

Effects of increased bedload on algal- and detrital-based stream food webs: Experimental manipulation of sediment and macroconsumers

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Abstract

Sedimentation poses a significant threat to stream ecosystems throughout the world, and increases in bedload can be especially detrimental to benthic communities. To examine how increased bedload affects algal- and detrital-based stream communities, we manipulated sediment (via daily sediment addition to 0.25-m² areas of stream bottom) and top-down effects of macroconsumers (fishes and crayfish, via electric exclusion) in two factorial experiments, one using tiles and one using leaf packs as sampling substrates. Sediment addition had significant effects on both algal- and detrital-based stream benthic communities, most notably via the alteration of macroconsumer-mediated biotic interactions; these effects largely were due to sediment transport across the stream bottom, rather than sediment deposition. In the tile experiment, macroconsumers reduced total insect biomass and biomass of several dominant insect taxa under ambient sediment conditions. Sediment addition eliminated all macroconsumer effects except their reduction of chironomid biomass. In the leaf pack experiment, sediment addition eliminated macroconsumer effects on fungal accumulation rates; in general, however, leaf packs were not as affected by sediment addition as tiles. Direct effects of sediment addition were minimal in both experiments: algal composition was altered on tiles, while dipteran predator biomass tended to decline in leaf packs. These experiments demonstrate that small, environmentally realistic increases in bedload affect benthic communities, primarily via the alteration of macroconsumer effects. Although indirect effects of sedimentation have been examined less frequently than direct biotic responses, this study demonstrates the importance of sediment regime in determining the outcome of fish- and crayfish-mediated species interactions.

Sediment is an integral component of stream ecosystems, but human activities such as agriculture and urbanization have altered stream sediment loading and transport, dramatically increasing the amount of inorganic material delivered to waterways (Waters 1995). Such anthropogenic sediment inputs are a significant source of stream impairment around the world (e.g., Waters 1995; Wood and Armitage 1997), and sedimentation poses a major threat to freshwater fauna (Richter et al. 1997). Numerous studies have shown that elevated sediment levels can negatively affect stream biota, including fishes (Berkman and Rabeni 1987), aquatic insects (Lemly 1982; Angradi 1999), other invertebrates (Brim Box and Mossa 1999), and algae (Biggs et al. 1999). However, most research examining the effects of sedimentation has focused either on sediment suspended in the water column or on sediment deposited on stream substrates; this focus is mirrored in the policy arena, where sediment regulations (e.g., total maximum daily load [TMDL] programs) are based largely on measures such as turbidity and total suspended solids (USEPA 1999). Fewer studies have explicitly

examined how stream biota are affected by increased bedload (sediment transported along the stream bottom), even though increased bedload can be more detrimental to stream benthic communities (Lemly 1982; Culp et al. 1986; Waters 1995) and may not be associated with increased turbidity or suspended sediments (Lane and Sheridan 2002).

Because sedimentation is often associated with other in-stream alterations (e.g., nutrient enrichment, decreased canopy cover), it can be difficult to separate sediment impacts from other factors. Sediment addition experiments provide one way of isolating sedimentation effects, and several studies have provided valuable insight into biotic responses via experimental elevation of sediment levels (e.g., Alexander and Hansen 1986; Barrett et al. 1992; Abrahams and Kattenfeld 1997). However, many of these studies have been short-term experiments conducted in aquaria or artificial stream channels (e.g., Runde and Hellenthal 2000). In addition, these studies often focus on the direct effects of sedimentation rather than on the indirect effects, such as the alteration of biotic interactions. Although several sediment addition studies have explicitly addressed species interactions, they generally have focused on suspended sediment and its repercussions for visually feeding fish predators (e.g., Barrett et al. 1992; Abrahams and Kattenfeld 1997). Few studies have considered the influence of increased bedload on species interactions. Rather, bedload addition studies have focused on measures such as total invertebrate drift and abundance (Culp et al. 1986) or individual species responses (Runde and Hellenthal 2000). Several studies have shown that the impacts of stream insect consumers on resources can be altered by deposited sediment (e.g., Peckarsky 1985; Walde 1986), but to our knowledge, no one has experimentally examined the influence of small-scale bedload sedimentation on macroconsumer-mediated biotic interactions.

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The relative importance of top-down interactions in structuring biotic communities depends on many factors, including disturbance or environmental stress (Peckarsky 1983; Menge and Sutherland 1987; Power 1992; Polis and Strong 1996). In general, disturbance (e.g., increased bedload transport) is expected to decrease the strength of biotic interactions (Peckarsky 1983; Menge and Sutherland 1987). In streams, the relative strength of top-down effects also depends on substrate type and its influence on prey vulnerability (e.g., Rosemond et al. 1998). For example, shrimps and fishes in a Costa Rican stream had a greater effect on insect densities on tiles (Pringle and Hamazaki 1998) than in leaf packs (Rosemond et al. 1998). In addition to providing invertebrates refugia from predation, detrital accumulations may shelter invertebrates from sediment transport and deposition, thereby reducing negative effects of elevated bedload. Thus, communities dependent on different basal resources (i.e., algae vs. detritus) may respond differently to increased bedload transport.

The objective of this study was to explore how small, yet environmentally realistic increases in bedload affect algal and detrital-based food webs in a forested southern Appalachian stream. Specifically, we examined the three questions that follow. (1) What are the direct effects of elevated bedload on aquatic insect assemblages, algal periphyton, fungal biomass, and leaf breakdown? (2) Does elevated bedload exert indirect influence via alteration of top-down effects of macroconsumers (fishes and crayfish)? (3) Do algal- and detrital-based communities differ in their susceptibility to the effects of elevated bedload? To address these questions, we simultaneously manipulated sediment and macroconsumers in situ in two separate factorial experiments, one using tiles and one using leaf packs as sampling substrates.

Methods

Study site—Experiments were conducted in Lower Ball Creek, a fourth-order stream at Coweeta Hydrologic Laboratory in western North Carolina (35°03'N, 83°30'W). Coweeta is a 2,185-ha facility managed by the U.S. Forest Service (USFS) and is located in the Blue Ridge physiographic province of the southern Appalachians. Mean monthly air temperature ranges from 3°C to 22°C, and annual precipitation ranges from 1.8 m at low elevation to 2.5 m at high elevation (Swank and Crossley 1988). During both experiments, continuous discharge data were collected at Lower Ball Creek by USFS researchers; continuous temperature data were collected by Dr. J. B. Wallace (Univ. of Georgia).

