Disturbance-Mediated Effects of Fishes on Stream Ecosystem Processes: Concepts and Results from Highly Variable Prairie Streams

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Abstract.—Stream fishes can have strong top-down and bottom-up effects on ecosystem processes. However, the dynamic nature of streams constrains our ability to generalize these effects across systems with different disturbance regimes and species composition. To evaluate the role of fishes following disturbance, we used a series of field and mesocosm experiments that quantified the influence of grazers and water column minnows on primary productivity, periphyton structure, organic matter pools, and invertebrate communities following either scouring floods or drying of prairie streams. Results from individual experiments revealed highly significant effects of fishes, but the direction or magnitude of effects varied among experiments. Meta-analyses across experiments indicated that grazers consistently reduced the relative amount of fine benthic organic matter (FBOM) and chironomid abundance within 2 weeks after disturbances. However, effect sizes (log response ratios) were heterogeneous across experiments for algal biomass and algal filament lengths measured more than 4 weeks after a disturbance and potentially associated with system productivity and grazer densities. A similar analysis of 3–4 experiments using water column minnows only found a consistent trend of decreasing FBOM in fish treatments relative to controls when measured less than 2 weeks after

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disturbances and increase in gross primary productivity measured more than 4 weeks after disturbance. These results, along with those of others, were used to develop a conceptual framework for predicting the potential role of fishes in streams following disturbances (flood and drying). Both theoretical and empirical research shows that recovery of stream ecosystem processes will depend on the resilience of autotrophic and heterotrophic communities following disturbance. Fish effects may vary among functional groups but are generally predicted to be greatest during early stages of succession when algal and invertebrate communities are less complex and their biomass is low relative to fish biomass. Our analysis underscores the context dependency of consumer effects on ecosystem structure and function in nonequilibrium conditions and suggests that factors regulating fish densities and colonization of algal and invertebrate taxa need to be evaluated to predict the consequences of biodiversity loss in streams with variable or human-modified disturbance regimes.

Introduction

Stream ecosystem functions, such as primary production, are influenced by the presence of fishes through both direct (e.g., predation) and indirect pathways (e.g., trophic cascades, nutrient mineralization). Our understanding of these pathways and how they shape stream ecosystems has progressed considerably over the past two decades. Early work focused on how fishes exerted direct top-down pressures on benthic macroinvertebrates (Gilliam et al. 1989; Flecker and Townsend 1994; Dahl and Greenberg 1996), algal communities (Grimm 1988; Power 1990; Gelwick and Matthews 1992), and detritus (Flecker 1996). The importance of indirect effects of stream fishes through trophic cascades (Power et al. 1985; Huryn 1998; Hargrave 2006; Hargrave et al. 2006) and alteration of nutrient cycling and stoichiometry (Gido and Matthews 2001; Vanni et al. 2002; McIntyre et al. 2007; McIntyre and Flecker 2010, this volume) were additional areas of research. More recent studies have evaluated the importance of fishes on whole stream ecosystem rates, such as productivity and nutrient uptake (Taylor et al. 2006; Bertrand and Gido 2007; Bertrand et al. 2009; Murdock et al., in press).

Although the number of studies testing the effects of fishes on ecosystem properties has increased, there is little consensus allowing us to predict when and where fishes will exert a strong effect on ecosystem properties. Rather, results from individual experiments and across systems tend to be context dependent (sensu Power et al. 1996). Theoretical and empirical studies suggest that consumer effects should vary with food web structure, nutrient limitation, and community composition (DeAngelis 1992; Worm et al. 2002; Power et al. 2008). Many streams, particularly intermittent streams, are nonequilibrium systems subject to frequent flooding or drying, and such streams are common globally (Dodds 1997). Drivers of stream ecosystem processes are likely to interact with these disturbances; yet little is known about spatial trends of animal-mediated processes with respect to ecosystem responses to flood and drought.

The context dependency of fish consumer influences on stream ecosystems was recently illustrated by Power et al. (2008), who used data from a long-term study to show that effects of steelhead *Oncorhynchus mykiss* and California roach *Hesperoleucus symmetricus* on benthic algae varied among years and seasons and was partly mediated by flood and drought effects on

algal and macroinvertebrate communities. Given the potential for complex interactions within stream food webs, predicting species interactions will require an understanding of multiple linkages among food web compartments and how these linkages vary over time.

Hydrologic regimes have variable influences on stream organisms with different life history traits (Poff and Ward 1989; Dodds et al. 2004), and organism responses to hydrology can mediate fish effects on stream ecosystems (Power et al. 2008). For example, fish can resist flooding better than benthic algae or invertebrates because they are mobile and can avoid being washed downstream by seeking refuge in low-velocity areas (Harvey 1987; Detenbeck et al. 1992; Franssen et al. 2006). Thus, fish densities may remain high while their resources are greatly diminished, potentially creating a strong demand for those resources after a disturbance. In contrast, extreme floods or stream drying may lower or eliminate populations of all organisms, and species that are good dispersers with rapid reproductive cycles (e.g., algae) may recolonize and recover more quickly than poor dispersers with slow reproductive cycles that may take weeks to years to recover. Under this scenario, recovery of poor dispersers will depend on proximity to refugia (Niemi et al. 1990). Accordingly, effects of fish on resilience of stream structure and function will likely be dependent on the type and magnitude of the disturbance, and if large enough to eradicate fishes and other organisms, recovery will depend on proximity to source populations, recolonization rates, and reproductive potential of new colonists.

In this chapter, we evaluate recent evidence of how fish effects on stream ecosystem properties vary in the context of stream disturbance regimes. Our definition of disturbances caused by floods and drying meets the criteria of Pickett et al. (1989) in that there is "a change in the minimal structure caused by a factor external to the level of interest." Ecosystem properties influenced by fishes were considered to be either structural or functional. Structural effects included changes in standing stocks of biota or size distributions of organisms and detritus, whereas functional effects include changes in ecosystem rates, such as algal accrual rates, primary production, and respiration by microbial communities. We focus on hydrologic disturbance (scouring floods and drying), although other types of disturbance may apply (e.g., natural or human-induced events that kill, displace, or reorganize biotic communities). We also focused on the roles of two dominant functional groups of stream fishes: grazers and water column minnows. The grazing minnow used in these experiments were the southern redbelly dace *Phoxinus erythrogaster* (hereafter dace), and the red shiner *Cyprinella lutrensis* (hereafter shiner) represented the water column minnow. These functional groups are prevalent in North American streams, as well as many other temperate and tropical streams, and interact directly and indirectly with stream periphyton communities that dominate ecosystem function (Figure 1).

Our overarching goals were to (1) summarize how stream ecosystems recover from disturbance, (2) describe the temporal effects of dace and shiners on this recovery process by testing for the consistency of fish effects (log response ratios) measured at different intervals since a disturbance, and (3) develop a conceptual model of potential effects of fishes in shaping the recovery of prairie stream ecosystems. To accomplish those goals, the chapter includes two main parts: (1) a meta-analysis of multiple experiments testing ecosystem effects of the target species, and (2) a synthesis of results from our studies and other research on the effect of fishes to develop a conceptual model of potential effect of fish on stream eco-
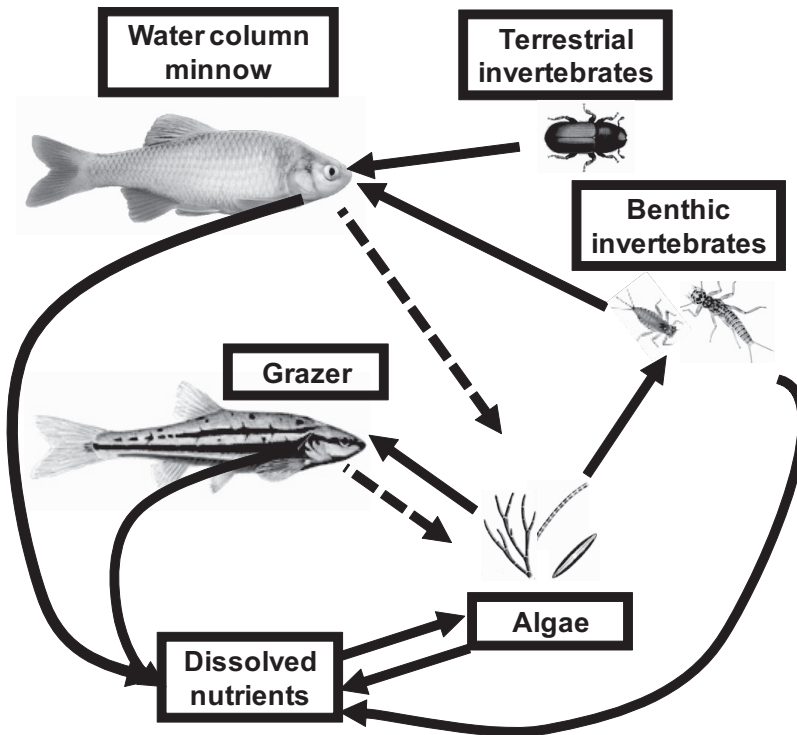
Figure 1. Functional roles of red shiner (water column minnow) and southern redbelly dace (grazing minnow) and potential interactions with different components of stream ecosystems. Solid lines represent energy flow between compartments and dashed lines represent potential indirect effects, such as bioturbation.

system structure and function following disturbance.

