Grazer–collector facilitation hypothesis supported by laboratory but not field experiments

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Abstract: Grazing invertebrates in streams feed by harvesting algal cells from surfaces, and in doing so release fine particulate organic matter (FPOM). The "grazer–collector facilitation hypothesis" holds that FPOM production by grazers facilitates growth and (or) survival of FPOM-collecting invertebrates. We tested for grazer–collector facilitation in laboratory and field experiments. In recirculating flumes in the laboratory, we tested for facilitation of the collector *Hydropsyche slossonae* by the grazers *Physa gyrina*, *Glossosoma intermedium*, and *Baetis tricaudatus*. All three grazers increased FPOM levels in flume water, but only *Physa* facilitated *Hydropsyche* growth. In the field, we manipulated *Physa* and *Glossosoma* densities to test for facilitation (at a local scale) of natural collector assemblages in an eastern Iowa stream. We did not detect facilitation of any collector by either grazer in the field, despite high power to detect such interactions. We suspect that grazer–collector facilitation was not observed in the field because (unlike in our laboratory flumes) field FPOM levels are often high and extremely variable in time and space and because organic particles can arise from sources other than grazer activity (= grazer-independent processing). Therefore, at local scales, collectors may not be significantly limited by the supply of grazer-derived FPOM.

Résumé : Les invertébrés brouteurs dans les cours d'eau se nourrissent en récoltant les cellules d'algues sur diverses surfaces et, ce faisant, ils libèrent de fines particules de matière organique (FPOM). L'hypothèse de « la facilitation brouteurs–collecteurs » veut que la production de FPOM par les brouteurs facilite la croissance et (ou) la survie des invertébrés collecteurs de FPOM. Nous avons vérifié l'existence des cette facilitation brouteurs–collecteurs dans des expériences en laboratoire et sur le terrain. Dans des canalisations de laboratoire avec recirculation de l'eau, nous avons vérifié la présence de facilitation chez le collecteur *Hydropsyche slossonae* par les brouteurs *Physa gyrina*, *Glossosoma intermedium* et *Baetis tricaudatus*. Les trois brouteurs augmentent les concentrations de FPOM dans l'eau des canalisations, mais seul *Physa* favorise la croissance d'*Hydropsyche*. Sur le terrain, dans un cours d'eau de l'est de l'Iowa, nous avons fait varier les densités de *Physa* et de *Glossosoma* afin de vérifier s'il y a de la facilitation (à l'échelle locale) dans la communauté naturelle de collecteurs. En nature, nous n'avons observé aucune facilitation chez les divers collecteurs par ni l'un ni l'autre des brouteurs, malgré notre capacité élevée de détecter de telles interactions. Nous soupçonnons que la facilitation brouteurs–collecteurs n'a pas été observée en nature car, contrairement à ce qui se passe dans les canalisations de laboratoire, les concentrations de FPOM y sont fortes et extrêmement variables dans le temps et dans l'espace et parce qu'il y a des sources de particules organiques autres que les brouteurs (= décomposition indépendante des brouteurs). Ainsi, aux échelles locales, les collecteurs ne sont peut-être pas limités significativement par l'apport de FPOM en provenance des brouteurs.

[Traduit par la Rédaction]

Introduction

Food webs in temperate streams are generally based on organic matter from two sources: detritus, largely in the form of coarse particulate organic matter (CPOM) of terrestrial origin; and primary production by periphyton (and to a lesser extent aquatic macrophytes). The processing of detrital material and periphyton to fine particulate organic matter (FPOM) has long been thought to play an important ecological role in stream communities. FPOM production has been an important element of conceptual models for stream ecosystem function (e.g., Minshall et al. 1985; Wallace and Webster 1996) and underlies hypothesized interactions among three functional groups of benthic stream invertebrates: shredders (that feed on CPOM), grazers (or "scrapers" that scrape or shear algal cells from periphyton), and collectors (that feed on FPOM filtered from the water column or collected from the substrate). Shredders process CPOM to FPOM as a byproduct of their feeding activity and therefore are widely assumed to facilitate growth and (or) survival of collectors (Heard and Richardson 1995). Similarly, grazers release FPOM as they feed, and as a result, they have been suggested to facilitate collectors (e.g., McCullough et al. 1979; Lamberti et al. 1987; Power et al. 1988). However, field experiments testing for either hypothesized interaction have been entirely lacking, with the shredder–collector and grazer–collector facilitation hypothe-

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ses supported instead by laboratory experiments and by correlative data (Heard and Richardson 1995). In this paper, we report laboratory- and field-based experimental tests of the grazer–collector facilitation hypothesis (in a future paper, we will report parallel tests of the shredder–collector facilitation hypothesis).

Grazing invertebrates are ubiquitous and often abundant members of benthic stream faunas. They are especially important in unshaded to moderately shaded streams in which primary productivity is relatively high: for instance, streams typical of grasslands, agricultural areas, aridlands, tundra, and other areas lacking continuous forest canopy. Effects of grazers on periphyton standing crop and productivity (review: Hillebrand 2002) and on stream nutrient transport and cycling (Lamberti et al. 1987, 1989; Sallenave et al. 1994) have been studied at length, but much less is known about how grazers interact with invertebrates in other feeding groups. Our focus is on the hypothesis that grazers, by processing algal cells and associated organic material to FPOM, facilitate growth and (or) survival of collectors downstream.

A grazer–collector interaction is plausible because grazers produce FPOM by several mechanisms: by dislodging particles as they move across the periphyton layer (Lamberti et al. 1987; Scrimgeour et al. 1991), by releasing harvested but uningested particles into the water column (Hart 1985), and by releasing fecal particles (Shepard and Minshall 1984; Lamberti et al. 1987, 1989). Particles of each origin enter the FPOM pool available to collectors (McCullough et al. 1979; Benke and Wallace 1980, 1997). Grazer-derived FPOM can be of high nutritional quality: dislodged but uningested algal particles can be three- to five-fold higher in quality compared with the overall detrital pool (Benke and Wallace 1980; Fuller and Mackay 1981), and even fecal particles can be superior to nonfecal detritus (Shepard and Minshall 1981) and can contribute significantly to collector production (Shepard and Minshall 1984; Wotton et al. 1998).

Grazer–collector interactions are not inevitable, however, because grazer activity is not the only route by which periphyton can be processed to particles. Other routes for periphyton processing, collectively referred to as "grazer-independent processing", include sloughing of dead and dying cells (Lamberti et al. 1987) and scouring of periphyton by inorganic particles in suspension (Chauvet et al. 1993). The nature of the interaction between grazers and collectors is likely to depend on the relative rates of grazer-dependent and grazer-independent processing of periphyton to FPOM: grazer–collector interactions should be facilitative when grazer-independent processing is slow but could be neutral or even amensal (negative) when grazer-independent processing is substantial (Heard 1994; Heard and Richardson 1995). Furthermore, periphyton is not the only source of particles in streams: FPOM also enters streams in runoff (Roeding and Smock 1989; Yule 1996; Wallace et al. 1999) and is produced by shredders feeding on CPOM (Heard and Richardson 1995), by mechanical abrasion of CPOM (Heard et al. 1999), and by flocculation of dissolved organic matter (Lush and Hynes 1973; Petersen 1986). In light of the variety of FPOM sources and agents of periphyton processing in streams, it is by no means inevitable that FPOM produced by grazer activity will limit collector growth or survival.