The Lower Ball Creek watershed is completely forested by mixed hardwood species such as red maple (*Acer rubrum*), tulip-poplar (*Liriodendron tulipifera*), and mixed oaks (*Quercus* spp.). Riparian areas are densely vegetated by rhododendron (*Rhododendron maximum*), mountain laurel (*Kalmia latifolia*), and dogwood (*Cornus florida*). Elevation at the study site is approximately 700 m, with a stream gradient of ~4 cm m⁻¹. Boulder, cobble, and gravel dominate the stream substratum, and substrates are relatively unembedded (0–25% embeddedness [Schofield unpubl. data]). Macroconsumer assemblages in Lower Ball Creek are dominated by

crayfish (*Cambarus bartonii*) and mottled sculpin (*Cottus bairdi*) at densities of approximately 2 m⁻² (Schofield et al. 2001) and 0.7 m⁻² (Grossman unpubl. data), respectively. Longnose dace (*Rhinichthys cataractae*), rosyside dace (*Clinostomus funduloides*), and rainbow trout (*Oncorhynchus mykiss*) are also present, but at very low densities (<0.2 m⁻² for all other fishes combined [Grossman unpubl. data]).

Tile experiment—In summer 1997, we conducted a 40-d (29 July–8 September) macroconsumer exclusion experiment using unglazed ceramic tiles as sampling substrates. Tiles (7.5 by 15 cm) were attached with cable ties and binder clips to polyvinyl chloride frames (0.25 m²) lined with copper wire; each frame contained eight tiles. Twenty frames (10 pairs) were placed in run habitats of Lower Ball Creek, along an approximately 0.5-km stream reach. Placement of pairs was determined by preliminary shear stress measurements using calibrated hemispheres (Statzner and Müller 1989); only sites that provided a suitable area with similar shear stresses were used. Water velocity and depth were measured at the four corners of each frame using a Marsh McBirney current meter and a meter stick. Canopy cover was measured over the center of each frame using a spherical densiometer.

To exclude macroconsumers, one frame in each pair was connected to a solar-powered fence charger (Parmak Model DF-SP-SS, Parker McCrory Manufacturing). Each charger contained a 6-V gel cell battery and delivered repeated electric pulses (~54–55 min⁻¹) to the 0.25-m² frame area at a maximum joule rating of 1.4 J. These electric pulses prevented the entry of fishes and crayfish but did not adversely affect smaller organisms such as aquatic insect larvae. Numerous studies have excluded macroconsumers with this technique (e.g., Pringle and Hamazaki 1998; March et al. 2001), which avoids artifacts associated with traditional cage enclosure experiments (e.g., reduced water flow, increased sedimentation). Researchers have used similar methods to exclude aquatic insects (e.g., Brown et al. 2000), but insect exclusion requires more powerful chargers and/or shorter distances between electrodes (e.g., 8.4 J across 9 cm in Brown et al. [2000] vs. 1.4 J across 20 cm in this study).

The unelectricized frame in each pair was accessible to macroconsumers and served as a control. Frames were placed approximately 0.5 m apart to minimize any influence of macroconsumer exclusion treatments on adjacent access treatments. Given that macroconsumers were frequently found immediately outside electrified frames, this distance appeared to be more than adequate. Throughout the experiment, fence charger batteries were replaced every 5 d to ensure a consistent 6-V charge. Frames also were cleared of any accumulated debris every 5 d to minimize flow alterations and prevent loss of frames during spates.

Ten frames (five pairs) were randomly chosen as sediment treatments. Each of these frames received 250 g of sand daily: sand was wetted and then added by hand as uniformly as possible to the entire frame area. Sand was used because the measurement of bedload transport rates in Lower Ball Creek and in a nearby pasture stream (Jones Creek) showed that bedload was dominated (>70%) by 0.25- to 2.00-mm particles (Sutherland unpubl. data). The average transport

rate in Lower Ball was $0.80 \pm 0.27 \text{ kg m}^{-1} \text{ d}^{-1}$ (Sutherland unpubl. data); by adding 250 g to each frame, we increased the bedload by approximately 60%. This increase was relatively small, and yet it was environmentally realistic (i.e., 35% lower than bedload transport rates measured in Jones Creek: $1.98 \pm 0.44 \text{ kg m}^{-1} \text{ d}^{-1}$ [Sutherland unpubl. data]). Sand was obtained from a point bar downstream of our study reach and was sieved (2-mm mesh) prior to application to remove larger inorganic particles and coarse particulate organic matter.

This experimental design resulted in four treatments (ambient sediment/macroconsumer access [AA]; ambient sediment/macroconsumer exclusion [AE]; sediment addition/macroconsumer access [SA]; and sediment addition/macroconsumer exclusion [SE]), each with five frames, or replicates. One tile was removed from each frame every 5 d. Fence chargers at exclusion frames were turned off briefly (5–10 min) for sampling. A 210- μm mesh hand net was held downstream of each tile as it was removed to retrieve any dislodged sediment or invertebrates. Tiles were placed in plastic bags and put on ice until they could be processed. Prior to tile removal, each frame was observed for 5 min, and visitation by any macroconsumers was recorded; observation time totaled $>11.5 \text{ h}$ during the course of the experiment.

Tiles were processed within 8 h of sampling. In the laboratory, each tile was rinsed, scraped with a razor blade, and brushed with a nylon toothbrush to remove invertebrates, algal periphyton, and sediment. Invertebrates were live-picked under a lighted magnifier and preserved in 70% ethanol. After invertebrates were removed, the volume of material scraped from each tile was brought to 500 ml and stirred continuously. A 10-ml subsample was preserved in 2% formalin for periphyton composition analysis. Equal subsamples (10–100 ml) were filtered onto two preashed 0.45- μm glass fiber filters. One filter was used to determine ash-free dry mass (AFDM) and inorganic sediment dry mass; the other was used for chlorophyll *a* (Chl *a*) analysis. Sediment filters were dried for 24 h at 70°C to obtain the dry mass and then ashed at 500°C for 1 h and reweighed to obtain AFDM. Chl *a* filters were processed according to standard methods for fluorometric analyses (APHA 1985), and concentrations were measured with a Turner Designs 10-AU fluorometer.

Taxonomic data were examined for the last day of the experiment (day 40). Invertebrate samples were identified to the lowest practical level (usually family or genus) using a dissecting microscope ($\times 10$ magnification). Individuals were measured to the nearest 0.5 mm using 1-mm grid paper, and biomass was calculated with family-specific, length-mass regressions from Benke et al. (1999). Organisms $<1.5 \text{ mm}$ were identified to order. To determine day 40 periphyton composition, the first 500 cells in a given volume were identified to genus. Biovolume for each taxon was estimated using values available in the literature (Greenwood pers. comm.).

