

Effects of grazing minnows and crayfish on stream ecosystem structure and function

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Abstract. We compared the effects of 2 common grazers, southern redbelly dace (*Phoxinus erythrogaster*) and crayfish (*Orconectes* spp.), on ecosystem structure and function in experimental streams with pool and riffle habitats. Our goal was to identify potentially overlapping roles of these grazers in these systems. Measures of ecosystem structure included algal filament length, particulate organic matter (POM), densities of invertebrate taxa, and algal biomass. Ecosystem function was measured as gross primary productivity (GPP). Biomass-dependent effects of crayfish and dace on ecosystem properties were compared in autumn 2005 when mean water temperature was 12.9°C (range 7.6–27.9°C). Increasing crayfish biomass did not influence ecosystem properties, but increasing dace biomass negatively affected algal filament length and chironomid abundance and positively affected chydorid abundance. Effects of moderately high biomasses of dace and crayfish were compared in spring 2006 when mean water temperature was 21.4°C (range 17.5–29.9°C). Algal filament lengths were generally low relative to values obtained in autumn 2005 in both dace and crayfish treatments. In addition, algal filament length was shorter and chironomid density was lower in crayfish than in dace streams. The contrasting effects of dace and crayfish across sampling days, seasons, and habitats led us to hypothesize that physiological and behavioral traits of these species might limit the redundancy of their effects on ecosystems across broad spatial and temporal scales.

Key words: primary production, context-dependent effects, experimental streams, prairie stream, periphyton, temperature, physiology, foraging behavior.

Aquatic ecosystems are under significant anthropogenic threats (Dudgeon et al. 2006). However, the effects of losing aquatic species on ecosystem function are difficult to predict because of the diverse forms of organisms and complex interactions among species (Giller et al. 2004). The ecosystem effects of many species might be predicted by grouping species into functional groups (e.g., trophic levels or feeding guilds) and assuming that all species within functional groups have similar effects. Such groupings imply that loss of a species within a functional group should have little effect on an ecosystem because other members of the group can compensate for the loss (i.e., species are redundant within groups; Lawton and Brown 1993). However, individual species can facilitate resource use

among species within functional groups (e.g., Cardinale et al. 2002), or species might partition resources over space or time (e.g., Loreau 2000, Cardinale et al. 2004). Thus, each species in a functional group might provide a unique contribution to the functioning of an ecosystem. The roles of individual species and functional groups and the context within which species in a community alter ecosystems must be characterized to understand fully the consequences of biodiversity losses (e.g., Wardle and Zackrisson 2005).

Aquatic grazers are an important group that can strongly influence stream ecosystem functioning (Feminella and Hawkins 1995, Steinman 1996, Hillebrand 2002). Grazers consume primary producers directly, and they affect primary producer species abundance and diversity, productivity, nutrient uptake, and mineralization in stream ecosystems. Grazers are likely to have overlapping effects in stream ecosystems, but they differ greatly in morphology, physiology, and behavior. Grazer effectiveness is dependent on grazer morphology and algal growth form (e.g., scraping and rasping grazers are more able than other types of grazers to feed on understory algae; Steinman 1996).

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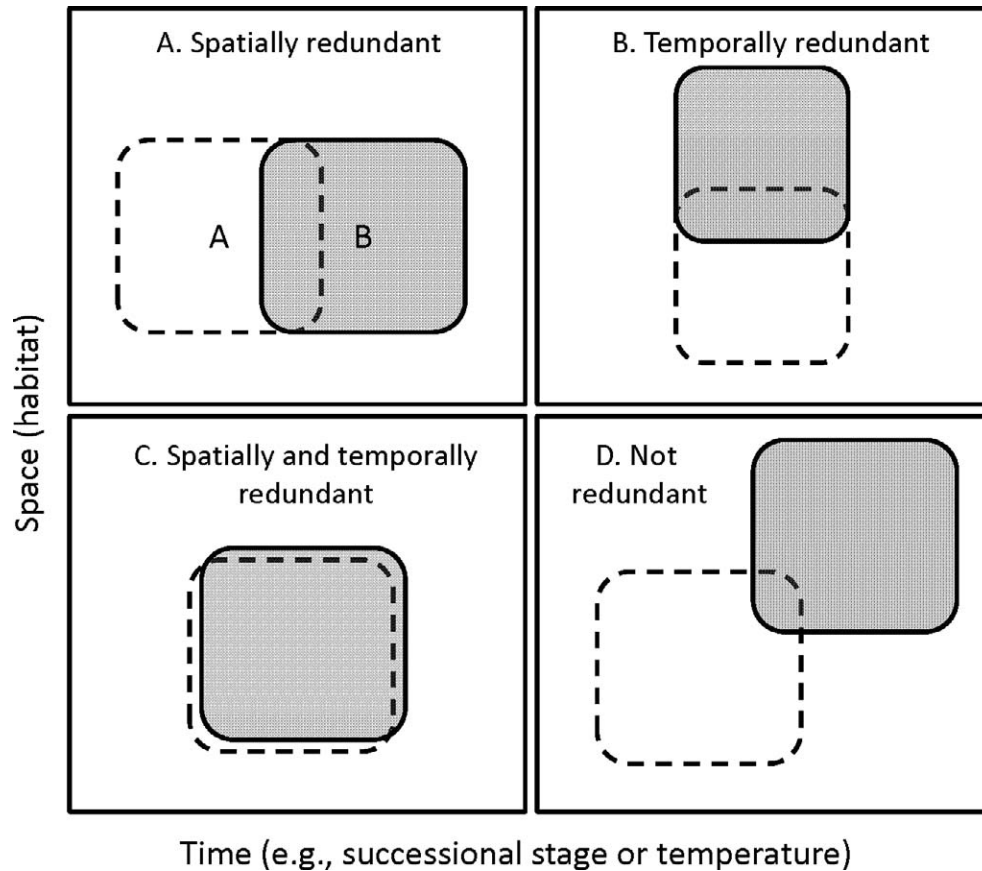