We tested for effects of grazers on collectors in both laboratory and field settings. For laboratory experiments, we chose one focal collector (the caddisfly *Hydropsyche slossonae*) and three grazers with distinct feeding ecologies: the snail *Physa gyrina*, the caddisfly *Glossosoma intermedium*, and the mayfly *Baetis tricaudatus*. Our laboratory experiments were intended to test for grazer–collector facilitation under ideal conditions: highly controlled experimental flumes with little spatial or temporal variation in FPOM except that associated with the presence or absence of grazers. In addition, we chose stocking densities of grazers and collectors to maximize the probability of detecting facilitation if it could exist. In the field, we manipulated two of the grazers that we studied in the laboratory (*Physa* and *Glossosoma*) in caging experiments to determine whether grazers facilitate collectors under natural conditions (which include higher and more variable amounts of FPOM). Our experiments were designed to test for interactions at a local scale, that is, effects of a local aggregation of grazers (≈50 individuals in ≈100 cm^2) on collector populations immediately downstream. Although grazer–collector interactions are also possible at the reach scale (integrating the effects of thousands to millions of collectors over hundreds to thousands of metres), such a hypothesis will require separate, quite different experimental tests and is not pursued here.

Methods

Laboratory flume experiments

Study species

In flume experiments, we tested for facilitation of a focal collector (the caddisfly *Hydropsyche slossonae* Banks (Trichoptera: Hydropsychidae)) by each of three grazers: the snail *Physa gyrina* Say (Gastropoda: Physidae), the caddisfly *Glossosoma intermedium* (Klapalek) (Trichoptera: Glossosomatidae), and the mayfly *Baetis tricaudatus* Dodds (Ephemeroptera: Baetidae). These species are among the dominant members of their guilds at our field site (Big Mill Creek, eastern Iowa; see below). We chose grazers differing in feeding behavior and mouthpart morphology because we suspected that they might differ in the quantity and quality of FPOM that they produced.

Hydropsyche larvae inhabit hard substrates where they spin nets to capture drifting organic particles including detritus, algal cells, and small invertebrates. They also collect and graze periphyton cells, and the relative importance of these items to the diet depends on availability and varies among species and instars (Fuller and Mackay 1980, 1981). *Hydropsyche slossonae* is widespread in cool and unpolluted streams across northeastern and central North America. In its later instars (used in our experiments), it makes nets with mesh sizes between 60 μm × 90 μm (third instar) and 180 μm × 300 μm (fifth instar) (Fuller and Mackay 1980). Its diet can include both algal and detrital particles (Fuller and Mackay 1981), with use of algal cells increasing in later instars (Fuller and Mackay 1980).

Physa snails (including *P. gyrina*) use their toothed radulae to scrape periphyton and other organics from hard substrates or to feed on plant tissues or occasionally carrion, with periphyton generally preferred (Brown 1991). *Physa*

gyrina ranges from the Arctic to the Gulf of Mexico and is abundant in both riffles and pools in Big Mill Creek.

Glossosoma larvae have cutting mandibles that shear and scrape periphyton at the substrate surface (McAuliffe 1984) and are important grazers in many cold-water streams (Kohler 1992). *Glossosoma intermedium* has a Holarctic distribution and is common and locally abundant in cool, fast streams in the midwestern United States.

Baetis larvae have brush-like mouthparts that sweep through the upper layers of periphyton to remove loosely attached diatoms and other algal, bacterial, and detrital particles (Dudley 1992). *Baetis tricaudatus* ranges across much of North America, prefers cold-water, rapid streams with hard substrate, and can be a dominant grazer in the Midwest (Kohler 1992). Both periphyton and detrital particles are important elements of baetid diets (Shapas and Hilsenhoff 1976).

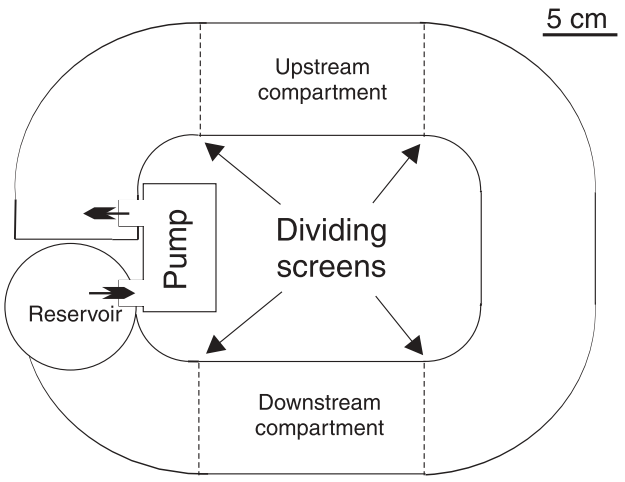
Flume setup

Recirculating flumes (Fig. 1) were constructed of 64-mm (inside diameter) polyvinyl chloride pipe cut lengthwise to give a semicircular cross section. Each flume was oval in layout, with a watercourse falling 3 cm over its 90-cm run, and held about 1.7 L of water recirculated at 0.1 $L \cdot s^{-1}$ by an aquarium pump (Aqua-Tech 5-15; Regent Pet Products, Moorpark, Calif.). Two experimental compartments were demarcated with screens of 2-mm mesh (fiberglass window screen): one upstream for grazers and one downstream for collectors. Each compartment was 15 cm long and 6 cm in wetted width and had water 15–20 mm deep. We kept the flumes in environmental chambers (Percival I36-LL; Percival Scientific, Boone, Iowa) set at 8 °C and a 12 h light – 12 h dark photoperiod.

We set up experiments with invertebrates, periphyton-covered gravel, and water collected from Big Mill Creek. We hand-picked invertebrates in the field, holding undamaged animals in stream water kept on ice and aerated by aquarium bubblers for return to the laboratory. We held all invertebrates in the environmental chambers for 7–10 days before use in flumes. Gravel was also kept on ice for transport to the laboratory and held (without invertebrates) in the environmental chambers until use. Water was filtered through 2-mm mesh to remove large debris and stored in the chambers until needed.

We compared FPOM production and *Hydropsyche* (collector) growth in flumes with and without each grazer. Each experimental run used 10 replicate flumes (five "control" and five "grazer"). We performed four runs with *Physa* (November–December 1998), four with *Baetis* (April–June 1999), and five with *Glossosoma* (October 1998 and February–March 1999). Each flume received, in its upstream compartment, 10 pieces (20–40 mm in diameter) of periphyton-covered gravel. In grazer flumes, but not in controls, this compartment also received 10 grazer individuals (*Physa*, *Glossosoma*, or *Baetis*). For all three grazers, this is toward the high end of the range of natural densities at Big Mill Creek. In the downstream compartment of each flume, we placed one third- or fourth-instar *Hydropsyche* larva along with several pieces of fine gravel (2–4 mm in diameter) and broken ceramic tile (10–40 mm × 10 mm × 6 mm)

Fig. 1. Design of recirculating laboratory flumes (top view). Water flow is clockwise. The compartment above is for grazers and periphyton-covered gravel; the compartment below is for *Hydropsyche* (the collector).



to which the *Hydropsyche* could anchor nets. *Hydropsyche* larvae were randomly assigned to grazer or control treatments. The grazer to collector ratio was held higher than typical for our field site deliberately to increase the potential impact of grazers on collectors and therefore maximize the probability of detecting facilitation if it could exist. Each experimental run lasted 2 weeks, during which time we replaced stream water lost by evaporation and cleaned screens with a toothbrush as necessary to maintain water flow. To the extent that cleaning of screens produces new FPOM (as opposed to resuspending FPOM filtered by the screens), it should make the detection of grazer–collector facilitation less likely, and therefore make our tests conservative.

