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PLANT ANIMAL INTERACTIONS

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How do grazers affect periphyton heterogeneity in streams?

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Abstract The effects of grazing by stream invertebrates on algal biomass and spatial heterogeneity were tested experimentally in flow-through microcosms with natural substrates (rocks). One experiment tested the effects of fixed densities of three species of grazers (the caddisfly *Allomyia* sp. and two mayflies, *Epeorus deceptivus* and *Baetis bicaudatus*) on periphyton. *Baetis* was tested with and without chemical cues from fish predators, which reduced grazer foraging activity to levels similar to the less mobile mayfly (*Epeorus*). Mean algal biomass (chlorophyll *a*; chl *a*) was reduced in grazer treatments compared to ungrazed controls, but there were no differences among grazer treatments. Algal heterogeneity (Morisita index) increased with grazer mobility, with the highest heterogeneity occurring in the *Baetis*-no fish treatment (most mobile grazer) and the lowest in the caddisfly treatment (most sedentary grazer). A second experiment used a three factorial design, and tested whether initial resource distribution (homogeneous vs. heterogeneous), *Baetis* density (high vs. low) and fish odor (present vs. absent) affected grazer impact on algal resources. Abundances of *Baetis* and chl *a* on individual rocks were recorded to explore the mechanisms responsible for the observed distributions of algae. Initial resource heterogeneity was maintained despite being subjected to grazing. Mean chl *a* was highest in controls, as in experiment I, and effects of *Baetis* on algal biomass increased with grazer density. There were no fish effects on algal biomass and no effects of grazer density or fish on algal heterogeneity. At the scale of individual rocks *Baetis* was unselective when food was homogeneously distributed, but chose high-food rocks when it was heterogeneously distributed. Results of these mechanistic experiments showed that *Baetis* can track resources at the scale of single rocks; and at moderate densities mobile grazers could potentially maintain periphyton distributions observed in natural streams.

Keywords Algae · Microcosms · Mobility · Morisita index · Stream invertebrates

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Introduction

Quantifying strengths of interactions in communities is a central issue in ecology (Mills et al. 1993; Laska and Wootton 1998; McPeek and Peckarsky 1998). Recent empirical studies of the effects of one species on the distribution and abundance of another have proposed different models to explore the strengths of consumer-resource interactions (Berlow et al. 1999; Wootton 1997; Chase et al. 2001). In particular, herbivore populations have been widely demonstrated to be influenced by (e.g., Laca and Demment 1991; Cyr and Pace 1993) and to affect both the structure and distribution of plant populations (e.g., Steinman et al. 1987; Mulholland et al. 1991; Hildrew 1996; Bigger and Marvier 1998).

Although many studies have focused on the effects of grazers on mean plant biomass, interest in how herbivores affect and respond to plant distribution is growing in both terrestrial (Bailey et al. 1996; Knapp et al. 1999; Hobbs et al. 2003) and aquatic systems (Wolcott and O'Connor 1992; Duffy et al. 2001; Gelwick 2000). In a terrestrial study, the presence of bison in a mesic North American grassland created a mosaic of patches with high and low biomass of resources (light and N) and enhanced plant species richness (Bakker et al. 2003). In contrast, selective grazing by Patagonian sheep reduced spatial heterogeneity in shrub steppes (Bisigato and Bertiller 1997). In a marine environment, Sommer (2000)

showed that spatially patchy grazing by a gastropod significantly increased the heterogeneity of microalgal assemblages, while random grazing of an algivorous isopod had no effect on the spatial distribution of periphyton. In a recent review, Adler et al. (2001) concluded that variation in the effects of grazing on the spatial heterogeneity of plants depends on the selectivity of the herbivore, the intensity of grazing, and the spatial patterns of both grazers and vegetation.

Although some studies have established that benthic herbivores respond to the spatial distribution of periphyton in streams (Hill et al. 1992; Chase et al. 2001), little is known about the importance of stream grazers in regulating algal patchiness itself (Flecker and Taylor 2004). Sarnelle et al. (1993) showed that foraging movements of randomly distributed snails grazing in artificial streams decreased the spatial heterogeneity of algal cover. Similarly, grazing catfish significantly reduced algal patchiness in a Panamanian stream characterized by high physical variability (Power 1984). Gelwick and Matthews (1997) also showed that grazing catfish reduced spatial heterogeneity of algal height in artificial streams compared to ungrazed artificial streams where spatial heterogeneity was more similar to that in natural pools.

The focus of studies of aquatic communities has also shifted from direct effects of consumers on resources (Hill and Knight 1987; Feminella and Resh 1990) to behaviorally-mediated indirect effects of other trophic levels on consumer-resource interactions (Bronmark et al. 1992; Miyasaka et al. 2003). For example, predators in streams have been shown to affect both emigration (e.g., Power 1990; Sih and Wooster 1994; Englund 1997) and feeding activities (Wooster 1994) of invertebrate prey. However, little is known about the indirect effects of predator-induced changes of prey foraging activity on resource distributions (McIntosh and Townsend 1996; Peckarsky and McIntosh 1998; McIntosh et al. 2004).

Theoretical analyses of grazer effects on spatial distribution of algal resources predict a humped relationship between grazer mobility (Abrams 2000) or grazer density (Lubchenco 1978; Poff and Nelson-Baker 1997) and resource heterogeneity. Based on these models we would expect that stream invertebrates at the extremes of mobility or density would homogenize algal resources relative to grazers with intermediate rates of mobility or intermediate densities. One objective of this study was to test theoretical predictions regarding the relationship between grazer mobility and resource heterogeneity at the scale of microcosms. We also predicted that invertebrate consumers foraging under perceived predation risk (chemical cues from brook trout) would reduce their mobility and have effects on algal resources similar to those of less mobile grazers.

A second objective of this study was to identify the mechanisms responsible for grazer effects on algal biomass and heterogeneity at the scale of individual rocks. However, to better understand the influence of organisms in generating and maintaining spatial heterogeneity in natural environments, experiments should be carried out at a variety at scales relevant to consumer-resource interactions and responsive to environmental variation (Peckarsky et al. 1997; Cooper et al. 1998). Thus, a third objective was to compare our results with others obtained at larger scales of observation. We predicted that results of microcosm studies may not extrapolate to larger scales because of the important influence of environmental complexity on the distribution and abundance of grazers and resources.

Materials and methods

Two experiments were designed to test mechanisms by which grazers influenced resources at a small scale. We manipulated the mobility of grazers, initial spatial distribution of algae, grazer density, and perceived predation risk to test whether increasing or decreasing grazer mobility, increasing grazing pressure directly by increasing grazer density or indirectly by removing predators would homogenize resources that were initially heterogeneous, and create heterogeneity where resources were initially homogeneous. We also observed the foraging behavior of grazers during experiments to help explain the mechanisms of grazer effects on resources (Flecker 1997).

Study area

We collected grazers for experiments from the East River and some of its tributaries, all high-elevation streams (> 2,950 m) located in the West Elk Mountains near the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado. The predominant grazers in these streams are insects (mayflies and caddisflies); these streams contain no grazing fish or snails (Peckarsky 1991). Some streams contain salmonid fishes, primarily the introduced brook trout (*Salvelinus fontinalis*); and others are completely fishless due to barriers to dispersal.