FIG. 1. Conceptual diagram illustrating the potential overlap in ecosystem effects of spatially redundant (A), temporally redundant (B), spatially and temporally redundant (C), and not redundant (D) species within functional groups across space and time. The loss of a species whose effects on ecosystem properties overlap with those of other species over space and time (i.e., C) is predicted not to alter ecosystem properties.

Body size of grazers also is important. For example, smaller-bodied snails probably are better able to crop small adnate algal taxa than are larger-bodied grazers, such as fishes (e.g., Vaughn et al. 1993). Grazers can differ greatly in reproductive turnover and physiology, and seasonal changes in grazer communities probably are associated with thermal tolerance and timing of reproduction. Therefore, species with similar ecological roles might not overlap in space or time (Fig. 1A–D), and the loss of a single species might affect ecosystem function when considered over broad spatial or temporal scales.

Aquatic biodiversity in prairie streams is threatened by numerous human activities (Cross and Moss 1987, Haslouer et al. 2005). Prairie streams are not heavily canopied, and they generally have high primary production (P) relative to respiration (R) ($P/R \approx 1$; Mulholland et al. 2001). Grazers in these streams might provide particularly important links between primary producers and ecosystem function. In North American prairie streams, grazing minnows and crayfish can

occur in high densities and potentially exert top-down (directly through grazing) and bottom-up (indirectly through nutrient recycling) control on primary production (Evans-White et al. 2003, Franssen et al. 2006, Bertrand and Gido 2007).

Crayfish and grazing minnows are dominant grazers in prairie streams and potentially have overlapping roles in these ecosystems. Both taxa can alter standing crops of attached algae, particle size of particulate organic matter (POM), and invertebrate community structure (Power et al. 1985, Gelwick and Matthews 1992, Vaughn et al. 1993, Creed 1994, Charlebois and Lamberti 1996, Bertrand 2007, Bertrand and Gido 2007). Crayfish also can have direct negative effects on invertebrates through predation (Momot 1995, Nyström et al. 1996, Stenroth and Nyström 2003, Usio and Townsend 2004). Morphological differences between grazing minnows and crayfish might cause different effects on primary producers at small spatial scales. Grazing minnows ingest periphyton directly, whereas crayfish have shredding mouth-

parts and feed by grasping and holding food items with their walking legs while tearing off pieces with their mandibles, maxillae, and maxillipeds. These differences between grazing minnows and crayfish call into question their functional redundancy in prairie streams.

We measured the effects of 2 dominant stream grazers, southern redbelly dace (*Phoxinus erythrogaster*) and crayfish (*Orconectes* spp.), on stream ecosystems. Our goals were to compare effects of these taxa on ecosystem properties and to determine how those effects varied with habitat (pools vs riffles), time since disturbance (14 vs 28 d), and season (cool vs warm). We hypothesized that loss or extirpation of one of these species would have minimal influence on prairie stream ecosystem function if their effects overlapped spatially and temporally (Fig. 1C).

Methods

Description of experimental streams

Twenty-four outdoor experimental streams at the Konza Prairie Biological Station (KPBS) in north-central Kansas (USA) were used to test the effects of grazer species biomass and identity on ecosystem properties. Each stream consisted of a 2.54-m² pool (mean depth = 0.5 m) connected to a 0.84-m² riffle (mean depth = 0.15 m) (see Matthews et al. 2006 for details of stream design). Ground water dripped into each stream at a rate of 1.4 to 11.5 mL/s (across experiments) and resulted in a turnover rate that ranged from 1.4 to 11.5 d. Water was recirculated within each riffle–pool unit by an electric trolling motor to simulate natural current velocities. Mean discharge was 4.3 L/s (± 1.5 L/s), and mean velocity in riffles was 7.9 cm/s (± 3.2 cm/s). 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 and occurred in abundances typical of nearby Kings Creek (Matthews et al. 2006).

Prior to each experiment, periphyton and macroinvertebrate species colonized the streams for 1 wk (2005) or 5 wk (2006), which was long enough for streams to develop filamentous algae and an invertebrate assemblage. After this colonization period, streams were flooded with water from a pressure sprayer to scour the substrata and stream walls. Most of the organic matter was exported through a large drain. Streams were refilled immediately and were stocked with grazers within 24 h after flooding (day 0). Results from a previous experiment indicated that flooding reduced algal biomass (chlorophyll [chl] $a < 3$ mg/m²) and kept biomass variation low among

streams (Bertrand and Gido 2007). Residual algae and invertebrates and aerial colonists allowed the stream community to recover within the time frame of the experiment. Thus, our experiments reflect post-flood recovery of ecosystem properties in prairie streams.

