002, algal filaments were, on average, more than two orders of magnitude shorter in riffles with *Phoxinus* ($F_{2,6} = 104.87$, $P < 0.01$, Fig. 2.4b). *Post hoc* comparisons among treatment means revealed that the control had significantly (Tukey HSD $P < 0.01$) longer algal filaments than both the small *Phoxinus* and the large *Phoxinus* treatments, but filament lengths in the small *Phoxinus* treatments were not significantly different than in the large *Phoxinus* treatments (Tukey HSD $P = 1.00$). In Summer 2003, using repeated-measures ANOVA, we found that the presence of *Phoxinus* significantly reduced mean algal filament length ($F_{1,6} = 6.24$, $P = 0.05$), but there also was a significant day x fish interaction effect ($F_{4,24} = 6.12$, sphericity-assumed $P < 0.01$; Fig.

2.4c). The difference in mean algal filament length between treatments was greatest on day 9 and diminished by day 36.

Invertebrate Assemblage structure—We did not observe an effect of *Phoxinus* on invertebrate assemblage structure in experimental streams (Appendix A). Redundancy analysis (RDA) showed that sampling date explained a significant fraction of the variability in invertebrate assemblage structure during Fall 2002 (1^{st} axis eigenvalue 0.47, F = 12.25, $P = 0.01$; Fig. 2.5). However, when sample date was included as a covariate, the presence of *Phoxinus* did not explain the remaining variability among samples (1^{st} axis eigenvalue 0.08, F = 2.24, $P = 0.25$). Using PRC in Summer 2003, we also did not find a significant effect of fish or a day x fish interaction on invertebrate assemblage structure (1^{st} axis eigenvalue 0.06, F = 7.44, $P = 0.26$; Fig. 2.6). In the four most abundant taxa, we found that *Bosmina* sp. and copepods decreased slightly where fish were present (*Bosmina* sp. density was 16% lower and copepod density was 90-95% lower in fish treatments but only on days 54 and 65), whereas oligochaetes and chironomids increased slightly (oligochaete density was 2% higher in the presence of fish and chironomid density was 7% higher in the presence of fish). Using repeated-measures ANOVA, the only significant effect of *Phoxinus* on individual taxa densities was a day*fish interaction on density of copepods ($F_{6,11.5} = 6.86$, $P < 0.01$).

Fine Particulate Organic Matter—In the experimental streams in Fall 2002, there was no significant difference in the relative mass of FPOM among the two fish treatments and the control for any size fraction. However, *Phoxinus* treatments had a greater proportion of the 99–1 μm size fraction than no fish treatments across sample days in Summer 2003 (Fig. 2.7). FPOM > 500 μm also was greater in the no fish treatments, but this effect diminished by day 42.

Although there was a significant day x fish interaction for FPOM 180 – 250 μm, there was not a consistent temporal trend that would indicate an effect of the fish treatments.

Diet—Phoxinus consumed diatoms and filamentous green algae in both the Fall 2002 and Summer 2003 experiments. We noted that one-third of the individuals examined had consumed some animal matter, but diatoms and filamentous green algae largely dominated gut contents. In Fall 2002, there was no significant difference ($t_4 = 0.55$, $P = 0.30$) in the ratio of filamentous green algae to diatoms consumed by small and large *Phoxinus*; overall, diet consisted of approximately 2 times more filamentous green algae than diatoms. In Summer 2003, *Phoxinus* ingested 5.4 times more filamentous green algae than diatoms. This was not significantly different ($t_7 = 0.26$, $P = 0.40$) from the ratio of available filamentous green algae to diatoms (i.e., 5.5 times more filamentous green algae than diatoms) measured from core samples.

DISCUSSION

Results from our experiments suggest that *Phoxinus* affected algal filament length, but had negligible effects on other aspects of ecosystem structure and whole stream primary productivity. Specifically, grazing by *Phoxinus* did not change GPP or NPP in the mesocosm studies, even though significantly shorter mean algal filaments in all three experiments distinctly characterized grazing treatments. Whereas the relative abundance of major algal taxa was not significantly affected by the presence of *Phoxinus* in the Summer 2003 experiment, the structural changes in the periphyton (i.e., decreased algal filament length and increased proportion of the smallest size fraction of FPOM) were apparent. In Kings Creek, algal filaments in exclosures grew markedly after the initial removal of *Phoxinus*, so much so that when juvenile *Phoxinus* and other grazing organisms (e.g., *Campostoma*) invaded, those fish were unable to crop the long filaments. Similarly, in Summer 2003 the ability of *Phoxinus* to control long algal filaments

disappeared by day 36, further suggesting that moderate densities of *Phoxinus* may not be able to maintain short algal turfs once long filamentous forms become established. Concordantly, the proportion of organic matter in the smallest size fraction increased in the presence of *Phoxinus* until day 36, likely a function of *Phoxinus* maintaining short algal turfs. Grazers typically reduce mean algal filament length (Power and Matthews 1983, Gelwick and Matthews 1992, Liess and Hillebrand 2004), but this structural change is usually linked with an increase in the relative abundance of adnate diatoms and turf-forming cyanobacteria in the grazer treatments, as was reported for *Campostoma* (Power et al. 1985, Power et al. 1988a, Gelwick and Matthews 1992). In contrast, *Phoxinus* grazing replaced long algal filaments that dominated the assemblage with more abundant, shorter filaments.

Although we were unable to measure GPP or NPP in Kings Creek, we assume rates of primary productivity in the experimental streams reflect processes that occur in a natural stream for several reasons. First, observations of reduced algal filament length and no change in algal biomass between fish treatments and controls in experimental streams was consistent with observations from field studies. Second, measurements of GPP and NPP in experimental streams are comparable with published estimates from Kings Creek. Finally, there was a significant positive association between irradiance and GPP ($r = 0.57$, $P < 0.01$), which indicates our measurements of GPP in the experimental streams were sensitive to factors known to influence photosynthetic rates. However, ecosystem metabolism may typically be more heterotrophic (P:R ratio = 0.75; Webster et al. 2003) and NPP slightly lower [(-0.01 to -0.19 g O_2 / m^2 / h (O'Brien 2006)] in Kings Creek than in the experimental streams, because the experimental stream studies began at an early successional stage in the algal assemblage

compared to that in Kings Creek. In the experimental streams, mean NPP was 0.12 g O_2 / m^2 / h in Fall 2002 and -0.08 g O_2 / m^2 / h in Summer 2003.

It is important to note differences in algal and invertebrate assemblage structure between Kings Creek and the experimental streams. The algal assemblage during the Kings Creek field study was in a late successional stage because the experiment was conducted during an interval with little precipitation and no flooding disturbances. In contrast, the experimental stream studies represented earlier successional stages of algal assemblage development. The temporal switch from net autotrophy to net heterotrophy during both mesocosm experiments illustrates this development of the algal community. Invertebrate grazers that could colonize by drift or over longer time scales were excluded from the experimental streams. Although lower invertebrate richness and nutrient limitation are potentially important components of ecosystem structure and function, the consistent effect of *Phoxinus* on structural components of the ecosystem in both the natural and experimental streams suggests our stream mesocosms reflect major processes occurring in the natural stream.

There are several explanations for the lack of a difference in productivity, algal biomass (chlorophyll *a*), and algal assemblage structure among treatments in the experimental streams. First, the densities at which we stocked *Phoxinus* may not have been high enough to significantly reduce biomass or productivity because the loss of algal cells by consumption may have been offset by increased production of remaining algal cells. Whereas the densities at which we stocked *Phoxinus* in the experimental streams (6.8 fish / m^2) was within the range of natural densities in Kings Creek (0.2 – 14.3 fish / m^2), this was higher than densities in previous studies of *Campostoma* that reported an effect on structure and function (mean density = 3.87; range

density: 0.4 – 10 fish / m^2). Thus, the lack of effect on the measurements was likely not due to low densities of *Phoxinus* in our experiments.

Second, at moderate densities, mechanical removal of algae by grazers may stimulate algal growth by increasing basal regeneration or mucilage secretions of algae (Power et al. 1988a), reducing shading, and increasing the rate of material transport across the boundary layer (Mulholland et al. 1991). In addition, excretion of limiting nutrients can further stimulate algal growth; assuming nutrient turnover by fish is great relative to the nutrient loading to the system (Vanni 2002). In the experimental streams, low nutrient concentrations in our water supply limit algal growth (Gido, unpublished data), thus excretion by fish could increase availability of soluble nutrients. For example, in Summer 2003 total N loading to experimental streams was estimated at 51.1 mg N / m^2 / d, assuming an average inflow of 1728 L / d and mean total N concentration of 99.9 ± 17.5 µg / L from inflow. Estimates of nutrient excretion by *Phoxinus* based on rates published for other stream fishes (Vanni 2002) range between 3 and 10 µmol N / g fish / h, which would yield a daily excretion rate between 13.4 and 44.8 mg N / m^2 / d, or 26 and 87% of the daily loading of nitrogen from spring water. These data suggest nutrient turnover by *Phoxinus* may play an important role in offsetting consumptive losses to grazing in these experiments.

Third, in the absence of *Phoxinus*, abundance of other grazers (i.e., fishes, crayfishes, snails, and insects) may have increased resulting in no difference between fishless controls and fish treatments. However, we found no measurable effect on the invertebrate assemblage among treatments in experimental streams, as the densities of invertebrates and species composition among grazing treatments were similar (e.g., between 50 and 70% of species were shared among treatments). This result was not surprising given the weak effect of *Phoxinus* on other measures

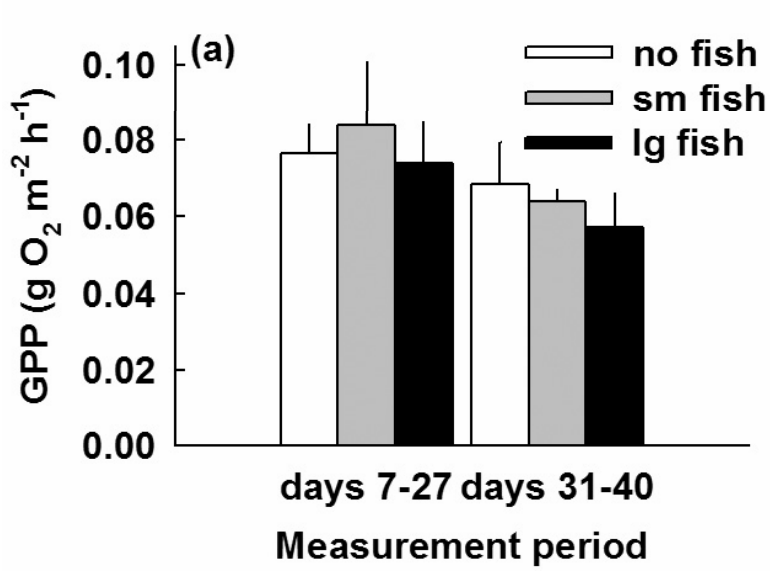
of system function and structure. That is, if exploitative or interference competition was intense, we also would have expected a decrease in the abundance of grazing invertebrates in *Phoxinus* treatments. Nevertheless, the presence of *Phoxinus* could have altered the behavior of grazing insects such that their grazing rates were higher in the no fish treatments (Vaughn et al. 1993; Peckarsky et al. 2001; Alvarez and Peckarsky 2005).

The inability of *Phoxinus* to alter area-specific GPP or NPP across the mesocosm experiments stands in contrast to grazing effects reported for other aquatic grazers (e.g., Hillebrand 2002) and for *Campostoma* (Stewart 1987, Gelwick and Matthews 1992), which decrease NPP / m^2 and increase NPP / g of benthic algae. However, there were several factors limiting a comparison of our results to studies of *Campostoma*. In particular, the spatial scale over which productivity was measured could strongly influence the effects of a grazer, as measurements over larger scales (e.g., entire pools) are likely to be less sensitive to grazer effects, particularly if the system has a higher relative abundance of heterotrophs (e.g., the stream is net heterotrophic). Production estimates reported in studies of *Campostoma* were based on artificial (i.e., ceramic quarry tiles, Stewart 1987) or natural (i.e., limestone cobbles, Gelwick and Matthews 1992) substrates placed in enclosed containers, whereas our measurements reflected metabolism of an entire mesocosm. Enclosed chamber measurements may be more sensitive to grazing effects because uptake rate of nutrients by the attached algae from the water column is influenced by a smaller amount of water relative to the amount of substratum and a lack of water movement within the chamber (Uehlinger and Brock 1991, Carpenter 1996, Bott et al. 1997). Moreover, whole stream estimates of productivity encompass a broader range of habitats (e.g., deeper hyporheic zone) and might mask the effects of grazers, which are likely most intense at the substrate-water interface. Finally, surface heterogeneity of substrates placed in enclosures

also could be an important source of bias, as Evans-White and Dodds (2001) found *Campostoma* prevented accumulation of algal biomass (chlorophyll *a* concentration) on artificial tile substrates but not on natural pebbles in experimental channels.

The ability of grazers to affect autochthonous primary productivity is particularly important for prairie streams in which allochthonous organic matter contributions are relatively low. Whereas our experiments suggest that *Phoxinus* at moderate densities affected some aspects of ecosystem structure, they did not change algal biomass or primary productivity. Because these results contrast studies of other grazing organisms, it will be important to evaluate if these differences were due to differences in interaction strengths among organisms or experimental design, as most tests of grazer effects were conducted at fine spatial and temporal scales. Whereas finer scale measurements of productivity and algal biomass help identify the mechanisms through which grazers affect ecosystem properties, tests of species effects at the scale of natural stream pools or reaches will provide a more comprehensive assessment of the role of these organisms in ecosystems.

Figure 2.1. Gross primary productivity (GPP; +1SE) of streams with and without Phoxinus erythrogaster in (a) nine experimental streams in Fall 2002 (n = 3), and (b) eight experimental streams in Summer 2003 (n = 4). Data in (b) are corrected for irradiance. Control (No fish) data points in (b) are offset one day later than data for streams with fish to prevent overlap.



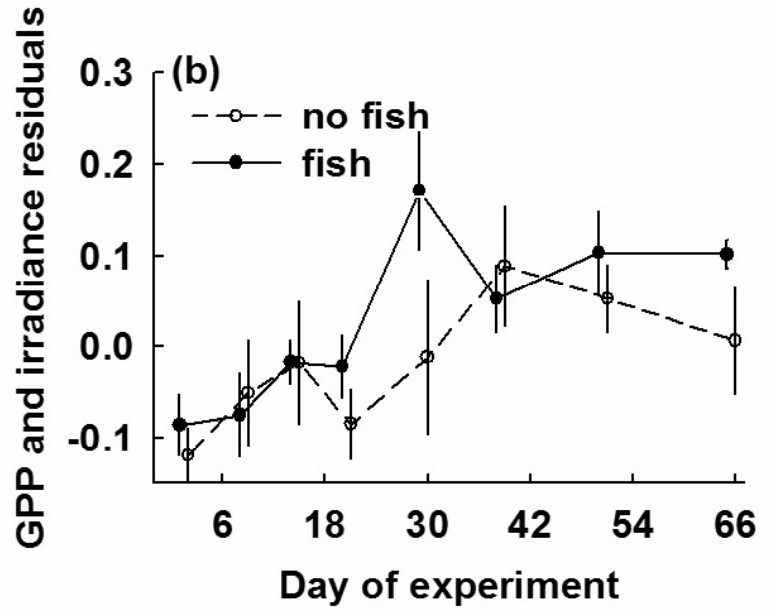


Figure 2.2. Gross primary productivity (GPP) of streams with and without fish as a function of mean daily solar irradiance in eight experimental streams in Summer 2003.

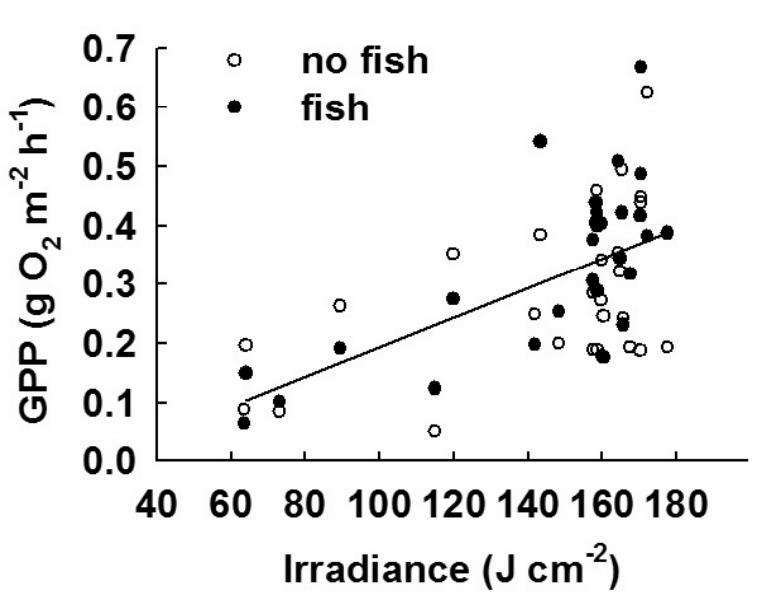
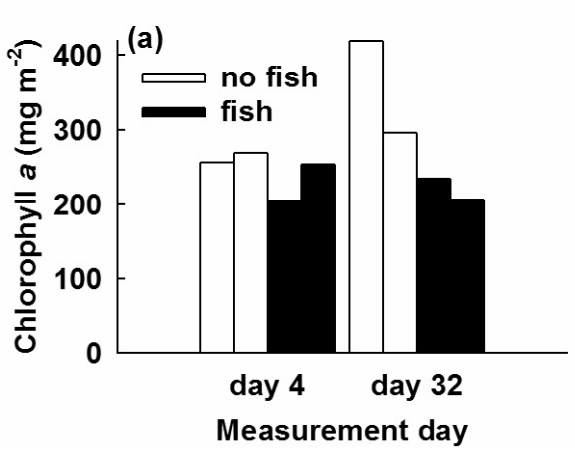
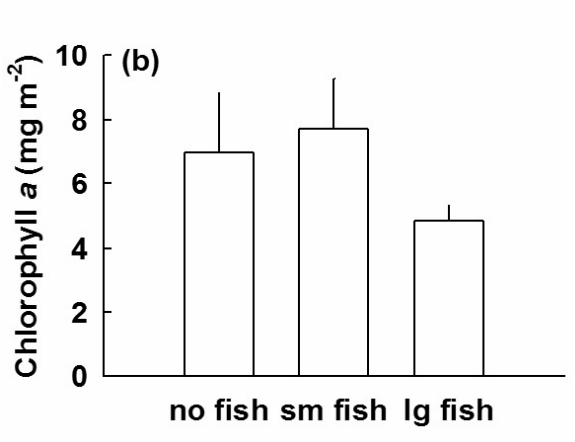


Figure 2.3. Algal biomass (chlorophyll *a*, +1SE) in stream pools and riffles with and without fish in (a) four Kings Creek pools in Fall 2002 (n = 2), (b) nine experimental stream riffles in Fall 2002 (n = 3), and (c) eight experimental stream pools in Summer 2003 (n = 4). Each bar in (a) represents data recorded in one pool in Kings Creek (P1, P2, P3, or P4). Control (No fish) data points in (c) are offset one day later to prevent overlap.





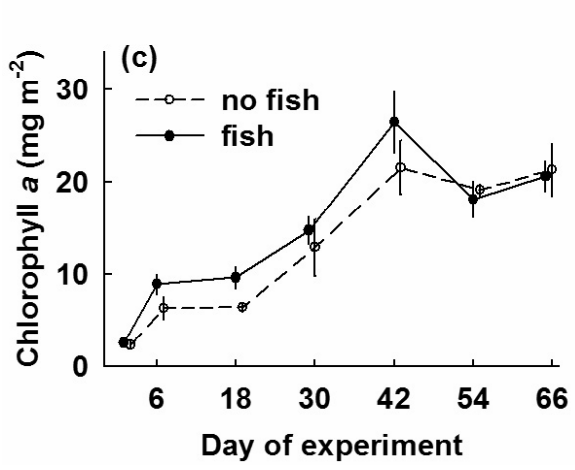


Figure 2.4. Algal (a) height and (b,c) filament length (+1SE) in (a) four Kings Creek pools in Fall 2002 (n = 2) on Day 39, (b) nine experimental stream riffles in Fall 2002 (n = 3) on Day 45, and (c) eight experimental stream pools in Summer 2003 (n = 4) with (grey and solid bars and symbols) and without (open bars and symbols) fish. Each bar in (a) represents data recorded in one pool in Kings Creek (P1, P2, P3, or P4). Control (No fish) data points in (c) are offset one day later to prevent overlap.

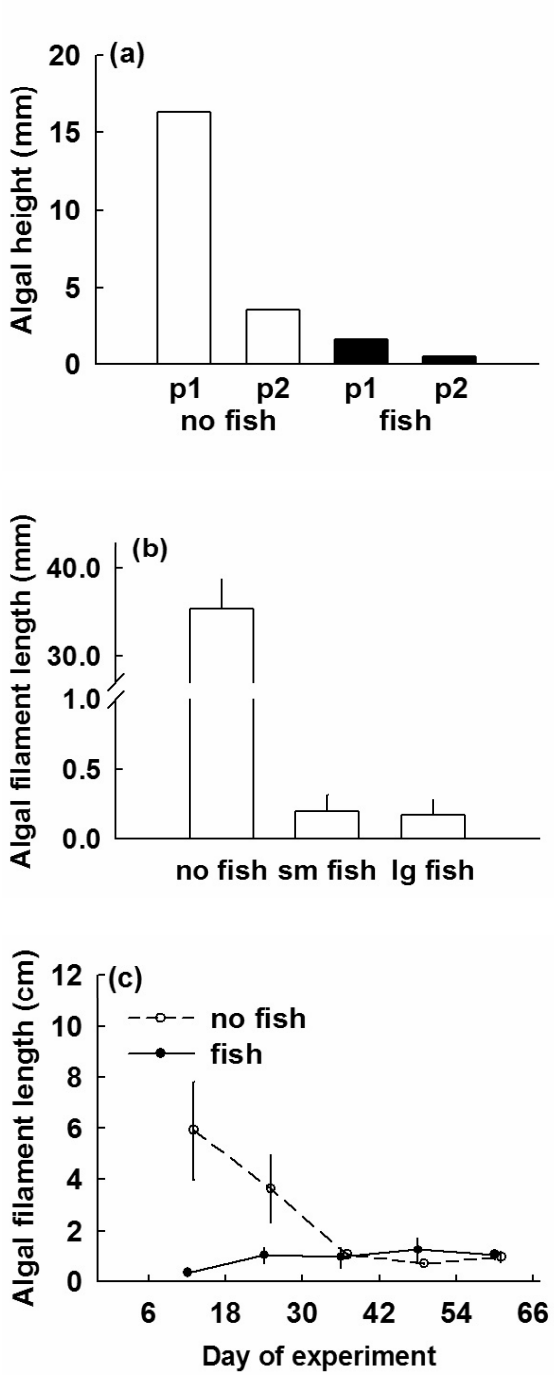


Figure 2.5. RDA of invertebrate assemblage structure data with and without fish on day 20 (circles) and 40 (squares) in nine experimental streams in Fall 2002. Small fish are represented by grey symbols; large fish by solid symbols and controls (No fish) are represented by open symbols. Plotted vectors are dominant invertebrate taxa. In parentheses is the cumulative percent variation explained by each axis.

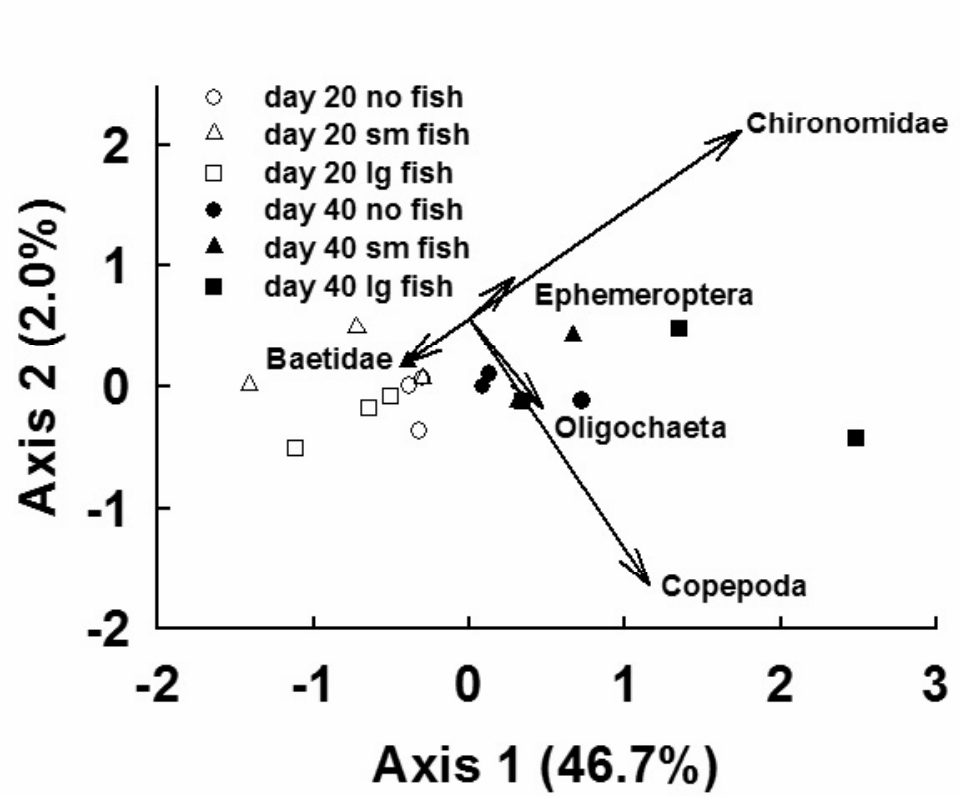


Figure 2.6. RDA of invertebrate assemblage structure data with and without fish in eight experimental streams in Summer 2003. Vectors plotted in bold are dominant invertebrate taxa, and numbered vectors indicate day of experiment. In parentheses is the cumulative percent variation explained by each axis.

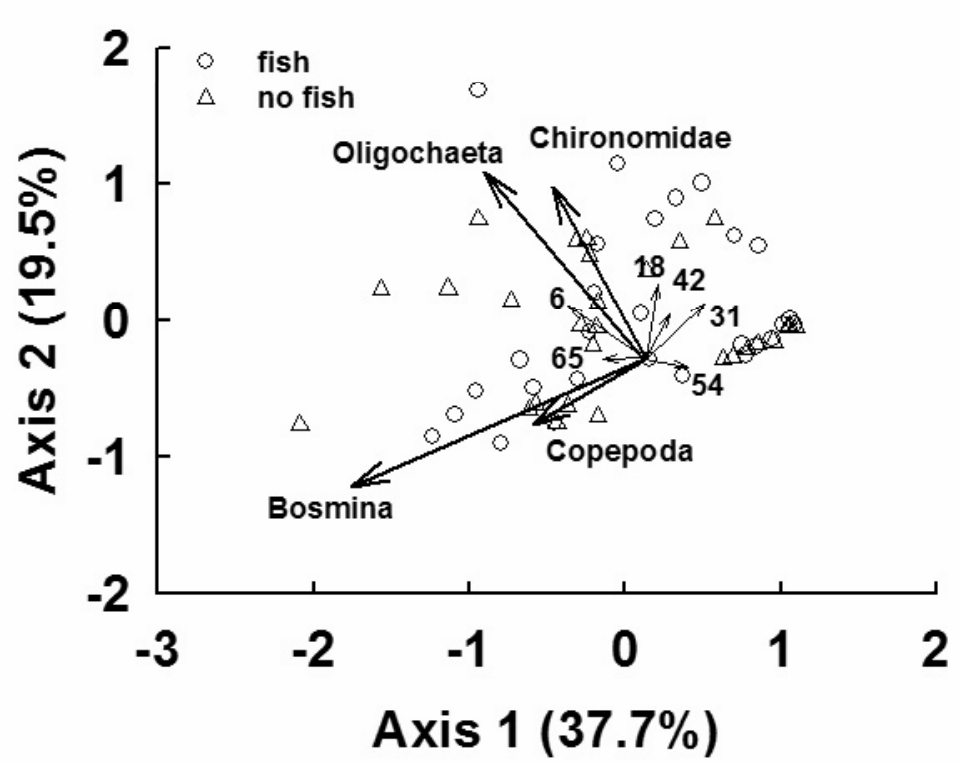
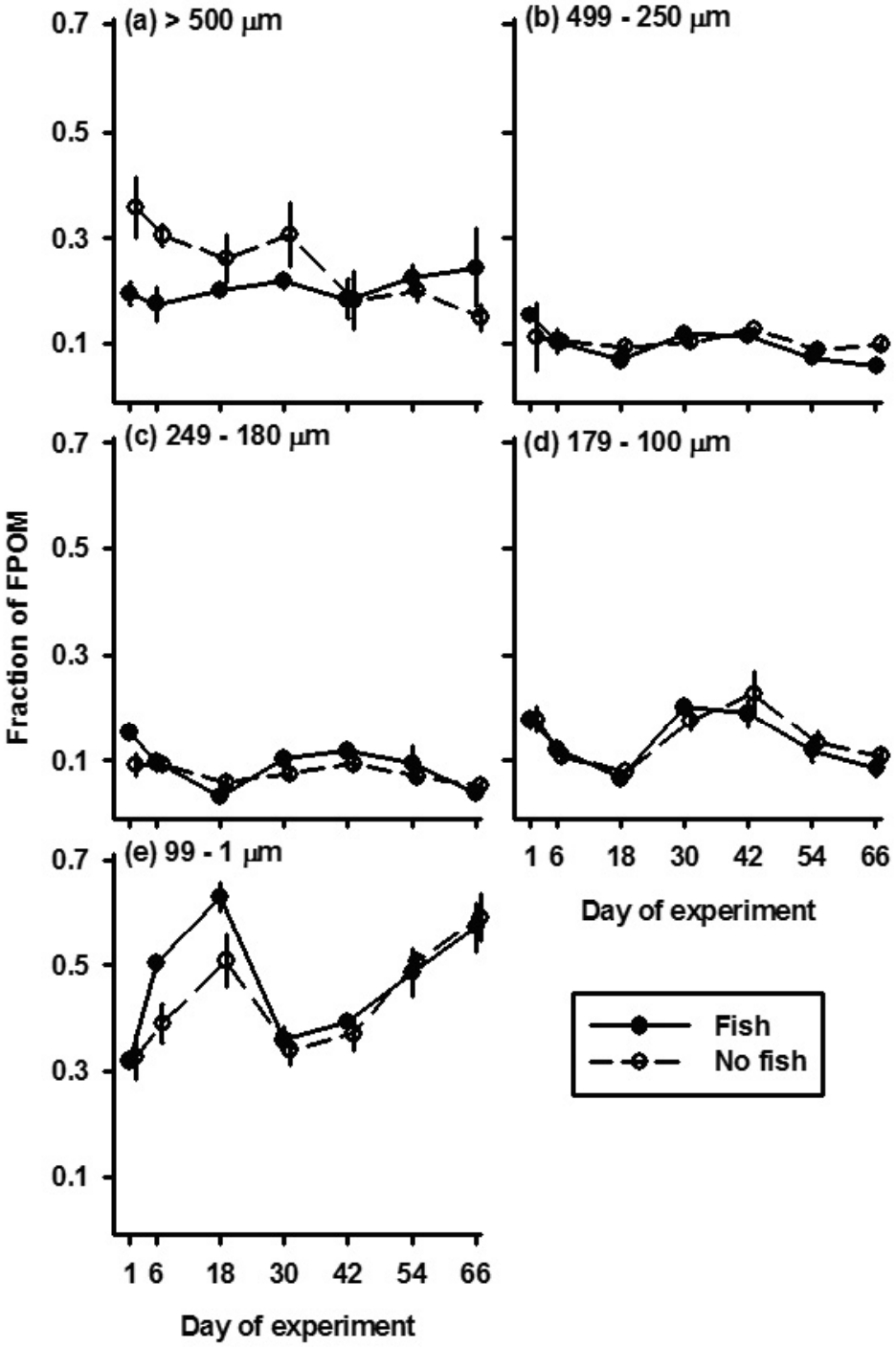


Figure 2.7. Mean fraction (±1SE) of total fine particulate organic matter (FPOM) in eight experimental stream pools with and without fish in five size classes (a) >500 µm (day*fish: F=2.74, P<0.05), (b) 499-250 µm, (c) 249-180 µm (day*fish: F=2.71, P<0.05), (d) 179-100 µm (day: F=7.09, P<0.01), and (e) 99-1 µm (day: F=16.37, P<0.01; fish: F=12.47, P<0.05) in Summer 2003. Control (No fish) data points are offset one day later to prevent overlap.