Artificial stream system

We conducted experiments in a streamside system of 60 circular plexiglass flow-through chambers of 15 cm diameter (described and illustrated in Peckarsky and Cowan 1991), housed in an opaque white portable greenhouse. Stream water was gravity-fed from a fishless first-order tributary of the East River and delivered through two water jets on opposite sides of each chamber. Current velocity was measured with a Nixon micro-propeller flow-meter (Charlton Kings Industrial Estate, Cheltenham, Gloucestersire). Water temperature was recorded continuously by an Onset Stowaway data logger (Onset Computer, Pocasset, Massachusetts)

placed in the outflow of the system. Experiments ran for ~3 weeks, and chambers were cleaned daily to avoid clogging and to replace dead or pupating individuals. Treatments were randomized among chambers to avoid position effects on algal growth or grazer behavior.

For treatments using chemical cues from fish, fishless stream water was delivered by gravity to a 110-l plastic bin containing two brook trout collected from the East River. Water from this bin was then dripped through tygon tubing to each chamber at a rate of 4.7 ± 0.2 ml^{-1} (mean ± 1 SE). Water from a holding tank with no fish was dripped into the fishless chambers at a similar rate. The trout were fed every 2 days a mixed diet of stream macroinvertebrates obtained from the same river. Mean fork length of the trout was 165.5 mm at the end of experiment I and 165.0 mm at the end of experiment II.

Design of experiment I (1 July 2002–22 July 2002)

The goal of this experiment was to test the effect of grazer mobility on the distribution and abundance of algal biomass. We collected small, periphyton-covered rocks from the East River, removed existing macroinvertebrates, and placed rocks in holding tanks with natural stream water for 48 h in an attempt to homogenize the starting algal biomass for the experiment. Each of 60 chambers received rocks of similar size (mean top surface area ± 1 SE, 18.3 ± 0.2 cm^2). Current velocity, which varied within chambers, was measured at three random positions in each chamber, and averaged (± 1 SE) 12.3 (± 0.8) cm s^{-1} . The average water temperature was 6.6°C and ranged from 4.2 to 11.4°C daily during the experiment.

To create a range of grazer mobility we used the sluggish dipteran *Bibliocephala* sp. (Blephariceridae), the caddisfly *Allomyia* sp. and two mayflies, *Epeorus deceptivus* and *Baetis bicaudatus*. Most of the *Bibliocephala* individuals pupated during the experiment, so we excluded this species from the analysis. *Allomyia* sp. (Apataniidae) is a relatively sedentary caddisfly that grazes algae from the upper surfaces of rocks in small, cold mountain streams (Wiggins 1996). Larvae were collected from a fishless tributary of the East River (Upper Benthette 3) and tested in fishless water only. *E. deceptivus* (Heptageniidae) is a moderately mobile mayfly that scrapes periphyton from rocks in cold, clear streams (Edmunds et al. 1976). Since *Epeorus* is most abundant in trout streams near RMBL (B. L. Peckarsky, unpublished data), larvae were collected from the East River, a trout stream, and were tested in fish water only. *B. bicaudatus* (Baetidae) is a highly mobile mayfly that feeds by browsing algae from the surfaces of rocks and is abundant in fish and fishless streams at this elevation. All *Baetis* individuals were collected from Marmot Creek, a fishless tributary of the East River, and were tested in both fishless water and water with fish cues, which has been shown to reduce their mobility (Peckarsky and McIntosh 1998).

This experiment included five treatments with ten replicates per treatment: (1) *Allomyia* sp. in fishless water, (2) *E. deceptivus* in fish water, (3) *B. bicaudatus* in fishless water, (4) *B. bicaudatus* in fish water, and (5) controls in fishless water with no grazers. We used the same density of grazers in each treatment, 12 larvae per chamber (~700 larvae m^{-2}), or two larvae per rock if evenly distributed. It would not be unusual to observe two individuals of any of these species on rocks of the size used in the experiment under natural conditions in streams (B. L. Peckarsky and A. R. McIntosh, unpublished observations).

Before (initial) and after (final) the experiment, head capsule widths (HCW, mm) of a random subsample of individuals of each grazer species were measured to the nearest 0.01 mm on a Wild dissecting microscope equipped with an ocular micrometer. HCW of *Allomyia* ranged from 0.45 to 0.92 mm ($n = 13$), *Baetis* from 0.56 to 0.86 mm ($n = 32$), and *Epeorus* from 1.2 to 2.4 mm ($n = 34$). Biomass was estimated using HCW (mm)–dry mass (DM, mg) regression equations. *Allomyia* and *Epeorus* were dried (at 60°C for 24 h) and weighed (0.001 mg) to obtain regression equations (*Allomyia*, $DM = 1.37 \times HCW^{3.37}$, $n = 48$, $R^2 = 0.66$; *Epeorus*, $DM = 0.09 \times HCW^{3.87}$, $n = 48$, $R^2 = 0.92$). DM of *Baetis* was estimated by averaging the HCW-mass regression equations for males and females published by Peckarsky et al. (2001) ($DM = 1.17 \times HCW^{3.64}$). Initial and final sizes were averaged to estimate the biomass of grazers present in the chambers throughout the experiment. The average biomass per individual per treatment (mg ± SE) was 0.53 ± 0.05 mg for *Baetis* in fish water ($n = 56$), 0.62 ± 0.05 mg for *Baetis* in fishless water ($n = 67$), 1.02 ± 0.05 mg for *Allomyia* ($n = 47$), and 1.35 ± 0.08 for *Epeorus* ($n = 73$).

Relative mobility of the grazers was qualitatively predicted *a priori* based on field observations, laboratory experiments and existing literature (Forrester 1994; Peckarsky 1996), and confirmed using visual observations on two occasions during this experiment: 8–9 July and 15–16 July, at 2200 and 1000 hours the next day. Nighttime observations were made using headlamps with red acetate filters, which did not affect the behavior of the species in this study (Peckarsky and Cowan 1995). Observers recorded the numbers of individuals drifting past a fixed transect during 1 min, and mean number drifting (day + night) was used to rank the grazers along the axis of mobility. Drifting or swimming resulted in movement from one rock to another, and has been shown to be involved in the search by mayflies for new patches of food (Kohler 1985).

Design of experiment II (22 July 2003–11 August 2003)

The goal of this experiment was to test the effects of initial resource distribution, grazer density and fish cues on grazer-mediated changes in algal resources. Small rocks were collected from Copper Creek, a tributary of

the East River, and suspended on a raft in the water column of the East River for 10 days to create similar starting resource levels. Rocks (mean top surface area = 19.7 ± 0.3 cm^2) in each chamber were numbered clockwise with respect to their location relative to the water jets (Fig. 1). Current velocity, measured above all rocks of ten randomly selected chambers, averaged (± 1 SE) 13.3 (± 0.8) cm s^{-1} . However, current velocity was high (21.2 ± 0.9 cm s^{-1}) above rocks immediately downstream of water jets (1 and 4), low (7.2 ± 0.7 cm s^{-1}) above rocks upstream of the jets (3 and 6) and intermediate (11.5 ± 0.9 cm s^{-1}) above rocks 2 and 5, providing two rocks with three different current velocities per chamber. The average water temperature was 6.3°C and ranged from 4.5 to 12.5°C daily during the experiment.

This experiment had a split-plot design with three factors varying between chambers: starting algal heterogeneity, grazer density and fish cues, and two factors varying within chambers (current velocity and food). Half of 60 chambers were randomly allocated to different starting distributions of algae: homogeneous or heterogeneous. Homogeneous treatments received six rocks straight from the raft. For heterogeneous treatments rocks 1, 3, 5 came directly from the raft, and rocks 2, 4, 6 were taken from the raft, then scrubbed and boiled to remove periphyton. Therefore, heterogeneous chambers provided rocks with two different levels of food (high and low) alternated so that each food level occurred at each current velocity (Fig. 1).