Part 1: Meta-Analysis of Dace and Shiner Effects on Recovery of Stream Ecosystem Properties in Field and Mesocosm Experiments

We have completed 10 experiments testing the effects of dace and shiners on stream ecosystem properties at the Konza Prairie Biological Station (KPBS) using either field experiments ($N = 3$) or large outdoor experimental streams ($N = 7$) (Table 1). Although specific objectives of each experiment varied, all included a no-fish control paired with treatments of either adult dace or shiners. These two species represent functional groups of fishes that are

common to the Great Plains and their trophic ecology in these systems is relatively well documented (Cross and Collins 1995). Although dace have been reported to consume both algae and invertebrates (e.g., Cross and Collins 1995), they primarily consumed algae in our experiments (Bertrand and Gido 2007; Bengtson et al. 2008). Shiners are omnivores that forage throughout the water column, primarily consuming aquatic and terrestrial insects and some algae (Gido and Matthews 2001; Bertrand 2007).

Field experiments were conducted in Kings Creek on the KPBS and included both enclosures and exclosures constructed with 5-mm mesh hardware cloth either stretched across the width of the stream (e.g., Bertrand et al. 2009) or in a diamond-shaped exclosure

Table 1. Conditions during experiments used to test effects of the presence of grazing and water-column (wc) minnow relative to controls on stream ecosystem properties. Reference number (Ref #) is used to link these experiments to results in Tables 2 and 3.

Year	Season	Venue	Duration (days)	Disturbance	Functional group	Algal accrual[a]	Fish biomass (g wet mass/m²)	Mean temperature (°C)	Ref #
2002	Fall	Experimental streams	40	Scour	grazer	4.88	24.3	7	1
2002	Fall	Kings Creek	32	Scour	grazer	–	–	–	2
2003	Summer	Experimental streams	65	Scour	grazer	0.85	14.9	22	3
2004	Summer	Experimental streams	80	Scour	wc minnow	0.99	11.5	22	4
2005	Summer	Kings Creek	56	Scour	grazer/wc minnow	3.11	6.0	22–38	5
2005	Fall	Experimental streams	28	Scour	grazer	2.67	17.0	13	6
2006	Spring	Kings Creek	63	Dry	grazer	13.85	3.1[b]	21	7
2006	Summer	Experimental streams	66	Dry	grazer/wc minnow	3.12	9.0	23	8
2006	Fall	Experimental streams	35	Scour	grazer	0.92	8.4	14	9
2007	Fall	Experimental streams	28	Scour	grazer/wc minnow	3.12	23.6	21	10

[a] Algal accrual rate (mg/m²/d) was calculated as chlorophyll a (mg/m²/d) ÷ days since disturbance at approximately 2 weeks (see Methods for specifics).
[b] This was a field exclosure experiment; thus, grazing minnow densities varied over time. This estimate was made at three weeks after the beginning of the experiment.

in the middle of the stream (Murdock et al., in press). We took advantage of natural events and followed successional trajectories of ecosystem properties after scouring floods or the rewetting of a dry stream channel. Nutrient concentrations in Kings Creek are relatively low because of the lack of anthropogenic or other sources of nutrients in the catchment. Nutrient concentrations typically increased moving downstream in the catchment. Total nitrogen (TN) averages about 750 µg/L (range 90–2,000 µg/L) downstream and 280 µg/L (range 90–700 µg/L) upstream. Total phosphorus (TP) averages about 40 µg/L (range <10–260 µg/L) downstream and 12 µg/L (range <10–100 µg/L) upstream.

Experimental streams were approximately 1,800 L and consisted of a 2.54-m^2 pool connected to a 0.84-m^2 riffle (Matthews et al. 2006). Water was drawn through a 15-cm-diameter pipe, buried beneath the substrata, by an electric trolling motor and propelled downstream through the riffle and pool at a mean discharge of about 10 L/s. In addition, low-nutrient groundwater was continuously added from a natural spring at a mean rate of about 1 L/min, which allows a complete replacement of water approximately each day. A shade canopy that blocked 57% of incoming solar irradiance simulated riparian cover. Substrata were a mixture of pebble, gravel, and fine sediment from a local quarry. Experiments were typically initiated after simulated disturbances in which the substrate was scoured with a high pressure hose or had been completely dried. Nutrient concentrations across experiments were representative of upstream conditions in Kings Creek and typically below detection (<10 µg/L) for TP and from 4 to 163 µg/L for TN.

Methods for measuring ecosystem properties were generally consistent across experiments and are described in other papers (Ber-

trand and Gido 2007; Bengtson et al. 2008; Bertrand et al. 2009; Murdock et al., in press). For this analysis, we focused on the recovery of gross primary productivity (GPP), algal biomass, algal filament lengths, proportion of fine benthic organic matter (FBOM), and benthic invertebrate assemblages following a disturbance because these were influenced by fishes in previous experiments. GPP was estimated by tracking diel fluctuations in dissolved oxygen and correcting for reaeration (Owens 1974). Benthic algal biomass was estimated by extracting chlorophyll *a* from pebbles in different treatments (Sartory and Grobbelaar 1984; Welschmeyer 1995). Benthic organic matter (BOM) and benthic invertebrates were collected using a modified core sampler (see Bertrand and Gido 2007 for details). FBOM was estimated by passing a slurry from the core sample through a series of filters and then measuring ash-free dry mass of those samples; FBOM was measured as the proportional weight of the size fraction <100 µm relative to the total weight of BOM. For benthic invertebrate abundances, we focused on the abundance of the family Chironomidae because other taxa varied considerably across experiments. Chironomids were often abundant and present in all experiments; mean percent of total abundance was 35.8% (range 6.6–76.9%), and mean percent of total invertebrate biomass measured in the four experiments in which biomass was measured was 29.7% (range 11.6–43.5%). The other numerically dominant taxa in these samples were zooplankton but were not considered here because they did not account for as much (<20%) of the total invertebrate biomass as chironomids. We also evaluated effects of fishes on invertebrate assemblage structure using a percent similarity index (PSI; Renkonen 1938) to evaluate differences between control and fish treatments. Val-

ues range from 0 to 1.0, with a 1.0 indicating identical proportional similarity of species in the invertebrate assemblages.

Data Analysis

The first step in our analysis was to use analysis of covariance (ANCOVA), with time since disturbance as the covariate, to test the effects of dace and shiners on ecosystem properties across experiments. For this, and other analyses, we did not distinguish between floods and drying, as there were only two drying experiments, thus making it difficult to evaluate effects of different disturbance type. Prior to this analysis, recovery trajectories of each response variable were standardized using z-scores (i.e., subtracted each response from the overall mean for that experiment and divided by the standard deviation) to allow comparisons across studies. After standardization, ANCOVA tested for differences between fish and no fish controls across experiments.