Some grazer individuals died during our experiments. There was little mortality among *Physa* or *Glossosoma* (never more than three per flume); to minimize disturbance to flumes, dead *Physa* or *Glossosoma* were not replaced. More *Baetis* died in our flumes, however, and we replaced dead *Baetis* as needed (average of seven replacements per flume). Disturbances to grazer flumes during *Baetis* replacement were replicated in controls. We found *Baetis* generally difficult to maintain in the laboratory, with substantial mortality in collection and maintenance. However, most dead *Baetis* had been feeding actively (they had algal cells in their guts).

Chlorophyll a

We measured chlorophyll *a* to test for effects of grazers on periphyton standing crops. We collected each flume's gravel after each run, extracted pigments in 90% acetone, and assayed chlorophyll *a* spectrophotometrically (LKB Ultraspec 2-D model 4050; UKB Biochrom Ltd., Cambridge, England) using standard methods (Steinman and Lamberti 1996). We used total chlorophyll *a* (micrograms) from the gravel in each flume as our index of periphyton standing crop. Periphyton on flume surfaces was not measured.

Table 1. Design summaries for field experiments.

Experiment	Start date	Duration (days)	Grazer species	Treatment	Replicates per treatment	Substrate sampling method	FPOM data?
Fall 1997	7 August	56	*Physa gyrina*	Grazers vs. no grazers Cobble vs. no cobble 2- vs. 12-mm-mesh cage[a]	5		Yes
Fall 1998	18 September	21	*Physa gyrina*	Grazers vs. no grazers	19	Hess samples and substrate trays	Yes
Spring 1999	17 April	28	*Glossosoma intermedium*	Grazers vs. no grazers	20	Hess samples	No

Note: FPOM, fine particulate organic matter.
[a]Incomplete factorial design: for 12-mm-mesh cages, grazers cannot be manipulated because the mesh size allows free entry and egress to benthic invertebrates. All other possible combinations were used for a total of six treatments.

FPOM

We measured FPOM production as ash-free dry mass per flume. After each run, we collected the entire water volume from each flume, after gentle brushing with a soft toothbrush to resuspend sedimented particles. We determined ash-free dry mass from a 300-mL subsample (and then corrected to total flume volume) by filtration through a preweighed 0.7-μm glass-fiber filter (Advantec MFS GF7547), drying at 60 °C for 48 h, and weighing before and after ashing for 1 h at 500 °C. Analyses based instead on dry mass after filtration through 0.22-μm polycarbonate membrane filters (to include grazer effects on small particles) were very similar, so we report only the ash-free dry mass data.

We also measured size distributions of organic particles (both uningested periphyton particles and grazer fecal particles) produced by each grazer. Size distribution data came from one control flume for each grazer species and were based on a 1-mL subsample from the flume's collected (as above) total water volume. From each subsample, we sized (longest axis) 100 fecal particles and 100 periphyton particles using an ocular micrometer at 400× magnification.

Collector performance

We measured fresh mass gain or loss of each *Hydropsyche* larva as an index of collector performance. Before and after the 2-week experiment, each larva was gently blotted with a paper towel, weighed to the nearest 1 μg on a microbalance (Mettler MT-5; Mettler-Toledo Inc., Switzerland), and immediately returned to water. Blotting and weighing took about 20 s and caused no apparent harm to the larvae.

Statistical analysis

For each grazer, we compared chlorophyll *a*, FPOM production, and collector performance between grazer and control flumes (fixed effect) and among runs (random effect) using mixed-model two-way analyses of variance (ANOVAs). Nonsignificant interactions ($P > 0.05$) were dropped and their sums of squares pooled with the error. We compared FPOM size distributions among grazers using one-way ANOVAs, evaluating significance of F values by randomization (10 000 randomizations) because size distributions were strongly nonnormal. Otherwise, all statistical analyses were conducted in SAS version 7.0 (SAS Institute Inc., Cary, N.C.) using Type III sums of squares.

Field caging experiments

Study site

We conducted experiments in Big Mill Creek (Jackson County, Iowa; 42°17′N, 90°33′W), a spring-fed second-order stream with approximately 50 $L \cdot s^{-1}$ baseflow, incomplete shading, and a limestone cobble–gravel substrate. Riffle sections are approximately 3–5 m wide and 10–20 cm deep at baseflow, and spring inputs occur within the study reach and along a ≈2 km upstream run. Upstream sections also drain some low-intensity pasture and a small pond. The dominant grazers are *P. gyrina*, *G. intermedium*, and *Baetis* spp., mostly *B. tricaudatus* and *B. brunneicolor* (Ephemeroptera: Baetidae). The dominant collectors are *Hydropsyche* spp. (mostly *H. slossonae*) and *Cheumatopsyche* spp. (Trichoptera: Hydropsychidae), and black flies (Diptera: Simuliidae).

General design

We conducted three caging experiments, which were similar in overall design but differed in some details (Table 1). Our strategy was to target local-scale interactions by comparing FPOM concentration and collector abundance immediately downstream of cages with or without high densities of grazing invertebrates. We used cages without grazers as controls, rather than no cage at all, to ensure that differences in local flow patterns could not drive apparent treatment effects. We ran experiments with two of the three dominant grazers at Big Mill Creek: *P. gyrina* and *G. intermedium*. We were unable to manipulate *Baetis* densities in the field, since they easily escaped through any mesh open enough to allow water flow through cages.

In most experiments, we used cages (13.5 cm × 8.5 cm × 4 cm) of 2-mm plastic mesh (Plastic Canvas; Darice, Strongsville, Ohio) sewn shut with fishing line. In one experiment (fall 1997), some treatments used cages of 12-mm-mesh metal hardware cloth fastened with florists' wire. Large-mesh cages tested for effects of flow restriction and shading by the smaller mesh material but did not allow grazer manipulation. Cages were stocked immediately before placement in the stream with the desired combinations of grazers and periphyton-covered cobbles. Grazers were hand-picked in Big Mill Creek the same day they were used. Periphyton-covered cobbles (20–50 mm in diameter) were collected from Big Mill Creek, cleaned of invertebrates, and allowed to stand 1 week in stream water in an environmental

chamber (at 8 °C and a 12 h light – 12 h dark photoperiod) to increase periphyton density. We used four to six cobbles per cage (enough to loosely fill the cage). We did not measure periphyton biomass at the end of the experiments, but a visible periphyton layer remained on the cobbles (so grazers still had access to food).