We crossed two levels of starting heterogeneity (homogeneous vs. heterogeneous), with two predator levels (fish cues present vs. absent) and two grazer densities (high vs. low), resulting in eight treatments with six replicates per treatment. The design also included 12 control chambers with no grazers, half starting with homogeneous algae and half heterogeneous, all with fishless water. As in experiment I, we did not allocate any chambers to test the effect of predators on control treatments without grazers, because previous studies (McIntosh et al. 2004) have shown that such low concentrations of fish odor do not affect algal growth. Low-density treatments had six *B. bicaudatus* (~350 larvae m^{-2}) collected from Marmot Creek (fishless), and high-density treatments were the same as in experiment I (12 individuals $chamber^{-1}$ = ~700 larvae m^{-2}). Initial HCW of a subsample of *Baetis* ranged from 0.54 to 0.90 mm (n = 30).

Night observations of grazer behavior were made using red light at 2200 hours on four occasions: 24 July, 31 July, 7 August and 10 August to test hypotheses about possible mechanisms explaining effects of treatments on

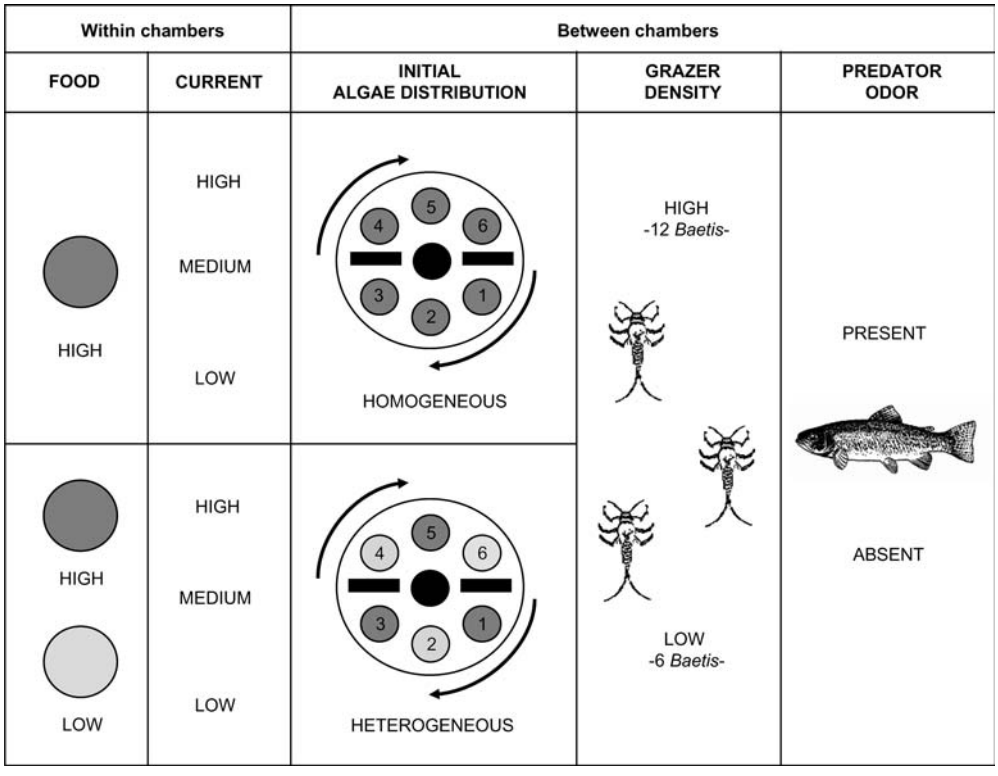

Fig. 1 Schematic of the split-plot design of experiment II. Initial algae distribution (homogeneous and heterogeneous) was completely cross-classified with grazer density (high and low) and predator odor (present or absent), which were applied between chambers (plots). Within chambers (subplots), food levels varied for the heterogeneous treatments only, and current velocity varied among rocks in all chambers (rocks *1* and *4* high velocity, *3* and *6* low velocity, *2* and *5* intermediate velocity). *Arrows* indicate the direction of current originating at two water jets (shown as *horizontal bars*) located between rocks *6* and *1* and *3* and *4* in each chamber

periphyton distribution. Observers recorded the number of individuals exposed on rocks 1–6, which had known food levels and current velocity. The response variable used in statistical analyses was mean percentage of individuals exposed on each rock rather than absolute numbers exposed, so that patterns could be compared between chambers with different densities of *Baetis*.

Measurements of periphyton biomass and distribution

To estimate starting periphyton biomass (as chl *a*) at the scale of individual rocks we took a random subsample of rocks from the batch used for the experiments, and put the rest in the chambers. In experiment I we subsampled 60 rocks (ten groups of six) and in experiment II we took 36 rocks (six groups of six) each from the homogeneous treatments and heterogeneous treatments. At the end of each experiment, final chl *a* was measured for all rocks from each chamber. Each rock was extracted in 90% ethanol for 24 h at 4°C in the dark, and the volume of extract was recorded. Chl *a* was measured using a spectrophotometer with corrections for degradation products, following the equation of Nusch (1980) for the use of ethanol {29.6×[abs(665)−abs(665acidified)]×[extract volume (ml)/area sampled (cm^2)]×path length of spectrophotometer cuvette (1 cm)}, where abs(665) is absorbance at 665 nm. To standardize algal biomass per unit area, the top surface of each rock was estimated from a regression equation obtained by tracing rocks on paper and then weighing the paper.

Algal heterogeneity within each chamber was estimated at the beginning and the end of each experiment using the Morisita index of aggregation (I_d), calculated from estimates of chl *a* on each group of six rocks. This index is commonly used to measure spatial heterogeneity and has the advantage of being relatively independent of sample mean and population density (Elliott 1977). Further details about the advantages and disadvantages of this index are discussed in McIntosh et al. (2004).

Biomass-specific grazer effects

The biomass-specific impact of each grazer species used in experiment I on mean algal biomass was calculated using an index modified from the dynamic index used by Osenberg and Mittelbach (1996) and Wootton (1997) to estimate per capita interaction strength. This index [defined here as grazer impact (GI) per unit grazer biomass; GI_B] was calculated as:

$$GI_B = \frac{\ln(G/R)}{DBT},$$

where, G is mean algal biomass when the consumers were present, R is mean resource level in the absence of consumers (control chambers), D is number of grazers per chamber (12), B is estimated biomass of the consumers in each treatment (mg per individual), and T is duration of the experiment (21 days).

Data analysis

We ran statistical analyses using SPSS for Windows (SPSS 10.1; SPSS Institute 2002). Contrast analyses between pairs of treatments in experiment II were carried out with JMPIN (JMPIN 4.0.2; SAS Institute 2000). Response variables were transformed where necessary to normalize data and homogenize variances.

Experiment I

A two-way ANOVA was used to test for differences in drift behavior among the four grazer treatments and time of observation (day vs. night). Effects of grazer treatments on two interdependent response variables, algal biomass [$\log(x+1)$-transformed chl *a*] and algal heterogeneity [$\log(x+1)$-transformed I_d], were determined using one-way multivariate ANOVA (MANOVA). Pillai's trace was used as the multivariate test criterion for *F*-tests, because it has been shown to be the most robust to violations of assumptions of MANOVA (Scheiner 2001). Where MANOVAs were significant, individual ANOVAs and post hoc Tukey tests identified the specific treatments responsible for significant effects. To test whether biomass-specific effects differed among treatments we conducted a one-way ANOVA on the values of GI_B calculated for each chamber.