CHAPTER 3 - INTERACTIVE EFFECTS OF FLOOD FREQUENCY AND FISHES ON STREAM STRUCTURE AND FUNCTION

Katie N. Bertrand, Keith B. Gido, Walter K. Dodds, Justin N. Murdock, and Matt R. Whiles

ABSTRACT

Global climate change may lead to less frequent but more severe precipitation events in the Great Plains, thus altering the hydrology of streams. Because changes in species composition are likely to accompany the predicted changes in hydrology, it is of interest to quantify how species influence the recovery of stream ecosystem structure and function after hydrologic disturbance. We tested the interactive effects of flood frequency and two common functional groups of fishes (benthic grazers and water column omnivores) on the resilience of stream ecosystem processes using experimental streams and a field experiment. Both recovery of stream ecosystem function (e.g., primary productivity) and structure (e.g., algal biomass, invertebrate assemblage structure, and particulate organic matter) were measured as response variables. Species from both functional groups affected recovery of ecosystem structure and function by stimulating primary production following simulated floods. However, some of these effects were temporally variable or dependent on flood frequency. In the natural stream experiment, recovery of ecosystem structure and function after a major flood was not influenced by fish treatment, rather ecosystem processes varied with position in the watershed. The lack of a species effect in the natural stream after a single, large flood, was generally consistent with

experimental streams treatments without repeated flooding. We also attributed the observed differences between field and mesocosm experiments to the inability of small (mean = 35.8 m^2) field enclosures to capture the influence of nutrient remineralization by fishes. Our results indicate that fishes from two dominant functional groups can influence the successional trajectory of stream ecosystems following scouring floods. However, the transient nature of these effects necessitates an understanding of the interaction between fishes and floods to predict the consequences of simultaneous changes in hydrology and species composition.

INTRODUCTION

Predicted effects of climate change in the Great Plains will likely include an increase in the occurrence of large flood disturbances with legacies that may influence subsequent ecosystem processes (Parsons et al. 2006). Climate change will be accompanied by changes in stream community structure including species invasions and extirpations, which also are likely to have effects on ecosystem processes (Resh et al. 1988). The resulting interaction between altered disturbance regime and community composition will make predicting ecosystem response difficult. For example, decreased disturbance frequency is likely to shift control of ecosystem processes from abiotic to biotic effects; however the interactive effects of disturbance and altered community structure are largely unknown (Power et al. 1988b; Uehlinger 2000).

Most streams are nonequilibrium systems that experience a wide range of disturbances that regulate densities of the biota (Resh et al. 1988, Dodds et al. 2004a). In frequently flooded streams, the disturbance regime also is predicted to constrain the species composition and mediate the interactions of species. Thus, frequent flooding that resets the community might limit the effect of species on ecosystem processes because resources are too unpredictable to maintain stable populations of consumers (Lepori and Hjerdt 2006). During inter-flood periods,

communities structured by the flood regime may influence ecosystem processes (Biggs et al. 2005), and consumer effects may intensify. In the absence of disturbance, periphyton growth is limited by self-shading, and grazers can have stronger effects on succession (Steinman et al. 1989). Alternatively, consumer effects may diminish during long inter-flood periods, as low densities of grazers may be insufficient to limit algal growth (Sarnelle et al. 1993).

Recovery of ecosystem processes following a disturbance is difficult to quantify in lotic algal assemblages (Steinman et al. 1987). However, accrual and senescence in benthic communities may be analogous to successional processes in terrestrial plant communities, with transitions from low- to high-profile growth forms (Hudon and Bourget 1981; Hoagland et al. 1982; Roemer et al. 1984), or early seres may be dominated by large, elongate diatoms (Bacillariophyceae) or colonial growth forms of algae (Oemke and Burton 1986; Steinman and McIntire 1986; Peterson and Stevenson 1989, 1990). Alternatively, succession is described as bi-phasic with rapid increases in taxa richness in early seres (i.e., days to weeks after flooding) as a result of r-strategist colonists (e.g., many diatoms) and moderate increases in taxa richness in later seres (i.e., one to several months after flooding) as a result of late-stage colonists (Biggs and Smith 2002).

Consumers can alter the successional trajectory of periphyton by returning it to an earlier sere, maintaining dominance of an early sere, or facilitating progress to a later sere. The influence of consumers on periphyton succession depends on consumer trophic position, consumer density, periphyton resource limitation, and timing during succession when the consumers are present (Steinman 1996; Rosemond et al. 2000). Primary consumers mechanically remove algae from the substrata (Gelwick and Matthews 1992; Bertrand and Gido 2007), and at high grazer densities, can change both ecosystem structure and function.

Secondary consumers may expedite succession through suppression of grazers or by remineralizing nutrients from autocthonous or allochthonous sources (Gido and Matthews 2001).

To quantify how changes in flood frequency and fish assemblage structure interact to affect prairie stream structure and function, we conducted two mesocosm studies and a natural stream study. Our aim was to develop a predictive framework for the effects of global change in aquatic systems and test the importance of consumer effects under non-equilibrium conditions. Experimental streams allowed us to replicate different flood-frequency scenarios and manipulate functional composition of consumers in a factorial design, where the mechanisms underlying ecosystem processes could be disentangled from the background noise and variability inherent in natural systems. A field experiment in Kings Creek provided a natural context for comparing experimental stream results. In the experimental streams, we predicted that fish effects would be greatest soon after flooding and the magnitude of their effects would depend on the balance between consumptive losses and stimulation through nutrient remineralization. In frequently flooded streams, fish effects might not be detected, because ecosystem rates and biomass accrual would be continuously reset to low levels (Biggs et al. 2005). We predicted that grazers would decrease primary productivity following flood disturbances, whereas water column omnivores would increase primary productivity following disturbances. In the natural stream, we predicted that fish effects would largely reflect local food web interactions (e.g., consumptive losses) because ecosystem processes are an integrated measure of catchment processes and food web interactions occur in local habitats such as stream pools (Houser et al. 2005).

METHODS

Study sites

Twenty-four experimental streams located on the Konza Prairie Biological Station (KPBS) in north central Kansas, USA were used to test the effects of floods and fish species on ecosystem processes. Each stream consisted of a 2.54 m^2 pool connected to a 0.84 m^2 riffle. The basic design of these streams is given in Matthews et al. (2006). Water was supplied by a natural spring and recirculated with electric trolling motors creating a mean discharge of 2.0 L s^{-1}. 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 stream was inoculated one week prior to the beginning of the experiment with a slurry of benthos from nearby Kings Creek to stimulate algal growth.

We simulated floods in experimental streams by scouring the substrata for 10 minutes with a high-pressure hose and a second trolling motor attached to the pool to keep dislodged material in suspension. A 500 mL grab sample of suspended organic matter was taken prior to draining the stream through a 13 cm drain hole in the bottom of each pool. Streams were immediately refilled with spring water. Flood intensity was consistent across streams, dates, and experiments.

Field enclosures were constructed in 20 pools in Kings Creek on the KPBS. A physicochemical and biological description of Kings Creek is in Gray et al. (1998) and Gray and Dodds (1998). The study pools were located in three reaches of the creek: a spring-fed headwater (HW; N=8), an intermittent middle reach (IM; N=8), and a perennial downstream reach (PD; N=4). Temperature was strongly 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, 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 was similar in size and texture to that in the mesocosms.

The fish assemblage in Kings Creek is dominated by two grazing minnows [*Campostoma anomalum* (central stoneroller), *Phoxinus erythrogaster* (southern redbelly dace)] and the orangethroat darter (*Etheostoma spectabile*) (Franssen et al. 2006). Red shiner (*Cyprinella lutrensis*) occur in the lower reaches of Kings Creek, but never in high abundance. Grazing insects, crayfish (*Orconectes* spp.) and snails (*Physa* and *Physella* spp.) are present in varying abundance.

Treatment organisms

We tested the interactive effects of flood frequency and two common functional feeding groups of stream fishes, grazers and water-column minnows, on stream ecosystem processes. Southern redbelly dace (hereafter referred to as dace) is one of several species of grazing minnows that occur in prairie streams and can influence stream ecosystem processes (Bertrand and Gido 2007). They prefer streambeds dominated by pebble, gravel, or sand and avoid reaches with greater proportions of silt or clay (Lennon and Parker 1960, McKee and Parker 1982, Slack et al. 1997). Dace are abundant in springfed headwater reaches but migrate throughout the stream when upstream and downstream reaches are connected (Hill and Jenssen 1968, Settles and Hoyt 1976, Felley and Hill 1983). Red shiner (hereafter referred to as shiners) are water-column omnivores broadly distributed throughout the Great Plains (Cross and Collins 1995) and also known to influence stream ecosystem processes (Gido and Matthews 2001). Because of their adaptations to reproduce quickly and tolerate high temperatures and high ammonia

concentrations typical of drying intermittent streams this species can reach extremely high densities (Matthews and Hill 1979).

Mesocosm experimental design

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. In nearby Kings Creek, a scouring flood capable of overturning and displacing large cobbles (i.e., discharge > 0.5 m^3 s^{-1}; Dodds et al. 1996) has a reoccurrence interval of approximately 1.2 y, which indicates that over ten years, Kings Creek will experience at least one scouring flood in eight out of ten years. However, it is not uncommon for multiple scouring events to occur within one year. For example, from 1995 – 2004, at a weir in the intermittent reach of Kings Creek (N4D), there were three years with at least four scouring floods, two years with three scouring floods, and four years with one scouring flood. We randomly assigned each of the six treatment combinations to four replicate experimental streams. All 24 streams 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, which ranged from 0 to 9 individuals m^{-2} (Bertrand et al. 2006, Franssen et al. 2006).

Within experimental streams, we sampled in both riffles and pools to evaluate effects of consumers and floods on the two habitats. We expected the two species in our experiments to

primarily occupy the deeper pool habitat. Thus, we expected direct consumptive effects in pools and indirect effects (i.e., nutrient excretion) to dominate in riffles.

Field experimental design

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 study 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 2005 and 2.1 m^3 s^{-1} flood on 10 June) in spring 2005. Substantial substrata scouring occurred throughout the stream and no visible periphyton were present in any of the study reaches at the start of the experiment. Following the second flood, discharge decreased steadily and there were no additional precipitation events or increases in discharge. Summertime baseflow (i.e., consistent surface discharge maintained by groundwater with little or no precipitation contribution) for this stream is approximately 0.01-0.10 m^3 s^{-1} (measured about 1km upstream of IM; USGS gauging station #06879650). A strong nutrient gradient exists from the upper to the lower reach. The headwater site is fed by low nutrient groundwater (mean levels during experiment: 34 μg L^{-1} NH_4^+-N, 7 μg L^{-1} NO_3^--N, and 3 μg L^{-1} soluble reactive phosphorus), whereas the lower portion of the watershed contained more agriculturally influenced groundwater, which increased the nutrient content of Kings Creek with distance downstream (IM: 28 μg L^{-1} NH_4^+-N, 56 μg L^{-1} NO_3^--N, 2 μg L^{-1} SRP; PD: 19 μg L^{-1} NH_4^+-N, 425 μg L^{-1} NO_3^--N). Leaf litter was removed from the mesh as needed to maintain natural stream flow through the study pools. Enclosures were assigned one of four treatments: fish exclosure, ambient fish assemblage enclosure, dace enclosure, or red shiner 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 8 weeks in all three reaches, ending on 9 August in the HW and approximately a week

later in the IM and PD reaches. We removed all fish and crayfish from the fish exclosure, dace enclosure, and red shiner enclosure treatment pools and re-stocked dace and shiner treatment pools at 8 fish m^{-2}.

We were unable to fully prevent movement of fish and other organisms in some field exclosures; young-of-year (YOY) fishes migrated through the wire mesh, crayfishes and some fishes were able to move through gravel under exclosure barriers. Thus, we used a backpack electrofisher to remove invaders on weeks 2 and 6. In addition, we conducted population censuses at the end of the experiment to evaluate the integrity of each treatment. One exclosure barrier was lost to beaver activity and another study pool dried up in week 6.

Data collection

Stream metabolism – Gross primary productivity (GPP) and net ecosystem productivity (NEP) were based on diurnal changes in dissolved oxygen measurements from YSI 600XLM sondes (Yellow Springs Instruments, Inc.). In the mesocosm experiments, we used a single sonde and the open-system single-station approach to get biweekly estimates of production (Owens 1974). Because water was recirculated and the effective channel length was increased (~1700 m), reareation was estimated using the surface renewal model (Owens 1974) and was assumed to be the same across all stream units.

In the field experiment, substrata specific metabolism was estimated from substrata baskets placed in recirculating chambers. Thirty plastic mesh baskets (10 cm x 10cm x 10cm) containing dried pebbles (16-64 mm) from the stream bank were placed in each pool. Baskets were arranged into three rows of ten baskets perpendicular to the channel in the downstream half of the pool. Baskets were buried approximately 10 cm in the streambed so basket tops were flush with the stream bottom. Three baskets were randomly selected from each pool once per week

and returned to the laboratory in moist, sealed plastic containers within 2 hours 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.

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

Nutrient retention and uptake – Nutrient retention was estimated in the mesocosm experiments by sampling inflowing and outflowing water for total nitrogen (TN) and total phosphorus (TP). In the dace experiment, we collected 125 mL of unfiltered water from the inflow and overflow for each stream. Samples were stored frozen until digestion and nutrient analysis following the methods of Dodds (2003). Because of high variability in nutrient measurements in 2003, we collected 500 mL water samples during the shiner experiment and filtered a homogenized 125 mL subsample through a 1 μm filter before analysis of dissolved nitrogen.

Kings Creek study pool ammonium uptake rates were measured directly following metabolism measurements using substrata baskets in the recirculating chambers. An ammonium spike was added to raise the water concentration by approximately 40 μg L^{-1} and filtered water samples were taken at 0, 15, 30, 45, 60, 90, and 120 minutes 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 and adjusted to μg NH_4^+-N m^{-2} s^{-1} and corrected for background concentrations (Dodds et al. 2002).

Algal filament length – We estimated algal filament length in the mesocosms every 12 days prior to flooding as the mean of the longest algal filaments 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 study pools, 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 taken from experimental streams or from substrata baskets from study pools (following metabolism and nutrient uptake measurements). Pebbles were collected on site and frozen within 4 hours of collection. Chlorophyll was extracted by submerging pebbles in a 78˚C, 95% EtOH solution as described in Sartory and Grobelaar (1984). Extracts were analyzed for chlorophyll *a* with a Turner Model 112 fluorometer (Turner Designs Inc., Sunnyvale, CA, USA) using an optical configuration optimized for the analysis of chlorophyll *a* without phaeophyton interference (Welschmeyer 1995). Algal biomass was reported as chlorophyll *a* per m^{-2} (cross-sectional area of pebbles or surface area of the substrata basket opening). In the mesocosm studies, we estimated biomass on days 1, 6, and every 12 days thereafter, with three haphazardly selected pebbles along algal filament length transects from the riffle and five from the pool. In the field study, we estimated algal biomass weekly from one of the three substratum baskets used for metabolism and nutrient uptake measurements.

Fine particulate organic matter – We used a modified core sampler that consisted of a 0.018 m^2 corer with an electric pump (0.1 L s^{-1}) to collect FPOM, invertebrates, and algae from the

substrata. 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 FPOM, and preserved it in formalin. One core sample was taken from the riffle and the pool in each experimental stream unit on days 1, 6, and every 12 days thereafter. Five replicate core samples were taken weekly from five equally spaced transects in each pool during the field study. Dry mass and AFDM of FPOM 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 9L slurry from the core sample was collected for algal assemblage structure and preserved in formalin. Because we were more concerned with physical structure of the assemblage than genera-level responses of algal taxa, we used coarse taxonomic groupings for algae. We described 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).

Diet – Twice during the dace experiment (days 54 and 78), we collected two dace from each stream to characterize diet. Because of the fine-grained diet of dace, a subsample from the foregut was examined at 200X power and the first 100 algal cells that crossed an ocular transect were classified as filamentous green algae or diatom (unicellular green and cyanobacteria were absent or in very low abundance) to give percentage occurrence of algal taxa for each individual. The occurrence of animal matter was also noted. In the shiner experiment, we collected at least two shiners from each stream on days 27, 48, and 79, and all diet items for each fish were

identified and enumerated under a stereomicroscope to estimate percent contribution of each diet item to the total diet of the individual as well as percent of shiners containing each diet item. Percent contribution of each diet item was estimated by counting the number of grid cells filled by a particular item relative to the total number of grid cells filled by the entire diet of the individual, and mean percent contribution was calculated for each diet item across all fish collected from a particular treatment and day of the experiment (Franssen and Gido 2006). In the Kings Creek field study, diet was quantified for all fishes collected during the 4th week of the experiment and for two individuals of each species collected at the end of the experiment (week 8). Where possible, diet was quantified for at least two individuals of each species from each enclosure. In the field study, diet of benthic grazers was quantified using the same method as was used for the dace experiment, whereas diet of all other fishes was quantified using the same method as was used for the shiner experiment.

Statistical analysis

Mesocosm experiments – Because streams were not flooded before the 12th day of the experiment, we tested for early effects of fish from days 1 through 11 on ecosystem processes using independent samples t-tests with fish as the main effect. Similarly, prior to the 24th day of the experiment, streams to be flooded at a 24-day interval were combined with no flood controls and were tested for interactive effects of fish and floods from days 12 through 23 on response variables using two-way ANOVAs with fish and flood as the two main effects. We tested the effects of all six treatment combinations from day 24 until the end of each experiment using repeated-measures ANOVA with presence of fish and flood frequency as the two main effects. Algal assemblage structure was only analyzed on two dates from each experiment, so on each date, we tested for interactive effects of fish and flood using two-way ANOVAs. A likelihood-

ratio test of homogeneity of variances was used to test if variance in response variables differed among treatments. We evaluated heteroscdasticity in our data and applied the best variance-stabilizing transformation wherever necessary. 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 primary production showed a strong significant dependence on mean daily solar irradiance in the dace study, 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 (SAS 2003). Irradiance was measured on the Konza Prairie Biological Station approximately 1 km from the experimental stream facility. The experimental streams were covered overhead by a shade canopy that blocked 57% of incoming solar irradiance. 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 chi-square tests, which compared reduced and full model -2 residual log likelihood values, to select the best model of our data. In a repeated measures design such as this, with different sized experimental units, the denominator degrees of freedom must be computed from a linear combination of mean squares, and the denominator is not chi-squared. Thus, we used the Kenward-Rogers approximation to find approximate degrees of freedom for the F-test, which produced fractional denominator degrees of freedom.

We used chi-square tests to evaluate diet shifts among fishes of the same species subjected to different flood frequencies. Tests were performed on fishes to compare mean proportions of diet items among individuals across treatments within a given sample day.

In addition to the above quantification of how fishes and floods influenced algal biomass and total organic matter from cores, we also tested these effects on organic matter export during simulated flooding using two-way ANOVA in the streams flooded on 12-day and 24-day intervals.

Field experiment – 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 experiment. We developed models to predict GPP, ammonium uptake rate, algal biomass, abundance of size fractions of FPOM, percent composition of four algal taxa groups individually, and invertebrate assemblage structure. To simplify the analysis of invertebrate assemblage structure, we summarized invertebrate data using a principle components analysis based on a correlation matrix of log-transformed densities. We chose a subset of candidate models that included individual predictor or groups of predictor variables that were thought to be important based on our previous experiments in the experimental streams. 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

Mesocosm experiments

Gross primary productivity –GPP was generally highest in the streams that were not flooded and in streams with shiners present. The lowest rates of GPP were recorded in those streams that were flooded every 12-days (Table 1; Fig. 3.1a-b). During the dace experiment, mean daily solar irradiance was a significant predictor of GPP on days 1 – 4 ($r^2 = 0.59$, $P = 0.03$), 20 – 23 ($r^2 = 0.64$, $P = 0.02$), and 29-65 ($r^2 = 0.15$, $P = 0.04$), and during the shiner experiment mean daily solar irradiance was a significant predictor of GPP on days 1 – 4 ($r^2 = 0.21$, $P = 0.03$) and days 30 – 77 ($r^2 = 0.04$, $P = 0.03$). Thus, we incorporated irradiance as a covariate for every date on which irradiance was a significant predictor of GPP except on days 30-77 of the shiner experiment, where irradiance explained a very small fraction of the total variance in GPP. Whereas the flood on the 12th day reduced GPP in the dace experiment relative to streams that were not flooded ($F_{1,20} = 9.09$, $P < 0.01$), we did not find a similar effect of flooding in the shiner experiment. After day 29, floods decreased GPP in both the dace ($F_{2,15.2} = 4.01$, $P = 0.04$) and the shiner ($F_{2,23.6} = 17.27$, $P < 0.01$) experiments relative to streams that were not flooded. In the dace experiment, streams that were not flooded had significantly higher rates of GPP than those that were flooded every 12 days (Tukey *P*-value = 0.03), but streams that were flooded every 24 days did not significantly differ from other flood treatments. In the shiner experiment, streams that were not flooded had significantly higher rates of GPP than those that were flooded every 12 or 24 days (both Tukey *P*-values < 0.01). Shiners only significantly increased GPP after day 29, and this effect was most notable in the streams flooded every 24 days ($F_{1,23.6} = 8.33$, $P < 0.01$).

Nutrient retention – The difference in total nitrogen (N) in water flowing in and out of the streams (i.e., retention) was not statistically different among flood treatments. However, compared to streams without fish, dace significantly increased N retention on days 42 and 56

(93.1 vs. –14.4 μg L^{-1}; $F_{1,13.6} = 5.63$, $P = 0.03$; Fig. 3.2a-b). We found no effect of shiners on N retention (Fig. 3.2c-d).

Algal filament length – Dace, shiners, and flood frequency affected algal filament lengths. In the dace experiment (Fig 3.3a-b), effects of flood frequency and fish changed with time. On day 23, pool filaments were longer in streams that had not been flooded than other treatments ($F_{1,20} = 4.66$, $P = 0.04$). Relative to streams without fish, dace significantly decreased mean algal filament length in pools on day 11 ($t_{22} = 8.05$, $P < 0.01$; means 0.2 versus 5.3 cm) and day 23 ($F_{1,20} = 16.65$, $P < 0.01$; means 0.4 versus 2.1 cm), but dace increased filament lengths after day 36 ($F_{1,18} = 8.50$, $P < 0.01$; means 1.1 versus 0.6 cm). In riffles, dace had no effect on filament lengths through the first 24 days of the experiment, but after 5 weeks, filaments were nearly twice as long in streams with dace compared to streams without dace ($F_{1,19.4} = 7.86$, $P = 0.01$; means 7.1 versus 4.1 cm) (Table 1 - 2).

In the shiner experiment the presence of shiners generally increased algal filament lengths and floods decreased filament lengths (Fig. 3c-d). On day 23, streams that were not flooded had longer algal filaments if shiners were present (mean = 1.5 cm) than if shiners were absent (mean = 0.3 cm; $F_{1,20} = 4.70$, $P = 0.04$). After the 5th week of the experiment, floods decreased filament lengths in pools ($F_{2,19.2} = 6.49$, $P < 0.01$) such that filaments were two to three times longer in streams that were not flooded (mean = 2.7 cm) compared with streams that were flooded every 12 days (Tukey P-value < 0.01; mean = 0.9 cm) or streams that were flooded every 24 days (Tukey P-value = 0.03; mean = 1.3 cm). In riffles, shiners increased filament lengths by day 23 compared to streams without fish ($F_{1,20} = 4.46$, $P = 0.05$; means 7.1 versus 3.6 cm). There also was a significant interaction between day of experiment, shiners, and flood frequency after week 5 in the riffles ($F_{6,36.5} = 4.02$, $P < 0.01$). On day 35, streams without fish

that were not flooded had significantly shorter filaments than streams with fish (all Tukey *P*-values < 0.04), and filaments in these streams grew significantly longer by days 47, 60, and 71 (all Tukey *P*-values < 0.01). On average, in streams that were not flooded, filaments were significantly shorter on day 35 than on days 47 and 60 (both Tukey *P*-values < 0.03) (Table 1 - 2).

Algal biomass – Both dace and shiners increased algal biomass, but the effects of dace were only apparent in the first 23 days, whereas the effects of shiners were only detectable after 29 days and were dependent on flood frequency. In the presence of dace, algal biomass was 30% and 43% greater in pools on days 6 (t_{22} = -2.09, $P < 0.05$; means 6.6 versus 8.6 mg m^{-2}) and 18 ($F_{1,20}$ = 10.16, $P < 0.01$; means 7.7 versus 10.9 mg m^{-2}), respectively, and biomass was nearly 50% greater in riffles on day 18 than in streams without fish ($F_{1,20}$ = 6.71, $P = 0.02$; means 28.1 versus 18.8 mg m^{-2}). After day 30, the effects of dace were undetectable, and flooding decreased biomass in pools (day*flood: $F_{6,37.9}$ = 3.93, $P < 0.01$; day 42: 12-day versus 65-day flood frequency Tukey *P*-value < 0.01) but not riffles relative to streams that were not flooded (Fig. 3.4a-b). There was no detectable effect of shiners or floods on algal biomass on days 6 or 18 (Fig. 3.4c-d). After day 30, shiners approximately doubled algal biomass in pools and riffles of streams that were flooded every 24 days relative to streams without shiners (fish*flood: both $P <$ 0.03; means 14.7 and 14.6 versus 28.9 and 22.7 mg m^{-2}; both Tukey *P*-values < 0.01) (Table 1 - 2).

Fine particulate organic matter – Total particulate organic matter in streams decreased with increasing flood frequency in both experiments, and fish effects were temporally variable (Figs. 3.5 – 3.8). On day 6, dace decreased the abundance of all size classes of FPOM in pools except 249-180 μm and decreased the abundance of the > 500 μm and 99-1 μm size classes in riffles in

comparison with streams without dace (decrease ranged from 20 to 43%). By day 18, there was a significant interaction between dace and flood in riffles, such that flooded streams with dace had significantly less FPOM in the > 500 μm and 499-250 μm size classes than flooded streams without dace (87 and 31% less in each of the two size classes, respectively). Thereafter, flood effects, not fish effects, determined the size distribution of FPOM (Table 1 - 2).

Shiners had no detectable early effect on FPOM size fractions, but by day 30, shiners increased the abundance of the smallest size fraction of FPOM in pools by 29% and riffles by 26% (pools: $F_{1,23.5} = 21.06$, $P < 0.01$; riffles: $F_{1,28.7} = 34.24$, $P < 0.01$), increased the abundance of the largest size fraction in pools by 75% and in riffles by 100% (pools: $F_{1,18} = 6.13$, $P = 0.02$; riffles: $F_{1,28.4} = 21.06$, $P < 0.01$), and increased the abundance of the 249-180 μm size class in riffles by 28% ($F_{1,19.7} = 6.42$, $P = 0.02$) relative to streams without shiners (Table 1 - 2).

Algal assemblage structure – Floods and shiners had significant effects on algal assemblage structure, but there was no significant effect of dace. Overall, green filaments were the most abundant type of algae present during the dace experiment (mean = 65% of assemblage; range: 1 – 99%), whereas cyanobacteria (mean = 17% of assemblage; range: 0 – 94%), diatoms (mean = 10% of assemblage; range: 0 – 84%), and green algae (mean = 6% of assemblage; range: 0 – 33%) comprised less of the total assemblage. In the shiner experiment, green filaments were the most abundant type of algae present (mean = 48% of assemblage; range: 0 – 94%), followed by diatoms (mean = 38% of assemblage; range: 0 – 98%), cyanobacteria (mean = 8% of assemblage; range: 0 – 99%), and green algae (mean = 5% of assemblage; range: 0 – 48%). Relative abundance of green algae was 2 to 4 times greater in pools and riffles of streams that were flooded than in streams that were not flooded on day 18 of the dace experiment (pool: $F_{1,20} = 10.89$, $P < 0.01$; riffle: $F_{1,20} = 9.90$, $P < 0.01$). By day 42 in pools, green algae was 4 times

more abundant in streams flooded every 12 days compared to streams that were not flooded ($F_{2,16} = 3.91$, $P = 0.04$; Tukey P-value = 0.04). Relative abundance of green filamentous algae on day 18 also was 50% greater in riffles of streams that were flooded during the dace experiment than in streams that were not flooded ($F_{1,20} = 6.95$, $P = 0.02$). Relative abundance of cyanobacteria showed trends opposite those of unicellular green and filamentous green algae. On day 18, there was 7 times more cyanobacteria in riffles of streams that were not flooded than in streams that were flooded ($F_{1,20} = 10.05$, $P < 0.01$). On day 42 in pools, we found relatively more cyanobacteria in the 24-day streams than in either the 12-day streams or the streams that were not flooded during the dace experiment, and we found the same result on day 42 during the shiner experiments (dace: $F_{2,16} = 4.01$, $P = 0.04$, 12-day vs. no flood Tukey P-value = 0.04; shiner: $F_{2,18} = 4.04$, $P = 0.04$, 24-day vs. no flood Tukey P-value < 0.05) (Table 1 – 2).