Experimental design

Autumn 2005.—Biomass-dependent effects of dace and crayfish on stream ecosystem properties were tested in independent experimental stream units stocked with 1 of 12 densities of either dace or crayfish (24 stream units). Density ranged from 0.9 to 10.7 individuals (ind.)/m² (3–36 ind./stream), and biomass ranged from 1.98 to 25.89 g/m² (dace) or 2.02 to 27.00 g/m² (crayfish). These densities were within the range observed in Kings Creek (Evans-White et al. 2003, Franssen et al. 2006, Bertrand and Gido 2007). Dace were captured by seining and crayfish were collected by electrofishing and baited minnow traps. A mixture of 2 crayfish species (*Orconectes neglectus* and *Orconectes nais*) was used. The species were not treated separately because both are common in Kings Creek, have similar diets, and have similar effects on ecosystem structure (Evans-White et al. 2003). The experiment began 4 October 2005 (day 0) and ended on 3 November 2005 (day 28). Mean water temperature during the experiment was 12.9°C (range 7.4–20.1°C). Low water-table levels made low-nutrient spring water unavailable, so high-nutrient ground water (mean \pm SD, NO₃ = 1991 \pm 1046 μ g/L) was used in the streams.

Spring 2006.—The relative effects of dace and crayfish on stream ecosystem properties were tested in independent experimental stream units stocked with moderately high densities/biomasses of dace or crayfish (12 stream units/species). Our intention was to attain a biomass (target wet biomass = 10 g/m²) in both treatments similar to those that resulted in significant effects in the autumn 2005 experiment or in previous experiments (Evans-White et al. 2003, Bertrand and Gido 2007). However, crayfish biomass in Kings Creek is lowest in spring (Evans-White et al. 2003), and it was difficult to find crayfish <50 mm total length. As a buffer against mortality, 20 individuals were stocked in each stream even though doing so elevated crayfish biomass relative to dace biomass. Thus, dace density was 12.4 ind./m² (8.5–12.5 g/m²), and crayfish density was 6.2 ind./m² (20.2–30.9 g/m²). A grazing control treatment (no dace or crayfish) was not included because our goal was to compare effects of the 2 grazers on ecosystem properties. The experiment began 17 May 2006 (day 0) and ended 4

June 2006 (day 28). Mean water temperature was 21.4°C (range 17.5–29.9°C). Higher water-table levels allowed use of low-nutrient spring water ($\text{NO}_3 = 63 \pm 23 \mu\text{g/L}$) in the streams.

Response variables

Response variables were measured on days 14 and 28. An open-system single-station method was used to estimate primary productivity (Bott 2006). A handheld dissolved O_2 (DO) sensor (YSI model 550; Yellow Springs Instruments, Yellow Springs, Ohio) placed in the riffle was used to measure DO in each experimental stream every 1 to 2 h from sunrise (minimum DO) until mid-afternoon when DO peaked. All experimental streams had similar inflow rates, recirculation rates, depths, and bed form. Therefore, turbulence-induced aeration was assumed to be similar across streams and experiments. Reaeration was estimated using a modified nighttime regression method (Owens 1974, Parkhill and Gulliver 1999).

Mean algal filament length was measured on pebbles collected at 3 to 5 points along each of 3 equally spaced transects oriented perpendicular to flow in the riffle and at 5 points in the pool (4 points around the perimeter and 1 point in the center) of each stream. The longest algal filament on each pebble was measured with a ruler. Algal biomass (as chl *a*) was measured on 3 pebbles (3–8 cm diameter) from the riffle and 5 pebbles from the pool. Pebbles were frozen within 2 h of collection. Later, chl *a* was extracted by submerging pebbles in a 78°C, 95% EtOH solution (Sartory and Grobbelaar 1984). The areas of pebbles were estimated using Sigmascan Pro (version 5; Hearne Scientific Software Pty. Ltd., Melbourne, Australia).

A modified core sampler consisting of a 180-cm² corer with an electric pump (0.1 L/s) was used to collect particulate organic material (POM) and invertebrates from riffle and pool substrata in the streams. Substrata inside the corer were agitated by hand until 9 L of water had been collected in a bucket. A 500-mL subsample of the homogenized slurry was collected for analysis of POM and preserved in formalin. The remaining slurry was passed through a 250- μm -mesh sieve to collect invertebrates, which also were preserved in formalin.

In the laboratory, the 500-mL POM subsample was separated into 3 size fractions (1–97 μm = fine POM [FPOM], 98–515 μm = medium POM [MPOM], and $\geq 516 \mu\text{m}$ = coarse POM [CPOM]) by filtering the slurry through a series of filters. Material from each size fraction was dried ($\sim 50^\circ\text{C}$, ≥ 24 h), weighed, combusted in a muffle furnace (500°C , >1 h), and

weighed again to estimate ash-free dry mass (AFDM) of each fraction.

Invertebrates were counted and identified with a dissecting microscope.

Data analysis

In autumn 2005, an analysis of covariance (ANCOVA) with habitat (riffle, pool) and sampling day (day 14, 28) as covariates was used to test the relationship between grazer densities and ecosystem response variables (SPSS version 11; SPSS Inc., Chicago, Illinois). Dependent variables were algal biomass (chl *a*), algal filament length, total POM, proportions of POM size fractions, and $\log_{10}(x)$ -transformed densities of 5 common invertebrate taxa (Chironomidae, Ephemeroptera, Chydoridae, Cyclopoida, and Ostracoda). Statistical significance was set at $p < 0.10$ because of potentially complex interactions and high variability in some responses.