Experiment II

Because of the complexity of the design we used two different analyses. First we conducted a three-way MANOVA to test the effects of three independent factors, starting resource heterogeneity (homogeneous vs. heterogeneous), predator presence (fish odor present vs. absent) and grazer density (high vs. low), on final algal biomass and heterogeneity (interdependent response variables). Individual ANOVAs identified the precise factors responsible for any significant effects. Control chambers were not included in this analysis because they were only partially crossed with the rest of treatments. Instead we used contrast analysis to test for differences between ungrazed chambers (controls with fishless water) and specific treatments.

Second, we used split-plot ANOVAs to test effects of treatment levels on two continuous response variables: (1) $\log(x+1)$−transformed chl *a*, and (2) arcsin $(\sqrt{x})$ -transformed mean percentages of *Baetis* on each rock. We constructed separate split-plot models for homogeneous and heterogeneous treatments to reduce the dimensionality of the data, after initially testing for significant interactions among the distribution of *Baetis*, the algal biomass among rocks (within chambers) and the starting

resource distribution (between chambers). For the heterogeneous treatments the split-plot model included two within-chamber factors: food availability (high on rocks 1, 3 and 5, and low on rocks 2, 4, and 6) and current velocity (high on rocks 1 and 4, low on rocks 3 and 6 and medium on rocks 2 and 5), and two between-chamber factors: predator presence and grazer density, each with two levels. Since resources were evenly distributed for the homogeneous treatments, there was only one within-chamber factor: current velocity regime.

Results

Experiment I

Grazer behavior

A two-way ANOVA showed that drift of grazers differed between day and night ($F_{1,\ 72} = 29.82$, $P < 0.001$), and among grazer treatments ($F_{3,\ 72} = 11.23$, $P < 0.001$). A significant interaction between periodicity and treatment ($F_{3,\ 72} = 5.84$, $P < 0.001$) occurred because caddisfly drift was aperiodic, while mayflies drifted mostly at night (Fig. 2). Pairwise comparisons of numbers of individuals drifting during day and night showed that the caddisfly *Allomyia* was the least mobile, followed by *Baetis* in fish water and *Epeorus*, then *Baetis* in fishless water (Fig. 2, Tukey tests, $P < 0.05$). Interestingly, fish chemical cues significantly reduced the mobility of *Baetis* to levels similar to the less mobile mayfly *Epeorus* (Fig. 2, Tukey test, $P > 0.05$).

Per capita grazer effects on mean algal biomass

Algal biomass (mean chl *a*) at the end of the experiment differed significantly among the treatments (one-way ANOVA, $F_{4,\ 45} = 5.41$, $P < 0.001$). Post hoc analysis showed that mean chl *a* was significantly higher in the ungrazed chambers (controls) than in all other treatments (Tukey test, $P < 0.05$), but did not differ among grazer treatments (Tukey test, $P > 0.05$) (Fig. 3a). Since density of grazers was the same in all treatments, these results indicate that the per capita grazing effects of all consumers were equivalent. Notably, after 21 days of feeding, all grazer treatments maintained algal biomass at levels similar to the starting levels (Fig. 3a).

Per capita grazer effects on algal heterogeneity

Resource heterogeneity significantly increased with increasing grazer mobility (one-way ANOVA, $F_{4,\ 45} = 3.54$, $P < 0.05$) (Fig. 3b). Post hoc analyses showed that algae was significantly more homogeneous in the controls and chambers with the low-mobility grazer *Allomyia* than in chambers containing the highly mobile *Baetis* in fishless water (Tukey test, $P < 0.05$), which had final resource heterogeneity most similar to the starting

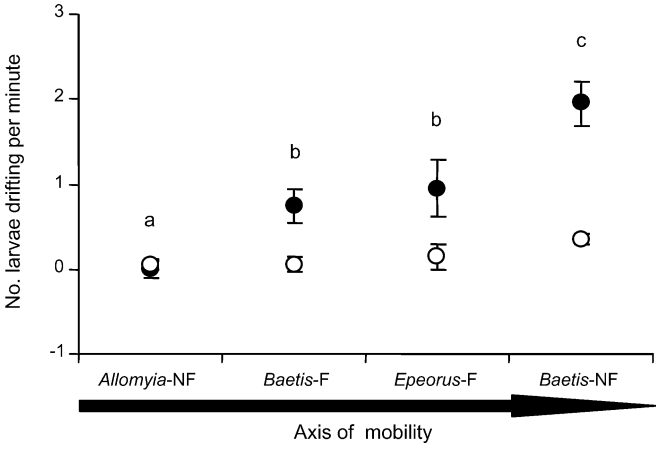

Fig. 2 Experiment I. Mean ± 1 SE number of larvae drifting in the water column observed during 1 min during the day (*open circles*) and at night (*solid circles*) for grazer species arranged along an axis of relative mobility. Values are means of chambers ± 1 SE. Treatments with the *same letter* were not significantly different. *F* fish water, *NF* fishless water ($n = 10$)

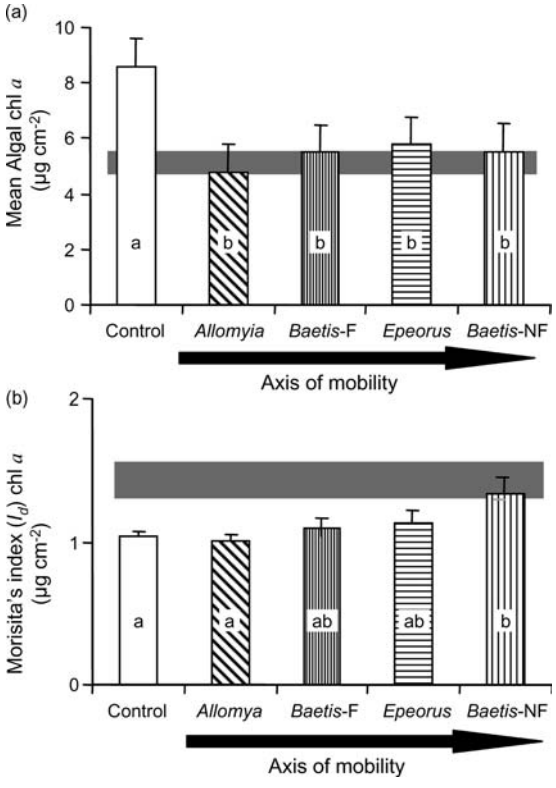

Fig. 3a, b Experiment I. Mean + 1 SE algal biomass estimated as chlorophyll *a* (chl *a*) (**a**) and algal heterogeneity estimated by Morisita's index (I_d) of aggregation (**b**) per grazer treatment arrayed along an axis of grazer mobility. Chl *a* was measured on all six rocks per chamber and ten chambers per treatment ($n = 10$). Starting values for chl *a* and I_d are indicated by *horizontal gray bars* showing the ± 1 SE of the mean initial values obtained from ten groups of six rocks taken from the same batch as the treatments. Histograms marked with the *same letters* were not significantly different (Tukey test, $P < 0.05$). For other abbreviations, see Fig. 2

algae distribution (Fig. 3b). Interestingly, subjecting *Baetis* to fish chemicals not only reduced its mobility to the level of the heptageniid mayfly, *Epeorus* (Fig. 2), but also altered its effect on algal heterogeneity to be more similar to that of *Epeorus* (Fig. 3b).

Biomass-specific grazer effects on mean algal biomass

Biomass-specific effects of grazers on mean algal biomass differed significantly among taxa (one-way ANOVA, $F_{3,\ 36} = 3.32$, $P < 0.05$). Per unit grazer biomass, the smallest grazer species, *Baetis*, was the most effective in reducing algal biomass, and the largest grazer, *Epeorus*, was the least effective grazer (Tukey test, $P < 0.05$). *Allomyia* had an intermediate effect on algal biomass (Fig. 4). Interestingly, the presence of fish chemicals did not affect either per capita or per unit biomass impact of *Baetis* on algal biomass (Tukey test, $P > 0.05$).

