KATHARINE ANN SCHOFIELD
Top-down interactions in southern Appalachian streams: an examination of temporal and spatial variability
(Under the direction of CATHERINE M. PRINGLE)

Macroconsumers (fish, crayfish, shrimp) can influence numerous aspects of the stream environment, including sediment accumulation, algal and invertebrate assemblages, and leaf breakdown. The relative strength and outcome of these macroconsumer (or top-down) interactions can depend upon many biotic and abiotic factors. The main objective of this research was to examine temporal and spatial variability in the top-down effects of southern Appalachian stream macroconsumers. To do this, we conducted a series of exclusion experiments, using electricity to exclude fishes and crayfishes from benthic areas of streams.

To assess temporal shifts in macroconsumer impacts on leaf breakdown, exclusion experiments were conducted in summer and autumn using rhododendron leaf packs. Although rhododendron is typically considered low quality food, crayfish played a significant role in rhododendron leaf breakdown during both summer and autumn. Insect shredder and predator biomass did not differ between macroconsumer exclusion and control areas, indicating that crayfish directly accelerated rhododendron decay via shredding.

In the second set of experiments, macroconsumers and sediment were simultaneously manipulated to determine whether sedimentation reduced the relative strength of top-down effects. Because macroconsumer impacts can vary with substrate type, experiments were run with tiles and leaf packs. Small yet environmentally realistic increases in bedload transport and deposition (obtained via daily sediment addition) directly and indirectly affected algal and detrital-based benthic communities. Macroconsumers reduced total insect biomass on tiles, but this effect was eliminated with sediment addition.

To assess the influence of watershed development on top-down effects, macroconsumers were excluded at five sites representing a range of human watershed development. Macroconsumers influenced lower trophic levels at all five sites, despite cross-site physical,

chemical, and biological differences. Although certain effects of watershed land use may tend to decrease the strength of top-down interactions (e.g., sedimentation), these reductions may be offset by other concurrent changes (e.g., increased nutrients).

Electric exclusion is a useful tool for assessing top-down effects, as it minimizes the artifacts associated with traditional cage experiments. However, the technique should be used wisely: the minimum voltages needed to exclude macroconsumers should be employed, and consistency of voltages both within and across sites should be maintained.

INDEX WORDS: Bedload, Cottus bairdi, Crayfish, Electric exclusion, Land use, Leaf breakdown, Macroconsumers, Sediment addition, Top-down, Variability

TOP-DOWN INTERACTIONS IN SOUTHERN APPALACHIAN STREAMS: AN EXAMINATION OF TEMPORAL AND SPATIAL VARIABILITY

by

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DEDICATION

For Mom and Dad,

who always taught me to ask a lot of questions.

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TABLE OF CONTENTS

CHAPTER 1

INTRODUCTION

The importance of macroconsumers (fish, shrimp, crayfish) in structuring stream communities has been documented by many researchers (e.g., Gelwick and Matthews 1992, Flecker 1996, Charlebois and Lamberti 1996). These relatively large organisms can influence numerous aspects of the stream environment, including sediment accumulation (e.g., Power 1990, Pringle and Blake 1994), algal and invertebrate assemblages (e.g., Gelwick and Matthews 1992, Pringle and Hamazaki 1998), and ecosystem processes such as leaf breakdown (e.g., Parkyn et al. 1997, March et al. 2001).

As with most ecological phenomena, the expression of macroconsumer (or top-down) effects is highly variable. The relative strength of top-down forces can depend upon many biotic and abiotic factors (Power 1992a, Polis and Strong 1996), including consumer identity (Biggs et al. 2000, Gelwick 2000), disturbance (Wootton et al. 1996), and habitat characteristics (Power 1992b, Flecker 1997, Rosenfeld 2000). For example, researchers have shown that macroconsumer effects are highly dependent upon species identities [e.g., crayfish versus minnows (Gelwick 2000); native versus introduced fishes (Biggs et al. 2000), overall assemblage composition (March et al. 2001)]. In addition, several studies have found that the relative strength of stream macroconsumer impacts can vary between habitats and/or substrates [e.g., riffles versus pools (Flecker 1997, Rosenfeld 2000); bedrock/boulder versus gravel (Power 1992b); tiles versus leaf packs (Pringle and Hamazaki 1998, Rosemond et al. 1998)]. Overall, the importance of environmental variation (physical, chemical, and biological) in determining the

strength and outcome of top-down interactions has been well-recognized (e.g., Hunter and Price 1992, Wellnitz and Ward 2000).

To date, most studies considering variability of top-down interactions have focused on systems minimally affected by human activities. However, human modification of the environment can significantly influence environmental variation and thus affect the strength and outcome of biotic interactions (e.g., Livingston et al. 1997). For example, human activities such as agriculture and urbanization have altered stream sediment loading and transport, drastically increasing the amount of fine inorganic material delivered to waterways (Waters 1995). Elevated sediment levels can exert a direct negative effect on fishes (Berkman and Rabeni 1987, Rowe et al. 2000), aquatic insects (e.g., Lemly 1982, Angradi 1999), other invertebrates (e.g., Brim Box and Mossa 1999), and periphyton (e.g., Horner et al. 1990, Biggs et al. 1999). Although such direct effects of sedimentation have received more attention, biotic interactions also can be affected. Several studies have shown that the influence of both invertebrate (e.g., Peckarsky 1985, Walde 1986) and vertebrate (e.g., Barrett et al. 1992, Johnson and Hines 1999) consumers on lower trophic levels can be altered by sedimentation.

Because anthropogenic sedimentation is often associated with other in-stream alterations (e.g., hydrologic changes, nutrient enrichment, decreased canopy-cover, sediment-associated contaminants), separating the influence of sediment from other factors is frequently difficult. Numerous studies have shown that human development of watersheds and/or riparian areas can have significant effects on myriad physical, chemical, and biological characteristics of streams (e.g., Jones and Clark 1987, Schlosser 1991, Lenat and Crawford 1994). In turn, these abiotic and biotic changes can affect top-down interactions (Dunson and Travis 1991, Hunter and Price 1992), either by weakening [e.g., increased sedimentation (Peckarsky 1985)] or strengthening [(e.g., increased irradiance (Wellnitz and Ward 2000)] consumer effects. Teasing apart the potentially contradictory effects of watershed development on top-down interactions complicates examination of consumer impacts. However, as anthropogenic landscape alteration becomes

increasingly prevalent worldwide, understanding species interactions in human-modified environments becomes especially important (McDonnell and Pickett 1990, Paul and Meyer 2001).

In the southern Appalachian Mountains, the impact of land use alterations on stream communities is a growing concern. The region supports highly diverse stream communities, including many endemic and imperiled species (Cooper and Braswell 1995, Morse et al. 1997). This diversity is being threatened, however, by human population growth and subsequent development throughout the region. Traditionally population density has been low in the area, but over the past 20 years the southern Appalachians have seen substantial growth, primarily due to residential development (SAMAB 1996). Much of this development has occurred in near-stream areas (Bolstad and Swank 1997). This changing land use mosaic provides a unique opportunity to examine how land use alterations influence top-down interactions.

The objective of this research was to examine temporal and spatial variability in the top-down effects of southern Appalachian stream macroconsumers. Dominant macroconsumers in these systems include omnivorous crayfishes (three species in the genus Cambarus) and fishes such as insectivorous mottled sculpins (Cottus bairdi), algivorous central stonerollers (Campostoma anomalum), and a suite of insectivorous shiners (Cyprinidae). We conducted a series of studies in which electricity was used to exclude fishes and crayfishes from benthic areas of different southern Appalachian streams. We then examined effects of macroconsumer exclusion on variables such as leaf breakdown, fungal biomass, sediment accumulation, and algal and insect assemblages, and compared these responses to patterns in macroconsumer access (control) areas.

Chapter 2 explores the role of macroconsumers in the breakdown of rhododendron leaf litter, which is generally considered a low quality food resource. Earlier work by Huryn and Wallace (1987) suggested that peak litter consumption by crayfish would occur between June and September, when relatively refractory leaves such as rhododendron comprise a significant portion of in-stream leaf litter. In Chapter 2, we consider whether macroconsumers (primarily crayfish)

influence rhododendron leaf breakdown in both summer (when leaves other than rhododendron are relatively scarce) and autumn (when other leaves are relatively abundant). To address this, we conducted two macroconsumer exclusion experiments, one in summer and one in autumn, using pre-conditioned rhododendron leaf packs as sampling substrates. We examined how leaf pack breakdown rates, fungal biomass, and insect assemblages differed in macroconsumer access versus macroconsumer exclusion treatments during the summer and autumn experiments. We predicted that exclusion of omnivorous crayfish would lead to decreased rhododendron breakdown in both summer and autumn.

Chapter 3 deals with top-down interactions in algal and detrital-based food webs, and whether these interactions can be altered by sedimentation. Few studies have explicitly examined the influence of elevated bedload on top-down forces [although see Alexander and Hansen (1986) for a notable exception]. Thus, we simultaneously manipulated sediment (via daily sediment addition) and top-down effects of macroconsumers in situ in two separate factorial experiments, one using tiles and one using leaf packs as sampling substrates. Both tiles and leaf packs were used because previous macroconsumer exclusion experiments indicated that the relative strength of top-down interactions differed between tile and leaf pack substrates (Pringle and Hamazaki 1998, Rosemond et al. 1998). We predicted that sediment addition would directly and indirectly affect benthic communities in both tile and leaf pack experiments, but that in general tile substrates would prove more vulnerable to sedimentation effects.

The objective of Chapter 4 was to examine how macroconsumer effects vary among streams with differing amounts of watershed development. Whereas the experiments in Chapter 3 examined the effects of elevated bedload in an otherwise unimpacted (e.g., hydrologically unaltered, unpolluted) southern Appalachian stream, stream sedimentation often results from human alteration of the landscape, which typically also changes numerous other physical, chemical, and biological stream characteristics. In Chapter 4, we examined whether top-down effects were altered by the suite of in-stream changes associated with increasing watershed

development. Using tiles as sampling substrates, we conducted macroconsumer exclusion experiments in five southern Appalachian streams; these sites represented a range of human watershed development, from 100% to < 50% forested. We expected that the biological, chemical, and physical changes associated with anthropogenic activity would interact to influence top-down interactions, and that the ultimate outcome of these changes would vary across sites. For example, we predicted that shifts in macroconsumer assemblages (e.g., from substrate to water column-oriented fish species) would tend to reduce top-down interactions, whereas greater light and nutrient availability would tend to increase macroconsumer effects.

Chapter 5 considers the electric exclusion technique used in these studies in greater detail. Many studies have used electricity to examine the effects of stream macroconsumers on benthic communities and processes (e.g., Pringle and Blake 1994, Pringle and Hamazaki 1998, Rosemond et al. 1998, March et al. 2001). All of these studies found that the electric current used to exclude macroconsumers did not exert a direct negative effect on insect assemblages. However, several researchers have found that insects can be adversely affected by electrical currents (e.g., Mesick and Tash 1980, Taylor et al. 2001). Chapter 5 examines the potential effects of electricity on southern Appalachian stream insect assemblages in greater detail, through re-analysis of previous experiments as well as analysis of insect drift before and after the start of four additional electric exclusion studies.

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CHAPTER 2

THE IMPORTANCE OF CRAYFISH IN THE BREAKDOWN OF RHODODENDRON LEAF LITTER [1]

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SUMMARY

1. Rhododendron (Rhododendron maximum) is a common evergreen shrub in riparian areas of the southern Appalachians, where its leaves can comprise a large proportion of leaf litter in streams. However, they are relatively refractory and generally considered a low quality food resource for detritivores.

2. Our objective was to assess whether macroconsumers (primarily crayfish (Cambarus bartonii)) influence rhododendron leaf breakdown in a forested southern Appalachian stream in both summer (when leaves other than rhododendron are relatively scarce) and autumn (when other leaves are relatively abundant). We conducted two leaf decay experiments, one in summer and one in autumn, using pre-conditioned leaves. Electric 'fences' were used to exclude macroconsumers from the benthos of a fourth-order stream; we predicted that excluding macroconsumers would reduce the decay rate of rhododendron leaves in both summer and autumn.

3. In both experiments, breakdown rate was lower in exclusion treatments. Macroconsumers accounted for approximately 33% and 54% of rhododendron decay in summer and autumn, respectively. We attribute this effect to direct shredding of rhododendron by crayfish. Biomass of insect shredders, insect predators and fungi did not differ between control and exclusion treatments, indicating that insectivorous sculpins (Cottus bairdi) did not affect rhododendron decay and that omnivorous crayfish did not exert an indirect effect via alteration of insect or fungal biomass.

4. The influence of shredding insects varied between summer and autumn. In summer, when other, more palatable leaf types were not available, rhododendron leaf packs appeared to provide 'resource islands' for insect shredders. There was a significant inverse relationship between insect shredders and leaf pack mass in the summer exclusion treatment: insects were the only organisms eating leaves in this treatment and, as shredder biomass increased, remaining leaf pack

mass decreased. In the control treatment, however, we did not see this relationship; here, the effect of insect shredders was presumably swamped by the impact of crayfish. In autumn, when other leaves were abundant, insect shredder biomass in rhododendron leaf packs was less than one-third of summer values.

5. Even at low density (approximately 2 m^{-2}) crayfish were able to influence an ecosystem process such as leaf decay in both summer and autumn. Given the threatened status of many crayfish species in the United States, this finding is especially relevant. Even small alterations in crayfish assemblages, whether via loss of native species and/or introduction of exotic species, may have significant repercussions for ecosystem function.

INTRODUCTION

The importance of macroconsumers (fish, shrimp, crayfish) in structuring stream communities has been documented by many researchers (e.g., Gelwick & Matthews, 1992; Pringle et al., 1993; Flecker, 1996; Charlebois & Lamberti, 1996). These relatively large organisms can influence numerous aspects of the stream environment, including sediment accumulation (e.g., Power, 1990a; Pringle & Blake, 1994), algal and invertebrate assemblages (e.g., Power, Matthews & Stewart, 1985; Power, 1990b; Flecker, 1992; Charlebois & Lamberti, 1996, Pringle & Hamazaki, 1998), and ecosystem processes such as leaf breakdown (e.g., Parkyn, Rabeni & Collier, 1997).

In many temperate streams, crayfish are a common component of the macrofaunal assemblage. Because crayfish are omnivorous, relatively long-lived and large-bodied (Momot, 1995), they can have significant impacts on in-stream resources, including algae, other invertebrates and detritus (e.g., Creed, 1994; Charlebois & Lamberti, 1996; Parkyn et al., 1997; Keller & Ruman, 1998). In addition, crayfish are one of the most threatened faunal groups, with 65% of species in the United States considered vulnerable, threatened or extinct (Richter et al.,

1997). Determining the role of crayfish in structuring benthic communities and influencing energy flow through stream ecosystems is of growing importance, given their imperiled status.

Crayfish are thought to feed primarily on detritus, especially as adults (Momot, 1995; Rabeni, Gossett & McClendon, 1995; Whitledge & Rabeni, 1997). Because of their low assimilation efficiency for detritus (typically ≤ 30%; Rabeni et al., 1995; Whitledge & Rabeni, 1997) crayfish may consume large quantities of this resource, thereby greatly accelerating leaf breakdown rates (e.g., Parkyn et al., 1997; Usio, 2000). Many leaf breakdown studies have been conducted at the Coweeta Hydrologic Laboratory, a US Forest Service (USFS) research facility in the southern Appalachian Mountains, USA (see Webster et al. (1999) for an overview). Most of these studies have focused on the role of aquatic insects (e.g., Webster & Waide, 1982; Wallace, Webster & Cuffney, 1982) and microbes (e.g., Paul & Meyer, 1996) in leaf breakdown; only one has explicitly addressed the influence of crayfish.

Huryn & Wallace (1987) conducted laboratory feeding trials which showed that leaf processing by Cambarus bartonii (Fabricius), a common crayfish at Coweeta, was positively correlated with water temperature. They predicted that peak litter consumption by crayfish would occur from June to September, when temperature was high, other shredding invertebrates were less active and litter standing crops were low. Consequently, they postulated that C. bartonii may play a significant role in the breakdown of rhododendron (Rhododendron maximum (L.)) leaves in summer. Rhododendron is an evergreen shrub that loses its leaves primarily in autumn, dropping approximately 9% of its leaf standing crop each year (Monk, McGinty & Day, 1985). It is one of the most refractory leaf species at Coweeta (Whiles, Wallace & Chung, 1993), so it may persist in stream channels for long periods. By mid-summer, when other leaf types are relatively scarce, rhododendron leaves can be well-conditioned and available for crayfish consumption (Huryn & Wallace, 1987).

Our objective was to assess whether macroconsumers (primarily crayfish) influence rhododendron leaf breakdown in a forested southern Appalachian stream in both summer (when leaves other than rhododendron are relatively scarce) and autumn (when other leaves are relatively abundant). To answer this question, we conducted two rhododendron decay studies, one in summer and one in autumn, using pre-conditioned leaves. Electric 'fences' were used to exclude macroconsumers from the benthos of a fourth-order stream; we hypothesized that macroconsumer exclusion would lead to a decreased rate of rhododendron breakdown in both summer and autumn.

METHODS

Study site

Experiments were conducted in Lower Ball Creek, a fourth-order stream at the USFS Coweeta Hydrologic Laboratory in western North Carolina, USA (35°N, 83°30'W). Coweeta is a 2185 ha facility located in the Blue Ridge physiographic province of the southern Appalachians. Mean monthly air temperature ranges from 3 to 22°C, and annual precipitation ranges from 180 cm at low altitude to 250 cm at high altitude (Swank & Crossley, 1988). During our experiments, continuous discharge data were collected at Lower Ball Creek by USFS researchers; continuous temperature data were collected by Dr. J.B. Wallace (University of Georgia, USA).

The Lower Ball Creek catchment is forested (approximately 100%) by mixed hardwood species such as red maple (Acer rubrum (L.)) and tulip-poplar (Liriodendron tulipifera (L.)). Riparian areas are densely vegetated by rhododendron (Rhododendron maximum), mountain laurel (Kalmia latifola (L.)) and dogwood (Cornus florida (L.)). Altitude at our study site is about 700 m, with a stream gradient of approximately 4 cm m^{-1}. Boulder, cobble and gravel comprise the stream substratum. Macroconsumer assemblages in Lower Ball Creek are dominated by crayfish (Cambarus bartonii) and mottled sculpin (Cottus bairdi (Girard)), but longnose dace

(Rhinichthys cataractae (Valienciennes)) and rosyside dace (Clinostomus funduloides (Girard)) are also present.

Experimental design

Rhododendron decay experiments were conducted in summer and autumn 1999. Freshly fallen rhododendron leaves (i.e., brown but not buried or decomposed) were collected near Lower Ball Creek on 17 March and 18 June for summer and autumn experiments, respectively. Previous research indicated that initial rhododendron decay is very slow (e.g., Webster & Waide, 1982; Benfield et al., 1991). Because we wanted to be able to detect a change in leaf mass over a limited experimental period, we used pre-conditioned leaves to accelerate the decay process. Leaves were placed in plastic mesh (5 mm) bags for pre-conditioning and secured in the stream with aluminium gutter nails. Summer leaves remained in the stream from 17 March to 15 July, for a pre-conditioning period of 1574 degree days (mean daily water temperature, 12.9°C). Autumn leaves remained in the stream from 18 June to 25 August (mean daily water temperature, 17.2°C). On 25 August, leaves were removed from the stream and rinsed to remove macroinvertebrates; they were then refrigerated at 4°C from 26 August to 2 October to slow decomposition and compensate for warmer pre-conditioning temperatures (i.e., relative to summer leaves). Pre-conditioning period for the autumn leaves was 1302 degree days.

On 7 July, 10 intact leaves were removed from summer pre-conditioning bags to determine a wet / dry mass conversion factor. Each leaf was weighed immediately upon removal from the stream to obtain a wet mass, then dried at 70°C for 24 h and reweighed to obtain a dry mass. The wet / dry mass ratio (mean ± 1 SE) was 5.25 ± 0.08; thus, we used 26.2 g wet mass per pack for approximately 5 g dry mass leaf packs. The same ratio was used for autumn leaf packs, and initial dry mass was similar between summer and autumn experiments (mean ± 1 SE, 4.49 g ± 0.08 in summer versus 4.88 ± 0.21 in autumn). All macroinvertebrates were rinsed from leaves prior to leaf pack assembly. Rinsed leaves were distributed into packs of appropriate mass, which

were held together by two plastic fasteners placed near leaf midribs. Because the pre-conditioned leaves were relatively fragile, packs also were wrapped in plastic mesh (2 cm) to minimize the loss of large leaf fragments; this mesh was large enough to allow access by macroinvertebrates, including crayfish.

Leaf packs were attached with nylon monofilament to polyvinylchloride frames (0.25 m^2) lined with copper wire. Each pack was weighted with a lead weight (85 g) to keep it flush with the substratum. In the summer experiment five leaf packs were secured in each frame. In the autumn experiment fewer intact leaves were available, so four packs were used per frame. During both summer and autumn, 10 frames (five 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 & Müller, 1989); only sites which provided suitable area (e.g., without large boulders) 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 centre of each frame using a spherical densiometer.

To exclude macroconsumers, one frame in each pair was chosen by coin toss to be the exclusion treatment. This frame was connected to a 6 V, solar-powered fence charger (Parmak Model DF-SP-SS, Parker McCrory Manufacturing Company) that delivered repeated pulses of electricity to the 0.25 m^2 frame area. These electric pulses prevented the entry of crayfish and fish, but did not adversely affect smaller organisms such as aquatic insect larvae. Many other studies have used this electric exclusion technique (e.g., Pringle & Blake, 1994; Pringle & Hamazaki, 1997), which avoids some artifacts associated with traditional cage enclosure experiments (e.g., reduced water flow and increased sedimentation). The other frame in each pair served as a control area to which macroconsumers had access. Frames were placed approximately 0.5 m apart to minimize the impact of exclusion treatments on controls; 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 days to ensure a consistent 6 V charge. Frames also were cleared of accumulated leaves every 5 days to minimize flow alterations and prevent loss of frames during spates.

Sampling

The summer experiment began on 16 July and ended on 29 August. One leaf pack was removed from each frame on days 5, 10, 20, 32 and 44. In addition, six packs were brought back to the lab on day 0 to determine initial leaf weights and fungal biomass. The autumn experiment began on 3 October and ended on 28 November. Leaf packs were sampled on days 8, 20, 35 and 56, and nine packs were used for day 0 assessments. Fence chargers at exclusion treatments were turned off briefly (5-10 min) for sampling. A 210 μm mesh hand net was held downstream of each leaf pack as it was removed from the stream to retrieve any dislodged invertebrates. Leaf packs were placed in plastic bags, put on ice and returned to the laboratory (2 h away) for processing. Prior to removing the leaf packs, all replicates were examined with a clear plastic viewing box to determine whether any macroconsumers were present. In previous experiments we observed replicates for 5 min, but limited visibility in the current study made these prolonged observations inefficient. Instead, we recorded presence or absence of macroconsumers during spot checks of all replicates on all sampling dates, as well as every five days when fence charger batteries were changed (n = 80 spot checks in summer, 100 in autumn). 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, and we conducted four spot checks of all replicates at night.

Leaf packs were processed within 24 h of sampling. Leaves were rinsed to remove invertebrates and sediment. Invertebrates were live-picked from the rinsed material and

preserved in 70% ethanol. We chose to focus on insect shredders and predators because they were the functional feeding groups most likely to affect rhododendron decomposition (shredders directly through leaf consumption, predators indirectly through consumption of shredders). Insects classified as shredders or predators by Merritt & Cummins (1996) were later identified to the lowest practical level (usually family or genus) using a dissecting microscope (10X magnification), and measured to the nearest 0.5 mm using 1 mm grid paper. Shredder and predator biomasses were calculated with family-specific, length-mass regressions from Benke et al. (1999). Organisms < 1.5 mm were identified to order and were not included in shredder or predator biomass values (typically they contributed < 0.01% of total invertebrate biomass). Shredders and predators from day 20, 32 and 44 (summer experiment) and day 20, 35 and 56 (autumn experiment) samples were identified.

After invertebrates were rinsed from leaf packs, 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, Arsuffi & Fallon, 1988; with slight modifications after Paul & Meyer, 1996). Ergosterol was extracted from day 0, 10, 20 and 32 (summer) and day 0, 8, 20 and 35 (autumn) samples. By day 44 of the summer experiment, only two control and two exclusion treatments had enough leaf material remaining for ergosterol analysis; by day 56 of the autumn experiment, none of the packs had enough leaf material remaining. Fungal biomass was estimated from ergosterol concentration using a conversion factor of 5 μg ergosterol / mg mycelial dry mass (Gessner & Chauvet, 1993; Paul & Meyer, 1996). The remaining 50 discs from each pack underwent the same drying and ashing process as the leaf packs. Packs were dried at 70°C for 3 d, weighed, then burned at 500°C for 6 h and reweighed. Total ash-free dry mass (AFDM) remaining was calculated by summing AFDM of each leaf pack and 2 x AFDM of the 50 leaf discs.

To quantify the availability of rhododendron and non-rhododendron leaves at the end of each experiment, we randomly selected 10 cross-stream transects (two near each treatment pair, each 1 m wide) and collected all leaves within each transect. These leaf collections were returned to the laboratory, rinsed free of macroinvertebrates, and sorted into rhododendron and non-rhododendron leaves. Leaves were dried at 70°C for approximately 1 wk, then weighed to determine dry weight (g m^{-2}) for the two leaf types.

To assess crayfish density, we sampled a 50 m transect within the experimental reach on 7 August and again on 4 November (none of the treatments were located inside the 50 m transect). On each date, 15 randomly located samples were taken using a quadrat sampler, which blocked off 1 m^2 of the stream bottom (i.e., total area sampled, 15 m^2). Crayfish from each sample were counted, identified and measured before being returned to the stream.

Statistical analysis

Initial physical parameters for each replicate were compared using a two-factor MANOVA (treatment and season), with water velocity, water depth, % canopy cover and shear stress as response variables. If MANOVA showed a significant effect, separate univariate two-factor ANOVAs were run for each physical parameter. Availability of rhododendron and non-rhododendron leaves was compared using a two-factor ANOVA (leaf type and season); if ANOVA showed a significant interaction between factors, separate paired *t*-tests were run for each season. To calculate leaf breakdown rate (*k*), we regressed the natural log of % AFDM remaining against day or degree day (where *k* is the slope of the regression). Breakdown rate was calculated for each replicate, then compared using two-factor ANOVA (treatment and season); separate ANOVAs were run for day and degree day calculations. A two-factor MANOVA (treatment and season), with predator and shredder biomass (average over three sample dates) as response variables, was run to test for any season or treatment differences in insect biomass. If significant effects were detected with MANOVA, univariate two-factor ANOVAs were run for

each response variable. To examine whether insect shredders were affecting leaf pack mass, we regressed AFDM remaining against shredder biomass for the summer and autumn experiments. Fungal biomass (average over three sample dates) was compared using a two-factor ANOVA (treatment and season). Prior to all statistical analyses, Levene's test was used to determine whether variances were equal; where necessary, data were transformed using a natural log or inverse transformation. For all analyses $\alpha = 0.05$, and all were conducted in SAS® System for Windows™, Release 6.12.

RESULTS

Mean daily water temperature during the summer experiment was 17.9°C (range 16.9-19.2°C) and 11.2°C (range 6.4-14.9°C) during the autumn experiment. Peak daily discharge was greater and more variable in autumn (mean ± SE, 217.5 l s^{-1} ± 54.7) than in summer (99.1 l s^{-1} ± 5.2), due largely to the occurrence of three distinct discharge peaks during the autumn experiment (Fig. 2.1). Water conductivity was similar in summer and autumn (mean ± SE, 12.5 μS cm^{-1} ± 0.26 in summer, 12.0 μS cm^{-1} ± 0.25 in autumn). Nutrient concentrations were relatively low in both summer and autumn, although concentrations were higher in summer: mean NO_3-N, NH_4-N, and soluble reactive phosphorus concentrations were 0.057, 0.004, and 0.009 mg L^{-1}, respectively, during the summer experiment, versus 0.004, 0.003, and 0.003 mg L^{-1} during the autumn experiment.

Initial physical parameters for treatment replicates are presented in Table 2.1. In the autumn experiment, one treatment pair differed significantly from the remaining four pairs in terms of these physical parameters. This pair was excluded from all analyses, leaving four replicate pairs for the autumn experiment and five replicate pairs for the summer experiment. Control and exclusion treatments did not differ in the measured parameters (MANOVA: Pillai's trace = 0.045, $F_{4,11} = 0.131$, $P = 0.968$), but there were significant seasonal (i.e., summer vs. autumn) differences

(MANOVA: Pillai's trace = 0.953, $F_{4,11} = 55.8$, $P < 0.0001$). Univariate analyses for each parameter indicated that water velocity (ANOVA: $F_{1,14} = 21.5$, $P = 0.0004$), water depth (ANOVA: $F_{1,14} = 6.25$, $P = 0.0254$), and % canopy cover (ANOVA: $F_{1,14} = 145$, $P < 0.0001$) contributed to this significant season effect: initial water velocities and depths were lower in autumn than in summer, while % canopy cover was greater (Table 2.1).

Macroconsumers were not observed in the electrified frames, indicating that the exclusion technique was effective. Crayfish and sculpins occasionally entered the exclusion treatment while fence chargers were turned off briefly for sampling, but they left immediately when chargers were reactivated. During the summer experiment a total of 11 crayfish were observed in control replicates (40 spot checks). During the autumn experiment large accumulations of leaves obscured spot checks, and only one crayfish and two sculpins were observed in control replicates (50 spot checks). Crayfish densities within the experimental reach were slightly higher in summer (mean ± SE, 2.33 m^{-2} ± 0.69) than in autumn (1.87 m^{-2} ± 0.50), although this difference was not significant.

Rhododendron leaves comprised more than 50% of the leaf material found in Lower Ball Creek at the end of the summer experiment (Table 2.2). Standing crop of rhododendron was similar in summer and autumn, whereas standing crop of non-rhododendron leaves (e.g., maple, birch, sycamore, dogwood) was nearly four times greater in autumn than in summer (Table 2.2). ANOVA showed a significant leaf type x season interaction (ANOVA: $F_{1,36} = 13.8$, $P = 0.0007$); subsequent paired *t*-tests indicated that there were significantly more non-rhododendron than rhododendron leaves in autumn (*t*-test: $t_9 = -5.13$, $P = 0.0003$), but not during the summer (*t*-test: $t_9 = 1.34$, $P = 0.106$).

Leaf breakdown

During both summer and autumn, exclusion of macroconsumers led to a decrease in rhododendron breakdown rate (Fig. 2.2). We estimated the amount of decay attributable to

macroconsumers in each experiment by dividing the difference between breakdown rates in control and exclusion treatments by the breakdown rate in the control treatment. Macroconsumers were responsible for approximately 33% of rhododendron decay during the summer experiment; this percentage increased to 54% in the autumn experiment. Comparison of individual replicate breakdown rates (k, day^{-1}) showed that there were significant treatment (P = 0.011) and season (P = 0.016, Table 2.3) effects: rhododendron breakdown was more rapid in autumn than in summer, and more rapid in control than in exclusion treatments (Fig. 2.2). No significant treatment x season interaction was found (P = 0.136, Table 3), although the difference between control and exclusion breakdown rates was much greater in autumn than in summer (Fig. 2.2).

To account for the shorter duration of the summer experiment (44 versus 56 days) we examined breakdown rates in two additional ways. When rates were calculated through day 32 (summer experiment) and day 35 (autumn experiment) significant treatment or season effects were not detected ($P \geq 0.121$, Table 2.3), indicating that treatment and season differences became pronounced only after more than a month of exclusion. We also calculated breakdown rates based on degree days. Although the autumn experiment lasted longer than the summer experiment, water temperatures were significantly lower. As a result, leaf packs in the summer experiment experienced more degree days during both pre-conditioning (1574 vs. 1302 degree days) and the experimental period (786 vs. 621 degree days), even though the summer experiment was of shorter duration. Comparison of individual replicate breakdown rates showed similar results whether k was calculated by day or by degree day (i.e., significant treatment and season effects, without significant treatment x season interaction).

Insect shredder and predator biomass

In each season, four taxa dominated the assemblage of insect shredders (> 90% biomass), although these taxa differed between seasons. The stoneflies Tallaperla and Pteronarcys were

among the dominant taxa in both summer and autumn; in addition, the stonefly Leuctra and the caddisfly Lepidostoma contributed to summer shredder biomass, while the stonefly Taeniopteryx and the cranefly Leptotarsus contributed to autumn shredder biomass. Similar predator taxa contributed the greatest biomass in both summer and autumn (i.e., perlid and perlodid stoneflies, dipteran predators such as Atherix, ceratopogonids and tanypodids).

Because Pteronarcys stoneflies can attain sizes comparable to small crayfish, they possibly could have been adversely affected by the exclusion treatment. Comparison of Pteronarcys biomass in control and exclusion treatments, however, did not show significant differences in either summer or autumn; in fact, the largest Pteronarcys individual obtained (length, 27 mm) was found in the exclusion treatment.

MANOVA (using total predator and shredder biomass per pack as response variables) showed no significant difference between control and exclusion treatments ($P = 0.332$, Table 2.4). However, there was a significant effect of season ($P = 0.005$), with greater predator and shredder biomass found in summer versus autumn (Fig. 2.3). Univariate ANOVAs indicated that both insect shredders ($F_{1,14} = 10.9$, $P = 0.005$) and predators ($F_{1,14} = 7.70$, $P = 0.015$) demonstrated a significant seasonal effect. Similar results were obtained when biomass was expressed in terms of mg g^{-1} AFDM rather than mg $pack^{-1}$. Although no significant treatment differences were detected, there was a tendency toward greater insect predator biomass in control versus exclusion treatments in the autumn experiment (Fig. 2.3). Higher predator biomass was not accompanied by a significant decrease in shredder biomass in the control treatment.

When AFDM remaining was regressed against insect shredder biomass on each date, a significant relationship ($r^2 = 0.482$, $P = 0.006$) was found in the exclusion treatment during the summer experiment: as shredder biomass increased, AFDM remaining decreased (Fig. 2.4). This pattern was not observed in the control treatment during the summer ($r^2 = 0.041$, $P = 0.467$), nor

was it observed in either control or exclusion treatments in the autumn experiment ($r^2 \leq 0.083$, $P \geq 0.364$).

Fungal biomass

Fungal biomass was not detected on day 0 samples in either the summer or the autumn experiment. Fungal biomass increased throughout each experiment but, by the end of both summer and autumn, most leaf packs did not contain enough material for ergosterol extraction. Therefore, days 44 (summer) and 56 (autumn) were excluded from analyses. Comparison by ANOVA indicated that there was a significant effect of season (ANOVA: $F_{1,14} = 78.2$, $P < 0.0001$), with greater fungal biomass in summer than autumn (Table 2.5). In both seasons, however, fungal biomass remained relatively low. There was not a significant effect of treatment (ANOVA: $F_{1,14} = 0.04$, $P = 0.844$), although there was a significant treatment x season interaction (ANOVA: $F_{1,14} = 12.2$, $P = 0.004$). In summer, fungal biomass tended to be greater in control than exclusion treatments; in autumn, this trend was reversed (i.e., there was greater biomass in exclusion versus control treatments), and the difference between treatments was more pronounced (Table 2.5).

DISCUSSION

Do macroconsumers influence rhododendron breakdown in both summer and autumn?

In both summer and autumn, breakdown rates (day^{-1} or degree day^{-1}) were slower when macroconsumers were excluded (Fig. 2.2), indicating that macroconsumers contribute to rhododendron breakdown. We attribute this macroconsumer effect to shredding by crayfish. In summer, when visibility was suitable for observations, crayfish were the only macroconsumers detected in control replicates. Although mottled sculpin are common in Lower Ball Creek, they are insectivorous, feeding primarily on aquatic insect larvae. In the study area, mottled sculpin feed predominantly on chironomids, heptageniid mayflies and hydropsychid caddisflies (i.e., taxa

that are not shredders or predators); many of the dominant shredders found in rhododendron leaf packs (e.g., peltoperlid and taeniopterygid stoneflies, Lepidostoma caddisflies) make up < 5% of mottled sculpin diets (Stouder, 1990).

Although sculpins (as well as crayfish) could have indirectly affected rhododendron breakdown via effects on insect shredders or predators (Short & Holomuzki, 1992; Malmqvist, 1993), differences in insect biomass (mg $pack^{-1}$ or mg g^{-1} AFDM) between control and exclusion treatments were not significant. Crayfish, however, have been shown to consume large quantities of detritus and to increase leaf breakdown (e.g., Huryn & Wallace, 1987; Parkyn et al., 1997; Whitledge & Rabeni, 1997; Usio, 2000). Crayfish density is relatively low in Lower Ball Creek (approximately 2 m^{-2}), but even so they are able to influence an ecosystem process such as leaf decay.

Based on the predictions of Huryn & Wallace (1987), we expected that the effect of macroconsumer exclusion on rhododendron breakdown would be greater during periods of low (i.e., summer) versus high (i.e., autumn) general leaf availability. Contrary to expectations, we did not find a significant season x treatment interaction in breakdown rates. Crayfish accounted for about 33% of rhododendron breakdown in summer versus 54% in autumn. Given that we observed fewer crayfish in the control treatment during autumn than summer, this finding was especially surprising. However, we probably underestimated crayfish visits to the autumn control treatment, because large accumulations of leaves obscured our view (this was not a problem during spot checks in summer). Summer and autumn crayfish sampling did not yield significantly different densities, supporting this contention.

Direct comparison of summer and autumn rhododendron decay is difficult, and the lesser effect of macroconsumer exclusion during summer may have been an artifact of our experimental design. Because summer and autumn leaf packs were collected at different times and subjected to different pre-conditioning regimes, initial leaf quality may have varied between our summer and

autumn experiments, even though initial fungal biomass did not differ. Summer treatments experienced more degree days than autumn treatments, and average fungal biomass was higher. This difference could have influenced crayfish shredding, although this seems unlikely given that fungal biomass was extremely low in both summer and autumn. For example, Paul & Meyer (1996) conducted leaf decay experiments in Lower Ball Creek using three leaf species and found that fungal biomass averaged > 40 mg DM g^{-1} AFDM on tulip-poplar, compared to the ≤ 3 mg DM g^{-1} AFDM we obtained on rhododendron (they reported similarly low values for rhododendron). Finally, summer and autumn experiments were run for different lengths of time (44 vs. 56 days), and effects of macroconsumer exclusion became pronounced only after 32-35 days. It is possible that, had we extended our summer experiment for an additional 12 days, we would have observed greater treatment differences.

Total biomass of insect shredders and predators was more than four-fold greater in summer than in autumn leaf packs (Fig. 2.3), probably because summer leaf packs served as 'resource islands' in a relatively leaf-poor environment (Table 2.2). This phenomenon has been noted in several other studies (e.g., Webster & Waide, 1982; Benfield & Webster, 1985; Benfield et al., 1991). When natural leaf litter is unavailable (e.g., because of season, disturbance, etc.), even leaf species that were previously ignored may be colonized (Webster & Waide, 1982). Thus, rhododendron may be an especially important resource during summer, when other leaves are relatively unavailable. Rhododendron has refractory leaves that can persist for long periods in streams (Monk et al., 1985; Huryn & Wallace, 1987; Whiles et al., 1993) and can comprise a large proportion of the leaves available in forested southern Appalachian streams (Stout, Benfield & Webster, 1993). Shredders that are active in spring and summer (e.g., Lepidostoma) may be especially reliant on slow-decaying leaf species such as rhododendron (Cummins et al., 1989).

This 'resource island' effect and subsequent concentration of insects on summer leaf packs may have led to the significant relationship observed between insect shredder biomass and

AFDM remaining. There was a significant inverse relationship between shredders and leaf pack mass in the summer macroconsumer exclusion treatment (Fig. 2.4). Insects were the only macroorganisms eating leaves in this treatment and, as shredder biomass increased, AFDM remaining decreased. In the control treatment, however, we did not see this relationship, and we speculate that the effect of insect shredders was swamped by crayfish impacts.

During autumn, natural leaf litter availability was much higher (Table 2.2), and rhododendron leaf packs were no longer resource islands. Although biomass of insect shredders was much lower on autumn leaf packs, the decay rate of rhododendron was faster. Physical fragmentation may have played a larger role in autumn, given that peak daily discharges were much greater. Paul & Meyer (1996) found that rhododendron decay was greatly enhanced following a flood. It seems likely that abiotic fragmentation (both in control and exclusion treatments) and crayfish effects (in the control treatment) were responsible for the majority of rhododendron breakdown in the autumn experiment. Thus, significant relationships between insect shredder biomass and leaf pack mass were not found in control or exclusion treatments in the autumn.

How do these results compare with other rhododendron breakdown experiments?

Many studies have examined rhododendron breakdown in southern Appalachian streams (Table 2.6). Our breakdown rates were similar to those reported in Hutchens (2000) and Paul & Meyer (1996), whether calculated by day or by degree day. For example, when the data in Hutchens (2000) are recalculated to obtain breakdown rates by degree day, a value of 0.003 is obtained (J.J. Hutchens, pers. comm.), while the data in Paul & Meyer (1996) yield a decay rate of 0.002. In comparison, our rhododendron decay rates calculated by degree day ranged from 0.001 to 0.003.