Daily water samples were collected throughout the experiment to determine total suspended solids. Conductivity was measured three times during the 40-d study, and water samples were collected every 5 d for nutrient analysis ($\text{NO}_3\text{-N}$,

$\text{NH}_4\text{-N}$, and soluble reactive phosphorus [SRP]). All water samples were collected midchannel, immediately downstream of all experimental frames.

Leaf pack experiment—In autumn 1999, we conducted a 56-d (9 October–4 December) macroconsumer exclusion experiment using sugar maple (*Acer saccharum*) leaf packs as our sampling substrate. The design of this experiment was similar to that of the tile experiment (e.g., in terms of exclusion, addition of sediment); only differences between the experiments will be discussed.

Leaves were shaken from trees 1 d before the experiment started and divided into approximately 5-g (wet weight) packs held together by two plastic I-shaped fasteners. Packs were wrapped in 2-cm plastic mesh to minimize the loss of large leaf fragments; this mesh was large enough to allow access by aquatic insect larvae and macroconsumers. Six leaf packs were secured in each of 20 frames using nylon monofilament. Each pack was weighted with 85 g of lead to keep it flush with the substratum. Between the time of the tile and leaf pack experiments, the sand point bar used as a source of sediment for the tile experiment was replaced by cobble. Thus, sand for addition to frames was obtained from a nearby sand and gravel distributor. As in the tile experiment, 10 frames (five pairs) were designated sediment treatments, and 250 g of sieved (2-mm mesh) sand was added daily to each frame.

One leaf pack was removed from each frame on days 5, 10, 20, 32, 44, and 56. In addition, 10 packs were brought back to the laboratory on day 0 to determine initial leaf pack AFDM. Prior to removing leaf packs, all replicates were examined with a clear plastic viewing box to determine whether macroconsumers were present. In the tile experiment, we observed replicates for 5 min, but limited visibility due to fallen leaves made prolonged observations inefficient in this experiment. Instead, we recorded the presence or absence of macroconsumers during spot checks of all replicates on all sampling dates as well as every 5 d when fence charger batteries were changed ($n = 320$ spot checks). In addition, any macroconsumers seen during leaf pack removal (i.e., that were hiding under leaf packs or cobbles during spot checks but were disturbed during sampling) were noted.

Leaf packs were processed within 24 h of sampling. Leaves were rinsed to remove invertebrates and sediment, and this material was preserved in 70% ethanol for later identification and determination of sediment mass. After rinsing, 100 leaf discs were randomly removed from each pack using a hole punch (6-mm diameter). Fifty discs were preserved in methanol for fungal biomass analysis via ergosterol extraction (Newell et al. 1988, with slight modifications after Paul and Meyer 1996); day 0, 10, 32, and 56 samples were analyzed. Fungal biomass was estimated from ergosterol concentration using a conversion factor of 5 μg of ergosterol mg^{-1} mycelial dry mass (Gessner and Chauvet 1993; Paul and Meyer 1996). Fungal accumulation rates (per day) then were calculated for each individual frame by regressing the natural log of fungal biomass against time (accumulation rate = slope). The remaining 50 discs from each pack underwent the same drying and ashing process as leaf packs. Packs were dried at 70°C for 3 d, weighed, and then

Table 1. Physical and chemical stream characteristics during tile and leaf pack experiments. Each value represents mean (standard error), with *n* indicated in brackets.

	Tiles	Leaf packs
Experimental period	29 Jul 97–08 Sep 97	09 Oct 99–4 Dec 99
Water temperature (°C)	16.9 (0.16) [41]	10.4 (0.34) [57]
Maximum daily discharge (liters s ⁻¹)	188.3 (39.1) [41]	217.3 (51.3) [57]
Total suspended solids (mg L ⁻¹)	7.5 (0.4) [37]	1.3 (0.1) [4]
Conductivity (ms cm ⁻¹)	13.5 (0.04) [3]	12.0 (0.25) [7]
Nutrients (mg L ⁻¹) NO ₃ -N	0.043 (0.001) [8]	0.004 (0.001) [7]
NH ₄ -N	0.003 (0.001) [8]	0.003 (0.000) [7]
SRP	0.008 (0.002) [8]	0.003 (0.001) [7]

burned at 500°C for 6 h and reweighed. Total AFDM remaining was calculated by summing AFDM of each leaf pack and 2× AFDM of the 50 leaf discs. Leaf breakdown rates (per day) were calculated for each individual frame by regressing the natural log of % AFDM remaining against time.

As in the tile experiment, taxonomic data were analyzed for the last day of the experiment (day 56). Invertebrate samples were sorted from preserved sediment using a dissecting microscope (×10 magnification) and identified to the lowest practical level, usually family or genus. Water samples were collected on sampling days for nutrient and conductivity analysis, and four samples were taken during the 56-d experiment to determine total suspended solids concentration.

Statistical analysis—In the tile experiment, one sediment replicate pair differed significantly from the remaining pairs in terms of initial water depth, velocity, and shear stress (Dixon's test [Sokal and Rohlf 1995]: $P < 0.05$). This pair was excluded from all analyses, leaving four replicate pairs (i.e., one macroconsumer access and one exclusion frame) for the tile/sediment addition treatment versus five replicate pairs for tile/ambient sediment, leaf pack/ambient sediment, and leaf pack/sediment addition treatments. In the tile experiment, one AA replicate was an outlier (Dixon's test: $P < 0.05$) in terms of insect biomass (because of one large [2.8 mg] *Stenonema* mayfly and two large [72.1 and 9.2 mg] *Pteronarcys* stoneflies); these individuals were omitted from all biomass values. Similarly, one SA replicate in the leaf pack experiment contained a 187.6-mg *Pteronarcys* (biomass outlier [$P < 0.05$]), and this individual also was omitted. In both experiments, Bartlett's test was used to test for equal variance; when necessary, data were natural log or arcsine($\sqrt{\quad}$) transformed.

Tile and leaf pack experiments were analyzed separately using two-factor (sediment and exclusion) analysis of variance tests (ANOVA, multivariate ANOVA [MANOVA], and repeated-measures ANOVA). Repeated-measures ANOVA was used for data analyzed through time (e.g., Chl *a*, AFDM, % AFDM, inorganic dry mass). Taxonomic data (i.e., periphyton and insect data, which were examined on the last day of each experiment), leaf breakdown rates, and fungal accumulation rates were analyzed using MANOVA and ANOVA. Two-tailed paired *t*-tests were used to compare access and exclusion pairs under each sediment regime when ANOVA indicated a significant sediment–exclusion interaction.