Experiment II

Treatment effects on periphyton

Contrast analysis showed that, as in experiment I, ungrazed treatments accumulated significantly more mean chl *a* than all grazed treatments ($F_{4,\ 55} = 10.18$, $P < 0.001$) (Fig. 5a, c). However, there were no significant differences in algal heterogeneity (I_d) between treatments and controls (least square means contrast analysis, $P > 0.05$) (Fig. 5b, d). The three-way MANOVA showed that, overall, both periphyton attributes (chl *a* and I_d) were significantly affected by the starting heterogeneity ($F_{2,\ 39} = 175$, $P < 0.001$) and grazer density ($F_{2,\ 39} = 175.6$, $P < 0.001$). However, there were no effects of predators ($F_{2,\ 39} = 0.013$, $P > 0.05$) and no significant interaction terms ($F_{2,\ 39} = 1.85$, $P > 0.05$). Individual ANOVAs showed that algal biomass was higher ($F_{1,\ 40} = 118$, $P < 0.001$) and heterogeneity was lower ($F_{1,\ 40} = 199$, $P < 0.001$) in treatments that started as homogeneous (Fig. 5c, d) compared to heterogeneous treatments (Fig. 5a, b), indicating that initial levels of heterogeneity were maintained throughout the duration of the experiment. Moreover, grazer density had a significant effect on mean chl *a* ($F_{1,\ 40} = 36.00$, $P < 0.001$); thus chambers with low grazer densities accumulated significantly more chl *a* than high grazer density treatments (Fig. 5a, c). However, there were no effects of grazer density on algal heterogeneity ($F_{1,\ 40} = 0.309$, $P > 0.05$) (Fig. 5b, d).

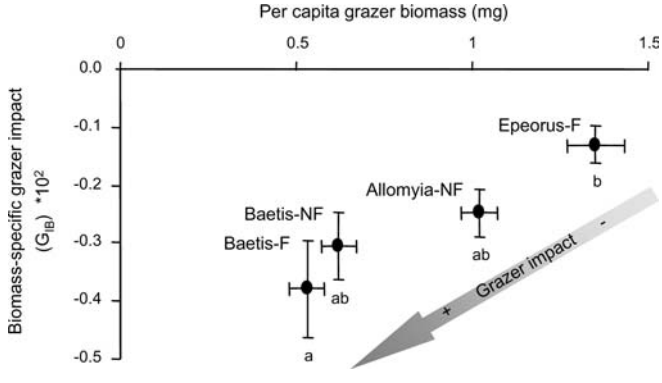

Fig. 4 Experiment 1. Mean ± 1 SE dynamic index of biomass-specific grazer impact (GI_B; see text for equation) plotted against per capita grazer biomass in the grazer treatments. Variation of mean grazer biomass within treatments is represented as a *horizontal line through each mean*. Note that grazers with high impact are lower on the *Y*-axis than ones with lower impact. Points marked with the *same letters* indicate no significant differences among treatments (Tukey test, $P < 0.05$). For other abbreviations, see Fig. 2

Mechanisms of effects: grazer behavior

The distribution of *Baetis* and of chl *a* differed among rocks, and those differences depended on starting heterogeneity (*Baetis*, two-way ANOVA rock×heterogeneity, $F_{5,\ 230} = 3.93$, $P < 0.05$, Fig. 6a, c; chl *a*, two-way ANOVA rock×heterogeneity, $F_{5,\ 230} = 80.61$, $P < 0.001$). Interestingly, all rocks with high starting chl *a* retained high chl *a* at the end of the experiment, and the level of food on the scrubbed rocks of the heterogeneous treatments (2, 4, 6) stayed low throughout the experiment (Fig. 6b, d).

In the heterogeneous treatments higher numbers of *Baetis* were visible on rocks with more food (food effect, split-plot ANOVA, $F_{1,20} = 38.29$, $P < 0.001$), but only at low grazer densities (food×density interaction, split-plot ANOVA, $F_{1,20} = 5.8$, $P < 0.05$) (Fig. 6a). A significant current velocity effect on the number of *Baetis* visible (split-plot ANOVA, $F_{2,40} = 3.93$, $P < 0.05$) was driven by an apparent affinity for rock number 5, which had high food and moderate current velocity, especially in the presence of predator cues (food×current×predator interaction, split-plot ANOVA, $F_{2,\ 40} = 4.23$, $P < 0.05$). Chl *a* remained high on rocks with high starting algae (Fig. 6b; rocks 1, 3, and 5) (food effect, split-plot ANOVA, $F_{1,20} = 856.24$, $P < 0.001$), and was lower on rocks in high grazer density treatments (Fig. 6b) (density effect, split-plot ANOVA, $F_{1,20} = 15.96$, $P < 0.001$; density×food interaction, split-plot ANOVA, $F_{1,20} = 9.24$, $P < 0.05$). There were no effects of fish cues or current velocity on the distribution of algal biomass among rocks.

In treatments with starting algae homogeneously distributed among rocks, both *Baetis* and chl *a* were also evenly distributed among rocks (Fig. 6c, d), independently of grazer density, predator cues or current velocity (split-plot ANOVA, $P > 0.05$). Interestingly, a three-way ANOVA showed that mean final grazer DM estimated from the HCW–DM regression equation was significantly lower for fish (0.54 ± 0.03 mg) ($n = 59$) than for fishless (0.64 ± 0.03 mg) ($n = 57$) treatments ($F_{1,108} = 6.41$, $P < 0.05$), as has been observed in previous studies of this species (Peckarsky et al. 2001). However this difference depended on starting heterogeneity