As a second step, we evaluated effects of fishes at different time intervals after disturbance events. Specifically, we used a meta-analysis to test if the log response ratio [LRR = ln (mean$_{fish}$/mean$_{no\ fish}$)] (Hedges et al. 1999) deviated significantly from zero for response variables measured early (within the first 2 weeks) and late (after 4 weeks) in the experiment. The program MetaWin 2.0 (Rosenberg et al. 2000) was used to calculate bootstrapped 95% confidence intervals for mean effect sizes and to test for heterogeneity of effects (Q_T) across experiments. Confidence intervals around mean effect sizes that did not overlap zero indicate the species had a consistent positive or negative effect on that response variable. Significant heterogeneity (Q_T) across experiments suggested that variance among effect sizes was greater than expected and other explanatory variables should be investigated (Rosenberg et al. 2000). Thus,

for variables that showed significant heterogeneity, we used simple correlation analysis to explore the associations of log response ratios and two potentially confounding factors: system productivity and fish density. System productivity was estimated by algal accrual rates measured as chlorophyll a (mg/m^2) in no fish controls ÷ days since disturbance. To standardize this estimate across experiments, we only used measurements taken either 14 d (five experiments) or 18 d (two experiments) post-disturbance. The one exception was for fall 2002, in which chlorophyll a was only measured 40 d post-disturbance. We corrected the accrual rate of this value (multiplied by 0.70) based on the relationship of measurements from other experiments that were taken around days 14 and 40. Algal accrual rates provided an index of productivity for each experiment that was independent of the fish effects because it was taken from the control stream. We set our alpha at 0.10 for all of the above-mentioned analysis because of the limited number of experiments available. Algal accrual rates were log-transformed prior to analysis to reduce the influence of extreme values.

Results

Nine experiments testing the effects of dace and four experiments testing the effects of shiners were conducted between 2002 and 2007 (Table 1). As expected, GPP, algal biomass (as chlorophyll a), BOM, and chironomid abundance was low following disturbance (scour or drying) and increased with time (Figures 2 and 3). This increase, however, was generally linear and did not appear to plateau in the time frame of our experiments. Across experiments, the only significant effect of fish was a general reduction of chironomid abundance in the presence of dace (ANCOVA; P = 0.091).
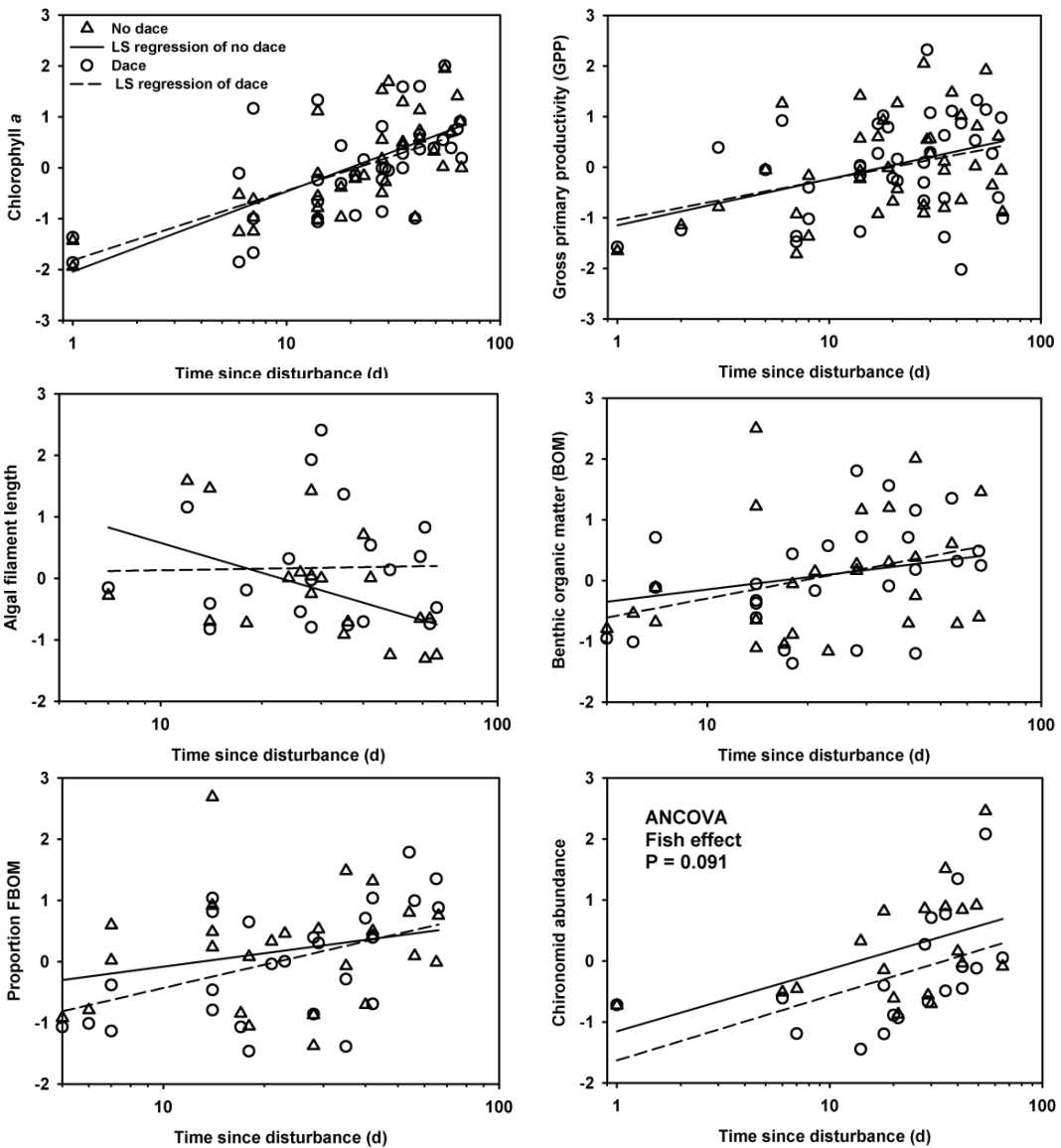
Figure 2. Ecosystem properties of field experiments and experimental streams as a function of time since disturbance (plotted on a log scale). Circles represent treatments with grazers (southern redbelly dace) and triangles are controls. Dependent variables (*y*-axis) are presented as standardized values (i.e., *z*-scores).

Meta-analysis of dace effects on response variables at different intervals after a disturbance indicated that the deviation of fish effects from zero (i.e., 95% confidence intervals did not overlap zero) only occurred for two response variables, FBOM and chironomid densities, measured less than 14 d post-disturbance (Table 2; Figure 4). Mean log response ratios were negative for both these variables, indicating a general reduction of the propor-
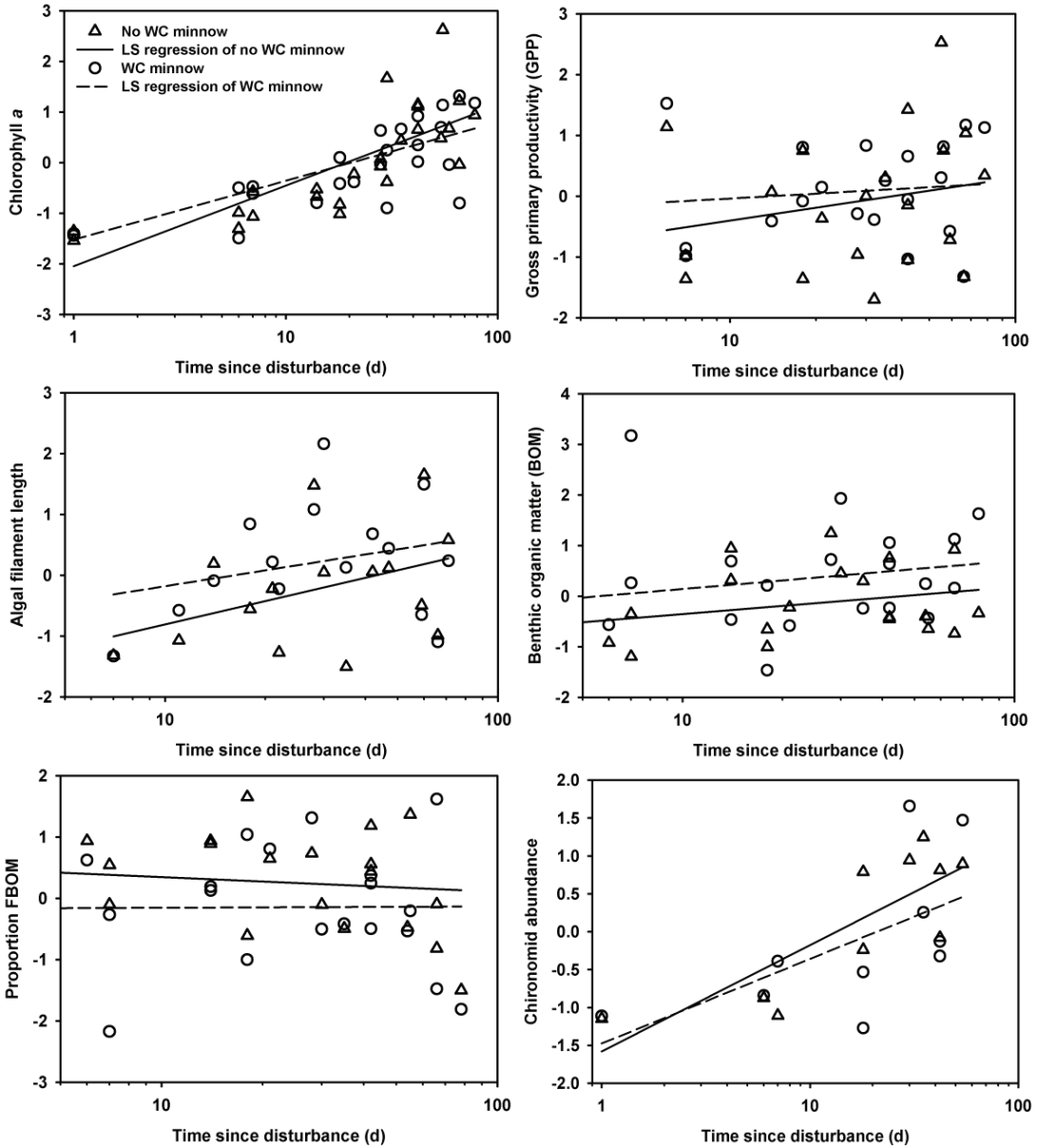
Figure 3. Ecosystem properties of Kings Creek and experimental streams as a function of time since disturbance (plotted on a log scale). Circles represent treatments with water column minnows (red shiner) and triangles are controls. Dependent variables (y-axis) are presented as standardized values (i.e., z-scores).