In the tile experiment, insect analyses focused on five groups composing ≥93% of total insect biomass in all treatments: chironomids (Tanypodinae and non-Tanypodinae Chironomidae [Diptera]); hydropterygids (Hydropterygidae [Trichoptera]); nondipteran predators (*Acronuria* and *Isoperla* [Plecoptera], *Rhyacophila* [Trichoptera]); mayflies (*Stenonema* and Leptophlebiidae [Ephemeroptera]); and leuctrids (*Leuctra* [Plecoptera]). In the leaf pack experiment, insect analyses focused on insect shredders and predators (dipteran and nondipteran) because these were the functional feeding groups most likely to affect leaf decomposition (shredders directly through leaf consumption and predators indirectly through consumption of shredders); they were also the groups contributing the most (>75%) to total insect biomass.

Similarity of periphyton and insect assemblages between replicate pairs (i.e., AA and AE frames, SA and SE frames) was calculated using a simplified Morisita index with natural log-transformed density and biomass or biovolume data (Wolda 1981). Ambient sediment and sediment addition similarity indices then were compared using *t*-tests to determine whether sediment addition increased similarity between macroconsumer access and exclusion treatments.

Unless otherwise noted, $\alpha = 0.05$ for all analyses. Analyses were conducted in SAS System for Windows™, release 6.12, and in JMPIN™ System for Windows, version 3.2.6.

Results

Treatments did not differ in terms of initial canopy cover (range = 86.2–96.8%), water depth (range = 0.13–0.17 m), water velocity (range = 0.16–0.26 m s⁻¹), or shear stress (range = 84–111 dyn cm⁻²) in either the tile (MANOVA: $F_{4,11} \leq 0.98$, $P \geq 0.458$) or the leaf pack experiment (MANOVA: $F_{4,13} \leq 2.42$, $P \geq 0.101$). Total suspended solids remained low throughout each experiment (Table 1), indicating that sediment addition did not significantly elevate suspended load.

Inorganic dry mass deposited on sampling substrates was greater in sediment addition than in ambient sediment treatments in both the tile (repeated-measures ANOVA: $F_{1,14} = 5.43$, $P = 0.035$) and leaf pack (repeated-measures ANOVA: $F_{1,16} = 7.82$, $P = 0.013$) experiments (Table 2). However, much of the added sediment was transported outside each 0.25-m² area: in both experiments, ≤4% of the total sediment added to each sediment replicate (10 kg in the tile

Table 2. Inorganic dry mass on sampling substrates in the tile and leaf pack experiments. Values represent mean (standard error) of five replicates (four replicates for sediment addition treatments [SA and SE] in the tile experiment) averaged through time (days 5–40 in the tile experiment and days 32 and 56 in the leaf pack experiment). AA, ambient sediment/macroconsumer access; AE, ambient sediment/macroconsumer exclusion; SA, sediment addition/macroconsumer access; SE, sediment addition/macroconsumer exclusion.

Experiment	Treatment	Inorganic dry mass (g m ⁻² or g pack ⁻¹)	
Tiles	AA	89.4 (14.9)	}
	AE	69.9 (11.3)	
	SA	148.2 (22.6)	
	SE	244.1 (71.8)	
Leaf packs	AA	13.6 (6.7)	}
	AE	9.8 (1.7)	
	SA	29.2 (6.7)	
	SE	21.5 (5.3)	

* Denotes a statistically significant ($P < 0.05$) difference between ambient sediment and sediment addition treatments.

experiment and 13 kg in the leaf pack experiment) remained by the last day. Sediment did not differ between macroconsumer access and exclusion treatments in either experiment (repeated-measures ANOVAs: $P \geq 0.515$).

Macroconsumers were not observed in exclusion replicates in either the tile or the leaf pack experiment (observation time = 315 min for tiles, 160 spot checks for leaf packs), indicating that the exclusion technique was successful. A total of five crayfish were observed in the tile AA treatment during the experiment (observation time = 175 min), and 10 crayfish and 1 sculpin were observed in the SA treatment (observation time = 140 min). During the leaf pack experiment, a total of four crayfish and two sculpins were observed in the AA treatment, and two crayfish and three sculpins were observed in the SA treatment ($n = 80$ spot checks for each treatment).

Tile experiment: Chl a, AFDM, and periphyton assemblages—Neither sediment addition nor macroconsumer exclusion had a significant effect on Chl *a* concentrations during the entire experimental period (repeated-measures ANOVA: $F_{1,14} \leq 2.83$, $P \geq 0.115$; Fig. 1). By day 40, however, macroconsumer exclusion led to higher Chl *a* concentrations under ambient sediment conditions (paired *t*-test: $t = -2.61$, $df = 4$, $P = 0.060$); this trend was not seen with sediment addition (Fig. 1). Sediment organic content (% AFDM) showed a similar pattern, with increased % AFDM in exclusion versus access treatments under ambient sediment conditions but not when sediment was added (repeated-measures ANOVA: $F_{1,14} = 5.02$, $P = 0.042$ [sediment \times exclusion]).

Total periphyton density and biovolume were not significantly altered by sediment addition or macroconsumer exclusion (ANOVAs: $F_{1,14} \leq 1.69$, $P \geq 0.215$; $F_{1,14} \leq 1.44$, $P \geq 0.250$). Although density and biovolume were at least twofold greater in AE than in AA treatments, variability was high (Fig. 2A). Macroconsumer access and exclusion pairs