To deploy cages, we attached them crosswise to the tops of standard clay bricks with plastic cable ties. Each brick was then dug into the stream bottom (parallel to the current) so the cage sat slightly above the surrounding substrate. We anchored bricks with steel reinforcing rods driven into the stream bottom. We placed cages in riffles at spots where water depth at baseflow was 12–20 cm. Cage exteriors were cleaned weekly of sediments and periphyton with a nylon brush to maintain water flow.

FPOM

In two experiments (Table 1), we used a direct count technique to measure FPOM levels in the field. At each sampling date, we took simultaneous 20-mL water samples immediately upstream and downstream of each cage (using syringes placed to sample water from the flow through the cage). Samples were returned to the laboratory on ice and then preserved in 4% formalin and stored at 4 °C. We stained (25 min at 0 °C) 500-µL subsamples with 5 nM 4′,6-diamidino-2-phenylindole, a DNA-binding fluorescent stain that allows discrimination of bacteria, protozoa, algae, and organic debris particles under epifluorescence microscopy (400×, excitation 365 nm). We filtered the subsamples onto 0.2-µm black polycarbonate membrane filters (Poretics K02CP02500), mounted the filters in immersion oil, and counted bacteria and organic particles in 10 haphazardly chosen microscope fields. The difference between upstream- and downstream-of-cage counts is an estimate of net particle production across the cage (possibly negative if cages tend to filter or sediment particles). We included bacterial counts because a variety of collectors have been shown either to consume bacterial cells directly or to strip bacteria from surfaces of more refractory detrital particles (e.g., Edwards and Meyer 1990).

Collector abundance

In two experiments (Table 1), we sampled invertebrates from artificial and (or) natural substrates downstream of our cages. Artificial substrates allowed control for fine-scale spatial heterogeneity in the streambed, whereas sampling natural substrate relaxed this control but provided a more realistic sample of the invertebrate community. Artificial substrates were made of 5-cm crushed limestone ballast (≈20 pieces, ≈800 g total) held in 12-mm-mesh hardware cloth trays 15 cm square and 2 cm deep. We positioned a tray 1 m downstream of each cage in the plume of water that passed through the cage (determined using food dye tracers). We set trays flush with the stream bottom, anchoring them with steel reinforcing rods. At the end of the experiment, each tray was gently lifted free and its contents (ballast and associated invertebrates) preserved in 70% ethanol. To sample invertebrates from natural substrate, we took a single sample with a 15-cm-diameter Hess sampler 50 cm downstream of each cage, preserving collected invertebrates in 70% ethanol. We identified collectors using standard references (Merritt and Cummins 1996; Wiggins 1996; black flies and chironomids to family and other taxa usually to genus). We counted individuals of each taxon and determined dry masses after drying for 48 h at 60 °C. Because our design allows migration of individuals to and from substrates during the course of the experiment, our collector abundance data will reflect differences between treatments in immigration or emigration, as well as growth and survival.

Fall 1997 experiment

In fall 1997, we caged *P. gyrina*. We used both 2- and 12-mm-mesh cages in six treatments with five replicates each (total 30 cages). The 2-mm-mesh cages were deployed in a two-way factorial design, with and without periphyton-covered cobble and with 0 or 50 *Physa* (four treatments). The 12-mm-mesh cages were set up with and without cobble (two treatments; local grazer populations had free access to these cages). Fifty *Physa* per cage ($4400 \cdot m^{-2}$) is a very high density for Big Mill Creek (and about fivefold higher than we used in our laboratory flumes). We chose such a dramatic treatment to achieve high grazer exploitation of available periphyton and therefore to maximize our likelihood of detecting grazer–collector interactions, if they existed. Treatments were interspersed randomly along the study reach with at least 5 m between cages. We took water samples for FPOM analysis weekly for 8 weeks but did not measure collector abundance.

Fall 1998 experiment

In fall 1998, we caged *Physa* again. Because there had been no significant treatment effects in our fall 1997 experiment, we simplified our design, using only the 2-mm-mesh cages and 19 replicates each of two treatments: (*i*) periphyton-covered cobble and (*ii*) periphyton-covered cobble plus 50 *Physa*. To further increase our power, we adopted a paired design, with control cages placed beside *Physa* cages across the breadth of the stream. Cages in a pair were separated by at least 1 m to ensure that downstream substrate samples were exposed to water flow passing through only one of the cages in a pair. Pairs of cages were at least 5 m apart, and *Physa* cages were alternated from left to right of their pairs every two cage sites. We ran this experiment later in the fall than the 1997 experiment (Table 1) and halted it after 3 weeks to avoid overlap with autumn leaf-fall (with its high organic matter availability). We took water samples for FPOM weekly and sampled invertebrates via both artificial substrate and Hess samples.

Spring 1999 experiment

In spring 1999, we caged *G. intermedium*. We used two treatments with 20 replicates of each: (*i*) periphyton-covered cobble and (*ii*) periphyton-covered cobble plus 38 *Glossosoma* ($3400 \cdot m^{-2}$, much higher than typical in the field). The design was again paired, but this time, we kept all *Glossosoma* cages on the same side of the stream. At these scales, mixing of particles across the width of the stream will be incomplete between pairs of cages (Heard et al. 2001); therefore, this design will tend to amplify differences between treatments as particles from one experimental cage are transported across the next. Randomized (fall 1997) or alternating designs (fall 1998) are more conservative for detecting local

Table 2. Chlorophyll *a*, fine particulate organic matter (FPOM, dry mass), and collector performance analyses for laboratory flume experiments.

		Physa flumes				*Glossosoma* flumes				*Baetis* flumes			
Measure	Source	df	MS[a]	*F*	*P*	df	MS[a]	*F*	*P*	df	MS[a]	*F*	*P*
Chlorophyll *a*	Grazer	1	94.9	5.47	0.026	1	245	6.97	0.012	1	7.0	0.59	0.45
	Run	3	826	47.6	<0.0001	4	167	4.76	0.0030	3	23	11.3	<0.0001
	Error	31	17.3			41	35.2			3	1	28.5	
FPOM	Grazer	1	0.507	13.22	0.0083	1	1.52	96.9	<0.0001	1	0.648	14.03	0.0007
	Run[b]	—	—	—	—	3[c]	0.097	6.19	0.0018	3	0.200	4.34	0.012
	Error	7	0.038			34	0.016			31	0.046		
Collector performance	Grazer	1	0.086	19.8	<0.0001	1	0.17	0.02	0.90	1	0.015	0.82	0.37
	Run	3	0.007	1.69	0.19	4	14.2	1.40	0.25	3	0.002	0.12	0.95
	Error	32	0.004			42	10.2			30	0.019		

Note: All *F* and *P* values are calculated after pooling nonsignificant grazer × run interactions with the error.
[a]Except for *Glossosoma* flume collector performance, MS = entry × 10^3.
[b]The analysis for *Physa* flume FPOM has no "run" effect because we determined ash-free dry mass for only one run of flumes. An analysis based on dry mass has similar results.
[c]We had five *Glossosoma* runs, but only four had associated ash-free dry mass measurements.

effects of grazers, but the same-side design includes some reach-level effects of high grazer densities and is therefore potentially more powerful. This experiment lasted 4 weeks, after which we sampled invertebrates using the Hess sampler (artificial substrates were lost in a spring freshet).