tion of FBOM and chironomids with dace relative to controls. In addition to reductions in chironomid abundance, mean differences in percent similarity of benthic invertebrate communities was notably lower soon after disturbance compared to after more than 28 d (72% versus 82%). Meta-analysis also indicated that LRR for algal biomass and algal filament lengths measured more than 28 d post-disturbance were highly heterogeneous

Table 2. Log response ratios and change in benthic invertebrate composition between southern redbelly dace (grazing minnow) and control treatments for individual experiments. Reference number in the first column refers to experiments described in Table 1. Values greater than zero indicate the value in the treatment with fish present was lower than in the control (no fish) treatment. Meta-analysis summary statistics are given below each variable, including mean log response ratio, bootstrapped 95% confidence intervals, total heterogeneity of sample (Q_T), degrees of freedom and P-value testing the significance of Q_T. GPP = gross primary productivity; FBOM = fine benthic organic matter; CI = confidence interval.

Ref. #	Replicates	GPP		Chlorophyll a		Algal filament length		FBOM		Chironomid density		Percent similarity change	
		<2 weeks	>4 weeks	<2 weeks	>4 weeks	<2 weeks	>4 weeks	<2 weeks	>4 weeks	<2 weeks	>4 weeks	<2 weeks	>4 weeks
1	3	0.03	−0.15	−0.10	−0.10	–	−4.60	–	–	−0.78	0.66	0.95	0.92
2	2	–	–	–	−3.98	–	–	–	–	–	–	–	–
3	12	0.00	0.16	0.22	0.13	−0.10	−0.02	−0.20	−0.10	−0.59	−0.92	0.69	0.54
5	5	−0.55	0.38	−0.46	−0.10	–	–	−0.15	−0.08	−0.47	−0.04	0.82	0.89
6	4	−0.20	0.02	−0.12	−0.31	−1.00	−0.57	−0.04	0.02	−1.30	−0.22	0.86	0.88
7	8	0.13	−0.37	−0.30	−0.38	–	−0.84	–	–	−0.53	−1.58	0.33	0.79
8	4	−0.07	0.01	−0.27	−0.53	0.27	0.69	−0.07	−0.01	–	−0.63	–	0.88
9	6	0.25	0.15	−0.03	0.34	–	0.64	−0.28	−0.74	−1.32	0.05	0.65	0.83
10	6	–	–	0.92	0.13	−0.05	0.49	−0.39	0.42	−1.29	−0.57	–	–
Mean		−0.06	0.03	−0.02	−0.53	−0.22	−0.60	−0.19	−0.08	−0.90	−0.41	0.72	0.82
Lower CI		−0.26	−0.14	−0.24	−1.50	−0.77	−2.15	−0.29*	−0.40	−1.20*	−0.81	0.53	0.71
Upper CI		0.09	0.18	0.32	0.00	0.11	0.34	−0.10*	0.16	−0.64*	0.06	0.86	0.88
Q_T		0.41	0.35	1.29	13.97	0.89	20.77	0.09	0.70	0.92	3.23	0.24	0.10
df		6	6	7	8	3	6	5	5	6	7	5	6
P-value		1.00	1.00	0.99	0.08	0.83	0.00	1.00	0.98	0.99	0.86	1.00	1.00

* indicates that 95% confidence intervals do not overlap zero.
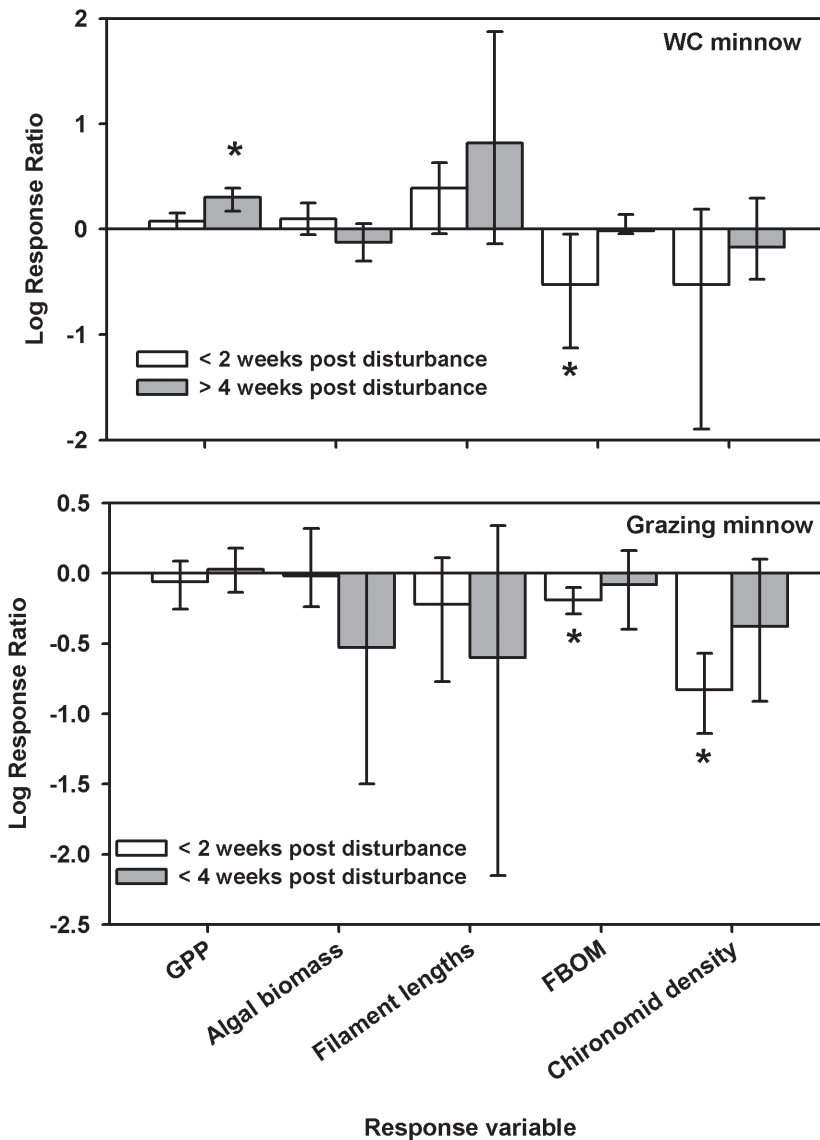
Figure 4. Mean log response ratios [ln (mean$_{fish}$/mean$_{no\ fish}$)] and bootstrapped 95% confidence intervals for response variables measured early (<2 weeks; open bars) and late (>4 weeks; gray bars) after disturbance for experiments with southern redbelly dace (grazing minnow) and red shiners (water column minnow).