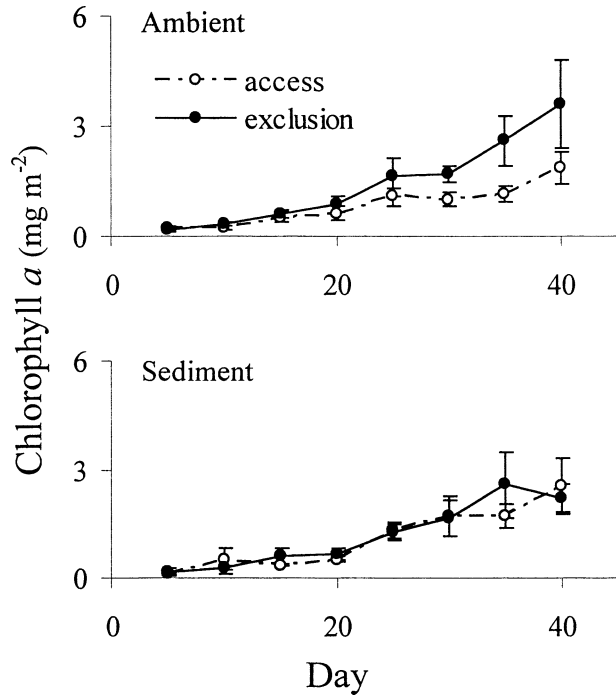


Fig. 1. Chlorophyll *a* concentrations in macroconsumer access and exclusion treatments on days 5–40 of the tile experiment. Ambient refers to ambient sediment conditions; sediment refers to the sediment addition treatment. Each point represents mean ($n = 5$ [ambient], $n = 4$ [sediment]) ± 1 SE.

had similar periphyton assemblages in both the ambient sediment and sediment addition treatments (similarity ≥ 0.88 for density and biovolume). Eight diatom genera (*Achnanthes*, *Navicula*, *Luticola*, *Cymbella*, *Gomphonema*, *Meridion*, *Eunotia*, and *Synedra*) composed $\geq 88\%$ of total periphyton density and biovolume in all treatments. However, sediment addition altered the relative biovolume contributions of these taxa (MANOVA: $F_{8,7} = 3.96$, $P = 0.043$): proportions of the motile genera *Navicula* and *Luticola* and the upright genus *Cymbella* decreased with sediment addition (ANOVAs: $F_{1,14} \geq 6.90$, $P \leq 0.020$), while the upright genus *Synedra* increased (ANOVA: $F_{1,14} = 8.80$, $P = 0.010$; Fig. 2B).

Tile experiment: Insect assemblages—Both macroconsumer exclusion and sediment addition significantly altered total insect biomass (ANOVA: $F_{1,14} = 5.17$, $P = 0.039$ [exclusion]; $F_{1,14} = 4.43$, $P = 0.054$ [sediment \times exclusion]). Biomass was fourfold greater in AE than in AA treatments (paired *t*-test: $t = 2.94$, $df = 4$, $P = 0.042$), but this difference disappeared when sediment was added (paired *t*-test: $t = 0.40$, $df = 3$, $P = 0.716$; Fig. 3). In addition, similarity between macroconsumer access and exclusion pairs in terms of insect biomass tended to increase with sediment addition (*t*-test: $t = 1.85$, $df = 4$, $P = 0.069$; Fig. 3), further suggesting a diminished influence of macroconsumers. Unlike biomass, total insect density was not affected by either macroconsumer exclusion or sediment addition (ANOVA: $F_{1,14} \leq 1.07$, $P \geq 0.318$).

Given their relatively large size, it is possible that certain insects (e.g., *Pteronarcys* stoneflies and large Heptageniidae

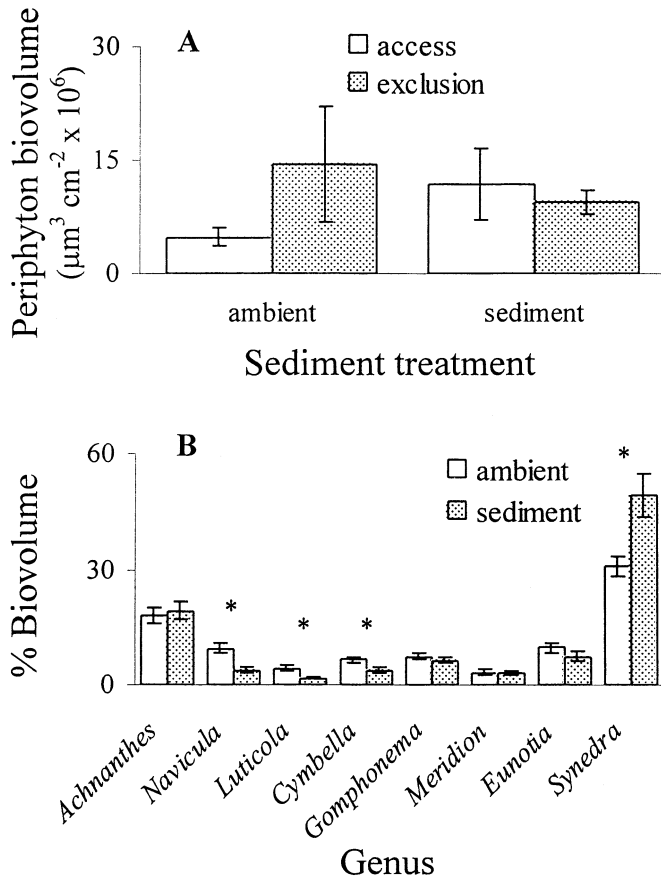


Fig. 2. (A) Total periphyton biovolume in macroconsumer access and exclusion treatments on day 40 of the tile experiment. Each bar represents mean ($n = 5$ [ambient], $n = 4$ [sediment]) ± 1 SE. (B) Percentage of total biovolume contributed by eight common ($\geq 2\%$ of total biovolume) genera in ambient and sediment treatments. Each bar represents mean of macroconsumer access and exclusion replicates ($n = 10$ [ambient], $n = 8$ [sediment]) ± 1 SE. * Denotes significant ($P < 0.05$) effect of sediment addition.

mayflies) were adversely affected by the electric exclusion technique. As mentioned earlier, three large individuals (two *Pteronarcys* individuals and one Heptageniidae individual) were excluded from biomass analyses, but all of these individuals were found in a single AA replicate. No other *Pteronarcys* individuals were collected from either access or exclusion tiles; although heptageniid biomass tended to be greater in access versus exclusion treatments, variability within treatments was high, and differences were not statistically significant. Hence, it is unlikely that exclusion results were influenced by either the presence or absence of these rare individuals.

Sediment addition and macroconsumer exclusion interacted to significantly affect biomass of the five insect groups we examined (MANOVA: $F_{5,10} = 3.56$, $P = 0.041$). Regardless of sediment regime, macroconsumer exclusion resulted in a $>70\%$ increase in chironomid biomass (ANOVA: $F_{1,14} = 5.20$, $P = 0.039$; Fig. 4). For both hydropsychid and nondipteran predator biomass, however, sediment regime influenced the outcome of macroconsumer exclusion (ANOVAs: $F_{1,14} = 7.00$, $P = 0.019$; $F_{1,14} = 13.10$, $P = 0.003$).