Statistical analysis

FPOM data (particle differences across cages) were analyzed with repeated-measures ANOVA. With one exception, we pooled nonsignificant ($P > 0.05$) interactions with the error. The exception was the time × grazer interaction, which we retained throughout because it was of strong a priori interest (an effect of grazers accumulating over time would produce such an interaction). In fall 1997, the main effect of mesh (2 versus 12 mm) was nonsignificant and was also pooled with the error (results would not differ if we simply omitted 12-mm-mesh cages). We report univariate tests of the time effect, but multivariate tests gave similar results. For the fall 1998 experiment, an alternative approach would take advantage of the paired design by summing particle differences across sampling dates and analyzing the totals using paired *t* tests; results of such tests did not differ from the repeated measures ANOVAs and are not reported. Collector abundance and mass data were analyzed using paired *t* tests contrasting control and experimental cages in a pair (our unpaired fall 1997 experiment did not include collector data). We analyzed abundance and mass of the most common collector taxa (*Hydropsyche* and black flies) individually and also analyzed total abundance and mass of all collectors. We calculated statistical power for effects on collector abundance and mass data using tables in Cohen (1988). We performed all analyses with SAS version 7.0 (SAS Institute Inc., Cary, N.C.) using Type III sums of squares.

Results

Laboratory flume experiments

Chlorophyll a

For *Physa* and *Glossosoma*, periphyton standing crop, measured as chlorophyll *a*, was significantly reduced (17% and 35%, respectively) in grazer flumes (Table 2; Fig. 2*a*). *Baetis* may also have reduced periphyton standing crop, but its effect (8%) was far from significant. Not surprisingly, there were often significant differences in periphyton growth among runs, but the effect of each grazer was consistent among runs (no grazer × run interactions).

FPOM

FPOM levels (ash-free dry mass) were significantly greater in flumes containing any of our three grazer species (Table 2; Fig. 2*b*). *Physa* and *Glossosoma* produced the most FPOM (100% and 86% more FPOM, respectively, than control flumes), whereas *Baetis* produced somewhat less (45% increase over controls). As for the chlorophyll analysis, there were significant run effects but no grazer × run interactions.

FPOM size distributions also differed among grazers for both uningested algal particles and fecal particles (algal particles: $F_{[2,297]} = 4.05$, $P = 0.018$; fecal particles: $F_{[2,297]} = 63.1$, $P < 0.0001$) (Fig. 3). For both particle types, *Physa* produced the largest particles, *Glossosoma* intermediate-sized particles, and *Baetis* the smallest particles. For all grazers, particles of uningested periphyton were much larger (three- to four-fold) than fecal particles.

Collector performance

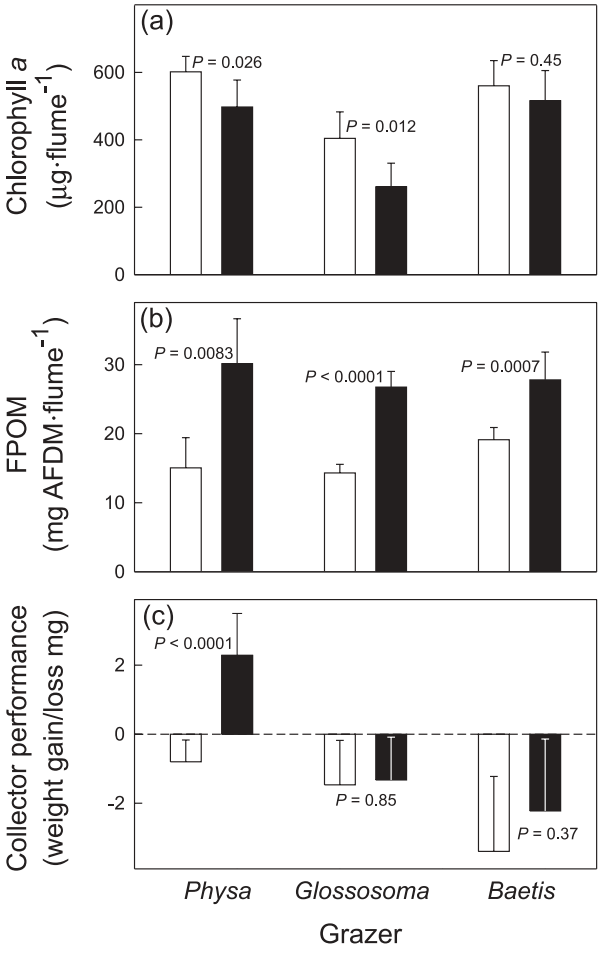
Hydropsyche larvae lost mass in the control flumes of all runs (Fig. 2*c*). In contrast, *Hydropsyche* gained mass in flumes with *Physa*, and *Physa*'s facilitation of *Hydropsyche* was highly significant (Table 2). In *Glossosoma* and *Baetis* flumes, *Hydropsyche* larvae lost less mass than in corresponding controls (Fig. 2*c*), but neither difference was significant. Once again, there were significant run effects but no significant grazer × run interactions.

Field experiments

FPOM

We measured particles in our first two experiments (fall 1997 and fall 1998). Particle densities and differences across cages were extremely variable (Fig. 4), a result consistent with other measurements in the system (S.B. Heard, unpub-

Fig. 2. Results from laboratory flume experiments for grazer (solid bars) and control (open bars) flumes. Error bars show ±2 SEs after removing run effects. (*a*) Periphyton standing crop measured as micrograms of chlorophyll *a* extracted from the gravel in the upstream compartment; (*b*) fine particulate organic matter (FPOM) production measured as milligrams ash-free dry mass (AFDM) filtered from the total water volume of each flume; (*c*) fresh mass gain or loss of the *Hydropsyche* larvae (collector) in each flume.



lished data). In neither experiment did particle differences across cages (for either particle type) differ significantly among treatments (Tables 3 and 4). (In 1998, we deleted from our analysis three cages with particle differences that were extreme outliers; however, none of our conclusions would be affected had we retained all of the cages.) None of the treatment (or treatment × time) effects were close to significance (all $F < 1$, all $P > 0.6$). In fact, there was never any significant change in particle densities across any set of cages (Fig. 4). Furthermore, changes in particle densities were never more positive (or less negative) across grazer cages, in contrast with the prediction from the grazer–collector facilitation hypothesis.

Collectors

We sampled collectors in our fall 1998 and spring 1999 experiments; in 1998, we used two parallel sampling techniques. In neither experiment (and for neither sampling technique) did collector abundance or dry mass differ between

Fig. 3. Particle sizes for fine particulate organic matter from grazer flumes (shaded bars, periphyton particles; open bars, fecal particles). For both particle types, differences among grazers are significant (periphyton, $P = 0.018$; fecal particles, $P < 0.0001$). Dots are means, center lines are medians, box boundaries are 25th and 75th percentiles, whiskers are 5th and 95th percentiles, and plus symbols represent extreme observations.