In spring 2006, split-plot repeated-measures analysis of variance (ANOVA) was used to test the main effects of grazer type and interactions with habitat (pool vs riffle) and sampling day (day 14 vs day 28) (PROC MIXED, SAS version 9.1; SAS Institute, Cary, North Carolina). Time was the repeated factor, grazer type was the whole-plot factor varying between streams, and habitats were the subplot factor varying among streams. The repeated measure was assumed to have similar variance between the 2 sampling dates (i.e., compound symmetry). A repeated measures ANOVA was used to test the effects of grazer type on GPP because it represented combined productivity of pools and riffles. Time was the repeated factor. Post hoc comparisons for all ANOVAs were based on Tukey's adjusted least square means.

Results

Recovery of crayfish and dace

In autumn 2005, on average, only 25% of the crayfish and 38% of the dace stocked in experimental streams were recovered at the end of the experiment. The number of grazers recovered from a stream was significantly linearly related to the number of stocked grazers (crayfish: $r^2 = 0.63$, $p < 0.001$; dace: $r^2 = 0.51$, $p = 0.009$), and a gradient of treatment densities was maintained for both taxa.

In spring 2006, on average, only 16% of the crayfish and 56% of the dace stocked in the experimental streams were recovered at the end of the experiment. Results of an analysis that excluded streams from which $<14\%$ of the stocked crayfish were recovered ($n_{\text{retained}} = 7$ of 12 crayfish streams) yielded the same significant relation-

TABLE 1. Results from an analysis of covariance testing the association between dace and crayfish biomass and ecosystem properties of experimental streams during autumn 2005. Partial correlation coefficients are given for time since disturbance (positive values indicate an increase from day 14 to day 28), habitat (positive values indicate higher values in riffles than pools), and grazer biomass. Chl *a* = chlorophyll *a*, POM = particulate organic matter, CPOM = coarse POM, MPOM = medium POM, FPOM = fine POM; ns = not significant ($p > 0.1$), * $p \leq 0.1$, ** $p \leq 0.05$.

Response variable	Partial <i>r</i> (dace)					Partial <i>r</i> (crayfish)				
	Adjusted R^2	<i>p</i>	Time	Habitat	Dace biomass	Adjusted R^2	<i>p</i>	Time	Habitat	Crayfish biomass
Benthic algae										
Biomass (chl <i>a</i>)	0.291	<0.001	0.546**	0.274*	ns	0.476	<0.001	0.647**	0.484**	ns
Filament length	0.286	<0.001	-0.355**	ns	-0.51	-0.022	0.584	ns	ns	ns
POM										
Total POM	0.584	<0.001	-0.777**	ns	ns	0.564	<0.001	-0.767**	ns	ns
CPOM ($\geq 516 \mu\text{m}$)	0.041	0.598	ns	ns	ns	0.002	0.390	ns	ns	ns
MPOM (98–515 μm)	0.234	0.002	0.497**	ns	-0.245*	0.397	<0.001	0.660**	ns	ns
FPOM (1–97 μm)	0.021	0.272	0.262*	ns	ns	0.285	<0.001	-0.563**	ns	ns
Benthic invertebrates										
Chydoridae	0.403	<0.001	0.603**	-0.375**	ns	0.447	<0.001	0.410**	-0.554**	0.374**
Cyclopoida	0.084	0.078	0.325**	ns	ns	0.05	0.156	ns	ns	ns
Ostracoda	0.282	0.001	0.558**	ns	ns	0.228	0.002	0.508**	ns	ns
Chironomidae	0.323	<0.001	0.568**	ns	-0.327**	0.157	0.014	0.287*	0.365**	ns
Ephemeroptera	0.086	0.074	ns	-0.303**	0.252*	-0.025	0.606	ns	ns	ns

ships as results using data from all streams, so all 12 streams were included in statistical analyses.

Ecosystem responses

GPP.—In autumn 2005, GPP was significantly greater on day 14 than on day 28 in streams with dace (partial $r = 0.446$, $p = 0.03$), but the effect of dace biomass was not statistically significant after controlling for sampling day (partial $r = 0.167$, $p = 0.45$). GPP was not significantly affected by sampling day or crayfish biomass in crayfish streams ($p > 0.17$).

In spring 2006, GPP was slightly greater ($p = 0.06$) on day 28 ($0.15 \text{ g O}_2 \text{ m}^{-2} \text{ h}^{-1}$) than on day 14 ($0.13 \text{ g O}_2 \text{ m}^{-2} \text{ h}^{-1}$), but it did not differ between dace and crayfish streams ($p = 0.79$; data not shown).

Algal structure.—In autumn 2005, algal filament length in dace streams was significantly longer on day 14 than on day 28 ($p = 0.02$), but it did not differ between riffle and pool habitat (Table 1). Algal filament length was significantly negatively related to dace biomass in pools and riffles on day 14 (Fig. 2A) but not on day 28 (Fig. 2B). Algal filament length in crayfish streams was not significantly affected by time, crayfish biomass, or habitat (Table 1, Fig. 2C, D). Algal biomass was greater on day 28 than on day 14 ($p < 0.001$) and was greater in riffle than in pool habitats ($p = 0.06$), but it was not related to the biomass of either taxon (Table 1).

In spring 2006, algal filament length was significantly shorter on day 14 than on day 28 ($p < 0.01$) and

was significantly greater in riffles than in pools ($p < 0.01$; Table 2). The grazer \times sampling day interaction was marginally significant ($p = 0.07$; Fig. 3A). Algal filament lengths were shorter in the crayfish than in the dace treatment on day 14 (Tukey-adjusted $p = 0.01$), but they did not differ between grazer treatments on day 28. Algal biomass was significantly greater in riffle than in pool habitats ($p < 0.01$), and the habitat \times grazer interaction was significant ($p = 0.04$; Fig. 3B). The 2 grazers had similar effects on algal biomass in pools, but algal biomass tended to be higher in riffles grazed by dace than in riffles grazed by crayfish (Tukey-adjusted $p = 0.06$).