across experiments (Table 2). An exploratory analysis suggests an association between the ratio of fish:algal biomass may explain some of the variability in the effect of dace on algal biomass (Figure 5). That is, the presence of dace increased algal biomass when they were stocked at high densities and there were low algal accrual rates and decreased algal biomass at low stocking densities and high algal accrual rates. There was no strong association between algal filament lengths and experimental conditions; however, the two experiments with the
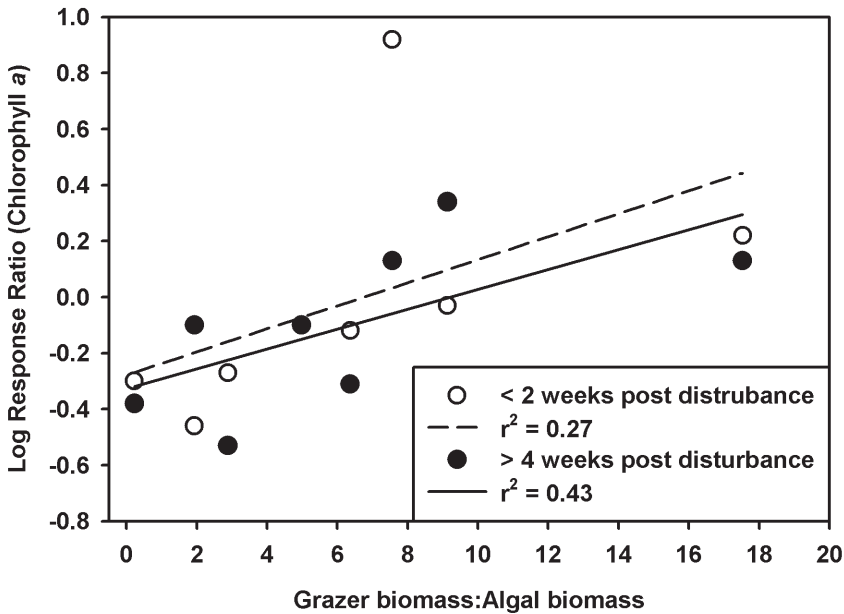
Figure 5. Relationship between fish:algae biomass (*x*-axis) and the effect (log response ratio) of southern redbelly dace (grazing minnows) on algal biomass (chlorophyll *a*). Log response ratios greater than zero indicate dace had a positive effect on algal biomass and negative numbers represent negative effects.

strongest negative effect of dace were also the two experiments with the highest algal accrual rates (Tables 1 and 2).

Two response variables showed consistent trends across experiments with shiners (Table 3; Figure 4). Similar to dace experiments, the presence of shiners consistently reduced the proportion of FBOM measured less than 14 d post-disturbance and mean differences in percent similarity of benthic invertebrate communities was notably lower soon after disturbance compared to after 28 d (73% versus 92%). Shiners also consistently increased primary productivity more than 28 d post-disturbance. Depending on the response variable measured, we did not attempt to attribute experimental conditions to variation in LRR because there were only three or four experiments conducted. Alternatively, we report heterogeneity of LRR for shiner experiments (Table 3).

Discussion

Role of Fishes in the Recovery of Periphyton

Regardless of significant effects of prairie stream fishes on algal biomass and filament lengths in individual experiments, when evaluated across experiments, there was little consensus on the direction and magnitude of these effects. The only consistent effect of fish (dace and shiners) was a reduction of FBOM within the first 2 weeks following a disturbance. It appears that foraging activities of fishes removes FBOM from substrates, either through consumption or bioturbation. Of the individual experiments evaluated, the strongest negative effects of dace on periphyton were during a field exclosure experiment following recovery from drought in spring 2006 when excluding dace and another species of grazing minnow, central stonerollers

Table 3. Log response ratios and change in benthic invertebrate composition between red shiner (water-column minnow) and control treatments for individual experiments. Reference number in the first column refers to experiments described in Table 1. Values greater than zero indicate the value in the treatment with fish present was lower than in the control (no fish) treatment. Meta-analysis summary statistics are given below each variable, including mean LRR, bootstrapped 95% confidence intervals, total heterogeneity of sample (Q_T), degrees of freedom and P-value testing the significance of Q_T. GPP = gross primary productivity; FBOM = fine benthic organic matter; CI = confidence interval.

Ref. #	Replicates	GPP		Chlorophyll a		Algal filament length		FBOM		Chironomid density		Percent similarity change	
		<2 weeks	>4 weeks	<2 weeks	>4 weeks	<2 weeks	>4 weeks	<2 weeks	>4 weeks	<2 weeks	>4 weeks	<2 weeks	>4 weeks
4	12	0.15	0.39	0.31	−0.31	0.52	1.87	−0.05	−0.07	0.12	0.29	0.71	0.93
5	5	0.00	0.35	−0.03	−0.06			−1.49	0.03	0.19	−0.19	0.91	0.89
8	4	0.07	0.17	−0.08	−0.30	0.69	0.72	−0.05	−0.01	−1.90	−0.62	0.56	0.94
10	6			0.18	0.17	−0.04	−0.14	−0.09	0.19				
Mean		0.07	0.30	0.10	−0.13	0.39	0.82	−0.53	−0.01	−0.53	−0.17	0.73	0.92
Lower CI		0.00	0.17*	−0.05	−0.30	−0.04	−0.14	−1.13*	−0.04	−1.90	−0.48	0.56	0.89
Upper CI		0.15	0.39*	0.25	0.05	0.63	1.87	−0.05*	0.14	0.19	0.29	0.91	0.94
Q_T		0.01	0.03	0.10	0.15	0.29	2.04	1.52	0.04	2.81	0.42	0.06	0.00
df		2	2	3	3	2	2	3	3	2	2	2	2
P-value		0.99	0.99	0.99	0.98	0.86	0.36	0.68	1.00	0.25	0.81	0.97	1.00

* indicates that 95% confidence intervals do not overlap zero.

Campostoma anomalum, initially (i.e., the first month after rewetting) resulted in 132% longer filament lengths, 113% higher algal biomass, and 45% higher primary productivity (Murdock et al., in press). In experimental streams, we also found significant negative effects of dace on algal filament lengths in three separate experiments, but those effects were restricted to the first 3 weeks of the experiments and not associated with declines in algal biomass (Bertrand and Gido 2007; Bengtson et al. 2008). In two studies in experimental streams, we found positive effects of dace on algal biomass (Bertrand 2007; D. J. Hoeinghaus, University of North Texas, unpublished data), and in the remaining three experiments, we either found no effect of dace on algal filament lengths or biomass or this effect included a complex interaction with habitat or other treatments. Shiners had strong positive effects on algal biomass and filament lengths in the experimental streams in 2004, but these effects were not consistent across experiments, with the exception of GPP measured more than 4 weeks post-disturbance.

The ability of fish to alter the structure and production of periphyton is likely dependent on algal community composition following disturbance and the susceptibility of those species to consumption or disruption by fishes (e.g., Power et al. 2008). The dominant algae following disturbances in Kings Creek and in experimental streams were filamentous green algae (*Spirogyra* spp. and *Ulothrix* spp.), which loosely attach to the substrate. Although diet data showed consumption of these algal taxa by dace, they could also shorten filaments by disturbing the upper part of the benthic habitat and knocking stalks loose (dashed line in Figure 1). Considering the general reduction in FPOM across experiments, it appears that foraging by dace also can reduce the abundance of small fragments.

High densities of dace increased algal biomass, but this was only apparent in experiments with low rates of algal accrual and is illustrated by examining how dace effects on algal biomass varied as a function of the ratio of dace:algal biomass (Figure 5). Dace were most likely to have a negative effect on algal biomass when their biomass was low relative to algal biomass and a positive effect when their biomass was high relative to algal biomass. This was in contrast to the prediction that at high densities, grazers should have the strongest effect. Apparently, the consumptive losses associated with high densities of dace were either compensated for by increased production of existing algal species or by increases in other algal taxa (e.g., diatoms). It is possible that a conversion to alternative algal taxa may have been facilitated by increased nutrients excreted by fishes. Negative effects of dace when algal biomass is high might also be a function of increased grazer efficiency. For example, in a recent meta-analysis of more than 800 experiments, Hillibrand (2009) found that grazers removed a higher proportion of periphyton in experiments with the highest algal biomass. He suggested increased efficiency may have been due to increase ingestibility or accessibility under these conditions. These somewhat complex results suggest the potential for compensatory responses of algae to grazers and points to the importance of algal community composition in mediating fish effects.