Most other studies, however, found much slower rhododendron breakdown rates (Table 2.6). With one exception (Paul & Meyer, 1996), previous studies were conducted in much smaller streams (first- and second- rather than fourth-order). Physical fragmentation by high flow may

have been reduced in these headwater streams. In addition, Pteronarcys stoneflies are frequently absent from these headwater reaches (e.g., Grubaugh, Wallace & Houston, 1996). These large-bodied shredders are present in Lower Ball Creek, and their presence may have contributed to the faster breakdown rates we observed. Most previous studies also used leaf packs made from 5 mm or smaller mesh. This may have limited access by larger crayfish, which are thought to be more detritivorous than smaller individuals (Momot, 1995; Whitledge & Rabeni, 1997). Webster & Waide (1982) compared rhododendron breakdown at Coweeta between leaf bags (3 mm mesh) and packs (loosely tied with fishing line), and found that decay rates more than doubled when packs were used. Finally, our breakdown rates were accelerated by using pre-conditioned rhododendron leaves. We attempted to account for this by comparing our decay rates with those obtained by Hutchens (2000) and Paul & Meyer (1996) for similar degree day periods (i.e., after their leaves had experienced 1300 degree days). In both studies, however, < 35% of rhododendron AFDM remained by the time 1300 degree days accumulated.

Comparing our results with other experimental manipulations is interesting. For example, Wallace et al. (1982) and Cuffney, Wallace & Lugthart (1990) found that rhododendron breakdown rates decreased by 62-78% in a headwater stream when shredders were greatly reduced by insecticide (Table 2.6). Our findings were similar, although the magnitude of change was not so great: when crayfish were excluded (here, by electricity), rhododendron breakdown was slowed by 33% in summer and by 54% in autumn. Whereas Wallace et al. (1982) and Cuffney et al. (1990) eliminated both insects and crayfish, our manipulation excluded only crayfish. Thus, our results suggest that a significant portion of decay rate decreases may be attributable to reductions in crayfish density.

In conclusion, crayfish play a significant role in the breakdown of rhododendron leaves during both summer and autumn, even though rhododendron is considered a low quality food. The influence of other factors (e.g., shredding insects, abiotic fragmentation) varies between

seasons. Crayfish exert a direct impact, increasing rhododendron decay via shredding rather than by altering biomass of insect shredders and/or predators. Even at the relatively low density found in Lower Ball Creek (2 m^{-2}), crayfish are able to affect an ecosystem process such as leaf decay. Given the threatened status of many crayfish species in the United States, this finding is especially relevant. Even small alterations in crayfish assemblages, whether via loss of native species and/or introduction of exotic species, may have significant repercussions for ecosystem function.

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Table 2.1. Initial physical parameters for control and macroconsumer exclusion treatments, summer and autumn experiments. Values are means of 5 (summer) or 4 (autumn) replicates, ± 1 SE.

	Summer		**Autumn**	
Physical parameter	***Control***	***Exclusion***	***Control***	***Exclusion***
Water velocity (m s^{-1})	0.20 ± 0.01	0.18 ± 0.02	0.07 ± 0.02	0.11 ± 0.02
Water depth (cm)	16.8 ± 0.1	15.5 ± 0.1	12.1 ± 3.5	11.0 ± 1.1
% Canopy cover	88.3 ± 0.9	87.6 ± 1.1	97.7 ± 0.3	98.6 ± 0.3
Shear stress (dyn cm^{-2})	160 ± 26	160 ± 26	145 ± 28	145 ± 28

Table 2.2. Dry weight of rhododendron and non-rhododendron leaves (g m^{-2}) collected from in-stream transects at the end of summer and autumn experiments. Values represent means of 10 transects, ± 1 SE.

Leaf type	Summer	Autumn
Rhododendron	3.17 ± 0.49	2.43 ± 0.59
Non-rhododendron	2.27 ± 0.69	9.78 ± 1.97

Table 2.3. Results of two-factor ANOVAs for leaf breakdown rates (k) calculated by day. Breakdown rates were also calculated through day 32 (summer) and day 35 (autumn) for comparison; these data were transformed (1/X) prior to analysis to correct for unequal variances. Each factor had two levels (control and macroconsumer exclusion for treatment, summer and autumn for season).

	Source	*df*	*Sum of squares*	*F*	*P*
***k* (day^{-1})**	**Treatment**	1	7.38×10^{-4}	8.47	0.011
	Season	1	6.48×10^{-4}	7.44	0.016
	Treatment x season	1	2.19×10^{-4}	2.51	0.136
	Error	14	1.22×10^{-3}		
***k* (day^{-1})**	**Treatment**	1	13652	2.73	0.121
through d32	**Season**	1	4026	0.80	0.385
or d35	**Treatment x season**	1	308	0.06	0.808
	Error	14	70071		

Table 2.4. Results of two-factor MANOVA for insect predator and shredder biomass (mg pack^{-1}). Values used in analysis were average biomass over 3 days (days 20, 32 and 44 in summer; days 20, 35 and 56 in autumn). Each factor had two levels (control and macroconsumer exclusion for treatment, summer and autumn for season).

Source	***df (num, den)***	***Pillai's trace***	***F***	***P***
Treatment	2, 13	0.156	1.20	0.332
Season	2, 13	0.563	8.38	0.005
Treatment x season	2, 13	0.039	0.26	0.773

Table 2.5. Fungal biomass (mg DM g^{-1} AFDM) in control and macroconsumer exclusion treatments during summer and autumn experiments. Values represent average biomass over 3 days (days 10, 20 and 32 in summer, days 8, 20 and 35 in autumn), ± 1 SE.

	Summer	**Autumn**
Control	3.85 ± 0.16	0.90 ± 0.17
Exclusion	3.06 ± 0.32	1.78 ± 0.23

Table 2.6. Summary of other rhododendron breakdown studies conducted at or near Coweeta. All studies were conducted in first- or second-order streams unless otherwise noted. Treatment refers to any manipulation or disturbance of the study stream.

Mesh size (mm)	Initial dry wt (g)	Duration	Treatment	Breakdown rate (day^{-1})	Reference
20	5	July - Aug	none	0.018	this study
20	5	Oct - Nov	none	0.037	this study
20	5	July - Aug	electric exclusion	0.013	this study
20	5	Oct - Nov	electric exclusion	0.017	this study
5	8	Dec - Aug	none	0.019	Hutchens (2000)
5	8	Dec - Aug	none	0.010	Hutchens (2000)
12	15	Oct - June	none	0.007	Paul & Meyer (1996)
12	15	Oct - June	none	0.017[a]	Paul & Meyer (1996)
5	15	Dec - Dec	none	0.005[b]	Chung, Wallace & Grubaugh (1993)
5	15	Dec - Dec	insecticide	0.002	Chung, Wallace & Grubaugh (1993)
5	15	Dec - Dec	insecticide recovery	0.006	Chung, Wallace & Grubaugh (1993)
5	10	Nov - June	none	0.002	Benfield et al. (1991)
5	10	Nov - June	forest disturbance	0.006[c]	Benfield et al. (1991)
5	15	Dec - Dec	none	0.004[d]	Cuffney, Wallace & Luthgart (1990)
5	15	Dec - Dec	insecticide	0.002	Cuffney, Wallace & Luthgart (1990)
5	15	Dec - Dec	Insecticide recovery	0.003[d]	Cuffney, Wallace & Luthgart (1990)
5	15	Feb - Feb	none	0.006	Wallace, Vogel & Cuffney (1986)
5	15	Feb - Feb	insecticide recovery	0.009	Wallace, Vogel & Cuffney (1986)
3	2-4	Oct - Oct	none	0.004[e]	Webster & Waide (1982)
3	2-4	Oct - May	logging	0.001	Webster & Waide (1982)
3	2-4	Oct - May	logging recovery	0.011[e]	Webster & Waide (1982)
5	15	Feb - Nov	none	0.005	Wallace, Webster & Cuffney (1982)
5	15	Feb - Nov	insecticide	0.001	Wallace, Webster & Cuffney (1982)

[a] study conducted in a fourth-order stream; [b] 4-year (1985, 1988-1990) average in reference strea; [c] average from three streams draining disturbed basins; [d] 3-year (1984-1987) average in reference stream; [e] average from three sites within 800 m reach

Figure 2.1. Peak daily discharge (L s^{-1}) of Lower Ball Creek during summer and autumn experiments.

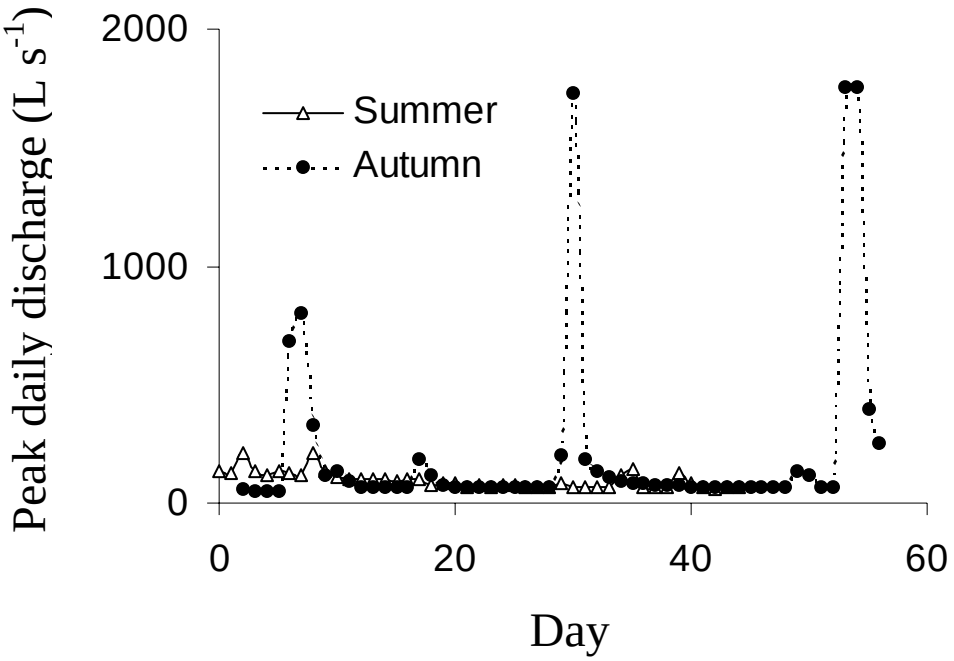

Peak daily discharge (L s-1)
2000
1000
0
Summer
Autumn
0
20
40
60
Day

Figure 2.2. Percent AFDM remaining versus day in control and macroconsumer exclusion treatments for (a) summer and (b) autumn experiments. Points represent means of 5 (summer) or 4 (autumn) replicates, ± 1 SE. Breakdown rates (k, day^{-1}) are given for control and exclusion treatments; these values represent means of individual replicate breakdown rates, ± 1 SE. Arrows indicate occurrence of high discharge events during the autumn experiment (see Fig. 2.1).

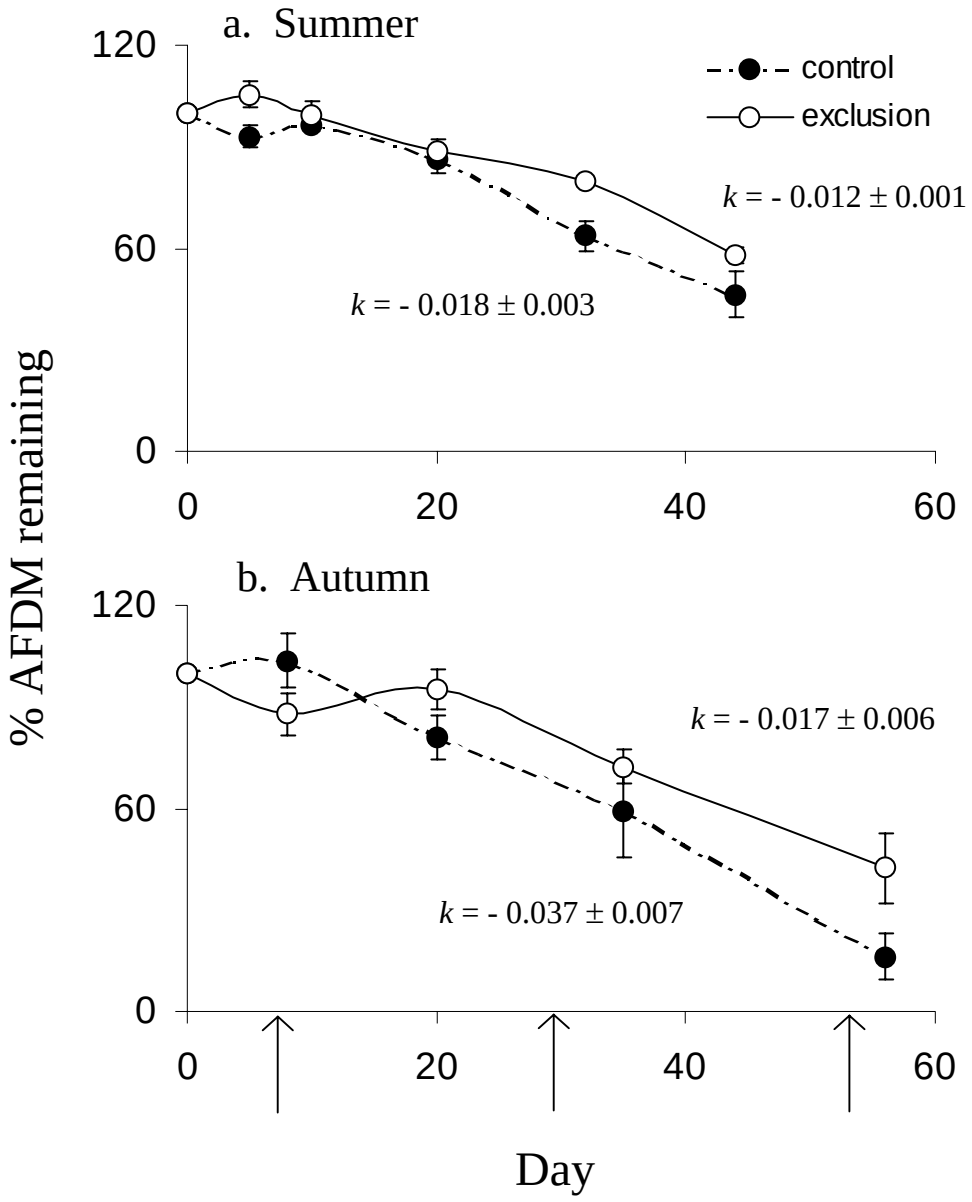

a. Summer
control
exclusion
k = - 0.012 ± 0.001
k = - 0.018 ± 0.003
b. Autumn
k = - 0.017 ± 0.006
k = - 0.037 ± 0.007
% AFDM remaining
Day
120
60
0
0
20
40
60

Figure 2.3. Biomass (mg pack^{-1}) of insect shredders and predators in control (white bars) and exclusion (shaded bars) treatments for (a) summer and (b) autumn experiments. Values represent average biomass over 3 days (days 20, 32 and 44 in summer; days 20, 35 and 56 in autumn), + 1 SE. Note the difference in scale between summer and autumn graphs. Similar patterns were obtained for biomass in terms of g^{-1} AFDM remaining.

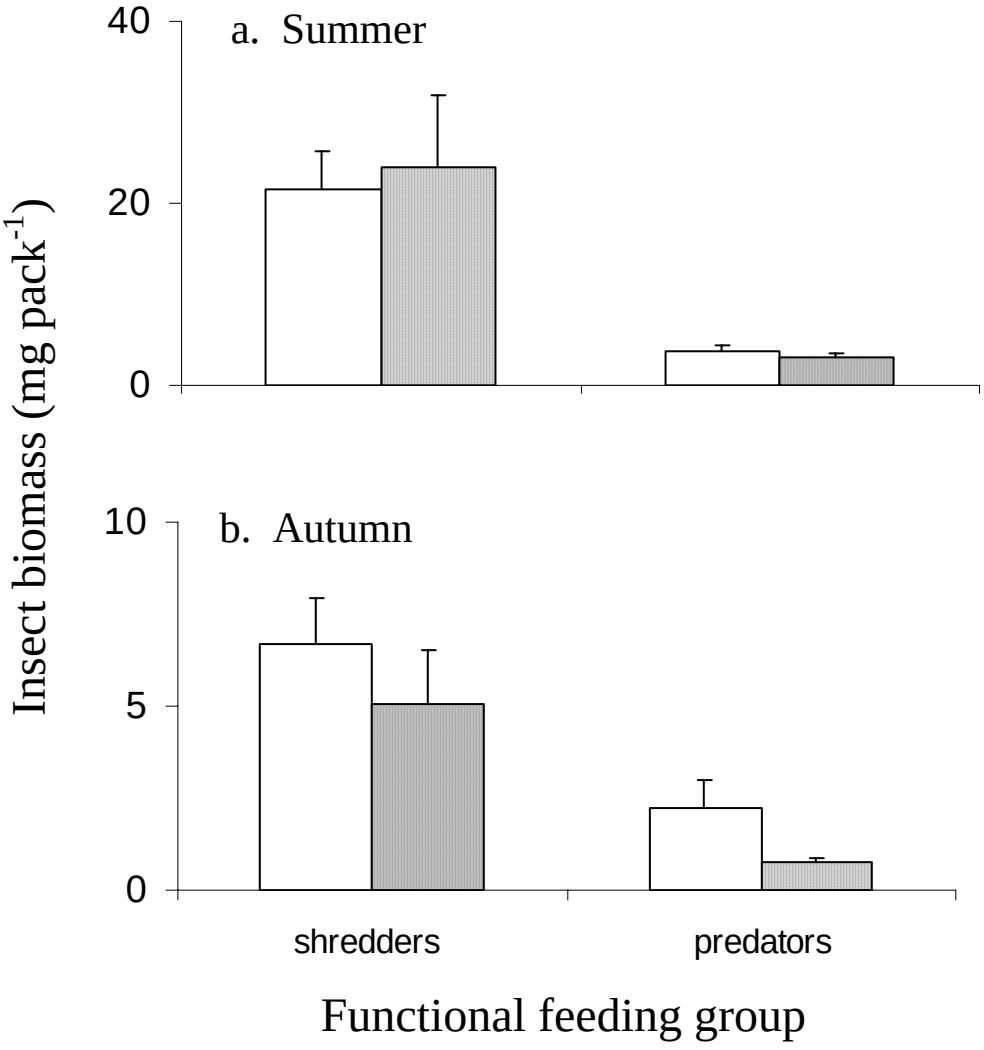
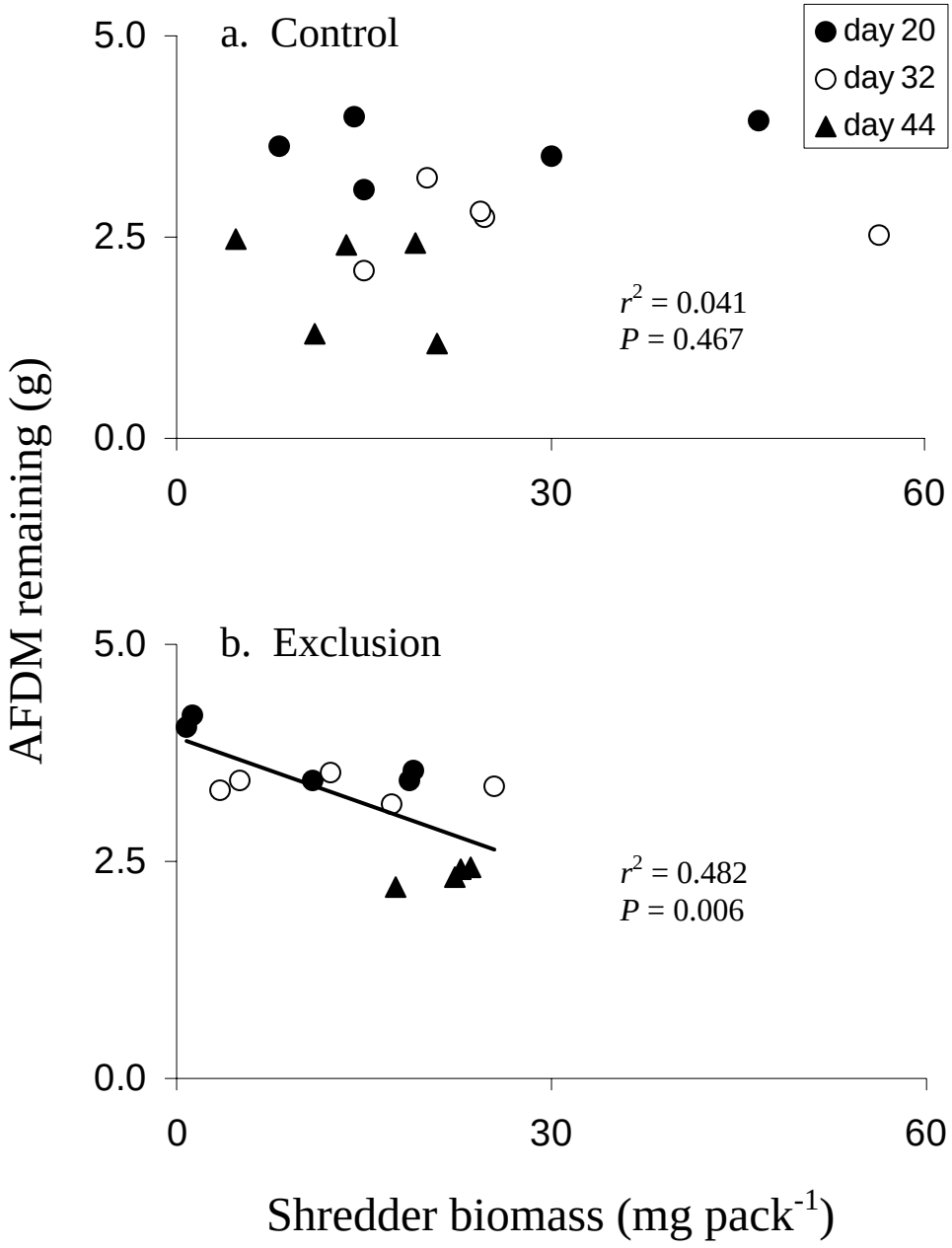

a. Summer
b. Autumn
40
20
0
10
5
0
Insect biomass (mg pack-1)
shredders
predators
Functional feeding group

Figure 2.4. AFDM remaining (g) versus shredder biomass (mg pack^{-1}) in (a) control and (b) macroconsumer exclusion treatments during the summer experiment. Each point represents one replicate on a given day; one day 44 exclusion replicate was omitted from the regression because it was considered an outlier (it contained a single 156 mg Pteronarcys).


a. Control
day 20
day 32
day 44
5.0
2.5
0.0
0
30
60
r^2 = 0.041
P = 0.467
b. Exclusion
5.0
2.5
0.0
0
30
60
r^2 = 0.482
P = 0.006
AFDM remaining (g)
Shredder biomass (mg pack^{-1})

CHAPTER 3

DIRECT AND INDIRECT EFFECTS OF INCREASED BEDLOAD ON ALGAL AND DETRITAL-BASED STREAM FOOD WEBS [1]

[1]Schofield, K.A., C.M. Pringle, and J.L. Meyer. Submitted to Ecological Applications 4/6/01.

ABSTRACT

Anthropogenic sedimentation poses a significant threat to stream ecosystems throughout the world. Increases in bedload (sediment transported and deposited on the stream bottom) can be especially detrimental for benthic communities. To examine how increased bedload directly and indirectly affects stream communities, we simultaneously manipulated sediment and top-down effects of macroconsumers (fishes and crayfish) in situ in two factorial experiments, one using tiles and one using leaf packs as sampling substrates. Bedload was increased (approximately 60% over normal transport rates) by daily addition of small amounts of sand to localized areas (0.25 m^2) of an otherwise unaltered stream. This increase in bedload had direct effects on basal resources in both the tile and leaf pack experiments. In the tile experiment algal composition was altered by sediment addition, while in the leaf pack experiment fungal biomass declined with sediment. The only direct effect of sediment on insect assemblages occurred in the leaf pack experiment, where sediment reduced predatory stonefly (Plecoptera) and Atherix (Diptera) biomass. However, sediment addition significantly altered top-down effects of macroconsumers in both experiments. In the tile experiment, macroconsumer reductions of total insect biomass, hydropsychid (Trichoptera) biomass, and predatory stonefly biomass were eliminated when sediment was added. The only effect of macroconsumers that was not eliminated in sediment treatments was their reduction of chironomid (Diptera) biomass. Increased bedload did not have as great an impact on top-down effects in the leaf pack experiment, although macroconsumer reductions of tanypodid (Diptera) abundance and biomass were eliminated in sediment treatments. These experiments show that small, environmentally realistic increases in bedload can directly and indirectly affect biota in both algal and detrital-based food webs. While indirect effects of sedimentation have been examined less frequently than direct biotic responses, this study demonstrates that alteration of top-down impacts can be an important effect of increased sedimentation. In these experiments, small amounts of sediment were added to localized areas of an otherwise unaltered stream. Even these relatively small-scale increases had significant effects

on stream communities, suggesting that the influence of larger scale sedimentation will be even greater.

KEY WORDS: bedload, Coweeta Hydrologic Laboratory, electric exclusion, indirect effects, macroconsumers, predator-prey, sedimentation, species interactions, stream, top-down

INTRODUCTION

Sediment is an integral component of stream ecosystems, influencing the physical, chemical, and biological conditions in lotic environments. However, human activities such as agriculture and urbanization have altered stream sediment loading and transport, drastically increasing the amount of fine inorganic material delivered to waterways (Waters 1995). These anthropogenic sediment inputs are a significant source of stream impairment around the world (e.g., Ryan 1991, Waters 1995, Wood and Armitage 1997). In the United States alone, siltation impacts 13% of river miles surveyed by the U.S. Environmental Protection Agency; 38% of rivers and streams classified as impaired are affected by anthropogenic sedimentation [USEPA, *public communication* (www.epa.gov/305b/98report, accessed 3/01)].

Consequently, sedimentation poses a major threat to freshwater fauna (Richter et al. 1997). Elevated sediment levels can negatively affect fishes (e.g., Berkman and Rabeni 1987, Rowe et al. 2000), aquatic insects (e.g., Lemly 1982, Gurtz and Wallace 1984, Angradi 1999), other invertebrates (e.g., Aldridge et al. 1987, Brim Box and Mossa 1999), and periphyton (e.g., Horner et al. 1990, Biggs et al. 1999). Biotic interactions can also be affected. Several studies have shown that effects of both invertebrate (e.g., Peckarsky 1985, Walde 1986) and vertebrate (e.g., Barrett et al. 1992, Johnson and Hines 1999) consumers on lower trophic levels can be altered by sedimentation. For example, predatory stoneflies significantly reduced prey density under ambient sediment conditions, but this predator effect was eliminated by silt deposition (Peckarsky 1985).

Stream sediments are generally classified as either suspended load (smaller particles suspended in the water column) or bedload (larger particles transported and deposited on the stream bottom) (Waters 1995). Bedload increases generally have the greatest negative impacts on stream benthic communities (Lemly 1982, Culp et al. 1986, Waters 1995). However, much of the research on sedimentation and species interactions has focused on suspended sediment and its repercussions for visually feeding fish predators (e.g., Gardner 1981, Barrett et al. 1992, Miner and Stein 1996). Fewer studies have considered the influence of elevated bedload on biotic interactions.

Because anthropogenic sedimentation is often associated with other in-stream alterations (e.g., hydrologic changes, nutrient enrichment, decreased canopy cover, sediment-associated contaminants), separating the influence of sediment from other factors is frequently difficult. Sediment addition experiments provide one way of isolating the effects of excess sedimentation. Several researchers have experimentally elevated sediment levels and examined biotic responses (Table 3.1), but these studies have limitations. Most have considered increases in suspended sediment rather than bedload (e.g., Horner et al. 1990, Doeg and Milledge 1991, Johnson and Hines 1999; Table 3.1). In addition, many were conducted ex situ and/or involved one-time or short-term additions of sediment (e.g., Culp et al. 1986, Strand and Merritt 1997; Table 1). One notable exception is a study by Alexander and Hansen (1986), who elevated bedload over ≈ 0.6 km in a Michigan stream by adding sand daily over a five year period; this bedload increase led to significant decreases in brook trout and benthic invertebrate abundances (Alexander and Hansen 1986).

The relative strength of biotic interactions, including top-down effects, depends upon many biotic and abiotic factors (Power 1992, Polis and Strong 1996). One important consideration is the dominant basal resource (i.e., leaf detritus versus periphyton). For example, macroconsumers (shrimps and fishes) in a Costa Rican stream had a greater effect on insect densities on tiles (Pringle and Hamazaki 1998) versus leaf packs (Rosemond et al. 1998). This difference was

attributed to sampling substrate, suggesting that the relative strength of top-down effects may depend on substrate type and its influence on prey vulnerability (Rosemond et al. 1998). In addition to providing invertebrates refugia from predation, detrital accumulations similarly may shelter invertebrates from sediment transport and deposition, thereby reducing negative effects of elevated bedload. Thus, communities dependent upon different basal resources also may respond differently to anthropogenic sedimentation.

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 wanted to examine three questions: (1) What are the direct effects of elevated bedload on stream structure (e.g., aquatic insect assemblages, periphyton, fungal biomass) and the ecosystem process of 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 direct and indirect effects of elevated bedload? To address these questions, we simultaneously manipulated sediment and top-down effects of macroconsumers in situ in two separate factorial experiments, one using tiles and one using leaf packs as sampling substrates. We hypothesized that sediment addition would directly and indirectly affect benthic communities in both tile and leaf pack experiments, but that in general tile substrates would prove more vulnerable to sedimentation effects.

METHODS

Study site

Experiments were conducted during summer and autumn in Lower Ball Creek, a fourth-order stream at Coweeta Hydrologic Laboratory in western North Carolina, USA (35°03′N, 83°30′W). Coweeta is a 2185 ha facility managed by the United States Forest Service (USFS), located in the Blue Ridge physiographic province of the southern Appalachians. Mean monthly air temperature

ranges from 3 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 [University of Georgia (UGA), USA].

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 latifola) and dogwood (Cornus florida). Elevation at the study site is approximately 700 m, with a stream gradient of about 4 cm m^{-1}. Boulder, cobble, and gravel comprise the stream substratum. 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. in press) and 0.7 m^{-2} (G. Grossman, UGA, *unpublished 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; G. Grossman, UGA, *unpublished data*).

Tile experiment

In Summer 1997, we conducted a 40 d macroconsumer exclusion experiment using unglazed ceramic tiles as sampling substrates. Tiles (7.5 cm x 15 cm) were attached with cable ties and binder clips to polyvinylchloride frames (0.25 m^2) lined with copper wire; each frame contained 8 tiles. Twenty frames (10 pairs) were placed in run habitats of Lower Ball Creek, along an approximately 0.5 km stream reach (Figure 3.1). Placement of pairs was determined by preliminary shear stress measurements using calibrated hemispheres (Statzner and Müller 1989); only sites that provided 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 6 V solar-powered fence charger (Parmak Model DF-SP-SS, Parker McCrory Manufacturing Company) that delivered repeated pulses of electricity to the 0.25 m^2 frame area. These electric pulses prevented the entry of crayfish and fish, but did not adversely affect smaller organisms such as aquatic insect larvae. Many other studies have used this electric exclusion technique (e.g., Pringle and Blake 1994, Pringle and Hamazaki 1998), which avoids artifacts associated with traditional cage enclosure experiments (e.g., reduced water flow and increased sedimentation). The unelectrified frame in each pair was accessible to macroconsumers and served as a control (Figure 3.1). Frames were placed approximately 0.5 m apart to minimize the impact of exclusion treatments on controls. 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 were also cleared of any accumulated debris every 5 d to minimize flow alterations and prevent loss of frames during spates.

Ten frames (5 pairs) were randomly chosen as sediment treatments (Figure 3.1). Each of these frames received 250 g of sand daily; sand was wetted, then added by hand as uniformly as possible to the entire frame area. Sand was used because measurement of bedload transport rates in Lower Ball Creek and in a nearby pasture stream (Jones Creek) showed that bedload was dominated by 0.25 - 2.00 mm particles (A. Sutherland, UGA, *unpublished data*). Average transport rate in Lower Ball was 0.80 ± 0.27 kg m^{-1} d^{-1} (A. Sutherland, UGA, *unpublished data*); by adding 250 g to each frame, we increased bedload by approximately 60%. This increase was relatively small yet environmentally realistic [i.e., 35% lower than bedload transport rates measured in Jones Creek (1.98 ± 0.44 kg m^{-1} d^{-1}; A. Sutherland, UGA, *unpublished data*)]. Sand

was obtained from a point bar downstream of our study reach and sieved (2 mm mesh) prior to application to remove coarse particulate organic matter.

The tile experiment began 29 July 1997 and ended 8 September 1997. 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 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 more than 11.5 h over 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, algae, 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 pre-ashed 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* analysis. Sediment filters were dried for 24 h at 70°C to obtain dry mass, then ashed at 500°C for 1 h and reweighed to obtain AFDM. Chlorophyll *a* filters were processed according to standard methods for fluorometric analyses (APHA 1985), and concentrations were measured with a Turner Designs 10-AU fluorometer.

Invertebrate samples were identified to the lowest practical level (usually family or genus) using a dissecting microscope (10X magnification), and sorted into functional feeding groups (Merritt and Cummins 1996). Individuals were measured to the nearest 0.5 mm using 1 mm grid paper. Biomass was calculated with family-specific, length-mass regressions from Benke et al. (1999). Organisms < 1.5 mm were identified to order and were not included in functional feeding

group abundance and biomass values. To determine periphyton species composition, the first 500 cells in a given volume were identified to genus. Taxa were classified according to growth form either as motile, adnate, or upright; biovolume for each taxon was estimated using values available in the literature (J. Greenwood, UGA, *personal communication*).

Daily water samples were collected throughout the experiment to determine total suspended solids. Conductivity was measured three times over the 40 d study, and water samples were collected every 5 d for nutrient analysis [NO_3-N, NH_4-N, and soluble reactive phosphorus (SRP)].

Leaf pack experiment

In Autumn 1999, we conducted a 56 d macroconsumer exclusion experiment using sugar maple (Acer saccharum) leaf packs as our sampling substrate. Design of this experiment was similar to the tile experiment (i.e., in terms of method of exclusion, addition of sediment, etc.; Figure 3.1); only differences between the experiments will be discussed here.

Leaves were shaken from trees one day before the experiment started and divided into approximately 5 g (wet weight) leaf packs held together by two plastic 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 twenty frames using nylon monofilament. Each pack was weighted with a lead weight (85 g) 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, ten frames (5 pairs) were designated as the sediment treatment, and 250 g of sieved (2 mm mesh) sand were added daily to each frame.

The leaf pack experiment began 9 October 1999 and ended 4 December 1999. One leaf pack was removed from each frame on days 5, 10, 20, 32, 44 and 56. In addition, ten packs were brought back to the lab on day 0 to determine initial leaf pack dry weights. Prior to removing leaf packs, all replicates were examined with a clear plastic viewing box to determine whether any

macroconsumers were present. In the tile experiment we observed replicates for 5 min, but limited visibility (i.e., because of fallen leaves) in this experiment made prolonged observations inefficient. Instead, we recorded 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). Fungal biomass was estimated from ergosterol concentration using a conversion factor of 5 μg ergosterol mg^{-1} mycelial dry mass (Gessner and Chauvet 1993, Paul and Meyer 1996). 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, then burned at 500°C for 6 h and reweighed. Total AFDM remaining was calculated by summing AFDM of each leaf pack and 2 x AFDM of the 50 leaf discs.

Invertebrates were later sorted from the preserved sediment using a dissecting microscope (10X magnification) and identified to the lowest practical level, usually family or genus. We chose to focus on insect shredders and predators because they were the functional feeding groups most likely to affect leaf decomposition (shredders directly through leaf consumption, predators indirectly through consumption of shredders); they were also the groups contributing most to total insect biomass.

Water samples were collected on sampling days for nutrient and conductivity analysis, and four samples were taken over the 56 d experiment to determine concentration of total suspended solids.

Statistical analysis

Each experiment (i.e., tile and leaf pack) was analyzed separately. Because chlorophyll *a* and AFDM (in the tile experiment) and fungal biomass (in the leaf pack experiment) accumulated steadily throughout each experiment, we consider only data from the last day of each experiment (day 40 for the tile experiment, day 56 for the leaf pack experiment) in this paper.

Data were analyzed in two ways: (1) using two-factor (sediment and exclusion) MANOVAs and ANOVAs, and (2) regressing response variables against inorganic sediment deposited on sampling substrates. These analyses were done to examine the effect of sediment addition and subsequent transport through frames and to take into account natural variability in sediment accumulation between treatment replicates. If MANOVAs showed a significant effect [$P \leq 0.10$, given the low power of MANOVA with several response variables (Scheiner 1993)], univariate ANOVAs were run for each response variable. When univariate ANOVAs yielded significant sediment x exclusion interactions, paired t-tests (ambient control versus ambient exclusion, sediment control versus sediment exclusion) were run to determine which relationships were driving the interaction.

Dixon's test (Sokal and Rohlf 1995) was used to test for outliers. In the tile experiment, one sediment replicate pair differed significantly from the remaining pairs in terms of initial water depth, velocity, and shear stress. This pair was excluded from all analyses, leaving four replicate pairs for the tile sediment treatment versus five replicate pairs for all other treatments (i.e., tile ambient, leaf pack ambient, and leaf pack sediment). In addition, one sediment exclusion replicate was an outlier ($P < 0.01$) for inorganic sediment, and was excluded from all correlations (exclusion from MANOVAs and ANOVAs did not alter results). One ambient control replicate

was an outlier ($P < 0.05$) in terms of insect biomass [due to a large (2.8 mg) heptageniid mayfly and two large (72.1 and 9.2 mg) Pteronarcys stoneflies]; therefore, biomass values for this replicate did not include these individuals. In the leaf pack experiment, one ambient control replicate was an outlier ($P < 0.01$) for inorganic sediment, and was excluded from all correlations. One sediment control replicate was an outlier ($P < 0.05$) for insect biomass [it contained a large (187.6 mg) Pteronarcys stonefly], so this individual was omitted from all biomass values. Finally, one ambient exclusion replicate was missing fungal biomass data from day 56.

Similarity of periphyton and insect assemblages between ambient and sediment control and exclusion pairs was calculated using a simplified Morisita index with natural log-transformed abundance and biomass or biovolume data (Wolda 1981). Ambient and sediment similarity indices were then compared using t-tests to determine whether sediment addition increased similarity between control and exclusion treatments in terms of periphyton and insect assemblages.

Prior to all statistical analyses, Levene's test (Underwood 1997) was used to determine whether variances were equal; where necessary, data were natural log or arcsine transformed. Unless otherwise noted, $\alpha = 0.05$ for all analyses, and all were conducted in SAS® System for Windows™, Release 6.12.

RESULTS

Physical and chemical stream characteristics during the tile and leaf pack experiments are presented in Table 3.2, and initial physical parameters for each treatment are presented in Table 3.3. Physical parameters did not differ significantly among sediment or macroconsumer treatments in the tile (MANOVA: Pillai's trace ≤ 0.26, $F_{4,11} \leq 0.98$, $P \geq 0.458$) or the leaf pack experiment (MANOVA: Pillai's trace ≤ 0.43, $F_{4,13} \leq 2.42$, $P \geq 0.101$). Total suspended sediment concentrations remained low throughout each experiment (Table 3.2), indicating that sediment

addition did not significantly elevate suspended load. Although it is possible that some added sand moved as suspended load rather than bedload, previous measurements indicated that bedload was composed largely of sand particles (A. Sutherland, UGA, *unpublished data*).

In the tile experiment, less than 1% of the total sediment added to each sediment replicate (10 kg) remained on tiles at day 40 (Table 3.4). Inorganic sediment was significantly greater on sediment versus ambient tiles (ANOVA: $F_{1,14} = 4.78$, $P = 0.046$), but did not differ between control and exclusion treatments (ANOVA: $F_{1,14} = 1.69$, $P = 0.214$). Assuming an average leaf pack size of 0.014 m^2, approximately 2% of the total sediment added to each replicate in the leaf pack experiment (13 kg) remained on leaf packs at day 56 (Table 3.4). Inorganic sediment tended to be greater on sediment versus ambient leaf packs (Table 3.4), but this difference was not statistically significant (ANOVA: $F_{1,16} = 1.75$, $P = 0.205$); inorganic sediment was similar between control and exclusion treatments (ANOVA: $F_{1,16} = 0.29$, $P = 0.600$).

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. Crayfish and sculpins occasionally entered exclusion frames when fence chargers were turned off briefly for sampling, but they exited immediately when chargers were reactivated. A total of five crayfish were observed in the tile ambient control treatment during the experiment (observation time = 175 min), and ten crayfish and one sculpin were observed in the sediment control treatment (observation time = 140 min). During the leaf pack experiment, a total of four crayfish and two sculpins were observed in the ambient control treatment, and two crayfish and three sculpins were observed in the sediment control treatment (n = 80 spot checks for each treatment).