POM.—In autumn 2005, total POM was significantly lower on day 28 than on day 14 ($p < 0.001$), but it did not vary with habitat or grazer biomass (Table 1). The proportion of FPOM was significantly higher on day 14 than on day 28 in crayfish streams ($p < 0.001$; Table 1), but the reverse was true in dace streams ($p < 0.08$). The proportion of MPOM was significantly higher on day 28 than on day 14 in all streams ($p < 0.001$), and it tended to decrease as dace biomass increased ($p = 0.10$; Table 1).

In spring 2006, total POM and proportions of POM size fractions differed significantly between habitats and sampling days (Table 2, Fig. 3C, D). Proportions of CPOM and MPOM were significantly greater and proportions of FPOM were significantly lower in riffles than in pools. Proportion of CPOM was significantly greater on day 28 than on day 14 (Fig. 3D), whereas

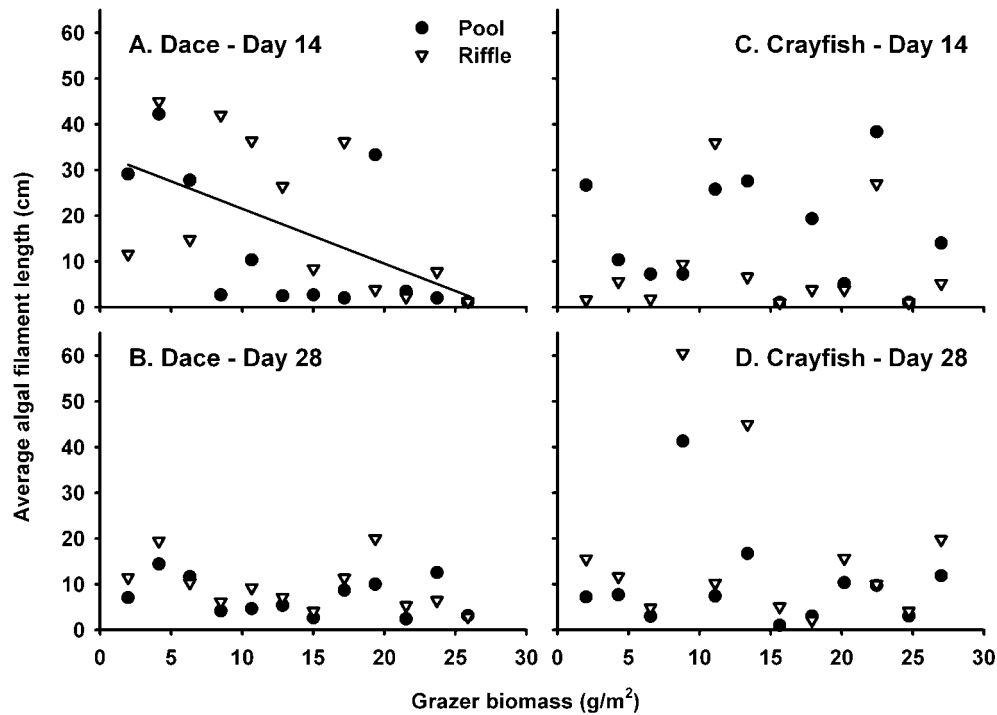


FIG. 2. Relationship between algal filament length and biomass of dace on days 14 (A) and 28 (B) and crayfish on days 14 (C) and 28 (D) in autumn 2005. Least-squares regression line indicates a significant relationship.

proportion of FPOM was significantly greater on day 14 than on day 28. Proportion of CPOM tended to be lower in crayfish than in dace streams (Tukey-adjusted $p = 0.06$; Fig. 3D).

Invertebrates.—In autumn 2005, invertebrate densities generally increased with time (Table 1). Chironomid density was significantly lower on day 14 than on day 28 ($p < 0.01$), and it decreased significantly as dace

TABLE 2. F statistics and p values from a split-plot repeated-measures analysis of variance testing the main effects of grazer type (G; crayfish vs dace), habitat (H; pool vs riffle), and time since disturbance (T; day 14 vs day 28) on ecosystem properties in experimental streams during spring 2006. Chl a = chlorophyll a , POM = particulate organic matter, CPOM = coarse POM, MPOM = medium POM, FPOM = fine POM. Bold font indicates a significant ($p < 0.1$) effect.