Relative to streams without fish, the abundance of filamentous green algae was twice as high ($F_{1,20} = 4.70$, $P = 0.04$) and diatoms half as high ($F_{1,20} = 8.72$, $P < 0.01$) in riffles of streams with shiners on day 18. Relative abundance of filamentous algae also was over 50% higher in pools with shiners on day 42 ($F_{1,18} = 6.01$, $P = 0.03$) (Table 1 – 2).

Invertebrate assemblage structure – Invertebrate abundance generally decreased with increasing flood frequency in both experiments (Table 1 – 2; Figs. 3.9 – 3.12). Some taxa were too rare to test temporal patterns or treatment effects, so we focused our analyses on the following major taxonomic groups: microcrustaceans (mean = 63% of total invertebrate biomass; SD = 30%; range: 0 – 100%; Calanoida, Cyclopoida, Chydoridae, Ostracoda, and Isopoda), oligochaetes (mean < 1%; SD = 3%; range: 0 – 26%), gastropods (mean = 3%; SD = 9%; range: 0 – 66%), and chironomids (mean = 20%; SD = 23%; range: 0 – 92%; Chironomini, Tanytarsini, Tanypodinae, and Orthocladiinae). In the presence of dace, chironomid density was 80% lower

than no fish treatments in riffles on day 18 ($F_{1,20} = 5.28$, $P = 0.03$). After day 24, microcrustacean, oligochaete, and chironomid densities were typically greatest in treatments with dace, but this effect varied with flood frequency. In pools, we found a significant interactive effect of fish and flood frequency on the density of microcrustaceans ($F_{2,17.5} = 7.53$, $P < 0.01$), such that microcrustaceans were 10 – 15 times denser in dace streams that were not flooded, compared with dace streams that were flooded (both Tukey *P*-values < 0.01). Furthermore, microcrustaceans were almost 20 times denser in unflooded streams with dace, than in unflooded streams without dace (Tukey *P*-value < 0.01). In riffles, we detected a different fish*flood interaction on the density of oligochaetes ($F_{2,18.9} = 5.68$, $P = 0.01$), such that streams without dace had 87 – 90% lower densities of oligochaetes if they were flooded every 12 days, as compared to streams that were flooded every 24 days (Tukey *P*-value = 0.02) or not flooded (Tukey *P*-value < 0.01). Additionally, streams with dace had 9 to 43 times denser oligochaetes in pools if they were not flooded than streams with dace that were flooded every 12 (Tukey *P*-value < 0.01) or 24 (Tukey *P*-value < 0.01) days, respectively. In streams that were flooded every 24 days, oligochaetes were approximately 4 times denser in riffles of streams without dace than in streams with dace (Tukey *P*-value = 0.04). In riffles, we detected a three-way interaction among day of experiment, presence of fish and flood frequency in the density of chironomids ($F_{4,20.2} = 3.19$, $P = 0.04$), such that on day 54, the difference in chironomid density between unflooded streams and streams that were flooded either every 12 days or every 24 days was greater in streams where dace were present than in streams without dace (both Tukey *P*-values = 0.03). Chironomids were 10 to 100 times denser in unflooded streams with dace than in flooded streams with dace, whereas chironomids were 4 to 6 times denser in unflooded streams without dace than in flooded streams without dace.

Prior to day 24, we did not detect an early effect of shiners on invertebrate abundances in riffles or pools. After day 24, we detected a significant fish*flood interaction in riffles ($F_{2,18.7}$ = 8.11, $P < 0.01$), such that in streams without shiners microcrustaceans were nearly three times denser in unflooded streams than in streams flooded every 12 days (Tukey *P*-value = 0.04). Furthermore, in streams with shiners, microcrustaceans were 36 to 86% denser in unflooded streams than in streams that were flooded (both Tukey *P*-values < 0.01).

Fish diet – Fish diet in the mesocosms varied by flood frequency and day of experiment. Dace diet consisted primarily of filamentous green algae and diatoms, but 27% of the fishes we examined ingested some animal matter (Table 3). On day 54, flood frequency significantly affected dace diet, such that dace consumed the most filaments in the no flood treatment and the least in the 24-day flood treatments (chi-square *P*-values < 0.01). On day 77, dace consumed more green filamentous algae than diatoms in the 24-day than in the no flood and 12-day flood treatments ($P < 0.01$).

The most frequent diet items among shiners examined were chironomids, chydorids, ostracods, and terrestrial invertebrates (Table 4). On day 27, shiners consumed a significantly greater proportion of ostracods (40%) in 12-day flood treatments than in the no flood (30%) or 24-day flood (2%) treatments (*P*-values < 0.03). On day 48, diet significantly differed between no flood and the two flood treatments (*P*-values < 0.01). Terrestrial invertebrates and chydorids each comprised more than 25% of the mean fraction in shiners from the no flood streams, whereas in the 12-day and 24-day streams, these items comprised less than 5% of the mean fraction of gut volume in shiners. Additionally, chironomids comprised 11% of the mean fraction of gut volume in shiners from the 24-day streams, whereas chironomids comprised 4% or less of the mean fraction of gut volume in shiners from either the 12-day or the no flood

streams. On day 79, we found significant differences in the proportion of diet items among all flood treatments ($P < 0.01$). Gut volumes occupied by chydorids and ostracods were greater in streams that were not flooded than in streams that were flooded every 12 days (chydorids: no flood = 12%, 12- and 24-day floods ≤ 2%; ostracods: 12-day floods = 1%, 24-day and no floods ≥ 22%). Finally, in 24-day streams, shiner gut volume was comprised of twice as many chironomids and almost no terrestrial invertebrates, compared with shiners from 12-day or no flood streams in which gut volume was filled with 6 to 9% terrestrial invertebrates.

Field experiment

Following the scouring flood in 2005, there was a strong temporal trend of increasing GPP and algal biomass that was dependent on study reach (Fig. 3.13 and 3.14) but not fish assemblage treatment and was consistent with the no flood treatment in the experimental streams. Productivity was greatest downstream and increased with days since flood disturbance. Nutrient uptake rate did not show a strong temporal trend, and was not as strongly associated with study reach (Fig. 3.15). Diet of fishes collected from Kings Creek was similar to that of fishes collected from the experimental stream mesocosms. Grazers, including dace and central stonerollers, primarily consumed diatoms (64 – 100% of diet item occurrence), filamentous green algae (0 – 19% of diet item occurrence), and unicellular green algae (0 -17% of diet item occurrence), whereas shiners primarily consumed terrestrial invertebrates (Table 5 - 6). Grazer diet varied slightly by reach, such that diet in HW differed significantly from IM and PD in weeks 4 and 8 (all P-values < 0.05), but grazer diets in IM and PD were similar in weeks 4 and 8 (both P-values ≥ 0.05). Red shiners had variable diets, but the most common items were terrestrial invertebrates (0 - 100% of diet item occurrence) (Table 6). We were unable to compare shiner diet by reaches in week 4 because no shiners were collected from PD during

week 4. In week 8, terrestrial invertebrates and unidentifiable algae/detritus were the only diet items found across all three reaches, so there were no significant differences among shiner diets by reach.

Time since the flood disturbance had the strongest associations with ecosystem response variables in Kings Creek study pools, based on our model ranking criteria (Table 7). Variance in GPP (Adjusted $r^2 = 0.10$) was best predicted with days since flood disturbance. The Akaike weight ($w_i = 0.38$) of this model suggests that is was approximately twice as likely to be the best approximating model as the next two candidate models which included measures of grazer density ($w_i = 0.21$), or shiner density ($w_i = 0.19$) with measures of days since flood. The best model for predicting ammonium uptake rate included measures of days since flood disturbance and explained approximately 28% of the variance in uptake rate. The Akaike weight ($w_i = 0.59$) of this model suggests that it was approximately 3 times more likely to be the best approximating model than the next two candidate models (both $w_i < 0.20$). Algal biomass was best predicted with a model including days since flood disturbance and explained approximately 32% of the variance in uptake rate. 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 ($w_i = 0.31$).

The principal components analysis of invertebrate assemblages structure sampled from enclosures revealed high species loadings for Chironomidae (Tanypodinae) and cyclopoid copepods on the first component axis. The second component axis distinguished samples based on the abundance of Oligochaeta and Cambaridae, the third component axis distinguished samples based on the abundance of Dytiscidae, Cambaridae, and Tabanidae, and the fourth component axis distinguished samples based on the abundance Tabanidae, *Physa* sp., and

Stenonema sp. (Table 3.8). The first component axis was best predicted (Adjusted $r^2 = 0.39$) by days since flood disturbance. The Akaike weight ($w_i = 0.59$) of this model suggests that it was approximately 3 times more likely to be the best approximating model than the next two best candidate models (both $w_i < 0.20$). The third component axis was best predicted by days since flood disturbance (Adjusted $r^2 = 0.10$). The Akaike weight ($w_i = 0.37$) of this model suggests that it was only 12% more likely to be the best approximating model than the next best candidate model which included grazer density ($w_i = 0.33$).

DISCUSSION

Our results indicate that fishes from two dominant functional groups can influence the successional trajectory of stream ecosystems following scouring floods. Because prairie streams are highly disturbed, non-equilibrium systems, measures of ecosystem rates such as stream metabolism, nutrient uptake, and nutrient retention, are critical in understanding their dynamics. Although we predicted grazers and omnivores should have opposite effects on primary production, our results demonstrated that both fishes stimulated some aspects of primary production (e.g., shiners increased GPP, whereas dace increased overall algal biomass and shiners increased biomass in the streams flooded every 24 days), presumably through nutrient remineralization or selective grazing. It is possible that grazing fishes consumed primarily elongate green filaments (i.e., later successional stages of the algal assemblage), which would have allowed the r-selected colonial species to accumulate, thus increasing productivity. Since fish diet and algal assemblage structure only represent a snapshot at a coarse taxonomic resolution of what a fish consumes and what is available, diet and algal assemblage structure analyses provide only a limited evaluation of selective feeding. However, based on our diet and algal assemblage structure analyses, we have no evidence to support selective feeding by grazing

minnows. As expected, red shiners consumed terrestrial invertebrates in both the experimental streams and in Kings Creek, and thus excreted remineralized nutrients from an allochthonous source. The net effect of each functional group appears to be dependent upon the balance between consumptive losses and nutrient stimulation.

In natural streams, flooding is clearly a driver of stream ecosystem processes (e.g., Biggs et al. 2005), and in the experimental streams, frequent floods dominated ecosystem processes. Productivity rates in experimental streams flooded every 12 days were lower than in less frequently flooded streams because they were continuously reset to an early successional stage with short algal filaments, low algal biomass, and low densities of invertebrates. In the absence of flooding, stream primary productivity rates were greater than grazing fishes could control, algal biomass increased to a plateau (i.e., recovered), and algal filaments were extremely long. Thus, the potential for fishes to influence ecosystem processes is most prevalent within the first 30 days after a flood (e.g., dace) or in systems that are flooded at intermediate frequencies (e.g., shiners).

For some responses, disturbance frequency interacted with the presence of dace or shiners. Most notably, in the shiner experiment, streams that were flooded with an intermediate return interval had significantly higher algal biomass if shiners were present than if there were no fish present, and fish effects were not detected in streams that were not flooded or in the most frequently flooded streams. The effect of shiners under intermediate disturbance frequency is consistent with other research, which 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. The potential for differential fish effects under varied disturbance frequencies also may depend on whether

nutrients, rather than grazing pressure, light, or temperature, are the most limiting resources for primary producers.

Mesocosm and field experiments allowed us to compare the interactive effects of fishes and flood disturbance regime at multiple spatial scales. Across these scales, we found transient effects of consumers on ecosystem structure and function. For example, in both the experimental streams and the natural stream, dace and shiners predominantly occupied pool habitats, but it was likely that nutrients excreted by those fishes affected production in the downstream riffle habitats. Thus, fish effects likely occurred in local habitats through consumption and excretion, whereas only excretion is transferred downstream and combined with other watershed-scale disturbances including terrestrial nutrient inputs (Houser et al. 2005). Because we found strong effects of consumers in experimental streams but not in our field enclosures, we hypothesize that advectional throughflow greatly diluted remineralized nutrients in stream enclosures as compared to the experimental streams. In the natural stream, study pools were between 12 and 20 meters in length whereas the experimental streams, as a result of their recirculating design and low rates of recharge, had an effective channel length of approximately 1700 meters. The patterns that we documented in the field also were driven largely by the long time required for recovery of primary producers following the intense scouring flood that exported organic matter and nutrients. Long algal filaments did not develop within the 8-week experiment in Kings Creek, possibly due to greater intensity of flooding (i.e., scour), lower nutrients, and grazing by a complex assemblage of invertebrates and vertebrates that re-colonized after the flood. Whereas algal biomass in the experimental streams typically recovered within 30 days to pre-flood levels (30 – 50 mg m^{-2}), in the field, algal biomass continued to increase through the 8th week of the experiment and reached values of over 150 mg m^{-2}. Similarly, GPP in the experimental streams

appeared to have reached recovery by 30 days after disturbance, but in Kings Creek, GPP continued to increase through the end of the experiment.

Surprisingly, nutrient uptake rate, which remained fairly constant throughout the experiment, did not match this trend in algal biomass and GPP, but it may have been related to uptake by heterotrophs or changing algal assemblage structure, such that nitrogen-fixing cyanobacteria may have affected the nutrient limitation of the assemblage as a whole. Invertebrate assemblages in the experimental streams were primarily colonized by taxa with winged adults, whereas the exclosures in Kings Creek were colonized by drifting invertebrates in addition to taxa with winged adults. Invertebrate assemblages also may have differed in terms of the relative abundance of functional feeding groups: in the lower reaches of Kings Creek there is a niche for shredders and collectors to process coarse particulate organic matter (CPOM; e.g., senesced leaves from riparian vegetation), whereas the experimental streams are largely void of this material.

Another difference that we noted between experimental streams and Kings Creek was the high density of microcrustaceans in the experimental streams. We hypothesize that this was a result of the floating mats of algae that accumulate and senesce in experimental streams, providing a refuge from predation for the microcrustaceans. These differences were supported by the analyses of field data, which suggested the most important factor driving ecosystem processes in the Kings Creek study pools was the number of days since flood disturbance. Even after 8 weeks post-flood, Kings Creek had not yet recovered, and most ecosystem processes and populations were still increasing at the end of our experiment.

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. In the streams that we flooded every 12 and 24 days, we found that dace decreased the amount of FPOM export during flooding by 10% (range: 9 – 12%), whereas shiners increased the amount of FPOM export by nearly 20% on average (range: 19 – 29%) but up to almost 30% in streams flooded every 24 days (Fig. 3.16). The increase in export in the shiner treatments was likely due to the increased productivity of these systems as a result of their nutrient excretion benefiting the primary producers. These differences, summed across many small grassland streams occupied by these species can have large cumulative impacts on downstream water quality (Dodds et al. 2004b). As fish effects depend on the balance between consumptive losses and the increased rate of supply of limiting nutrients, dace increased productivity but incorporated some of the surplus algal production into fish tissue, so that it was not exported downstream during flooding. Alternatively, shiners increased productivity but did not directly consume the surplus algal production, and the excesses were exported downstream. Differences in export also could be linked to the retention or loss of nutrients from the systems.

Fish might also influence basin-wide nutrient dynamics by altering nutrient retention of streams. On day 42, we found that dace increased nutrient retention by 50 $\mu g\ L^{-1}$, whereas shiners only increased nutrient retention by 15 $\mu g\ L^{-1}$, relative to fishless controls. This supports the hypothesis that more of the excess organic matter and nutrients should be lost to downstream advection where water column omnivores dominate as compared to streams dominated by grazing minnows, in which more of the organic matter and nutrients should be recycled within the system. It is important to note that our nitrogen retention estimates in the experimental streams were calculated as a budget of concentration in the inflow versus concentration in the outflow over the course of the experiments, and we did not measure denitrification. Although we assume that reductions in nitrogen were primarily due to incorporation in the biota because

coarse substrate was likely well aerated, we cannot rule out the possibility that fish altered denitrification rates in the experimental streams.

General considerations

Prairie streams carry nearly 30% of global runoff and thus play important roles in controlling downstream water quality (Dodds 1997, Peterson et al. 2001). In North America, 95% of the prairie biome has been converted to agriculture or urban areas (Samson and Knopf 1994) and very few of the remaining fragments contain entire watersheds, or unaltered structure and function (Dodds et al. 2004a). Our results suggest that fishes may play important, but transitional roles in regulating ecosystem processes in these non-equilibrial systems. Furthermore, using time-integrated measures of whole ecosystem processes such as total downstream export of organic matter, we found that regional changes in fish assemblage structure might affect ecosystem services in large river basins. We conclude that global change, by altering species composition and disturbance regime in once-abundant prairie streams, may have far-reaching effects on downstream water quality. However, because species effects can be offsetting, predicting those effects will require a comprehensive understanding of the functional roles of species in these aquatic systems.

Table 3.1. Mean differences from experimental stream pools; boldface terms indicate significant differences ($P < 0.05$). Fish effects were calculated by subtracting the mean of the no fish treatment from the mean of the fish treatment, whereas flood effects were calculated by subtracting the mean of the streams that were not flooded from the mean of the streams that were flooded.

	Effect	Flood			fish				
	Day of experiment	12 – 23	> 24		6 - 11	12 - 23		> 24	
	Comparison	flood v no flood	12-day v no flood	24-day v no flood	all	12-day	24-day + no flood	12-day	24-day	no flood
Response	Fish treatment									
Gross primary productivity (g O_2 m^{-2} h^{-1})	dace	d14: **-0.08** d20: 0.02	**-0.18**	0.20	-0.04	d14:-0.03 d20: 0.04	d14:0.00 d20: 0.04	0.13	0.00	0.05
	red shiner	0.03	**-0.10**	**-0.08**	**0.02**	-0.01	0.06	**0.02**	**0.08**	**0.03**
Algal filament length (cm)	dace	-0.89	-0.23	-0.10	**-5.03**	**-1.40**	**-1.92**	**1.19**	**0.39**	**0.10**
	red shiner	-0.34	**-1.76**	**-1.43**	0.72	**0.27**	**1.17**	0.44	1.07	0.45
Algal biomass (mg m^{-2})	dace	0.50	**-6.82**	-3.99	**1.97**	**4.68**	**1.89**	2.19	3.14	1.30
	red shiner	-7.37	**-3.28**	**1.41**	2.13	2.95	-3.95	**3.29**	**14.23**	**-0.64**
FPOM > 500 µm (mg)	dace	**-1.82**	**-3.26**	**-2.81**	**-1.32**	**-1.77**	**0.38**	-0.57	-1.22	0.77
	red shiner	-0.64	**-6.56**	**-7.47**	0.39	-0.20	0.93	**0.63**	**0.55**	**5.13**
FPOM 499 - 250 µm (mg)	dace	-0.17	**-0.95**	**-0.68**	**-0.56**	-0.24	0.27	-0.05	-0.03	-0.18
	red shiner	**-0.43**	**-0.44**	-0.69	0.18	0.04	0.23	0.06	0.28	0.39
FPOM 249 - 180 µm (mg)	dace	0.19	**-0.58**	**-0.52**	-0.18	-0.16	-0.17	0.01	0.25	0.33
	red shiner	-0.28	**-0.33**	**-0.06**	0.08	0.00	0.04	-0.04	0.15	0.26
FPOM 179 – 100 µm (mg)	dace	-0.34	**-1.70**	**-1.45**	**-0.51**	-0.28	-0.13	-0.25	0.01	-0.04
	red shiner	**-0.44**	**-1.06**	-0.20	0.22	0.30	0.19	0.04	0.29	0.64
FPOM 99 – 1 µm (mg)	dace	**-3.49**	**-7.28**	**-6.33**	**-0.84**	-1.12	2.27	-0.04	-0.16	1.06
	red shiner	**-2.15**	**-2.63**	**-2.50**	0.41	0.55	1.76	**0.32**	**1.37**	**3.21**
Green algae (%)	dace	**10.84**	**4.67**	9.30	N/A	-9.40	-2.08	2.93	5.13	0.31
	red shiner	4.54	-0.25	0.63	N/A	10.50	1.41	-11.30	-9.57	-12.50
Green filamentous algae (%)	dace	9.85	-2.98	-29.55	N/A	28.71	-2.92	19.83	-23.85	-3.20
	red shiner	-3.80	-7.07	-6.83	N/A	4.68	13.13	**21.95**	**19.70**	**27.43**
Cyanobacteria (%)	dace	-5.98	-10.70	10.27	N/A	-13.84	10.06	3.05	17.42	1.04
	red shiner	-10.02	-2.32	0.44	N/A	-0.72	0.46	-0.70	-2.43	-0.73
Diatoms (%)	dace	-14.71	-1.63	9.34	N/A	-5.47	-5.06	-5.80	1.29	0.57
	red shiner	10.63	11.00	6.98	N/A	-14.48	-18.51	-9.95	-7.40	-11.48

Chironomidae (ind. m^{-2})	dace	-205.16	**-6968.20**	-5146.35	**-23.86**	3.67	-315.15	-1115.59	-1139.81	3914.24
	red shiner	**-960.41**	**-3245.22**	**-2977.55**	-220.29	31.69	-59.56	-13.12	216.82	2668.12
Microcrustacea (ind. m^{-2})	dace	-20506.2	**-15464.99**	**-15605.08**	210.2	-3879.4	5915.87	1747.02	1072.73	**32278.12**
	red shiner	**-34165.30**	**-63495.61**	**-41849.39**	9255.06	4076.60	14867.35	**7445.76**	**29665.27**	**18348.26**
Oligochaeta (ind. m^{-2})	dace	-821.82	**-19463.67**	**-16514.03**	-15.8	-231.04	1539.86	-502.85	-3430.29	-1637.02
	red shiner	-197.36	-544.98	-549.98	-79.21	0.00	436.6	4.57	15.14	1099.1
Physa sp. (ind. m^{-2})	dace	7.74	-47.81	35.93	N/A	44.56	-5.28	6.35	-64.2	21.58
	red shiner	N/A	-38.39	-51.73	-18.25	N/A	N/A	86.95	-31.34	-56.86

Table 3.2. Mean differences from experimental stream riffles; boldface terms indicate significant differences ($P < 0.05$). Fish effects were calculated by subtracting the mean of the no fish treatment from the mean of the fish treatment, whereas flood effects were calculated by subtracting the mean of the streams that were not flooded from the mean of the streams that were flooded.

	Effect	Flood			fish					
	Day of experiment	12 – 23	> 24		6 - 11	12 - 23		> 24		
	Comparison	flood v no flood	12-day v no flood	24-day v no flood	all	12-day	24-day + no flood	12-day	24-day	no flood
Response	Fish treatment									
Algal filament length (cm)	dace	-0.31	-0.57	-1.48	-3.42	-1.15	0.76	**4.16**	**1.98**	**3.06**
	red shiner	-1.39	**-0.93**	**-0.80**	1.5	**1.18**	**6.10**	**0.50**	**1.64**	**0.64**
Algal biomass (mg chla m^{-2})	dace	1.29	-9.83	-7.87	-2.08	**7.88**	**10.62**	6.46	3.17	5.87
	red shiner	-1.51	-20.64	-18.62	1.8	-0.88	-0.45	4.69	**8.16**	-5.05
FPOM > 500 µm (mg)	dace	**-4.78**	**-3.86**	**-3.48**	**-2.39**	**-5.10**	**3.03**	0.08	0.19	1.36
	red shiner	-0.81	**-3.44**	**-2.50**	0.33	-0.22	1.84	**0.41**	**1.54**	**3.82**
FPOM 499 - 250 µm (mg)	dace	**-0.54**	**-1.09**	**-1.00**	-0.12	**-0.53**	**0.31**	0.02	0.15	-0.11
	red shiner	-0.26	**-0.42**	**-0.08**	0.11	-0.13	0.47	0.03	0.21	0.36
FPOM 249 - 180 µm (mg)	dace	**-0.36**	**-0.67**	**-0.71**	2.67	-0.28	0.18	0.11	0.01	0.06
	red shiner	-0.02	-0.1	0.13	0.24	-0.06	0.21	**0.12**	**0.48**	**0.13**
FPOM 179 – 100 µm (mg)	dace	-0.27	**-1.86**	**-1.57**	-0.37	-0.28	0.25	-0.25	0.01	0.37
	red shiner	0.01	-0.26	0.08	0.26	-0.12	0.30	**0.19**	**0.52**	**0.44**
FPOM 99 – 1 µm (mg)	dace	**-5.28**	**-6.96**	**-5.84**	**-1.75**	-1.66	2.51	-0.23	0.23	2.75
	red shiner	**-1.62**	**-1.33**	**-0.46**	0.55	-0.19	2.01	**0.27**	**1.44**	**1.66**
Green algae (%)	dace	**5.05**	7.34	4.76	N/A	-1.72	-0.42	1.65	-8.52	0.47
	red shiner	3.68	0.07	-5.12	N/A	5.76	-0.39	-3.52	0.12	-8.98
Green filamentous algae (%)	dace	**25.15**	-0.14	-17.21	N/A	-7.37	13.52	-11.30	17.04	-2.63
	red shiner	6.98	-11.70	-25.95	N/A	**25.40**	**20.11**	21.43	21.75	33.64
Cyanobacteria (%)	dace	**-27.36**	-2.91	-4.79	N/A	11.29	-6.62	11.44	0.27	-0.75
	red shiner	0.44	6.03	**38.77**	N/A	11.72	0.70	-13.74	-29.27	0.66
Diatoms (%)	dace	0.44	-3.97	9.65	N/A	-1.57	-0.89	-2.45	6.35	2.92
	red shiner	-12.94	16.64	3.34	N/A	**-42.88**	**-24.10**	-4.17	7.40	-3.26
Chironomidae (ind. m^{-2})	dace	-173.89	**-4555.82**	**-3427.91**	-92.31	**-185.30**	**-424.36**	**-1111.63**	**-1862.03**	**-3044.88**
	red shiner	N/A	**-2606.19**	**-2158.58**	-21.74	N/A	N/A	-226.12	-386.19	470.96
Microcrustacea (ind. m^{-2})	dace	**-28280.80**	**-24682.49**	-22914.75	-1844.03	-2934.01	-12942.5	1357.81	-493.49	6695.8

	red shiner	N/A	**-54139.71**	**-22460.65**	-1071.98	N/A	N/A	**-653.93**	**59853.97**	**54642.30**
Oligochaeta (ind. m^{-2})	dace	**-2782.43**	**-13303.42**	**-8846.84**	-57.7	-633.87	425.23	-1244.52	**-6807.90**	5848.81
	red shiner	N/A	-309.75	-283.01	20.57	N/A	N/A	24	72.88	479.46
Physa sp. (ind. m^{-2})	dace	0.64	-30.85	52.16	N/A	3.43	-0.86	-16.93	56.33	35.46
	red shiner	N/A	**-98.17**	**-92.38**	7.42	N/A	N/A	24	0.22	-94.7

Table 3.3. Diet of southern redbelly dace (*Phoxinus erythrogaster)* collected from experimental stream mesocosms on the Konza Prairie Biological Station on two days (54 and 77) during the dace study of summer 2003. Percentages of diet items represent the mean number of cells of each type per 100 total cells counted in each fish.

Trt	Day	N	% unicellular green algae	% filamentous green algae	% diatoms	ratio filaments:diatoms	% fish with inverts in diet
12-day	54	6	0	60	40	1.50	0
	77	11	1	41	56	0.73	27
	mean		1	51	48	1.12	
24-day	54	7	1	38	60	0.63	14
	77	8	3	74	23	3.22	13
	mean		2	56	42	1.93	
65-day	54	8	0	79	21	3.82	50
	77	8	0	56	44	1.29	50
	mean		0	68	32	2.56	
Overall	mean		1	58	41	1.87	26

Table 3.4. Diet of red shiner (*Cyprinella lutrensis*) collected from experimental stream mesocosms on the Konza Prairie Biological Station on three days (27, 48 and 79) during the shiner study of summer 2004. Diet is reported as percent occurrence, which is the percent of individuals in which the diet item was found, and as gut volume (mean squares), which is the mean number of grid cells (cell area 4 mm^2) that were filled by each type of diet item.

			terrestrial invertebrate		Chydoridae		Ostracoda		Chironomidae		algae/detritus
Trt	Day	N	% occurrence	mean squares	% occurrence	mean squares	% occurrence	mean squares	% occurrence	mean squares	mean squares
12-day	27	6	50	1	17	<1	67	1	17	<1	7
	48	6	50	2	50	3	83	2	67	3	58
	79	7	43	1	43	2	43	<1	57	1	27
24-day	27	4	75	3	50	<1	50	1	0	0	75
	48	6	0	<1	50	<1	0	0	83	4	41
	79	7	14	<1	14	<1	86	17	43	1	38
80-day	27	6	67	2	50	<1	33	6	33	<1	18
	48	7	43	2	57	16	71	2	14	<1	20
	79	8	38	1	63	10	88	3	63	1	36

Table 3.5. Diet of southern redbelly dace (*Phoxinus erythrogaster)* and central stoneroller (*Campostoma anomalum*) collected from 20 Kings Creek study pools on the Konza Prairie Biological Station during weeks 4 and 8 of the summer 2005 field study. Percentages of diet items represent the mean number of cells of each type per 100 total cells counted in each fish.