Tile experiment

Chlorophyll *a*, AFDM, and periphyton biovolume

Chlorophyll *a* and AFDM data for each treatment are presented in Table 3.5. Comparison of treatments by MANOVA (with chlorophyll, AFDM, chlorophyll:AFDM, and % AFDM as response variables) showed a significant effect of sediment (MANOVA: Pillai's trace = 0.685, $F_{4,11} = 5.99$, $P = 0.008$), as well as a significant sediment x exclusion interaction (MANOVA: Pillai's trace = 0.663, $F_{4,11} = 5.41$, $P = 0.012$). Subsequent ANOVAs indicated that % AFDM was the only response variable that differed significantly among treatments, demonstrating a significant sediment x exclusion interaction (ANOVA: $F_{1,14} = 9.46$, $P = 0.008$). Percent AFDM was greater in the exclusion treatment under ambient conditions (paired t-test: $t_4 = 4.91$, $P = 0.004$), but this difference disappeared when sediment was added (paired t-test: $t_3 = 1.10$, $P = 0.176$). Sediment organic content differed between control and exclusion treatments only under ambient conditions (Table 3.5).

Neither sediment nor exclusion had a significant effect on total periphyton abundance (ANOVA: $F_{1,14} \leq 1.64$, $P \geq 0.221$) or biovolume (ANOVA: $F_{1,14} \leq 1.50$, $P \geq 0.241$), although under ambient conditions both mean abundance and biovolume were at least two-fold greater in exclusion versus control treatments (Table 3.5). Periphyton in all treatments was dominated by the diatom genera Synedra, Achnanthes, and Eunotia, and similarity between control and exclusion pairs did not differ in ambient or sediment treatments (similarity ≥ 0.88 for abundance and biovolume). However, sediment did have a significant effect on the proportion of periphyton biovolume contributed by different growth forms (MANOVA: Pillai's trace = 0.69, $F_{3,12} = 9.07$, $P = 0.002$). ANOVAs for each growth form indicated that in sediment treatments the proportion of motile taxa decreased (ANOVA: $F_{1,14} = 28.41$, $P < 0.0001$) and the proportion of upright taxa increased (ANOVA: $F_{1,14} = 8.32$, $P = 0.012$; Figure 3.2 and Table 3.5). While total abundance

and biovolume were not significantly affected by sediment addition, periphyton composition (i.e., biovolume proportions) was altered.

Insect abundance and biomass

Total insect abundance and biomass on day 40 are presented in Table 6. Total abundance did not differ significantly between treatments (ANOVA: $F_{1,14} \leq 1.07$, $P \geq 0.318$), but total biomass demonstrated a statistically significant exclusion effect (ANOVA: $F_{1,14} = 5.17$, $P = 0.039$) as well as a borderline significant sediment x exclusion interaction (ANOVA: $F_{1,14} = 4.43$, $P = 0.054$). Total biomass was four-fold greater in the exclusion versus control treatment under ambient conditions ($t_4 = 2.94$, $P = 0.021$), but this difference disappeared when sediment was added ($t_3 = 0.40$, $P = 0.358$; Table 3.6).

Given their relatively large size, it is possible that certain insects (e.g., Pteronarcys stoneflies and some Heptageniidae mayflies) could have been adversely affected by the exclusion treatment. As mentioned earlier, three large individuals (two Pternonarcys and one Heptageniidae) were excluded from biomass analyses, but all of these individuals were found in a single control replicate. No other Pteronarcys individuals were collected from either control or exclusion tiles; although heptageniid biomass tended to be greater in control versus exclusion treatments, variability within treatments was high and differences were not statistically significant.

Control and exclusion pairs in the sediment treatment were more similar in terms of both total insect abundance and biomass than ambient pairs (Table 3.6), but these differences were not statistically significant (t-tests: $t_7 = 1.64$, $P = 0.073$ for abundance; $t_7 = 1.64$, $P = 0.072$ for biomass). Plots of abundance and biomass versus sediment showed that neither variable was significantly correlated with inorganic sediment. Thus, addition of sediment eliminated the effect of macroconsumer exclusion on total insect biomass (and tended to make control and exclusion pairs more similar), but insect biomass was not correlated with the amount of sediment deposited on tiles.

Abundance of functional feeding groups did not show significant sediment or exclusion effects (MANOVA: Pillai's trace ≤ 0.31, $F_{5,10} \leq 0.90$, $P \geq 0.516$), but biomass showed a significant sediment x exclusion interaction (MANOVA: Pillai's trace = 0.57, $F_{5,10} = 2.67$, $P = 0.087$). This interaction effect was due largely to the response of gatherers and predators. Gatherer biomass demonstrated a significant exclusion effect (ANOVA: $F_{1,14} = 5.59$, $P = 0.033$), with biomass in exclusion treatments at least two-fold greater than in control treatments (Figure 3.3). For predator biomass, there was a significant sediment x exclusion interaction (ANOVA: $F_{1,14} = 10.85$, $P = 0.005$): under ambient conditions predator biomass was 20 times greater in the exclusion treatment (paired t-test: $t_4 = 3.00$, $P = 0.020$), but this exclusion effect disappeared when sediment was added (paired t-test: $t_3 = 1.82$, $P = 0.083$; Figure 3.3). Comparison of individual gatherer and predator taxa indicated that these functional feeding group differences were driven by the response of non-Tanypodinae chironomids (exclusion effect; ANOVA: $F_{1,14} = 5.78$, $P = 0.031$) and predatory stoneflies (sediment x exclusion interaction; ANOVA: $F_{1,14} = 14.63$, $P = 0.002$), respectively. Macroconsumers reduced the biomass of non-Tanypodinae chironomids by 50% or more in ambient and sediment treatments, and sediment addition eliminated the stimulatory effect of macroconsumer exclusion on predatory stonefly biomass.

Insect gatherer and predator biomass were not correlated with inorganic sediment in control or exclusion treatments. Although mean insect filterer (primarily hydropsychid caddisfly) biomass was nearly 25 times greater in exclusion versus control replicates in the ambient but not the sediment treatment, these differences were not statistically significant (ANOVA: $F_{1,14} \leq 3.67$, $P \geq 0.076$; Figure 3.3). However, when hydropsychid biomass was regressed against inorganic sediment, a statistically significant pattern was evident: in exclusion treatments, hydropsychid biomass decreased as inorganic dry mass increased ($r^2 = 0.69$, $P = 0.011$).

To summarize, sediment both directly and indirectly affected benthic communities in the tile experiment (Figure 3.4a). Sediment addition altered periphyton composition, increasing the

proportion of biovolume contributed by upright growth forms. In addition, it eliminated the influence of macroconsumers on sediment organic content, as well as biomass of total insects, predatory stoneflies and hydropsychid caddisflies. The only effect of macroconsumers that was not altered by sediment addition was their reduction of chironomid biomass.

Leaf pack experiment

Leaf breakdown and fungal biomass

Over the 56-day experiment, individual leaf packs lost 13 - 46% of their initial AFDM. Sediment and macroconsumer treatments did not differ in terms of average remaining leaf pack AFDM or fungal biomass (MANOVA: Pillai's trace ≤ 0.21, $F_{2,14} \leq 1.84$, $P \geq 0.195$; Table 3.7), although fungal biomass was highest in the ambient control treatment and lowest in the ambient exclusion treatment (Table 3.7). Fungal biomass decreased with increasing inorganic sediment in both the control and exclusion treatments (Figure 3.5), and was negatively correlated with AFDM remaining ($r^2 \geq 0.53$, $P \leq 0.017$).

Insect abundance and biomass

Abundance and biomass of total insects, shredders, and predators are presented in Table 3.7. Total insect biomass was greater in exclusion versus control replicates in both ambient and sediment treatments, but among-treatment differences were not statistically significant for either biomass or abundance (ANOVAs: $F_{1,16} \leq 2.28$, $P \geq 0.151$; Table 3.7). Similarity between control and exclusion pairs in terms of total abundance and biomass did not differ between ambient and sediment treatments (t-tests: $t_8 \leq 0.92$, $P \geq 0.193$). Regression of total insect abundance and biomass against inorganic sediment likewise revealed no significant correlations. Neither addition of sediment nor the amount of sediment deposited on leaf packs significantly affected total insect abundance or biomass in leaf packs.

Total abundance and biomass of insect shredders also showed no statistically significant differences between treatments (ANOVAs: $F_{1,16} \leq 2.60$, $P \geq 0.126$; Table 3.7), and no significant

correlation with the amount of sediment in leaf packs. However, insect predator abundance and biomass were affected by sediment. Comparison of treatments in terms of total predator abundance showed a significant treatment interaction (i.e., sediment x exclusion; ANOVA: $F_{1,16} = 5.75$, $P = 0.029$). Subsequent ANOVAs for individual predator taxa indicated that this effect was largely driven by abundance of Tanypodinae chironomids (ANOVA: $F_{1,16} = 6.15$, $P = 0.025$). Tanypodids were twice as abundant in the ambient exclusion than the ambient control treatment (paired t-test: $t_4 = 2.29$, $P = 0.042$), but this effect disappeared when sediment was added (paired t-test: $t_4 = 0.50$, $P = 0.321$; Table 3.7). Addition of sediment eliminated the effect of exclusion on tanypodid abundance.

Total predator biomass demonstrated a significant effect of sediment (ANOVA: $F_{1,16} = 6.06$, $P = 0.026$), with reduced biomass in both sediment treatments relative to ambient treatments (Table 7); predator biomass also showed a borderline-significant sediment x exclusion interaction (ANOVA: $F_{1,16} = 4.13$, $P = 0.059$). Subsequent ANOVAs for individual taxa suggested that these effects were largely driven by three taxa: tanypodids and, to a lesser extent, predatory stoneflies (i.e., perlids and perlodids) and the dipteran Atherix. Tanypodid biomass demonstrated a significant sediment x exclusion interaction (ANOVA: $F_{1,16} = 5.73$, $P = 0.029$). Biomass was twice as high in the ambient exclusion than the ambient control treatment (paired t-test: $t_4 = 3.32$, $P = 0.015$), but this pattern did not hold in the sediment treatments (paired t-test: $t_4 = 1.27$, $P = 0.136$; Table 3.7). In addition, both predatory stoneflies and Atherix showed borderline-significant effects of sediment (ANOVAs: $F_{1,16} = 3.51$, $P = 0.079$ and $F_{1,16} = 4.32$, $P = 0.054$, respectively). Of these three taxa, only predatory stonefly biomass showed a significant relationship when regressed against inorganic sediment. In control treatments, predatory stonefly biomass decreased as inorganic dry mass increased ($r^2 = 0.86$, $P = 0.0003$); this correlation was not evident in exclusion treatments, where predatory stonefly biomass was always low.

As in the tile experiment, sediment both directly and indirectly affected benthic communities in the leaf pack experiment (Figure 3.4b). Sediment addition led to decreased biomass of fungi,

predatory stoneflies and the dipteran Atherix, and eliminated the effect of macroconsumers on tanypodid abundance and biomass.

DISCUSSION

Small yet environmentally realistic increases in bedload transport and deposition directly and indirectly affected algal and detrital-based benthic communities in an otherwise unimpacted (e.g., hydrologically unaltered, unpolluted) southern Appalachian stream. To our knowledge, this study represents the first in situ experimental manipulation of bedload that explicitly considers sedimentation impacts on both algal and detrital-based stream food webs. In addition, this study experimentally examines (via macroconsumer exclusion) the indirect effects of bedload increases -- specifically, how sedimentation alters the outcome of species interactions. The importance of pollutant impacts on biotic interactions has been stressed for other contaminants [e.g., heavy metals (Clements 1999), hydrocarbons (Carman et al. 1997)], but relatively few studies have explicitly examined the effect of sedimentation on these interactions. Of the sediment addition studies that have considered indirect effects, most have focused on suspended sediment (Table 3.1), which is typically less influential than bedload in altering lotic benthic communities (Lemly 1982, Waters 1995).

Direct effects of elevated bedload

Basal resources in both tile and leaf pack experiments were directly affected by bedload increases. In the tile experiment, periphyton community composition changed in response to sedimentation. Total periphyton abundance and biovolume did not differ between treatments, but sediment addition led to an increase in the proportion of biovolume composed of upright taxa (e.g., Synedra and Eunotia spp.) and a decrease in the proportion of motile taxa (e.g., Navicula and Luticola spp.; Figure 3.2 and Table 3.5). Motile diatoms are generally considered to be more tolerant of siltation than other algal growth forms (Kutka and Richards 1996), given that they can reposition themselves on top of deposited sediment. However, these taxa are more loosely

attached to the substrate than many upright taxa, and they may have been more readily scoured by daily addition of sediment and subsequent bedload transport (Hudon and Legendre 1987, Peterson 1996).

In the leaf pack experiment, fungal biomass in both control and exclusion treatments decreased as inorganic sediment increased (Figure 3.5). Leaf pack AFDM was negatively correlated with fungal biomass, suggesting that sediment indirectly affected leaf breakdown via its negative effects on fungi, which play an important role in leaf decay (e.g., Suberkropp and Klug 1980, Suberkropp and Arsuffi 1984). Insect shredders did not appear to be important in leaf pack breakdown in this experiment, as neither shredder abundance nor biomass were correlated with leaf pack AFDM. Although sediment can accelerate leaf breakdown via physical abrasion (Webster and Waide 1982), in our experiment leaf pack AFDM remaining tended to increase with inorganic sediment. Burial of leaf packs may make them inaccessible to shredders, thereby slowing leaf breakdown (Webster and Waide 1982, Parkyn et al. 1997); burial did not occur in this experiment, however, as < 3% of the total sediment added remained on packs by day 56 (Table 3.4).

The only direct effect of sediment addition on insect assemblages occurred in the leaf pack experiment, where biomass of predatory stoneflies and Atherix dipterans tended to decline with increased sediment (Table 3.7 and Figure 3.4b). Bedload increases did not directly affect insects in the tile experiment, even though these substrates may offer less shelter from saltating bedload (i.e., bedload transported along the stream bottom) than leaf packs. This relative lack of direct sediment effects was unexpected, as many studies have shown significant reductions in benthic insect abundance and biomass with sedimentation (e.g., Lenat et al. 1981, Lemly 1982, Angradi 1999). For example, other sediment addition studies have shown increased drift (Rosenberg and Wiens 1978, Culp et al. 1986, Doeg and Milledge 1991) and reduced densities (Alexander and Hansen 1986, Culp et al. 1986) of benthic insects with sedimentation. Culp et al. (1986) found

that saltating sediment was especially influential, reducing benthic invertebrate densities by more than 50% within 24 hours of application.

The apparent absence of direct effects in this study may reflect the small scale of our experiments. Sediment addition could have resulted in immediate decreases in insect abundance and biomass, which were then offset by immigration from adjacent, unaltered areas of the stream (Cooper et al. 1990). Because sediment was added to only localized areas within a larger, unaltered stream landscape, total insect standing stocks were not diminished; prey movement into sediment addition treatments may have obscured localized effects of elevated bedload.

Indirect effects of elevated bedload – alteration of macroconsumer effects

Sediment addition altered macroconsumer effects in both tile and leaf pack experiments, although sediment impacts were much greater on tiles (Figure 3.4). In the tile experiment, macroconsumers reduced both total insect and predatory stonefly biomass under ambient conditions; when sediment was added, these macroconsumer effects disappeared, and insect assemblages in control and exclusion treatments became more similar (Table 3.5, Figure 3.3). In addition, hydropsychid biomass declined with increasing sedimentation, but only when these organisms were released from predation pressure (i.e., in exclusion treatments). In general, prey taxa preferred by mottled sculpin [chironomids and hydropsychids (Stouder 1990)] were reduced in ambient control versus exclusion treatments. These taxa also may be likely prey for omnivorous crayfish, as they are relatively immobile and easy to catch (Momot 1995).

This reduction of predator effects with increased sedimentation has been found for both vertebrate and invertebrate predators (e.g., Gardner 1981, Peckarsky 1985, Walde 1986, Barrett et al. 1992, Johnson and Hines 1999). However, few sediment addition experiments have focused on bedload increases and their potential alteration of top-down effects (Table 1). One exception is a five-year 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 the top-down effects of brook trout were not altered by bedload increases, which contrasts with the results obtained in our tile experiment. This is not surprising, given that macroconsumers in the tile experiment were predominantly obligate benthic feeders (i.e., mottled sculpins and crayfish), whereas brook trout feed upon aquatic and terrestrially-derived invertebrate drift.

Peckarsky (1983) postulated that harsh abiotic conditions (e.g., elevated bedload transport) can diminish the influence of biotic interactions such as competition and predation in stream communities. Results of the tile experiment support this contention, although the mechanisms are not clear. Sedimentation (or any other abiotic disturbance) may alter top-down forces via effects on macroconsumers and/or prey taxa. For example, elevated sediment may change macroconsumer behavior, decrease macroconsumer feeding efficiency, and/or alter prey density or behavior (Walde 1986). Our observations do not suggest that macroconsumers visited sediment controls less frequently than ambient controls, arguing 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). However, total insect biomass was not consistently reduced by sediment addition: the sediment control treatment actually had higher insect biomass than the ambient control treatment (Table 3.6).

The mechanisms behind bedload and macroconsumer interactions were likely taxon specific. Few predatory stoneflies were found in sediment control or exclusion treatments, suggesting that sediment-related changes in stonefly density may have affected macroconsumer impacts on predatory stoneflies. In contrast, biomass of hydropsychid caddisflies was not consistently reduced by sediment addition. Biomass in control treatments was greater with sediment added, whereas biomass in exclusion treatments was greater under ambient conditions. Thus, direct response of hydropsychids to sediment addition does not appear to explain differences in macroconsumer effects. This lack of a consistent hydropsychid response may have reflected

species specific differences in sediment susceptibility (Strand and Merritt 1997, Runde and Hellenthal 2000a and 2000b). The only impact of macroconsumers that was not altered by sediment addition was their reduction of chironomid biomass. Top-down effects on sediment-sensitive taxa (stoneflies and caddisflies) were eliminated, whereas top-down effects on relatively sediment-tolerant taxa (chironomids) were not affected.

Our results further illustrate that studies that consider only abundance measures may fail to detect ecologically relevant results (Benke et al. 1999). Significant treatment effects generally were not evident when insect abundances were considered. In both the tile and leaf pack experiments, sediment and macroconsumer effects on insect assemblages were observed only when insect biomass was considered, with the exception of tanypodid abundance in the leaf pack experiment (Figure 3.4).

Macroconsumers had minimal effects on insect assemblages in the leaf pack experiment relative to their effects in the tile experiment. 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). In contrast, tiles provide a homogeneous and relatively refuge-free habitat, potentially facilitating predation. Of the insects we considered, only tanypodid dipterans differed significantly between control and exclusion treatments in the leaf pack experiment. Abundance and biomass of tanypodids were reduced in the ambient control treatment, but this effect disappeared when sediment was added (Table 3.6). This contrasts with what we observed for chironomid biomass in the tile experiment, where macroconsumers had a significant effect under both ambient and sediment conditions (Figure 3.4a).

This difference may be explained, at least in part, by insect predation. In the leaf pack experiment, predatory stonefly abundance and biomass were greater in ambient control versus exclusion treatments, although these differences were not statistically significant; in sediment treatments, abundance and biomass of these predators were always low. Leaf packs may have provided tanypodids refuge from macroconsumer predation, but insect predators may have been

harder to avoid (Wooster 1994). Stonefly predators may have contributed to reduced tanypodid abundance and biomass in the ambient control treatment, while in the ambient exclusion treatment tanypodids were released from both macroconsumer and insect predation pressure. In the sediment treatments, where large stonefly predators were rare in both control and exclusion treatments, tanypodid abundance and biomass were higher.

Implications

Throughout the world, anthropogenic sedimentation poses a significant threat to freshwater ecosystems (e.g., Ryan 1991, Waters 1995, Richter et al. 1997, Wood and Armitage 1997); in the United States, sediment impairs more stream and river miles than any other pollutant (USEPA 1998). These experiments indicate that increases in bedload can directly affect biota in both algal and detrital-based food webs. Perhaps more important, elevated bedload can alter the outcome of species interactions (Figure 3.4). These indirect influences of sedimentation are examined less frequently than direct biotic responses, but our results suggest that alteration of top-down effects may be an important aspect of bedload increases.

These findings have significant implications for the response of stream systems to anthropogenic sedimentation. In our experiments, small amounts of sediment were added to localized areas (0.25 m^2) of the stream bottom. Despite the small scale of these additions, bedload increases had significant direct and indirect effects on benthic communities. In reality, sedimentation affects entire stream reaches, and adjacent, sediment-free areas, which may have offset aquatic insect reductions in our experiments, will be less common. Thus, the influence of larger scale sedimentation is likely to be even greater than observed in these experiments.

Our experiments demonstrate that even small increases in bedload can affect algal and detrital-based food webs. However, much larger bedload increases may be common, with correspondingly greater impacts on benthic communities. Bedload transport rates in Lower Ball Creek were naturally very low (0.80 ± 0.27 kg m^{-1} d^{-1}; A. Sutherland, UGA, *unpublished data*).

By adding 250 g of sand daily to each frame, we simulated a 60% increase over natural bedload transport rates; this increase was still 35% lower than transport rates in a nearby pasture stream (1.98 ± 0.44 kg m^{-1} d^{-1}; A. Sutherland, unpublished data). Land-clearing activities can lead to much greater increases [e.g., 20-fold bedload transport rate increases after a forest fire (Beaty 1994)], so the transport rates we considered were exceptionally low. For example, Kunhle (1992) recorded bedload transport rates of 78 to 55,000 kg m^{-1} d^{-1} in two gravel-bed northern Mississippi streams -- more than 35 to 20,000 times greater than the "high" pasture stream transport rate.

An additional concern with anthropogenic sedimentation is the prevalence of sediment-associated contaminants (e.g., heavy metals, hydrocarbons), which adsorb to sediment particles and are thereby transported into streams. Benthic organisms live in close proximity to these contaminated sediments, and can be adversely affected by these pollutants (e.g., Forrow and Maltby 2000). Because "clean" sediment was used in our experiments, these results do not reflect potential pollutant effects; sedimentation impacts observed here may be exacerbated by sediment-associated contaminants.

Finally, our experiments suggest that biotic interactions in autotrophic systems (i.e., the tile experiment) may be especially vulnerable to sedimentation (Figure 3.4). Increased sediment delivery to stream systems is often accompanied by other alterations, including decreases in riparian cover. Decreases in allochthonous inputs and stream shading can induce shifts from primarily heterotrophic systems based upon leaf litter to more autotrophic systems based upon periphyton. As a result, streams may face a negative feedback effect: increases in bedload may coincide with development of more sediment-susceptible habitats and communities.

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Table 3.1. Summary of selected sediment addition experiments. Only studies which involved experimental manipulation of sediment levels are included; studies which primarily focused on particle size effects are not included. NTU were not converted to mg L^{-1} values, given differences in sediment type and turbidity measurements. Response variables are parameters measured in experiments, and other factors are additional independent variables that were manipulated. S = suspended sediment; B = bedload (deposited or transported).

		Sediment addition				
Reference	**Study system**	***Type***	***Amount***	***Duration***	**Response variables**	**Other factors**
Ciesielka and Bailey 2001	in-stream areas	B	4.59 kg m^{-2}	one-time addition	benthic invert abundance	--
Runde and Hellenthal 2000a	artificial streams	B	up to 8.11 kg m^{-2}	daily for 9 d or one-time addition	hydropsychid drift, mortality, behavior	--
Runde and Hellenthal 2000b	artificial streams	S	667-6000 mg L^{-1}	continuously for 24 hr	hydropsychid drift, mortality, behavior	--
Johnson and Hines 1999	aquaria	S	0-2000 mg L^{-1}	one-time addition	razorback larvae preference, susceptibility to predation	--
Strand and Merritt 1997	aquaria	S	11 g day^{-1}; daily max of 23 NTU	daily for 16 d	hydropsychid growth	--
Abrahams and Kattenfeld 1997	aquaria	S	0-11 NTU	added as needed to maintain NTU	fathead minnow predator avoidance, mortality	--
Miner and Stein 1996	aquaria	S	0-100 NTU	one-time addition	bluegill predator detection, habitat choice	alternative prey availability
Gregory 1993	aquaria	S	0-22.7 NTU	added as needed to maintain NTU	juvenile chinook salmon predator avoidance, spatial distribution	predator type (bird vs. fish)

Barrett et al. 1992	weir pond channels	S	8.3-96.6 mg L^{-1}	continuously during feeding trials	rainbow trout reactive distance, pursuit speed	--
Doeg and Milledge 1991	in-stream riffle channels	S	20-133 mg L^{-1}	continuously for 1.5 hr	invert drift	--
Horner et al. 1990	artificial streams	S	25 mg L^{-1}	continuously for 4-7 d	periphyton accrual, export, composition	phosphorus, current velocity
Aldridge et al. 1987	aquaria	S	0-750 mg L^{-1}	one-time addition	unionid food clearance rates, O_2 uptake rates, N excretion rates	turbulence
Culp et al. 1986	in-stream riffles	B	increased proportion of sand by 10%	one-time addition	invert drift and benthic densities	--
Alexander and Hansen 1986	≈ 0.6 km stream reach	B	3x daily sediment discharge	daily for 5 y	brook trout abundance, biomass, growth, food consumption; benthic invert densities	--
Gardner 1981	aquaria	S	0-190 NTU	one-time addition	bluegill feeding rate, size selectivity	--
Rosenberg and Wiens 1978	in-stream riffle channels	S	7-8 mg L^{-1}	continuously for 5 hr	invert drift and benthic densities	--
Ciborowski et al. 1977	artificial streams	S	0-2680 mg L^{-1}	one-time addition	invert drift	current velocity, light

Table 3.2. Physical and chemical stream characteristics during tile and leaf pack experiments. Values represent means ± 1 SE; sample size is indicated by number in brackets.

		TILES	LEAF PACKS
Experimental period		7/29-9/8/97	10/9-12/4/99
Water temperature (°C)		16.9 ± 0.16 [41]	10.4 ± 0.34 [57]
Maximum daily discharge (L 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 (µS 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]

Table 3.3. Physical parameters at the start of each experiment. All values represent means of five quadrats ± 1 SE except the sediment added values for the tile experiment (means of four quadrats ± 1 SE).

Experiment	Sediment treatment	Macroconsumer treatment	Canopy cover (%)	Water depth (m)	Water velocity ($m\ s^{-1}$)	Shear stress ($dyn\ cm^{-2}$)
TILES	*Ambient*	Control	85.4 ± 1.6	0.17 ± 0.01	0.200 ± 0.009	83.6 ± 0.0
		Exclusion	86.3 ± 1.2	0.17 ± 0.02	0.257 ± 0.022	89.1 ± 5.5
	Sediment	Control	86.5 ± 0.5	0.14 ± 0.01	0.221 ± 0.032	90.2 ± 17.7
		Exclusion	86.2 ± 1.0	0.13 ± 0.01	0.223 ± 0.021	90.2 ± 17.7
LEAF PACKS	*Ambient*	Control	96.0 ± 0.9	0.14 ± 0.02	0.191 ± 0.050	111 ± 24.6
		Exclusion	95.1 ± 1.5	0.16 ± 0.01	0.214 ± 0.057	111 ± 24.6
	Sediment	Control	96.3 ± 0.9	0.16 ± 0.02	0.158 ± 0.024	88.6 ± 16.4
		Exclusion	96.8 ± 0.5	0.17 ± 0.03	0.179 ± 0.051	88.6 ± 16.4

Table 3.4. Inorganic dry mass on day 40 of the tile experiment and day 56 of the leaf pack experiment. Leaf pack sediments were converted to g m^{-2} using an average leaf pack size of 0.0144 m^2; g $pack^{-1}$ values are shown in brackets. To calculate the % of added sediment that remained on experimental substrates, g m^{-2} values were divided by the total amount of sediment added to each replicate over each experiment (40 kg m^{-2} in tile experiment, 53 kg m^{-2} in leaf pack experiment). Values represent mean of four (tile sediment values) or five replicates ± 1 SE, unless otherwise noted. Dashed lines indicate that sediment was not added to ambient treatments.

Experiment	Sediment treatment	Macroconsumer treatment	Inorganic dry mass (g m^{-2})	% Total added
TILES	Ambient	Control	130 ± 26	------
		Exclusion	113 ± 18	------
	Sediment	Control	219 ± 65	0.5 ± 0.2
		Exclusion [a]	298 ± 111	0.7 ± 0.3
LEAF PACKS	Ambient	Control	848 ± 393 [12.2 ± 5.7]	------
		Exclusion	905 ± 298 [13.0 ± 4.3]	------
	Sediment	Control [b]	1117 ± 83 [16.1 ± 1.2]	2.1 ± 0.2
		Exclusion	1234 ± 476 [17.8 ± 6.9]	2.3 ± 0.9

[a] Values based on three replicates [one outlier (1299 g m^{-2}, 3.3%) omitted].

[b] Values based on four replicates [one outlier (4620 g m^{-2}, 8.7%) omitted].

Table 3.5. Chlorophyll *a*, organic matter, and periphyton composition on day 40 of the tile experiment. Ambient values represent means of five quadrats ± 1 SE; sediment values represent means of four quadrats ± 1 SE.

	AMBIENT		**SEDIMENT**	
RESPONSE VARIABLE	***Control***	***Exclusion***	***Control***	***Exclusion***
Chlorophyll *a* (mg m^{-2})	1.83 ± 0.44	3.61 ± 1.20	2.52 ± 0.76	2.21 ± 0.38
AFDM (g m^{-2})	11.32 ± 1.81	16.31 ± 2.67	31.27 ± 18.55	29.35 ± 10.52
Chl a : AFDM (x 10^{4})	1.76 ± 0.54	2.08 ± 0.35	1.31 ± 0.51	1.15 ± 0.40
Sediment organic content (% AFDM)	0.08 ± 0.01	0.13 ± 0.00	0.10 ± 0.03	0.06 ± 0.01
Total periphyton abundance (# cm^{-2} x 10^{-4})	1.66 ± 0.38	4.27 ± 1.95	3.22 ± 1.33	2.51 ± 0.56
Adnate	0.75 ± 0.25	1.54 ± 0.78	1.50 ± 0.69	1.23 ± 0.38
Motile	0.19 ± 0.03	0.68 ± 0.27	0.20 ± 0.07	0.17 ± 0.03
Upright	0.72 ± 0.15	2.05 ± 0.90	1.52 ± 0.57	1.11 ± 0.17
Total periphyton biovolume (μm^{3} cm^{-2} x 10^{-6})	4.84 ± 1.22	14.45 ± 7.72	11.79 ± 4.67	9.42 ± 1.51
Adnate	1.13 ± 0.45	2.41 ± 1.41	2.45 ± 1.23	1.89 ± 0.50
Motile	0.75 ± 0.13	2.74 ± 1.11	0.81 ± 0.35	0.70 ± 0.11
Upright	2.96 ± 0.73	9.30 ± 5.22	8.53 ± 3.17	6.83 ± 1.19

Table 3.6. Total insect abundance and biomass on day 40 of the tile experiment. Ambient values represent means of five quadrats ± 1 SE; sediment values represent means of four quadrats ± 1 SE. Similarity between control and exclusion quadrats was calculated using a simplified Morisita index with ln-transformed data (Wolda 1981).

Sediment treatment	**Macroconsumer treatment**	**Abundance (# m^{-2})**	**Similarity**	**Biomass (mg m^{-2})**	**Similarity**
Ambient	***Control***	1316 ± 240	0.64 ± 0.05	63 ± 20	0.50 ± 0.08
	Exclusion	2027 ± 482		248 ± 58	
Sediment	*Control*	1445 ± 365	0.74 ± 0.04	102 ± 30	0.64 ± 0.01
	Exclusion	1689 ± 695		109 ± 46	

Table 3.7. Percent AFDM remaining, fungal biomass, and abundance and biomass of total insects, shredders and predators on day 56 of the leaf pack experiment. All values represent means of five replicates ± 1 SE unless otherwise noted.

	AMBIENT		**SEDIMENT**	
RESPONSE VARIABLE	***Control***	***Exclusion***	***Control***	***Exclusion***
% AFDM remaining	65.8 ± 5.3	67.7 ± 2.7	64.4 ± 3.6	66.4 ± 3.9
Fungal biomass (mg g^{-1} AFDM)	56.1 ± 6.9	33.2 ± 2.3[a]	44.5 ± 3.6	44.3 ± 13.8
Total insect abundance (# $pack^{-1}$)	163 ± 36	229 ± 23	199 ± 11	184 ± 32
Shredders	8.4 ± 1.8	5.8 ± 1.8	10.0 ± 3.5	4.6 ± 1.4
Predators	28.2 ± 7.1	50.0 ± 4.8	43.0 ± 4.0	35.8 ± 7.5
Tanypodinae	18.2 ± 5.6	39.8 ± 4.0	31.4 ± 5.7	26.8 ± 5.6
Atherix	1.0 ± 0.5	0.2 ± 0.2	0.0 ± 0.0	0.2 ± 0.2
Stoneflies	0.8 ± 0.4	0.4 ± 0.4	0.8 ± 0.6	1.0 ± 1.0
Total insect biomass (mg $pack^{-1}$)	40.2 ± 6.5	21.3 ± 8.1	47.6 ± 14.0	29.1 ± 17.5
Shredders	21.6 ± 4.2	13.2 ± 8.0	37.3 ± 13.3	21.1 ± 17.3
Predators	10.6 ± 3.1	3.9 ± 1.2	2.8 ± 0.3	3.1 ± 0.8
Tanypodinae	0.2 ± 0.0	0.4 ± 0.0	0.4 ± 0.1	0.3 ± 0.1
Atherix	3.9 ± 1.6	0.8 ± 0.8	0.0 ± 0.0	0.2 ± 0.2
Stoneflies	4.6 ± 2.5	0.4 ± 0.4	0.1 ± 0.0	0.1 ± 0.1

[a] Value based on four replicates (one replicate was missing data).

Figure 3.1. Illustration of the experimental design for sediment addition experiments (figure not to scale). White squares represent frames to which macroconsumers had access (i.e., control treatment); gray squares represent frames from which macroconsumers were excluded (i.e., exclusion treatment). Ovals represent pairs to which sediment was added. This design was used twice, once with tiles and once with leaf packs as sampling substrates.

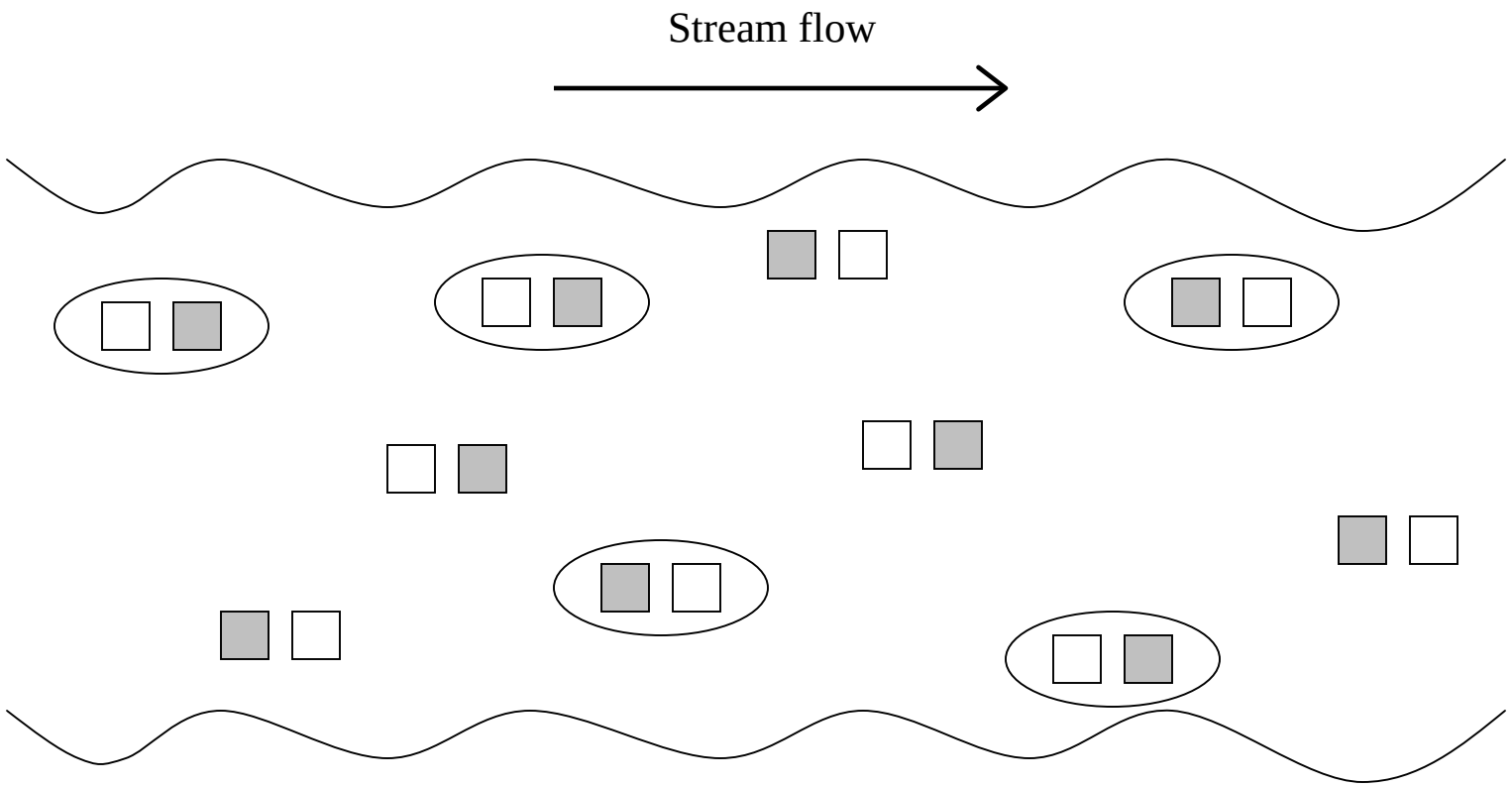

Stream flow

Figure 3.2. Percentage of day 40 periphyton biovolume composed of motile, adnate, and upright taxa in the ambient and sediment treatments of the tile experiment; C = control, E = macroconsumer exclusion.

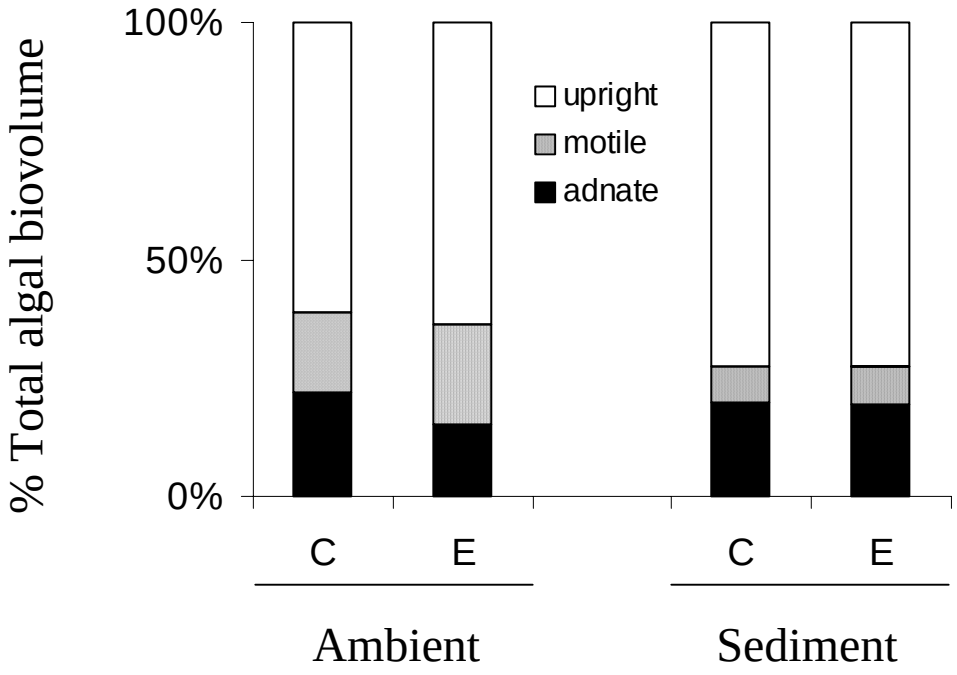

% Total algal biovolume
100%
50%
0%
upright
motile
adnate
C
E
C
E
Ambient
Sediment

Figure 3.3. Day 40 biomass (mg m^{-2}) of insect functional feeding groups in (a) ambient and (b) sediment treatments of the tile experiment; white bars = control, shaded bars = macroconsumer exclusion.