The lack of or positive effect of grazers on periphyton structure and biomass is counter to other studies that indicate that grazers should reduce algal biomass when the fish:algal biomass is high. For example, Winemiller et al. (2006) found negative effects of herbivorous fishes on algal biomass (as chlorophyll *a*) when high densities of migratory fishes occupied a tropical stream, but low densities of resident fishes were not able to reduce algal biomass.

They predicted that a lack of a stable equilibrium between consumer and resource biomass should result in oscillating effects of herbivores on algal biomass. Low biomass of consumers also may stimulate primary producers. Power (1990) showed that at low densities, foraging activities by grazers can clear sediments and increase growth of algae. Moreover, low densities of secondary consumers (i.e., water column minnows) can elicit a behavioral response of invertebrate prey that can decrease invertebrate grazing rates (Peckarsky et al. 1993), and this could influence rates of primary production. Although we did not conduct a rigorous test of confounding factors, our experiments suggest that dace had a positive effect on algal biomass when their biomass was high relative to algal biomass. These conditions typically occurred after disturbances or in experiments with low nutrient-loading rates. We hypothesize that the net effect of dace was positive because consumption was balanced by stimulation of algal growth directly through remineralization of nutrients (Bertrand and Gido 2007) or indirectly by reducing chironomid abundances or through bioturbation. Alternatively, negative effects of dace when algal biomass was high relative to fish biomass may have resulted because nutrients were less limiting; thus the net effect of dace was negative.

Although identifying the context in which fish exert a strong effect on periphyton is still a challenge, factors influencing algal community composition and accrual rates are potentially good predictors of these effects. Both nutrient loading and disturbance are strong drivers of algal community dynamics and are potential factors that will influence the balance between dace and algal biomass. Quantifying the consumptive demand by fishes relative to algal community dynamics should be an informative way of predicting the direction and magnitude of fish effects on periphyton com-

munities. However, models that describe these interactions may be complex and may require an understanding of the complex behavioral dynamics, lagged responses, and spatial distribution of fishes.

Fish Effect on Invertebrate Communities Following Disturbance

Although similarity of invertebrate assemblages between fish and no fish treatments was often high, several of our experiments documented differences in abundance or biomass of invertebrate taxa between fish and no fish treatments. The most notable effect of fishes was a general reduction of chironomids in the presence of grazers. Diet analysis from the experiments suggests only minimal (presumed to be incidental) consumption of midges by dace, indicating that these negative effects were indirect. The reduction of chironomids by dace was most pronounced in our spring 2006 field experiment following stream drying. In this experiment, the presence of dace strongly reduced algal biomass and chironomid densities. In other experiments, because algal biomass was generally not reduced or increased by grazers, we hypothesized that indirect mechanisms limited colonization of midge larvae. These midge assemblages were dominated by *Rheotanytarus* spp., which build tubes on coarse substrates. Dace likely interfered with and inhibited *Rheotanytarsus*, directly and indirectly, through their feeding activities. Although not included in our analysis, we also noted in several experiments that microcrustacean densities tended to track algal filament lengths and biomass, indicating that changes in periphyton structure by fishes might also influence invertebrate communities. Our results are consistent with Flecker (1992) who reported that the presence of herbivorous and detritivorous fishes reduced benthic invertebrates in Rio Las Marias, Venezuela as a result of sediment pro-

cessing and, for some invertebrate taxa, by in-timidation. As with periphyton communities, predicting the influence of fishes on stream invertebrate communities remains a challenge. Clearly identifying trophic linkages and indi-rect effects among fishes and invertebrates will help deduce the relative importance of fish in regulating invertebrate abundances.

Predicting Ecosystem Effects of Stream Fish

We expect the greatest effect of fish consumers to occur shortly after a disturbance, assuming that the biomass of fishes was high relative to the biomass of resources. This outcome was the case in several of our experiments, in which dace negatively affected algal filament lengths in streams soon after disturbance, but this ef-fect diminished after 2 weeks (Bertrand 2007; Bengtson et al. 2008). Positive effects of dace and shiners on algal biomass were also great-est within the first few weeks after disturbance (Bertrand 2007; Murdock 2008). Assuming that the role of fishes in structuring stream ecosystems is greatest soon after a disturbance, frequently disturbed streams may be more likely to be influenced by fishes than those that are more stable. However, this influence is contingent on the ability of fishes to maintain high densities or rapidly colonize frequently disturbed systems. Thus, differences in dis-turbance regimes and other conditions across geographic regions may lead to context-spe-cific predictions of fish effects on ecosystems. Our synthesis is based on a series of experi-ments on the effects of two functional groups of fishes in prairie streams and may not extend to other systems such as tropical streams that are more heavily dominated by grazers and de-tritivores (Wootton and Oemke 1992).

The scale of measurement also may con-strain the predictive capacity of experiments. In several of our experiments, we noted dif-ferent responses of periphyton communities in riffle and pool habitats (Bertrand 2007; Murdock 2008). Grazing and water column minnows are often observed foraging in clus-ters and are not evenly dispersed within these pools (e.g., Harvey 1991). Greater densities of fishes can also occur at the interface between pools and riffles. Biomass of fishes used in our experiments ranged from 6 to 24 g/m², which was representative of mean densities of fishes in pools found in Kings Creek (Franssen et al. 2006; Bertrand et al. 2007). These densi-ties also were consistent with other studies testing the effects of fish on algal communi-ties (Table 4). However, using mean densi-ties may miss strong effects related to large schools of fishes moving into and out of areas. In general, it is important to consider a range of densities that represent the scale at which fishes interact with benthic communities, and we are currently pursuing such studies. More research on movement patterns of fishes and effect of aggregations of fishes would help evaluate the appropriate scale for conducting these experiments (e.g., Flecker et al. 2010, this volume).

Effects of fishes on streams are likely to vary over longer time scales than most field experi-ments, which are typically less than 4 weeks. One exception was Gelwick and Matthews (1992), who found strong effects early in field experiment after scouring flood, but effects di-minished after 6 weeks with the senescence of algae communities. Our temporal trajectories commonly showed differences in ecosystem rates that were mediated by consumers in the first few weeks following disturbance, but after a month or more treatments converge and in some instances reversed (e.g., Bertrand et al. 2009). Our experiments were scaled to match the approximate temporal sequence of distur-bances (drying or flooding every month or two). The dependence of these results on the

Table 4. Densities and biomass (wet mass) of grazing fishes in previous experiments evaluating their influence on stream periphyton.

Source	Density (#/m²)	Biomass (g/m²)	Venue	Results
Power 1990	4	10	Field	Grazers stimulated algal growth.
Gelwick and Matthews 1992	1.8	<10 g/m²	Field	Grazers reduced periphyton biomass.
Gelwick and Matthews 1997	9		Mesocosm	Grazers reduced periphyton biomass.
Power and Matthews 1983	~1–6		Field	Grazers reduced algal height.
Flecker 1992	1.1 and 3.7		Field	Grazers reduced periphyton biomass.
Vaughn et al. 1993	7.8	12.01–14.34	Mesocosm	Grazers effected algal community composition.
Evans-White et al. 2003	9.0 and 18.0	1.5 and 14.4[a]	Mesocosm	Grazers reduced periphyton biomass at high densities.
Inoue and Miyayoshi 2006	5.0		Field	Grazers reduced periphyton biomass.
Abe et al. 2007		15 and 74	Mesocosm	Grazing fish reduced algal accumulation rate.

[a] Estimated wet mass from dry mass given in paper; assuming wet mass is = dry mass $\times$ 2.

temporal component suggests a consideration of intervals between disturbances is necessary to evaluate the importance of fishes in structuring stream ecosystems. Additionally, more long-term manipulative experiments, similar to those in terrestrial systems (e.g., Brown et al. 2001), conducted over multiple years may yield insight into seasonal and annual variation in the strengths of fish effects on ecosystem processes.