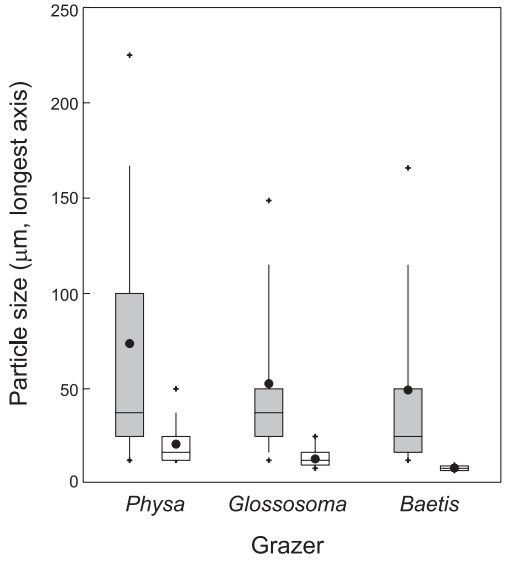
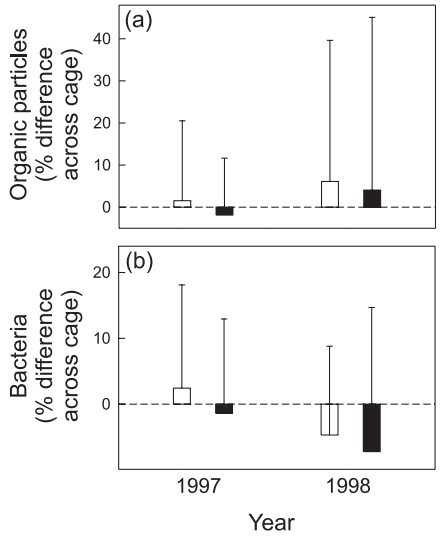


Fig. 4. Effects of control and grazer cages on particle densities (4′,6-diamidino-2-phenylindole counts) in water samples (expressed as downstream count minus upstream count, as a percentage of upstream count). Solid bars, grazer cages; open bars, control cages. Counts are pooled across the nonsignificant effect of date. For 1997, differences are also pooled across nonsignificant mesh and rock treatments. No bars are significantly different from zero height (no effect of treatment, all $P > 0.6$). Error bars show ±2 SEs.



samples taken downstream of control and grazer cages. This held true for collectors as a guild and also for the two dominant collectors (*Hydropsyche* spp. and black flies) considered separately (Fig. 5). Two grazer effects were nearly significant (black fly abundance in 1998 Hess samples and

Table 3. Repeated-measures ANOVAs for particle counts (fall 1997 field experiment).

	Bacteria				Organic particles			
Source	df	MS[a]	*F*	*P*	df	MS[a]	*F*	*P*
Between-subjects effects								
Time	5	213	1.65	0.15	5	4.88	0.63	0.68
Time × grazers	5	80.8	0.62	0.68	5	5.2	0.66	0.65
Error	110	129			110	7.8		
Within-subjects effects								
Cobble	1	74.9	0.32	0.58	1	9.25	0.99	0.33
Grazers	1	0.466	0.00	0.96	1	0.32	0.03	0.85
Error	22	233			22	9.32		

[a]MS = entry × 10^3.

Table 4. Repeated-measures ANOVAs for particle counts (fall 1998 field experiment).

	Bacteria				Organic particles			
Source	df	MS[a]	*F*	*P*	df	MS[a]	*F*	*P*
Between-subjects effects								
Time	1	147	1.51	0.23	1	30.4	1.93	0.17
Time × grazers	1	9.02	0.09	0.76	1	3.05	0.19	0.66
Error	32	97			32	15.7		
Within-subjects effects								
Grazers	1	9.82	0.21	0.65	1	0.287	0.03	0.87
Error	32	46			32	11		

[a]MS = entry × 10^3.

Hydropsyche weight in 1999 Hess samples), but both effects were negative and therefore inconsistent with the grazer–collector facilitation hypothesis.

Our designs had substantial power to detect grazer–collector facilitation, had it been present. All individual comparisons (i.e., one taxon's abundance or mass measured in one experiment by one sampling method) had >98% power for effects giving $r^2 > 0.2$ (20% of total variance in mass or abundance explained by treatment; Cohen 1988). The aggregate power of our combined experiments was very high: probabilities of our detecting facilitation for at least one collector in at least one experiment were >99% and >94% for effects giving $r^2 = 0.06$ and $r^2 = 0.04$, respectively (treatment explaining only 6% and 4% of total variance).

Discussion

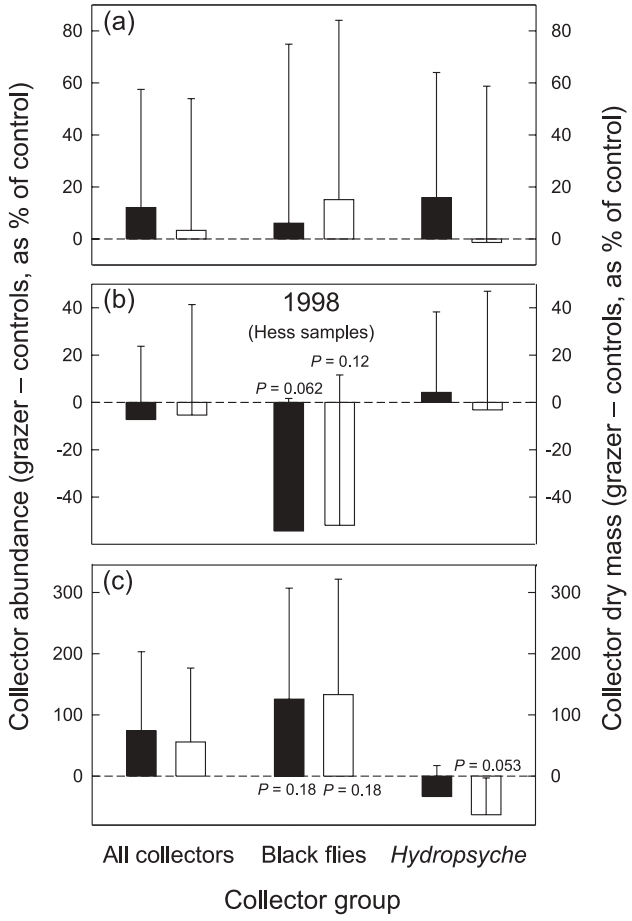
Although the grazer–collector facilitation hypothesis is certainly plausible, few studies have focused on grazer–collector interactions and none have directly tested the facilitation hypothesis in natural streams. Our results suggest that grazer–collector facilitation can be detected in highly controlled laboratory experiments but that local-scale facilitation does not play an important role in natural populations at our field site. Of course, we cannot rule out interactions over larger spatial scales or at other sites.

Grazer–collector facilitation in laboratory flumes

Grazers in our laboratory flumes processed periphyton to FPOM and thereby depressed periphyton standing crop (significantly so for two of three grazers). Flumes with grazers experienced substantial increases in FPOM levels (45–100% depending on grazer species and including both dislodged but uningested periphyton cells and fecal particles). These results are consistent with previous experiments documenting periphyton removal and FPOM production by grazers, with effects varying among grazer species (e.g., Lamberti et al. 1987; Scrimgeour et al. 1991; Hillebrand 2002).