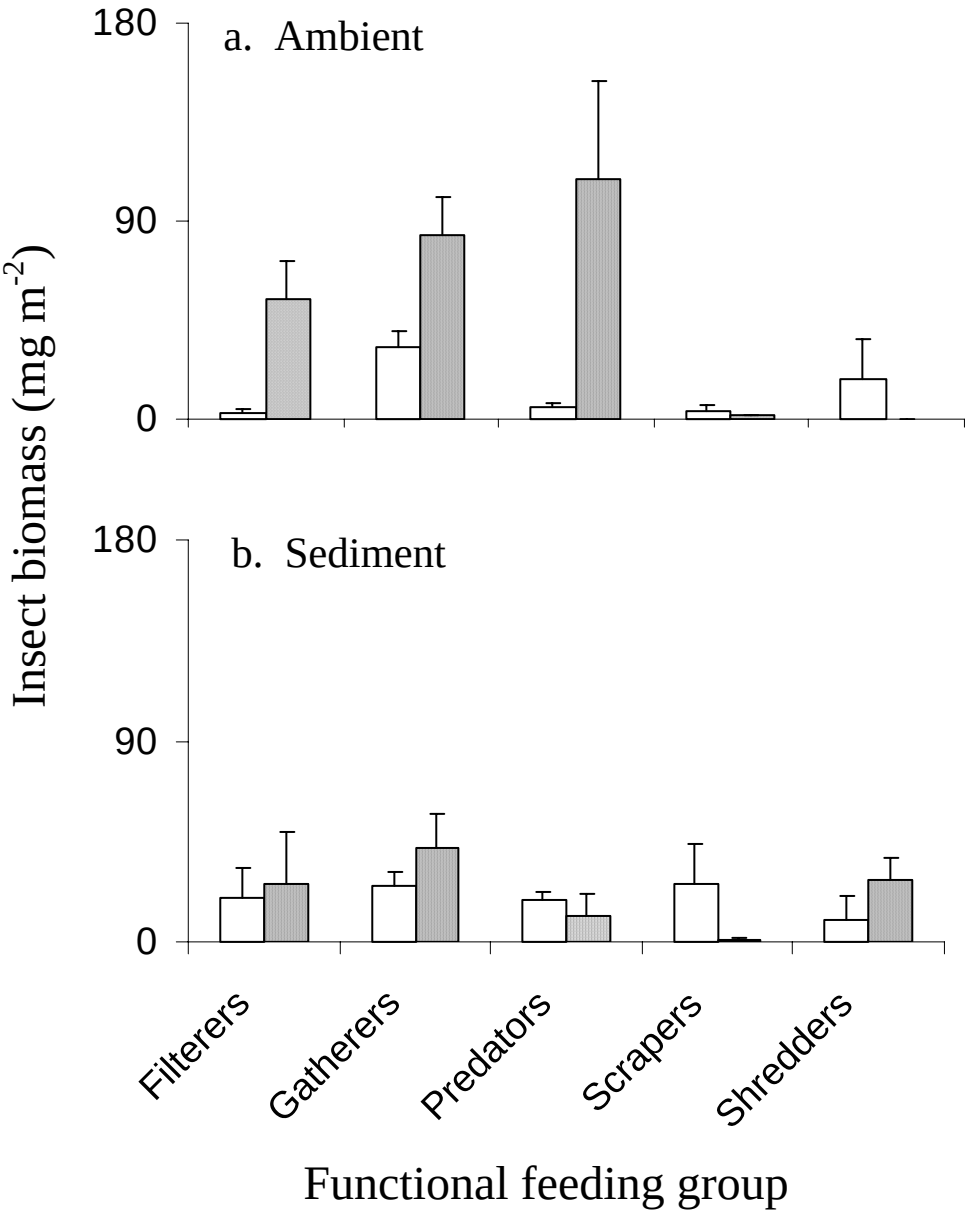
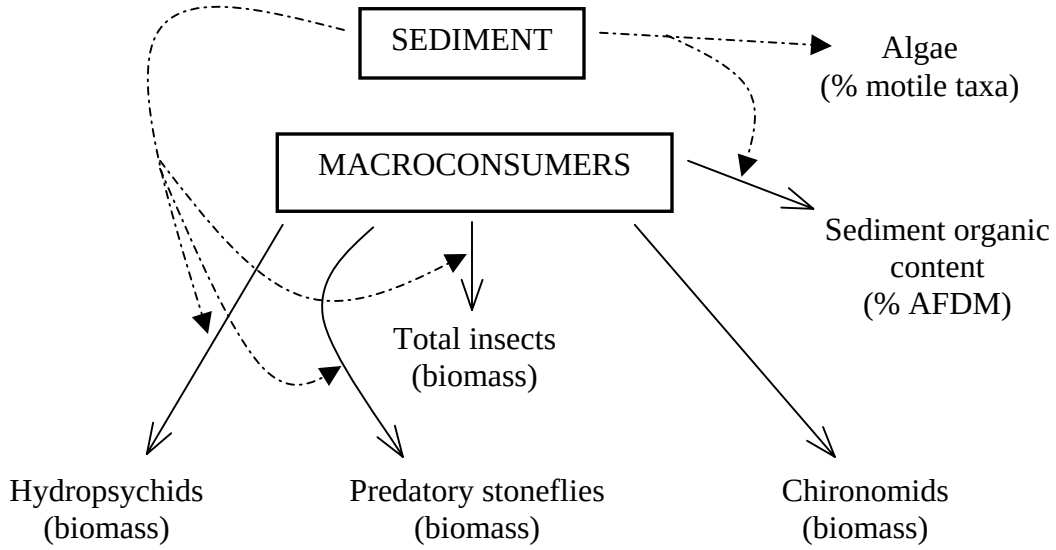

a. Ambient
b. Sediment
180
90
0
Insect biomass (mg m-2)
Filterers
Gatherers
Predators
Scrapers
Shredders
Functional feeding group

Figure 3.4. (a) Summary of tile experiment results, and (b) summary of leaf pack experiment results. Boxes indicate factors that were manipulated in the experimental design; other parameters were response variables. All arrows indicate negative effects. Dashed arrows represent influence of sediment (i.e., there was a significant sediment effect or a significant correlation with inorganic sediment in both control and exclusion treatments). Solid arrows represent influence of macroconsumers (i.e., there was a significant exclusion effect). Dashed arrows pointing to solid arrows indicate that macroconsumer impacts were altered by sediment addition (i.e., there was a significant sediment x exclusion interaction, or a significant correlation with inorganic sediment in either the control or exclusion treatment).

a. Tile experiment



b. Leaf pack experiment

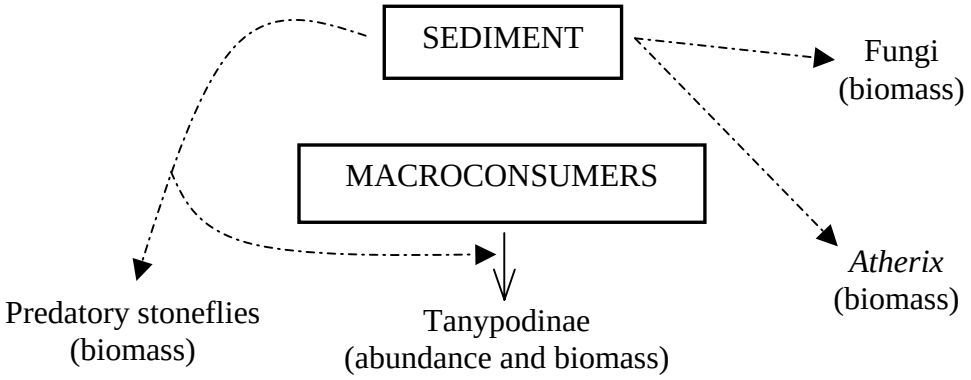
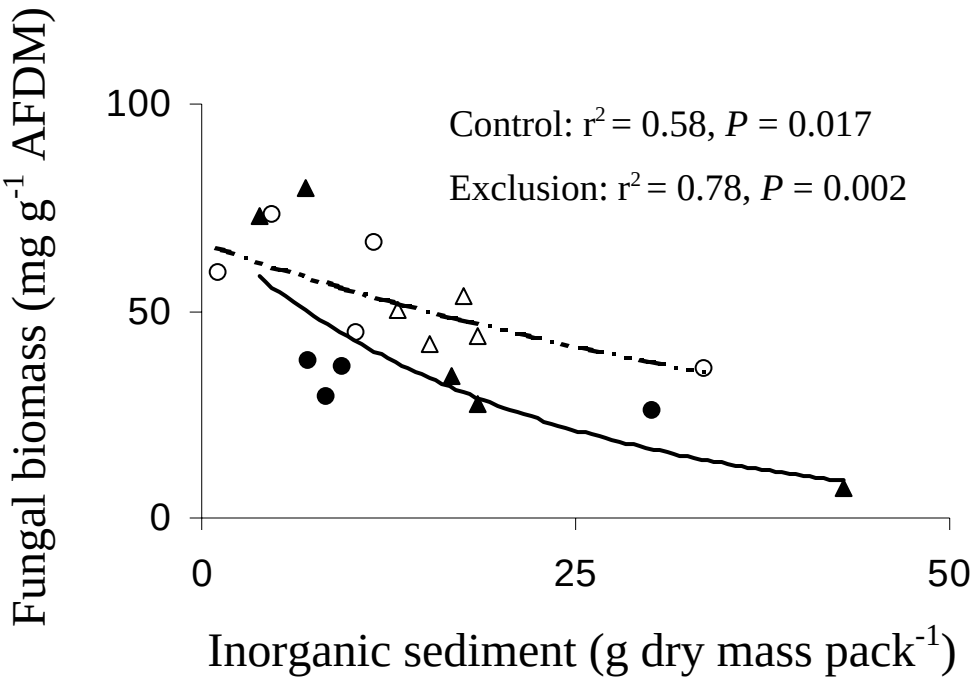


Figure 3.5. Fungal biomass (mg g^{-1} AFDM) versus inorganic sediment (g dry mass m^{-2}) on day 56 of the leaf pack experiment. White symbols = control replicates; black symbols = exclusion replicates; circles = ambient replicates; triangles = sediment replicates. Dashed line indicates significant regression for control treatments, while solid line indicates significant regression for exclusion treatments.


Fungal biomass (mg g-1 AFDM)
100
50
0
0
25
50
Inorganic sediment (g dry mass pack-1)
Control: r2 = 0.58, P = 0.017
Exclusion: r2 = 0.78, P = 0.002

CHAPTER 4

TOP-DOWN INTERACTIONS IN STREAMS DRAINING HUMAN-MODIFIED LANDSCAPES [1]

[1] Schofield, K.A., C.M. Pringle, J.L. Meyer, E.J. Rosi, and K.D. Kearns. To be submitted to Ecological Monographs.

ABSTRACT

Spatial and temporal variability of consumer-controlled forces have been the subject of much debate in ecology. To date, most studies considering variability of these top-down interactions have focused on systems minimally impacted by human activities. However, human modification of the landscape is prevalent, and it can significantly affect the strength and outcome of species interactions. The objective of this study was to examine how top-down interactions vary among streams with differing amounts of human disturbance in their watersheds. To address this issue, we experimentally excluded macroconsumers (fishes and crayfishes) from benthic areas of five southern Appalachian streams. These sites represented a range of human watershed development, from 100% to < 50% forested; macroconsumer assemblages at low development sites were dominated by benthic insectivores (Cottus bairdi) and crayfishes, whereas algivores (Campostoma anomalum) and general insectivores (e.g., Notropis leuciodus) were common at more developed sites. Using ceramic tiles as sampling substrates, we compared sediment, algal assemblages (chlorophyll *a*, AFDM, abundance, biovolume, and composition), and insect assemblages (abundance, biomass, and composition) in macroconsumer exclusion and control areas. In general, water chemistry variables (e.g., nutrient concentrations, conductivity, total suspended solids, and temperature) increased from low to high development sites. Significant cross-site differences were found for every response variable, but macroconsumer exclusion often had relatively similar effects among all sites. Response of chlorophyll *a* and AFDM to exclusion varied across sites, but at most sites there was a tendency for concentrations to be greater in the absence of macroconsumers. Macroconsumer exclusion did not have a significant effect on total algal abundance or biovolume across all sites, but exclusion did influence algal composition. Adnate diatom taxa (e.g., Achnanthes spp.) comprised a significantly greater proportion of total biovolume in controls, whereas upright diatom taxa (e.g., Melosira varians, Cymbella spp.) were more dominant in exclusion treatments. Insect abundance and biomass were greater in exclusion

versus control treatments at all sites, indicating that macroconsumers had a negative effect on insect assemblages. These results indicate that top-down effects were not diminished by increasing watershed development. Macroconsumers significantly affected benthic communities at all five sites, despite cross-site differences in physical, chemical, and biological characteristics. Although certain effects of watershed disturbance may tend to decrease the strength of top-down interactions (e.g., increased sedimentation or shifts in macroconsumer assemblages), these reductions may be offset by other concurrent changes (e.g., increased light and nutrient availability).

INTRODUCTION

The influence of top-down (i.e., consumer-controlled) forces in structuring biotic communities has been debated in both terrestrial and aquatic systems (e.g., Hunter and Price 1992, Power 1992, Strong 1992, Polis and Strong 1996). As with most ecological phenomena, variability (both spatial and temporal) of top-down effects is prevalent. For example, the strength of top-down interactions in aquatic systems can be affected by disturbance [e.g., floods (Wootton et al. 1996, Angeler et al. 2000)], consumer identity [e.g., native versus non-native species (Biggs et al. 2000), vertebrate versus invertebrate consumers (Gelwick 2000), longitudinal assemblage shifts (March et al. 2001)], and habitat characteristics [e.g., riffles versus pools (Flecker 1997, Rosenfeld 2000)].

To date, most studies considering variability of top-down interactions have focused on systems minimally affected by human activities. However, human modification of the environment can significantly alter the strength and outcome of trophic interactions (e.g., Livingston et al. 1997, Wardle et al. 1998). Numerous studies have shown that human development of watersheds and/or riparian areas can have significant impacts on physical, chemical, and biological characteristics of streams (e.g., Jones and Clark 1987, Schlosser 1991,

Lenat and Crawford 1994). In turn, these abiotic and biotic changes can affect top-down interactions (Dunson and Travis 1991, Hunter and Price 1992), either by weakening [e.g., increased sedimentation (Peckarsky 1985, Schofield et al., in review)] or strengthening [e.g., increased irradiance (Wellnitz and Ward 2000)] consumer effects. Separating the potentially contradictory effects of watershed development on top-down interactions complicates examination of consumer impacts. However, as anthropogenic landscape alteration becomes increasingly prevalent worldwide, understanding species interactions in human-modified environments becomes especially important (McDonnell and Pickett 1990, Paul and Meyer 2001).

One common result of watershed development is the alteration of stream biotic communities, including macroconsumer assemblages. Several studies have found that watershed land use (i.e., increased agriculture or urbanization) can result in decreased abundance of streambed-dependent fishes (e.g., sculpins and darters) and increased abundance of less benthos-restricted fishes (e.g., minnows and sunfishes) (Schlosser 1982, Weaver and Garman 1994, Rabeni and Smale 1995, Harding et al. 1998). In addition, benthic insectivores tend to be replaced by omnivorous and/or algivorous fishes in modified systems (e.g., Schlosser 1982, Weaver and Garman 1994). These shifts in fish assemblage structure may affect the relative strength of top-down interactions, as the influence of different fishes (e.g., streambed versus water column species, insectivores versus algivores) on benthic communities will vary.

In the southern Appalachian Mountains, the effect of land use alterations on stream communities is a growing concern. The region supports highly diverse stream communities, including many endemic and imperiled species (Cooper and Braswell 1995, Taylor et al. 1996, Morse et al. 1997). This diversity is being threatened by human population growth and subsequent development throughout the region. Traditionally, population density has been low in the area, but over the past 20 years the southern Appalachians have seen substantial growth,

primarily due to residential development (SAMAB 1996). Much of this development has occurred in near-stream areas (Bolstad and Swank 1997). This changing land use mosaic provides a unique opportunity to examine how land use alterations influence the outcome of top-down interactions.

The objective of this study was to examine how macroconsumer effects (i.e., top-down interactions) vary among streams with differing amounts of development in their watersheds. Specifically, we wanted to address the following question: are top-down effects altered by increasing watershed development? We experimentally excluded macroconsumers (fishes and crayfishes) from benthic areas within five southern Appalachian streams; these sites represented a range of watershed development, from 100% to < 50% forested. We expected that biological, chemical, and physical changes associated with anthropogenic activity would interact to influence top-down forces, and that the ultimate outcome of these changes would vary across sites (Figure 4.1). Based on shifts in vertebrate macroconsumers (e.g., from largely substrate-oriented fishes at forested sites to water column-oriented fishes at more developed sites), we predicted that top-down effects would diminish with watershed development (e.g., Gido and Matthews 2001). We also expected that sedimentation would increase with watershed development, further reducing top-down effects at human-modified sites (e.g., Peckarsky 1985, Schofield et al. in review). However, we speculated that reductions in top-down effects might be at least partially offset by other development-associated changes. For example, increased light and nutrient availability at more developed sites could increase algal resources, thereby enhancing top-down pressure (Oksanen et al. 1981).

METHODS

Study sites

Experiments were conducted at five sites in the southern Appalachian Mountains of western North Carolina. Sites were located in the Little Tennessee River basin (Lower Ball Creek and Jones Creek) and the French Broad River basin (Upper Davidson River, Beaverdam Creek, and Sweeten Creek; Figure 4.2). These streams are a subset of 36 sites varying in watershed land use, at which Coweeta Long Term Ecological Research (LTER) scientists have been collecting baseline physical, chemical, and biological data for several years. The five sites examined here were chosen because their watersheds vary in extent and type of watershed development, resulting in significant among-site differences in macroconsumer assemblages (Tables 4.1 and 4.2).

Ball Creek (Ball) and Upper Davidson River (Davidson) are relatively unaltered by human activities (Ball is located at the Coweeta Hydrologic Laboratory, and Davidson is in Pisgah National Forest). Their watersheds are completely forested (Table 4.1), and the streams are bordered by dense riparian vegetation (e.g., Rhododendron maximum). However, Davidson is a much wider stream than Ball Creek, and thus receives more light. Substrate at both sites is predominantly unembedded boulder, cobble, and gravel. Dominant macroconsumers are mottled sculpin (Cottus bairdi), a benthic insectivore, and omnivorous crayfishes (Cambarus bartonii and C. robustus, Table 4.2).

Although the Jones Creek (Jones) watershed also is predominantly forested (Table 4.1), extensive sections of the riparian zone are used for cattle pasture, and low-density residential development is scattered throughout the basin. Substrate is predominantly cobble and gravel, and is highly embedded with sand. As at Ball and Davidson, dominant macroconsumers are mottled sculpin and omnivorous crayfishes (C. bartonii and C. georgiae, Table 4.2).

The Beaverdam Creek (Beaverdam) study site is located at the upstream edge of a golf course in northern Asheville, North Carolina. Although the study reach does not receive much drainage from the golf course, a residential community (with septic tanks) is located immediately upstream. Riparian areas immediately adjacent to the study reach consist primarily of mowed grass, although a large sycamore (Plantanus occidentalis) tree and a clump of shrubs are present. Substrate is predominantly sand, with occasional embedded cobble and gravel. The dominant macroconsumers at this site are the algivorous central stoneroller (Campostoma anomalum) and omnivorous crayfish (C. bartonii, Table 4.2).

Sweeten Creek (Sweeten) is located in an industrial section of southern Asheville, North Carolina. The study area has relatively steep-sloped banks covered with herbaceous vegetation and shrubs (i.e., without trees), and is flanked by parking lots, a gas station, and an oil company. Substrate is primarily sand and embedded cobble and gravel, covered with a fine, oily layer of organic material; larger substrate is present, but it is typically large pieces of concrete rather than boulders. The macroconsumer assemblage is dominated by a mix of general insectivores [e.g., Tennessee shiner (Notropis leuciodus), warpaint shiner (Luxilus coccogenis), creek chub (Semotilus atromaculatus)], and omnivorous crayfishes (C. bartonii and C. robustus, Table 4.2).

Experimental design

During the summers of 1997 and 1998, 40 d electric exclusion experiments were conducted at the five study sites (two sites in 1997, three sites in 1998). Rainfall and temperature patterns were relatively similar between years (e.g., other than infrequent, brief rainfalls, significant storms did not occur during experiments in either year), and all experiments were conducted during low flow conditions.

Unglazed brown ceramic tiles (7.5 cm x 15 cm) were attached with cable ties and binder clips to polyvinylchloride (PVC) frames (0.25 m^2) lined with copper wire; each frame contained 6 or 8 tiles. Tiles were used as sampling substrates to provide standardized sampling units across the

five sites. However, tiles were more representative of habitat conditions at Jones, Beaverdam, and Sweeten (i.e., embedded substrate with few interstitial spaces), and may have artificially elevated macroconsumer predation at Ball and Davidson (i.e., where interstitial spaces were abundant).

Ten PVC frames (five pairs) were placed in run habitats at each site (Figure 4.3). Placement of pairs was determined by preliminary shear stress measurements taken with calibrated hemispheres (Statzner and Müller 1989). Water velocity and depth were measured with a Marsh McBirney® current meter [Marsh McBirney, Inc., Frederick, MD] and a meter stick at the four corners of each frame. Canopy cover was measured over the center of each frame with a spherical densiometer [Forest Densiometers, Bartlesville, OK].

To exclude macroconsumers, one frame in each pair was connected to a 6 V solar-powered fence charger (Parmak Model DF-SP-SS, Parker McCrory Manufacturing Company, Kansas City, MO) that delivered repeated pulses of electricity to the 0.25 m^2 frame area (Figure 4.3). These electric pulses prevented the entry of crayfishes and fishes, but did not adversely affect smaller organisms such as aquatic insect larvae. Many other studies have used this electric exclusion technique (e.g., Pringle and Hamazaki 1998, March et al. 2001), which avoids artifacts associated with traditional cage enclosure/exclosure experiments (e.g., reduced water flow and increased sedimentation). The unelectrified frame in each pair was accessible to macroconsumers and served as a control. Frames were placed approximately 0.5 m apart to minimize the influence of exclusion treatments on controls. 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 were also cleared of any accumulated debris every 5 d to minimize flow alterations and prevent loss of frames during spates.

Sampling

Water samples were taken every 5 d for nutrient analysis [NO_3-N, NH_4-N, and soluble reactive phosphorus (SRP)] and conductivity measurements. Total suspended solids were measured every day at Ball and Jones, and every 5 d at the remaining three sites. Continuous temperature data were collected during each experiment except the one at Jones.

Beginning on day 15, one tile was removed from each frame every 5 d (Ball and Jones were also sampled on days 5 and 10, but those data are not included here). 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 invertebrates and/or sediment. 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 ≥ 250 min at each site.

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, algae and sediment. Invertebrates were live-picked under a lighted magnifier and preserved in 70% ethanol. Given relatively low abundances at Ball, all invertebrates were picked at this site; at the remaining four sites, only large (≥ 4 mm) organisms were picked from whole samples. After invertebrates were removed, the volume of material scraped from each tile was brought to 500 ml and stirred continuously. In some cases, so much sediment had been deposited on tiles that homogenizing this material was impossible. This bulk sediment (usually coarse sand and gravel) was rinsed and brushed as well as possible, then placed in pans to be dried, weighed, and ashed. At Davidson, Jones, Beaverdam, and Sweeten, small invertebrates were picked from a 100 ml subsample and preserved for later identification. A 10 ml subsample was preserved in 2% formalin for periphyton composition analysis. Equal subsamples (10-100 ml) were filtered onto two pre-ashed glass fiber filters. One filter was used to determine ash-free dry mass (AFDM) and

inorganic sediment dry mass, and the other was used for chlorophyll *a* analysis. Sediment filters were dried for 24 h at 70 °C to obtain dry mass, then ashed at 500 °C for 1 h and reweighed to obtain AFDM. Bulk sediments underwent a similar process. Total sediments deposited on tiles were then calculated as AFDM + inorganic dry mass (from filters) + bulk sediment dry mass (from pans). Chlorophyll *a* filters were processed according to standard methods for fluorometric analyses (APHA 1985), and concentrations were measured with a Turner Designs 10-AU fluorometer.

Invertebrates were sorted into insect and non-insect taxa. Non-insect taxa were classified as mites, oligochaetes, limpets, or snails and counted. Insects were identified to the lowest practical level (usually family or genus) with a dissecting microscope (10X magnification), and sorted into functional feeding groups (Merritt and Cummins 1996). Individuals were measured to the nearest 0.5 mm with 1 mm grid paper. Biomass was calculated using family-specific length-mass regressions from Benke et al. (1999). Organisms < 1.5 mm were identified to order and were not included in functional feeding group analyses. To determine periphyton species 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, and taxa were classified according to growth form as either adnate, motile, or upright (J. Greenwood, UGA, *personal communication*).

Statistical analysis

Data were analyzed in two ways: (1) by combining data from all five experiments to examine overall response to macroconsumer exclusion across all five sites; and (2) by examining each site independently, to determine site-specific responses to exclusion. For cross-site analyses, two-factor (site and exclusion) MANOVAs and ANOVAs were used. If MANOVAs showed a significant effect ($P < 0.05$), univariate ANOVAs were run for each response variable. Tukey's HSD test was used to assess site-by-site differences.

Although site-specific responses would, to a certain extent, be reflected in the overall analyses (i.e., in site x exclusion interactions), separate analysis of each experiment allowed us to take into account the paired nature of our experimental design. Thus, for within-site analyses, paired t-tests (control versus exclusion) were run for parameters of interest. Bonferroni corrections were used when multiple paired t-tests were conducted on explicitly correlated data (e.g., algal assemblage proportions). These corrections were not used for insect functional feeding group analyses, as we were interested in the individual response of each functional group. Because a small proportion of tests may show significant results by chance any time numerous statistical tests are run (i.e., inflated Type I error), keeping in mind the number of paired comparisons conducted per site [11 at Ball; 20 at Davidson; 16 at Jones; 18 at Beaverdam; and 28 at Sweeten (total = 93 across all sites)] is helpful. *P*-values are given for each individual test interpreted to be statistically significant.

Repeated measures ANOVA was used to analyze chlorophyll *a*, AFDM, and total deposited sediment data for all days (day 15 to day 40),. Because chlorophyll *a* and AFDM tended to accumulate through time at each site (and because the number of samples that could be processed was limited) usually only day 40 data for algal and insect assemblages were analyzed. Two exceptions, however, were day 15 data at Jones and day 35 data at Sweeten. Given the somewhat anomalous chlorophyll *a* patterns observed at these sites, consideration of these additional days was necessary.

At Beaverdam, one replicate pair was excluded from all analyses because the exclusion treatment fence charger was not working properly; thus, there were only four replicate pairs at Beaverdam versus five replicate pairs at the remaining four sites. The only exception to this was insect samples at Davidson, which were also based on four replicate pairs (one control sample was misplaced). Insect shredders were included in total insect abundance and biomass values, but because they were relatively rare (shredders were collected in only 5 out of 46 total replicates),

they were omitted from functional feeding group analyses. One control replicate at Ball was a significant outlier [Dixon's test (Sokal and Rohlf 1995): $P < 0.01$] in terms of insect biomass, due to the presence of two large Pteronarcys stoneflies and one large Stenonema mayfly (biomass of three individuals = 7480 mg m^{-2}, versus total biomass of all other individuals in replicate = 55 mg m^{-2}). These three individuals were omitted from all biomass analyses. In addition, an exclusion replicate at Sweeten contained one large Stenonema (biomass = 623 mg m^{-2}) which was a significant outlier (Dixon's test: $P < 0.01$); this individual also was omitted from all biomass analyses.

Prior to all statistical analyses, Levene's test (Underwood 1997) was used to determine whether variances were equal. Where necessary, data were transformed [usually natural log, although occasionally square-root or inverse transformations were used; for proportional data, an arcsine square-root transformation was used (Zar 1999)]. Unless otherwise noted, $\alpha = 0.05$ for all analyses, and all were conducted in SAS® System for Windows™, Release 6.12 (SAS Institute, Cary, NC).

RESULTS

Across all sites, physical habitat characteristics were similar between control and exclusion treatments (MANOVA: Pillai's trace = 0.08, $F_{4,35} = 0.81$, $P = 0.527$), but there were significant differences among sites (Pillai's trace = 2.17, $F_{16,152} = 11.22$, $P < 0.0001$). Water velocity, water depth, shear stress, and canopy cover were all significantly different across sites (ANOVAs: $F_{4,38} \geq 9.06$, $P < 0.0001$; Table 4.3). Similarly, water quality variables demonstrated significant among-site differences (ANOVAs: $P < 0.0001$ for each variable). In general, water quality measures increased as one moved from relatively unaltered sites (Ball and Davidson) to more human-influenced watersheds (Beaverdam and Sweeten; Table 4.3). The total amount of sediment deposited on tiles did not differ between control and exclusion treatments across all sites

(rmANOVA: $F_{1,19} = 0$, $P = 0.953$). Comparison of mean sediment levels at each site indicated that there were significant differences among sites (Kruskal-Wallis test: $P < 0.001$), with relatively low sediment levels at Ball and Davidson and > 300-fold higher levels at Sweeten (Figure 4.4).

Observation of control and exclusion treatments (total observation time ≥ 250 minutes per site) indicated that the exclusion technique effectively excluded fishes and crayfishes at each site. Although macroconsumers occasionally entered exclusion treatments when the electricity was shut off for sampling, they exited immediately when fence chargers were reactivated. The following macroconsumers were observed in control replicates at each site: 5 crayfish at Ball; 20 sculpin at Davidson; 4 sculpin and 2 crayfish at Jones; 14 fishes at Beaverdam; and 11 fishes at Sweeten (fishes at Beaverdam and Sweeten were too small to identify reliably).

Chlorophyll* a *and AFDM

Chlorophyll *a* concentrations differed by more than two orders of magnitude across the five sites (Figure 4.5). In general, chlorophyll *a* tended to increase over time at each site; the only exception to this pattern was Jones, where chlorophyll peaked on day 15 and then decreased over the course of the experiment (Figure 4.5c). Accrual of AFDM was more variable, increasing over time at some sites but remaining essentially constant at others (Figure 4.6).

Analysis by repeated measures ANOVA showed site x exclusion interactions for both chlorophyll *a* and AFDM ($F_{4,19} = 4.33$, $P = 0.012$; $F_{4,19} = 4.12$, $P = 0.014$, respectively). When each site was analyzed independently, only Beaverdam showed a significant effect of exclusion on both chlorophyll *a* and AFDM (Table 4.4): chlorophyll *a* concentration and AFDM were greater in macroconsumer exclusion versus control treatments (Figures 4.5d and 4.6d). Exclusion also had a significant effect on AFDM at Jones, with greater AFDM in the exclusion treatment (Figure 4.6c and Table 4.4). Although chlorophyll *a* was consistently higher in exclusion versus

control treatments at Ball, this effect was not statistically significant ($P = 0.107$, Figure 4.5a and Table 4.4).

In general, similar results were obtained when chlorophyll *a* and AFDM data from day 40 were considered in isolation. However, an interesting pattern developed at Sweeten between days 35 and 40. Chlorophyll *a* concentrations were nearly equal in control and exclusion treatments on day 35, but chlorophyll was more than twice as high in the exclusion treatment by day 40 (Figure 4.5e). Response of chlorophyll *a* and AFDM to macroconsumer exclusion varied across sites, but at Ball, Beaverdam, Jones (for AFDM), and Sweeten there was a tendancy (at least by day 40) for levels to be greater in the absence of macroconsumers.

Algal biovolume

At all sites, algal assemblages were dominated by diatoms, which made up > 88% of total algal abundance and > 90% total algal biomass in every replicate. Abundance and biovolume differed by about two orders of magnitude across the five sites (Figure 4.7 and Table 4.5), and MANOVA showed a highly significant site effect (Pillai's trace = 0.63, $F_{8,76} = 4.33$, $P = 0.0002$). Subsequent ANOVAs indicated that both total abundance and biovolume were significantly different across sites (ANOVAs: $F_{4,38} \geq 10.82$, $P < 0.0001$). Although both abundance and biovolume tended to increase incrementally across the five sites (from Ball to Sweeten, Figure 4.7), only Ball had significantly lower abundance and biovolume relative to the other sites (Table 4.5). Because algal abundance and biovolume data generally showed similar trends, only biovolume data will be discussed further.

When macroconsumers were present (i.e., in controls), algal biovolume at each site was positively correlated with nutrients (NO_3-N, NH_4-N, SRP) and negatively correlated with % canopy cover (Table 4.6); in exclusion treatments, these relationships were not significant. Across all sites, macroconsumer exclusion did not have a significant effect on total algal biovolume (ANOVA: $F_{1,38} = 3.39$, $P = 0.074$). When sites were examined individually, only Ball

showed a significant effect of exclusion, with greater total biovolume in the exclusion versus control treatment (paired t-test: $|t_4| = 4.33$, $P = 0.006$; Figure 4.7b). However, this pattern was not consistent across sites. Total biovolume was greater in control versus exclusion treatments at Davidson, although this difference was not statistically significant ($|t_4| = 1.42$, $P = 0.114$; Figure 4.7b). This general lack of significant exclusion effects probably was at least partially related to high variability within each site: across all sites, coefficients of variation (CVs) for total algal biovolume ranged from 0.55 - 1.86. To examine compositional changes (and minimize the effect of total algal biovolume variability), proportional data for three physiognomic forms (adnate, motile, and upright algal taxa) were examined (Figure 4.8). Percentages of adnate, motile, and upright taxa showed a significant site x exclusion interaction (MANOVA: Pillai's trace = 0.63, $F_{12,114} = 2.51$, $P = 0.006$). Subsequent ANOVAs indicated that the proportion of each form differed significantly across sites (ANOVAs: $F_{4,38} \geq 8.67$, $P < 0.0001$). For example, upright diatom taxa dominated algal biovolume at Ball and Davidson, whereas motile diatom taxa made up a greater percentage of the biovolume at Jones, Beaverdam, and Sweeten (Figure 4.8 and Table 4.5).

Across all sites, macroconsumer exclusion had a significant effect on the proportions of adnate and upright taxa (ANOVAs: $F_{1,38} \geq 4.35$, $P \leq 0.044$), but not on the proportion of motile taxa (ANOVA: $F_{1,38} = 0.22$, $P = 0.640$). Adnate taxa tended to make up a greater percentage of total biovolume in control versus exclusion treatments at all sites (Figure 4.8). Upright taxa generally showed the opposite trend, although at Davidson and Jones the proportion of upright taxa was relatively similar between treatments (Figure 4.8).

When sites were analyzed independently, only Davidson, Beaverdam, and Sweeten demonstrated significant exclusion versus control differences in terms of algal composition. Adnate taxa (primarily Achnanthes spp. and Achnanthidium minutissima) comprised a significantly greater biovolume percentage in control versus exclusion treatments at both

Davidson and Beaverdam (paired t-tests: $|t_4| = 12.58$, $P < 0.0001$ for Davidson; $|t_3| = 5.56$, $P = 0.006$ for Beaverdam; Figure 4.8). This pattern also was evident at Sweeten ($|t_4| = 9.61$, $P = 0.0003$), but at this site proportions of motile and upright taxa differed between treatments as well. Motile diatom taxa (primarily Navicula and Nitzschia spp.) comprised a greater biovolume proportion in the control ($|t_4| = 6.19$, $P = 0.002$), whereas the proportion of upright taxa (primarily Melosira varians) was greater in the exclusion treatment ($|t_4| = 6.36$, $P = 0.002$; Figure 4.8).

Taxon-specific responses to exclusion did not always mirror overall physiognomic group responses. Dominant taxa at Davidson, Beaverdam, and Sweeten (defined as ≥ 2% total biovolume in either the control or exclusion treatment at a given site) are shown in Figure 4.9 (because Ball and Jones did not show differences in overall physiognomic groups, taxon-specific responses were not considered at these sites). Although adnate taxa as a whole demonstrated a significant response as a group at Davidson, only Eunotia spp. (an upright taxon) comprised significantly different biovolume proportions in control versus exclusion treatments (paired t-test: $|t_4| = 4.38$, $P = 0.006$; Figure 4.9a). At Beaverdam, the biovolume percentages contributed by Achnanthes and Cymbella spp. were significantly reduced in the exclusion treatment, whereas Surirella spp. increased significantly ($|t_3| \geq 5.56$, $P \leq 0.006$; Figure 4.9b). Five individual taxa showed significant exclusion responses at Sweeten: Achnanthes spp., Achnanthidium minutissima, Nitzschia spp., and Synedra spp. contributed smaller biovolume proportions in the exclusion treatment, while the proportion of Melosira varians increased ($|t_4| \geq 4.94$, $P \leq 0.004$; Figure 4.9c).

As mentioned earlier, chlorophyll *a* concentration at Jones peaked at day 15, then decreased throughout the experiment (Figure 4.5c). This pattern was not explained by total algal biovolume, which did not differ between days 15 and 40 (ANOVA: $F_{1,16} = 0.23$, $P = 0.637$). However, algal composition varied between days. The percentages of adnate, motile, and upright physiognomic forms were significantly different between days 15 and 40 (MANOVA: Pillai's

trace = 0.73, $F_{3,14}$ = 12.53, P = 0.0003). Motile taxa (primarily Navicula and Nitzschia spp.) increased from approximately 10% of total biovolume on day 15 to more than 30% on day 40 (ANOVA: $F_{1,16}$ = 14.68, P = 0.002), whereas upright taxa (primarily Cymbella and Synedra spp.) decreased from more than 55% of total biovolume on day 15 to approximately 25% by day 40 (ANOVA: $F_{1,16}$ = 35.11 P < 0.0001; Figure 4.10a).

The opposite pattern developed at Sweeten between days 35 and 40. Chlorophyll *a* levels nearly doubled in the exclusion treatment between day 35 and day 40, while levels in the control did not change (Figure 4.5e). Total algal biovolume in the exclusion treatment did not differ between days 35 and 40 (paired t-test: $|t_4|$ = 0.54, P = 0.309), but there was a compositional shift. Biovolume of motile diatom taxa (primarily Navicula and Nitzschia spp.) was proportionally greater on day 35 (paired t-test: $|t_4|$ = 3.93, P = 0.009), whereas the biovolume proportion contributed by upright diatom taxa (primarily Melosira varians) was higher on day 40 ($|t_4|$ = 5.36, P = 0.003; Figure 4.10b).

Macroconsumer effects on total algal biovolume differed across sites: at some sites (e.g., Ball, Beaverdam) biovolume was greater in exclusion treatments, whereas at other sites (e.g., Davidson) the opposite pattern held. Only at Ball did macroconsumers significantly reduce total algal biovolume. Compositional shifts were more consistent, as the proportion of adnate taxa (e.g., Achnanthes spp.) tended to decrease and the proportion of upright taxa (e.g., Melosira varians) tended to increase with macroconsumer exclusion across all sites. However, algal responses to macroconsumer exclusion were often taxon-specific.

Invertebrate abundance and biomass

Abundances of non-insect taxa (mites, snails, limpets, and oligochaetes) were highly variable both among and within sites (Table 4.7). Oligochaetes were not found at predominantly forested sites (Ball and Davidson), but were abundant at sites with greater watershed development (Beaverdam and Sweeten). In general, abundance of non-insect groups did not differ between

control and exclusion treatments at any site. However, mites were significantly more abundant in the exclusion versus control treatment at Davidson (paired t-test: $|t_3| = 5.22$, $P = 0.007$; Table 4.7). Oligochaetes tended to be more abundant in exclusion versus control treatments at Sweeten, but this difference was not statistically significant (paired t-test: $|t_4| = 1.65$, $P = 0.087$; Table 4.7).

There were significant cross-site differences in total insect abundance and biomass (MANOVA: Pillai's trace = 1.33, $F_{8,72} = 17.92$, $P < 0.0001$). Across sites, insect biomass in both control and exclusion treatments was positively correlated with nutrient concentrations (NO_3-N, NH_4-N, SRP) and negatively correlated with % canopy cover (Table 4.6); significant relationships were not seen for insect abundance. Insect abundance and biomass were lowest at Ball, while abundance and biomass were highest at Jones and Sweeten, respectively (both more than a ten-fold increase over Ball, Table 4.5). However, as with algal biovolume there was a great deal of variability within each site (CVs ranged from 0.41 - 0.82 for abundance and 0.41 - 1.46 for biomass across all sites).

Both abundance and biomass differed between control and exclusion treatments (MANOVA: Pillai's trace = 0.28, $F_{2,35} = 6.68$, $P = 0.004$). Overall, total insect abundance and biomass were significantly greater in macroconsumer exclusion versus control treatments (Table 4.8); this general trend held at all five sites for biomass, and at all sites except Jones for abundance (Figure 4.11). Because insect abundance and biomass generally showed similar trends (in terms of totals and functional feeding groups), only biomass data will be discussed in greater detail.

When biomass at each site was considered independently, significant control versus exclusion differences were seen at Ball (paired t-test: $|t_4| = 2.66$, $P = 0.028$), Davidson ($|t_3| = 3.28$, $P = 0.023$), Jones ($|t_4| = 2.51$, $P = 0.033$) and Beaverdam ($|t_3| = 2.80$, $P = 0.034$; Figure 4.11b). Functional feeding groups generally followed the same pattern as total insect biomass, and values were greater in exclusion versus control treatments at most sites (MANOVA: Pillai's trace = 0.39, $F_{4,33} = 5.22$, $P = 0.002$; Figure 4.12). Significant among-site differences were found for

gatherer, scraper, and predator biomass (Tables 4.5 and 4.8). Biomass of gatherers and predators also showed significant responses to exclusion across all sites, with greater biomass in macroconsumer exclusion versus control treatments (Figure 4.12b and 4.12d, Table 4.8). Significant site x exclusion interactions were not seen for total insect biomass or biomass of any functional feeding group (Table 4.8).

In contrast, functional feeding group responses to macroconsumer exclusion differed among sites when sites were examined independently. Only Ball showed significantly greater filterer (primarily hydropsychid caddisfly) biomass in the exclusion treatment (paired t-test: $|t_4| = 7.59$, $P = 0.0008$), although this trend was evident at all sites (Figure 4.12a). Gatherer (primarily non-Tanypodinae chironomid) biomass also was higher in exclusion treatments at each site, but only differences at Jones ($|t_4| = 4.48$, $P = 0.005$), Beaverdam ($|t_3| = 2.87$, $P = 0.032$), and Sweeten ($|t_4| = 2.31$, $P = 0.041$) were statistically significant (Figure 4.12b). Control and exclusion treatments differed in terms of predator biomass at Ball ($|t_4| = 2.72$, $P = 0.027$) and Beaverdam ($|t_3| = 4.70$, $P = 0.009$; Figure 4.12d); at Ball this response was largely to due to greater biomass of predatory stoneflies in the exclusion treatment, whereas at Beaverdam it resulted primarily from dipteran predators such as Tanypodinae chironomids. Scraper biomass was not significantly different between control and exclusion treatments at any site ($P \geq 0.118$; Figure 4.12c).