Variable	G		H		T		G × H		G × T		H × T		G × H × T	
	df = 22		df = 22		df = 22		df = 22		df = 44		df = 44		df = 44	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Benthic algae														
Biomass (chl a)	0.44	0.514	29.92	0.010	4.25	0.045	4.63	0.042	0.00	0.992	0.08	0.782	1.25	0.270
Filament length	4.18	0.053	13.60	0.001	27.76	0.0100	0.10	0.761	3.49	0.069	0.02	0.883	2.13	0.151
POM														
Total POM	1.28	0.269	25.87	0.000	1.33	0.255	0.14	0.710	0.83	0.369	0.07	0.796	1.62	0.210
CPOM ($\geq 516 \mu\text{m}$)	3.95	0.059	5.71	0.026	23.10	0.000	0.10	0.751	0.53	0.470	1.06	0.309	2.02	0.162
MPOM (98–515 μm)	1.70	0.206	29.12	0.000	0.11	0.747	0.11	0.747	1.51	0.225	0.81	0.373	2.81	0.101
FPOM (1–97 μm)	1.24	0.277	16.68	0.001	4.52	0.039	0.02	0.894	1.05	0.312	5.30	0.026	2.93	0.094
Benthic invertebrates														
Chydoridae	3.55	0.073	0.33	0.570	0.32	0.575	3.57	0.072	0.84	0.365	0.09	0.770	2.53	0.119
Cyclopoida	0.01	0.920	5.54	0.028	0.00	0.953	0.02	0.898	0.66	0.422	0.08	0.783	0.30	0.585
Chironomidae	3.72	0.067	24.46	0.000	0.25	0.623	1.01	0.325	0.73	0.398	10.27	0.003	0.71	0.403
Ostracoda	0.87	0.360	13.46	0.001	0.75	0.391	4.45	0.047	0.01	0.919	1.01	0.320	1.51	0.226
Ephemeroptera	2.07	0.164	6.00	0.023	0.05	0.822	0.68	0.420	0.68	0.413	0.25	0.617	0.34	0.563

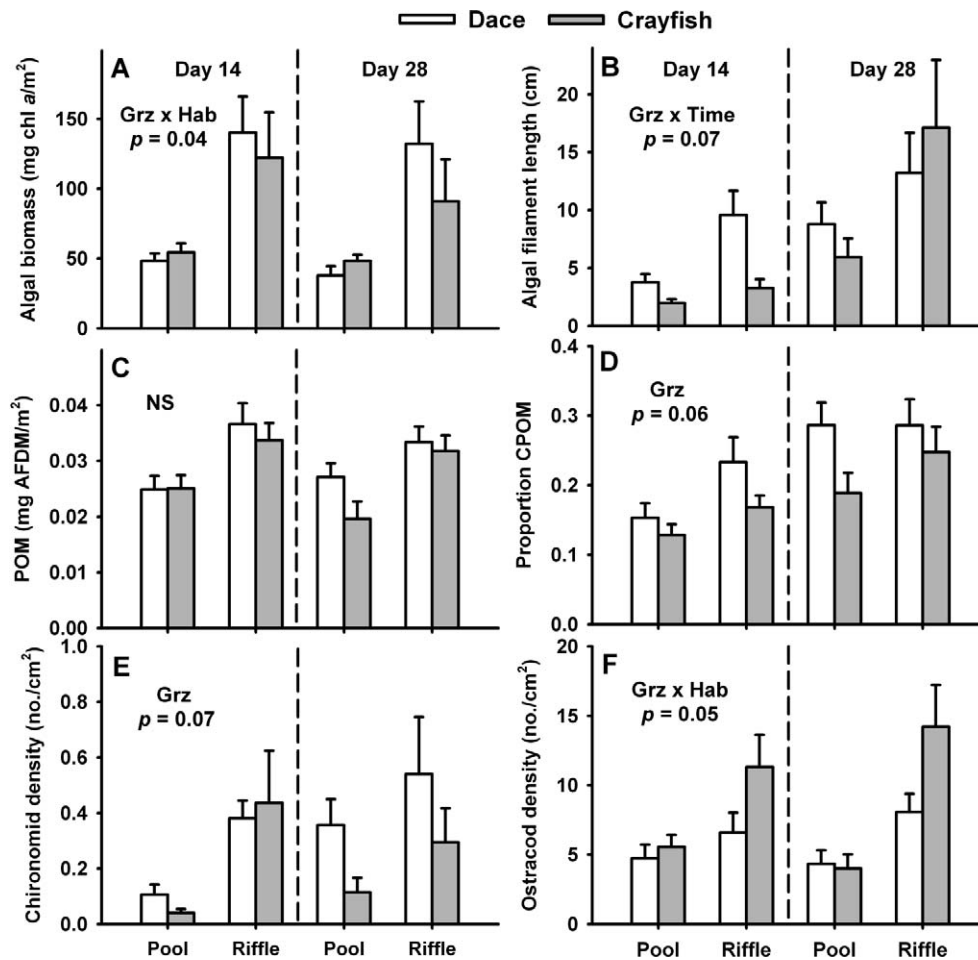


FIG. 3. Mean (+1 SE) algal filament length (A), algal biomass (as chlorophyll [chl] *a*) (B), total particulate organic matter (POM) ash-free dry mass (AFDM) (C), proportion of POM > 516 μm (CPOM) (D), chironomid density (E), and ostracod density (F) from spring 2006. Graphs are presented only for ecosystem properties in which dace and crayfish differed significantly. Grz = grazer, Hab = habitat, NS = not significant.

biomass increased ($p = 0.04$) on day 14 but not on day 28 (Fig. 4A, B). Chironomid density was not significantly affected by crayfish biomass (Table 1, Fig. 4C, D). Chydorid density was significantly greater in pools than riffles ($p < 0.05$) and increased significantly as crayfish biomass increased ($p = 0.01$; Table 1). Ephemeropteran density tended to increase as dace biomass increased ($p = 0.09$; Table 1).

In spring 2006, chironomid density tended to be lower in the crayfish than in the dace treatment ($p = 0.07$; Fig. 3E). Ostracod density tended to be higher in riffles than in pools in crayfish streams ($p = 0.05$; Fig. 3F).