Trt	Reach	Week	N	% unicellular green	% green filaments	% diatoms	ratio filaments:diatoms	% fish with inverts in diet
no fish	HW	4	4	2	17	80	0.21	0
no fish	IM	4	5	4	1	95	0.01	0
no fish	IM	8	5	1	3	96	0.03	0
no fish	PD	8	2	1	2	80	0.03	0
control	HW	4	6	1	5	93	0.05	0
control	HW	8	7	<1	6	94	0.06	0
control	IM	4	5	7	1	93	0.01	0
control	IM	8	7	<1	1	99	0.01	0
control	PD	4	3	5	<1	95	0.01	0
control	PD	8	4	0	<1	>99	0.01	0
dace	HW	4	6	6	1	92	0.01	0
dace	HW	8	6	<1	11	89	0.12	0
dace	IM	4	3	17	19	64	0.30	0
dace	IM	8	5	1	3	96	0.03	0
dace	PD	4	3	10	2	88	0.02	0
dace	PD	8	4	0	0	100	0	0
red shiner	HW	4	4	2	4	93	0.04	0
red shiner	HW	8	7	0	12	88	0.14	14
red shiner	IM	4	3	<1	1	99	0.01	33
red shiner	IM	8	8	1	11	88	0.13	0
red shiner	PD	8	2	1	2	98	0.02	50

Table 3.6. Diet of red shiner (*Cyprinella lutrensis*) collected from 20 Kings Creek pools on the Konza Prairie Biological Station during weeks 4 and 8 of the summer 2005 field study. Diet is reported as percent occurrence, which is the percent of individuals in which the diet item was found, and as gut volume (mean squares), which is the mean number of grid cells that were filled by each type of diet item.

				terrestrial invertebrates		Chydoridae		Ostracoda		Chironomidae		algae/detritus
				%	mean	%	mean	%	mean	%	mean	
Trt	Reach	Week	N	occurrence	squares	occurrence	squares	occurrence	squares	occurrence	squares	mean squares
no fish	HW	4	5	80	34.4	0	0	20	<1	20	<1	6
no fish	HW	8	1	0	0	0	0	0	0	0	0	20
control	IM	8	2	100	4	0	0	0	0	0	0	0
dace	HW	8	2	100	4	0	0	0	0	0	0	1
dace	PD	8	1	100	6	0	0	0	0	0	0	0
red shiner	HW	4	6	88	12	0	0	67	<1	0	0	12
red shiner	HW	8	3	100	5	0	0	0	0	0	0	3
red shiner	IM	4	4	100	9	0	0	0	0	25	<1	2
red shiner	IM	8	1	50	3	0	0	0	0	0	0	5
red shiner	PD	8	2	50	2	0	0	0	0	0	0	<1

Table 3.7. 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
Invertebrate PCA AX1	Day	0.39	-13.56	3	0.00	0.59
Invertebrate PCA AX1	day, grazer	0.37	-11.23	4	2.33	0.19
Invertebrate PCA AX1	day, shiner	0.37	-11.07	4	2.49	0.17
Invertebrate PCA AX3	Day	0.10	1.41	3	0.00	0.37
Invertebrate PCA AX3	day, grazer	0.13	1.63	4	0.22	0.33
Invertebrate PCA AX3	day, shiner	0.08	3.74	4	2.33	0.11
Invertebrate PCA AX3	day, shiner, grazer	0.11	4.11	5	2.70	0.09
Invertebrate PCA AX3	Grazer	0.02	4.84	3	3.43	0.07

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.

Table 3.8. Species loadings on first four axes of principle components analysis of invertebrate assemblage structure in Kings Creek study pools during summer 2005.

Taxon	Axis 1	Axis 2	Axis 3	Axis 4
MOLLUSCA				
Gastropoda				
Physa	0.1441	0.1449	0.1856	0.4371
Helisoma	0.0001	0.0494	0.1703	0.2555
Hydrobiidae	0.1635	0.2289	0.3987	0.5792
Bivalvia				
Sphaerium	0.0008	0.4759	0.4905	0.5359
ANNELIDA				
Clitellata (Oligochaeta)	0.0055	0.2164	0.2304	0.2395
NEMATODA	0.1594	0.1999	0.2086	0.2564
ARTHROPODA				
Arachnida				
Hydracarina	0.3561	0.482	0.4981	0.5252
Crustacea				
Amphipoda	0.0134	0.025	0.4109	0.5741
Isopoda	0.2935	0.2972	0.523	0.5374
Cambaridae	0.0721	0.3953	0.3997	0.4182
Ostracoda	0.6574	0.6636	0.6885	0.6935
Copepoda				
Cyclopoid	0.819	0.821	0.8439	0.8541
Harpacticoid	0.0575	0.1344	0.5461	0.5737
Insecta				
Trichoptera				
Polycentropodidae	0.3098	0.3143	0.5015	0.5019
Diptera				
Chironomidae (Tanypodinae)	0.8536	0.8576	0.8579	0.8597
Chironomidae (non-Tanypodinae)	0.7854	0.8044	0.8422	0.8437

Taxon	Axis 1	Axis 2	Axis 3	Axis 4
Chironomidae (pupae)	0.4929	0.5465	0.6139	0.6159
Ceratopogonidae	0.1419	0.5894	0.6095	0.6096
Tipulidae	0.413	0.5502	0.6848	0.6901
Tabanidae	0.0573	0.0574	0.1951	0.6337
Coleoptera				
Dytiscidae (larvae)	0.0266	0.1135	0.4914	0.6533
Elmidae (larvae)	0.1512	0.4299	0.4747	0.5912
Ephemeroptera				
Baetidae	0.1878	0.3649	0.3792	0.5669
Caenidae (Caenis)	0.5609	0.5848	0.6103	0.6151
Leptophlebiidae	0.5101	0.5607	0.5714	0.5738
Heptageniidae (Stenonema)	0.5575	0.5956	0.7607	0.7839

Figure 3.1. Gross primary production (GPP + SE) in dace study (a) and shiner study (b). Control (no fish; open symbols) data points are offset one day later to prevent overlap.

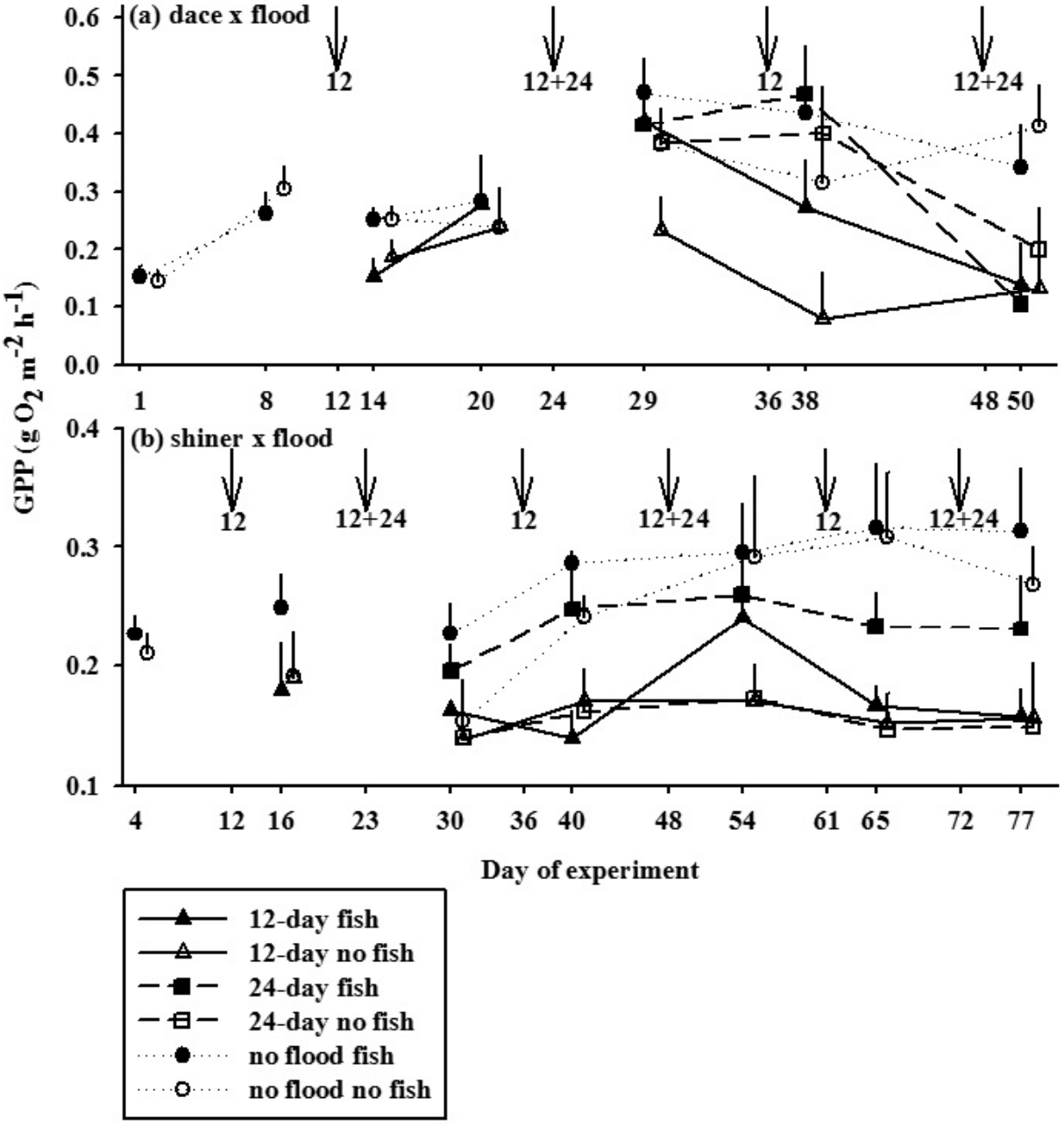


Figure 3.2. Mean concentration (+ SE) of total nitrogen retained in experimental streams with (gray bars) and without (black bars) fish during the dace (a)-(b) and shiner (c)-(d) mesocosm studies. Values of bars were calculated by subtracting the concentration of total nitrogen measured in the outflow from that measured in the inflow of each stream. Note that y-axis scale differs among panels.

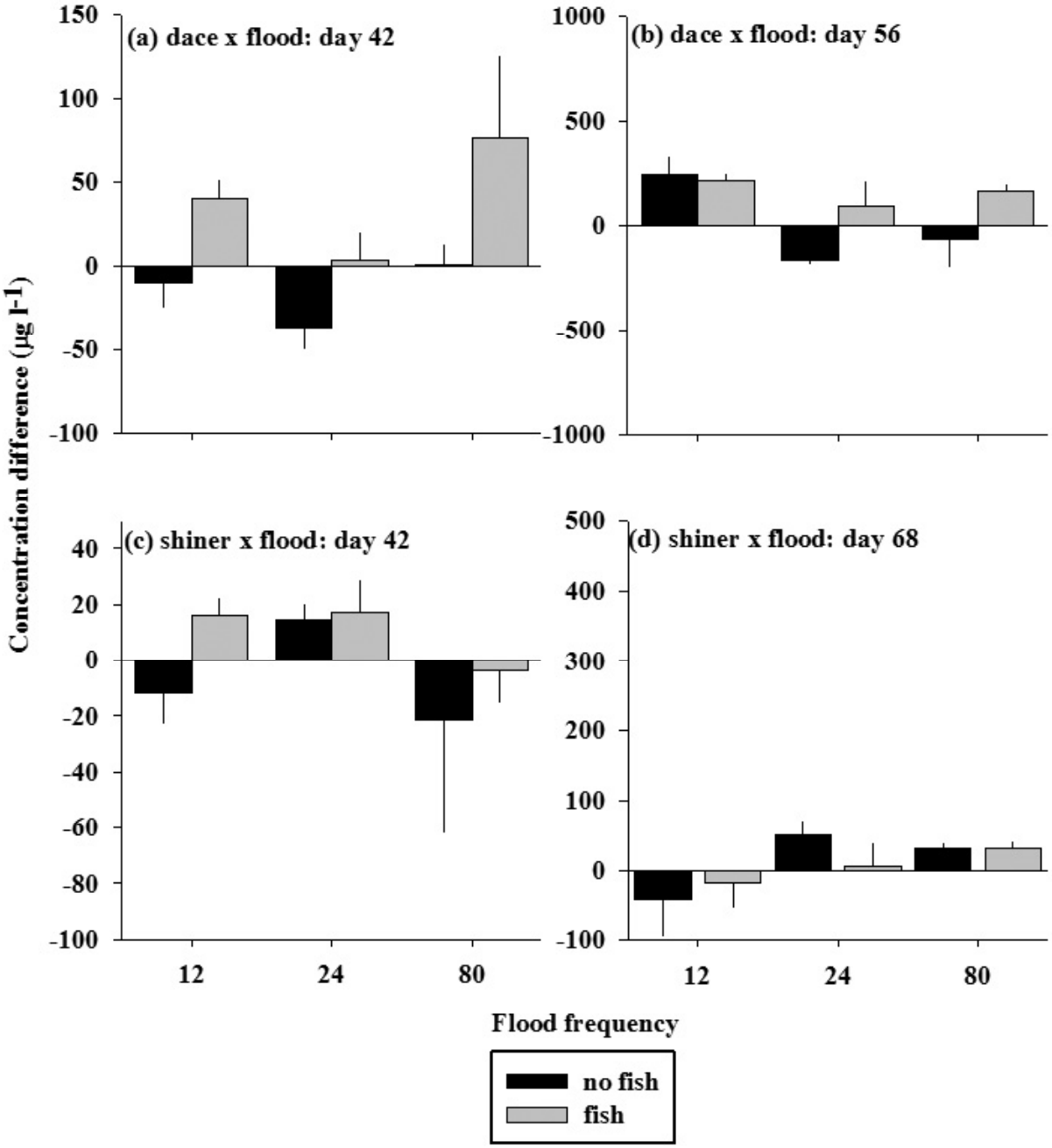


Figure 3.3. Mean algal filament length (+ SE) in dace mesocosm pools (a) and riffles (b) and in shiner mesocosm pools (c) and riffles (d). Control (no fish; open symbols) data points are offset one day later to prevent overlap.

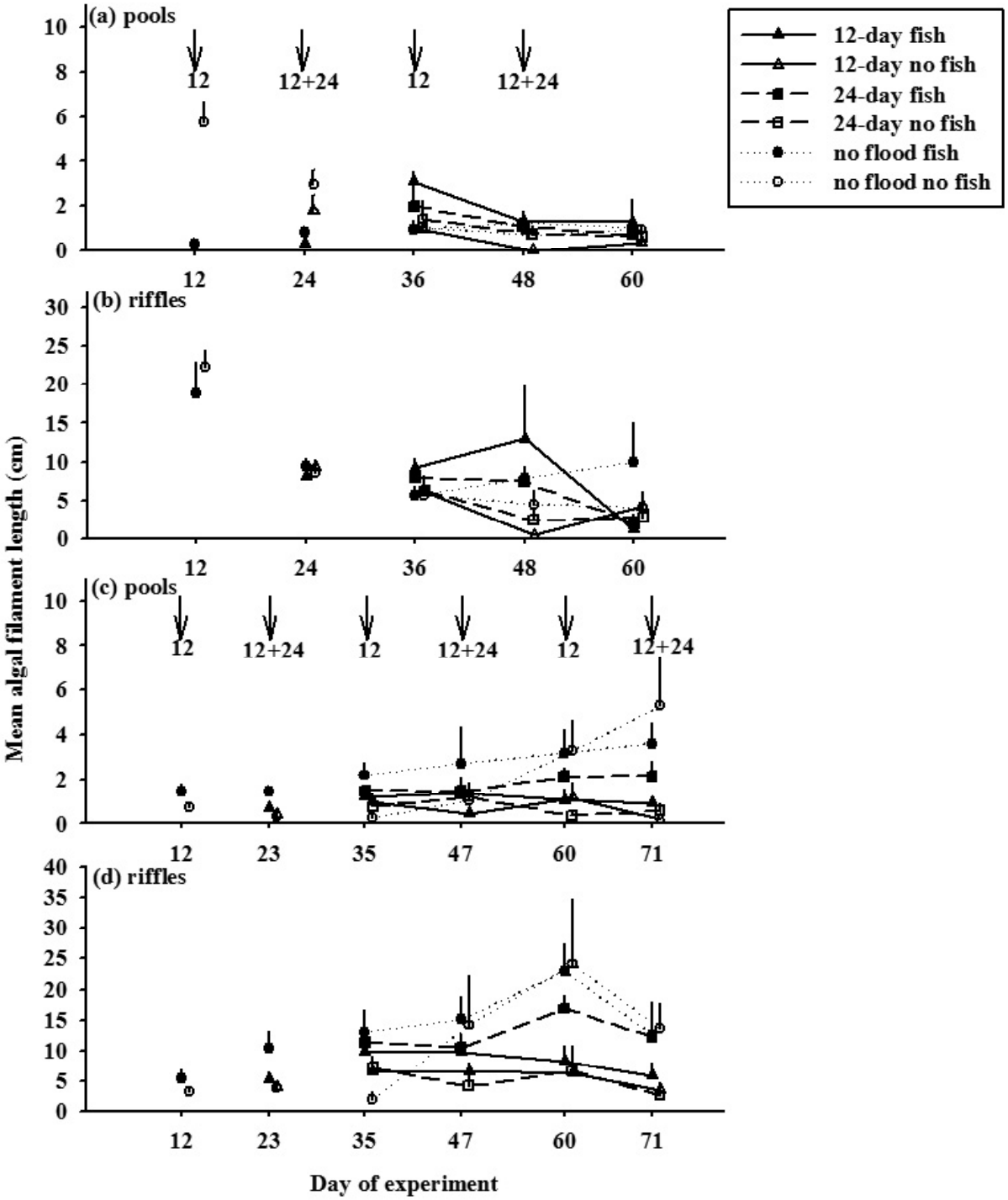


Figure 3.4. Algal biomass (chlorophyll *a*; + SE) in dace mesocosm pools (a) and riffles (b) and in shiner mesocosm pools (c) and riffles (d). Control (no fish; open symbols) data points are offset one day later to prevent overlap.

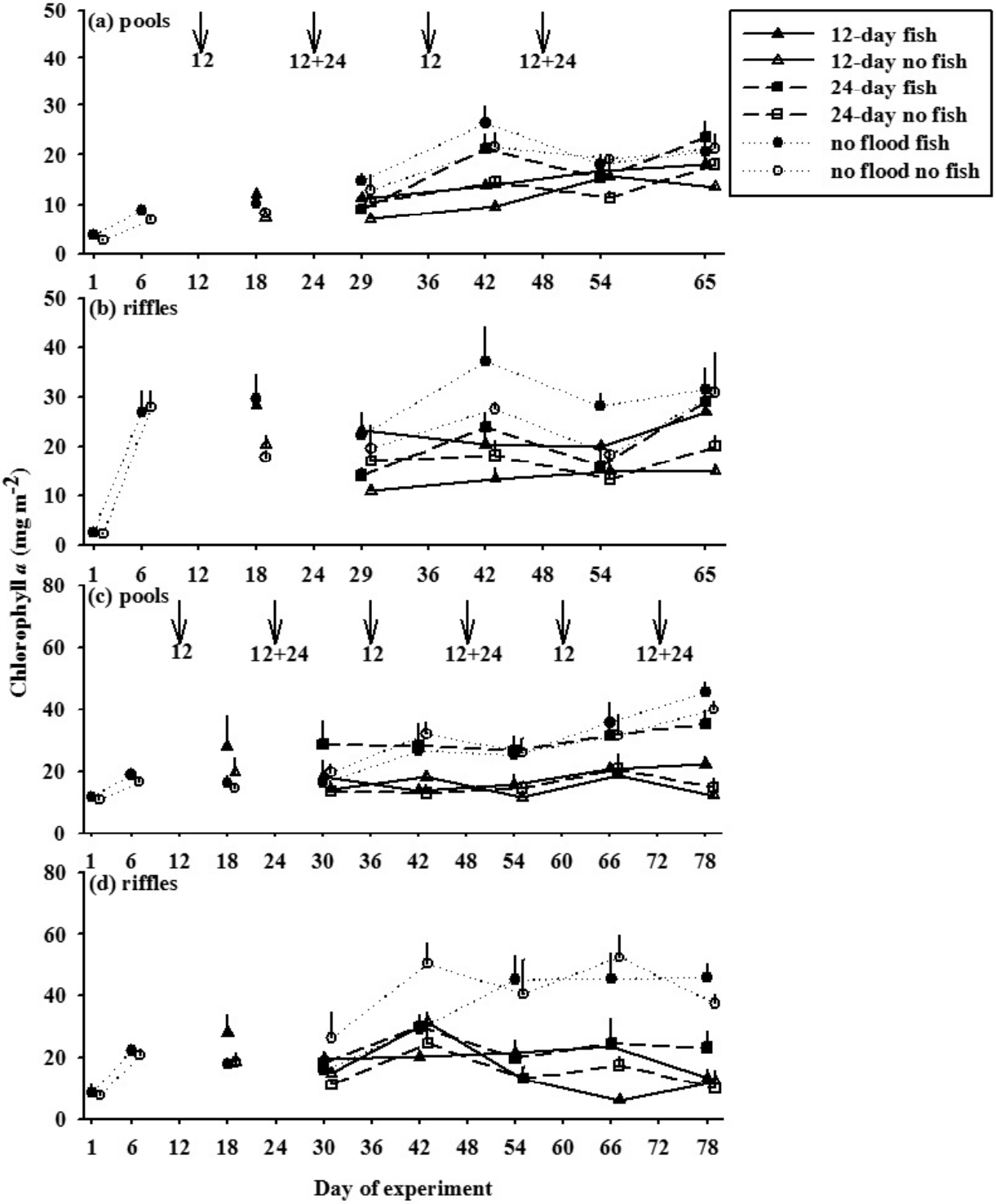


Figure 3.5. Mean mass (+ SE) of total fine particulate organic matter (FPOM) in experimental stream pools with (filled symbols) and without (open symbols; offset 1 day later) fish in five size classes during the dace study: (a) >500 μm, (b) 499-250 μm, (c) 249-180 μm, (d) 179-100 μm, and (e) 99-1 μm.

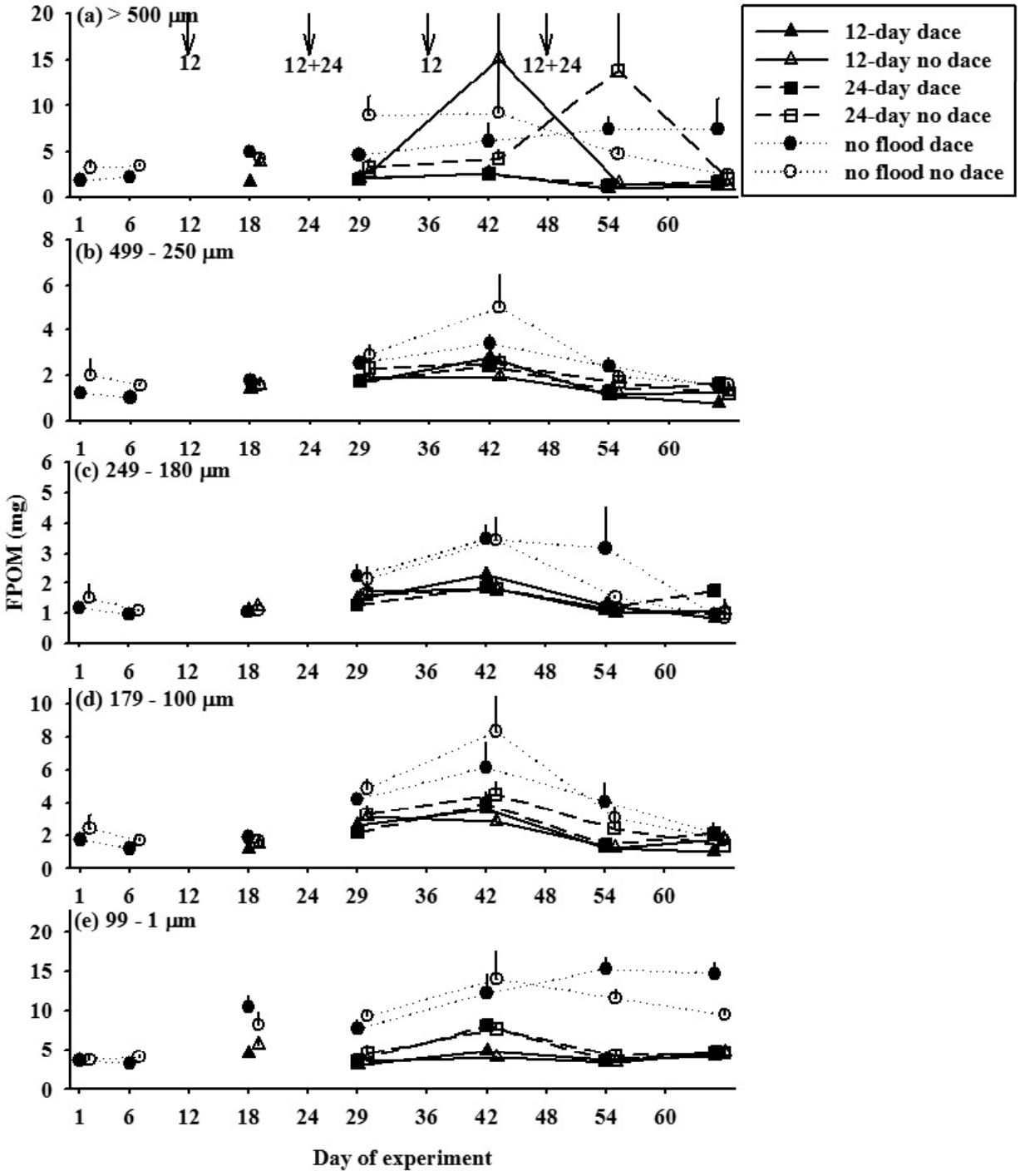


Figure 3.6. Mean mass (+ SE) of total fine particulate organic matter (FPOM) in experimental stream riffles with (filled symbols) and without (open symbols; offset 1 day later) fish in five size classes during the dace study: (a) >500 μm, (b) 499-250 μm, (c) 249-180 μm, (d) 179-100 μm, and (e) 99-1 μm.

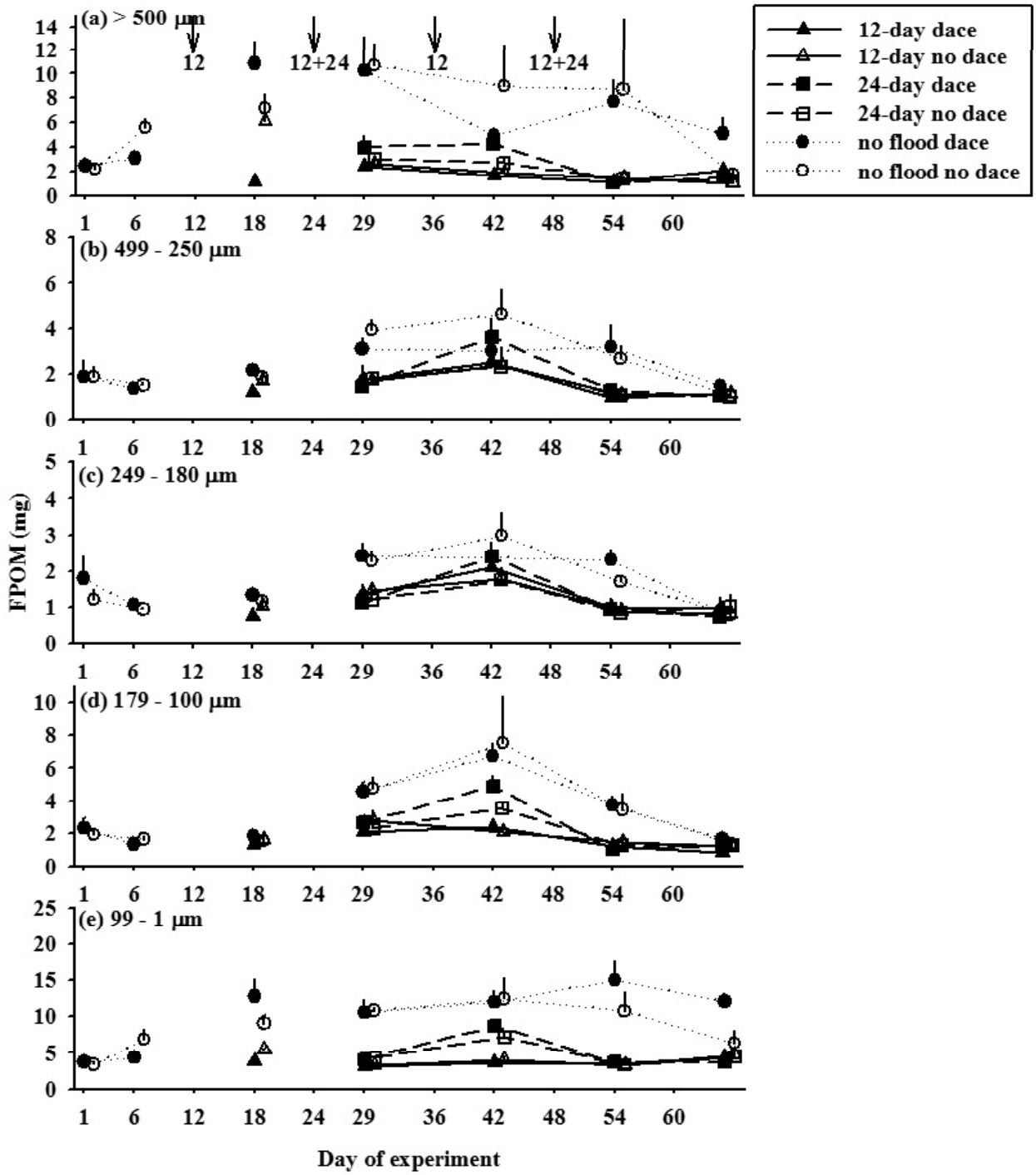


Figure 3.7. Mean mass (+ SE) of total fine particulate organic matter (FPOM) in experimental stream pools with (filled symbols) and without (open symbols; offset 1 day later) fish in five size classes during the shiner experiment: (a) >500 μm, (b) 499-250 μm, (c) 249-180 μm, (d) 179-100 μm, and (e) 99-1 μm.