Given the somewhat anomalous chlorophyll *a* and algal composition patterns seen at Jones and Sweeten, insect biomass data for days 15 (at Jones) and 35 (at Sweeten) also were examined. At Jones, chlorophyll *a* in both the control and exclusion treatments peaked on day 15 and decreased throughout the experiment (Figure 4.5c). However, total insect biomass (averaged over both control and exclusion treatments) increased significantly between days 15 and 40 (ANOVA: $F_{1,16} = 11.45$, $P = 0.004$), primarily due to increases in gatherer biomass ($F_{1,16} = 71.00$, $P < 0.0001$; Figure 4.13a).

Chlorophyll *a* and algal composition at Sweeten showed marked changes between days 35 and 40 in the exclusion treatment (Figures 4.5e and 4.10b). Although total insect biomass in the exclusion treatment did not differ between days (paired t-test: $|t_4| = 0.49$, $P = 0.324$), there were differences among individual functional feeding groups. Between days 35 and 40, gatherer (primarily chironomid) biomass in the exclusion treatment increased significantly ($|t_4| = 3.33$, $P = 0.015$), whereas scraper (primarily baetid mayfly) biomass showed a significant decline ($|t_4| = 4.67$, $P = 0.005$; Figure 4.13b).

To summarize, macroconsumer exclusion showed remarkably similar patterns across the five study sites (Table 4.9). Although chlorophyll *a* and AFDM were not consistently elevated in exclusion treatments (only Jones and Beaverdam showed statistically significant relationships), at most sites there was a tendency (at least by day 40) towards higher levels in the absence of macroconsumers. Only Ball showed a significant effect of macroconsumer exclusion on total algal biovolume, with increased biovolume in the exclusion treatment; responses at other sites were highly variable. At all sites, the proportion of algal biovolume contributed by adnate taxa was consistently higher when macroconsumers were present, whereas upright taxa tended to decrease. In terms of insect biomass, macroconsumers consistently had a negative effect: across all sites, biomass was greater in exclusion versus control treatments. Total, gatherer, and predator biomass were significantly reduced in the presence of macroconsumers across all sites, and a similar tendency was seen with filterers, although this relationship was not statistically significant. Only scraper biomass at a single site showed even a tendency towards a positive macroconsumer effect (i.e., greater biomass in control versus exclusion).

DISCUSSION

Top-down effects of stream macroconsumers were not eliminated by changes associated with increasing watershed development. Macroconsumers (fishes and crayfishes) significantly

affected benthic communities at five sites representing a range of human watershed development, despite cross-site differences in physical, chemical, and biological characteristics. We predicted that alteration of factors such as macroconsumer assemblage composition, nutrient and light availability, and sedimentation with watershed development would cause exclusion responses to vary across sites (Figure 4.1). Contrary to our predictions, only two response variables (chlorophyll *a* and AFDM) showed statistically significant interaction (i.e., site x exclusion) effects, and responses to macroconsumer exclusion were frequently similar across sites.

At all five sites, response of insects to exclusion was remarkably consistent: irrespective of macroconsumer assemblage, exclusion resulted in greater insect abundance and biomass. None of the insect response variables demonstrated a significant site x exclusion interaction, and three variables (total, gatherer, and predator biomass) were significantly reduced by macroconsumers across all five sites. Given that the relative strength of top-down forces may be lessened at basal components of the food web (e.g., McQueen et al. 1986, Forrester et al. 1999), perhaps more surprising is that certain algal responses also were relatively consistent among sites. For example, the proportion of total algal biovolume composed of upright diatom taxa increased in macroconsumer exclusion treatments, whereas the proportion of adnate diatom taxa decreased. Our experimental design does not allow us to separate trophic and non-trophic interactions, so these results do not necessarily mean that macroconsumers at all sites consumed insects and algae; rather, it indicates that macroconsumer activity directly (e.g., by consumption) and/or indirectly (e.g., by alteration of food/habitat or accidental dislodgement) affected insect and algal assemblages at five streams differing in their extent of watershed development.

Because conductivity differed across the five sites (range = 13 - 109 $\mu S\ cm^{-1}$), strength of the electric exclusion technique varied somewhat among sites. In low conductivity water, the voltage gradient to which organisms are subjected (i.e., the number of volts / the distance between the two copper wire loops in each PVC frame) is relatively high. Thus, organisms feel a stronger

shock at low conductivity versus high conductivity sites, where the voltage gradient is reduced. This cross-site difference potentially raises two concerns: (1) fishes and crayfishes may not have been effectively excluded at higher conductivity sites; and (2) insects (especially larger ones) may have been adversely affected by the exclusion technique at lower, but not higher, conductivity sites. We did not observe any fishes or crayfishes in exclusion treatments, even at high conductivity sites. Perhaps more important, the observed significant differences between control and exclusion treatments at high conductivity sites indicates that fishes and crayfishes were effectively excluded. We found large insects in exclusion treatments at low and high conductivity sites, and consistently observed greater insect biomass in exclusion versus control treatments. These findings support the contention that large insects were not adversely affected by the exclusion technique at high or low conductivity sites. However, even if these concerns were founded (i.e., macroconsumers did enter exclusion treatments at high conductivity sites and large insects were reduced in exclusion treatments at low conductivity sites), our results, which showed significant effects of macroconsumer exclusion at each site, would only be an underestimation of actual macroconsumer effects.

The cross-site physical, chemical, and biological trends we observed were similar to those reported in numerous other studies examining anthropogenic alteration of streams. For example, water temperature, nutrient concentrations, total suspended solids, and deposited sediment generally increased from low development to high development sites, while % canopy cover decreased (Waters 1995, Bolstad and Swank 1997, Johnson et al. 1997, Herlihy et al. 1998). Insect assemblages became dominated by relatively tolerant taxa (e.g., chironomids and hydropsychids) as watershed development increased (Jones and Clark 1987), and sediment-tolerant diatoms (i.e., motile taxa) comprised a greater proportion of total algal biovolume (Kutka and Richards 1996, Hill et al. 2000). Fish assemblages shifted from predominantly benthic feeding, substrate-oriented species (i.e., mottled sculpin) to algivorous and more water column-

oriented species (Schlosser 1982, Weaver and Garman 1994, Rabeni and Smale 1995, Harding et al. 1998). Little is known about the influence of land use alteration on crayfish assemblages. Guiasu and Dunham (1999) found that C. robustus can outcompete C. bartonii for limited shelter (e.g., crevices under boulders), suggesting that C. robustus may be more tolerant of stream sedimentation and substrate embeddedness. Accordingly, C. robustus was collected only at the most developed study site (Sweeten), which had extremely high sediment levels and little unembedded substrate.

Light, nutrient, and temperature increases resulting from watershed development often stimulate algal and insect biomass (e.g., Jones and Clark 1987, Quinn et al. 1997). Both algal biovolume and insect biomass were significantly correlated with nutrient and light availability at each site (Table 4.6). For algal biovolume, this relationship was found only when macroconsumers were present. Across all sites algal biovolume in controls was positively correlated with nutrient concentrations and negatively correlated with % canopy cover, which indicates that algae responded to increased resource levels associated with watershed disturbance. In exclusion treatments this relationship did not hold, primarily because of the large increase in algal biovolume observed at Beaverdam (i.e., when Campostoma was excluded; Figure 4.7b). Correlations between insect biomass and light and nutrients levels were even more significant, and relationships were seen in both control and exclusion treatments. Insect biomass was consistently reduced by macroconsumers at all sites, indicating that biomass was significantly affected by top-down influences. Significant relationships between insect biomass and primary producer resources (i.e., light and nutrients) suggest that bottom-up influences also were important determinants of insect biomass, most likely due to increased algal standing crops providing increased food and/or habitat.

Predictions revisited

Ball Creek, Upper Davidson River, and Jones Creek

At Ball, Davidson, and Jones, we predicted that mottled sculpins and crayfishes would reduce biomass of non-predator insects (e.g., filterers and gatherers) via predation, but have minimal impact on larger insect predators (Figure 4.1a, b, and c). Overall, macroconsumer exclusion resulted in significantly greater total insect biomass at all three sites (Figure 4.14a, b and c). Filterer (primarily hydropsychid caddisfly) and gatherer (primarily chironomid) biomass tended to be greater in exclusion treatments at each site, although these differences were not always statistically significant. Although other studies have found that sculpins do not significantly affect insect abundance (e.g., Flecker 1984, Flecker and Allan 1984), insect abundance and biomass were reduced by sculpins and crayfishes in this study.

Hydropsychids and chironomids can comprise a large portion of mottled sculpin diets (Stouder 1990), and these relatively sessile taxa also may be heavily preyed upon by crayfishes (Momot 1995). Our results suggest that macroconsumer exclusion released these taxa from predation pressure, despite the fact that total macroconsumer density was relatively low (< 3 m^{-2} for crayfishes and fishes combined) at each site. However, fish density estimates are most likely underestimations of actual densities, as they were based on one-pass electroshocking data. For example, long-term studies at Ball Creek indicate that mottled sculpin density is approximately 0.7 m^{-2} (G. Grossman et al., UGA, *unpublished data*), versus the 0.2 m^{-2} estimate we obtained from one-pass electroshocking (Table 4.2)

Although macroconsumers did not significantly affect insect predator biomass at Davidson or Jones, biomass of predatory stoneflies increased with macroconsumer exclusion at Ball (Figure 4.14a). Mottled sculpins do not regularly consume large predatory stoneflies (Stouder 1990), which suggests that reduction of stonefly predators in the control was not related to direct trophic interactions. Instead, this treatment difference probably resulted from avoidance of sculpins by

stoneflies. Similar non-trophic interactions between predatory stoneflies and mottled sculpins have been found in other studies (e.g., Soluk and Collins 1988, Gibson 1999). At Davidson and Jones, predatory stoneflies were rare in both control and exclusion treatments.

Our predictions about macroconsumer effects on algal assemblages differed among Ball, Davidson, and Jones. We expected algal resources to be relatively scarce at Ball, and predicted that macroconsumers would have little influence on algae at this site. We anticipated greater algal standing stocks at Davidson and Jones, given increased light and nutrients at these sites. Thus, we predicted that macroconsumers would influence algal assemblages at both Davidson and Jones. However, we were unsure of the direction of this response, as both positive and negative effects were expected (e.g., direct reduction of algae by crayfish, coupled with indirect release of algae from insect grazing pressure).

Contrary to our predictions, macroconsumer exclusion affected total algal biovolume at Ball: biovolume was significantly greater in exclusion versus control treatments, despite relatively scarce algal resources (Figure 4.14a). A similar trend was seen with chlorophyll *a* concentration, although this relationship was not statistically significant. Algal composition did not differ between control and exclusion treatments, arguing against any kind of selective algal consumption by macroconsumers; however, omnivorous crayfish may have uniformly reduced diatom assemblages in the control treatment (Keller and Ruman 1998). Biomass of insect scrapers tended to be higher in control versus exclusion treatments, although this trend was not statistically significant (Figure 4.12c). This reduction of scraper (primarily Ephemeroptera) biomass in exclusion treatments may have resulted from increased biomass of predatory stoneflies (Figure 4.12d). Thus, the patterns observed in algal biovolume may have resulted from a trophic cascade: predatory stoneflies reducing insect scrapers in exclusion treatments, thereby increasing algal biovolume. Alternatively, increased algal biovolume may have been an indirect consequence of macroconsumer effects on hydropsychid caddisflies. Larval hydropsychid

caddisflies construct nets and use them to catch food particles. Hydropsychid abundance and biomass, and thus net surface area, were greater in the exclusion treatment. This increased net area may have led to increased surface area for algal entrainment and growth (O'Connor 1993), thereby increasing total algal biovolume.

At Davidson, we did not observe a significant difference in algal biovolume, chlorophyll *a*, or AFDM between control and exclusion treatments. However, Davidson was the only site that showed a decrease in total algal biovolume in the exclusion treatment, although this relationship was not statistically significant (Figure 4.14b). A weak trophic cascade may have occurred at Davidson, with macroconsumers reducing insect biomass in the control, thereby releasing algae from grazing pressure and increasing algal biovolume. Total algal abundance and biovolume were significantly higher at Davidson than at Ball, most likely because of differences in canopy cover and nutrient availability between the two sites. At Davidson, the enhancement of primary producers (through increased light and nutrients) may have enhanced the top-down influence of insects (Oksanen et al. 1981), thereby establishing a weak trophic cascade.

Algal composition at Davidson was significantly altered by macroconsumer exclusion. Adnate taxa (primarily Achnanthidium minutissima) comprised a greater proportion of total biovolume in control versus exclusion treatments at Davidson; this trend was evident at Ball and Jones, but these differences were not statistically significant. Grazing commonly leads to increased proportions of understory algae (Steinman 1996). Biomass of insect scrapers did not differ between control and exclusion treatments, so this increase in adnate taxa suggests that algal taxa may have been responding to reduced crayfish grazing pressure in exclusion treatments (Keller and Ruman 1998).

At Jones, algal abundance, biovolume, and composition were not affected by macroconsumer exclusion. Despite enhanced algal resources (relative to Ball and Davidson), the weak trophic cascade seen at Davidson was not observed at Jones (Figure 4.14c). In part this may have been a

reflection of different algal assemblages at the two sites. At Davidson, upright taxa dominated algal biovolume (~ 75%), and these taxa tend to be more susceptible to herbivory (Steinman et al. 1987, Steinman 1996). At Jones, algal biovolume was dominated by motile and adnate diatom taxa, which are generally considered less grazer-susceptible.

Differences between algal responses at Davidson and Jones also may have been related to sediment levels at each site. Sedimentation can reduce the influence of consumers on lower trophic levels (e.g., Barrett et al. 1982, Peckarsky 1985, Schofield et al., in review). At Davidson relatively little sediment deposited on tiles, but at Jones sediment levels were higher. Thus, sedimentation at Jones may have been a more significant influence on algal assemblages than insect herbivory. This possibility is bolstered by changes in algal composition over the course of the experiment. Jones was the only site at which chlorophyll *a* declined throughout the experiment, although total algal biovolume did not differ between days 15 and 40. Similar patterns were seen in control and exclusion treatments, which indicated that this trend was not a macroconsumer-mediated response. Rather, algal composition in both control and exclusion treatments shifted between days 15 and 40: motile diatom taxa comprised a greater proportion of total biovolume by day 40, while the proportion of upright taxa declined.

In contrast, daily addition of sand to Ball Creek resulted in the opposite pattern: the biovolume proportion of motile taxa decreased, while the proportion of upright taxa increased (Schofield et al., in review). Differences in sediment regime between the two experiments are most likely responsible for these opposite patterns. Motile diatom taxa generally are considered more sediment tolerant than other adnate or upright taxa, because they can reposition themselves on top of deposited sediment (Kutka and Richards 1996, Hill et al. 2000). However, motile taxa also tend to be more loosely attached to the substrate and may have been more readily scoured by daily addition of sediment and subsequent bedload transport in Ball Creek (Hudon and Legendre 1987, Peterson 1996).

Beaverdam Creek

Numerous studies have shown that the central stoneroller (Campostoma anomalum) can significantly affect both algal and insect assemblages (e.g., Gelwick and Matthews 1992, Vaughn et al. 1993, Gelwick and Matthews 1997). Because macroconsumer assemblages at Beaverdam were dominated by this algivorous fish, we predicted that reduced grazing pressure in the exclusion treatment would cause algae to increase. We also expected insect biomass to increase, as greater algal resources resulted in increased food and habitat availability and incidental ingestion and/or disruption were eliminated in exclusion treatments (Figure 4.1d). In general, both of these predictions were supported by our results. Chlorophyll *a* and AFDM were significantly higher in the macroconsumer exclusion treatment (Figure 4.14d), although differences between control and exclusion treatments only became pronounced after day 20. This contrasts with previous studies, which found that algal assemblages were altered by Campostoma within as quickly as five minutes (Power et al. 1988). This lag time is likely related to Campostoma density differences between the two study sites [< 2 m^{-2} in this study versus up to 50 m^{-2} in Power et al. (1988)]. Although total algal biovolume also increased with macroconsumer exclusion, high between-replicate variability obscured any statistically significant effect.

Significant differences in algal composition were observed between control and exclusion treatments. In the control (i.e., Campostoma grazed areas), adnate diatom taxa (primarily Achnanthes spp.) comprised a greater proportion of total algal biovolume. As mentioned earlier, this shift towards increased dominance of adnate, tightly adhering algae taxa is common in grazed systems (Vaughn et al. 1993, Steinman 1996). Although overall proportions of motile and upright taxa were not statistically different between control and exclusion treatments, individual taxa (e.g., Surirella and Cymbella spp.) demonstrated significant exclusion responses. These responses were not always consistent within physiognomic classifications. For example, the

proportion of upright Cymbella diatoms was significantly reduced by macroconsumer exclusion, whereas the proportion of Melosira varians, another upright taxon, tended to be elevated in the exclusion treatment (exclusion frames generally had long Melosira filaments hanging from them). This indicates that algal responses to macroconsumer exclusion were often taxon-specific, and suggests that broad physiognomic characteristics may be limited in reflecting actual susceptibility to grazing (Wellnitz and Ward 2000).

Macroconsumer exclusion also led to significant increases in total insect abundance and biomass, largely because of gatherer (primarily non-Tanypodinae chironomids) and predator (primarily Tanypodinae chironomids) responses. Previous studies have shown both increases [e.g., Gelwick et al. (1997)] and decreases [e.g., Gelwick and Matthews (1992)] in chironomid abundance with Campostoma exclusion. Here, Campostoma may have reduced chironomid abundance through alteration of food and shelter provided by algae, incidental ingestion, and/or dislodgement (Matthews et al. 1987). In addition, chironomids are common prey items for crayfish (Momot 1995, Whitledge and Rabeni 1997).

Sweeten Creek

Because macroconsumer density was relatively low (< 1.5 m^{-2} for fishes and crayfishes combined) and fish assemblages were dominated by water column species, we predicted that macroconsumers would have minimal effects on algae and insects at Sweeten Creek (Figure 4.1e). As expected, chlorophyll *a* and AFDM in control and exclusion treatments were not consistently different over the 40-day experiment, and total algal abundance and biovolume were similar between treatments on day 40. Total insect biomass tended to be greater in exclusion versus control treatments, but this difference was not statistically significant. Only insect gatherers (primarily chironomids) were significantly affected by macroconsumer exclusion, with greater biomass in exclusion versus control treatments by day 40 (Figure 4.14e). Contrary to our predictions, this indicates that macroconsumers significantly affected at least some benthic taxa.

Macroconsumers influenced chironomid biomass despite high sediment levels at Sweeten. In contrast, we found that daily addition of sediment to a forested stream eliminated macroconsumer effects (Schofield et al., in review). However, sediment regime in that study (i.e., daily addition) differed greatly from what was observed at Sweeten (i.e., most sediment was deposited on tiles early in the experiment, after a brief rainfall). In addition, insect assemblages at these sites were very different. Insects (e.g., chironomids) at Sweeten generally are sediment tolerant, whereas assemblages at the forested site were dominated by relatively sediment-intolerant taxa (e.g., mayflies and stoneflies). These sediment-tolerant taxa also are generally sessile, which may make them more susceptible to predation or dislodgement by macroconsumers. In disturbed systems, the expected decreases in top-down effects (e.g., due to shifts from benthic-feeding, substrate-associated fishes to more generalist, water column fishes) possibly may be offset by (1) increased susceptibility of tolerant, relatively sessile insect taxa (e.g., chironomids, hydropsychids) to macroconsumer effects, (2) increased macroconsumer feeding efficiency on relatively embedded substrates with few refugia (e.g., Brusven and Rose 1981), and/or (3) decreased availability of terrestrial insects due to alteration of riparian vegetation (e.g., Edwards and Huryn 1996, Nakano et al. 1999). As a result, generalist fishes may affect benthic insect assemblages in human-modified streams as significantly as obligate benthic-feeding fishes do in relatively unaltered systems.

Although total algal abundance and biovolume at Sweeten were not affected by macroconsumer exclusion, algal composition differed between control and exclusion treatments by day 40. In the exclusion treatment upright algal taxa comprised a greater proportion of total biovolume, while motile and adnate taxa were more dominant in the control. Insect scraper biomass did not differ between treatments, suggesting that this compositional shift was caused by macroconsumer effects. Decreases in upperstory taxa in the presence of macroconsumers may have resulted from herbivory [Campostoma were present in the stream, but at very low density (<

0.05 m^{-2})] or from incidental dislodgement and/or ingestion while preying upon chironomids (Steinman 1996). As at Beaverdam, taxon-specific responses to macroconsumer exclusion varied within these broad physiognomic groups. Most of the upperstory increase in the exclusion treatment was due to increases Melosira varians; other upright taxa, however, were significantly reduced with macroconsumer exclusion (e.g., Synedra spp.).

Chlorophyll *a* concentration did not differ consistently between control and exclusion treatments over the entire experiment, but a significant difference had developed by day 40. Between days 35 and 40 chlorophyll *a* in the exclusion treatment nearly doubled, while levels in the control did not change. Total algal biovolume on days 35 and 40 did not differ, but algal composition varied significantly: the biovolume proportion contributed by motile taxa decreased by day 40, while the proportion of upright taxa increased. This increase in upperstory taxa coincided with a decrease in insect scraper biomass (primarily baetid mayflies), which suggests that changes in chlorophyll *a* and algal composition in the exclusion treatment were mediated by insect scrapers. Gatherer (primarily chironomid) biomass in the exclusion treatment also increased between days 35 and 40, potentially because of increased habitat provided by upperstory algae (Creed 1994, Wootton et al. 1996). Thus, day 40 differences in chironomid biomass between control and exclusion treatments probably resulted from (1) direct macroconsumer effects on chironomids, and (2) indirect effects of insect scrapers. Abiotic factors (e.g., discharge, sediment) did not differ during this five-day period, suggesting that direct and indirect biotic interactions (between algae, baetids, and chironomids) influenced the expression of top-down control. Had we only examined data from day 40, we would not have detected these species interactions. These between-day differences demonstrate that there can be significant temporal variation in top-down effects over relatively brief time periods, suggesting that the detection of significant macroconsumer effects may be very dependent on both experimental duration and sampling frequency.

Conclusions

Macroconsumers consistently affected lower trophic levels in streams representing a range of human watershed development, despite physical, chemical, and biological differences between study sites. This indicates that macroconsumers can be important top-down interactors in southern Appalachian streams, and that this role is not necessarily eliminated by in-stream changes associated with human development (e.g., decreased abundance of obligate benthic fishes, sedimentation). Although certain effects of watershed land use may tend to decrease the strength of top-down interactions, these reductions may be offset by other concurrent changes. For example, the abundance of relatively tolerant insect taxa (e.g., chironomids, hydropsychids) tends to increase in human-modified streams, and these relatively sessile taxa may be more susceptible to macroconsumer predation. In addition, increased light and nutrient availability these systems may enhance top-down effects. Thus, human modification of the landscape can influence the spatial and temporal variability of top-down interactions via multiple pathways. Although many studies have examined direct effects of watershed development and associated in-stream changes, few have considered the repercussions of these changes for species interactions (Paul and Meyer 2001). Given the potential importance of top-down interactions in determining stream structure and function, and the prevalence of anthropogenic watershed disturbance, further examination of this issue will greatly improve our understanding of stream ecosystems in a human-modified world.

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Table 4.1. Watershed characteristics at the five study sites (1990 data). Sites represent a range of human watershed development, from undeveloped watersheds on the left (Ball and Davidson) to more developed watershed on the right (Beaverdam and Sweeten). All sites are located in the Little Tennessee River or French Broad River drainages in western North Carolina, USA.

CHARACTERISTIC	BALL	DAVIDSON	JONES	BEAVERDAM	SWEETEN
Watershed area (ha)	711	1830	4317	1927	1401
Elevation (m)	689	791	665	644	604
Distance to headwaters (km)	3.96	5.74	10.06	6.39	6.88
% Forested -- total	100	100	95	88	41
% Non-forested -- 30 m buffer [1]	0	0	14	21	60

[1] 30 m buffer for 1 km reach upstream of study site.

Table 4.2. Macroconsumer assemblages at the five study sites. Sites represent a range of human watershed development, from undeveloped watersheds on the left (Ball and Davidson) to more developed watersheds on the right (Beaverdam and Sweeten).

MACROCONSUMER	BALL	DAVIDSON	JONES	BEAVERDAM	SWEETEN
CRAYFISHES[1]					
Species	*Cambarus bartonii*	*Cambarus bartonii* *Cambarus robustus*	*Cambarus bartonii* *Cambarus georgiae*	*Cambarus bartonii*	*Cambarus bartonii* *Cambarus robustus*
Density[2] (# m^{-2})	2.1	1.6	1.1	2.2	0.6
FISHES[3]					
Total # species	6	3	9	11	15
Species[4]	Mottled sculpin (74) Rosyside dace (12) Rainbow trout (7) Longnose dace (5)	Mottled sculpin (74) Longnose dace (20) Blacknose dace (6)	Mottled sculpin (81) Tennessee shiner (6) Rosyside dace (5)	Central stoneroller (76) Redbreast sunfish (7) Northern hogsucker (5)	Tennessee shiner (28) Warpaint shiner (19) Blacknose dace(19) Creek chub (10)
Density[2] (# m^{-2})	0.2	0.2	0.9	1.9	0.7

[1] Crayfishes were sampled twice at each site (Summer and Autumn 1999) using a 1 m^2 quadrat sampler.
[2] Total density, all species.
[3] Fishes were sampled with a backpack electroshocker (one-pass) at the conclusion of each experiment.
[4] Only species representing ≥ 5% total individuals caught are listed; % given in parentheses.

Table 4.3. Physical and chemical parameters for each experiment. Physical parameters were measured at the start of each experiment; chemical parameters were measured throughout each experimental period. Values represent mean ± 1 SE. For physical parameters, n = 5 at all sites except Beaverdam (n = 4). For chemical parameters, numbers in brackets indicate sample size for each value. Letters beside brackets denote significant differences among sites by Tukey's HSD Test (i.e., sites with the same letter are not statistically different at an overall $\alpha = 0.05$). na = not available (temperature data were not recorded at Jones).

PARAMETER	BALL	DAVIDSON	JONES	BEAVERDAM	SWEETEN
Duration of experiment	7/29-9/8/97	6/29-8/8/98	7/31-9/9/97	7/1-8/10/98	6/30-8/9/98
Physical parameters					
Canopy cover (%)	85.9 ± 1.0 [a]	77.1 ± 4.9 [ab]	59.1 ± 3.2 [c]	67.8 ± 5.7 [bc]	16.1 ± 2.5 [d]
Water depth (m)	0.17 ± 0.01 [ab]	0.20 ± 0.02 [b]	0.20 ± 0.01 [b]	0.12 ± 0.01 [c]	0.14 ± 0.01 [ac]
Water velocity (m s^{-1})	0.23 ± 0.01 [a]	0.12 ± 0.02 [b]	0.33 ± 0.02 [c]	0.20 ± 0.01 [a]	0.16 ± 0.02 [ab]
Shear stress (dyn cm^{-2})	86.4 ± 2.8 [a]	80.3 ± 7.8 [ac]	149.9 ± 7.2 [b]	54.7 ± 0 [c]	77.4 ± 8.2 [ac]
Chemical parameters					
Water temp (°C) [1]	17.5 ± 0.2 [41] [a]	18.1 ± 0.1 [38] [b]	na	22.8 ± 0.1 [40] [c]	23.3 ± 0.2 [40] [c]
Temp range (°C) [2]	1.2 ± 0.1 [41] [a]	1.7 ± 0.1 [38] [b]	na	4.1 ± 0.2 [40] [c]	3.5 ± 0.1 [40] [d]
TSS (mg L^{-1})	7.5 ± 0.4 [40] [a]	4.5 ± 0.3 [7] [a]	8.0 ± 0.5 [40] [a]	10.1 ± 1.7 [8] [a]	20.8 ± 4.3 [8] [b]
Conductivity (μS cm^{-1})	13.5 ± 0.0 [3] [a]	14.5 ± 0.1 [7] [a]	33.6 ± 0.3 [3] [b]	71.7 ± 0.9 [6] [c]	109 ± 1.8 [7] [d]
NO_3-N (mg L^{-1})	0.04 ± 0.00 [9] [a]	0.13 ± 0.00 [7] [b]	0.10 ± 0.01 [9] [c]	0.33 ± 0.01 [6] [d]	0.86 ± 0.04 [7] [e]
NH_4-N (mg L^{-1})	0.003 ± 0.001 [9] [a]	0.003 ± 0.000 [7] [a]	0.006 ± 0.001 [9] [a]	0.008 ± 0.001 [6] [a]	0.249 ± 0.023 [7] [b]
SRP (mg L^{-1}) [3]	0.008 ± 0.002 [9] [a]	0.014 ± 0.001 [7] [a]	0.011 ± 0.001 [9] [a]	0.027 ± 0.002 [6] [b]	0.079 ± 0.006 [7] [c]

[1] Daily maximum temperature
[2] Daily maximum - daily minimum temperature
[3] Soluble reactive phosphorus

Table 4.4. Results of repeated measures ANOVAs for chlorophyll *a* (μg m^{-2}) and AFDM (g m^{-2}) on days 15-40, when each site was analyzed independently. Site represent a range of human watershed development, from 100% forested watersheds (Ball and Davidson) to watersheds < 50% forested (Sweeten). Exclusion refers to treatment differences between macroconsumer (fishes and crayfishes) access and macroconsumer exclusion treatments.

		EXCLUSION		**DAY**		**EXCLUSION x DAY**	
REPSONSE VARIABLE	**SITE**	$\mathbf{F_{1,8}}$	***P***	$\mathbf{F_{5,40}}$	***P***	$\mathbf{F_{5,40}}$	***P***
Chlorophyll *a* (μg m^{-2})	Ball	3.30	0.107	29.31	< 0.0001	2.45	0.094
	Davidson	0.04	0.849	16.25	< 0.0001	1.41	0.258
	Jones	0.19	0.671	14.60	< 0.0001	0.45	0.699
	Beaverdam [1]	6.08	0.049	10.20	0.002	3.02	0.077
	Sweeten	1.89	0.206	16.69	< 0.0001	1.72	0.191
AFDM (g m^{-2})	Ball	1.25	0.296	17.61	< 0.0001	0.34	0.810
	Davidson	0.00	0.952	3.02	0.050	0.84	0.484
	Jones	11.97	0.009	1.92	0.162	0.69	0.552
	Beaverdam [1]	8.89	0.025	3.15	0.067	3.55	0.050
	Sweeten	0.37	0.560	10.19	< 0.0001	2.43	0.075

[1] Because there were 4 replicates at Beaverdam (vs. 5 at other sites), degrees of freedom for this site were treatment = $F_{1,6}$, day and treatment x day = $F_{5,30}$.

Table 4.5. Among-site differences in algal abudance and biovolume and insect abundance and biomass on day 40 of each experiment. Values represent overall means for control and exclusion replicates ± 1 SE; n = 10 at all sites except for algal and insect values at Beaverdam and insect values at Davidson (n = 8). Letters denote significant differences among sites by Tukey's HSD Test (i.e., sites with the same letter are not statistically different at an overall $\alpha = 0.05$).

RESPONSE VARIABLE	BALL	DAVIDSON	JONES	BEAVERDAM	SWEETEN
Algal abundance (# $cm^{-2} * 10^{-3}$)					
Total	28.0 ± 8.8 ^{a}	217.7 ± 86.4 ^{b}	300.8 ± 109.6 ^{b}	1218.9 ± 717.8 ^{b}	2094.1 ± 951.9 ^{b}
Algal biovolume (μm^3 $cm^{-2} * 10^{-5}$)					
Total	96.8 ± 40.2 ^{a}	520.8 ± 201.4 ^{b}	784.5 ± 269.9 ^{b}	5635.2 ± 3741.9 ^{b}	9124.7 ± 4354.3 ^{b}
% Adnate	0.18 ± 0.02 ^{a}	0.13 ± 0.01 ^{a}	0.42 ± 0.05 ^{b}	0.17 ± 0.04 ^{a}	0.05 ± 0.01 ^{c}
% Motile	0.19 ± 0.02 ^{ab}	0.14 ± 0.03 ^{b}	0.33 ± 0.06 ^{ac}	0.33 ± 0.03 ^{ac}	0.40 ± 0.05 ^{c}
% Upright	0.62 ± 0.02 ^{ab}	0.74 ± 0.02 ^{b}	0.25 ± 0.03 ^{c}	0.50 ± 0.04 ^{a}	0.55 ± 0.05 ^{a}
Insect abundance (# m^{-2})					
Total	1680 ± 288 ^{a}	18291 ± 3766 ^{bc}	27253 ± 5941 ^{b}	16439 ± 4352 ^{bc}	10064 ± 1766 ^{c}
Insect biomass (mg m^{-2})					
Total	155.1 ± 42.2 ^{a}	500.8 ± 214.1 ^{ab}	981.5 ± 198.6 ^{bc}	879.5 ± 204.6 ^{bc}	2114.0 ± 910.2 ^{c}
Filterers	28.5 ± 11.8 ^{a}	134.8 ± 116.1 ^{a}	196.6 ± 99.5 ^{a}	40.6 ± 21.0 ^{a}	894.0 ± 623.1 ^{a}
Gatherers	57.5 ± 11.9 ^{a}	250.9 ± 78.7 ^{b}	486.9 ± 80.6 ^{bc}	606.0 ± 187.6 ^{bc}	675.2 ± 105.1 ^{c}
Scrapers	2.6 ± 1.2 ^{ab}	27.2 ± 15.7 ^{bc}	104.0 ± 40.2 ^{cd}	159.7 ± 23.8 ^{d}	14.1 ± 8.1 ^{a}
Predators	57.3 ± 27.3 ^{a}	70.4 ± 31.9 ^{ab}	171.9 ± 74.0 ^{b}	66.5 ± 8.0 ^{ab}	530.6 ± 290.3 ^{b}

Table 4.6. Correlation coefficients and significance values for nutrient concentrations and % canopy cover versus algal biovolume and insect biomass, in control and exclusion treatments. Each correlation is based on five points (each point = mean of control or exclusion replicates at each site for each parameter versus mean nutrient concentration or % canopy cover at that site). Correlation is positive unless marked with a negative sign (-).

		NO_3-N		NH_4-N		SRP		% Canopy cover	
VARIABLE	**TREATMENT**	r^2	***P***	r^2	***P***	r^2	**P**	r^2	***P***
Algal biovolume	Control	0.97	0.002	0.97	0.002	0.99	0.001	0.90 (-)	0.015
	Exclusion	0.56	0.147	0.27	0.366	0.48	0.195	0.36 (-)	0.282
Insect biomass	Control	0.84	0.030	0.85	0.027	0.84	0.028	0.99 (-)	< 0.0001
	Exclusion	0.89	0.015	0.83	0.033	0.88	0.018	0.98 (-)	0.001

Table 4.7. Abundance (# m^{-2}) of non-insect taxa on day 40 at the five study sites. Values represent mean ± 1 SE; n = 5 at all sites except Davidson and Beaverdam (n = 4).

SITE	TREATMENT	MITES	SNAILS	LIMPETS	OLIGOCHAETES
Ball	Control	36 ± 22	0	0	0
	Exclusion	71 ± 52	0	0	0
Davidson	Control	2400 ± 509	0	0	0
	Exclusion	5889 ± 1032	0	0	0
Jones	Control	89 ± 89	0	267 ± 178	196 ± 174
	Exclusion	89 ± 89	0	284 ± 240	0
Beaverdam	Control	333 ± 213	200 ± 99	322 ± 164	111 ± 111
	Exclusion	111 ± 111	156 ± 76	329 ± 193	229 ± 175
Sweeten	Control	0	18 ± 18	209 ± 128	1631 ± 190
	Exclusion	0	0	249 ± 248	3173 ± 890

Table 4.8. Results of individual ANOVAs for total insect abundance and biomass and functional feeding group biomass on day 40, across all sites.

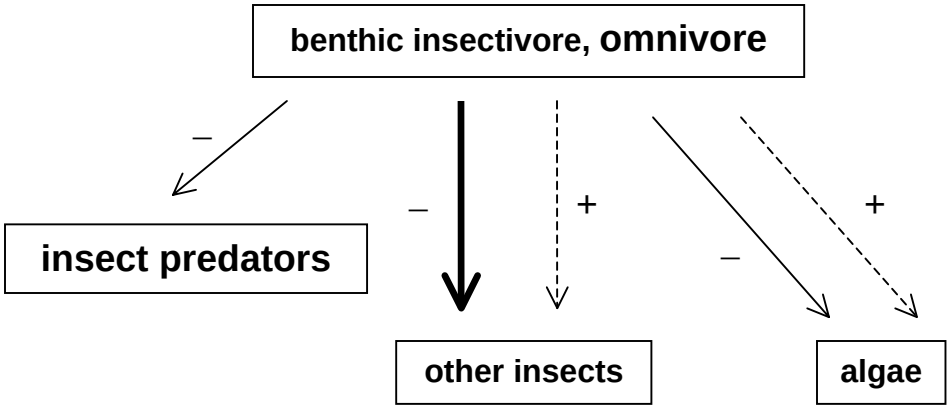
	SITE		EXCLUSION		SITE x EXCLUSION	
VARIABLE	$\mathbf{F_{4,36}}$	***P***	$\mathbf{F_{1,36}}$	***P***	$\mathbf{F_{4,36}}$	***P***
Total abundance (# m^{-2})	28.70	< 0.0001	10.64	0.002	0.85	0.505
Total biomass (mg m^{-2})	14.47	< 0.0001	12.50	0.001	0.61	0.659
Filterers	1.03	0.404	3.20	0.082	0.61	0.658
Gatherers	18.62	< 0.0001	19.42	< 0.0001	1.02	0.411
Scrapers	9.01	< 0.0001	0.17	0.685	0.72	0.584
Predators	4.90	0.003	5.01	0.032	1.42	0.247

Table 4.9. Summary of exclusion results at five study sites. – indicates macroconsumer exclusion led to a decrease in a given parameter (control > exclusion); + indicates macroconsumer exclusion led to an increase in a given parameter (control < exclusion); 0 indicates macroconsumers generally had no effect (control ≈ exclusion). † indicates that an overall significant effect was seen across all five sites. * denotes statistically significant relationship at $\alpha = 0.05$ level within a given site (for % data, $\alpha = 0.05/3 = 0.017$).

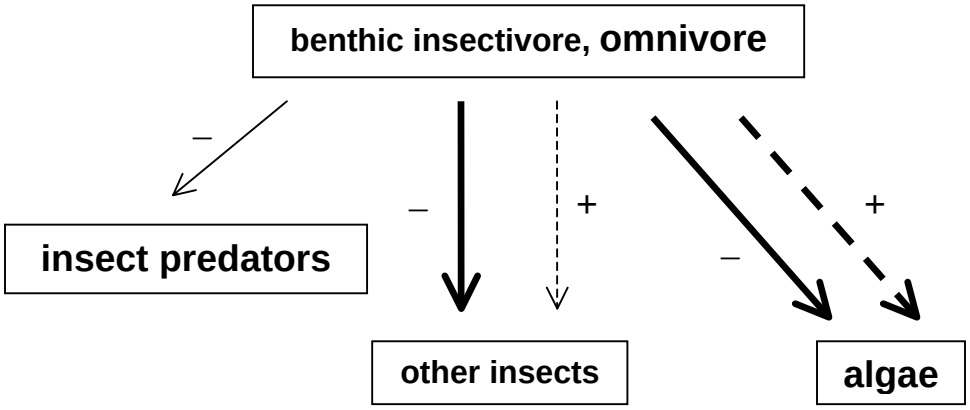
RESPONSE VARIABLE	BALL	DAVIDSON	JONES	BEAVERDAM	SWEETEN
Chlorophyll *a*	+	0	0	+ *	0
AFDM	+	0	+ *	+ *	0
Algal biovolume					
Total	+	–	+	+	0
% Adnate †	–	– *	–	– *	– *
% Motile	+	+	+	+	– *
% Upright †	0	0	0	+	+ *
Insect biomass					
Total †	+ *	+ *	+ *	+ *	+
Filterers	+ *	+	+	+	+
Gatherers †	+	+	+ *	+ *	+ *
Scrapers	–	+	+	0	0
Predators †	+ *	+	+	+ *	0

Figure 4.1. Predicted outcomes of macroconsumer exclusion experiments at each site. Text size indicates relative biomass (high versus low) of different biotic components across five sites. Solid arrows represent direct effects of macroconsumers, while dashed arrows represent indirect effects (i.e., effects mediated through insect consumers); bold arrows indicate interactions likely to be significant. Signs adjacent to arrows indicate positive (+) or negative (-) effect of macroconsumers. At Ball (1a), macroconsumers were expected to reduce biomass of insect filterers and gatherers. Given relatively scarce algal resources at this site, effects on algae were expected to be minimal. Similar effects on insect biomass were expected at Davidson (1b) and Jones (1c); given greater algal resources at these sites, macroconsumers also were expected to significantly iinfluence algal assemblages (both positively and negatively). At Beaverdam (1d), algivorous macroconsumers were expected to significantly reduce algae (via ingestion) and insects (via incidental ingestion or disruption). At Sweeten (1e), relatively low densities of general insectivores (i.e., not obligate benthic-feeding species) and omnivores were not expected to significantly affect benthic insect biomass or algal resources.