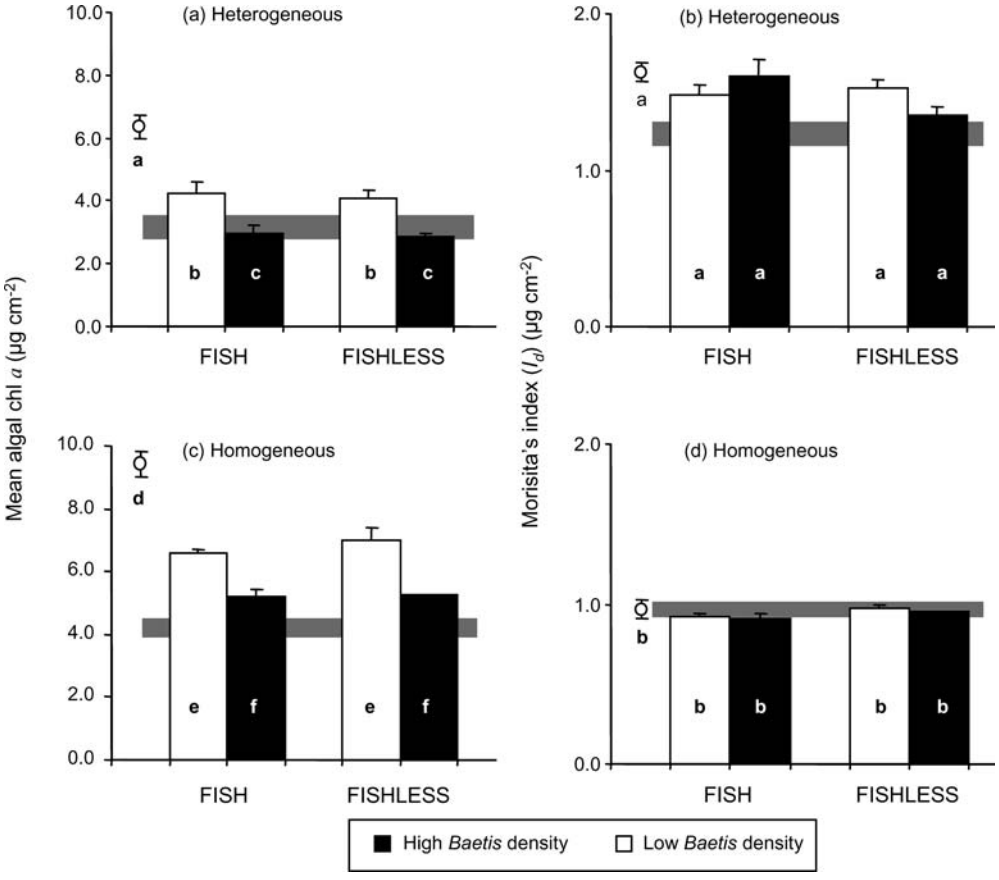

Fig. 5a–d Experiment II. Histograms show mean + 1 SE algal chl *a* (**a, c**) and I_d (**b, d**) in the grazed treatments. The *circles* indicate means (± 1 SE) of the ungrazed controls. Data are based on chl *a* measured on six rocks per chamber and six chambers per treatment ($n = 6$). *Horizontal grey bars* show ± 1 SE of the mean initial values of chl *a* and I_d of six groups of six rocks taken from the same batch as the treatment rocks. Histograms marked with the *same letters* were not significantly different (Tukey test, $P < 0.05$)

(predator×heterogeneity interaction, $F_{1,108} = 10.94$, $P < 0.001$). In heterogeneous treatments, the average final biomass per individual (mg ± SE) was 0.50 ± 0.04 for *Baetis* in fish water ($n = 29$) and 0.74 ± 0.03 for *Baetis* in fishless water ($n = 28$), which suggests a potential cost to *Baetis* feeding on heterogeneous resources in the presence of fish.

Discussion

The distribution and abundance of benthic algae are controlled by factors affecting biomass accrual (e.g., nutrients and light) and biomass loss (e.g., physical disturbance and grazing) (Biggs 1996). Herbivores may reduce algal biomass (top-down control) only if grazer density and consumption rates are sufficient to counteract rates of algal accrual (Steinman 1996). Conversely, if rates of grazing or grazer density are low, grazer feeding morphology is not well matched with the dominant algal growth form, or biomass accrual is constrained by limited resources irrespective of grazers, algal biomass may not be affected by grazing (bottom-up control) (Steinman 1996).

In both experiments of this study all grazer treatments reduced mean algal biomass at the scale of microcosm chambers, consistent with other experiments conducted at larger scales (e.g., Lamberti et al. 1987; Taylor et al. 2002). Interestingly, all grazers used in this study prevented the accumulation of algal biomass, reducing chl *a* to levels similar to the rocks from the source stream. These results suggest that renewal rates of algae in the microcosms were high enough to swamp resource depression due to grazing (Cyr and Pace 1993). However, the detailed observations conducted at the scale of individual rocks suggested that *Baetis* was tracking their resources (chose good food rocks) rather than depressing them. Thus, at the scale of individual rocks, top-down effects of grazers on algal biomass may be balanced by rapid rates of accrual in microcosms receiving natural stream water containing algal propagules.

Other studies have reported that *Baetis* perceives and responds to spatial heterogeneity in periphyton abundance among rocks by selecting patches with high periphyton (Kohler 1984; Richards and Minshall 1988). Similarly, previous studies in microcosms showed that grazing mayflies consistently selected high-food rocks,

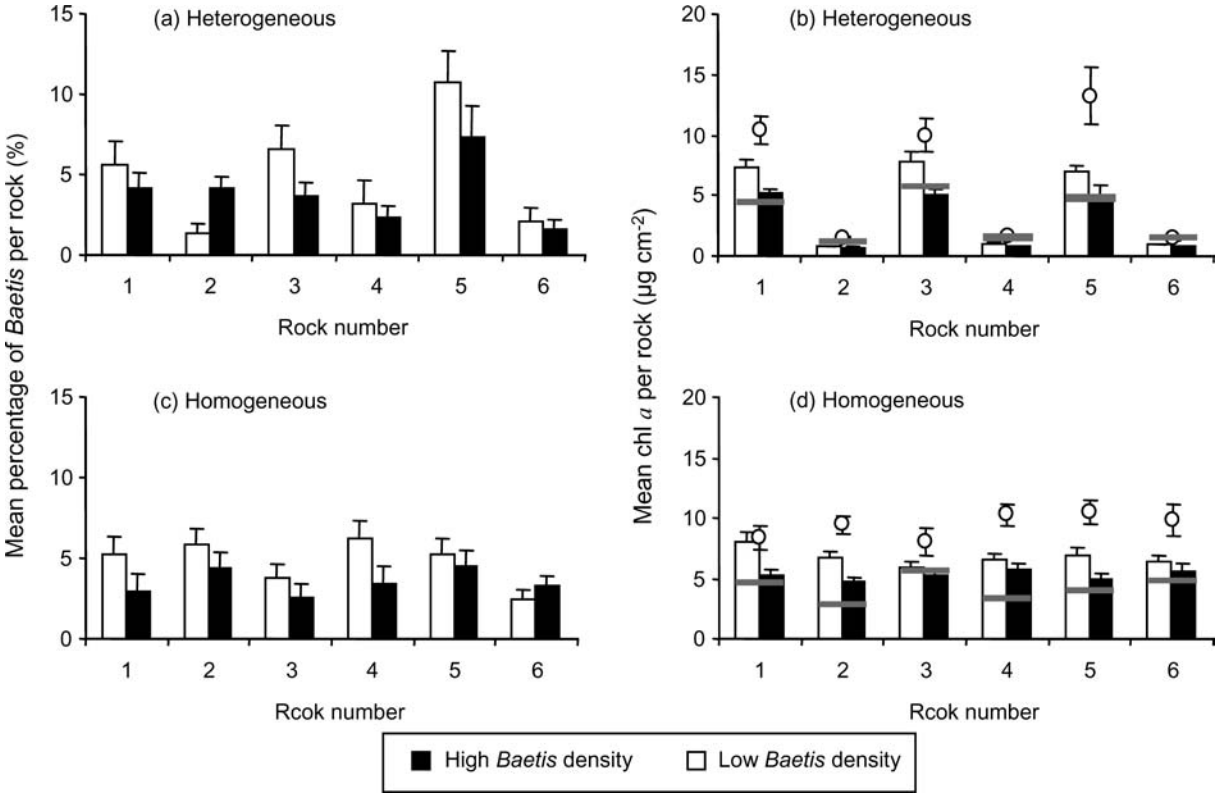

Fig. 6a–d Experiment II. Mean + 1 SE percentage of *Baetis* (**a, c**) and chl *a* (**b, d**) per rock for initially heterogeneous (**a**, **b**) and homogeneous (**c**, **d**) treatments. **b**, **d**: *Horizontal grey bars* indicate ± 1 SE of the mean initial values of chl *a* and the *circles* indicate means (± 1 SE) of the ungrazed controls. Since there was no significant fish effect, fish and no fish chambers were combined for illustration (but not for analysis). Values are based on grazers and chl *a* measured on each rock

even though predatory stoneflies increased *Baetis* drift from all rocks (Peckarsky 1996). Interestingly, in this study *Baetis* was less selective in high-density treatments, possibly because of interference with other grazers foraging at higher densities.