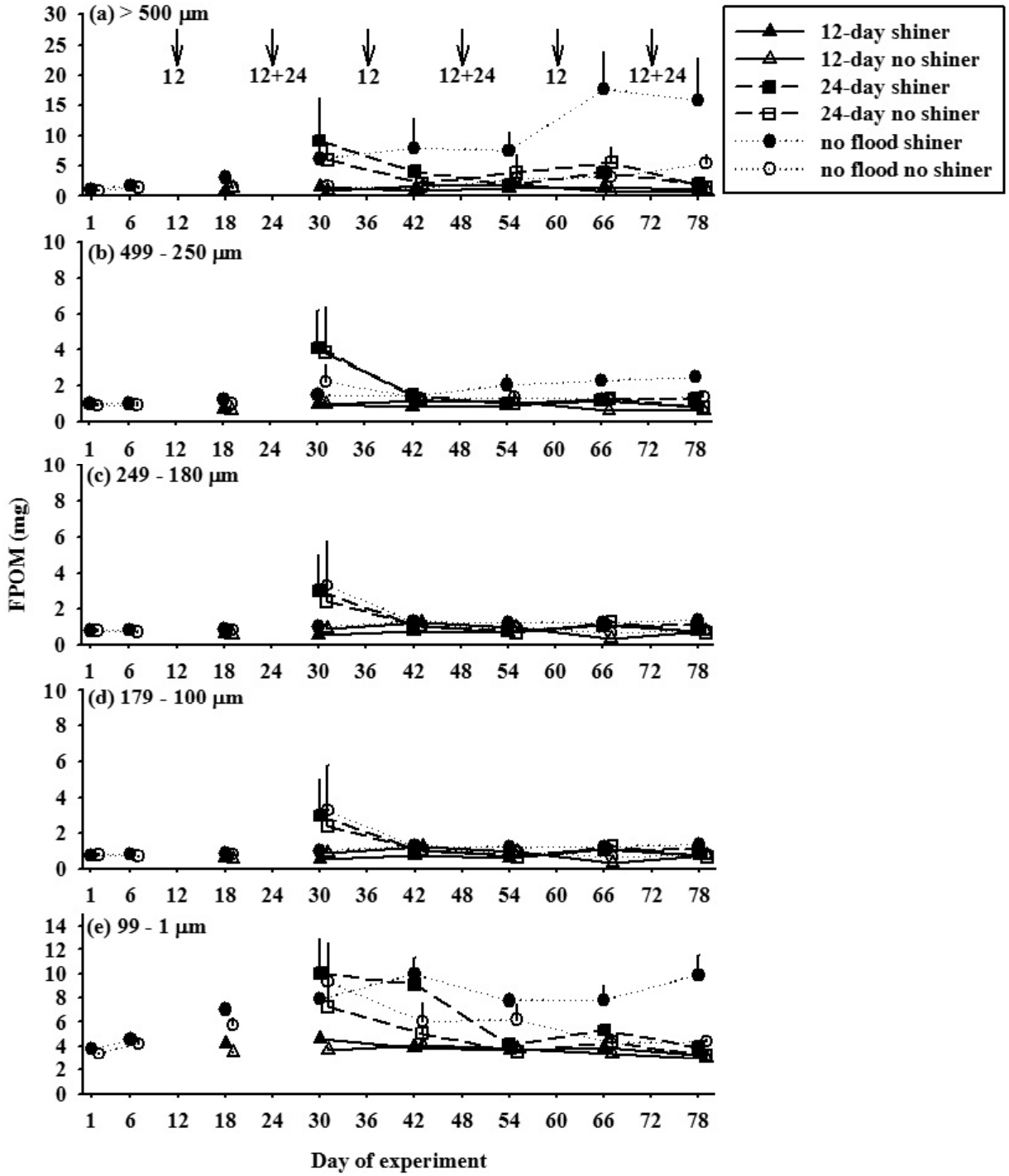


Figure 3.8. Mean mass (+ SE) of total fine particulate organic matter (FPOM) in experimental stream riffles with (filled symbols) and without (open symbols; offset 1 day later) fish in five size classes during the shiner experiment: (a) >500 μm, (b) 499-250 μm, (c) 249-180 μm, (d) 179-100 μm, and (e) 99-1 μm.

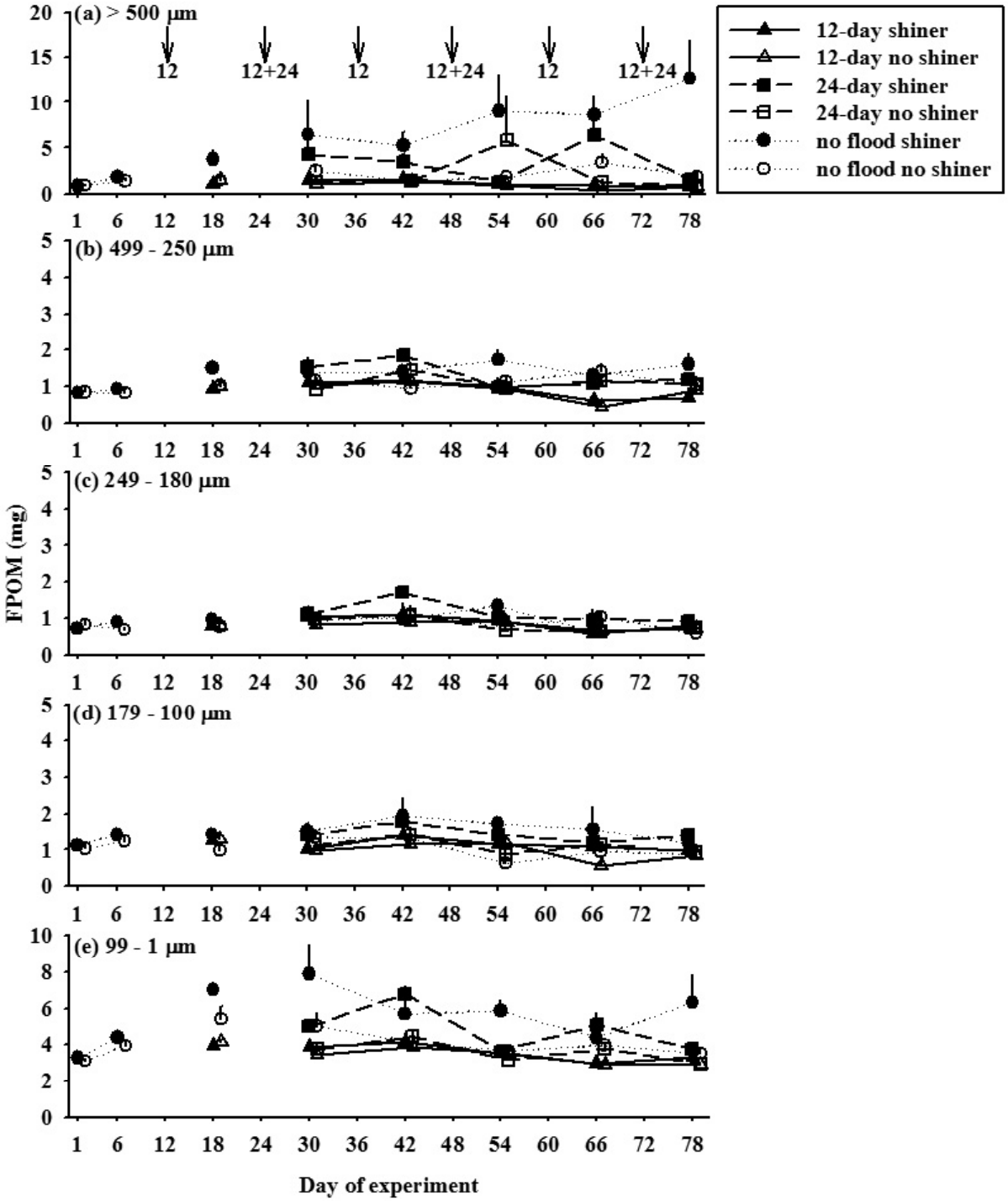


Figure 3.9. Mean densities (+ SE) of (a) Chironomidae, (b) microcrustacea, (c) Oligochaeta, and (d) *Physa* / *Physella* spp. in experimental stream pools with (closed symbols) and without (open symbols; offset 1 day later) dace.

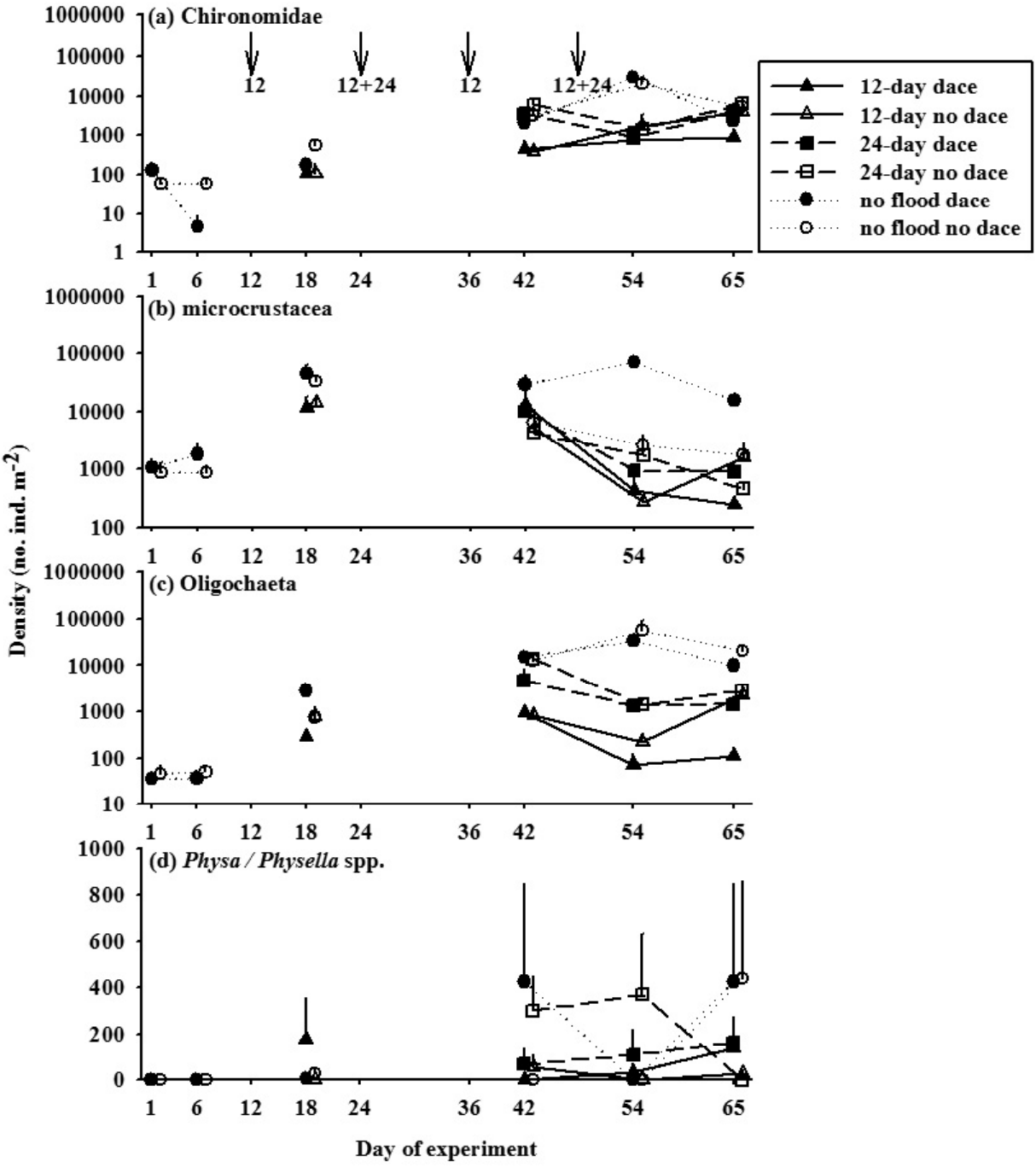


Figure 3.10. Mean densities (+ SE) of (a) Chironomidae, (b) microcrustacea, (c) Oligochaeta, and (d) *Physa* / *Physella* spp. in experimental stream riffles with (closed symbols) and without (open symbols; offset 1 day later) dace.

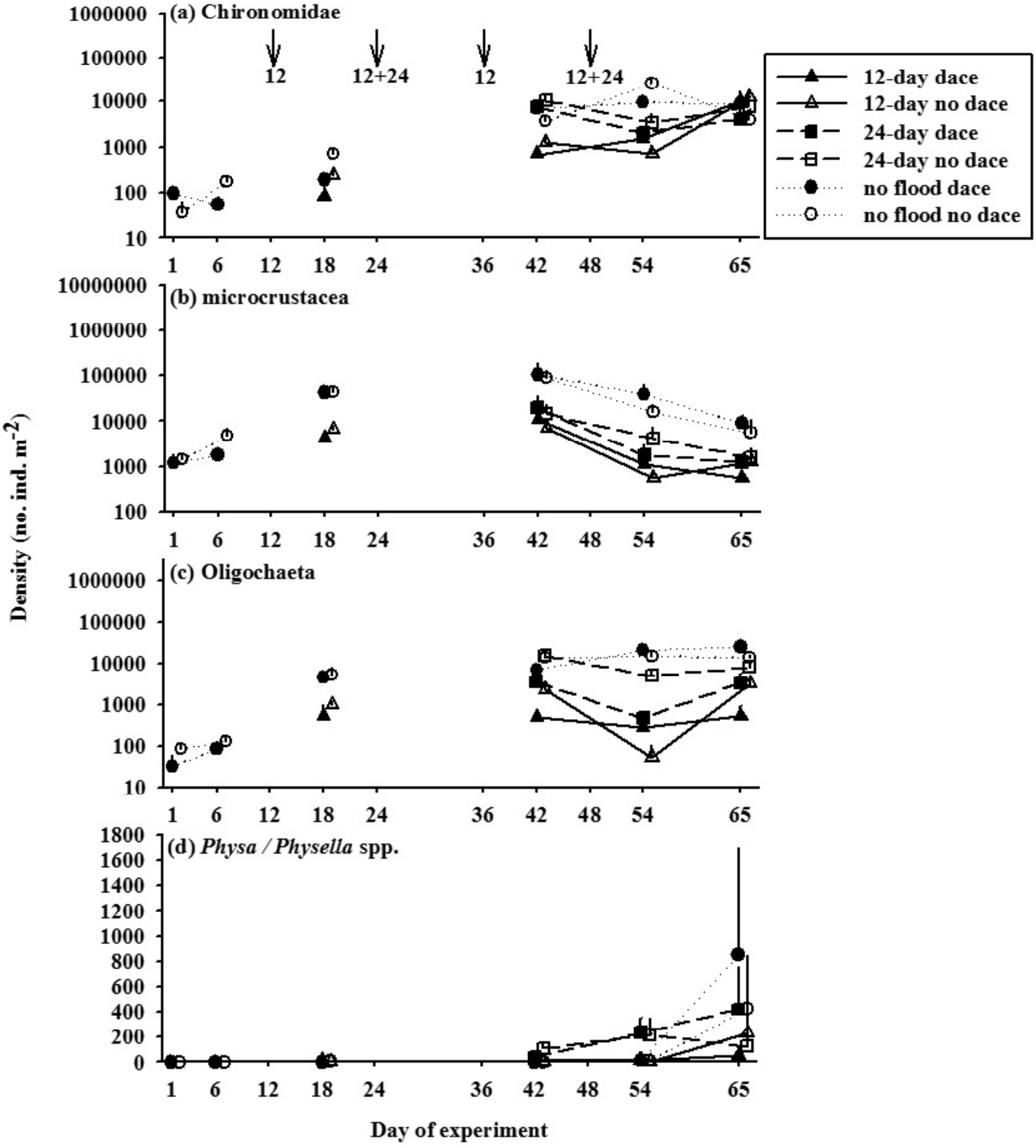


Figure 3.11. Mean densities (+ SE) of (a) Chironomidae, (b) microcrustacea, (c) Oligochaeta, and (d) *Physa* / *Physella* spp. in experimental stream pools with (closed symbols) and without (open symbols; offset 1 day later) shiners.

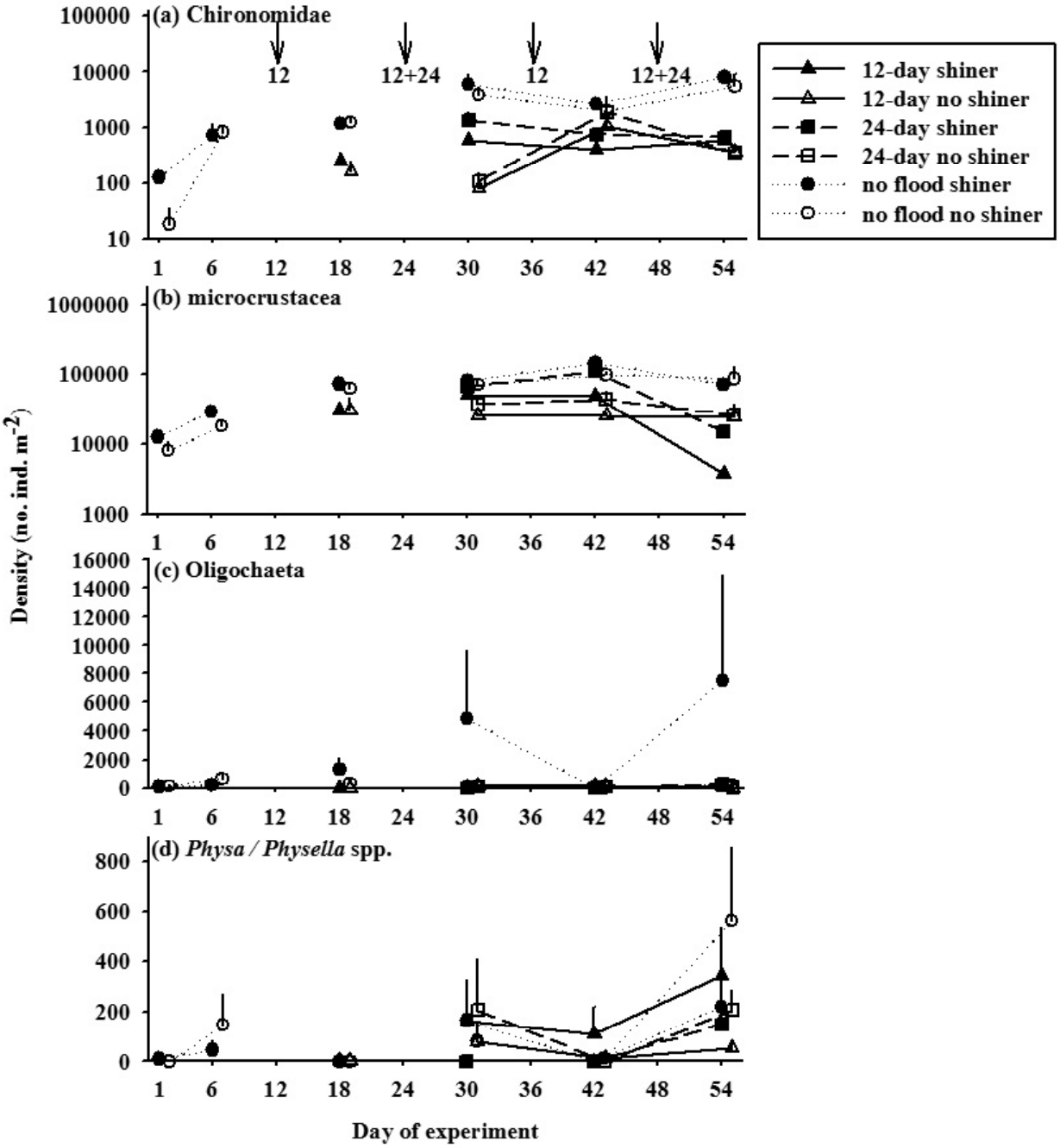


Figure 3.12. Mean densities (+ SE) of (a) Chironomidae, (b) microcrustacea, (c) Oligochaeta, and (d) *Physa* / *Physella* spp. in experimental stream riffles with (closed symbols) and without (open symbols; offset 1 day later) shiners.

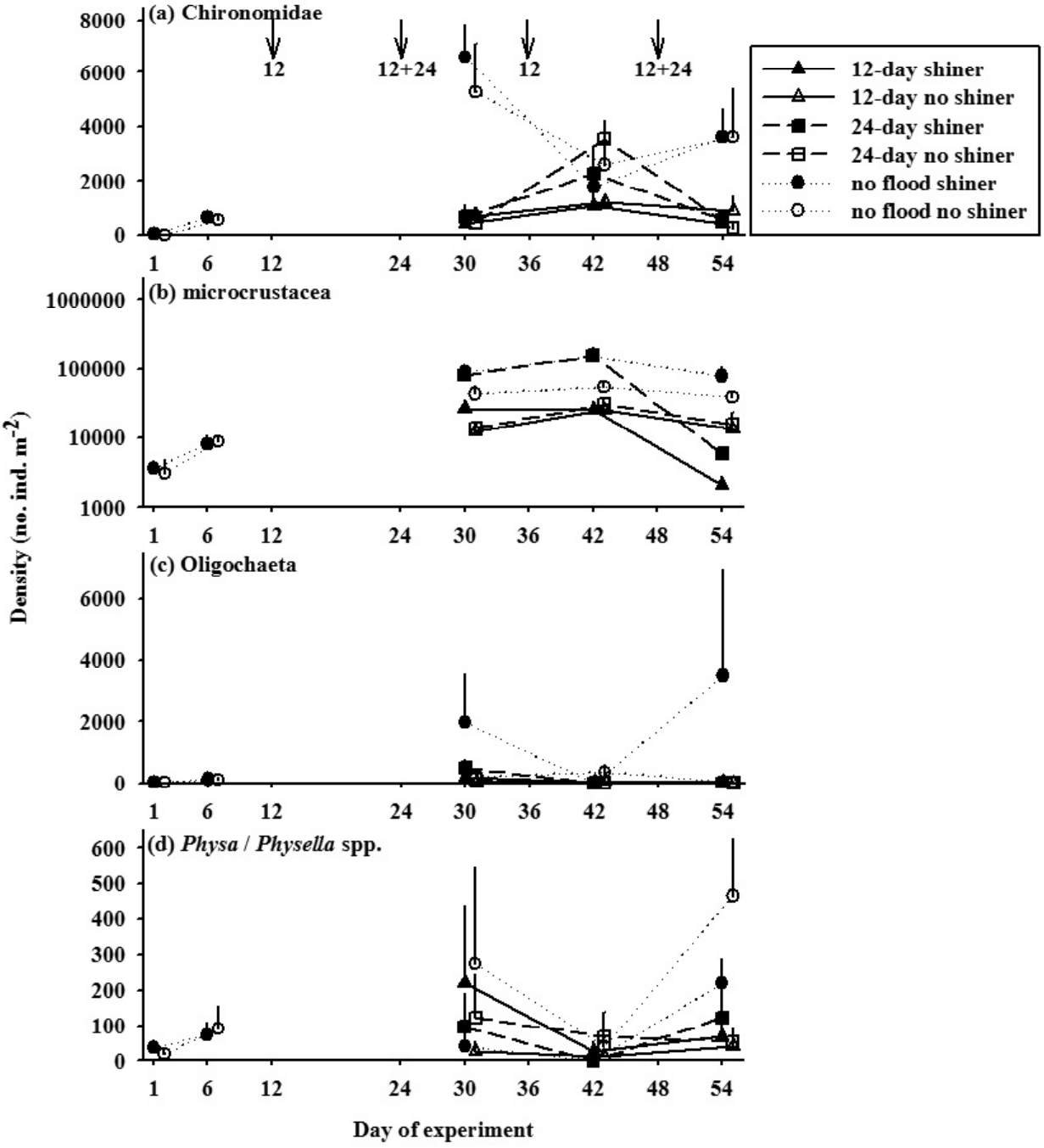


Figure 3.13. GPP measured in recirculating chambers on substrate baskets incubated during the field experiment in 20 Kings Creek pools.

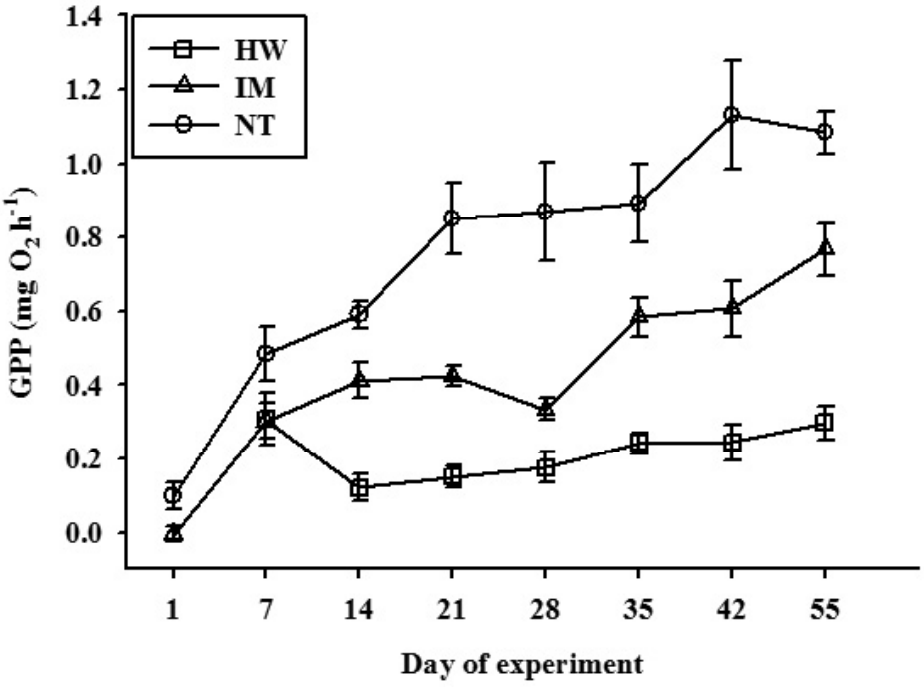


Figure 3.14. Algal biomass on substrate baskets collected from 20 Kings Creek pools.

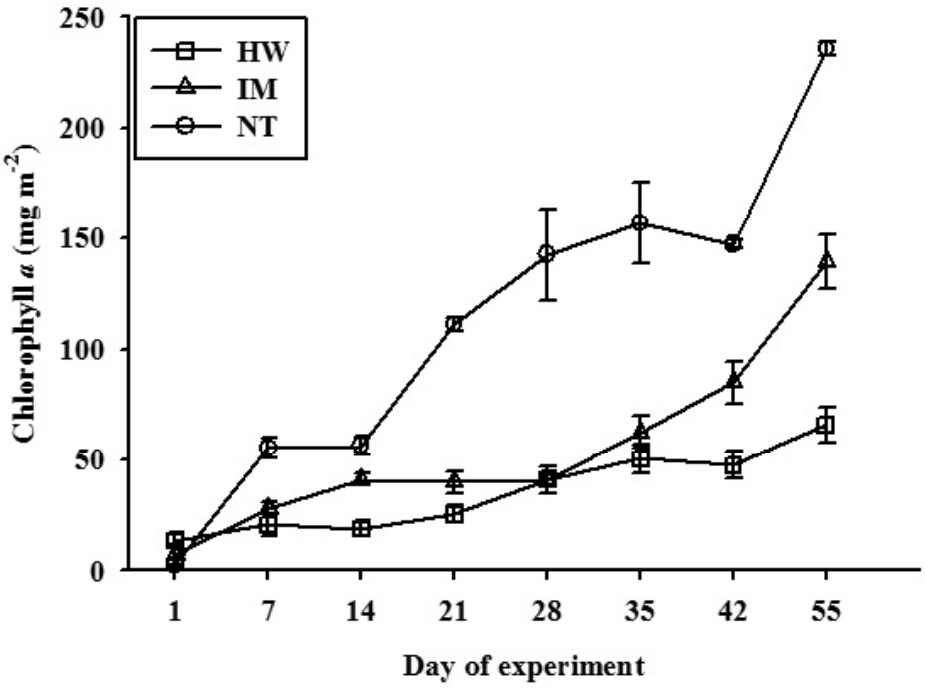


Figure 3.15. Uptake rates of ammonium in recirculating chambers by substrate baskets collected from 20 Kings Creek pools.