What is the relative merit of field experiments and experimental streams? Field experiments come closest to matching "real" conditions. However, these experiments can still have limitations, including potential cage effects (e.g., Cooper et al. 1990); difficulties with replication; and the potential for extreme hydrologic events destroying cages during the course of the experiment. While mesocoms are not as "real," they allow for better replication and isolation of specific variables of interest. For example, based on our studies, gross primary productivity of whole stream channels cannot be measured in reaches less than ~30 m in local streams. This length of

experimental reach is difficult to manipulate for any length of time and it is difficult to find reaches that are similar enough to serve as replicates and are independent (i.e., not directly downstream from another treatment). Given the limitations of both approaches, we have adopted an approach of paired field and mesocosm experiment, using mesocosms to identify mechanisms underlying patterns and relationships and field studies to test the importance of those mechanisms in the context of natural communities and environmental conditions.

Part 2: Potential Interactions of Stream Fishes in Prairie Stream Ecosystem Recovery Following Floods and Drought

Recovery of Stream Ecosystems from Disturbance

We used data from the published literature (e.g., Power and Stewart 1987; Peterson 1996) and our own work on prairie streams to de-

velop predictions on how stream ecosystem structure and function change after disturbances. Our experience in prairie streams suggests that stream nutrient concentrations can change rapidly with disturbance, but often stabilize with time. In particular, an initial pulse of nutrients occurs following floods and is shortly followed by a decrease in dissolved nutrients because of dilution (Figure 6A). The magnitude of variability and duration of these effects are likely dependent on nutrient sources in the catchment. In contrast to flooding, dissolved nutrients in prairie streams are relatively high when dry channels are rewetted because of leaching of materials from the dry streambed and dominance by high-nutrient groundwater inflows. In the absence of consumers, stream algal biomass increases until resource limitation (e.g., nutrients or light) slows growth (Figure 6B). During accumulation, early successional species dominance gives way to late successional species (Hoagland et al. 1982), and understory algal cells may senesce and detach (Townsend and Padovan 2005). The initial algal community after drought can vary as desiccation resistant species in dry biofilms influence successional trajectories upon rewetting (Peterson 1996; Robson and Matthews 2004). These successional trajectories can lead to assemblages that respond differentially to grazing (Wellnitz and Radar 2003).

Organic matter is removed by a scouring flood and accrues at a decelerating rate with time after a disturbance. Gentle flow returning to a dry streambed has minimal effects on the amount of benthic organic matter, whereas FBOM may gradually increase following a flood as consumers breakdown coarse organic fractions (Figure 6C). Invertebrate consumer diversity should increase in a stair-step manner because some colonists facilitate colonization of subsequent groups (e.g., shredders
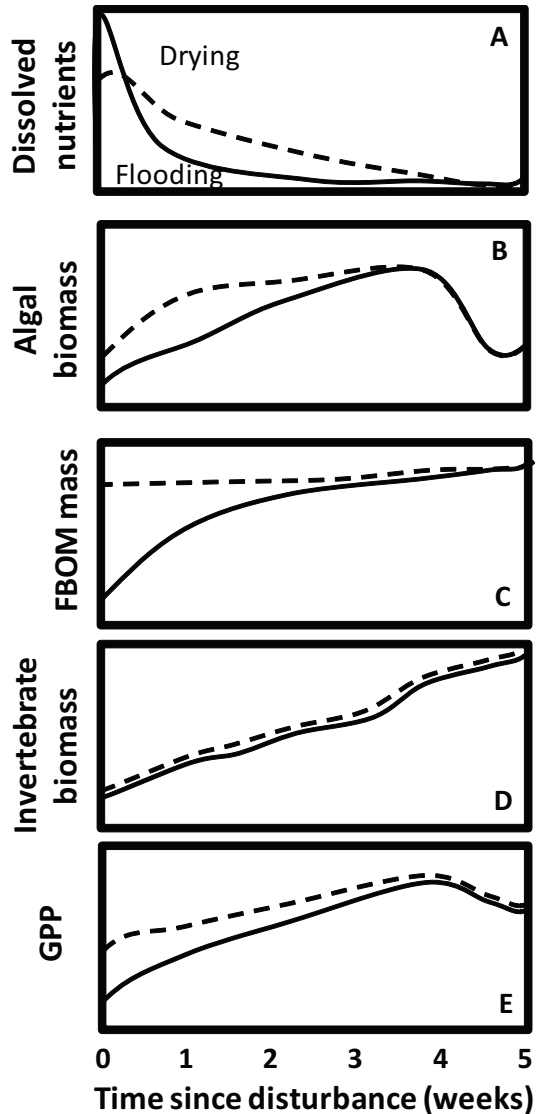

Figure 6. Predicted recovery of stream ecosystem properties after scouring floods (solid lines) or stream drying (dashed lines). FBOM (fine benthic organic matter) is the proportion or abundance of fine particulate organic matter and GPP (gross primary productivity) is the gross primary productivity of the stream.

producing FBOM and facilitating collectors [Cummins 1973]), periods of dispersal and colonization (e.g., adult emergences) vary among taxa, and there should be a lag response to the accumulation of algae and de-

tritus in the system (Figure 6D). Invertebrate biomass, on the other hand, should increase in a generally linear fashion as overall abundance increases and larger individuals and taxa colonize. As biomass of grazers and detritivores accumulates in the system, their consumption of algae and detritus may alter the biomass and abundance of those resources. In general, ecosystem rates (metabolism and nutrient retention) should track changes in algal biomass, algal efficiency, and total organic matter. These rates should increase with time since disturbance but stabilize or decline if algal communities begin to slough (Figure 6E).

The experiments we evaluated above in prairie streams illustrate these general patterns of recovery (Dodds et al. 2004; Bertrand 2007; Murdock 2008) and provide a basis for predicting how fishes can alter patterns of recovery of these stream ecosystem properties. Our work, along with others (Dodds et al. 2004; Takimoto et al. 2009), suggest that a major factor determining interactions between fishes and stream ecosystem properties is relative turnover rates of biota. In prairie streams, we hypothesize that resistance and resilience of organisms can affect recovery trajectories of ecosystem properties, such as GPP, nutrient retention, and standing stocks of organisms. In general, recovery of microbial assemblages occurs within hours to days, and some macroinvertebrates can recover within days to weeks (Fritz and Dodds 2002). Fishes typically resist flooding or rapidly recolonize intermittent streams if the disturbed area was in close proximity to a source population (Murdock 2008).

Role of Fishes in the Recovery of stream Ecosystems

Nutrients

Stream fishes influence nutrient availability and stoichiometry (Vanni 2002; Hood et al.

2005; Hendrixson et al. 2007, McIntyre et al. 2007, McIntyre and Flecker 2010). Characteristics of species (e.g., body nutrient ratios) and their functional roles may dictate their effect on nutrient release and uptake by microbes, and we generally expect the effects of fishes on dissolved nutrients to diminish with time since disturbance as algal mats thicken and algae may rely more on internal recycling of nutrients or other factors, such as light, become limiting.

Soon after disturbance, grazing fishes can have variable but positive effects on dissolved nutrient concentrations directly through excretion or indirectly by removing algae that takes up nutrients (Figure 7A). Water column minnows can increase nutrients through excretion, but also, by feeding on terrestrial materials, they should increase transfer rates of those nutrients into soluble forms. If water column minnows consume herbivorous invertebrates, water column nutrients might also decline as increasing periphyton released from grazing increases nutrient uptake. Over longer time scales, both functional groups could serve as a net sink of nutrients by assimilating available nutrients into body tissue (Vanni 2002).