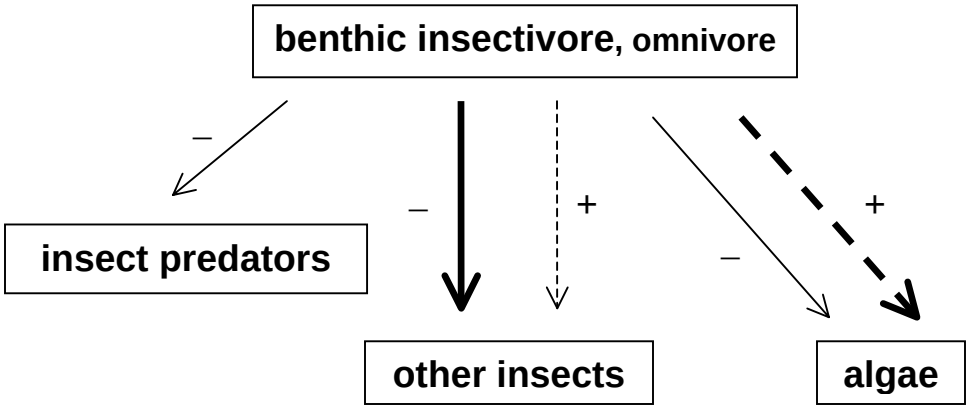
a. Ball



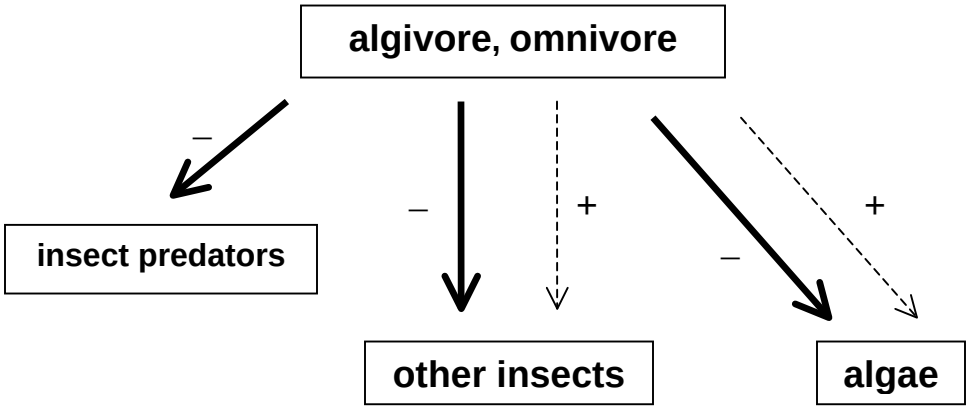
b. Davidson



c. Jones



d. Beaverdam



e. Sweeten

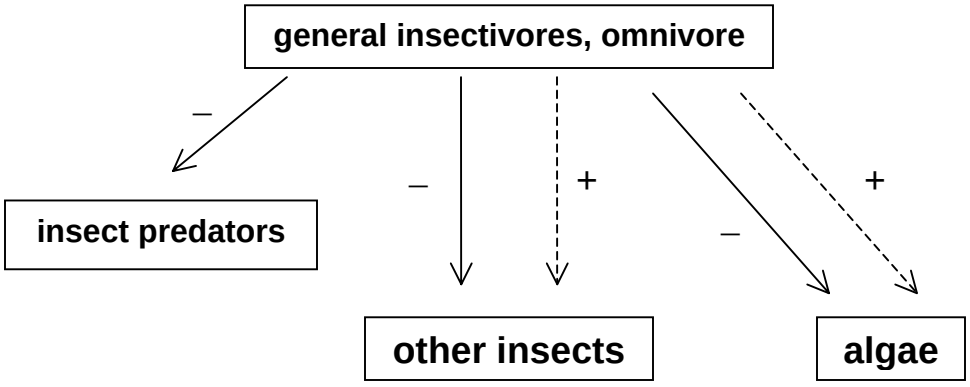


Figure 4.2. Map of the five study sites. Lower Ball Creek and Jones Creek are in the Little Tennessee River drainage, while Upper Davidson River, Beaverdam Creek, and Sweeten Creek are in the French Broad River drainage.

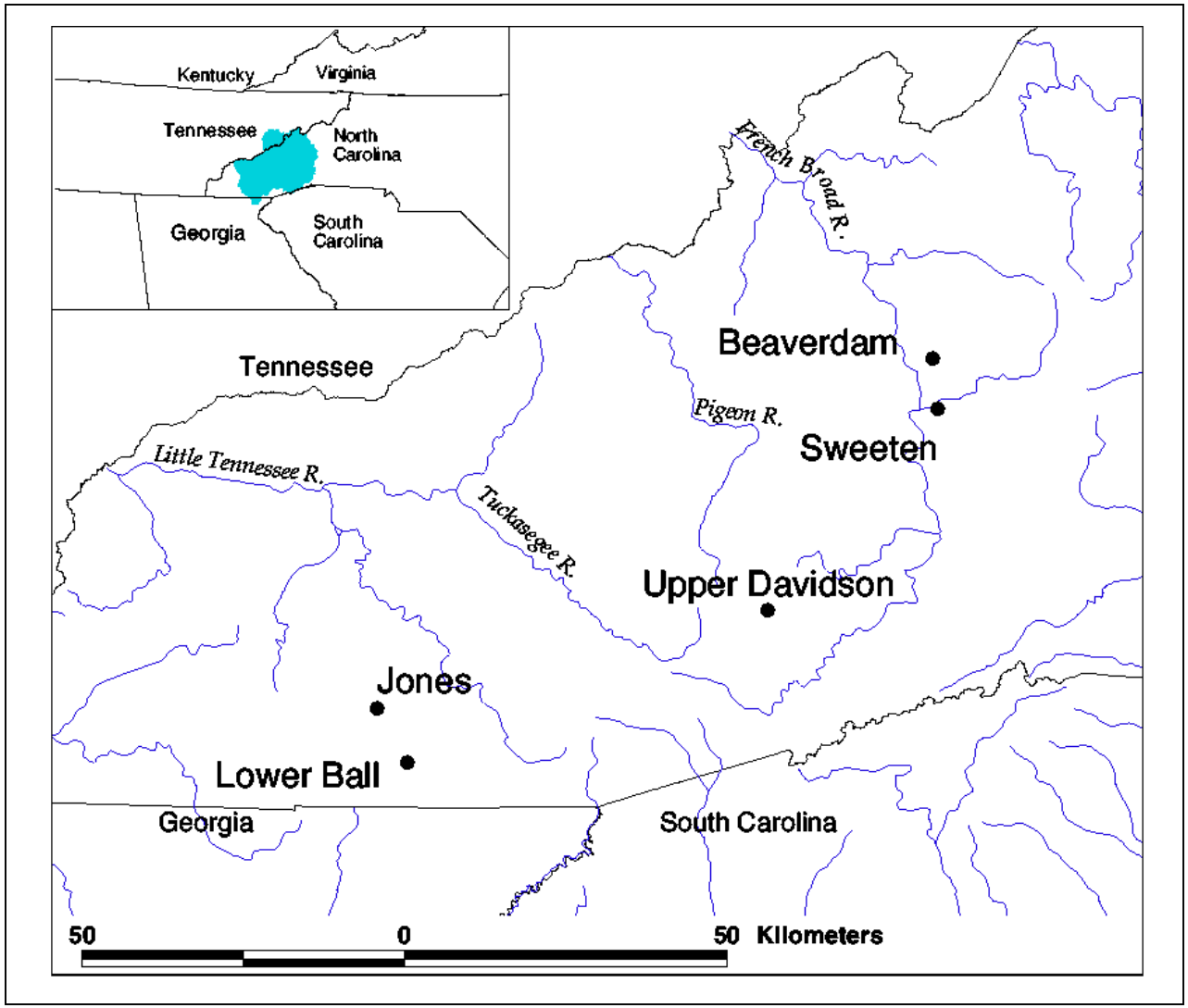

Kentucky
Virginia
Tennessee
North Carolina
Georgia
South Carolina
French Broad R.
Beaverdam
Tennessee
Pigeon R.
Sweeten
Little Tennessee R.
Tuckasegee R.
Upper Davidson
Jones
Lower Ball
Georgia
South Carolina
50
0
50 Kilometers

Figure 4.3. Illustration of the experimental design (figure not to scale). White squares represent frames to which macroconsumers had access (i.e., control treatment); gray squares represent frames from which macroconsumers were excluded (i.e., exclusion treatment). An exclusion experiment was conducted in each of five streams (Ball, Davidson, Jones, Beaverdam, and Sweeten), which varied in their amount of watershed development (0% to > 50% of non-forested watershed area.

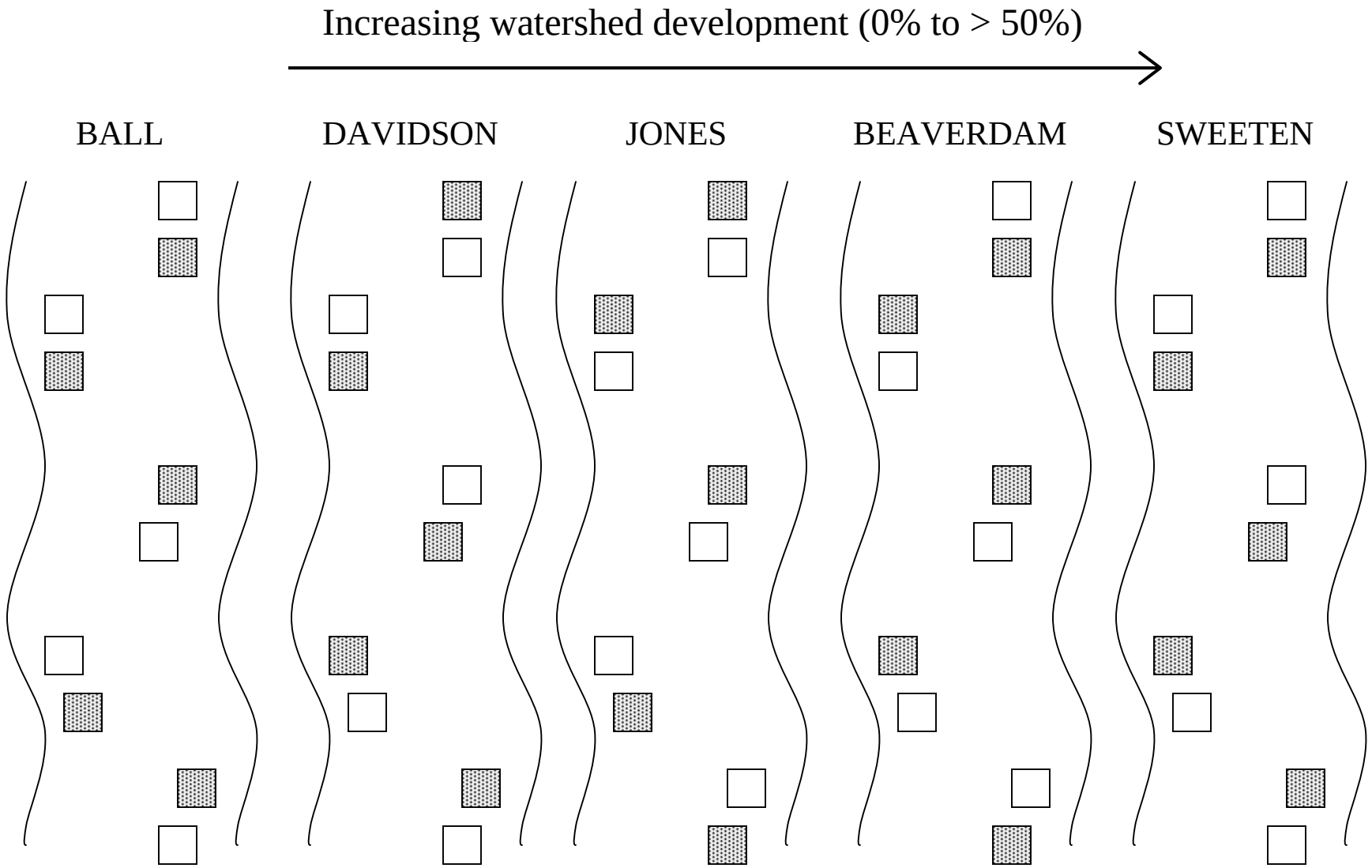

Increasing watershed development (0% to > 50%)
BALL
DAVIDSON
JONES
BEAVERDAM
SWEETEN

Figure 4.4. Total sediment deposited on tiles (g m^{-2}) at each site. Each value represents mean of control and exclusion treatments over days 15 - 40, + 1 SE. Letters above each bar indicate significant site differences as determined by Tukey's HSD test (i.e., sites with the same letter are not statistically different). B = Ball, D = Davidson, J = Jones, V = Beaverdam, S = Sweeten.

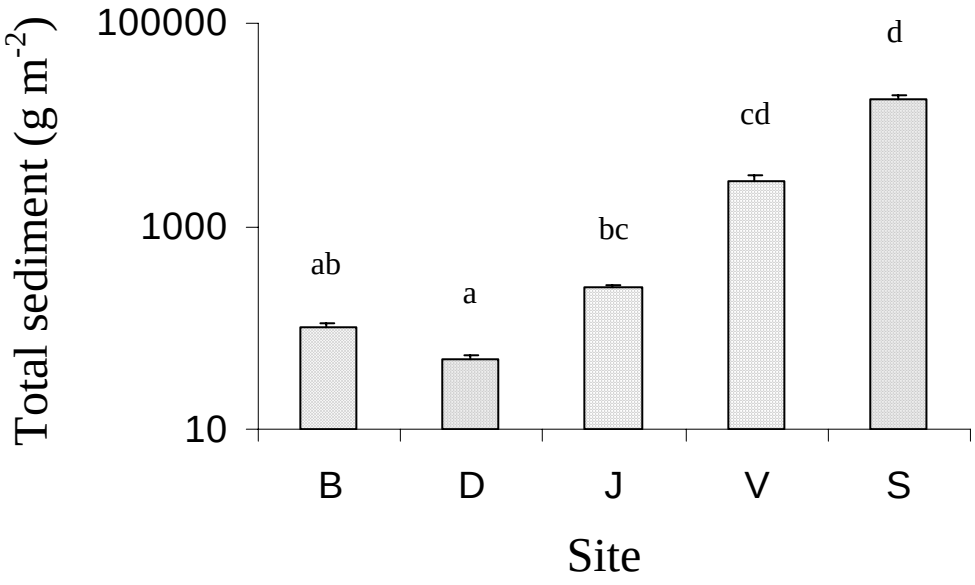
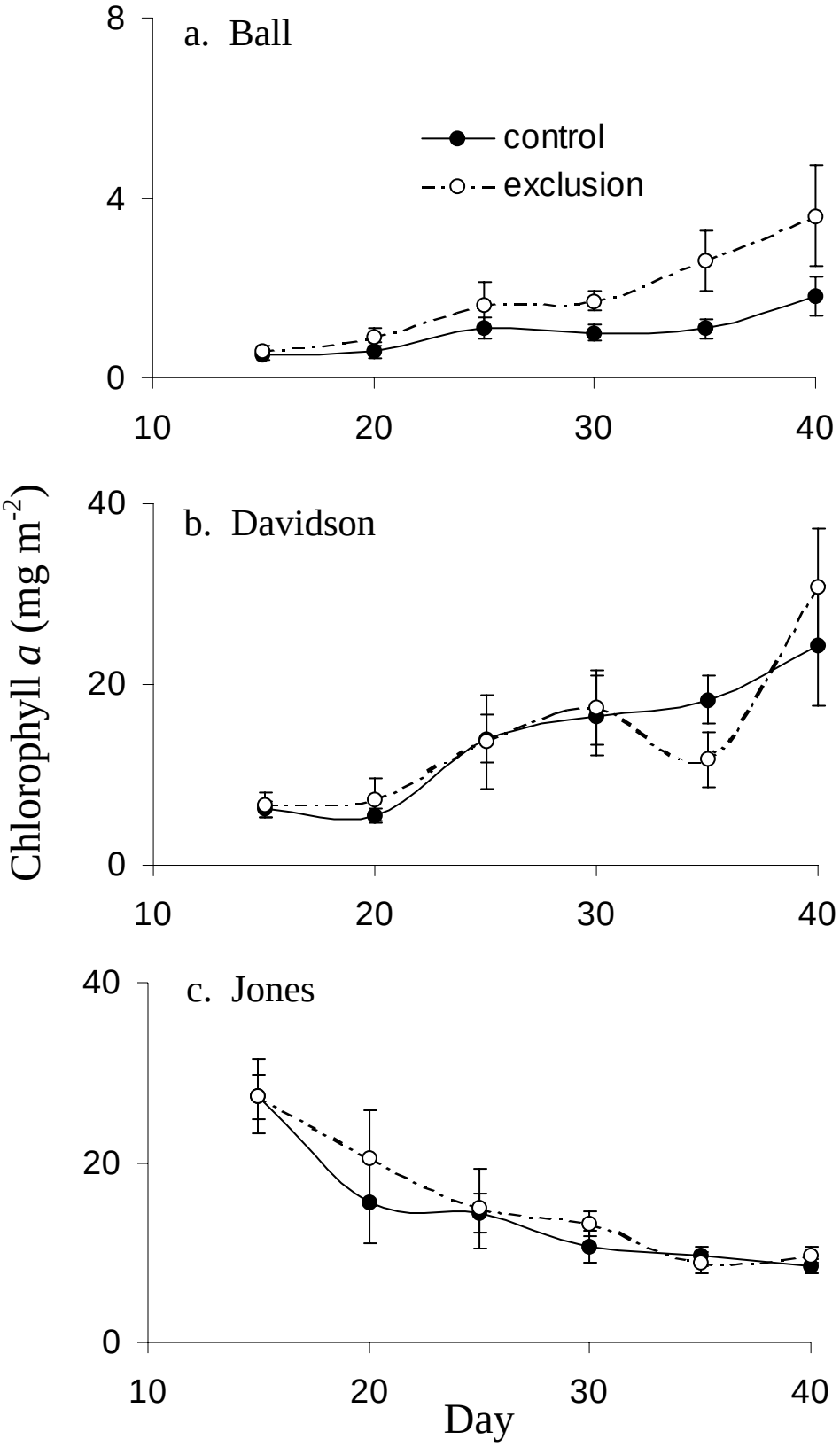

100000
1000
10
Total sediment (g m-2)
ab
a
bc
cd
d
B
D
J
V
S
Site

Figure 4.5. Chlorophyll *a* concentration (mg m^{-2}) on days 15 - 40 at (a) Ball, (b) Davidson, (c) Jones, (d) Beaverdam, and (e) Sweeten. Each point represents mean of five replicates ± 1 SE, except for Beaverdam (mean of four replicates ± 1 SE); note the differences in scale between y-axes. Only Beaverdam (d) showed a significant effect of exclusion through time (repeated measures ANOVA: $F_{1,6} = 6.08$, $P = 0.049$).


a. Ball
control
exclusion
b. Davidson
c. Jones
Chlorophyll a (mg m-2)
Day
0
4
8
20
40
10
20
30
40

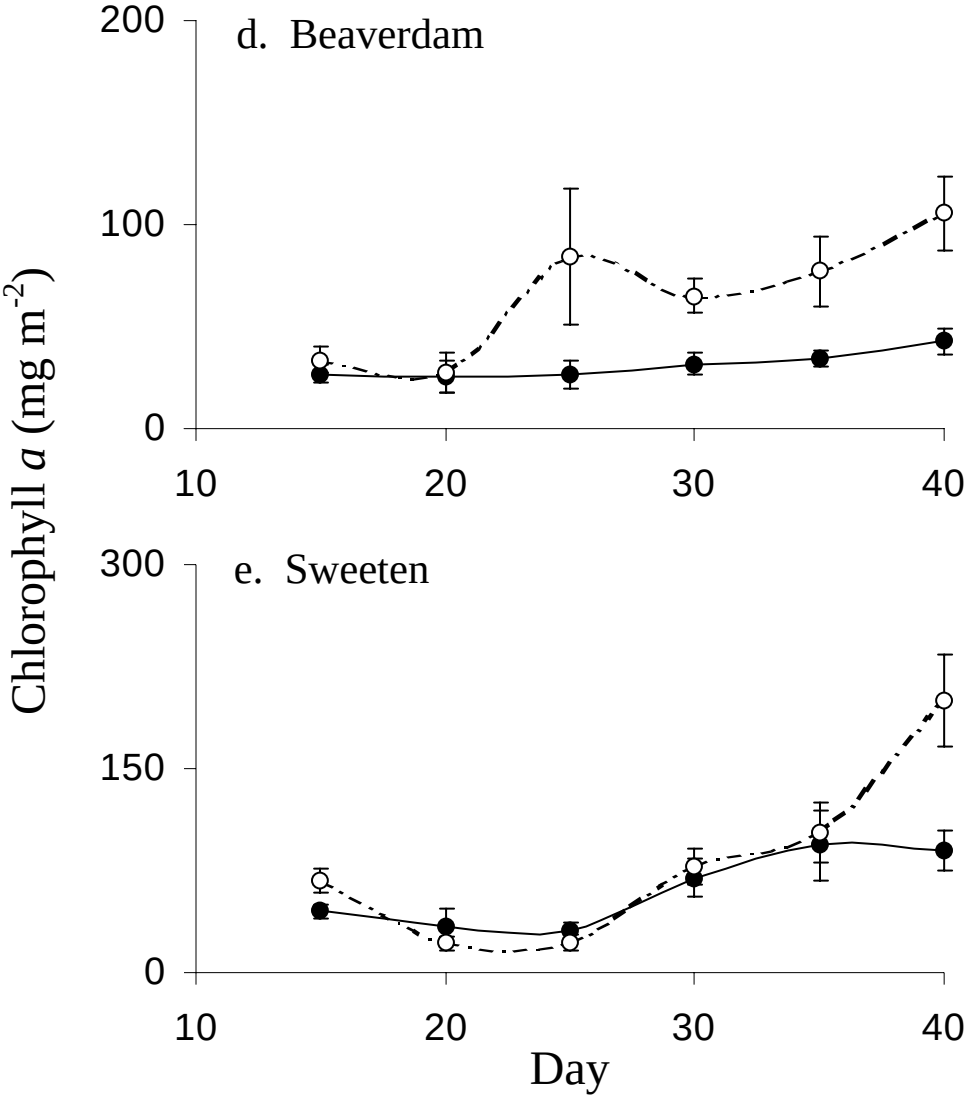
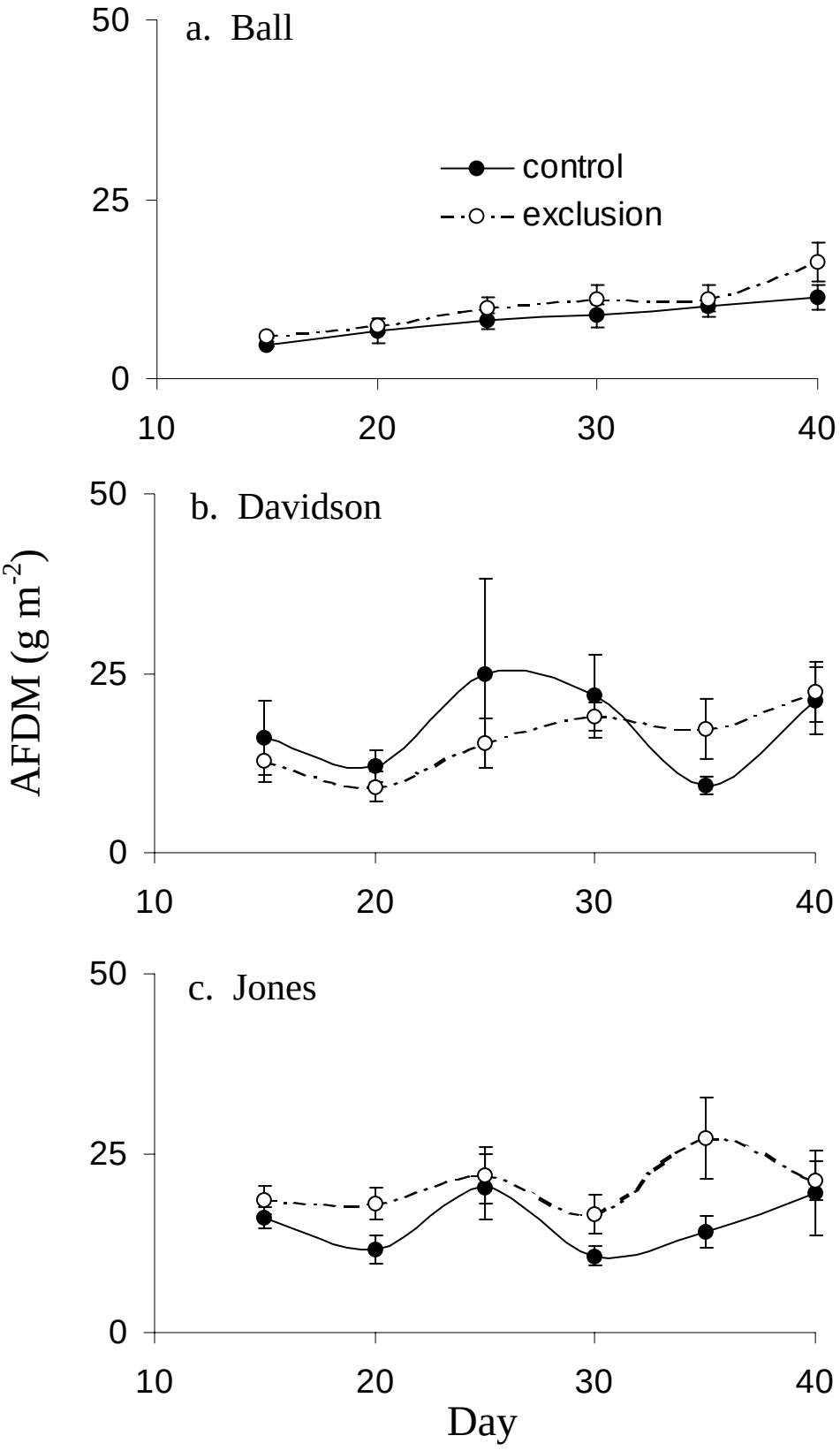

d. Beaverdam
e. Sweeten
Chlorophyll a (mg m-2)
Day
200
100
0
300
150
0
10
20
30
40

Figure 4.6. AFDM concentration (g m^{-2}) on days 15 - 40 at (a) Ball, (b) Davidson, (c) Jones, (d) Beaverdam, and (e) Sweeten. Each point represents mean of five replicates ± 1 SE, except for Beaverdam (mean of four replicates ± 1 SE); note the differences in scale between y-axes. Jones (c) and Beaverdam (d) showed significant effects of exclusion through time (repeated measures ANOVAs: $F_{1,8} = 11.97$, $P = 0.009$ and $F_{1,6} = 8.89$, $P = 0.025$, respectively).


a. Ball
control
exclusion
b. Davidson
c. Jones
AFDM (g m-2)
Day
50
25
0
10
20
30
40

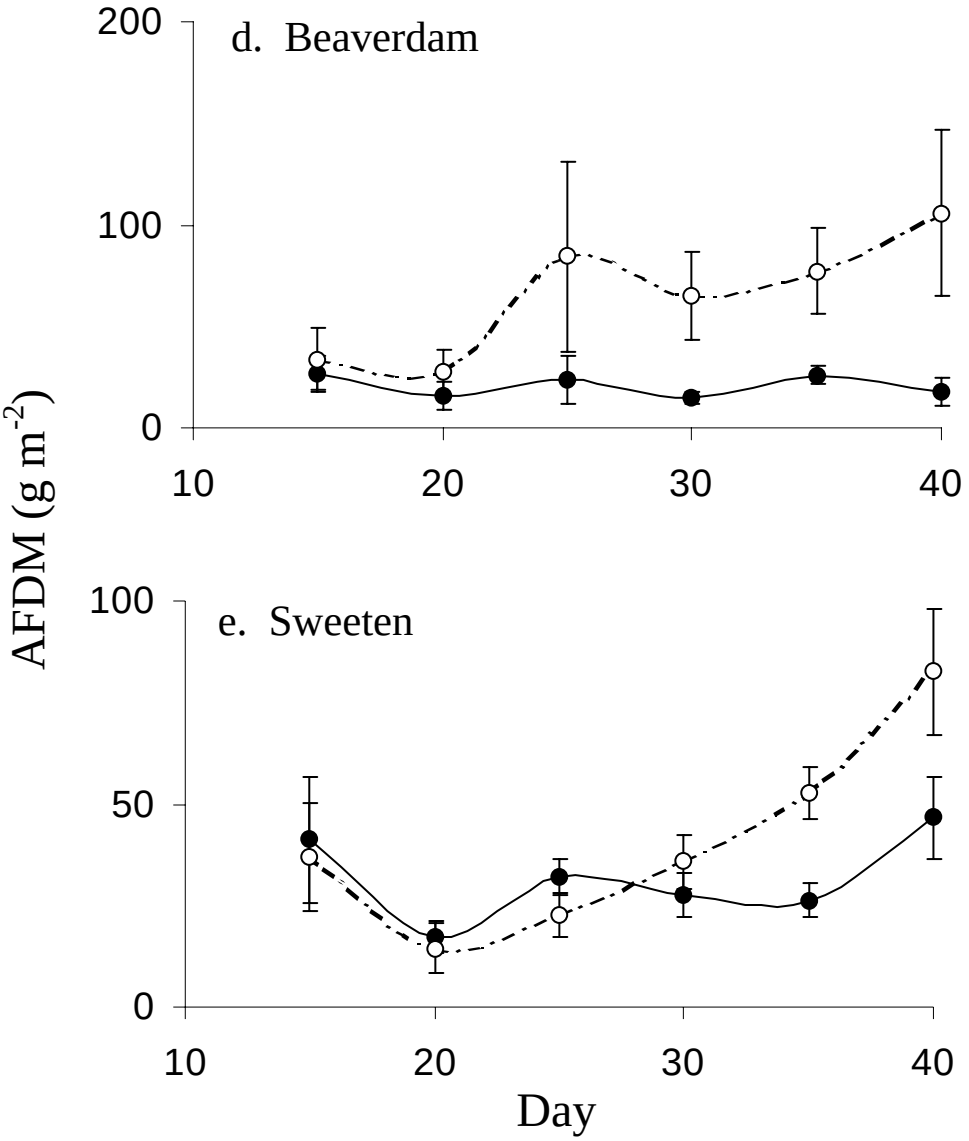

d. Beaverdam
e. Sweeten
AFDM (g m-2)
Day
200
100
0
50
10
20
30
40

Figure 4.7. Total algal (a) abundance (# cells $cm^{-2} * 10^{-2}$) and (b) biovolume (μm^3 $cm^{-2} * 10^{-5}$) on day 40 at each site; white bars = control, shaded bars = macroconsumer exclusion. Each value represents mean of five replicates + 1 SE, except for Beaverdam (mean of four replicates + 1 SE). * indicates significant ($P < 0.05$) difference between control and exclusion treatments when each site examined individually (by paired t-test). B = Ball, D = Davidson, J = Jones, V = Beaverdam, S = Sweeten.

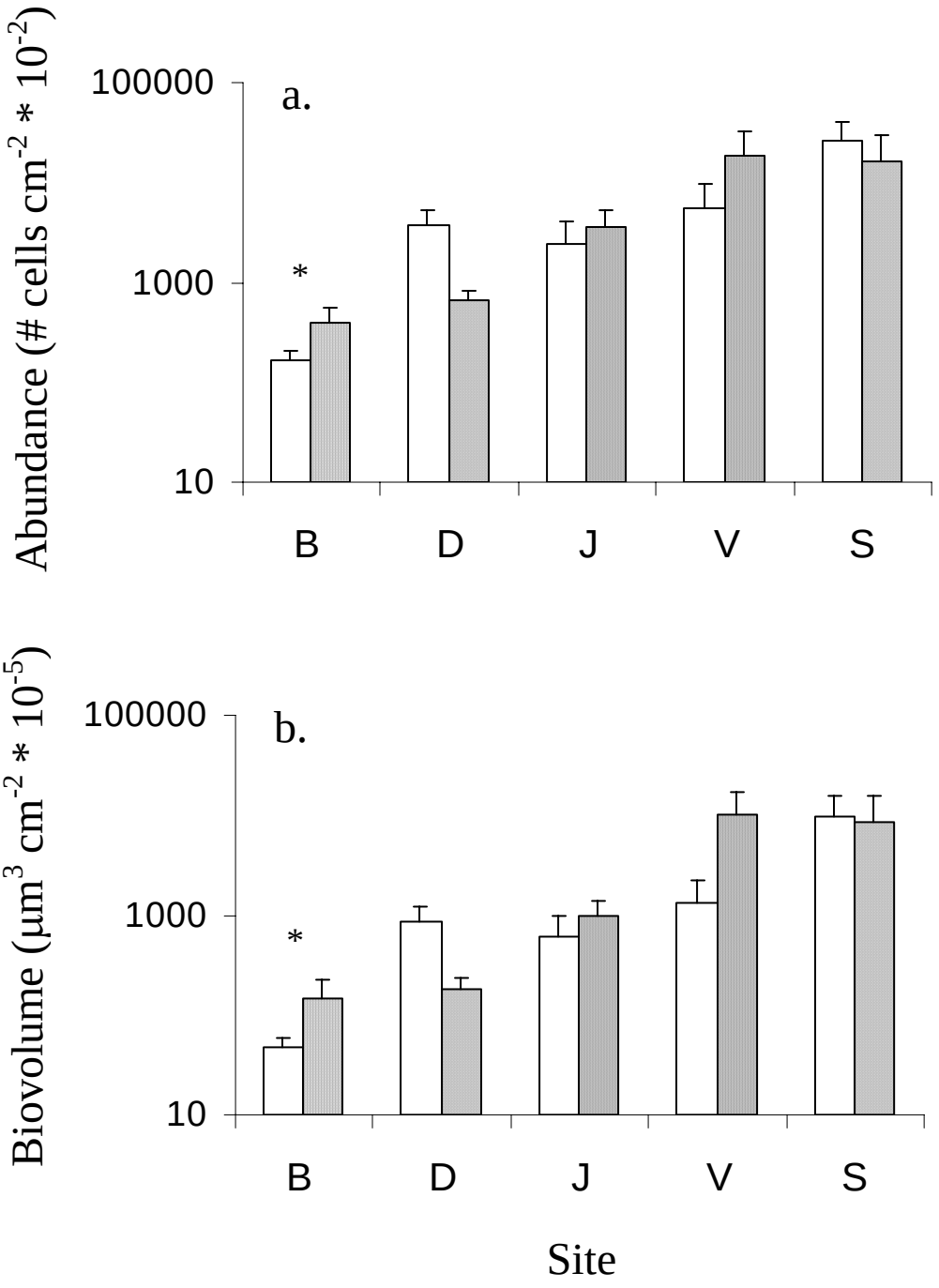

a.
100000
1000
10
*
Abundance (# cells cm-2 * 10-2)
B
D
J
V
S
b.
100000
1000
10
*
Biovolume (µm3 cm-2 * 10-5)
B
D
J
V
S
Site

Figure 4.8. Percentage of day 40 total algal biovolume composed of upright (e.g., Melosira varians and Synedra spp.), motile (e.g., Navicula and Nitzschia spp.), and adnate (e.g., Achnanthes spp.) taxa at each site. Each value represents mean of five replicates, except for Beaverdam (mean of four replicates). C = control, E = exclusion; B = Ball, D = Davidson, J = Jones, V = Beaverdam, S = Sweeten.

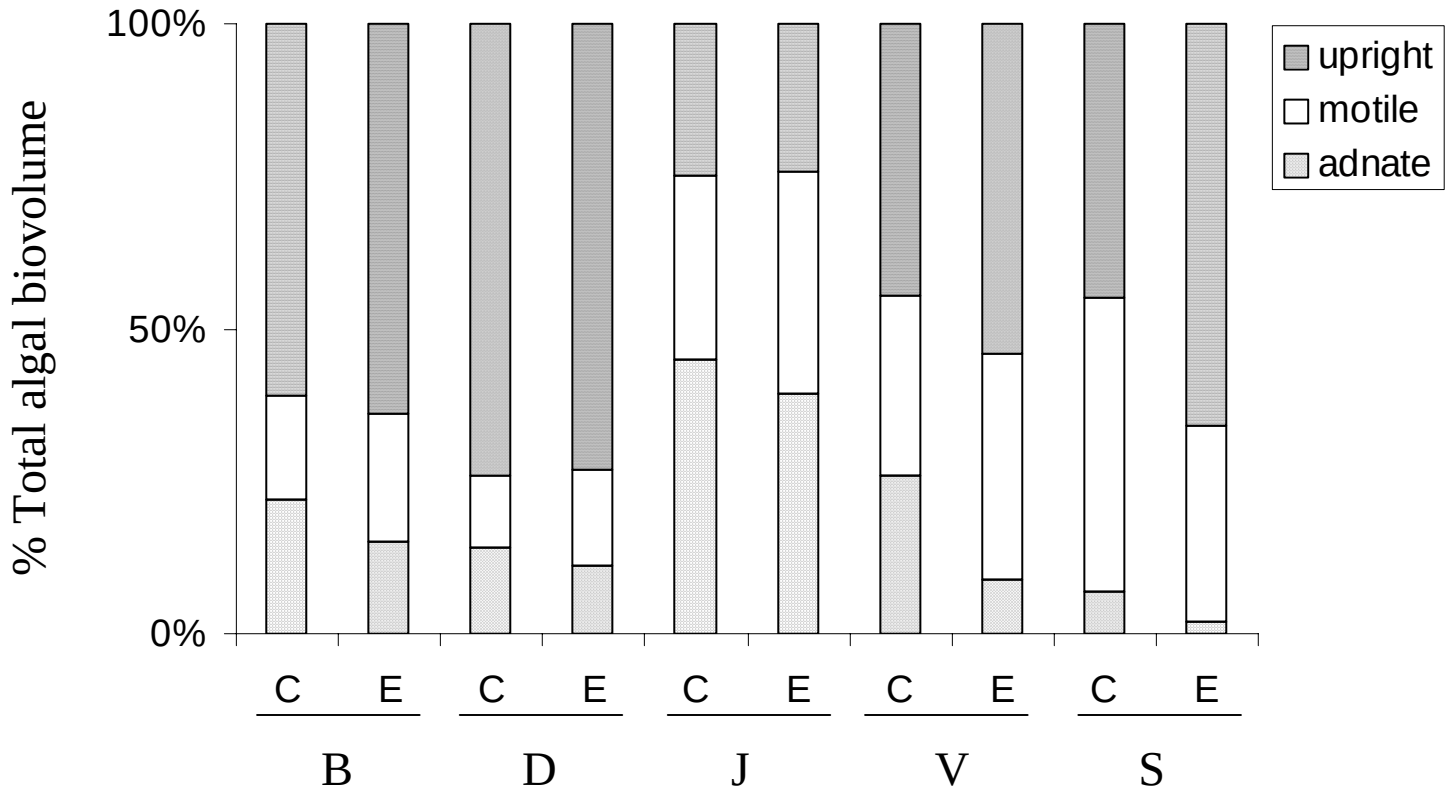
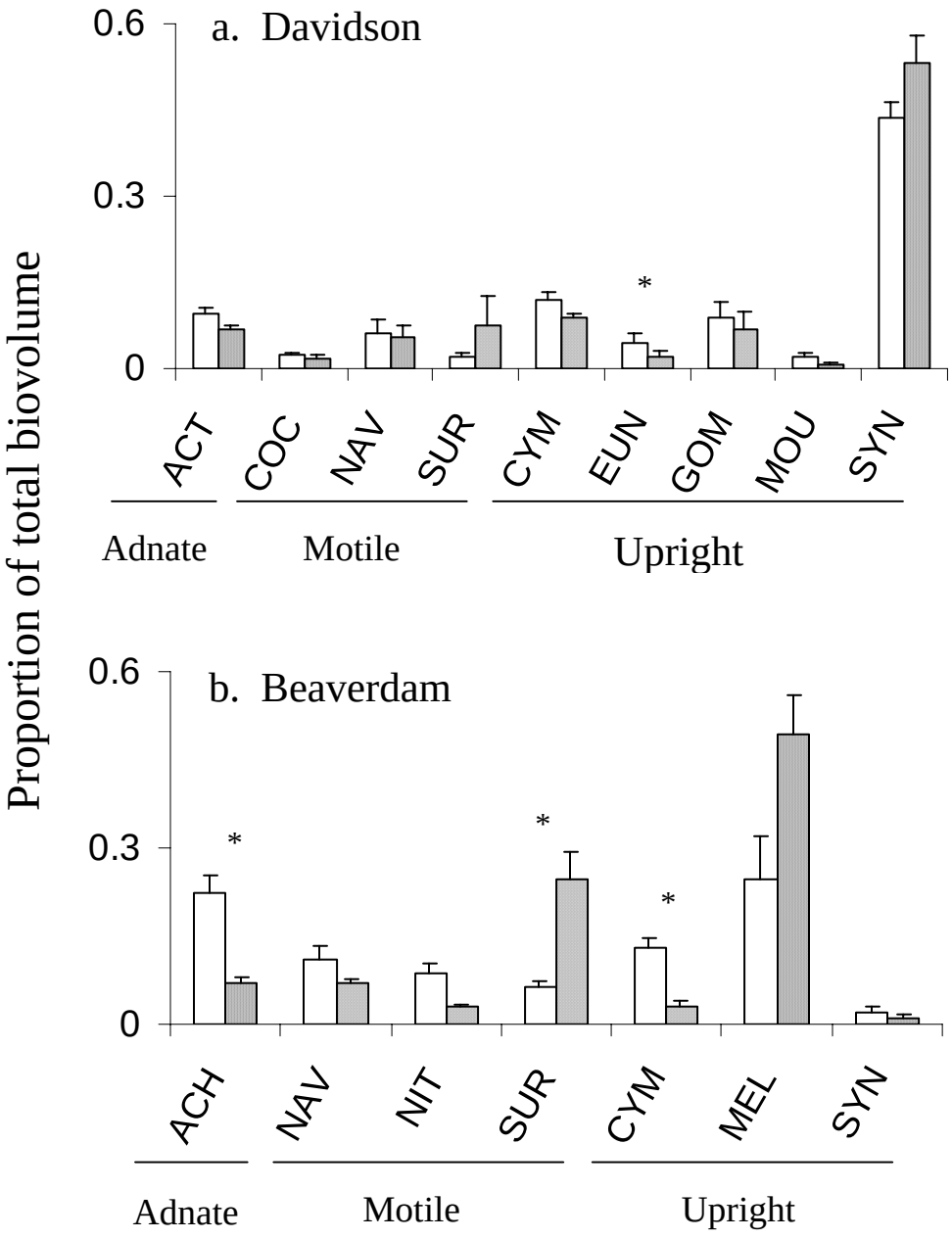

% Total algal biovolume
100%
50%
0%
upright
motile
adnate
C
E
B
D
J
V
S

Figure 4.9. Proportion of day 40 biovolume composed of dominant algal taxa (mean total biovolume ≥ 2% in either control or exclusion treatment) at (a) Davidson, (b) Beaverdam, and (c) Sweeten. White bars = control, shaded bars = exclusion. For Davidson and Sweeten, each value represents mean of five replicates + 1 SE; for Beaverdam, each represents mean of four replicates + 1 SE. * indicates significant difference between control and exclusion for individual taxa, as determined by paired t-tests; with Bonferroni corrections, $P = 0.05/9$ at Davidson, 0.05/7 at Beaverdam, and 0.05/8 at Sweeten. Adnate taxa: ACH = Achnanthes spp., ACT = Achnanthidium minutissima; motile taxa: COC = Cocconeis placentula, NAV = Navicula spp., NIT = Nitzschia spp., SUR = Surirella spp., PIN = Pinnularia spp.; upright taxa: CYM = Cymbella spp., EUN = Eunotia spp., GOM = Gomphonema spp., MEL = Melosira varians, MOU = Mougeotia spp., SYN = Synedra spp.