Although all three grazers generated substantial FPOM, only one had a detectable effect on collector growth: *Physa* significantly facilitated *Hydropsyche*, whereas *Baetis* and *Glossosoma* did not. We believe that ours is the first experiment to connect FPOM production by grazers to increases in collector growth (although Sallenave et al. (1994) documented collector ingestion of grazer-released FPOM). Two important points follow: first, it is indeed possible for collectors to profit from FPOM production by grazers, but second, there may be differences in the occurrence or strength of these interactions among species. Our three grazers may have differed in their effects for several reasons. Although *Physa* produced the most FPOM, this cannot entirely explain our results because *Physa* and *Glossosoma* differed only by about 20% in FPOM production but differed dramatically in their effects on collector growth. FPOM particle size may also be important: *Physa* produced the largest particles of the three grazers and, in particular, by far the most particles >50 μm, a size range important in our experiments because nets spun by late-instar *H. slossonae* have relatively large openings (between 60 μm × 90 μm and 180 μm × 300 μm; Fuller and Mackay 1980). Finally (although we did not attempt to measure this), the nutrient content and (or) digestibility of particles produced could have differed among grazer species (e.g., Shepard and Minshall 1984; Wotton 1994).

Fig. 5. Collector abundance (solid bars) and dry mass (open bars) contrasts between (paired) substrate samples downstream of grazer control and grazer cages. (*a*) 1998 experiment, data from artificial substrates; (*b*) 1998 experiment, data from Hess samples; (*c*) 1999 experiment, data from Hess samples. All contrasts are expressed as a percentage of control; error bars show ±2 SEs. *P* values (from paired *t* tests) not shown were >0.20.



No grazer–collector facilitation in the field

We could detect neither particle production nor local-scale collector facilitation by grazers in any of our field experiments. This was true even though our experiments were designed to maximize the probability of detecting such effects: we used very high local grazer densities, we used grazers known to produce large amounts of FPOM in laboratory flumes, and we used increasingly powerful experimental designs in our later experiments. In particular, in our third experiment, we kept all grazer cages on one side of the stream so that treatment effects would be amplified by incomplete mixing of suspended particles (Heard et al. 2001) along the study reach. Our failure to detect local grazer–collector facilitation is not an artifact of low statistical power: combined, the two experiments yielding data on collectors had over 94% power to detect effects so small as to account for only 4% of the variance in collector mass or abundance. Although we cannot rule out even smaller effects of grazers on collectors, we expect that most ecologists would consider such weak effects to be of limited interest.

Our negative field results must be interpreted in light of the spatial scale at which our investigations were directed. We cannot rule out the possibility that, even though grazer–collector interactions appear negligible at a local scale, taken together, all of the grazers in a stream reach produce enough FPOM to significantly facilitate collectors downstream. Patterns observed in stream (and other) communities can depend strongly on spatial scale, with small-scale patterns either intensified (e.g., Cooper et al. 1998) or dissipated (e.g., McAuliffe 1984) at larger spatial scales. No reach-scale experimental tests of the grazer–collector facilitation hypothesis have been performed. Such tests will be very difficult in natural streams, as selective removal of grazers from whole reaches is probably impossible, while grazer addition at that scale would require logistically fearsome numbers of individuals. Whole-stream manipulations using chemical insecticides have reduced FPOM export (Cuffney et al. 1990), but these treatments cannot isolate effects of one functional group because they remove all insects. A more promising approach would be to manipulate grazer densities in artificial stream channels large enough for the operation of reach-level effects but small enough for stocking to produce significant differences in grazer densities.

Reconciling laboratory and field results

Whether or not grazer–collector facilitation might be detectable at larger scales, we are left with an apparent conflict between our local-scale laboratory and field results. In the laboratory, we detected FPOM production by all three grazers and facilitation of *Hydropsyche* by *Physa*, but in the field, neither *Physa* nor *Glossosoma* had detectable effects on FPOM or on collectors. We believe that these contrasting results have important implications for our understanding of benthic stream communities.

The grazer–collector facilitation hypothesis focuses on the role of grazers in converting periphyton to FPOM, which is then available to collectors. Our laboratory experiments confirm that grazers in Big Mill Creek produce FPOM and that this FPOM can increase collector growth. However, laboratory experiments cannot test a critical component of the grazer–collector facilitation hypothesis: that the rate of FPOM production by grazers can limit collector performance (growth or survival) in the field. Our field data strongly suggest that, at the local scale at which we worked, collectors in Big Mill Creek are not limited by grazer-derived FPOM. It may be that collectors are not limited by FPOM supply at all; or perhaps collectors are limited by FPOM but local grazer populations do not contribute significantly to local-scale variation in FPOM levels.

Surprisingly, it remains an open question whether (or how often) collectors are limited by FPOM in natural streams (Heard and Richardson 1995). Even if collectors are limited by particles, however, grazer–collector facilitation is not assured. In the field, there are many sources of FPOM other than grazer activity (Heard and Richardson 1995), including runoff, mechanical abrasion of CPOM and periphyton, CPOM processing by shredders, and flocculation of dissolved organic matter. No study (including ours) has ever quantified the proportional contribution of grazers to total FPOM production, but if it is small, detection of grazer–

collector facilitation will be difficult. Perhaps more important, given the local scale of our study, is the contribution of grazers to spatial variance in FPOM levels: if variation ascribable to other factors swamps the contribution of local grazer populations, then grazers will not explain a significant proportion of variance in collector performance even if collectors are particle limited. Studies of benthic FPOM generally find high fine-scale spatial heterogeneity (e.g., Hill et al. 1992; Martinez et al. 1998), and in Big Mill Creek, suspended FPOM is highly heterogeneous even on small (submetre and subminute) spatial and temporal scales (S.B. Heard, unpublished data). In this light, perhaps it should not be surprising that (according to our power analyses) local-scale patterns in grazer abundance are unlikely to account for more than a tiny fraction of variance in collector performance.

In summary, we suspect that the different outcomes of our laboratory and field experiments can be explained by differences between laboratory and field in quantity and heterogeneity of suspended FPOM. In our flumes, conditions were highly controlled (suppressing FPOM heterogeneity) and FPOM levels were relatively low (because we prevented or minimized gains through runoff, mechanical abrasion, and flocculation). Therefore, our flume experiments magnified the relative contribution of grazer-derived particles to overall FPOM abundance. This was a deliberate feature of our design: our flume experiments were not intended to mimic field conditions but rather to maximize our likelihood of detecting grazer–collector interactions if they could ever exist. Our laboratory experiments show that collectors can profit from FPOM produced by grazers, but our field experiments strongly suggest that, at least at a very local scale, they do not. Further experimental effort will be necessary to test the hypothesis that grazer–collector interactions might exist at reach or larger spatial scales.

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References

Benke, A.C., and Wallace, J.B. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology, **61**: 108–118.

Benke, A.C., and Wallace, J.B. 1997. Trophic basis of production among riverine caddisflies: implications for food web analysis. Ecology, **78**: 1132–1145.

Brown, K.M. 1991. Mollusca: Gastropoda. *In* Ecology and classification of North American freshwater invertebrates. *Edited by* J.H. Thorp and A.P. Covich. Academic Press, New York. pp. 285–314.