Discussion

Effects on algae and organic matter

Our study contributes information on the relative effects of 2 important prairie stream grazers on GPP,

periphyton communities, benthic POM standing stocks and size distribution, and invertebrate communities in experimental streams. Our ability to examine the magnitudes of each grazer effect is limited because we chose to compare grazer treatments with each other rather than with ungrazed treatments. However, previous experiments have quantified crayfish (Evans-White et al. 2001) and dace (Bertrand and Gido 2007) effects on algal biomass and filament length in prairie streams. Our study showed that ecosystem properties of streams exposed to crayfish or dace grazing can differ depending upon time since disturbance, habitat, and season. Our results suggest that grazer biomass and individual traits (i.e., physiology or behavior) can mediate their roles in stream communities and ecosystems. However, we recommend caution in interpreting quantitative results because grazer biomasses changed during our experiments (we did not recover all grazers).

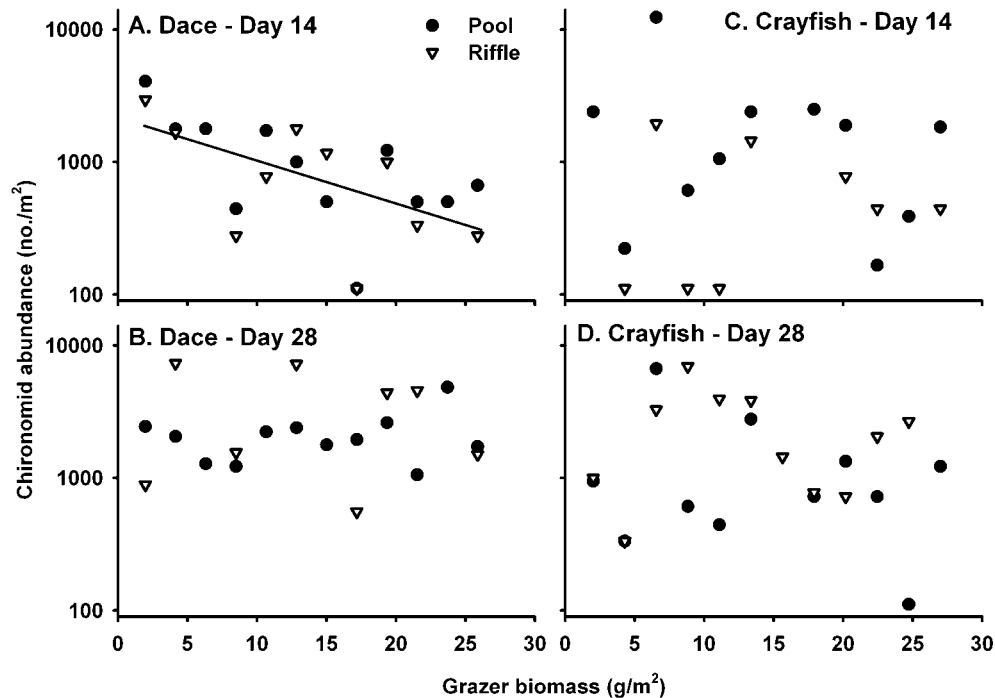


FIG. 4. Relationship between chironomid density and biomass of dace on days 14 (A) and 28 (B) and crayfish on days 14 (C) and 28 (D) in autumn 2005. Least-squares regression line indicates a significant relationship.

Algal filament lengths were sensitive to grazer biomass and taxon. Differences in algal filament length between dace and crayfish streams were more pronounced on day 14 than on day 28 in both experiments. This pattern is consistent with the results of a previous study in these experimental streams, which showed that negative effects of dace on algal filament lengths diminished after 18 d (Bertrand and Gido 2007). The experimental streams were scoured prior to stocking grazers; thus, the benthic communities were recovering from this disturbance. Our data suggest that grazer effects on filamentous algae are strongest soon after disturbance when algae and invertebrates are colonizing the experimental streams, and that the effects diminish as these communities develop. This time effect could be caused by shifts in the periphyton community from more scour-resistant forms (Petersen 1996) to more filamentous forms (Steinman 1996), an increase in the complexity of the grazer assemblage as larvae of winged invertebrates colonize these systems, changes in the feeding behavior of grazers, or a reduction in grazer biomass during the experiment (e.g., mortality and escape). The identity of the specific mechanism that limits grazer effects after several weeks is equivocal, but the relationship of these effects to time since a disturbance has potentially interesting implications. For example, if grazer effects or differences between taxa are distur-

bance dependent, then grazer effects should be strongest in streams that experience frequent flooding and weaker in streams with stable flow.

Studies in natural prairie streams indicate that resource consumption by crayfish and cyprinid fishes affects stream organic matter (Stagliano and Whiles 2002, Evans-White et al. 2003) and nutrient dynamics (Dodds et al. 2000). Our study indicates that these 2 grazers might alter organic matter dynamics via consumption of algal and invertebrate food resources. CPOM and MPOM in our experimental streams probably consisted mostly of filamentous algae and invertebrates because inputs of allochthonous vegetation were minimal. The decrease in the proportion of MPOM as dace density increased coincided with decreases in algal filament length and chironomid density. Furthermore, lower proportions of CPOM in crayfish streams than in dace streams in spring 2006 coincided with decreases in algal filament length and chironomid density. Algal filament length in pools on day 28 also tended to be shorter in crayfish streams than in dace streams. On the other hand, densities of some invertebrates responded positively to grazers (i.e., Ephemeroptera in 2005 and Chydoridae in 2006). Future experiments should measure invertebrate biomass to examine how grazer effects on invertebrate taxa influence POM dynamics in these streams. Regardless of the mechanism, our study indicates that