Proportion of total biovolume
a. Davidson
0.6
0.3
0
*
ACT
COC
NAV
SUR
CYM
EUN
GOM
MOU
SYN
Adnate
Motile
Upright
b. Beaverdam
0.6
0.3
0
*
*
*
ACH
NAV
NIT
SUR
CYM
MEL
SYN
Adnate
Motile
Upright

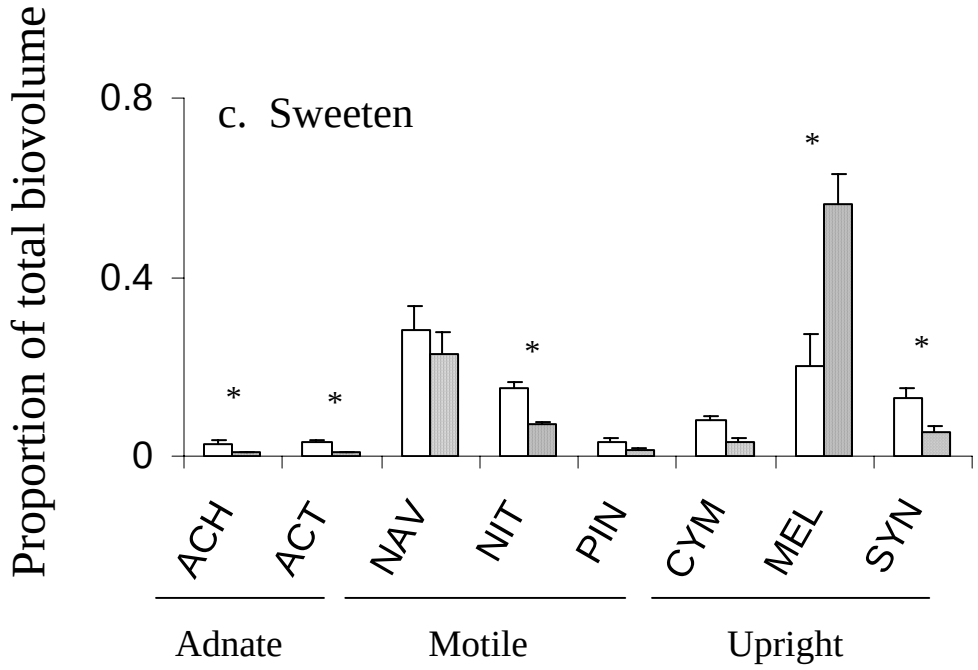

Proportion of total biovolume
0.8
0.4
0
c. Sweeten
*
*
*
*
ACH
ACT
NAV
NIT
PIN
CYM
MEL
SYN
Adnate
Motile
Upright

Figure 4.10. Proportion of total algal biovolume composed of upright, motile, and adnate diatom taxa on (a) day 15 (white bars) and day 40 (shaded bars) at Jones, and (b) day 35 (white bars) and day 40 (shaded bars) at Sweeten. In (a), each bar represents mean of control and exclusion treatments (n = 10), + 1 SE; * denotes significant ($P < 0.05$) difference between days when each form was examined individually (by ANOVA, with day and exclusion as response variables). In (b), each bar represents mean of exclusion treatment (n = 5), + 1 SE; * denotes significant ($P < 0.05/3$) difference between days when each form was examined individually (by paired t-test).

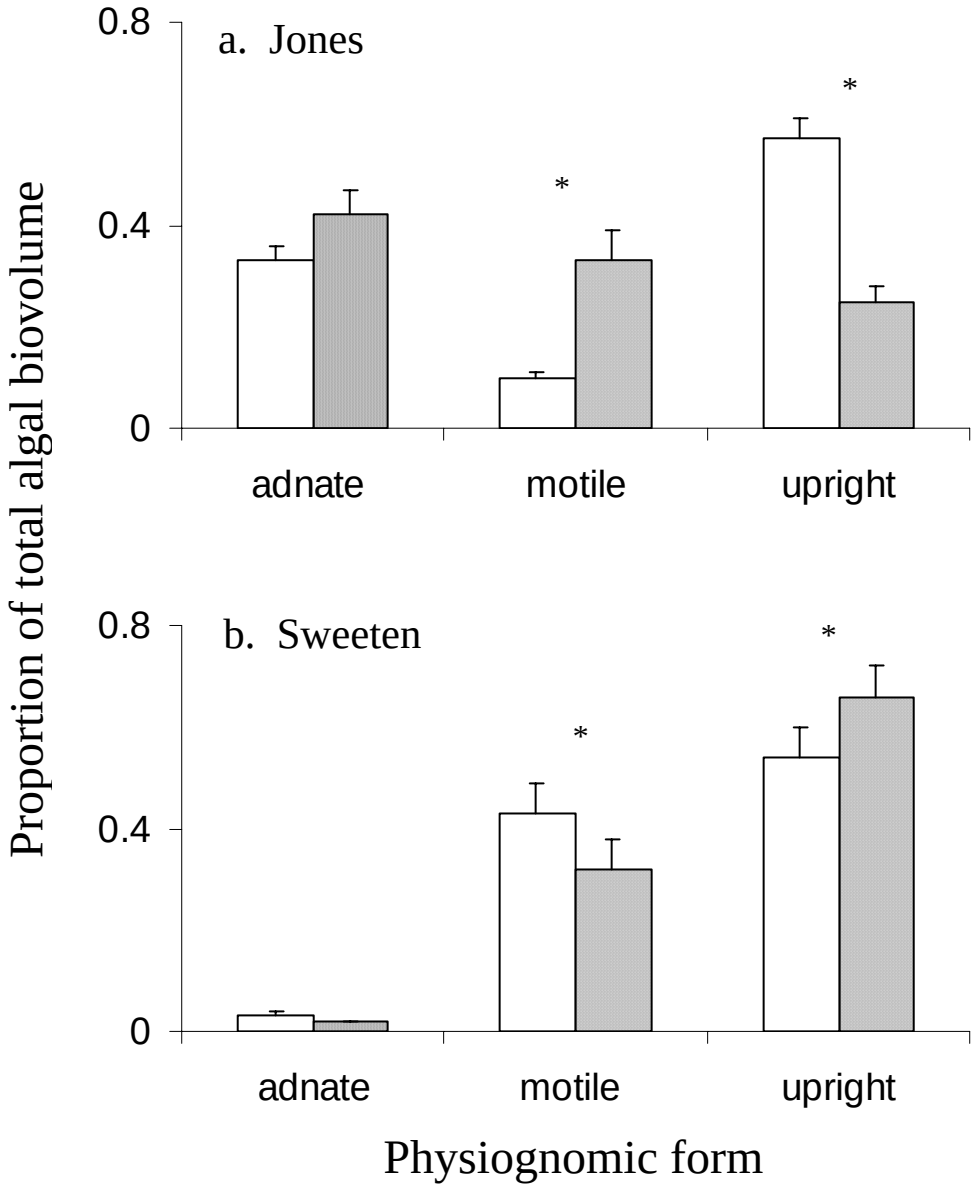

a. Jones
b. Sweeten
0.8
0.4
0
*
adnate
motile
upright
Proportion of total algal biovolume
Physiognomic form

Figure 4.11. Total insect (a) abundance (# m^{-2}) and (b) biomass (mg m^{-2}) in control (white bars) and exclusion treatments (shaded bars) at each site. Each value represents mean of five replicates + 1 SE, except for Davidson and Beaverdam (mean of four replicates + 1 SE). * indicates significant ($P < 0.05$) difference between control and exclusion treatments when each site examined individually (by paired t-test). B = Ball, D = Davidson, J = Jones, V = Beaverdam, S = Sweeten.

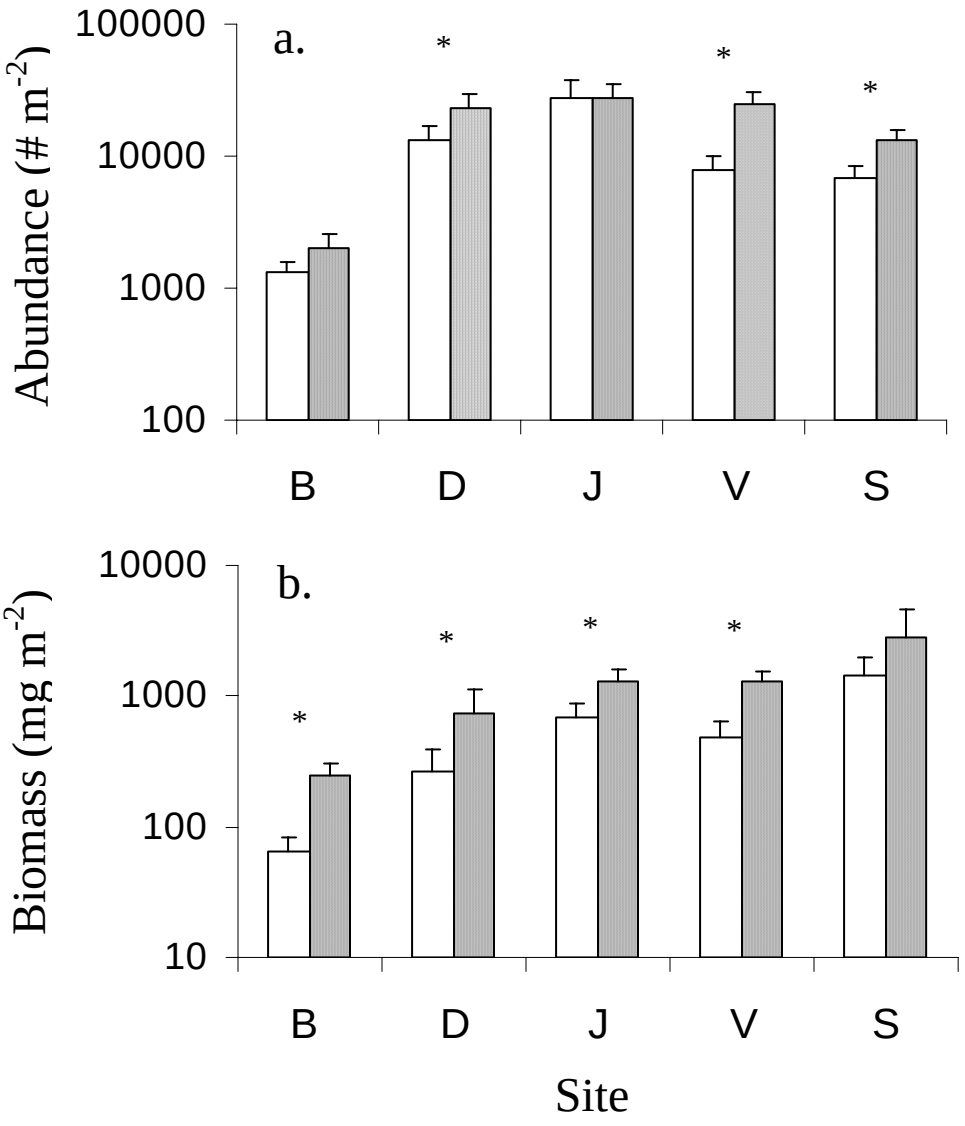
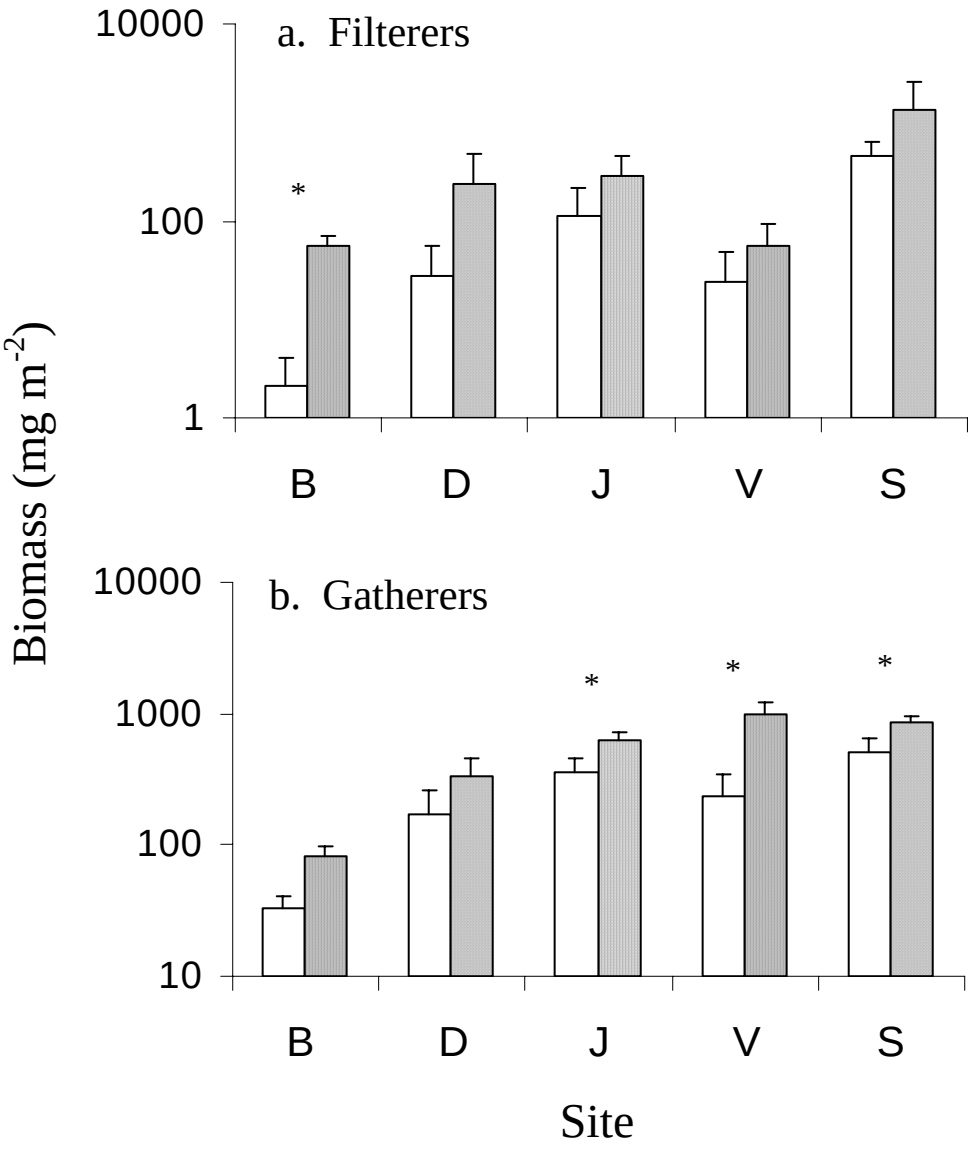

a.
b.
Abundance (# m-2)
Biomass (mg m-2)
100000
10000
1000
100
10
B
D
J
V
S
Site
*

Figure 4.12. Biomass (mg m^{-2}) of (a) insect filterers, (b) insect gatherers, (c) insect scrapers, and (d) insect predators on day 40 in control (white bars) and exclusion (shaded bars) treatments at each site. Each value represents mean of five replicates + 1 SE, except for Davidson and Beaverdam (mean of four replicates + 1 SE). * indicates significant ($P < 0.05$) difference between control and exclusion treatments when each site examined individually (by paired t-test). B = Ball, D = Davidson, J = Jones, V = Beaverdam, S = Sweeten.


a. Filterers
10000
100
1
*
B
D
J
V
S
b. Gatherers
10000
1000
100
10
*
*
*
B
D
J
V
S
Site
Biomass (mg m-2)

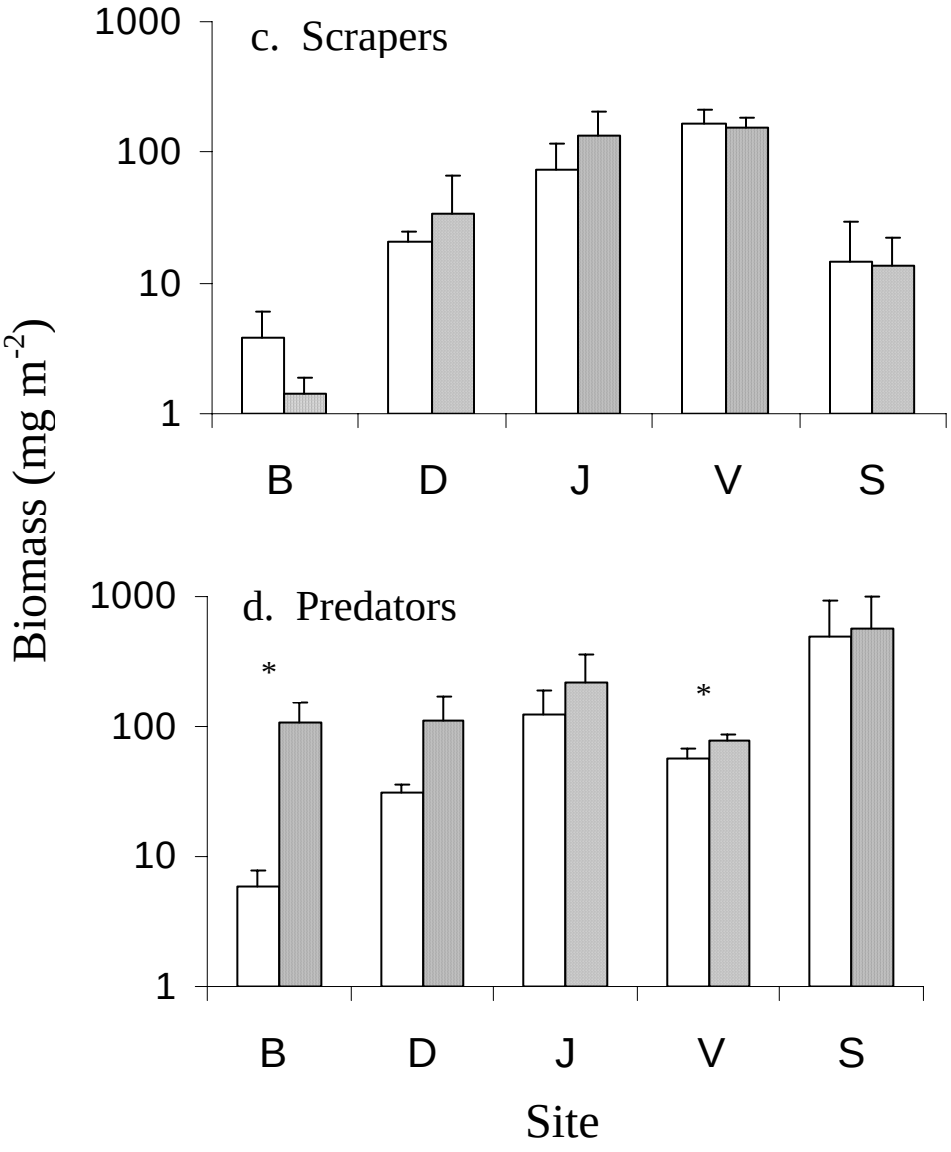

c. Scrapers
d. Predators
Biomass (mg m-2)
1000
100
10
1
B
D
J
V
S
*
*
Site

Figure 4.13. Functional feeding group biomass (mg m^{-2}) on (a) day 15 (white bars) and day 40 (shaded bars) at Jones, and (b) day 35 (white bars) and day 40 (shaded bars) at Sweeten. In (a), each bar represents mean of control and exclusion treatments (n = 10), + 1 SE; * denotes significant ($P < 0.05$) difference between days when each form was examined individually (by ANOVA, with day and exclusion as response variables). In (b), each bar represents mean of exclusion treatment (n = 5), + 1 SE; * denotes significant ($P < 0.05$) difference between days when each form was examined individually (by paired t-test).

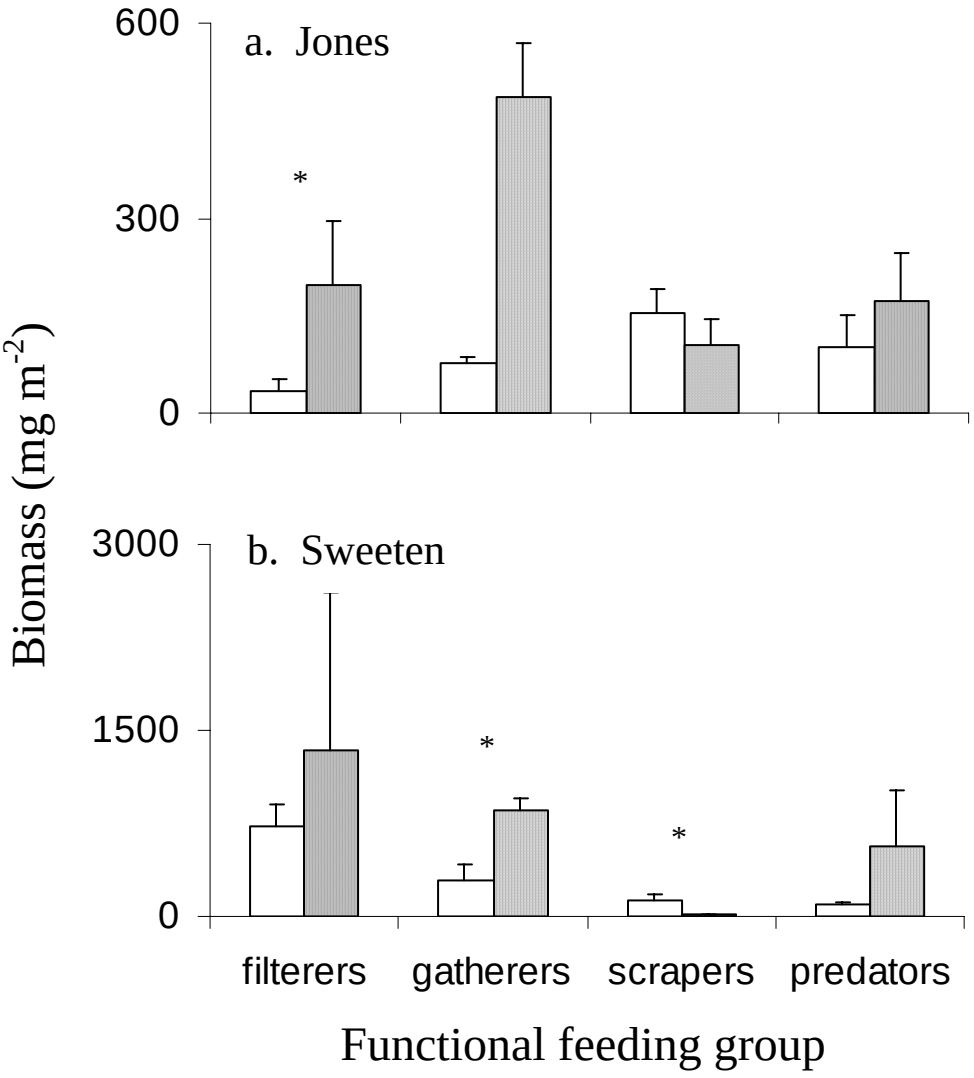
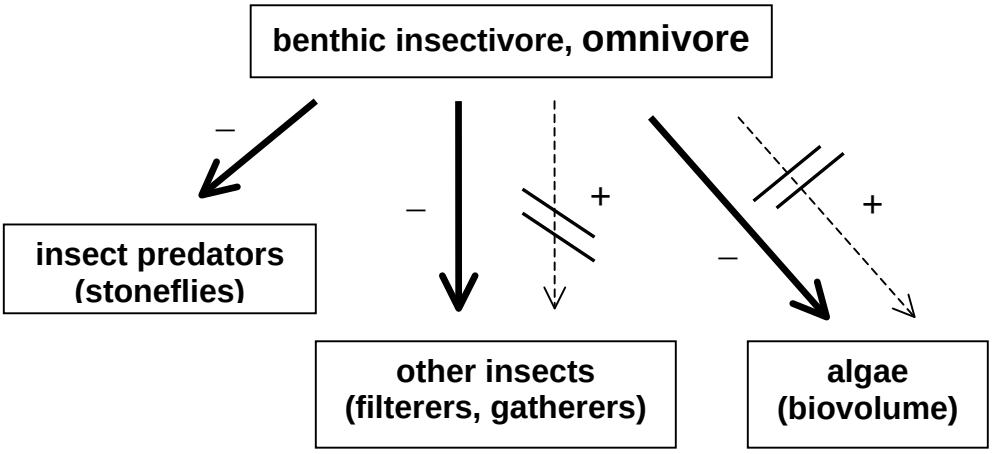
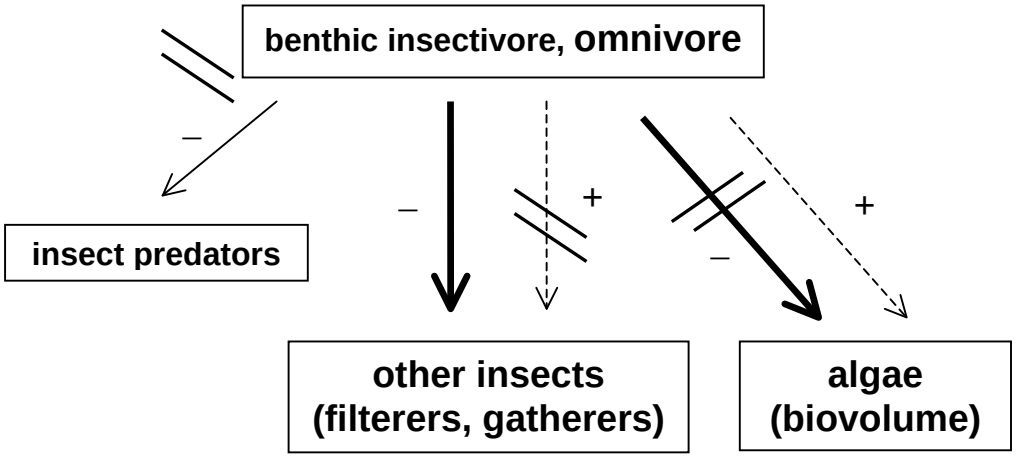

600
300
0
a. Jones
*
3000
1500
0
b. Sweeten
*
*
Biomass (mg m-2)
filterers
gatherers
scrapers
predators
Functional feeding group

Figure 4.14. Results of macroconsumer exclusion experiments at each site. Text size indicates relative biomass (high versus low) of different biotic components across five sites. Solid arrows represent direct effects of macroconsumers; dashed arrows represent indirect effects (i.e., effects mediated through insect consumers). Arrows crossed by double hatch marks indicate we predicted a macroconsumer effect (see Figure 1) that was not seen in our results. Bold arrows indicate statistically significant interactions ($P < 0.05$); regular arrows indicate trends that were not statistically significant (generally $0.05 < P < 0.10$). Signs adjacent to arrows show positive (+) or negative (-) effect of macroconsumers.

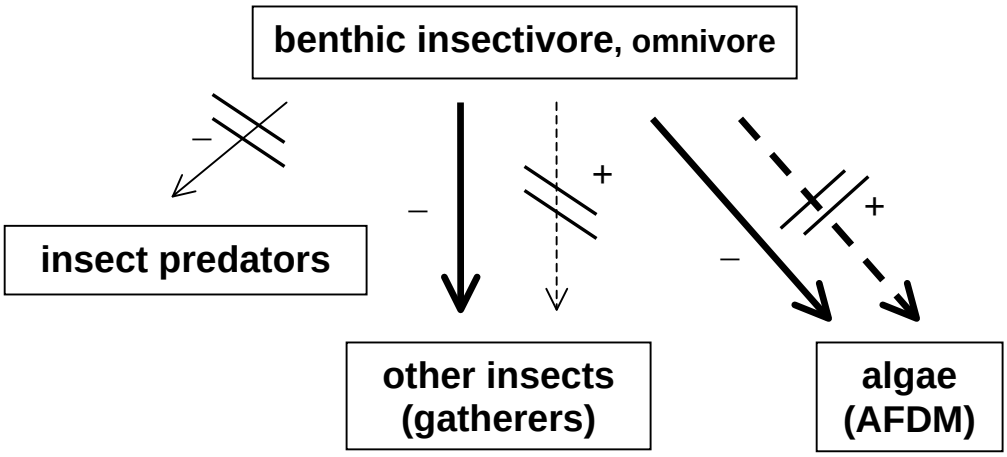
a. Ball



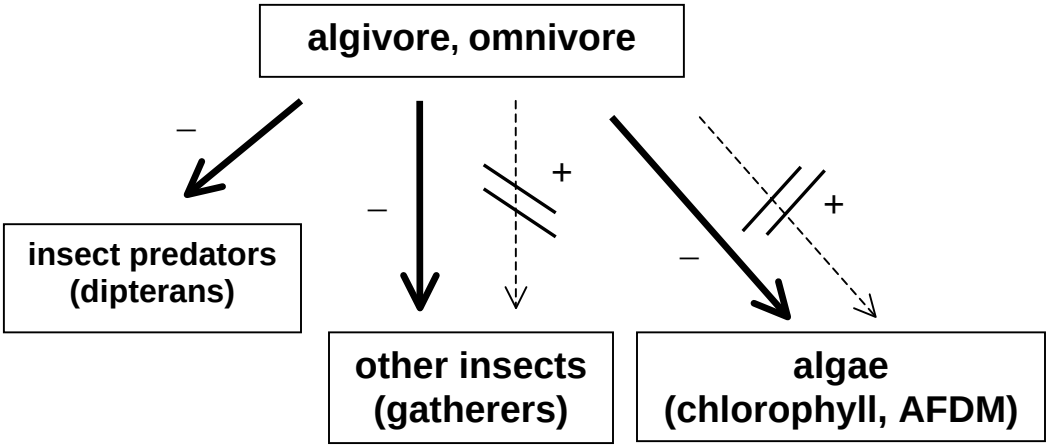
b. Davidson



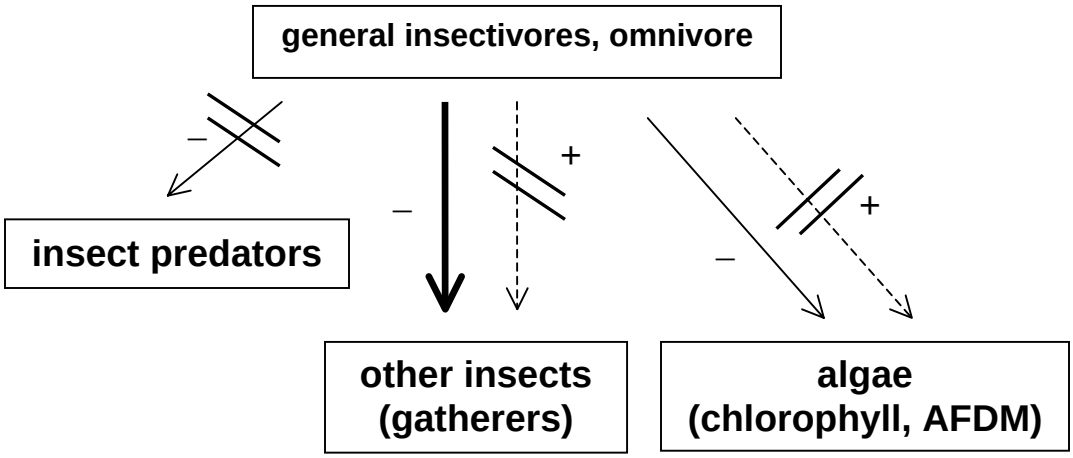
c. Jones



d. Beaverdam



e. Sweeten



CHAPTER 5

REVISITING THE USE OF ELECTRICITY FOR EXPERIMENTAL EXCLUSION: PAST, PRESENT AND FUTURE [1]

[1] Schofield, K.A. C.M. Pringle, and D.D. Schofield. To be submitted to Canadian Journal of Fisheries and Aquatic Sciences.

ABSTRACT

Studies using electricity to exclude stream macroconsumers (i.e., fishes, shrimps, crayfishes) have shown that aquatic insects are not directly affected by the electric current. However, many of these studies were conducted in tropical streams characterized by assemblages of small benthic insects (e.g., chironomids and baetid mayflies). The main objective of this chapter was to examine in greater detail whether this electric exclusion technique had any direct negative effect on insect assemblages in southern Appalachian study streams, which are characterized by larger, more diverse insect assemblages. We compared insect drift before and after the start of four electric exclusion studies, as well as re-examined data from Chapter 4 in terms of common insect taxa collected across multiple sites. Activation of fence chargers significantly elevated drift abundance and biomass (approximately 50% and 120%, respectively), indicating that insects initially were adversely affected by the electrical charge. Although size frequency distributions of drifting insects were relatively similar between treatments, five individuals > 5 mm drifted in exclusion treatments versus one individual > 5 mm in controls. In contrast, most insect taxa commonly colonizing tiles were not negatively affected by electricity; insect abundance and/or biomass (here chironomids, hydropsychids, and baetids) were significantly greater in electrified treatments, as has been observed in several other studies conducted in tropical streams. While heptageniid abundance and biomass were lowered by electricity, large individuals were collected in exclusion replicates and average individual biomass did not differ between treatments. These results suggest that insects in close proximity to electrically charged wires can be affected by the current, but most substrate-associated insects (i.e., those colonizing tiles) are not significantly impacted at the voltages generated by 6 V fence chargers. On level ground, the copper wire loops between which current is generated are approximately 5 cm above the ground; thus, current most probably does not reach the substrate surface, where insects are most abundant. Certain modifications of the electric exclusion technique (e.g., use of high voltage wire) may maximize

in-stream field strength, but these modifications may not be necessary or desirable. Since tile and drift data suggest that some insect taxa (e.g., heptageniid mayflies) may be adversely impacted at relatively low voltages, maximizing field strength may increase the probability that these insects will be affected while having little effect on macroconsumer exclusion capabilities of the method. Improved consistency of electrical field strength among replicates within a given site and across sites can be achieved by standardizing connections between fence chargers and in-stream frames, as well as through the use of voltage-limiting resistors. This increased standardization of experimental conditions will facilitate both within- and cross-site comparisons.

INTRODUCTION

Many researchers have used electricity to exclude stream macroconsumers (e.g., fishes, shrimps, crayfishes) from benthic areas (e.g., Pringle and Hamazaki 1998, Rosemond et al. 1998, March et al. 2001). This technique was originally developed by Pringle and Blake (1994), who first used it to exclude shrimps in tropical Puerto Rican streams. Since then, the technique has been modified and used to exclude macroconsumers in tropical (e.g., Pringle and Hamazaki 1997, Rosemond et al. 1998, Silveira and Moulton 2000, March et al. 2001) and temperate (e.g., Powell 2001, Schofield et al. 2001, Uieda and Uieda 2001) stream systems.

Benefits of electric exclusion include minimization of artifacts commonly associated with traditional cage enclosure/exclosure experiments (e.g., reduced water flow and increased sedimentation) and increased resistance of experimental units to high discharges (Pringle and Blake 1994). The technique allows researchers to examine stream macroconsumer impacts under natural abiotic conditions (e.g., natural hydrologic regimes), using natural organism densities. As a result, it provides a means to examine in situ how abiotic and biotic factors interact to structure stream ecosystems. For example, Pringle and Hamazaki (1997) used electric exclusion methods to examine how fishes control algal response to high discharge events; because most previous

exclusion studies had been conducted during baseflow conditions (e.g., Pringle et al. 1993), this interaction between disturbance and biotic assemblages had not been observed.

Other studies have used electric exclusion methods to examine (1) the role of different macroconsumers (e.g., shrimps, fishes, crayfishes) in structuring benthic communities (e.g., Pringle and Blake 1994, Pringle and Hamazaki 1998, Rosemond et al. 1998, Powell 2001, Schofield et al. 2001); (2) top-down effects in streams with low versus high phosphorus concentrations (e.g., Ramírez 2001, Rosemond et al. in press); and (3) the spatial variability of top-down effects along an stream elevational gradient (e.g., March et al. 2001, March et al. in press). By combining electric exclusion experiments with larger scale stream surveys, Pringle et al. (1999) were able to link macroconsumer assemblages to interstream differences in the quality and quantity of organic matter. Recently, several researchers have modified the technique by increasing in-stream electrical current, thereby leading to exclusion of grazing insects (e.g., Moulton et al. 1999, Brown et al. 2000, Opsahl et al. 2001).

In Costa Rican and Puerto Rican study streams, organisms < 1 cm (i.e., most aquatic insects) do not appear to be adversely affected by the electric current generated by 6 V or 12 V fence chargers (e.g., Pringle and Blake 1994, Pringle and Hamazaki 1997, Rosemond et al. 1998, March et al. 2001, Ramírez 2001). However, these experiments were conducted in tropical streams characterized by assemblages of small benthic insects (e.g., chironomids and baetid mayflies). It is possible that insect assemblages in temperate systems may be more susceptible to these electrical pulses (e.g., due to increased insect size, compositional differences, water conductivity differences, etc.). The main objective of this chapter is to examine in greater detail whether electricity had any direct negative effect on insect assemblages. We compare insect drift before and after the start of electric exclusion experiments at four sites, as well as re-examine data from Chapter 4 in terms of insect taxa found across multiple study sites. In addition, we suggest

improvements to the electric exclusion technique that may facilitate both within- and cross-site comparisons, as well as future research directions that may be taken with this methodology.

BRIEF DESCRIPTION OF THE ELECTRIC EXCLUSION TECHNIQUE

The electric exclusion technique used throughout this dissertation is a slight modification of the technique developed by Pringle and Blake (1994) and later refined by Pringle and Hamazaki (1997). Square polyvinylchloride (PVC) frames (0.25 m^{-2} each) are lined with two rings of stranded, uninsulated, 12-gauge copper wire. Sampling substrates (i.e., tiles or leaf packs) are secured in each frame, and frames are placed in a paired design into run habitats of a given stream (Figure 5.1). One frame in each pair is randomly chosen as the exclusion treatment. This frame is connected to a fence charger (Parmak Model DF-SP-SS, Parker McCrory Manufacturing Company, Kansas City, MO) with insulated 12-gauge copper wire (Figure 5.2).