Chauvet, E., Giani, N., and Gessner, M.O. 1993. Breakdown and invertebrate colonization of leaf litter in two contrasting streams: significance of oligochaetes in a large river. Can. J. Fish. Aquat. Sci. **50**: 488–495.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences. Lawrence Erlbaum Associates, Hillsdale, N.J.

Cooper, S.D., Diehl, S., Kratz, K., and Sarnelle, O. 1998. Implications of scale for patterns and processes in stream ecology. Aust. J. Ecol. **23**: 27–40.

Cuffney, T.F., Wallace, J.B., and Lugthart, G.J. 1990. Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. Freshw. Biol. **23**: 281–299.

Dudley, T.L. 1992. Beneficial effects of herbivores on stream macroalgae via epiphyte removal. Oikos, **65**: 121–127.

Edwards, R.T., and Meyer, J.L. 1990. Bacterivory by deposit-feeding mayfly larvae (*Stenonema* spp.). Freshw. Biol. **24**: 453–462.

Fuller, R.L., and Mackay, R.J. 1980. Feeding ecology of three species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. Can. J. Zool. **58**: 2239–2251.

Fuller, R.L., and Mackay, R.J. 1981. Effects of food quality on the growth of three *Hydropsyce* species (Trichoptera: Hydropsychidae). Can. J. Zool. **59**: 1133–1140.

Hart, D.D. 1985. Grazing insects mediate algal interactions in a stream benthic community. Oikos, **44**: 40–46.

Heard, S.B. 1994. Processing chain ecology: resource condition and interspecific interactions. J. Anim. Ecol. **63**: 451–464.

Heard, S.B., and Richardson, J.S. 1995. Shredder–collector facilitation in stream detrital food webs: is there enough evidence? Oikos, **72**: 359–366.

Heard, S.B., Schultz, G.A., Ogden, C.B., and Griesel, T.C. 1999. Mechanical abrasion and organic matter processing in an Iowa stream. Hydrobiologia, **400**: 179–196.

Heard, S.B., Gienapp, C.B., Lemire, J.F., and Heard, K.S. 2001. Transverse mixing of transported material in simple and complex stream reaches. Hydrobiologia, **464**: 207–218.

Hill, B.H., Gardner, T.J., and Ekisola, O.F. 1992. Benthic organic matter dynamics in Texas prairie streams. Hydrobiologia, **242**: 1–5.

Hillebrand, H. 2002. Top-down versus bottom-up control of autotrophic biomass — a meta-analysis on experiments with periphyton. J. North Am. Benthol. Soc. **21**: 349–369.

Kohler, S.L. 1992. Competition and the structure of a benthic stream community. Ecol. Monogr. **62**: 165–188.

Lamberti, G.A., Ashkenas, L.R., Gregory, S.V., and Steinman, A.D. 1987. Effects of three herbivores on periphyton communities in laboratory streams. J. North Am. Benthol. Soc. **6**: 92–104.

Lamberti, G.A., Gregory, S.V., Ashkenas, L.R., Steinman, A.D., and McIntire, C.D. 1989. Productive capacity of periphyton as a determinant of plant–herbivore interactions in streams. Ecology, **70**: 1840–1856.

Lush, D.L., and Hynes, H.B.N. 1973. The formation of particles in freshwater leachates of dead leaves. Limnol. Oceanogr. **18**: 968–977.

Martinez, B., Velasco, J., Suarez, M.L., and Vidal-Abarca, M.R. 1998. Benthic organic matter dynamics in an intermittent stream in south-east Spain. Arch. Hydrobiol. **141**: 303–320.

McAuliffe, J.R. 1984. Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. Oikos, **42**: 327–333.

McCullough, D.A., Minshall, G.W., and Cushing, C.E. 1979. Bioenergetics of lotic filter-feeding insects *Simulium* spp. (Diptera) and *Hydropsyche occidentalis* (Trichoptera) and their function in controlling organic transport in streams. Ecology, **60**: 585–596.

Merritt, R.W., and Cummins, K.W. (*Editors*). 1996. An introduction to the aquatic insects of North America. 3rd ed. Kendall-Hunt, Dubuque, Iowa.

Minshall, G.W., Cummins, K.W., Petersen, R.C., Cushing, C.E., Bruns, D.A., Sedell, J.R., and Vannote, R.L. 1985. Developments in stream ecosystem theory. Can. J. Fish. Aquat. Sci. **42**: 1045–1055.

Petersen, R.C., Jr. 1986. In situ particle generation in a southern Swedish stream. Limnol. Oceanogr. **31**: 432–437.

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

Roeding, C.E., and Smock, L.A. 1989. Ecology of macroinvertebrate shredders in a low-gradient sandy-bottomed stream. J. North Am. Benthol. Soc. **8**: 149–161.

Sallenave, R.M., Day, K.E., and Kreutzweiser, D.P. 1994. The role of grazers and shredders in the retention and downstream transport of a PCB in lotic environments. Environ. Toxicol. Chem. **13**: 1843–1847.

Scrimgeour, G.J., Culp, J.M., Bothwell, M.L., Wrona, F.J., and McKee, M.H. 1991. Mechanisms of algal patch depletion: importance of consumptive and non-consumptive losses in mayfly–diatom streams. Oecologia, **85**: 343–348.

Shapas, T.J., and Hilsenhoff, W.L. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera, and Trichoptera. Gt. Lakes Entomol. **9**: 175–188.

Shepard, R.B., and Minshall, G.W. 1981. Nutritional value of lotic insect feces compared with allochthonous materials. Arch. Hydrobiol. **90**: 467–488.

Shepard, R.B., and Minshall, G.W. 1984. Role of benthic insect feces in a Rocky Mountain stream: fecal production and support of consumer growth. Holarct. Ecol. **7**: 119–127.

Steinman, A.D., and Lamberti, G.A. 1996. Biomass and pigments of benthic algae. *In* Methods in stream ecology. *Edited by* F.R. Hauer and G.A. Lamberti. Academic Press, New York. pp. 295–313.

Wallace, J.B., and Webster, J.R. 1996. The role of macroinvertebrates in stream ecosystem function. Annu. Rev. Entomol. **41**: 115–139.

Wallace, J.B., Eggert, S.L., Meyer, J.L., and Webster, J.R. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecol. Monogr. **69**: 409–442.

Wiggins, G.B. 1996. Larvae of the North American caddisfly genera (Trichoptera). 2nd ed. University of Toronto Press, Toronto, Ont.

Wotton, R.S. 1994. Particulate and dissolved organic matter as food. *In* The biology of particles in aquatic systems. 2nd ed. *Edited by* R.S. Wotton. Lewis Publishers, Boca Raton, Fla. pp. 235–288.

Wotton, R.S., Malmqvist, B., Muotka, T., and Larsson, K. 1998. Fecal pellets from a dense aggregation of suspension-feeders in a stream: an example of ecosystem engineering. Limnol. Oceanogr. **43**: 719–725.

Yule, C.M. 1996. Trophic relationships and food webs of the benthic invertebrate fauna of two aseasonal tropical streams on Bougainville Island, Papua New Guinea. J. Trop. Ecol. **12**: 517–534.