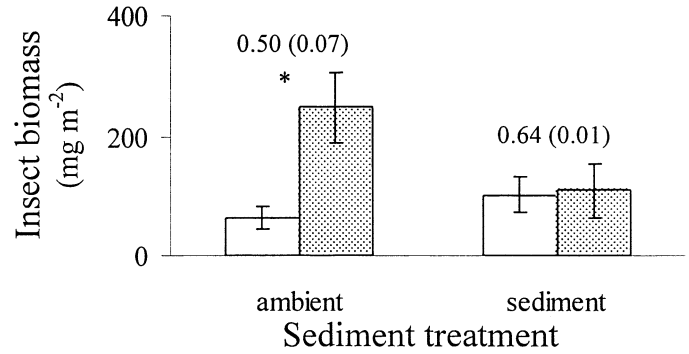


Fig. 3. Total insect biomass in macroconsumer access and exclusion treatments on day 40 of the tile experiment. Each bar represents mean ($n = 5$ [ambient], $n = 4$ [sediment]) ± 1 SE. Each number indicates similarity (0–1.0 scale, mean of four or five replicates [standard error]) between paired macroconsumer access and exclusion replicates. * Denotes significant ($P < 0.05$) effect of macroconsumer exclusion.

Under ambient sediment conditions, hydropsychid and nondipteran predator biomass values were ≥ 20 times higher when macroconsumers were excluded (paired t -tests: $t = -7.59$, $df = 4$, $P = 0.002$; $t = -2.77$, $df = 4$, $P = 0.050$); in both cases, sediment addition eliminated this exclusion effect (Fig. 4). Similar patterns were observed for density, but, as with total density, differences were not statistically significant.

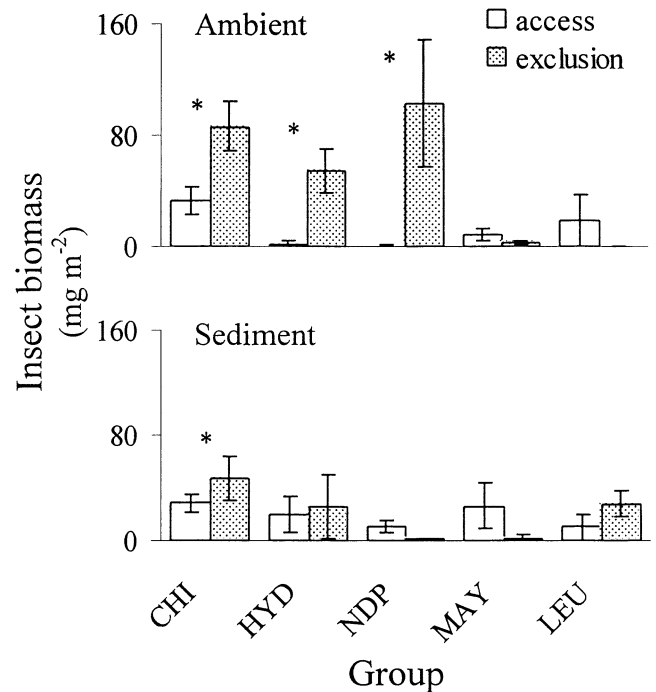


Fig. 4. Biomass of five common insect groups on day 40 of the tile experiment. Ambient refers to ambient sediment conditions; sediment refers to the sediment addition treatment. Each bar represents mean ($n = 5$ [ambient], $n = 4$ [sediment]) ± 1 SE. CHI, chironomids; HYD, hydropsychids; NDP, nondipteran predators; MAY, mayflies; LEU, leuctrids; * Denotes significant ($P < 0.05$) effect of macroconsumer exclusion.

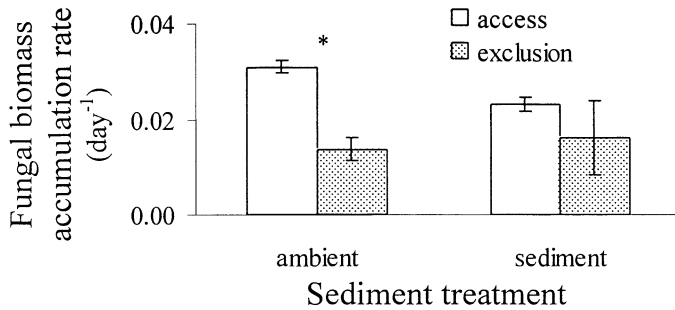


Fig. 5. Fungal biomass accumulation rates in macroconsumer access and exclusion treatments during the leaf pack experiment. Each bar represents mean ($n = 5$) \pm 1 SE; * Denotes significant ($P < 0.01$) effect of macroconsumer exclusion.

Leaf pack experiment: Leaf breakdown and fungal biomass—Leaf breakdown rates (per day) did not differ significantly among treatments (ANOVA: $F_{1,16} \leq 0.26$, $P \geq 0.618$), ranging from 0.0054 ± 0.0005 (AE) to 0.0062 ± 0.0012 (AA). Rates of fungal biomass accumulation were affected by macroconsumers and sediment addition, however. Biomass accumulation rates were significantly elevated in AA versus AE treatments (nonparametric Nemenyi test: $q = 4.54$, $P < 0.01$), but this macroconsumer effect was not evident when sediment was added (Fig. 5).

Leaf pack experiment: Insect assemblages—Neither total insect density nor biomass was significantly altered by sediment addition or macroconsumer exclusion in the leaf pack experiment (ANOVAs: $F_{1,16} \leq 2.28$, $P \geq 0.151$), although there was a tendency toward greater biomass in macroconsumer access versus exclusion treatments under both sediment regimes (Fig. 6). Similarity between macroconsumer access and exclusion pairs in terms of insect biomass was not affected by sediment addition (t -test: $t = 0.32$, $df = 7$, $P = 0.759$; Fig. 6).

Sediment addition tended to decrease biomass of dipteran predators (primarily Tanyptodinae, Ceratopogonidae, and *Atherix*) in both macroconsumer access and exclusion treatments (ANOVA: $F_{1,16} = 4.42$, $P = 0.052$). In contrast, biomass of insect shredders (primarily the dipteran *Leptotarsus* and the plecopterans *Pteronarcys*, *Taeniopteryx*, and *Tallaperla*) and nondipteran predators (primarily perlid and perlotid stoneflies and the trichopteran *Rhyacophila*) did not differ between macroconsumer or sediment treatments (ANOVAs: $F_{1,16} \leq 1.08$, $P \geq 0.314$; $F_{1,16} \leq 2.97$, $P \geq 0.104$).