Periphyton

Herbivorous stream fishes can have negative (Power et al. 1985; Gelwick and Matthews 1992; Bengtson et al. 2008), positive (Power 1990; Bertrand 2007), and neutral (Bertrand and Gido 2007) effects on algal biomass. Based on our work and that of others (Gelwick and Matthews 1992), the effects of fishes should diminish with time (Figure 7C). Conflicting patterns are likely due to the balance between consumptive losses and stimulation, which vary with functional roles of fishes and algal community composition. Stimulation of algal growth may occur through increased nutrients, removal of sediments (Power 1990), or altering of community structure (e.g., Abe et al. 2007),
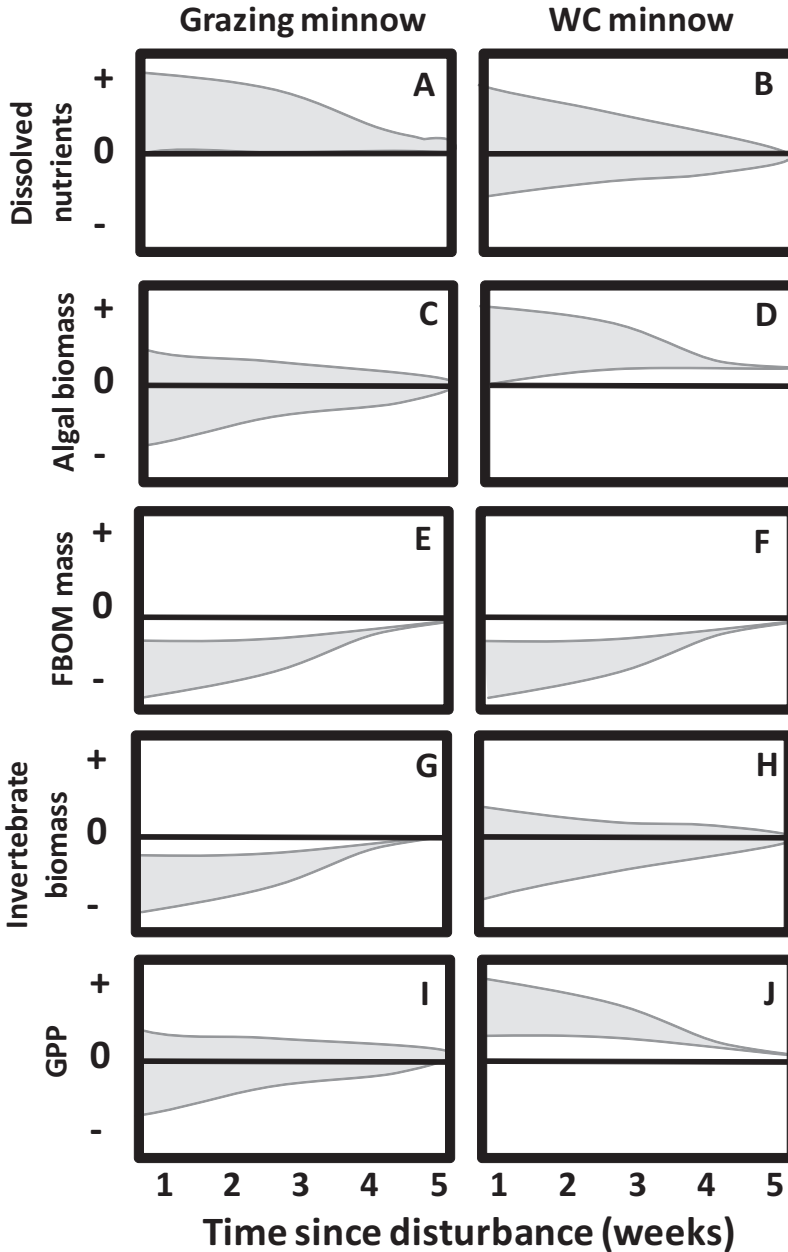
Figure 7. Predicted effects of grazing and water column minnows on the recovery of stream ecosystem properties after a disturbance. Shaded areas represent the expected range of effect sizes based on a literature review and observations from prairie streams.

and if grazer densities are high, consumption rates may, but not always, exceed stimulatory effects. Water column minnows can influence periphyton communities through both trophic cascades and excretion of soluble nutrients. In a 3-trophic-level system as is commonly seen in prairie streams (fish as the top predator, invertebrates as herbivores, and periphyton), the

presence of water column minnows is predicted to have a generally positive effect on periphyton (Figure 7D). The effect of grazers and water column minnows on periphyton communities is predicted to diminish with time since disturbance as the microbial and invertebrate communities develop and food web interactions become more complex. In addition, the biomass and consumptive demand by fishes relative to periphyton biomass declines.

Organic Matter Pool

Fishes may influence the distribution of living and dead matter as well as the size fractions of that material. In general, the presence of large nonfiltering consumers decreases the amount of fine particulate organic matter (results presented above, Gelwick and Matthews 1992; Figure 7E, 7F). It appears that the breakdown of large particulate organic matter into feces is offset by the removal of small organic particles due to consumption or advective losses resulting from benthic foraging. Moreover, fish may stimulate the growth of larger forms of algae (i.e., filaments) or invertebrates, thus reducing the relative proportion of fine particles in the system (not shown in Figure 7). Fish influences on BOM pools may diminish with time since disturbance because the relative mass of BOM processed by fish will become smaller as the total organic matter pool increases.

Benthic Invertebrate Communities

Herbivorous fishes should generally have a negative effect on benthic invertebrates through either direct consumption (in which case they are actually functioning as omnivores, see Evans-White et al. 2003) or indirectly by competition for resources or physical disturbance of the substrata (e.g., Flecker 1992; Figure 7G). Because most stream food webs are 3-trophic-level systems, we also predict that water column minnows should decrease total abundance of invertebrates or alter community structure to favor predator-resistant taxa (Figure 7H). However, fishes also can alter conditions to favor invertebrates. For example, stream fishes can facilitate foraging by invertebrates (e.g., Vaughn et al. 1993), consume predators of grazing and detritivorous invertebrates (e.g., Power et al. 1985), or subsidize primary producers by excreting nutrients obtained from external sources (Gido and Matthews 2001). Invertebrate communities change markedly with time since disturbance. Thus, we predict that the magnitude of fish effects on total invertebrate biomass will dampen with time since disturbance, as predator-resistant taxa become more abundant.

Stream Metabolism

Fishes can influence stream metabolism by altering primary production or respiration. We expect only moderate influences on respiration because a majority of stream heterotrophs are in the subsurface and not directly influenced by fishes. While fish reduced the proportional abundance in FBOM in core samples, this did not seem to influence respiration (e.g., Bertrand et al. 2009). Algal production is more susceptible to top-down and bottom-up control by fishes than heterotrophic components of stream ecosystems. Thus, overall effects of fishes on whole-stream metabolism are predicted to be greatest in stream with high primary production to respiration ratios (i.e., $P/R > 1$). In general, grazers could positively or negatively influence primary production (Figure 7I), whereas water column minnow effects should generally be positive (Figure 7J). Grazing fishes may remove inactive materials in stream algal biofilms and reduce self shading in mats leading to increased production efficiency (rate of primary production per unit al-

gal biomass). Increased nutrients provided by mineralization should also increase efficiency, so both water column and herbivorous fishes should increase production efficiency. Grazing fishes could also have a positive effect on photosynthesis if their foraging favors faster growing forms of algae. For example, if herbivorous fish remove a modest amount of algal biomass, yet stimulate the remaining algae (by relaxing a limiting factor such as nutrients or light), they could increase algal productivity, particularly productivity per unit algal biomass (production efficiency). Although we are unaware of publications establishing such relationships for fishes, grazing snails can increase periphyton productivity under low light (Lamberti et al. 1989), and they feed with rasping mouthparts in a fashion similar to some herbivorous fishes.

Conclusions

Escalating demands on water resources, balanced with a desire to maintain biological integrity require that ecologists predict the dynamics of these systems and how the loss or addition of components will influence stream biodiversity and associated ecosystem services (e.g., Lundberg and Moberg 2003; Dobson et al. 2006; Thebault and Loreau 2006; Power et al. 2008). Our results confirm that large consumers, in particular grazing and water column minnows, can influence stream ecosystem structure and function. The magnitudes and directions of those influences depend upon numerous factors, including time since disturbance, fish biomass, algal accrual rates, and identity of consumers and producers. We cannot yet predict the outcome of a specific manipulation of consumer densities in spite of numerous experiments in a variety of systems. Nevertheless, the context dependency of fish effects is apparent. Thus, human modifications to ecosystems that alter the disturbance regime

of streams are likely to alter the roles of species in these systems. Specifically, alteration of hydrology, nutrient loading, riparian vegetation, and community characteristics can potentially modify trophic interactions of stream fishes. Further work elucidating the context in which stream consumers regulate ecosystem processes will help predict and hopefully mitigate the consequences of losing fish diversity in highly threatened stream ecosystems.

Acknowledgments

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