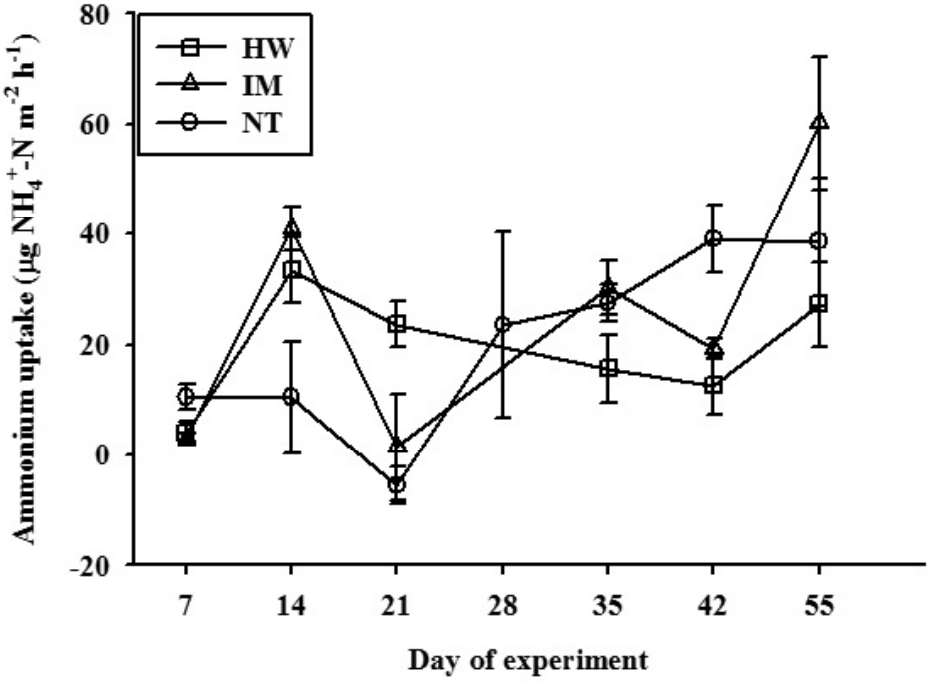
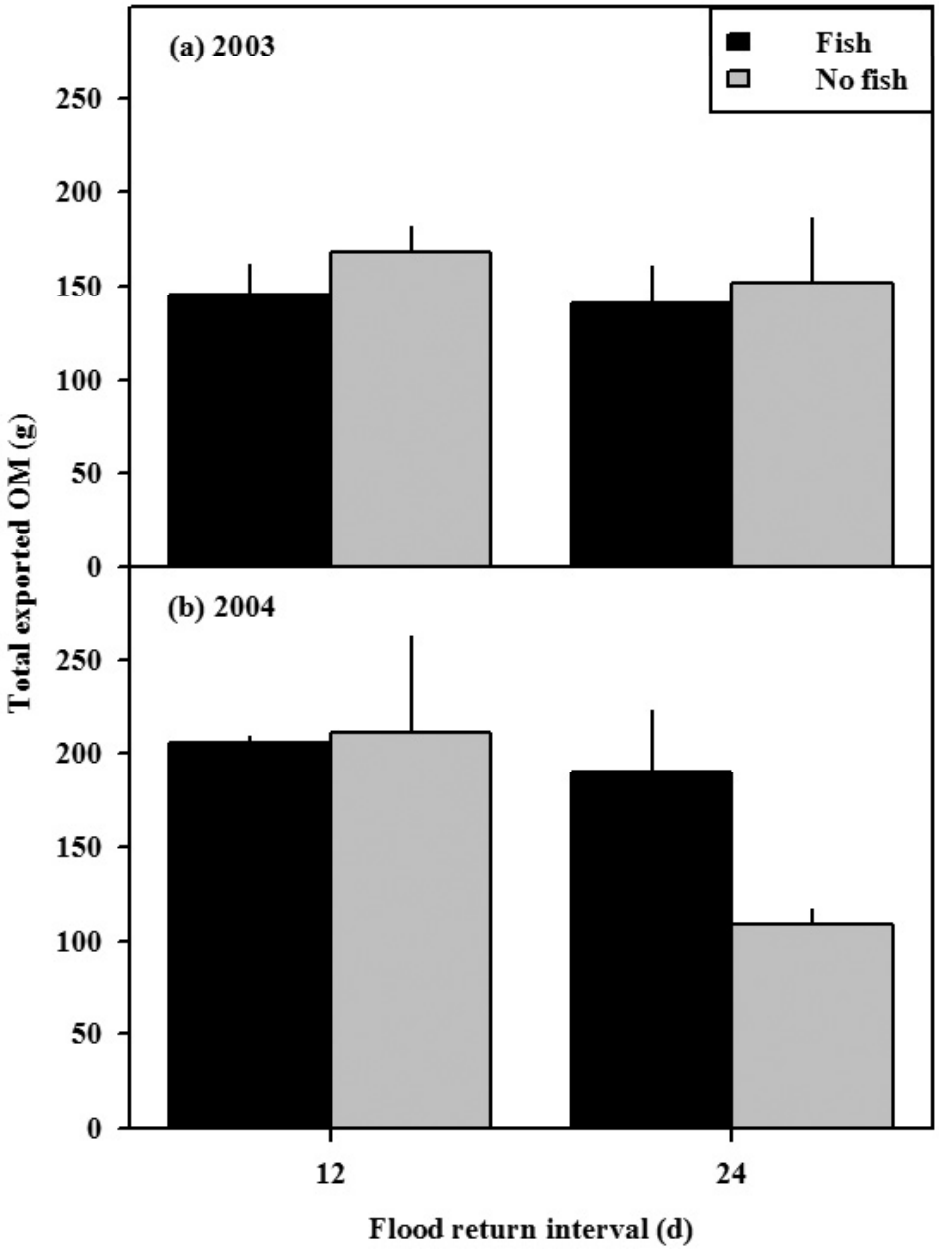


Figure 3.16. Mean mass (+ SE) of exported particulate organic matter (FPOM) during flooding in 24 experimental streams with (black bars) and without (grey bars) fish in (a) dace and (b) shiner studies.



CHAPTER 4 - CONSEQUENCES OF GRAZER LOSS ON PRAIRIE STREAM ECOSYSTEM FUNCTION

Katie N. Bertrand

ABSTRACT

I tested the overlapping effects of three common grazers on stream ecosystem structure and function in experimental stream mesocosms by either removing them from a community containing a full complement of grazers or evaluating their effects across a range of variable densities. The presence of southern redbelly dace (*Phoxinus erythrogaster*), a grazing minnow, and crayfish (*Orconectes nais*), a grazing decapod, was experimentally manipulated, whereas variation in grazing snail abundance was tested with analysis of covariance. Ecosystem structure was quantified as algal filament length, algal biomass, size fractionation of fine particulate organic matter (FPOM), algal assemblage structure, and invertebrate assemblage structure. Ecosystem function was assessed using gross and net primary productivity, respiration, nutrient uptake, and nutrient limitation. Significant effects of grazer removal included an increase in nutrient limitation when crayfish were removed and idiosyncratic effects of dace and crayfish removal on abundance of size fractions of FPOM and invertebrate assemblage structure. The general lack of response to herbivore diversity is consistent with the effects of herbivore diversity on ecosystem function in estuary mesocosms, but could also be related to the spatial and temporal scale at which my study was conducted or the context of physical conditions present during the experiment.

INTRODUCTION

Species loss is a global phenomenon that is accelerating in recent decades (Millenium Assessment 2005; Balvanera et al. 2006) because of global climate change, altered land use patterns, altered biogeochemical cycles, and the introduction of nonnative species (Loreau 2000). In many situations, extinction is a non-random result of these anthropogenic disturbances, and the outcome of continued species loss is not well-understood. Traits of surviving species in altered communities structured by resource partitioning or facilitation will determine the functional consequences of these extinctions (Gross and Cardinale 2005). In spite of the gaps in current understanding, accumulating evidence links biodiversity and ecosystem function and substantiates the argument for conserving biodiversity (Hector et al. 2001).

Whereas several studies have examined the effects of microconsumer biodiversity on ecosystem function at small spatial scales (e.g., Lawton et al. 1993), few studies have investigated multiple trophic level systems or the effect of biodiversity within consumer functional groups of streams. Within aquatic systems, Covich et al. (2004) reviewed 18 studies of the effects of benthic biodiversity on ecosystem function, of which only 8 were stream studies, and none included gastropods, decapods, or fishes. Furthermore, only three functional groups were considered in these 8 studies: decomposers (1), filter-feeders (2), and shredders (5). Although the ecosystem effects of aquatic grazers have been well characterized for many taxa, the effects of diversity within the grazer functional feeding group is understudied, with a few exceptions in marine systems. In estuary mesocosms, isopod and amphipod diversity did not affect eelgrass, periphyton, or herbivore production (Duffy et al. 2001). However, in marine microcosms, consumer richness was associated with reduced algal biomass and increased

consumer biomass (Gamfeldt et al. 2005). These contrasting studies make it difficult to extrapolate these results to the role of herbivore diversity in freshwater streasms.

Whereas ecological stability may depend more on the diversity of functional groups than the species diversity within functional groups, species within those groups may respond to environmental cues at different spatial and temporal scales (Peterson et al. 1998). That is, if two or more grazers are functionally redundant (*sensu* Lawton 1994) but use different habitats, the loss of one grazer from the community would potentially alter ecosystem function. For example, many grazing aquatic insects (e.g., mayflies) are found at substantially higher densities in riffle, than in pool habitats, because the faster water velocities and shallower water provide greater concentrations of dissolved oxygen (Cummins and Merritt 1995). In contrast, grazing minnows are typically found in greater densities in pool habitats, because riffles that separate the pools are too shallow for fish passage and may expose fish to avian predators (Power et al. 1985). In addition to partitioning longitudinal habitats, grazer size and motility also may play a role in resource partitioning. Larger, more motile vertebrate grazers such as cyprinids, are predicted to graze on longer filaments in the algal overstory, whereas smaller grazers (e.g., snails) graze more effectively on the algal understory (Vaughn et al. 1993; Steinman et al. 1987). Grazers also may perform similar functions over different temporal scales, in that species with shorter generation times may be able to recolonize and restore the grazing function more rapidly following a disturbance than larger, longer-lived taxa. Peak abundances of different grazer taxa also may vary depending upon their timing of reproduction. Thus, although they may perform similar ecological functions, it is important to consider the effects of species loss within the grazer functional feeding group because the loss of a species may eliminate existing complementarity in the community and potentially change ecosystem function.

My primary objective was to investigate the functional effects of species loss in the grazer functional feeding group of prairie stream ecosystems. In open-canopied prairie streams, where primary production dominates total respiration, autochthonous production plays a dominant role in energy flow through the system. Grazers are closely associated with primary producers, often responsible for regulating their abundance, and in prairie streams, they potentially affect ecosystem functioning through their consumption of primary production. Grazing minnows such as *Phoxinus erythrogaster* (southern redbelly dace), crayfish (*Orconectes* spp.) and snails (*Physa* and *Physella* spp.) are present in varying abundance but are typical occupants of prairie streams. Using these three commonly abundant grazers from nearby Kings Creek, on the Konza Prairie Biological Station, I tested the redundancy of a grazing minnow, a crayfish, and snails. If these species were largely similar in the ecological roles they performed, and are able to compensate for the loss of a member of that group, I expected to find no response of ecosystem structure and function to grazer diversity (Loreau 2000). However, if one species in the grazer assemblage performed the majority of the measured ecosystem function (e.g., drivers and passengers hypothesis), I would expect significant differences in ecosystem processes as result of removing the "driver" species from the grazer assemblage (Walker 1992).

METHODS

Study design

Eighteen experimental streams located on the Konza Prairie Biological Station (KPBS) in north central Kansas, USA were used to test the effects of grazer species loss on ecosystem processes. Each stream consisted of a 2.54 m^2 pool connected to a 0.84 m^2 riffle. The basic design of these streams is given in Matthews et al. (2006). Water was supplied by a low-nutrient

(NO_3^--N < 100 μg L^{-1}) natural spring until day 33, when drought conditions necessitated the use of higher-nutrient well water (NO_3^--N ≈ 2000 μg L^{-1}) through the end of the experiment. Water was recirculated with electric trolling motors creating a mean discharge of 2.0 L s^{-1}. 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. Streams were filled three weeks prior to the beginning of the experiment, and each stream was inoculated one week prior to the beginning of the experiment with a slurry of benthos from nearby Kings Creek to stimulate algal growth.

Experiments began after scouring the substrata with a high-pressure hose to homogenize streams. After 10 minutes of scouring, streams were rapidly drained through a 13 cm drain hole in the bottom of each pool. Streams were immediately refilled with new spring water after scouring was complete. This procedure was sufficient to remove the majority of the organic matter in the streams (e.g., overturned pebbles were dislocated from the riffle into the pool), and scour intensity was consistent across streams.

To test the effects of losing a member of the grazer assemblage in prairie streams, I compared ecosystem structure and function among experimental streams containing different grazer assemblages: a full assemblage (control; fish + crayfish + snails) and two reduced assemblages (the full assemblage minus fish or crayfish). In addition, analysis of covariance was used to test for interactive effects of these treatments and snail densities. I randomly assigned each of the three assemblages to six replicate experimental streams. All 18 streams were scoured and homogenized on 8 July 2005 (day 0 of experiment), and the last measurements were recorded on 25 August 2005 (day 48). Mean water temperature was 23°C (range: 20-25°C). Fish and crayfish were stocked at densities typical in Kings Creek, which ranged from 0 to 9

individuals m^{-2} (Evans-White 2001, Bertrand and Gido 2006, Franssen et al. 2006). To prevent escape of crayfish and fish from streams, I installed mesh hardware cloth coverings at the upstream and downstream ends of each stream. Streams were observed regularly for mortalities, and dead crayfish or dace were replaced immediately. Five plastic mesh baskets (10 x 10 x 10 cm) were filled with pebbles (16-64 mm dia.) and incubated in the pool of each stream to allow colonization by algae and invertebrates. Baskets were removed for measurement of ecosystem function in recirculating chambers.

Ecosystem function measurements

Gross primary productivity (GPP), net primary productivity (NPP), and respiration (R) in experimental streams were based on diurnal changes in dissolved oxygen measurements from YSI 600XLM sondes (Yellow Springs Instruments, Inc.) using the open-system single-station approach (Bott 1996). Water was recirculated at the same velocity and the bed-form was similar in all experimental units so turbulence-induced aeration was similar across experimental stream channels. Reareation was estimated using the surface renewal model, which is calculated from velocity (V, in cm s^{-1}) and mean depth (H, in cm) using the formula

$$f_{(20°C)} = 50.8\ V^{0.67}\ H^{-0.85} \quad (1)$$

(Owens 1974). The flow-through rates were the same for all experimental units leading to an approximate turnover time of 13 hrs. Because of the recirculating design of the experimental streams, I estimated that the effective channel length (i.e., discharge/inflow * length of the experimental stream) was approximately 1700 m. The prolonged exposure to stream biota to recirculated water assured that diurnal changes in water oxygen concentration reflected biotic processes in these stream units. NPP was estimated by averaging the mean hourly rate of R at night (from 2300 – 0400 hours) and the mean hourly rate of production during day (from 0800 –

1600 hours), whereas GPP was estimated by adding the mean hourly rate of R at night to the mean daytime production. Sondes were deployed in six streams for 24h then transferred to another stream, such that metabolism in all eighteen experimental streams was measured over a period of three days. GPP was estimated for each stream at the conclusion of the experiment between days 45 and 47.

Primary productivity also was estimated from substrate baskets in recirculating chambers. Four baskets were selected from each of eight pools once per day from days 45 through 47 and returned to the laboratory in moist, sealed plastic containers within 2 hours of collection. Baskets were analyzed for benthic metabolism (GPP, R, and NPP) and ammonium (NH_4^+) uptake rates in 22 L recirculating chambers (Dodds and Brock 1998) filled with streamwater collected from the experimental streams.

The baskets from each pool were sealed airtight in one of eight chambers, which incorporated an YSI oxygen probe, with water circulated at approximately 10 cm s^{-1}. Light was excluded from the chambers and the decline in dissolved oxygen concentration was measured for 1.5 hours. After measuring R, chambers were exposed to overhanging fluorescent grow lights (approximately 300 μmol quanta m^{-2} s^{-1} PAR) and dissolved oxygen monitored for another 1.5 hours. Respiration and NPP were calculated using linear regression as the change in water oxygen concentration over time per the total area of the three baskets (300 cm^2) and adjusted to mg O_2 m^{-2} hr^{-1}. Gross primary productivity was calculated as NPP + R.

Ammonium uptake rates were measured directly following metabolism measurements using substrata baskets. An ammonium spike was added to raise the water concentration by approximately 40 μg L^{-1} and filtered water samples were taken at 0, 15, 30, 45, 60, 90, and 120 minutes 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 and adjusted to μg NH_4^+-N m^{-2} s^{-1} and corrected for background concentrations (Dodds et al. 2002).

Nutrient limitation was assessed with nutrient diffusing substrata incubated in the center of each stream pool for 39 days and subsequently removed for analysis (Tank and Dodds 2003). I extracted chlorophyll *a* from the porous silica caps to estimate algal biomass by submerging caps in a 78˚C, 95% EtOH solution as described in Sartory and Grobelaar (1984). Extracts were analyzed for chlorophyll *a* with a Turner Model 112 fluorometer (Turner Designs Inc., Sunnyvale, CA, USA) using an optical configuration optimized for the analysis of chlorophyll *a* without phaeophyton interference (Welschmeyer 1995).

Ecosystem structure measurements

The length of the longest algal filament (vertical or horizontal) was measured along each of the same three transects used for collecting algal biomass (9 points per stream riffle, and 5 points per stream pool) on day 47.

Algal biomass was estimated as the concentration of chlorophyll *a* extracted from pebbles taken from study pools or experimental streams. Pebbles were collected on site, frozen within four hours of collection, and later analyzed for chlorophyll *a* as described above. To capture any spatial heterogeneity, I collected one pebble from each of three transects (upstream, middle, and downstream) in the riffles, and I collected four pebbles from the edges of the pools and one from the deep center of the pools on days 2, 7, 18, 31, and 47.

I used a modified core sampler that consisted of a 0.018 m^2 corer with an electric pump (0.1 L s^{-1}) to collect fine particulate organic matter (FPOM), invertebrates, and algae from the substrata. Substrata inside the corer were agitated by hand, and 9 L were pumped from each riffle or pool, homogenized in a bucket, and subsampled for fine particulate organic matter

(FPOM; 500 mL) and algal assemblage structure (AAS; 50 mL). Remaining invertebrates and detritus in the bucket were concentrated on a 250 μm sieve, preserved in formalin, and later identified to order, family, or genus. Fine particulate organic matter samples were preserved in 5% formalin, and dry as well as ash-free dry mass (AFDM) was measured for five size classes: >500 μm, 500-250 μm, 249-180 μm, 179-100 μm and 99-1 μm. I took separate core samples from both the riffle and the pool on days 2, 7, 18, 31, and 47. Algal assemblage structure samples also were preserved in formalin and later categorized into four general taxonomic groups (unicellular green, filamentous green, diatom, or cyanobacteria). The first 100 algal cells that intersected the ocular transect were placed in these categories.

At the conclusion of the experiment, I preserved at least two individual *Phoxinus* and at least one crayfish captured from each experimental stream to later characterize diet. Diet items in the foregut of *Phoxinus* were identified and enumerated using a transect method similar to the procedure for quantifying algal assemblage structure; we categorized the first 100 algal cells as filamentous green algae or diatoms (unicellular green and cyanobacteria were absent or in very low abundance), and noted the occurrence of animal matter. Diet items in the crayfish stomach were identified using a stereomicroscope and the percent of total diet volume that each item comprised was recorded.

Statistical analysis

ANCOVA, with snail density (Table 1) as the covariate, was used to test for differences among treatments in algal filament length, wholestream metabolism (i.e., NPP, R, and GPP), basket metabolism (i.e., NPP, R, and GPP), basket nutrient uptake, and the concentration of chlorophyll *a* on nutrient diffusing substrata. The overall ANCOVA test was followed with Bonferroni *post hoc* comparisons among grazer assemblages. Using repeated-measures

ANCOVA with sample date as the repeated factor, I tested for grazer assemblage effects on ecosystem structure (including algal biomass and FPOM size fractionation) over time in the experimental streams. I followed the overall repeated-measures ANCOVA with Tukey *post hoc* comparisons among grazer assemblages. Levene's test was used to check for heterogeneity of error variances among treatment groups and any necessary transformations were applied to correct heteroscedasticity. Discriminant function analysis (DFA, SPSS 2001), discriminated among grazer assemblage treatments using: (1) algal assemblage structure and (2) invertebrate assemblage structure. Stepwise model entry was used to identify taxa responding to the grazer assemblage structure treatments, and cross-validated classification was used to predict group membership. The analyses were based on log-transformed abundances of invertebrates (i.e., number of individuals per core) or arcsin square-root transformed proportional abundances of algae. Only invertebrates that occurred in more than 10% of samples were included in the analysis.

RESULTS

Whereas no crayfish were found dead during the experiment, I was unable to recover the majority of crayfish from the experimental streams (mean = 13% of initial stocking). In an experiment conducted in these streams in fall 2005, an average of 25% of the crayfish were recovered from experimental streams, but the number recovered was significantly associated with initial stocking density ($r^2 = 0.63$, $P < 0.01$) (Bengtson et al., in prep). Although I cannot rule out mortality or escape, it is likely the deep substrate (> 50 cm in some locations) and complexity of the experimental stream units limited my ability to recover crayfish. I successfully recovered the majority (mean = 57%) of the dace that were stocked into streams.

Ecosystem function

The snail density covariate was not significant and there was no significant difference among the two reduced assemblage treatments and the control assemblage in wholestream metabolism (i.e., NPP, R, and GPP), metabolism (i.e., NPP, R, and GPP) measured from substrate baskets in recirculating chambers, or ammonium uptake measured in recirculating chambers.

There was no effect of the snail covariate on algal biomass on nutrient diffusing substrata, but the no crayfish assemblage accumulated significantly more algal biomass on the combined nitrogen and phosphorus releasing substrata than the no fish assemblage (mean difference = 3.79 mg m^{-2} chlorophyll *a*; Bonferroni $P < 0.01$; Fig. 4.1).

Ecosystem structure

Neither grazer assemblage treatment nor the snail covariate affected algal filament length (Fig. 4.2), or algal biomass (Fig. 4.3). In riffles, there was no effect of the snail covariate or grazer assemblage treatment on abundance of any of the size fractions of FPOM (Fig. 4.4). In pools, there was no effect of the snail covariate, but grazer assemblage treatment did affect the abundance of 249 – 180 μm FPOM, where there was a significant interaction between day of experiment and grazer assemblage treatment (Fig. 4.5). On days 2 and 7, the greatest mass of this size fraction was found in the no fish assemblage, whereas on days 31 and 48, the greatest mass of this size class was found in the no crayfish assemblage on day 31.

Effects of grazer assemblage treatments on invertebrate assemblage structure varied between days 18 and 48 of the experiment and between riffles and pools. Invertebrate assemblage structure was numerically dominated in the experimental streams by zooplankton and dipteran larvae. Overall, DFA classified the no crayfish treatments most accurately (mean

correct classifications = 83%) followed by the no fish treatments (mean = 56%) and then the full grazer assemblages (< 50%; Table 2). In riffles on day 18, DFA revealed two taxa that discriminated among the three grazer assemblages: early-instar chironomids (Wilks' $\Lambda = 0.49$, $F_{2,14} = 7.17$, $P < 0.01$) and cyclopoid copepods (Wilks' $\Lambda = 0.28$, $F_{4,26} = 5.72$, $P < 0.01$) (Fig. 4.6). Early-instar chironomids were only found in 3 of the 6 no fish assemblage streams (mean = 46 m^{-2}; SD = 54 m^{-2}) as compared to full grazer assemblage streams (mean = 714 m^{-2}; SD = 1115 m^{-2}) and no crayfish assemblage streams (mean = 516 m^{-2}; SD = 430 m^{-2}), that each had at least one early-instar chironomid. In riffles on day 48, two taxa discriminated among the three grazer assemblages: baetid mayflies (Wilks' $\Lambda = 0.60$, $F_{2,15} = 5.01$, $P = 0.02$) and oligochaetes (Wilks' $\Lambda = 0.38$, $F_{4,28} = 4.34$, $P < 0.01$) (Fig. 4.7). In the absence of fish, baetid mayflies and oligochates were approximately half as dense as that of the full grazer and no crayfish assemblages. In pools on day 18, DFA did not identify any taxa that discriminated among the treatments (no variables were selected). In pools on day 48, two taxa discriminated among the three grazer assemblages: chironomids (Wilks' $\Lambda = 0.61$, $F_{2,15} = 4.75$, $P = 0.03$) and chydorids (Wilks' $\Lambda = 0.39$, $F_{4,28} = 4.18$, $P < 0.01$) (Fig. 4.8). Chironomids were more abundant in the no crayfish assemblage streams (mean = 1400 m^{-2}; SD = 1116 m^{-2}) than they were in either the full grazer assemblage streams (mean = 192 m^{-2}; SD = 186 m^{-2}) or the no fish assemblage streams (mean = 220 m^{-2}; SD = 220 m^{-2}).

Algal assemblage structure was dominated by filamentous green algae and diatoms, but desmid green algae, unicellular green algae, and cyanobacteria also appeared consistently in the assemblage. Based on stepwise DFA, grazer assemblage structure did not affect algal assemblage structure (no variables were selected).

Grazer diet varied by species, but dace diet was dominated by filamentous green algae and diatoms (Table 3), which matched the proportions of algal taxa available for grazing. The majority of crayfish guts were empty, but one individual consumed aquatic nymphs (Table 4). I was unable to compare the diets of dace and crayfish after finding predominantly empty stomachs in the crayfish.

DISCUSSION

There was not a significant effect of the snail covariate on any of the measured response variables, despite densities of snails in the experimental streams that did not vary by treatment and ranged from 0 – 17130 individuals m^{-2} (mean = 1303 individuals m^{-2}), which exceeded densities from previous studies that found effects of snails (i.e., 200 – 1400 individuals m^{-2}; Hill et al. 1992; Rosemond 1993). This stands in contrast to other studies of snails (e.g., Steinman et al. 1987; Hill et al. 1992) that have reported significant reductions in algal biomass, biomass specific primary productivity, and changes in taxonomic composition and morphology of the primary producer assemblage. One explanation for the lack of effect of snails could be a perceived or real predation threat from the presence of other grazers, particularly crayfish (Turner 1997). There is some observational evidence to support this hypotheis: on day 13, I observed that there were very few snails in pools of streams with crayfish present. However, the density and biomass of snails across treatments suggests that crayfish were not effective predators.

Although there have been relatively few studies on crayfish effects in streams, Creed (1994) demonstrated that crayfish reduced biomass of filamentous green algae (*Cladophora* sp.), and Gelwick (2000) demonstrated that crayfish reduced algal filament lengths in stream pools. Either of these effects may inhibit grazing by other invertebrate herbivores (Nystroem et al.

1996). In contrast, crayfish in the experimental streams had no unique effect on algal biomass or algal filament length when compared to other grazer assemblages. Removal of crayfish may have been compensated by the presence of other grazers, but as with snails, the lack of a unique ecosystem response to crayfish removal could be explained by several other factors including insufficient densities to produce a measureable effect. Assuming the inability to recover crayfish was due to ineffective sampling, rather than mortality, densities in the experimental streams (2.3 crayfish m^{-2}) were within the range of natural densities (0.12 – 8.15 m^{-2}) observed in nearby Kings Creek (Evans-White and Dodds 2001).

The effects of grazing minnows in prairie streams have been relatively well documented in the literature. Studies of central stoneroller (*Campostoma anomalum*) demonstrated that grazing fishes have potentially strong effects on both ecosystem structure and function including reduced algal filament length, algal biomass, and mean particle size of organic matter as well as altered algal assemblage structure and primary productivity (Matthews 1998; Gelwick and Matthews 1992). Studies of *Phoxinus* demonstrated that these fishes decreased algal filament length and mean particle size of FPOM (Bertrand and Gido 2007). Additional studies in the context of varied flood frequencies demonstrated that *Phoxinus* actually increase algal biomass, presumably through their nutrient remineralization (Bertrand et al., in prep). In contrast, this study found no significant effect of removing *Phoxinus* from the grazer assemblage on algal filament length or algal biomass. Since fishes were stocked at the same densities as in the previous study by Bertrand and Gido (2007), densities were sufficient to find an effect. Moreover, short algal filaments lengths (< 5 cm) were typical of grazed treatments from previous experiments, compared to 19 cm in ungrazed treatments (Bertrand and Gido 2007). Thus, removal of *Phoxinus* may have been compensated by the presence of other grazers.

Given the spatial and temporal constraints of this experimental stream study, it appeared that variation in snail density or the removal of crayfish or dace had minimal effects on stream ecosystem structure or function. Because I used an additive design (i.e., I did not equalize biomass across grazer assemblage treatments), finding a lack of effect of grazer removal is synonymous with finding a lack of effect of decreased grazer biomass. In a study of the effects of grazing caddisflies on periphyton biomass, Anderson et al. (1999) found that the effect of grazers decreased with increasing grazer biomass. There were significant differences in periphyton biomass between grazed and ungrazed treatments, but the differences among varied levels of grazer biomass were small. Therefore, in prairie streams, ecosystem processes may depend on the presence of at least one grazer, but there may not be strong effects of removing one species from an assemblage with multiple grazers.

Grazer assemblage structure appeared to elicit idiosyncratic effects on nutrient limitation, distribution of FPOM size fractions, and macroinvertebrate assemblage structure. By removing crayfish from the grazer assemblage, algal growth on substrates supplemented with nitrogen and phosphorus increased, whereas removing dace from the assemblage decreased algal growth on substrates supplemented by nitrogen and phosphorus. Because the degree of limitation in the full assemblage was intermediate to those of the two reduced assemblages, it is uncertain what mechanism underlies the difference. However, since nutrient releasing substrates were unprotected from grazing by dace, crayfish, or snails, it's possible that the grazer assemblages directly removed algae from the substrates. It's also possible that under the low ambient nutrient concentrations (TN $\approx$ 100 $\mu g\ L^{-1}$; TP < 10 $\mu g\ L^{-1}$), identities of grazers in the assemblage affected nutrient limitation through grazer-specific excretion stoichiometry (Evans-White and Lamberti 2006).

Although grazers consume benthic algae, I only found an interactive effect of grazer assemblage structure and day of experiment on size fractionation of FPOM in pools for the 249 – 180 μm size class, which, on average, accounted for only 6% (range: 0 – 30%) of the total mass of FPOM. Similar to nutrient limitation, the mass of this size class in streams with the full grazer assemblage was intermediate to the two reduced grazer assemblages throughout the experiment, again making it difficult to predict what mechanism might be driving differences in ecosystem properties among grazer assemblages. Given the small proportional abundance of this size class, it seems possible that this was a spurious result.

Differences in invertebrate assemblage structure among the full and reduced assemblages suggest that grazer assemblage structure may have indirect effects on ecosystem processes over longer time intervals. Since crayfish are omnivorous, I expected that if crayfish were preferentially consuming invertebrates there would be a significant increase in the abundance of invertebrates in the no crayfish assemblage streams. However, there were no consistent effects of removing crayfish on invertebrate assemblage structure. For example, chironomid abundance helped discriminate among grazer assemblages in samples from day 18 riffles and day 48 pools, but they were consistently found in low abundance in the no fish assemblage streams, as opposed to the no crayfish assemblage streams. It is possible that the unexplained differences in invertebrate assemblage structure could translate into differences in other ecosystem processes (e.g., productivity and algal community structure) given time for additional generations to develop and ameliorate the differences in invertebrate assemblage structure.

Overall, I did not find sufficient evidence to reject the hypothesis that prairie stream grazers perform similar ecological roles under the spatial and temporal constraints of this experiment. Although this is a coarser spatial and temporal scale than those over which many

other studies of biodiversity and ecosystem function have been conducted (Covich et al. 2004), the importance of biodiversity is likely scale dependent (Peterson et al. 1998) and may not have been adequately represented in my study. It is possible that since benthic biodiversity effects are dependent on flow, nutrient limitation, light, and other physical characteristics in the stream, grazer biodiversity may be critical to ecosystem function under conditions other than those in which my study was conducted. Moreover, grazers vary greatly in body size and life history characteristics, and it is likely that r-selected species such as snails regenerate quickly following disturbances (e.g., floods), whereas longer-lived species such as fishes require more time to re-establish sufficient population sizes to produce grazing effects. Thus, in non-equilibrium prairie stream systems the effect of grazers will be continuous if snails are present early, and then crayfishes and fishes return later. In contrast, if one of these species were absent, ecosystem recovery post-disturbance might be drastically altered.