Discussion

Small, yet environmentally realistic increases in bedload had significant effects on both algal- and detrital-based stream benthic communities, most notably via the alteration of macroconsumer-mediated biotic interactions (Fig. 7). These effects largely were due to sediment transport across the stream bottom, rather than sediment deposition. Although previous studies have shown that sediment deposition can diminish the top-down effects of insects (e.g., Peckarsky 1985; Walde 1986), to our knowledge, this study is the first in situ sediment manipulation to experimentally demonstrate that elevated bed-

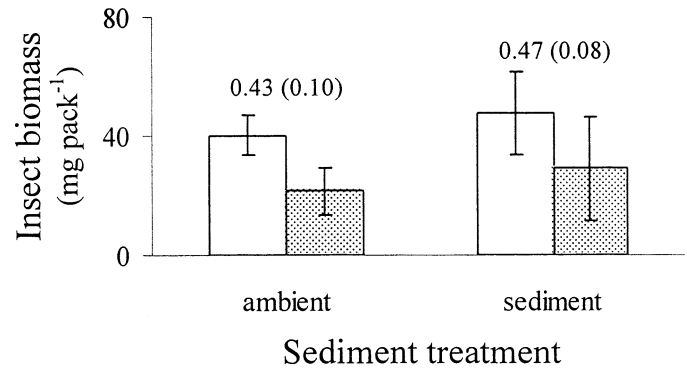


Fig. 6. Total insect biomass in macroconsumer access and exclusion treatments on day 56 of the leaf pack experiment. Each bar represents mean ($n = 5$) \pm 1 SE. Each number indicates similarity (0–1.0 scale, mean of five replicates [standard error]) between paired macroconsumer access and exclusion replicates.

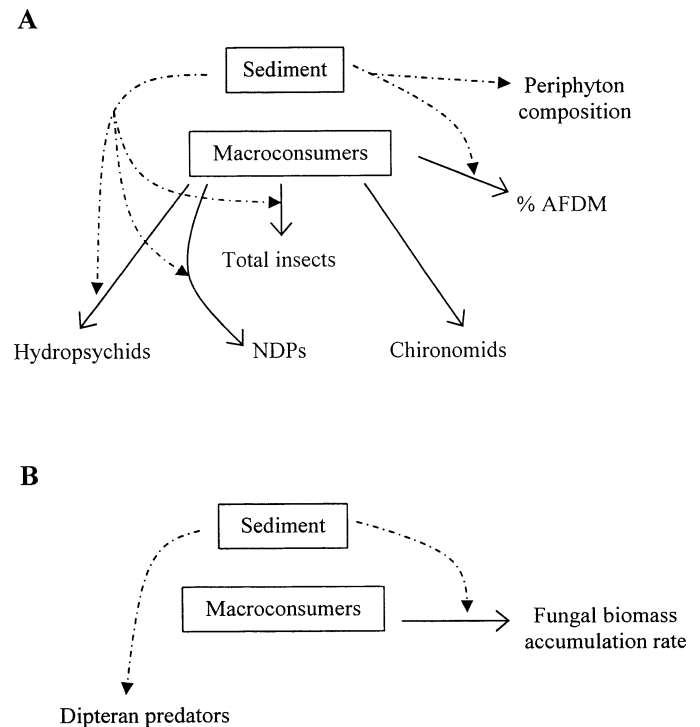


Fig. 7. Summary of (A) tile experiment and (B) leaf pack experiment results. Boxes indicate factors that were manipulated in the experimental design; other parameters indicate response variables. All arrows indicate negative effects. Dashed arrows represent influence of sediment (i.e., there was a significant sediment effect); solid arrows represent influence of macroconsumers (i.e., there was a significant exclusion effect). Dashed arrows pointing to solid arrows indicate that macroconsumer effects were altered by sediment addition (i.e., there was a significant sediment–exclusion interaction). NDPs, nondipteran predators (primarily predatory stoneflies). Response variables that were unaffected by sediment addition or macroconsumer exclusion are not shown.

load and subsequent sediment transport can alter the outcome of species interactions mediated by fishes and crayfish.

Direct effects of elevated bedload—In both the tile and leaf pack experiments, the direct effects of increased bedload were relatively minor (Fig. 7). Sediment addition altered periphyton composition on tiles, decreasing the proportion of motile diatoms such as *Navicula* and *Luticola* (Fig. 2B). Although motile diatom taxa are often considered more tolerant of deposited sediment than other algal growth forms (Kutka and Richards 1996), these taxa are more loosely attached to the substrate than many upright taxa. Thus, *Navicula* and *Luticola* may have been more readily scoured by the daily addition of sediment and the subsequent bedload transport (Hudon and Legendre 1987; Peterson 1996), resulting in a relative increase in other taxa (e.g., the upright diatom *Synedra*).

In the leaf pack experiment, sediment addition did not alter leaf decay rates: the relatively small amount of sediment added did not accelerate leaf breakdown via physical abrasion (Webster and Waide 1982), nor did it slow breakdown by burying leaf packs and making them inaccessible to shredders (Webster and Waide 1982; Parkyn et al. 1997). However, the only direct effect of sediment addition on insect assemblages occurred in the leaf pack experiment, where dipteran predator biomass tended to decline in both macroconsumer access and exclusion treatments when sediment was added. Small bedload increases did not directly affect insects in the tile experiment, even though these substrates may offer less shelter from saltating sediment.

In contrast to our results, many studies have demonstrated significant direct effects of sedimentation on stream benthic communities (Waters 1995; Wood and Armitage 1997). As stated earlier, many of these studies focused on suspended and/or deposited sediment rather than on sediment transported along stream bottoms (e.g., Angradi 1999; Runde and Hellenthal 2000). Given that <4% of the total sediment added to each replicate remained at the end of each experiment, this study did not focus on the effects of sediment deposition; instead, it addressed the impacts of sediment transport through localized benthic areas. For example, sediment addition tiles and leaf packs (and the underlying stream substrate) remained relatively unembedded, and substrate particle size within each replicate was not significantly reduced. Adverse effects of sedimentation are often associated with increases in substrate embeddedness and/or decreases in particle size (Waters 1995), but these factors were not significantly altered in these experiments.