The equivalent per capita effect of all grazers on mean algal biomass was unexpected, because most previous investigations have shown that scraping caddisflies have a stronger effect on algal biomass than mayflies (Hill and Knight 1988; Feminella et al. 1989; but see Dudley 1992). However, higher grazer density had greater effects on algal biomass than did low grazer densities, as has been reported previously in this system (Taylor et al. 2002) and in other studies conducted at various spatial scales with different grazers (Hill and Knight 1987; Kohler and Wiley 1997).

While all grazer species used in this study had the same per capita effect on chl *a* biomass, per grazer biomass effects differed. The largest grazer, *Epeorus*, had the lowest per biomass impact, and the smallest grazer, *Baetis*, the highest impact per unit biomass. These results are consistent with other studies in laboratory streams, where *Baetis* effects on periphyton, corrected for body mass, were comparable to those of the larger *Juga* snails (Lamberti et al. 1995). The per unit biomass grazer impacts estimated in this study also showed that the effects of grazers on mean chl *a* were not simply a function of variation in total invertebrate biomass per chamber (Taylor et al. 2002). Although total grazer biomass differed per chamber, final algal biomass did not differ among chambers with different grazer species. Thus, neither differences among grazer body sizes nor differences in grazer mobility caused variation in algal biomass among grazer treatments.

One of the most striking results of this study was the observed increase in algal heterogeneity with increasing consumer mobility (experiment I). Using simple two-patch models, Abrams (2000) predicted that the pattern of resource heterogeneity (measured as the difference between two resource patches) along an axis of grazer mobility should fit a hump-shaped curve. Assuming that grazers have homogeneous distributions and equal access to all patches, he predicted that immobile grazers should homogenize resources, variability among resource patches should be greatest for intermediate rates of movement, and highly mobile consumers should decrease spatial variation in food abundance by overexploitation. Based on these models we originally hypothesized that stream invertebrates with low and high mobility (caddisflies and *Baetis* in fishless water, respectively) would homogenize algal resources and that grazers with intermediate rates of mobility (e.g., crawling mayfly larvae: *Epeorus* and *Baetis* in fish water) would increase the spatial heterogeneity of algae.

Consistent with Abrams' (2000) predictions, at this small scale (microcosms) the most sedentary consumer (the caddisfly *Allomyia*) homogenized algal resources. However, the most mobile grazer (*Baetis* in fishless water) increased differences in algal biomass among patches (rocks) compared to *Allomyia* and ungrazed treatments, maintaining algal heterogeneity at the levels established at the beginning of the experiment. If the grazer species tested in this experiment were relatively sedentary, these results would be consistent with the left side of a hump-shaped curve. However, mayflies were more mobile in microcosms than in larger chambers (mesocosms) (B. L. Peckarsky, unpublished data), suggesting that overall movement rates of *Baetis* were inflated in microcosms compared to mesocosms. Furthermore, consumers with higher mobility (fishless *Baetis*) homogenized algal resources in mesocosms compared to less mobile *Baetis* in fish water (McIntosh et al. 2004). Thus, the inconsistency between results using the same species of grazers at different scales suggests that factors other than grazer mobility, such as variation in grazer density and physical habitat complexity contributed to observed variation in algal heterogeneity at larger scales.

Using a spatially explicit simulation model Poff and Nelson-Baker (1997) predicted that resource heterogeneity should increase with higher grazer densities until some threshold, above which grazers combined small patches thereby homogenizing resources. As predicted by this model, increasing grazing snail densities resulted in more homogeneous distributions of filamentous algae in artificial streams, consistent with effects observed in natural streams with higher ranges of grazer densities (100–3,500 larvae m^{-2}) (Sarnelle et al. 1993). However, over the range of *Baetis* densities tested in experiment II (350–700 larvae m^{-2}) grazer density did not affect I_d, which is consistent with experiments conducted in small streams with a similar range of densities of the same grazer taxa (200–800 larvae m^{-2}) with or without added fish cues (McIntosh et al. 2004). In contrast, McIntosh et al. (2004) observed that in unmanipulated streams with a wider range of grazer densities ($\sim$100–2,000/m^2), resource heterogeneity decreased with increasing grazer densities, but only in fishless streams where grazer movements were unconstrained. Furthermore, McIntosh et al. (2004) demonstrated that suppression of mayfly grazing by predators indirectly increased resource heterogeneity under controlled abiotic conditions in mesocosms and small stream experiments, but not in natural (unmanipulated) streams where multiple interacting factors can affect algal distributions.

McIntosh et al. (2004) argued that physical factors should predominantly control resource heterogeneity when consumer-resource (biotic) interactions are weak. Thus, reduced feeding activity of grazers, via low densities or by predator-induced changes in grazer behavior, could indirectly increase the influence of abiotic factors on resource heterogeneity, especially in natural streams with a high degree of abiotic heterogeneity. Therefore, we speculate that low variation in physical variables, such as current and substrate, and narrow ranges of grazer density in the microcosms may have prevented natural bottom-up processes from generating resource heterogeneity in these small-scale experiments. Clearly, more experiments across a range of grazer densities and physical conditions are needed to enable us to generalize regarding the effects of grazers on resource heterogeneity.

Finally, important insights can be gained from interpreting conflicting results observed in the same system at different scales. While the goal of this study was to test theoretical models on herbivore-plant interactions at the microcosm scale, our results also illustrate that experiments conducted at small scales may fail to predict larger scale responses (Carpenter 1996). The different effects of grazing stream insects on periphyton biomass and distribution at different scales may be attributed to differences in environmental complexity and scale-dependent constraints on mechanisms involved in consumer–algal interactions (Englund 1997). However, development of theory for extrapolation of experimental results across scales still remains a major challenge in ecology (Levin 1992)

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References

Abrams PA (2000) The impact of habitat selection on the spatial heterogeneity of resources in varying environments. Ecology 81:2902–2913

Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479

Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL (1996) Mechanisms that result in large herbivore grazing distribution patterns. J Range Manage 49:386–400

Bakker C, Blair JM, Knapp AK (2003) Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grasslands? Oecologia 137:385–391

Berlow EL, Navarrete SA, Briggs CJ, Power ME, Menge BA (1999) Quantifying variation in the strengths of species interaction. Ecology 80:2206–2224

Bigger DS and Marvier MA (1998) How different would a world without herbivory be? A search for generality in ecology. Integr Biol 1:60–67