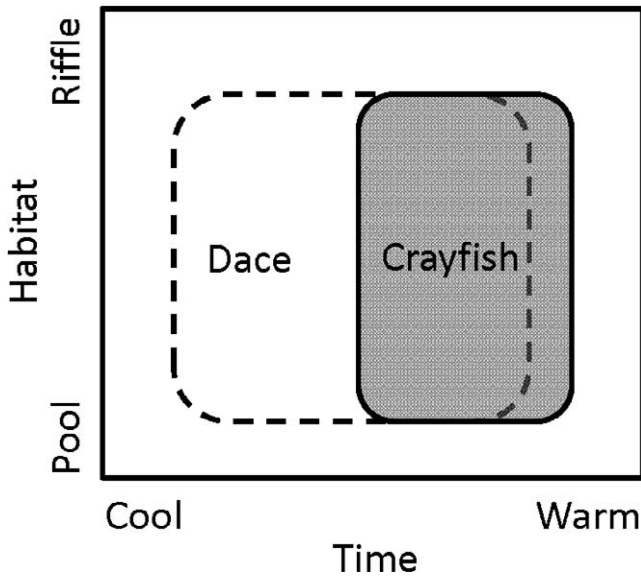


FIG. 5. Hypothesized overlap in effects of dace and crayfish on benthic communities in streams based on experimental stream results.

crayfish and dace can alter stream organic matter dynamics by reducing CPOM and MPOM.

Complementary resource use

Differences in foraging behavior among habitats and over time might result in complementary resource use. Crayfish were observed feeding at night in pools and riffles, but dace were observed feeding in pools during the day. However, the effects of dace on ecosystem properties were similar in pools and riffles in autumn 2005, a result that suggests that dace forage in both habitats. Grazer effects were habitat specific in spring 2006 but were not always consistent. For example, algal biomass generally was higher in riffles grazed by dace than in riffles grazed by crayfish on day 14. Nevertheless, grazers generally had similar effects in riffles and pools, and we have little evidence that grazer roles differ by habitat in our streams. However, differences in the foraging behavior of these taxa might exist at smaller temporal or spatial scales than we were able to measure in our study. For example, crayfish grazing can be localized around burrows, creating heterogeneity within pool habitats (Gelwick 2000). Grazer activity also is likely to vary between day and night. Greater quantification of the spatial distribution of foraging might clarify overlapping roles among these grazers in prairie streams.

The relative effects of dace and crayfish on stream ecosystems might be mediated by seasonally variable factors. For example, crayfish biomass had no effect on experimental stream communities in autumn 2005.

However, algal filament length was shorter, algal biomass was lower in riffles, and chironomid densities were lower in crayfish than in dace streams in spring 2006. Lack of grazer controls and potentially confounding effects between autumn and spring experiments (e.g., nutrient loading and grazer biomass) limit our ability to identify the specific environmental gradients that mediated grazer effects. However, we do know that both temperature, which can regulate crayfish growth (Evans-White et al. 2003) and (potentially) grazing activity, and nutrients, which can limit algal growth (Tank and Dodds 2003), differed between experiments. Therefore, future experiments should examine grazing effects across temperature and nutrient gradients to help clarify the potential role of these factors in mediating grazer effects across seasons in prairie streams.

Functional redundancy

Algal filament lengths, POM composition, and invertebrate density varied between experiments, grazer treatments, habitats, and with time since disturbance. These results suggest that biomass and individual traits (i.e., physiology or behavior) of grazers might mediate their relative roles in stream communities and ecosystems. Our results from autumn 2005 differed from those of previous work conducted during summer, which showed negative effects of crayfish on periphyton communities (Evans-White et al. 2001). This difference suggests that crayfish effects might have been restricted by water temperature or high nutrient concentration during the autumn experiment (Fig. 5). Crayfish growth can be regulated by temperature in prairie streams (Evans-White et al. 2003), and previous studies have indicated that temperature (Kishi et al. 2005) and nutrients (Rosemond et al. 1993) can mediate consumer effects in other ecosystems. Habitat (i.e., pool vs riffle) was an important factor regulating algae, POM, and invertebrate density in our experimental streams, but we found minimal differences between pool and riffle habitat in the responses of stream ecosystem properties to grazer biomass or identity. In addition, the differences in effect between grazers might be limited to the early stages of the development of microbial communities after flooding. Our results suggest that the major separation between these grazing species appears to be across a temporal gradient (Fig. 5) and that future experiments should examine grazers within the context of seasonally variable factors, such as temperature and nutrient levels.

Species identity within functional groups or guilds might mediate species effects on communities and

ecosystems (Cardinale et al. 2002, Evans-White and Lamberti 2005, 2006, Vaughn et al. 2007). Our experimental results and those of others (Spooner and Vaughn 2006, Vaughn et al. 2007) indicate that functional roles of species can vary spatially or temporally, perhaps because of variations in abiotic and biotic factors. Species might appear to be redundant at small temporal scales, but at larger temporal scales that include seasonal variations in temperature and resource availability, they might not have overlapping roles (Cardinale et al. 2004). Our results suggest that conservation of both crayfish and dace could be necessary to sustain the ecosystems in Kings Creek and other prairie streams. Food webs are a complex chain of reactions (Winemiller 1990) that are difficult to characterize fully. Studies examining the importance of individual species must be conducted over larger temporal scales and should identify factors controlling species effects.

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