However, some studies have demonstrated significant direct effects of bedload transport on stream biota (e.g., Alexander and Hansen 1986; Culp et al. 1986). In fact, Culp et al. (1986) found that saltating sediment was especially detrimental to insect assemblages, with a 10% increase in sand particles reducing benthic invertebrate densities by >50% within 24 h. In part, the relative absence of direct sediment effects in this study likely reflects the small scale of sediment addition, in terms of both areal extent and total amount. Because sediment was added to small (0.25 m²), discrete areas within a larger, unaltered landscape, any sediment-related decreases in insect density or biomass may

have been offset by immigration from adjacent, unaffected stream areas (Cooper et al. 1990). In addition, relatively small amounts of sand were added to each replicate.

Indirect effects of elevated bedload: Alteration of macroconsumer effects—The most noticeable effect of increased bedload transport was the alteration of top-down macroconsumer effects. Macroconsumers influenced lower trophic levels in both the tile and leaf pack experiments, despite relatively low macroconsumer densities (total fishes and crayfish <3 m⁻²) in Lower Ball Creek. Sediment addition altered many of these macroconsumer-mediated effects. In the tile experiment, macroconsumers reduced sediment organic content under ambient sediment conditions but had no effect when sediment was added; by day 40, Chl *a* tended to show a similar pattern (Fig. 1). Fungal accumulation rates in the leaf pack experiment showed the opposite macroconsumer effect: macroconsumers accelerated fungal accumulation under ambient sediment conditions, but this effect also disappeared with sediment addition (Fig. 5). In each experiment, the interaction between macroconsumers and sediment regime was a key factor influencing basal resources (i.e., algae and fungi).

Macroconsumer effects on insect assemblages also were affected by sediment addition. In the tile experiment, macroconsumers reduced insect biomass under ambient sediment conditions. When sediment was added, these macroconsumer effects disappeared, and insect assemblages in access and exclusion treatments became more similar (Figs. 3, 4). Prey taxa preferred by mottled sculpins (chironomids and hydropterygids [Stouder 1990]) were affected, as were nondipteran predators (primarily predatory stoneflies). Because sculpins do not regularly consume large predatory stoneflies (Stouder 1990), the reduction in nondipteran predators probably resulted from the avoidance of sculpins by stoneflies rather than direct predation (e.g., Soluk and Collins 1988; Gibson 1999).

Harsh abiotic conditions (e.g., elevated bedload transport) may diminish the influence of biotic interactions such as competition and predation in stream communities (Peckarsky 1983; Menge and Sutherland 1987). Results of the tile experiment support this contention, as sediment addition diminished the influence of macroconsumers. Sedimentation (or any other abiotic disturbance) may alter top-down forces via effects on macroconsumers and/or prey taxa (e.g., through changes in macroconsumer behavior, macroconsumer feeding efficiency, prey density, prey behavior [Walde 1986]). Macroconsumers did not visit sediment addition replicates less frequently than ambient sediment replicates, which argues against an alteration of macroconsumer behavior. Sediment-related alterations in prey density may be more important, as patch selection by mottled sculpin is consistently related to invertebrate abundance (Petty and Grossman 1996). This is supported by the fact that top-down effects on sediment-sensitive taxa (hydropterygids and nondipteran predators) were diminished by sediment addition, while top-down effects on relatively sediment-tolerant taxa (chironomids) were unaffected.

Macroconsumers had minimal effects on insect assemblages in the leaf pack experiment relative to their effects in

the tile experiment (Fig. 7). Leaf packs provide a food source for invertebrates, but they also can shelter these organisms from predation (e.g., Reice 1991; Rosemond et al. 1998) and scouring by sediment transport. In contrast, tiles provide a homogeneous and relatively refuge-free habitat, potentially facilitating predation and scouring. Our results suggest that increased sediment transport will affect communities based on algal resources more significantly than leaf pack-associated communities.

Comparison with other studies—Previous studies have shown diminished consumer effects with increased sedimentation, but these studies have focused on either insect predators (e.g., Peckarsky 1985; Walde 1986) or the influence of increased suspended sediment on fish predators (e.g., Barrett et al. 1992; Abrahams and Kattenfeld 1997). Few sediment addition experiments have focused on the potential alteration of top-down effects by bedload increases. One notable exception is a 5-yr sediment addition study by Alexander and Hansen (1986), which found that the amount of food eaten per individual brook trout did not change with sediment addition, although overall brook trout and benthic insect numbers decreased. This suggests that top-down effects of brook trout were not altered by bedload increases, which contrasts with results of our tile experiment. This difference is not surprising, given that, in our study, macroconsumers were predominantly obligate benthic feeders (i.e., mottled sculpins and crayfish), whereas brook trout feed on aquatic and terrestrially derived invertebrate drift.

Other sediment addition studies have examined bedload effects on benthic insects (e.g., Culp et al. 1986; Runde and Hellenthal 2000; Ciesielka and Bailey 2001). Generally, these studies have been relatively short term, mimicking one-time increases in sediment transport and deposition. In our experiments, daily sediment additions mimicked “pulsed” sediment inputs (e.g., after brief rainstorms) over longer timescales (40–56 d) or impacts of saltating bedload moving downstream after a massive input of sediments upstream (e.g., because of bank failure). Furthermore, our experiments involved the addition of relatively large-sized particles. Other studies have shown that sediment effects can be size-dependent, with smaller particles frequently having more adverse effects than large particles (Waters 1995; Runde and Hellenthal 2000). While it is possible that the use of smaller particles (e.g., silt) may have increased sedimentation effects, larger sand particles compose the bulk of sediment naturally moving as bedload in Lower Ball Creek.

Our experiments likely underestimate sedimentation effects on stream communities. While we added small amounts of sediment to localized areas (0.25 m²) of the stream bottom, land clearing activities can lead to much greater bedload increases (e.g., 20-fold bedload transport rate increases after forest fires [Beatty 1994]). Sedimentation also affects entire stream reaches, and adjacent, sediment-free areas (which may have offset aquatic insect reductions in these experiments) may not exist. Finally, our results do not reflect the potential effects of sediment-associated contaminants (e.g., heavy metals, hydrocarbons), which can adversely affect benthic organisms (e.g., Forrow and Maltby 2000).

In conclusion, our experiments demonstrate that small in-

creases in bedload affect benthic communities, largely by altering the outcome of species interactions. Given that current sediment regulatory programs (e.g., TMDL requirements) typically focus on turbidity and suspended sediments, these findings are especially significant. Algal-based food webs (and, to a more limited extent, detrital-based food webs) were affected by small additions of sand bedload in the absence of increased suspended sediments. Thus, regulatory programs based solely on suspended sediment levels may not adequately address increases in sediment transport along the stream bottom and its direct and indirect effects on biotic communities.

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