Biggs BJF (1996) Patterns in benthic algae of streams. In: Stevenson RJ, Bothwell ML, Lowe RL (eds) Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego, Calif., pp 31–56
Bisigato AJ, Bertiller MB (1997) Grazing effects on patchy dry land vegetation in northern Patagonia. J Arid Environ 36:639–653
Bronmark C, Klosiewski SP, Stein RA (1992) Indirect effects of predation in a freshwater, benthic food chain. Ecology 73:1662–1674
Carpenter SR (1996) Microcosms have limited relevance for community and ecosystem ecology. Ecology 77:677–680
Chase JM, Wilson W, Richards S (2001) Foraging trade-offs and resource patchiness: theory and experiments with a freshwater snail community. Ecol Lett 4:304–312
Cooper SD, Diehl S, Kratz S, Sarnelle O (1998) Implications of scale for patterns and processes in stream ecology. Aust Ecol 23:27–40
Cyr H, Pace ML (1993) Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. Nature 361:148–150
Dudley TL (1992) Beneficial effects of herbivores on stream macroalgae via epiphyte removal. Oikos 65:121–127
Duffy JE, Macdonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. Ecology 82:2417–2434
Edmunds GF, Jensen SL, Berner L (1976) The mayflies of North and Central America. University of Minnesota Press, Minneapolis, Minn.
Elliott JM (1977) Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol Assoc Sci Publ 25:50–79
Englund G (1997) Importance of spatial scale and prey movements in predator caging experiments. Ecology 78:2316–2325
Feminella JW, Resh VH (1990) Hydrologic influences, disturbance, and intraspecific competition in a stream caddisfly population. Ecology 71:2083–2094
Feminella JW, Power ME, Resh VH (1989) Periphyton response to grazing invertebrates and riparian canopy in three northern California coastal streams. Freshwater Biol 22:445–457
Flecker AS (1997) Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength. J North Am Benthol Soc 16:286–295
Flecker AS, Taylor BW (2004) Tropical fishes as biological bulldozers: density effects on resource heterogeneity and species diversity. Ecology 85:2267–2278
Forrester GE (1994) Influences of predatory fish on the drift dispersal and local density of stream insects. Ecology 75:1208–1218
Gelwick FP (2000) Grazer identity changes the spatial distribution of cascading trophic effects in stream pools. Oecologia 125:573–583
Gelwick FP, Matthews WJ (1997) Effects of algivorous minnows (*Campostoma*) on spatial and temporal heterogeneity of stream periphyton. Oecologia 112:386–392
Hildrew AG (1996) Food webs and species interactions. In: Petts GE, Calow P (eds) River biota, diversity and dynamics. Blackwell, Oxford, pp 123–144
Hill WR, Knight AW (1987) Experimental analysis of the grazing interaction between a mayfly and stream algae. Ecology 68:1955–1965
Hill WR, Knight AW (1988) Concurrent grazing effects of two stream insects on periphyton. Limnol Oceanogr 33:15–26
Hill WR, Weber SC, Stewart AJ (1992) Food limitation of two lotic grazers: quantity, quality, and size-specificity. J North Am Benthol Soc 11:420–432
Hobbs NT, Gross JE, Shipley LA, Spalinger DE, Wunder BA (2003) Herbivore functional response in heterogeneous environments: a contest among models. Ecology 84:666–681
Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG (1999) The keystone role of bison in North American tallgrass prairie. BioScience 49:39–50
Kohler SL (1984) Search mechanism of a stream grazer in patchy environments: the role of food abundance. Oecologia 62:209–218
Kohler SL (1985) Identification of stream drift mechanisms: an experimental and observational approach. Ecology 66:1749–1761
Kohler SL, Wiley MJ (1997) Pathogen outbreaks reveal large-scale effects of competition in stream communities. Ecology 78:2164–2176
Laca EA, Demment M (1991) Herbivory: the dilemma of foraging in a spatially heterogeneous food environment. In: Palo RT, Robbins CT (eds) Plant defenses against mammalian herbivory. CRC, Boca Raton, Fla., pp 29–44
Lamberti GA, Ashkenas LR, Gregory SV, Steinman AD (1987) Effects of three herbivores on periphyton communities in laboratory streams. J North Am Benthol Soc 6:92–104
Lamberti GA, Gregory SV, Ashkenas LR, Li JL, Steinman AD, McIntire CD (1995) Influences of grazer type and abundance on plant-herbivore interactions in streams. Hydrobiologia 306:179–188
Laska MS, Wootton JT (1998) Theoretical concepts and empirical approaches to measuring interaction strength. Ecology 79:461–476
Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967
Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am Nat 112:23–39
McIntosh AR, Townsend CR (1996) Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behavior. Oecologia 108:174–181
McIntosh AR, Peckarsky BL, Taylor BW (2004) Predator-induced resource heterogeneity in a stream food web. Ecology 85:2279–2290
McPeek MA, Peckarsky BL (1998) Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. Ecology 79:867–879
Mills LS, Soule ME, Doak DF (1993) The keystone species concept in ecology and conservation. BioScience 43:219–224
Miyasaka H, Genkai-Kato M, Kuhara N, Nakano S (2003) Predatory fish impact on competition between stream insect grazers: a consideration of behaviorally- and density-mediated effects on an apparent coexistence pattern. Oikos 101:511–520
Mulholland PJ, Steinman AD, Palumbo AV, Elwood JW (1991) Role of nutrient cycling and herbivory in regulating periphyton communities in laboratory streams. Ecology 72:966–982
Nusch EA (1980) Comparison of different methods for chlorophyll and phaeopigments. Arch Hydrobiol Beih Ergebg Limnol 14:14–36
Osenberg CW, Mittelbach GG (1996) The relative importance of resource limitation and predator limitation in food chains. In: Polis GA, Winemiller KO (eds) Food webs: integration of patterns and dynamics. Chapman and Hall, New York, pp 134–148
Peckarsky BL (1991) Habitat selection by stream-dwelling predatory stoneflies. Can J Fish Aquat Sci 48:1069–1976
Peckarsky BL (1996) Alternative predator avoidance syndromes in stream-dwelling mayflies. Ecology 77:1888–1905
Peckarsky BL, Cowan CA (1991) Consequences of larval intraspecific interference to stonefly growth and fecundity. Oecologia 88:277–288
Peckarsky BL, Cowan CA (1995) Microhabitat and activity periodicity of predatory stoneflies and their mayfly prey in a western Colorado stream. Oikos 74:513–521
Peckarsky BL, McIntosh A (1998) Fitness and community consequences of avoiding multiple predators. Oecologia 113:565–576
Peckarsky BL, Cooper SD, McIntosh AR (1997) Extrapolating from individual behavior to populations and communities in streams. J North Am Benthol Soc 16:375–390
Peckarsky BL, Taylor BW, McIntosh AR, McPeek MA, Lytle DA (2001) Variation in mayfly size at metamorphosis as a developmental response to risk of predation. Ecology 82:740–757
Poff NL, Nelson-Baker K (1997) Habitat heterogeneity and algal grazer interactions in streams: explorations with a spatially explicit model. J North Am Benthol Soc 16:263–276

Power ME (1984) Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. J Anim Ecol 53:357–374

Power ME (1990) Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. Ecology 71:897–904

Richards C, Minshall GW (1988) The influence of periphyton abundance on *Baetis bicaudatus* distribution and colonization in a small stream. J North Am Benthol Soc 7:77–86

Sarnelle OK, Kratz W, Cooper SD (1993) Effects of an invertebrate grazer on the spatial arrangement of a benthic microhabitat. Oecologia 96:208–218

Scheiner SM (2001) MANOVA: multiple response variables and multispecies interactions. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Oxford University Press, New York, pp 99–115

Sih A, Wooster D (1994) Prey behavior, prey dispersal and predator impacts on stream prey. Ecology 68:1199–1207

Sommer U (2000) Benthic microalgal diversity enhanced by spatial heterogeneity of grazing. Oecologia 122:284–287

Steinman AD (1996) Effects of grazers on freshwater benthic algae. In: Stevenson RJ, Bothwell ML, Lowe RL (eds) Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego, Calif., pp 341–373

Steinman AD, McIntire CD, Gregory SV, Lamberti GA, Ashkenas LR (1987) Effects of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. J North Am Benthol Soc 6:175–188

Taylor BW, McIntosh AR, Peckarsky BL (2002) Reach-scale invertebrate manipulations show invertebrate grazers depress algal resources in natural streams. Limnol Oceanogr 47:893–899

Wiggins GB (1996) Larvae of the North American caddisfly genera, 2nd edn. University of Toronto Press, Toronto

Wolcott DL, O'Connor NJ (1992) Herbivory in crabs: adaptations and ecological considerations. Am Zool 32:370–381

Wooster D (1994) Predator impacts on stream benthic prey. Oecologia 99:7–15

Wootton JT (1997) Estimates and test of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecol Monogr 67:45–64