Table 4.1. Mean (and range) of snail densities from core samples and mean (and range) of snail densities and biomasses from substrata baskets across treatments (All = full grazer assemblage, NC = no crayfish assemblage, and NF = no fish assemblage) in 18 experimental streams on the Konza Prairie Biological Station.

Sample method	Day of experiment	Response variable	All	NC	NF
Core	18	Density (ind. m^{-2})	1812 (0 - 4008)	1876 (0 - 4392)	2608 (0 - 7906)
Core	48	Density (ind. m^{-2})	4209 (220 - 17130)	1766 (0 - 9663)	439 (0 - 1318)
Basket	34	Density (ind. m^{-2})	920 (0 - 2810)	520 (0 - 1650)	400 (0 - 870)
Basket	34	Biomass (g m^{-2})	290 (0 – 720)	273 (0 – 858)	159 (0 – 763)

Table 4.2. Summary of discriminant function analysis classifications into three grazer assemblage treatments (All = full grazer assemblage, NC = no crayfish assemblage, or NF = no fish assemblage) based on invertebrate data from 18 experimental streams on the Konza Prairie Biological Station. Values represent the percent of correct classifications using the stepwise procedure and "leave-one-out" cross-validation.

Habitat	Day of experiment	All	NC	NF
Riffle	18	17	83	83
Riffle	48	17	100	67
Pool	18	N/A	N/A	N/A
Pool	48	33	67	17

Table 4.3. Diet of *Phoxinus erythrogaster* collected from experimental stream mesocosms on the Konza Prairie Biological Station at the conclusion of the grazer assemblage study of summer 2005. Percentages of diet items represent the mean number of cells of each type per 100 total cells counted in each fish from grazer assemblage treatments (Trt) with all species present (ALL) and with crayfish removed (NC).

Trt	Species	N	% cyanobacteria	% desmid green algae	% filamentous green algae	% diatoms	Total invertebrates	Total fish with inverts in diet
All	dace	6	1	42	35	23	2	2
NC	dace	8	< 1	23	46	28	1	1

Table 4.4. Diet of *Orconectes nais* collected from experimental stream mesocosms on the Konza Prairie Biological Station at the conclusion of the grazer assemblage study of summer 2005. Diet is reported as percent occurrence, which is the percent of individuals in which the diet item was found, and as percent gut fullness, which is the mean number of grid cells that were filled by each type of diet item divided by the total number of grid cells filled by the entire diet of all individuals examined from grazer assemblage treatments (Trt) with all species present (ALL) and with fish removed (NF).

			Aquatic nymphs		Snails		Microcrustacea		Chironomids		Algae / detritus
Trt	species	N	% occur	% gut fullness	% occur	% gut fullness	% occur	% gut fullness	% occur	% gut fullness	% gut fullness
All	crayfish	5	0	0	0	0	1	1	0	0	99
NF	crayfish	2	50	3	50	90	0	0	50	1	0

Figure 4.1. Mean algal biomass (+ SE) grown on nutrient releasing substrates (C = control, N + P = nitrogen and phosphorus) in 18 experimental streams on the Konza Prairie Biological Station. Treatments included two reduced grazer assemblages (N=6; NC = no crayfish; NF = no fish), which were compared to a control (N=6; All = full grazer assemblage).

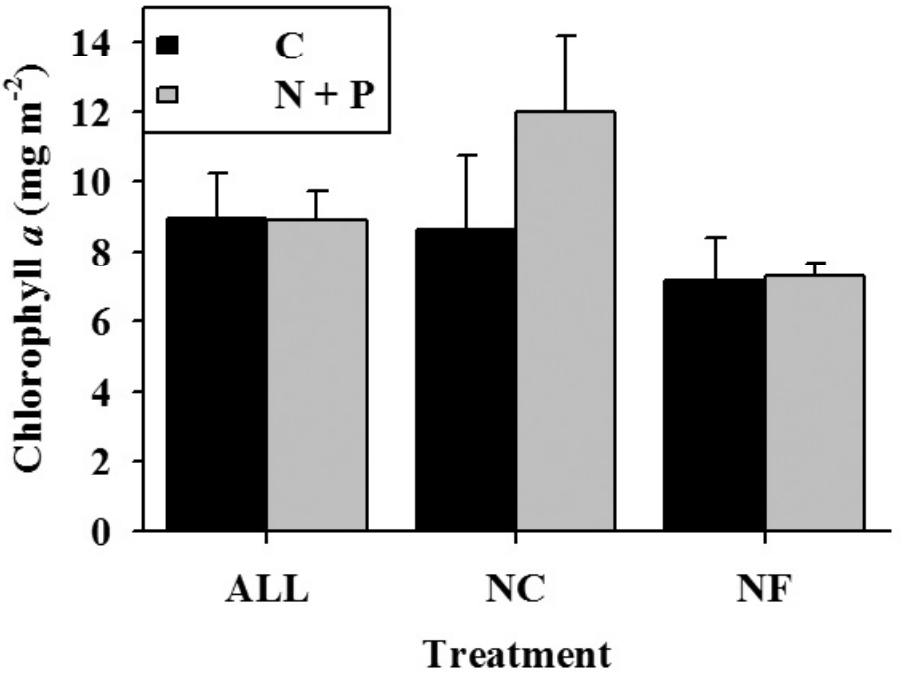


Figure 4.2. Mean algal filament length (+ SE) in 18 experimental streams on the Konza Prairie Biological Station. Treatments included two reduced grazer assemblages (N=6; NC = no crayfish; NF = no fish), which were compared to a control (N=6; All = full grazer assemblage).

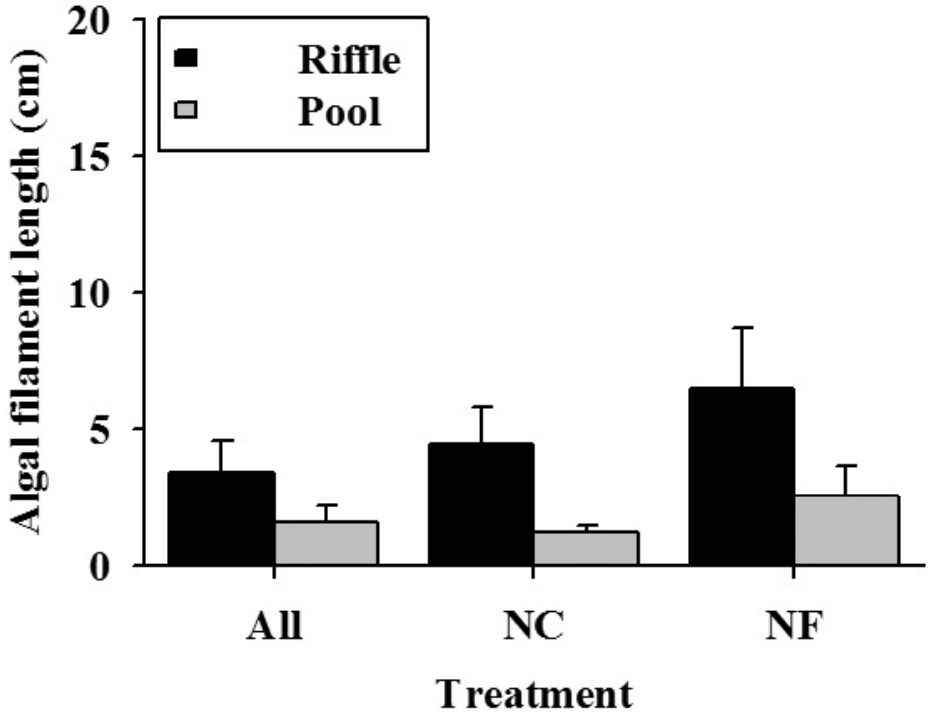


Figure 4.3. Mean algal biomass (+ SE) in riffles (a) and pools (b) in 18 experimental streams on the Konza Prairie Biological Station. Treatments included two reduced grazer assemblages (N=6; NC = no crayfish; NF = no fish), which were compared to a control (N=6; All = full grazer assemblage). Reduced grazer assemblages (open symbols) data points are offset ½ day later to improve visibility.

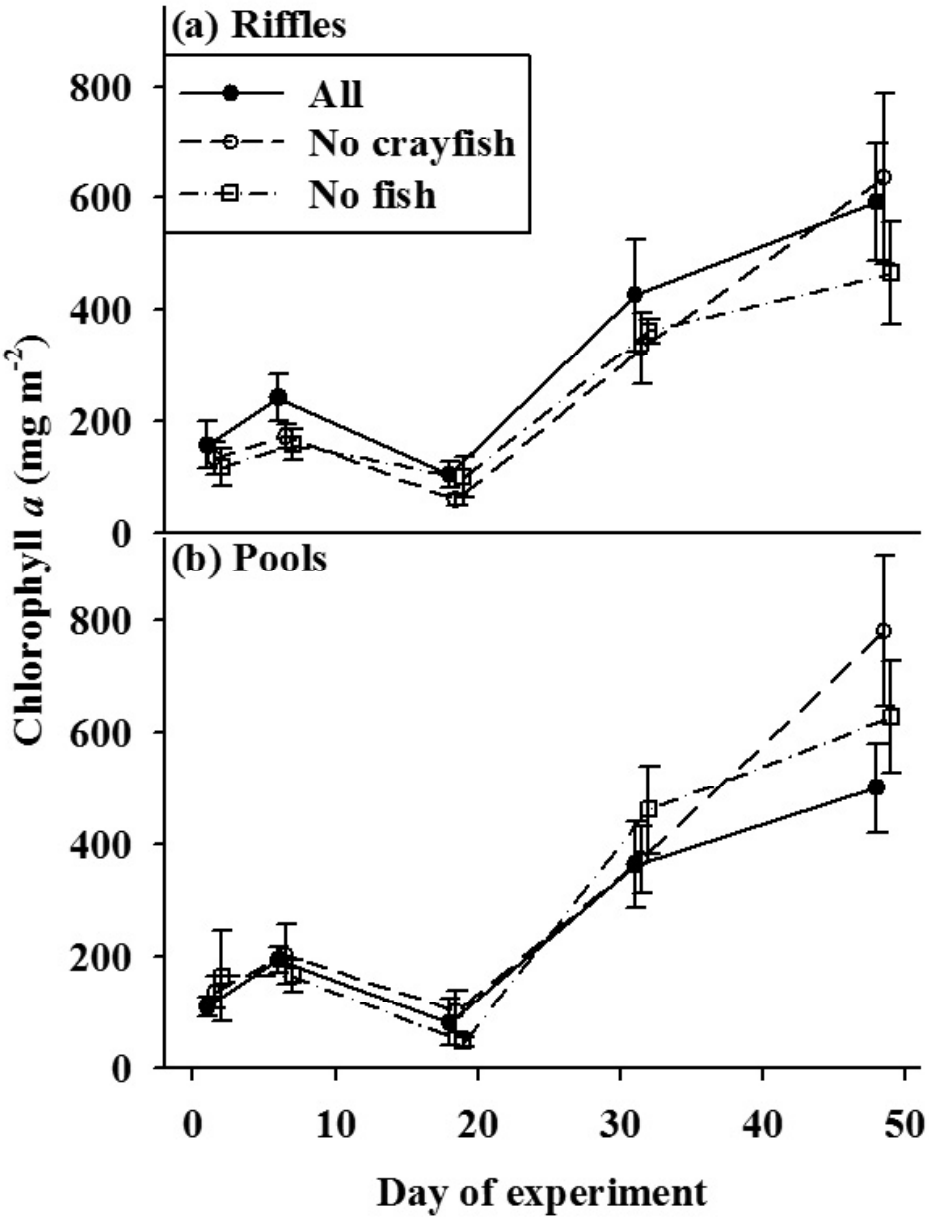


Figure 4.4. Mean fractions (+ SE) of fine particulate organic matter (FPOM) sized (a) > 500 µm, (b) 499 – 250 µm, (c) 249 – 180 µm, (d) 179 – 100 µm, and (e) 99 – 1 µm in riffles of 18 experimental streams on the Konza Prairie Biological Station. Treatments included two reduced grazer assemblages (N=6; NC = no crayfish; NF = no fish; open symbols; offset ½ day later), which were compared to a control (N=6; All = full grazer assemblage).

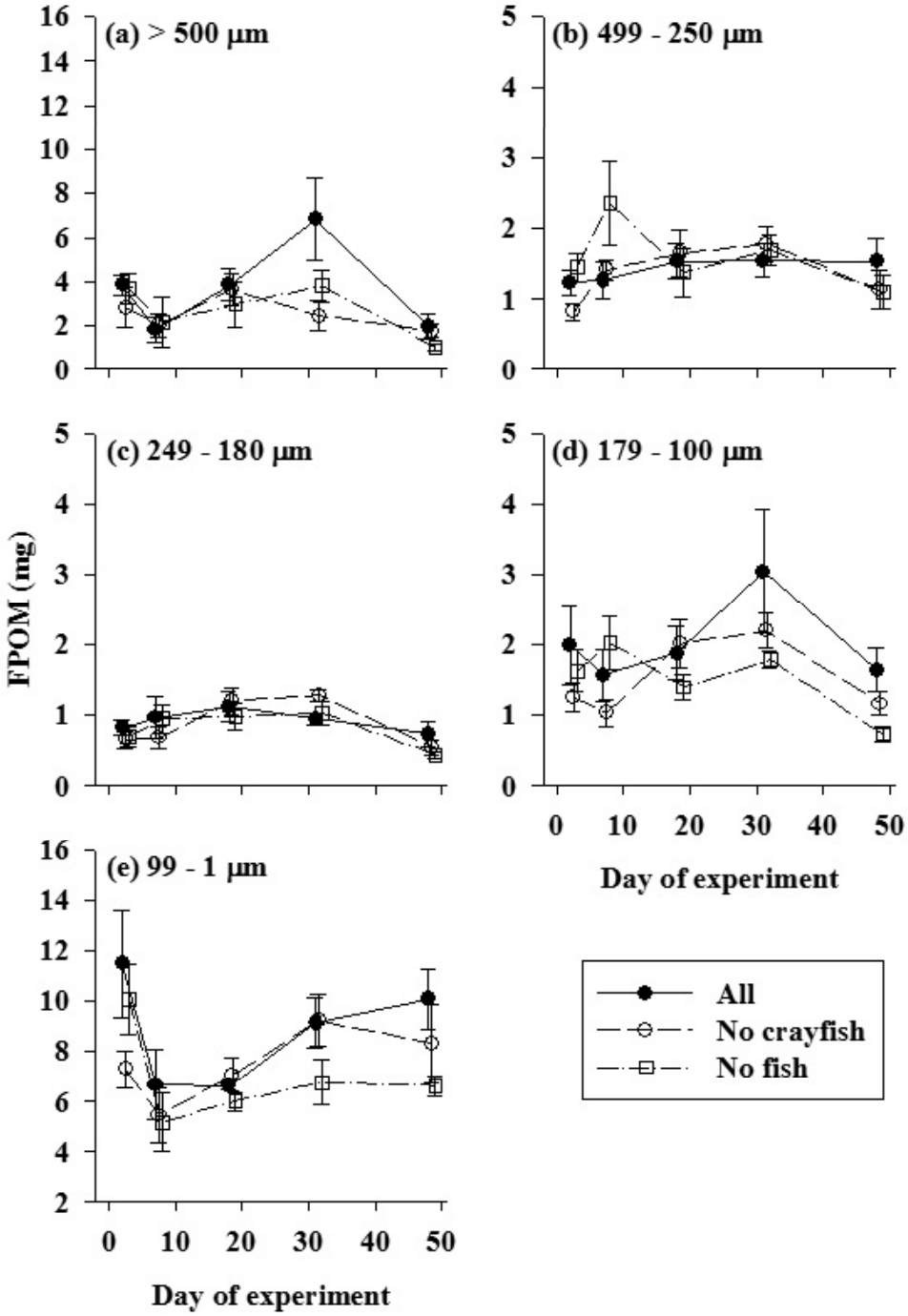


Figure 4.5. Mean fractions (+ SE) of fine particulate organic matter (FPOM) sized (a) > 500 µm, (b) 499 – 250 µm, (c) 249 – 180 µm, (d) 179 – 100 µm, and (e) 99 – 1 µm in pools of 18 experimental streams on the Konza Prairie Biological Station. Treatments included two reduced grazer assemblages (N=6; NC = no crayfish; NF = no fish; open symbols; offset ½ day later), which were compared to a control (N=6; All = full grazer assemblage).

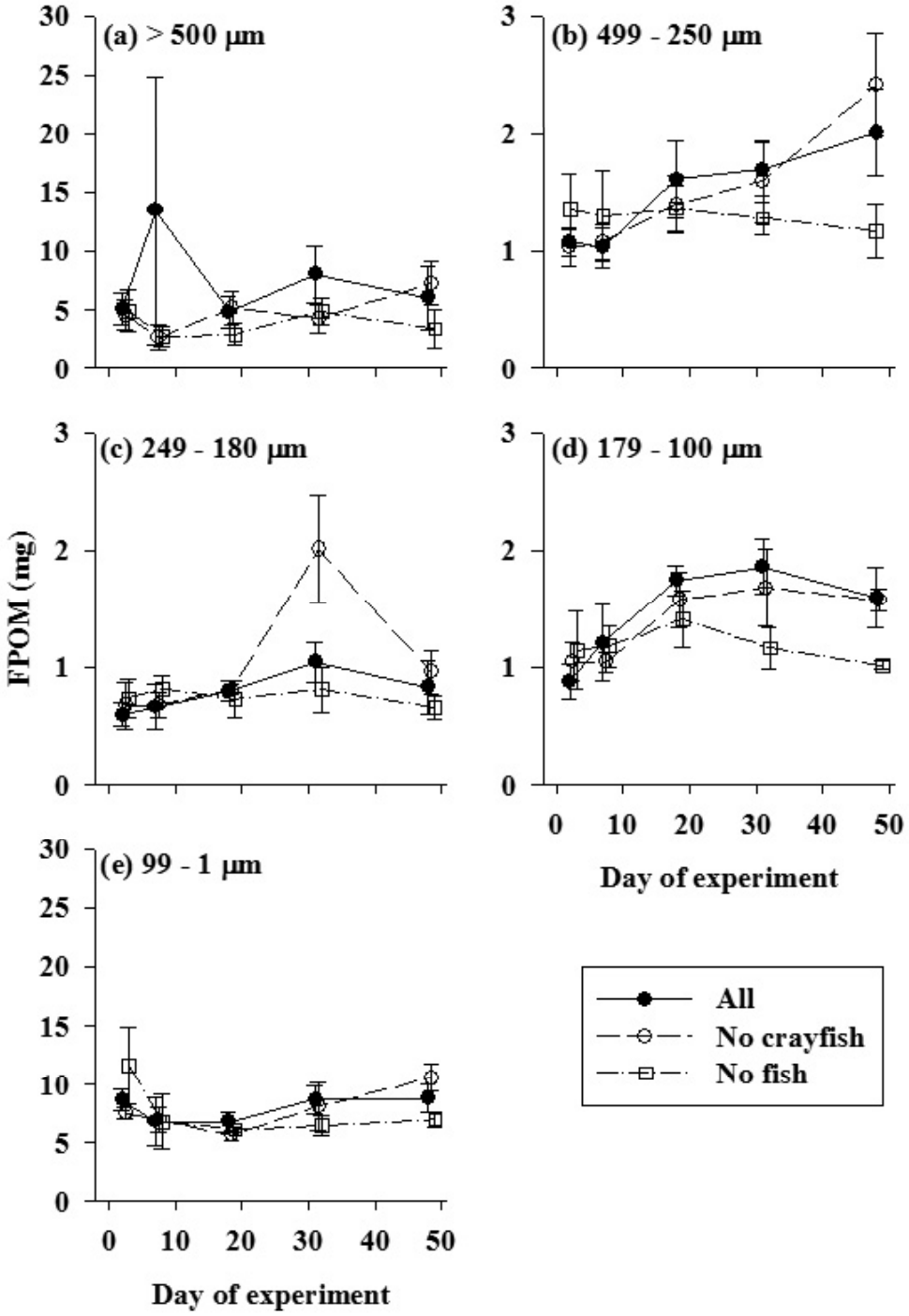


Figure 4.6. Boxplots representing 25th, 50th and 75th percentile densities of (a) early instar chironomids and (b) cyclopoid copepods in riffles of 18 experimental streams on the Konza Prairie Biological Station on day 18. Treatments included two reduced grazer assemblages (N=6; NC = no crayfish; NF = no fish), which were compared to a control (N=6; All = crayfish + fish).

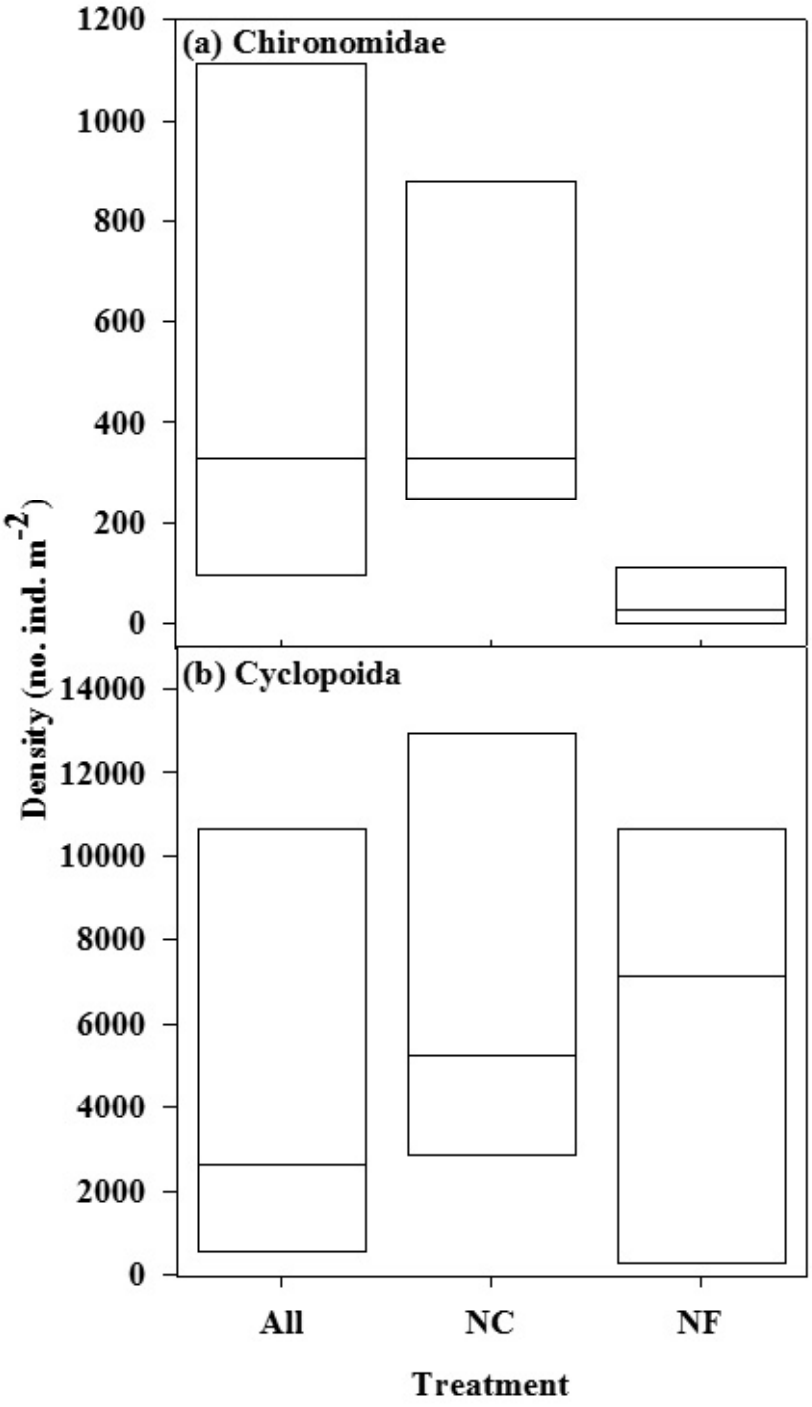


Figure 4.7. Boxplots representing 25th, 50th and 75th percentile densities of (a) baetid mayflies and (b) oligochaetes in riffles of 18 experimental streams on the Konza Prairie Biological Station on day 48. Treatments included two reduced grazer assemblages (N=6; NC = no crayfish; NF = no fish), which were compared to a control (N=6; All = crayfish + fish).

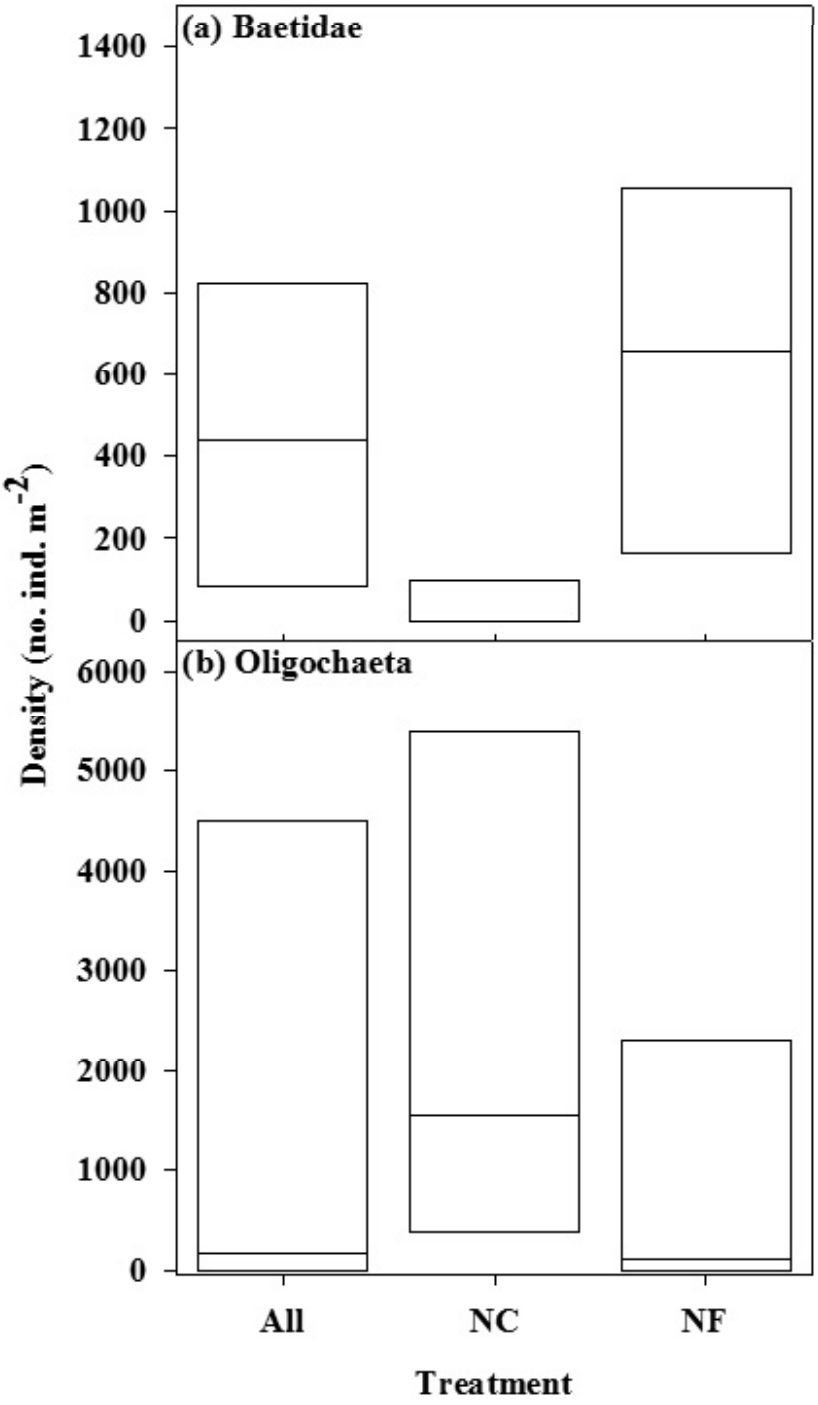
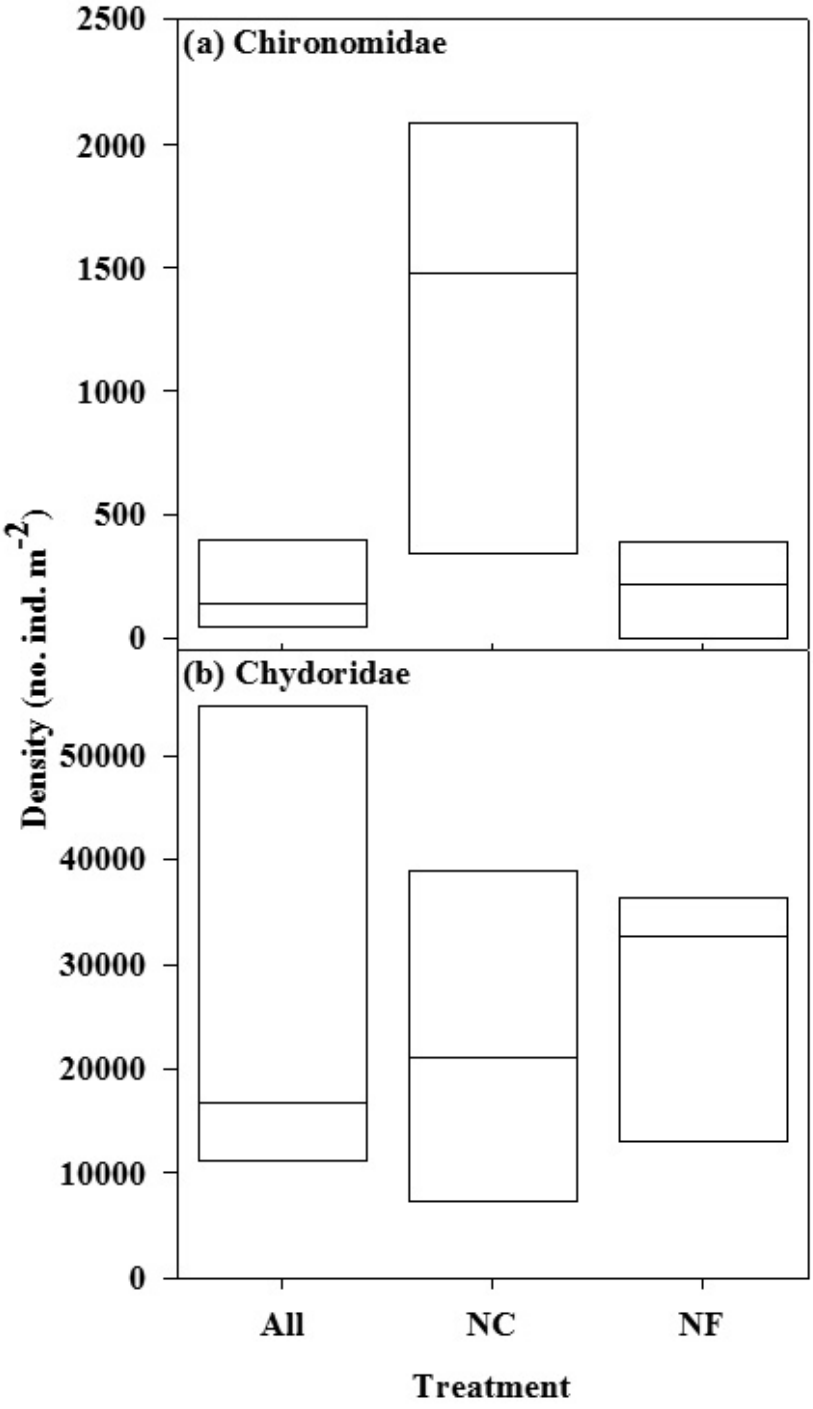


Figure 4.8. Boxplots representing 25th, 50th and 75th percentile densities of (a) early instar chironomids and (b) chydorids in pools of 18 experimental streams on the Konza Prairie Biological Station on day 48. Treatments included two reduced grazer assemblages (N=6; NC = no crayfish; NF = no fish), which were compared to a control (N=6; All = crayfish + fish).



CHAPTER 5 - CONCLUSIONS

Species extirpations and altered disturbance regimes of grassland streams will likely continue if global change progresses according to predictive climate models. It is critical then to understand the role of species in Great Plains streams in order to prevent and mitigate the effects of potentially altered ecosystem function. Although knowledge of consumer effects on stream ecosystem structure and function has increased greatly over the past 30 years, questions still remain about the generality of species effects within functional feeding groups, the interactive effects of species and disturbance regime, and the effects of within-functional group diversity on stream ecosystem structure and function. To address these research needs, I (1) characterized the effects of a grazing minnow, southern redbelly dace (*Phoxinus erythrogaster*), on ecosystem structure and function, (2) examined the interactive effects of two fishes (a grazer and a water column omnivore) and flood frequency on ecosystem structure and function, and (3) tested the hypothesis of functional redundancy among grazing fish, crayfish, and snails. Moderate densities of *Phoxinus* temporarily reduced mean algal filament length and mean size of particulate organic matter relative to fishless controls, but there was no detectable effect on algal biomass or ecosystem primary productivity. Both benthic grazers and water column omnivores affected recovery of ecosystem structure and function by stimulating primary production following simulated floods, but some of these effects were temporally variable or dependent on flood frequency. In the natural stream, recovery of ecosystem structure and function after a major flood was not influenced by fish treatment, rather ecosystem processes varied with position in the watershed. When single grazer species were removed from the assemblage, effects included an increase in nutrient limitation when crayfish were removed and transient

effects of dace and crayfish removal on abundance of size fractions of FPOM and invertebrate assemblage structure.

The transient nature of these effects necessitates an understanding of contingency effects on ecosystem studies. For example, several factors could explain the lack of effect of *Phoxinus* on primary productivity including increased algal production efficiency in grazed treatments or increased grazing by other organisms in fishless treatments. Environmental venue and the spatial and temporal scale of ecosystem measurements also can greatly influence the outcome of these experiments. This was illustrated by the lack of a species effect in the natural stream after a single, large flood. Whereas this was generally consistent with experimental streams treatments without repeated flooding, the observed differences between field and mesocosm experiments were more likely related to the inability of small (mean = 35.8 m^2) field enclosures to capture the influence of nutrient remineralization by fishes. Finally, the general lack of unique ecosystem effects among grazer assemblages could be related to the spatial and temporal scale at which my study was conducted or the context of physical conditions present during the experiment. My research suggests that it is important to identify major factors driving experimental results and to perform experiments that characterize the interaction of species effects and confounding factors.

Prairie streams are ideal systems for studying the effects of disturbance and species composition on ecosystem processes. Characteristically harsh disturbance regimes and the global importance in carrying runoff make understanding these systems critical. To this end, my investigations indicate that the inhabitants of prairie streams may provide ecosystem services in terms of mitigating downstream water quality. Dace decreased organic matter export during flooding and increased short-term nutrient retention, whereas shiners increased organic matter export. Given that these systems carry nearly 30% of global runoff (Dodds 1997), it is likely that

differences in organic matter export and nutrient retention may translate into larger economic differences in the availability of clean water or the commercial fisheries in the Gulf of Mexico. Although assigning dollar values is not possible at this time, the potential services provided by intact communities in grassland streams are another reason for continued investigation and further understanding of the dynamics of these important systems.

LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum-likelihood principle. In Petrov, B. N., F. Csaki (eds.). Second International Symposium on Information Theory. Akademiai Kiado: Budapest, Hungary.

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control AC-19:716-723.

Alvarez, M., and B. L. Peckarsky. 2005. How do grazers affect periphyton heterogeneity in streams? Oecologia **142**:576-587.

Anderson, E. L., E. B. Welch, J. M. Jacoby, G. M. Schimek, and R. R. Horner. 1999. Periphyton removal related to phosphorus and grazer biomass level. Freshwater Biology **41**:633-651.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J-S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters **9**:1146 – 1156.

Bengtson, J. R., M. A. Evans-White, and K. B. Gido. *In preparation*. Effects of grazing minnows (*Phoxinus erythrogaster*) and crayfish (*Orconectes nais* and *O. neglectus*) on ecosystem structure and function.

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

Bertrand, K. N., K. B. Gido, and C. S. Guy. 2006. An evaluation of single-pass versus multiple-pass backpack electrofishing to estimate trends in species abundance and richness in prairie streams. Transactions of the Kansas Academy of Science 109: 131 – 138.

Bertrand, K. N., K. B. Gido, J. N. Murdock, W. K. Dodds, and M. R. Whiles. *In preparation*. Fishes and floods: stream ecosystem drivers in the Great Plains.

Biggs, B. J. F., and R. A. Smith. 2002. Taxonomic richness of stream benthic algae: effects of flood disturbance and nutrients. Limnology and Oceanography **47**:1175-1186.

Biggs, B. J. F., V. I. Nikora, and T. H. Snelder. 2005. Linking scales of flow variability to loti ecosystem structure and function. River Research and Applications **21**:283-298.

Bott, T. L. 1996. Primary productivity and community respiration. Pages 533-556 *in* Hauer, F. R., and G. A. Lamberti, editors. Methods in Stream Ecology. Academic Press, New York.

Bott, T. L., J. T. Brock, A. Baatrup-Pedersen, P. A. Chambers, W. K. Dodds, K. T. Himbeault, J. R. Lawrence, D. Planas, E. Snyder, and G. M. Wolfaardt. 1997. An evaluation of techniques for measuring periphyton metabolism in chambers. Canadian Journal of Fisheries and Aquatic Sciences **54**:715-725.

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

Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. Nature **415**:426-429.

Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology **77**:677-680.

Carpenter, S. R., and J. F. Kitchell. 1984. Plankton community structure and limnetic primary production. American Naturalist **124**:159-172.

Cooper, D. C. 1973. Enhancement of net primary productivity by herbivore grazing in aquatic laboratory microcosms. Limnology and Oceanography **18**:31-37.

Covich, A. P., M. C. Austen, F. Bärlocher, E. Chauvet, B. J. Cardinale, C. L. Biles, P. Inchausti, O. Dangles, M. Solan, M. O. Gessner, B. Statzner, and B. Moss. 2004. The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. Bioscience **54**:767-775.

Creed, R. P. Jr. 1994. Direct and indirect effects of crayfish grazing in a stream community. Ecology **75**:2091-2103.

Cross, F. B., and J. T. Collins. 1995. Fishes in Kansas. University of Kansas Natural History Museum, Lawrence.

Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. American Midland Naturalist **67**:477-504.

Cummins, K. W., and R. W. Merritt. 1996. Ecology and distribution of aquatic insects. Pages 74 – 86 *in* Merritt, R. W., and K. W. Cummins, editors. An introduction to the aquatic insects of North America, 3rd edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Dodds W. K. 1997. Distribution of runoff and rivers related to vegetative characteristics, latitude, and slope: a global perspective. Journal of the North American Benthological Society **16**:162-168.

Dodds W. K. 2003. Misuse of inorganic N and soluble reactive P concentrations to indicate nutrient status of surface waters. Journal of the North American Benthological Society **22**:171-181.

Dodds, W. K., and J. Brock. 1998. A portable chamber for *in situ* determination of benthic metabolism. Freshwater Biology **39**:49-59.

Dodds W. K., K. Gido, M. R. Whiles, K. M. Fritz, and W. J. Matthews. 2004a. Life on the edge: the ecology of great plains prairie streams. BioScience **54**:205-216.

Dodds, W. K., A. C. Huston, M. A. Evans, D. A. Gudder, K. M. Fritz, and L. Gray. 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., A. J. Lopez, W. B. Bowden, S. Gregory, N. B. Grimm, S. K. Hamilton, A. E. Hershey, E. Marti, W. H. McDowell, J. L. Meyer, D. Morrall, P. J. Mulholland, B. J. Peterson, J. L. Tank, H. M. Valett, J. R. Webster, and W. Wollheim. 2002. N uptake as a function of concentration in streams. Journal of the North American Benthological Society **21**:206-220.

Dodds W. K., E. Marti, J. L. Tank, J. Pontius, S. K. Hamilton, N. B. Grimm, W. B. Bowden, W. H. McDowell, B. J. Peterson, H. M. Valett, J. R. Webster, S. Gregory. 2004b. Carbon and nitrogen stoichiometry and nitrogen cycling rates in streams. Oecologia 140: 458 – 467.

Duffy, J. E., K. S. McDonald, J. M. Rhode, and J. D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: and experimental test. Ecology **82**:2417-2434.

Erlich, P. R. and A. H. Erlich. 1981. Extinction: the causes and consequences of the disappearance of species. Random House, New York.

Evans-White, M. A., and W. K. Dodds. 2001. A comparison of the trophic ecology of the crayfishes (*Orconectes nais* (Faxon) and *Orconectes neglectus* (Faxon)) and the central stoneroller minnow (*Campostoma anomalum* (Rafinesque)): omnivory in a tallgrass prairie stream. Hydrobiologia **462**:131-144.

Evans-White, M. A., and W. K. Dodds. 2003. Ecosystem significance of crayfishes and stonerollers in a prairie stream: Functional differences between co-occurring omnivores. Journal of the North American Benthological Society **22**:423-441.

Evans-White, M. A., and G. A. Lamberti. 2006. Stoichiometry of consuer-driven nutrient recycling across nutrient regimes in streams. Ecology Letters **9**:1186-1197.

Felley, J. D., and L. G. Hill. 1983. Multivariate assessment of environmental preferences of cyprinid fishes of the Illinois river, Oklahoma. American Midland Naturalist **109**:209-221.

Flecker, A. S., B. W. Taylor, E. S. Bernhardt, J. M. Hood, W. K. Cornwell, S. R. Cassatt, M. J. Vanni, and N. S. Altman. 2002. Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. Ecology **83**:1831-1844.

Forbes, S. A., and R. E. Richardson. 1920. The fishes of Illinois. Illinois Department of Registration and Education, Division of Natural History Survey, Champaign, Illinois.

Franssen, N. R., and K. B. Gido. 2006. Use of stable isotopes to test literature-based trophic classifications of small-bodied stream fishes. American Midland Naturalist **156**:1-10.

Franssen, N. R., K. B. Gido, C. S. Guy, J. A. Tripe, S. J. Shrank, T. R. Strakosh, K. N. Bertrand, C. M. Franssen, K. L. Pitts, and C. P. Paukert. 2006. Effects of floods on fish assemblages in an intermittent prairie stream. Freshwater Biology **51**:2072-2086.

Gamfeldt, L., H. Hillebrand, and P. R. Johnson. 2005. Species richness across two trophic levels simulataneously affect prey and consumer biomass. Ecology Letters **8**:696-703.

Gelwick, F. P. 2000. Grazer identity changes the spatial distribution of cascading trophic effects in stream pools. Oecologia **125**:573-583.

Gelwick, F. P., and W. J. Matthews. 1992. Effects of an algivorous minnow on temperate stream ecosystem properties. Ecology **73**:1630-1645.

Gido, K. B., and W. J. Matthews. 2001. Ecosystem effects of water column minnows in experimental streams. Oecologia **126**:247-253.

Ghilarov, A. M. 2000. Ecosystem functioning and intrinsic value of biodiversity. Oikos **90**:408-412.

Gray, L. J., and W. K. Dodds. 1998. Structure and dynamics of aquatic communities. Pages 177-189 *in* Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. Grassland dynamics: Long-term ecological research in tallgrass prairie. Oxford University Press, New York.

Gray, L. J., G. L. Macpherson, J. K. Koelliker, and W. K. Dodds. 1998. Hydrology and aquatic chemistry. Pages 159-176 *in* Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. Grassland dynamics: Long-term ecological research in tallgrass prairie. Oxford University Press, New York.

Gross, K., and B. J. Cardinale. 2005. The functional consequences of random vs. ordered species extinctions. Ecology Letters **8**:409-418.

Haslouer, S. G., M. E. Eberle, D. R. Edds, K. B. Gido, C. S. Mammoliti, J. R. Triplett, J. T. Collins, D. A. Distler, D. G. Huggins, and W. J. Stark. 2005. Current status of native fish species in Kansas. Transactions of the Kansas Academy of Science **108**:32-46.

Hector, A., J. Joshi, S. P. Lawler, E. M. Spehn, and A. Wilby. 2001. Conservation implications of the link between biodiversity and ecosystem functioning. Oecologia **129**:624-628.

Hill, W. R., H. L. Boston, and A. D. Steinman. 1992. Grazers and nutrients simultaneously limit lotic primary productivity. Canadian Journal of Fisheries and Aquatic Sciences **49**:504-512.

Hill, L. G., and T. A. Jenssen. 1968. A meristic study of the redbelly dace, *Chrosomus erythrogaster* (Cyprinidae), from a stream in southern Oklahoma. Southwestern Naturalist **13**:55-60.

Hillebrand, H. 2002. Top-down versus bottom-up control of autotrophic biomass--a meta-analysis on experiments with periphyton. Journal of the North American Benthological Society **21**:349-369.

Hoagland K. D., S. C. Roemer, and J. R. Rosowski. 1982. Colonization and community structure of two periphyton assemblages, with emphasis on the diatoms (bacillariophyceae). American Journal of Botany **69**:188-213.

Hooper, D. U., F. S. Chapin III, J. J. Ewel, A Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs **75**:3-35.

Houser, J. N., P. J. Mulholland, and K. O. Maloney. 2005. Catchment disturbance and stream metabolism: patterns in ecosystem respiration and gross primary productivity along a

gradient of upland soil and vegetation disturbance. Journal of the North American Benthological Society **24**:538-552.

Hudon, C., and E. Bourget. 1981. Initial colonization of artificial substrate: Community development and structure studied by scanning electron microscopy. Canadian Journal of Fisheries and Aquatic Sciences **38**:1371-1384.

Krebs, C. J. 2001. Ecology: The experimental analysis of distribution and abundance. Benjamin Cummings, San Francisco.

Lawton, J. H. 1994. What do species do in ecosystems? Oikos **71**:367-374.

Lawton, J. H., and R. M. May. 1995. Extinction rates. Oxford University Press, Cambridge, UK.

Lawton, J. H., S. Naeem, R. M. Woodfin, V. K. Brown, A. Gange, H. J. C. Godfray, P. A. Heads, S. Lawler, D. Magda, C. D. Thomas, L. J. Thompson, and S. Young. 1993. The ecotron: a controlled environmental facility for the investigation of population and ecosystem processes. Philosophical Transactions: Biological Sciences **341**:181-194.

Lennon, R. E., and P. S. Parker. 1960. The stoneroller, *Campostoma anomalum* (Rafinesque), in Great Smoky Mountains National Park. Transactions of the American Fisheries Society **89**:263-270.

Lepori, F., and N. Hjerdt. 2006. Disturbance and aquatic biodiversity: reconciling contrasting views. BioScience **56**:809-818.

Liess, A., and H. Hillebrand. 2004. Invited review: Direct and indirect effects in herbivore - periphyton interactions. Archiv für Hydrobiologia **159**:433-453.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos **91**:3-17.

Matthews, W. J. 1998. Patterns in freshwater fish ecology. Chapman & Hall, New York, New York, USA.

Matthews, W.J., K.B. Gido, G.P. Garrett, F.P. Gelwick, J. Stewart, and J. Schaefer. 2006. Modular experimental riffle-pool stream system. Transactions of the American Fisheries Society **135**:1559-1566.

Matthews W. J., and L. G. Hill. 1979. Influence of physico-chemical factors on habitat selection by red shiners (Notropis lutrensis) (Pisces: Cyprinidae). Copeia **1979**:70-81.

Matthews, W. J., M. E. Power, and A. J. Stewart. 1986. Depth distribution of grazing scars in an Ozark stream. Environmental Biology of Fishes **17**:291-297.

Matthews, W. J., and E. G. Zimmerman. 1990. Potential effects of global warming on native fishes of the southern Great Plains and the Southwest. Fisheries **15**:26-32.

McKee, P. M., and B. J. Parker. 1982. The distribution, biology, and status of the fishes *Campostoma anomalum*, *Clinostomus elongatus*, *Notropis photogenis* (Cyprinidae), and *Fundulus notatus* (Cyprinodontidae) in Canada. Canadian Journal of Zoology **60**:1347-1358.

Miller, R. J., and H. W. Robinson. 2004. Fishes of Oklahoma. University of Oklahoma Press, Norman, OK.

Milliken, G. A., and D. E. Johnson. 2002. Analysis of Messy Data, Volume III: Analysis of Covariance. Chapman & Hall, London, UK.

Millenium Assessment. 2005. Ecosystems and Human Well-Being: Synthesis. Island Press, Washington, D.C.

Mulholland, P. J., A. D. Steinman, A. V. Palumbo, J. W. Elwood, and D. B. Kirschtel. 1991. Role of nutrient cycling and herbivory in regulating periphyton communities in laboratory streams. Ecology **72**:966-982 .

Naeem, S., and A. C. Baker. 2005. Paradise sustained. Nature **433**:370-371.

Napolitano, G. E., N. C. Shantha, W. R. Hill, and A. E. Luttrell. 1996. Lipid and fatty acid compositions of stream periphyton and stoneroller minnows (*Campostoma anomalum*): Trophic and environmental implications. Archiv für Hydrobiologie 137:211-225

Newbold, J. D., R. V. O'Neill, J. W. Elwood, and W. Van Winkle. 1982. Nutrient spiralling in streams: Implications for nutrient limitation and invertebrate activity. American Naturalist 120:628-652.

Nystrom, P., and K. Abjornsson. 2000. Effects of fish chemical cues on the interactions between tadpoles and crayfish. Oikos **88**:181-190.

Nystroem, P., C. Broanmark, and W. Graneli. 1996. Patterns in benthic food webs: A role for omnivorous crayfish? Freshwater Biology **36**:631-646.

O'Brien, J. 2006. Controls of nitrogen spiraling in Kansas streams. PhD Dissertation. Kansas State University.

Oemke, M. P., and T. M. Burton. 1986. Diatom colonization dynamics in a lotic system. Hydrobiologia **139**:153-166.

Owens, M. 1974. Measurements on non-isolated natural communities in running waters. Pages 111-119 *in* Vollenweider, R. A., editor. A manual on methods for measuring primary production in aquatic environments. Blackwell Scientific, Oxford.

Parsons, M., C. A. McLoughlin, M. W. Roundtree, and K. H. Rogers. 2006. The biotic and abiotic legacy of a large infrequent flood disturbance in the Sabie River, South Africa. River Research and Applications **22**:187-201.

Peckarsky, B. L., B. W. Taylor, A. R. McIntosh, M. A. McPeek, and D. A. Lytle. 2001. Variation in mayfly size at metamorphosis as a developmental response to risk of predation. Ecology **82**:740-757.

Peterson, C. G., and R. J. Stevenson. 1989. Substratum conditioning and diatom colonization in different current regimes. Journal of Phycology **25**:790-793.

Peterson, C. G., and R. J. Stevenson. 1990. Post-spate development of epilithic algal communities in different current environments. Canadian Journal of Botany **68**:2092-2102.

Peterson B. J., W. M. Wollheim, P. J. Mulholland, J. R. Webster, J. L. Meyer, J. L. Tank, E. Marti, W. B. Bowden, H. M. Valet, A. E. Hershey, W. B. McDowell, W. K. Dodds, S. K. Hamilton, S. Gregory, and D. D. Morrall. 2001. Control of nitrogen export from watersheds by headwater streams. Science **292**:86-90.

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity and scale. Ecosystems **1**:6-18.

Phillips, G. L. 1969. Diet of minnow *Chrosomus erythrogaster* (Cyprinidae) in a Minnesota stream. American Midland Naturalist **82**:99-109.

Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. Science **269**:347-350.

Power, M. E. 1990. Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. Ecology **71**:897-904.

Power, M. E., and W. J. Matthews. 1983. Algae-grazing minnows (*Campostoma anomalum*), piscivorous bass (*Micropterus* sp.), and the distribution of attached algae in a small prairie-margin stream. Oecologia **60**:328-332.

Power, M. E., W. J. Matthews, A. J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. Ecology **66**:1448-1456.

Power, M. E., A. J. Stewart, and W. J. Matthews. 1988*a*. Grazer control of algae in an Ozark mountain stream: Effects of short-term exclusion. Ecology **69**:1894-1898.

Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, B. Statzner, and I. R. Wais De Badgen. 1988*b*. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society **7**:456-479.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society **7**:433-455.

Roemer, S. C., K. D. Hoagland, and J. R. Rosowski. 1984. Development of a freshwater periphyton community as influenced by diatom mucilages. Canadian Journal of Botany **62**:1799-1813.

Rosemond, A. D. 1993. Interactions among irradiance, nutrients, and herbivores constrain a stream algal community. Oecologia **94**:585-594.

Rosemond, A. D., P. J. Mulholland, and S. H. Brawley. 2000. Seasonally shifting limitation of stream periphyton: Response of algal populations and assemblage biomass and productivity to variation in light, nutrients, and herbivores. Canadian Journal of Fisheries and Aquatic Sciences **57**:66-75.

Rosenfeld, J. S. 2002. Logical fallacies in the assessment of functional redundancy. Conservation Biology **16**:837-839.

Rosenzweig, M. L. 1999. Heeding the warning in biodiversity's basic law. Science **284**:276-277.

Sala, O. E., F. S. Chapin III, J. J. Armesto, E. L. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Sarnelle, O., K. W. Kratz, and S. D. Cooper. 1993. Effects of an invertebrate grazer on the spatial arrangement of a benthic microhabitat. Oecologia **96**:208-218.

Sartory, D. P., and J. E. Grobbelaar. 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia **114**:177-187.

SAS. 2003. SAS for Windows. Version 9.1.

Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia **122**:297-305.

Settles, W. H., R. D. Hoyt. 1976. Age structure, growth patterns, and food habits of the southern redbelly dace *Chrosomus erythrogaster* in Kentucky. Transactions of the Kentucky Academy of Science **37**:1-10.

Slack, W. T., M. T. O'Connell, T. L. Peterson, J. A. Ewing III, and S. T. Ross. 1997. Ichthyofaunal and habitat associations of disjunct populations of southern redbelly dace. *Phoxinus erythrogaster* (teleostei: Cyprinidae) in Mississippi. American Midland Naturalist 137:251-265.

SPSS. 2001. SPSS for Windows: Standard version. Release 11.0.1.

Stewart, A. J. 1987. Responses of stream algae to grazing minnows and nutrients: A field test for interactions. Oecologia **72**:1-7.

Steinman, A. D. 1996. Effects of grazers on freshwater benthic algae. Pages 341-373 *in* Stevenson, R. J., M. L. Bothwell, and R. L. Lowe, editors. Algal ecology: Freshwater benthic ecosystems. Academic Press, San Diego, pp 341-373.

Steinman, A. D., and C. D. McIntire. 1986. Effects of current velocity and light energy on the structure of periphyton assemblages in laboratory streams. Journal of Phycology **22**:352-361.

Steinman, A. D., C. D. McIntire, S. V. Gregory, and G. A. Lamberti. 1989. Effects of irradiance and grazing on lotic algal assemblages. Journal of Phycology **25**:478-485.

Steinman, A. D., C. D. McIntire, S. V. Gregory, G. A. Lamberti, and L. R. Ashkenas. 1987. Effects of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. Journal of the North American Benthological Society **6**:175-188.

Tank, J., and W. K. Dodds. 2003. Responses of heterotrophic and autotrophic biofilms to nutrients in ten streams. Freshwater Biology **48**:1031-1049.

ter Braak, C. J., and P. Smilauer. 2002. Canoco for Windows version 4.5. Biometris-Plant Research International, Wageningen, The Netherlands.

Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. Science **294**:843-845.

Turner, A. M. 1997. Contrasting short-term and long-term effects of predation risk on consumer habitat use and resources. Behavioral Ecology **8**:120-125.

Uehlinger, U. 2000. Periphyton biomass in an unpredictable environment: exploring the temporal variability with a dynamic model. Verhandlung Internationale Vereinigung für theoretische und angewande Limnologie **27**:3162-3165.

Uehlinger, U., and J. T. Brock. 1991. The assessment of river periphyton metabolism; A method and some problems. Pages 175-181 *in* Whitton, B. A., E. Rott, and G. Friedrich, editors. Use of algae for monitoring rivers. Institut for Botanik, Universität Innsbruck, Innsbruck, Austria.

Van Deventer, J. A., and W. S. Platts. 1989. Microcomputer software system for generating population statistics from electrofishing data-user's guide for MicroFish 3.0. U.S. Forest Service General Technical Report INT-254.

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annual Reviews in Ecology and Systematics **33**:341-370.

Vaughn, C. C., F. P. Gelwick, and W. J. Matthews. 1993. Effects of algivorous minnows on production of grazing stream invertebrates. Oikos **66**:119-128.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's Ecosystems. Science **277**:494-499.

Walker, B. 1992. Biological diversity and ecological redundancy. Conservation Biology **6**:18-23.

Wallace, B. J., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology **41**:115-139.

Webster, J. R., P. J. Mulholland, J. L. Tank, H. M. Valett, W. K. Dodds, B. J. Peterson, W. B. Bowden, C. N. Dahm, S. Findlay, S. V. Gregory, N. B. Grimm, S. K. Hamilton, S. L. Johnson, E. Martí, W. H. McDowell, J. L. Meyer, D. D. Morrall, S. A. Thomas, and W.

M. Wollheim. 2003. Factors affecting ammonium uptake in streams - an inter-biome perspective. Freshwater Biology **48**:1329-1352.

Welschmeyer, N. A. 1995. Flourometric analysis of chlorophyll a in the presence of chlorophyll b and phaeopigments. Limnology and Oceanography **39**:1985-1992.

Appendix A - ELECTRONIC SUPPLEMENTARY MATERIAL TO CHAPTER 2

Table A. Mean (range) of invertebrate densities (individuals / m^2) across the three experimental venues. Means were not presented for Kings Creek study pools because there were only two replicates for each of the fish and no fish treatments. No fish and fish treatments were reported separately in the experimental streams, but not in Kings Creek, where data are from day 4 of the experiment.

	Kings Creek	Experimental Streams 2002		Experimental Streams 2003	
Taxon		no fish	fish	no fish	fish
COLLEMBOLA	(0-3)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
INSECTA					
Ephemeroptera					
Baetidae	(0-23)	4 (1-7)	2 (0-4)	4 (1-8)	3 (0-6)
Caenidae	(8-38)	0 (0-0)	0 (0-0)	1 (0-3)	1 (0-3)
Heptageniidae	(8-49)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-1)
Leptophlebiidae	(0-8)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Libellulidae		0 (0-0)		0 (0-8)	
Megaloptera					
Sialidae	(0-8)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Coleoptera					
Dytiscidae		1 (0-2)		0 (0-2)	
Elmidae	(0-4)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Diptera					
Ceratopogonidae		0 (0-0)		0 (0-1)	
Chironomidae	(4-87)	25 (22-27)	31 (10-53)	465 (3-2257)	436 (2-1987)
Simuliidae		0 (0-0)		0 (0-1)	
Pupae	(0-11)	0 (0-0)	0 (0-0)	5 (0-15)	4 (0-14)

Adults			0 (0-0)	0 (0-0)	0 (0-1)
Trichoptera					
Philopotamidae	(0-8)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
CRUSTACEA					
Cladocera					
Bosmina sp.		0 (0-0)		2383 (150-7982)	
Copepoda	(0-72)	15 (14-16)	16 (7-26)	325 (5-1317)	448 (24-1421)
Isopoda					
Caccidotea					
tridentata	(0-3)	0 (0-0)	0 (0-0)	0 (0-1)	0 (0-1)
ARACHNIDA					
Acari	(0-15)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
ANNELIDA					
Oligochaeta	(0-30)	1 (0-3)	1 (0-2)	1042 (2-3561)	1026 (3-2744)
MOLLUSCA					
Gastropoda		0 (0-0)		10 (0-43)	
Terrestrial			0 (0-0)	0 (0-0)	2 (0-8)
22 TOTAL TAXA					
mean abundance	6.51	2.10	2.35	192.68	217.54

Appendix B - PERMISSION TO INCLUDE CHAPTER 2

Figure A. License agreement with Springer to include a published manuscript (Chapter 2) in dissertation.

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