Six volt chargers were used in this series of experiments. The fence chargers are solar-powered, but they also contain 6 V gel cell batteries (in forested sites with dense canopy cover and low light, batteries generally begin to drop below 6 V after 3 to 4 days). According to Parker McCrory specifications, peak charger voltage is approximately 9000 V; however, our measurements with a Parker McCrory peak voltage reader indicate charger output is > 11,000 V when the charger is in isolation. When attached to in-stream frames, the charger delivers pulsed direct current electricity (~ 54 – 55 pulses min^{-1}) to the 0.25 m^{-2} area, generating electric current between the outer and inner copper wire loops. This field does not appear to extend beyond the 0.25 m^{-2} area, as macroconsumers (fishes and crayfishes) are often found immediately outside PVC frames. Field strength in the water is much weaker than 11,000 V, as energy dissipates both through the wires connecting fence chargers to PVC frames and through the water. Peak voltages measured at fence chargers during experiments (i.e., voltages completing the circuit from fence chargers to in-stream frames and back) are generally ~ 10 – 60 V.

DOES THE ELECTRIC EXCLUSION TECHNIQUE DIRECTLY AFFECT STREAM INSECTS?

METHODS

Drift experiments

Between July 10 and July 19, 1997, drift experiments were conducted at four sites in the Little Tennessee River basin (Lower Ball Creek, Betty Creek, Coweeta Creek, and Jones Creek). These sites are located in western North Carolina and northern Georgia, in the southern Appalachian Mountains. Conductivity ranged between approximately 13 $\mu S\ cm^{-1}$ at Lower Ball Creek to 35 $\mu S\ cm^{-1}$ at Jones Creek. Substrate was predominantly cobble, gravel, and sand at all sites except Ball, where boulders also were prevalent.

Electric exclusion experiments were set up at each site (five replicate pairs per site). After replicates were installed, they were left undisturbed for 10 min. Before each experiment began (i.e., before fence chargers connected to exclusion replicates were turned on), insect drift was sampled for 5 min with 363 μm mesh nets positioned immediately downstream of each replicate. Following these pre-exclusion (control) samples, fence chargers were turned on and drift was collected for an additional five minutes at each exclusion replicate (exclusion samples). Drift at all sites was collected between 10:00 and 15:00. Because samples were collected in a paired design over a 10-15 min period, discharge was assumed to be equal between control and exclusion pairs. Samples were preserved in 70% ETOH; organisms were later identified to family and measured to the nearest 0.5 mm. Insect biomass was calculated with family-level length-mass regressions from Benke et al. 1999.

Control and exclusion drift samples were compared in terms of total insects, Ephemeroptera, and Diptera taxa (ephemeropterans and dipterans were each collected in 35 out of 40 total replicates, versus 8 and 17 replicates for plecopterans and trichopterans, respectively). Total, ephemeropteran, and dipteran abundance (# $sample^{-1}$) were compared across all sites with paired

t-tests (control versus exclusion, n = 20, using square root-transformed data). Variance assumptions of paired t-tests (i.e., equal variance between samples) could not be met for biomass parameters, given the overwhelming influence of rare, large individuals. This problem was dealt with in two ways. First, total, ephemeropteran, and dipteran biomass were compared with non-parametric Wilcoxon rank sum tests. Second, individuals > 5 mm were omitted from analyses [total = 6 individuals over 40 replicates]. Omission of these individuals equalized variance between control and exclusion samples; paired t-tests were then conducted for total, ephemeropteran, and dipteran biomass across all sites (control versus exclusion, n = 20), with these large individuals omitted.

The fence chargers used at Betty Creek were a newer model than those used at the remaining three sites, and the manufacturers advertised them as having "more shocking power" (these chargers were not used in any other exclusion experiments). Because of this, we examined drift abundance and biomass with Betty omitted from analyses. Water conductivity differed among the four sites; therefore, abundance and biomass of total insects, ephemeropterans, and dipterans also were compared within each site with paired t-tests (n = 5). By comparing each site independently, we were able to at least qualitatively examine whether drift response to electric exclusion differed among sites.

Because multiple paired t-tests were run, there is an elevated probability of Type I error (i.e., that we will declare treatments statistically different when in fact they are not). However, overall α (= 0.05) was not adjusted, given (1) the conservative nature of adjustment procedures, and (2) the fact that each site represented a separate experiment. *P*-values are reported for each test, and the total numbers of tests run both within and across sites are presented in Table 5.1.

Tile experiments

Detailed methods for the tile experiments are given in Chapter 4. Briefly, electric exclusion experiments were conducted at five study sites (Lower Ball Creek, Jones Creek, Upper Davidson

River, Beaverdam Creek, and Sweeten Creek) during the summers of 1997 and 1998. These sites varied in physical, chemical, and biological characteristics; conductivity ranged from approximately 13 μS cm^{-1} at Lower Ball Creek to 110 μS cm^{-1} at Sweeten Creek. Forty days after the start of each experiment, unglazed brown ceramic tiles (7.5 cm x 15 cm) were collected from paired macroconsumer exclusion and control treatments at each site (5 replicate pairs at Ball, Jones, and Sweeten; 4 pairs at Davidson and Beaverdam), and insects that colonized tiles were removed, identified, and measured.

To examine direct effects of the exclusion technique on insect abundance and biomass, we focused on five insect families that were relatively common across all sites: Chironomidae (found in all 46 replicates); Hydropsychidae (26 replicates); Heptageniidae (18 replicates); Baetidae (15 replicates); and Tipulidae (20 replicates). Paired t-tests were used to compare abundance (# m^{-2}) and biomass (mg m^{-2}) of each family across all sites (control versus exclusion, n = 23). Data were natural log-transformed to equalize variances. In addition, we calculated each family's average individual biomass in each replicate (biomass/abundance, units = mg $individual^{-1}$). Both within and among sites, occurrence of these five insect taxa was highly variable; with the exception of Chironomidae, rarely was any family consistently found in both the control and exclusion treatment of a given replicate pair. Thus, we were able to compare only average individual Chironomidae biomass by paired t-test (control versus exclusion, n = 23, square root-transformed data). For the remaining four families, average individual biomass in control and exclusion treatments were compared with non-parametric Mann-Whitney-U tests.

Because conductivity differed among the five sites, we also examined each site independently (n = 4 or 5, depending upon the site). Paired t-tests were used for chironomid and hydropsychid abundance and biomass, but the assumption of equal variance could not be met for the remaining taxa; thus, these taxa were compared by non-parametric Wilcoxon rank sum tests. Although these site-specific analyses had reduced power relative to tests with all sites pooled, they allowed

us to qualitatively examine cross-site differences in taxa response to exclusion. For example, if a given taxon was significantly less abundant in exclusion treatments at low conductivity sites (i.e., Ball and Davidson) but not at high conductivity sites (i.e., Beaverdam and Sweeten), this may suggest that this taxon may be adversely affected by the exclusion technique at low conductivities. As with the drift study, overall α (= 0.05) was not adjusted for multiple tests; the total number of comparisons is given in Table 5.1.

RESULTS

Drift experiments

When all four sites were analyzed together, total drift abundance was higher in electric exclusion versus control samples (Table 5.2, Figure 5.3a). This pattern held for dipteran abundance, but ephemeropteran abundance did not differ between control and exclusion treatments ($P > 0.40$, Table 2 and Figure 5.3a). Size frequency distributions for drifting organisms at each site are presented in Figures 5.4 – 5.6. Size distributions were relatively similar between control and exclusion treatments at each site, although large organisms were generally more abundant in electric exclusion samples. One individual (a dipteran) > 5 mm occurred in control samples; five individuals (one ephemeropteran, one plecopteran, one dipteran, and two trichopterans) > 5 mm were found in exclusion samples. Wilcoxon rank sum tests on all biomass data (including individuals > 5 mm) showed that total, ephemeropteran, and dipteran biomass were all greater in exclusion versus control drift ($P < 0.05$, Figure 5.3b). If individuals > 5 mm were omitted from biomass analyses, both ephemeropteran and dipteran biomass remained greater in exclusion samples (Table 2, Figure 5.3c). However, total drift response to exclusion became non-significant ($P = 0.076$, Table 5.2).

Total and ephemeropteran drift abundance and biomass did not differ between control and exclusion treatments when data from all sites but Betty (i.e., the site with “more shocking power” fence chargers) were analyzed ($P \geq 0.138$, Table 5.2). In contrast, dipteran abundance and

biomass remained higher in exclusion drift samples, even when Betty was omitted from analyses ($P \leq 0.045$, Table 5.2).

Drift response to exclusion was variable among sites. In terms of abundance, only total drift abundance at Betty showed an even borderline effect of exclusion when sites were examined independently ($P = 0.062$; Table 5.3, Figure 5.7). More significant differences were seen with biomass, as total biomass at Ball and total and ephemeropteran biomass at Betty were greater in exclusion versus control treatments (Table 5.3, Figure 5.8).

These experiments indicate that, across all four sites, drift of aquatic insect larvae was enhanced by activation of electric exclusion treatments, and that larger individuals (> 5 mm) seemed especially susceptible to these effects. Within-site analyses suggest that insect responses were strongest at Betty and Ball.

Tile experiments

Across all sites, abundance and biomass of chironomids, hydropsychids, and baetids were greater in exclusion versus control treatments. The opposite pattern was seen for heptageniids, whereas tipulid abundance and biomass did not differ between treatments (Tables 5.4 - 5.6, Figure 5.9). Average individual biomass for chironomids was significantly higher in exclusion versus control treatments (paired t-test: $t_{22} = -2.23$, $P = 0.018$; Table 5.6), but no significant differences were seen for the remaining four taxa (Mann-Whitney tests: $P > 0.05$; Table 5.7).

In general, cross-site trends in chironomid and hydropsychid abundance and biomass were observed at all sites: at each site abundance and biomass of these taxa usually tended to be greater in exclusion versus control treatments (Tables 5.4 and 5.5), although these differences were not always statistically significant (Table 5.8). Within-site differences were not observed for abundance or biomass of the remaining three taxa (Wilcoxon rank sum tests: $P > 0.05$; Tables 5.4 and 5.5). Only Chironomidae average individual biomass demonstrated significant differences between control and exclusion treatments at any site, with higher average biomass in

exclusion treatments at Jones (paired t-test: $t_4 = -2.77$, $P = 0.025$) and Beaverdam ($t_3 = -2.60$, $P = 0.040$; Figure 5.10). Differences in average individual biomass for other taxa were highly variable across sites (Figure 5.10).

DISCUSSION

Activation of fence chargers significantly elevated drift abundance (an approximately 50% increase) and biomass (an approximately 120% increase), indicating that, at least initially, insects were adversely affected by the electrical charge. Several other studies have demonstrated similar drift increases in response to electricity (e.g., Bisson 1976, Mesick and Tash 1980, Taylor et al. 2001). As expected, these effects were especially evident with large insects: five insects > 5 mm were collected in exclusion drift samples, versus one in control samples. When these insects were excluded from biomass analyses, the increase in total biomass between control and exclusion treatments dropped from 120% to < 25%.

Six large insects across 40 samples is a relatively small number. These low drift densities, even in exclusion replicates, may have resulted from three factors: (1) insects were adversely affected by the electrical pulses but unable to drift; (2) insects were adversely affected but responded by moving into interstitial spaces; and (3) only insects that were in close proximity to the copper wires were adversely affected. As mentioned earlier, the electrical field dissipates quickly with distance from the copper wires, and electric pulses are undetectable by the human hand approximately 5 cm beyond the outermost wire. It seems likely that electric current will dissipate as rapidly in the vertical dimension. On level ground, the copper wire loops sit approximately 5 cm above the ground; thus, the electric field generated between wires most probably does not extend to the substrate surface, where insects are most abundant.

In both control and exclusion replicates, ephemeropterans and dipterans comprised most of the drift; although plecopterans and trichopterans were collected in drift samples, they were relatively uncommon. When all four sites were examined together, both ephemeropteran and

dipteran drift biomass (as well as dipteran drift abundance) were significantly higher in exclusion treatments. Studies have shown that these taxa can be especially susceptible to adverse electrical effects. Bisson (1976) found that chironomids demonstrated greater drift increases than other taxa when electroshocked with a battery-powered backpack shocker. Mesick and Tash (1980) found that drift of certain ephemeropteran taxa was prompted by charges as little as 0.16 V. However, there are several key differences between the drift experiment described here and these previous studies. For example, the study by Mesick and Tash (1980) was conducted in a small aquarium (36 cm x 20 cm), which likely affected dissipation of the electric current. In addition, the voltage applied by Bisson (1976) [~ 500 V] was much greater than the 40 – 60 V charge obtained with this electric exclusion method.

As mentioned earlier, several researchers have modified the electric exclusion technique to exclude stream insects from benthic areas. Usually these techniques effectively exclude mayflies, but dipterans generally are not adversely affected (e.g., Moulton et al. 1999, Brown et al. 2000). This contrasts with results of our drift experiments, which showed that dipteran abundance and biomass were initially elevated by fence charger activation (≥ 80% increase for both abundance and biomass).

Drift patterns differed across the four sites. Insects in Betty Creek showed a relatively strong adverse reaction to the electrical charge, which was likely (at least in part) an artifact of the chargers used at this site (these chargers were not used in any other exclusion experiments). Water conductivity did not have an obvious influence on insect drift across the four sites, although comparisons among sites are complicated by the fact that conductivity was not the only cross-site difference. Because sites differed in conductivity (range ≈ 13 – 35 $\mu S \quad cm^{-1}$), field strength and therefore insect response also may have varied. In low conductivity water, the voltage gradient to which organisms are subjected (i.e., the number of volts / the distance between the two copper wire loops in each PVC frame) is relatively high. Thus, organisms feel a stronger

shock at low conductivity versus high conductivity sites, where the voltage gradient is reduced. Total drift biomass was greater in exclusion versus control replicates at Ball, the lowest conductivity site; however, ephemeropteran and dipteran biomass were not significantly elevated in exclusion samples.

Electric exclusion did not appear to negatively affect most common insect taxa colonizing tiles in our experiments. In fact, abundance and biomass of chironomids and hydropsychids were significantly greater in electrified treatments, as was biomass of baetid mayflies. Tipulid abundance and biomass did not differ between control and exclusion treatments, but abundance and biomass of heptageniid mayflies were significantly lower in exclusion versus control replicates. Although this suggests that heptageniids were adversely affected by the electrical charge, average individual biomass of heptageniids did not differ between control and exclusion treatments. Across all sites, average individual heptageniid biomass was greater in exclusion treatments, largely due to two large individuals collected in exclusion replicates (one at Davidson, one at Sweeten). In addition, heptageniid abundance and biomass in both control and exclusion treatments were highly variable (coefficient of variation at all sites ≥ 0.77).

Although the abundance and biomass of dipteran drift (primarily chironomids) were significantly elevated in electric exclusion replicates, chironomid abundance, biomass, and average individual biomass were significantly higher in exclusion treatments. This finding supports the contention that substrate-associated insects are not affected by the electric current.

CONCLUSIONS

Does the use of electricity to exclude stream macroconsumers directly affect stream insects? Insect drift was elevated by the exclusion technique (drift abundance increased by 50%, drift biomass by 120%), suggesting that insects initially avoided the electrical current. Larger insects (> 5 mm) seemed especially vulnerable to direct electrical impacts, although size frequency distributions for drifting insects were relatively similar between control and exclusion replicates.

However, the abundance, biomass, and individual size of most insects colonizing tiles within electrified treatments were not adversely affected; in fact, insects tended to respond positively to macroconsumer exclusion. Substrate-associated insects generally occur below the charged area, and may only respond to electrical pulses when they approach charger wires. Heptageniid mayflies warrant more attention, as results suggest that heptageniids may be especially sensitive to electric current. Other scrapers (e.g., baetid mayflies) did not show similar sensitivity, and overall scraper abundance and biomass did not differ between control and exclusion treatments in our exclusion experiments.

MODIFICATION AND IMPROVEMENT OF THE ELECTRIC EXCLUSION TECHNIQUE

Modification and improvement of the electric exclusion technique should focus on two criteria: strength of the electrical charge, and consistency of the charge both within and across study systems. Currently, voltages delivered to in-stream frames are not maximized. The copper wire used in these experiments is 600 V wire, which means that any charges greater than 600 V will not be conserved (i.e., voltage will be lost through the wire). This can be remedied by using high voltage wire to connect fence chargers to frames. Length and alignment of the wires connecting fence chargers to frames also will influence field strength. Longer connecting wires will allow more charge to dissipate before reaching the frames, so connecting wires should be kept as short as possible. In addition, the two wires connecting each fence charger to a frame should be kept as far apart as possible. In past experiments these wires have been tied together, which does not maximize field strength.

However, maximizing the electrical charge within each frame may not be necessary or desirable at the range of water conductivities examined here (~ 13 - 110 $\mu S\ cm^{-1}$). In all experiments conducted thus far, electrical charges were strong enough to effectively exclude

macroconsumers. Since drift and tile data suggest that some taxa (e.g., heptageniid mayflies) may be adversely affected by the exclusion technique at relatively low voltages, maximizing field strength may increase the probability that these insects will be negatively affected, but have little effect on the macroconsumer exclusion capabilities of the technique.

Maintaining a consistent electrical charge both within and across study systems presents a more significant concern. In a given electric exclusion experiment, all exclusion replicates ideally should have similar in-stream field strengths. However, field strength will be affected by numerous factors, including water conductivity, temperature, moisture, length and placement of connecting wires, and uniformity of connections (i.e., between connecting wires and fence chargers and connecting wires and frames). In the field, temperature and moisture are difficult to control, especially across multiple sites. Connecting wires can be placed in PVC tubes to help standardize moisture and temperature conditions across replicates, but this may prove relatively impractical in the field.

Length and placement of connecting wires and connection uniformity are easier to standardize. Connecting wires of equal length should be used for all replicates, since wire length will influence field strength (i.e., longer wires = weaker field). In addition, the connecting wires attached to each fence charger should be kept a standardized distance apart from each other (e.g., the distance between the fence charger electrodes). Standard ring terminals should be used to attach connecting wires to fence chargers. These terminals clamp onto the ends of the connecting wires, and establish relatively uniform connections to fence chargers. In past experiments connecting wires have been wrapped around fence charger electrodes, but this can introduce field strength variability. Ideally the attachments between connecting wires and frame wires would be similarly standardized, but finding an attachment method that can withstand high water discharges has proven difficult.

When conducting electric exclusion experiments at multiple sites, water conductivity differences potentially can pose a problem. As discussed earlier, water conductivity will affect field strength (i.e., higher conductivity = weaker field), which complicates cross-site comparisons. In theory, water conductivity differences can be corrected for by attaching a variable, voltage-limiting resistor at the fence charger electrodes. However, insect response to electricity at the sites examined here was not obviously influenced by water conductivity, suggesting that this resistor may not be necessary within this range of conductivities (~ 13 - 110 $\mu S\ cm^{-1}$). This voltage-limiting apparatus may be useful for ensuring that the minimum voltage needed to exclude macroconsumers is used. Using the weakest electrical current that effectively excludes macroconsumers would minimize the chance for potentially sensitive insect taxa (e.g., heptageniids) to be adversely affected by the exclusion technique.

FUTURE APPLICATIONS

The use of electric exclusion methods allows in situ examination of interactions between biotic and abiotic forces influencing stream ecosystems. It provides a powerful experimental tool, and future applications of the technique could lead in several directions, including:

- Examination of scale effects: Several studies have shown that the scale at which exclusion experiments are conducted can significantly influence experimental results (e.g., Englund 1997). Electricity could be used to exclude macroconsumers from different sized areas (< 0.25 m^2 to entire stream reaches), allowing comparison of macroconsumer impacts across multiple scales.
- Simultaneous examination of top-down versus bottom-up influences: The relative importance of top-down (i.e., consumer-controlled) and bottom-up (i.e., resource-controlled) forces in structuring ecosystem dynamics has been the subject of much debate in ecology (e.g., Power 1992, Hunter and Price 1992). By placing nutrient

diffusing substrates in macroconsumer access and exclusion treatments, one could conduct an elegant experiment assessing the relative importance of macroconsumers versus nutrients, as well as interactions between the two. These experiments could be combined with exclusion experiments at different scales, which would provide an interesting examination of the spatial variability of top-down versus bottom-up impacts.

New applications pf the original electric exclusion technique (i.e., for the exclusion of stream macroconsumers) are already underway. As mentioned earlier, researchers have begun to use electricity for the exclusion of insects as well as macroconsumers, to determine the relative importance of different consumer assemblages (e.g., Moulton et al. 1999, Brown et al. 2000, Opsahl et al. 2001).

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Table 5.1. Number of paired tests conducted across sites (i.e., with all data pooled) and within sites (i.e., with each site analyzed independently) in the drift and tile experiments. All tests were paired t-tests using natural log or square root-transformed data unless otherwise noted.

EXPERIMENT	VARIABLE	ACROSS SITES	WITHIN SITES
Drift	Abundance	3	3
	Biomass	3 (+ 3 Wilcoxon)	3
Tiles	Abundance	5	2 (+ 3 Wilcoxon)
	Biomass	5	2 (+ 3 Wilcoxon)
	Average individual biomass	1 (+ 4 Mann-Whitney)	1

Table 5.2. Results of paired t-tests (control versus electric exclusion) for drift abundance and biomass, when all sites (Lower Ball Creek, Betty Creek, Coweeta Creek, and Jones Creek) were included in analyses and when Betty was omitted from analyses. Data were square root-transformed before analysis, and individuals > 5 mm (total = 6 across all sites) were omitted from biomass comparisons.

	ALL SITES		**BETTY OMITTED**	
	t_{19}	***P***	t_{14}	***P***
Abundance **(# sample^{-1})**				
Total	- 1.96	0.032	- 1.13	0.138
Ephemeroptera	- 0.24	0.406	0.02	0.490
Diptera	- 2.49	0.011	- 1.82	0.045
Biomass **(mg sample^{-1})**				
Total	- 1.49	0.076	- 0.80	0.219
Ephemeroptera	- 1.75	0.048	- 0.82	0.212
Diptera	- 2.60	0.009	- 2.63	0.010

Table 5.3. Results of individual paired t-tests (control versus electric exclusion) for drift abundance and biomass at Lower Ball Creek, Betty Creek, Coweeta Creek, and Jones Creek. Individuals > 5 mm (total = 6 across all sites) were omitted from biomass analyses.

		ABUNDANCE		BIOMASS	
SITE	**INSECTS**	t_4	***P***	t_4	***P***
Ball	Total	- 1.52	0.102	- 2.40	0.037
	Ephemeropteran	- 0.46	0.336	- 0.41	0.351
	Dipteran	- 1.07	0.173	- 1.28	0.135
Betty	Total	- 1.94	0.062	- 2.21	0.046
	Ephemeropteran	- 1.10	0.166	- 2.24	0.044
	Dipteran	- 1.49	0.106	- 0.65	0.275
Coweeta	Total	- 0.18	0.432	0.18	0.431
	Ephemeropteran	0.71	0.258	- 0.47	0.331
	Dipteran	- 1.43	0.113	- 1.34	0.125
Jones	Total	- 0.41	0.352	- 0.71	0.259
	Ephemeropteran	- 0.12	0.455	- 0.48	0.329
	Dipteran	- 0.91	0.208	- 1.80	0.073

Table 5.4. Abundance (# m^{-2}) of common insect taxa collected on day 40 tiles at each tile experiment sites. Values represent mean of 4 replicates (Davidson, Beaverdam) or 5 replicates (Ball, Jones, Sweeten), ± 1 SE.

SITE	TREATMENT	CHIRONOMIDAE	HYDROPSYCHIDAE	HEPTAGENIIDAE	BAETIDAE	TIPULIDAE
Ball	Control	1014 ± 211	36 ± 22	89 ± 40	0	0
	Exclusion	1547 ± 363	284 ± 90	89 ± 28	0	0
Davidson	Control	11229 ± 3469	367 ± 367	373 ± 213	111 ± 111	22 ± 22
	Exclusion	18311 ± 4314	1589 ± 1559	22 ± 22	0	22 ± 22
Jones	Control	24658 ± 8572	622 ± 411	71 ± 33	391 ± 241	53 ± 36
	Exclusion	23875 ± 6347	427 ± 165	0	1013 ± 652	231 ± 107
Beaverdam	Control	6245 ± 2140	22 ± 22	289 ± 105	422 ± 293	222 ± 147
	Exclusion	21884 ± 5944	189 ± 161	0	1063 ± 191	178 ± 150
Sweeten	Control	6395 ± 1449	142 ± 66	0	36 ± 36	258 ± 126
	Exclusion	12169 ± 2110	658 ± 493	18 ± 18	53 ± 36	276 ± 190

Table 5.5. Biomass (mg m^{-2}) of common insect taxa collected on day 40 tiles at each tile experiment site. Values represent mean of 4 replicates (Davidson, Beaverdam) or 5 replicates (Ball, Jones, Sweeten), ± 1 SE.

SITE	TREATMENT	CHIRONOMIDAE	HYDROPSYCHIDAE	HDEPTAGENIIDAE	BAETIDAE	TIPULIDAE
Ball	Control	32.9 ± 10.1	2.1 ± 2.0	53.1 ± 48.6	0	0
	Exclusion	84.6 ± 17.4	54.3 ± 16.3	1.4 ± 0.5	0	0
Davidson	Control	192.6 ± 85.7	28.3 ± 28.3	16.6 ± 6.4	4.3 ± 4.3	4.8 ± 4.8
	Exclusion	331.7 ± 95.0	223.9 ± 216.1	33.4 ± 33.4	0	6.2 ± 6.2
Jones	Control	401.6 ± 105.9	111.1 ± 101.9	28.5 ± 17.1	41.8 ± 34.2	11.4 ± 9.7
	Exclusion	669.5 ± 115.9	193.4 ± 100.3	0	57.5 ± 36.3	12.1 ± 5.5
Beaverdam	Control	170.2 ± 52.3	24.5 ± 24.5	67.0 ± 51.8	11.4 ± 7.0	25.6 ± 17.2
	Exclusion	970.4 ± 241.1	56.7 ± 35.7	0	73.8 ± 31.9	28.6 ± 16.5
Sweeten	Control	507.0 ± 163.7	450.4 ± 189.7	0	14.7 ± 14.7	68.4 ± 30.3
	Exclusion	905.6 ± 135.0	1337.7 ± 1267.6	124.6 ± 124.4	13.6 ± 8.7	71.0 ± 32.2

Table 5.6. Results of paired t-tests (control versus electric exclusion) for abundance and biomass of common insect taxa collected on tiles. Each test was done on pooled day 40 data from five sites (Ball, Davidson, Jones, Beaverdam, and Sweeten). Data were natural log-transformed before analysis.

	ABUNDANCE		BIOMASS	
TAXON	t_{22}	***P***	t_{22}	***P***
Chironomidae	- 4.23	0.0002	- 5.46	< 0.0001
Hydropsychidae	- 3.04	0.003	- 2.26	0.017
Heptageniidae	2.11	0.023	2.00	0.030
Baetidae	- 1.51	0.072	- 1.85	0.039
Tipulidae	- 0.14	0.445	- 0.05	0.479

Table 5.7. Average individual biomass (mg individual^{-1}) of five insect taxa commonly collected on tiles. Values represent mean ± 1 SE across all five sites; the number of replicates each average is based upon (i.e., total number of replicates in which each taxon was found) is indicated in brackets.

TAXON	CONTROL	EXCLUSION
Chironomidae	0.04 ± 0.01 [23]	0.05 ± 0.01 [23]
Hydropsychidae	1.17 ± 0.50 [10]	0.04 ± 0.01 [16]
Heptageniidae	0.33 ± 0.13 [12]	1.43 ± 1.14 [6]
Baetidae	0.12 ± 0.06 [6]	0.11 ± 0.03 [9]
Tipulidae	0.24 ± 0.06 [10]	0.27 ± 0.07 [10]

Table 5.8. Results of individual paired t-tests (control versus electric exclusion) for day 40 abundance and biomass of Chironomidae and Hydropsychidae at each tile experiment site. Data were natural log-transformed before analysis. Values represent t-statistic and *P*-value for each test; degrees of freedom = 4 for Ball, Jones, and Sweeten, 3 for Davidson and Beaverdam.

	CHIRONOMIDAE		**HYDROPSYCHIDAE**	
SITE	**Abundance (t / *P*)**	**Biomass (t / *P*)**	**Abundance (t / *P*)**	**Biomass (t / *P*)**
Ball	- 1.35 / 0.125	- 1.85 / 0.069	- 4.47 / 0.006	- 7.51 / 0.001
Davidson	- 5.29 / 0.007	- 2.79 / 0.034	- 1.40 / 0.128	- 1.65 / 0.099
Jones	- 0.60 / 0.292	- 4.37 / 0.006	- 0.83 / 0.227	- 1.27 / 0.136
Beaverdam	- 3.39 / 0.021	- 5.53 / 0.006	- 1.52 / 0.113	- 0.94 / 0.208
Sweeten	- 2.60 / 0.030	- 2.27 / 0.043	- 0.31 / 0.386	0.22 / 0.417

Figure 5.1. Illustration of a typical electric exclusion experiment at one site, using a paired design. White squares = control frames, shaded squares = electrified frames; each square represents a 0.25 m^{-2} area (figure not to scale). The stream reach length over which the five replicate pairs are distributed depends on the number of suitable areas (i.e., in terms of water velocity, substrate, etc.) within a given area.

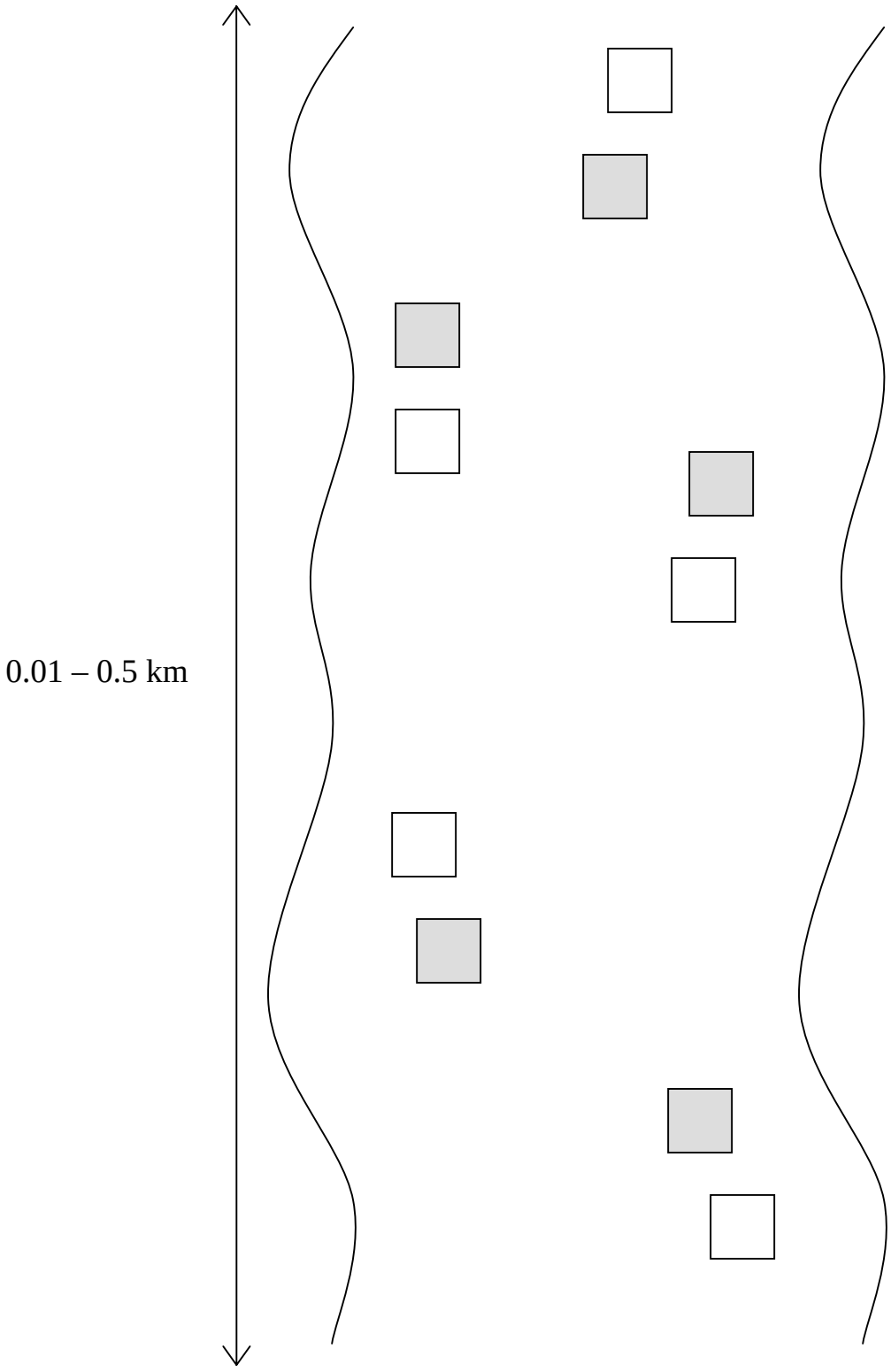

0.01 – 0.5 km

Figure 5.2. Illustration of an electrified frame in an exclusion experiment (figure not to scale).

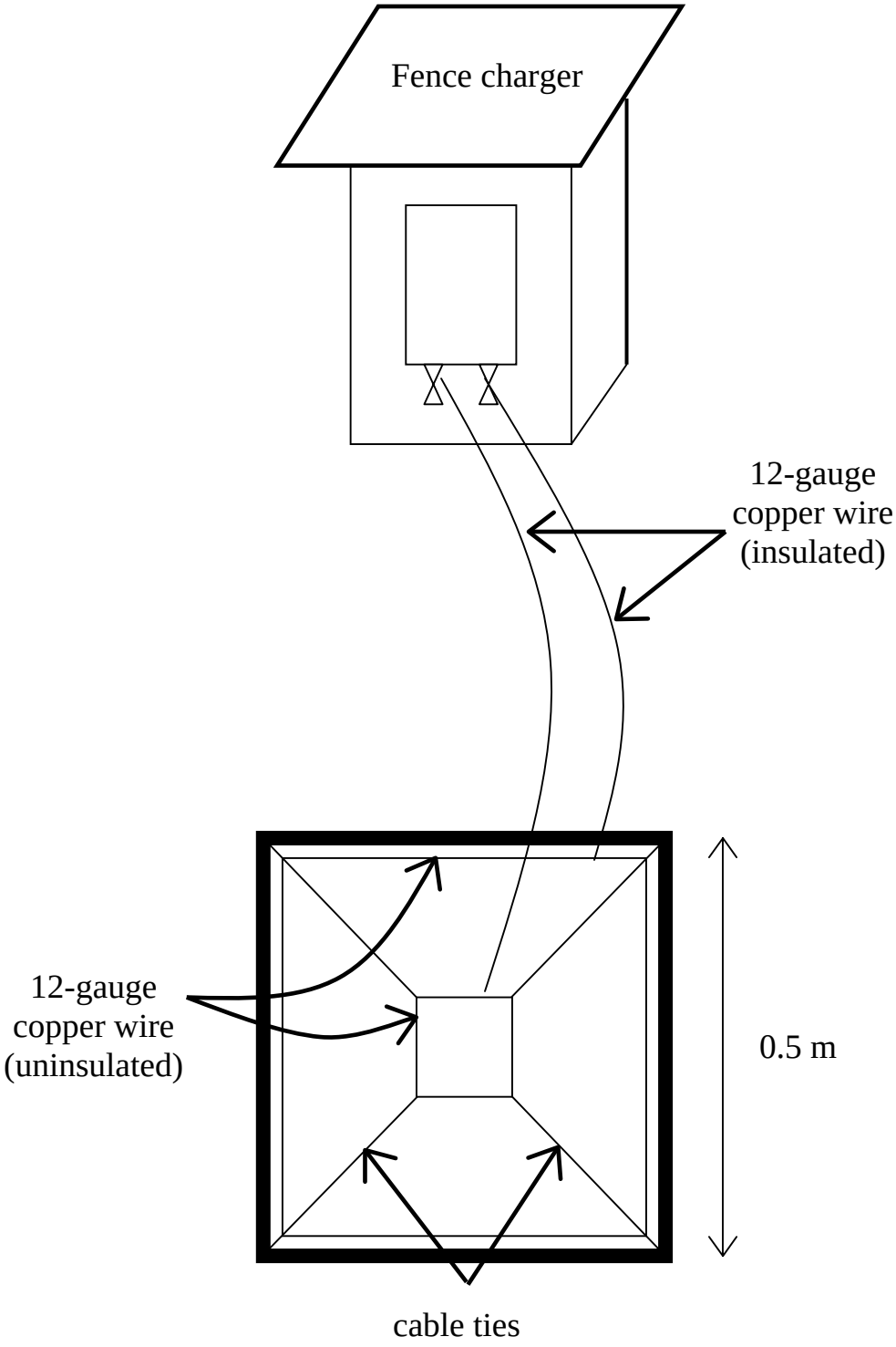

Fence charger
12-gauge
copper wire
(insulated)
12-gauge
copper wire
(uninsulated)
0.5 m
cable ties

Figure 5.3. Total, ephemeropteran, and dipteran drift abundance (a) and biomass (b and c) in control (white bars) and electric exclusion (shaded bars) replicates, averaged across all four sites. Biomass values are shown with large individuals (> 5 mm) included (b), and with these individuals (total = 6 individuals across 40 replicates) removed (c). Values represent mean (n = 20) + 1 SE. * indicates paired t-test with $P < 0.05$.

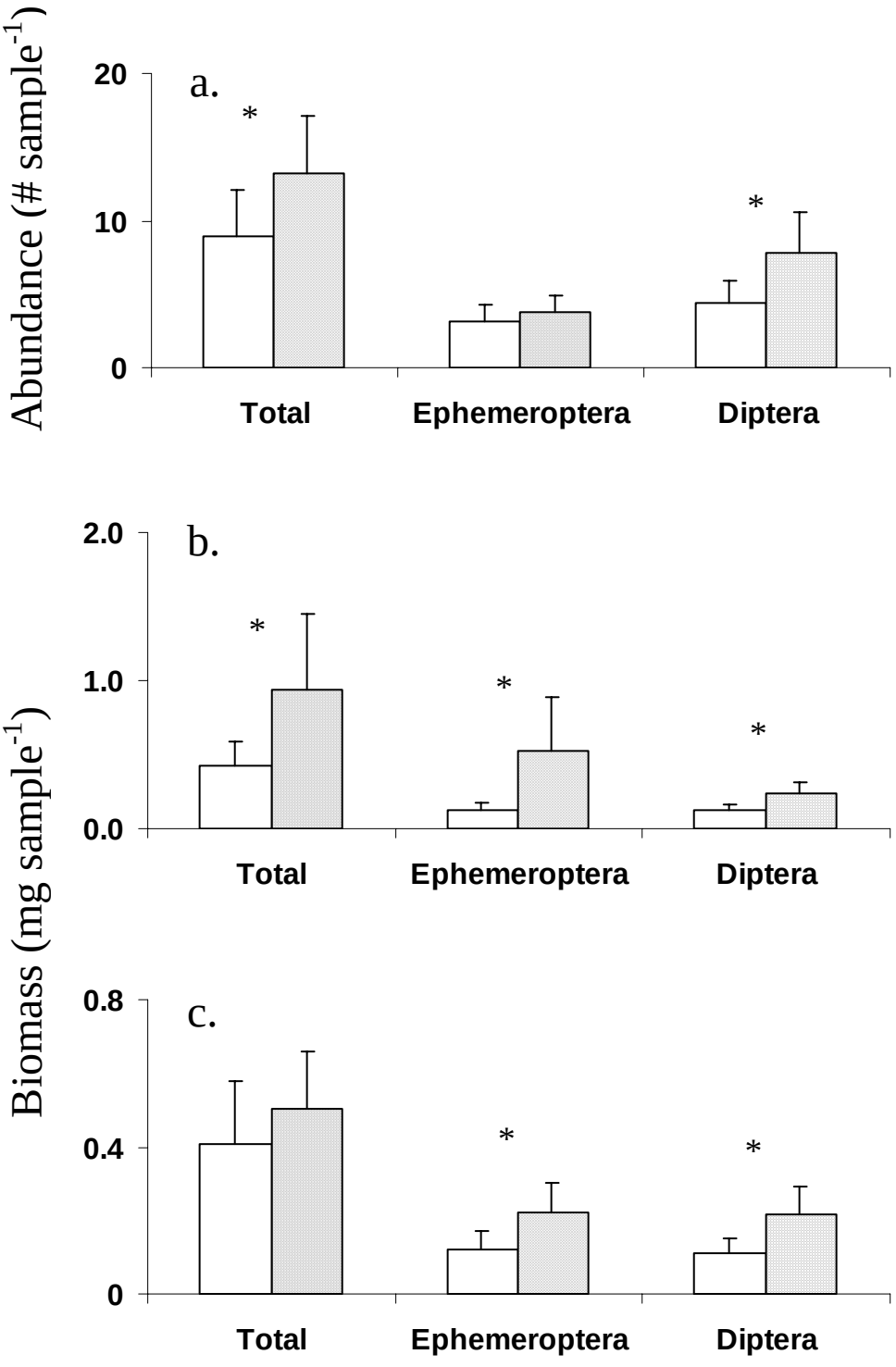

Abundance (# sample-1)
a.
20
10
0
*
*
Total
Ephemeroptera
Diptera
Biomass (mg sample-1)
b.
2.0
1.0
0.0
*
*
*
Total
Ephemeroptera
Diptera
c.
0.8
0.4
0
*
*
Total
Ephemeroptera
Diptera

Figure 5.4. Size frequency distributions for total aquatic insect drift in control (white bars) and exclusion (shaded bars) replicates, at (a) Ball, (b) Betty, (c) Coweeta, and (d) Jones. Each value represents sum across five replicates.

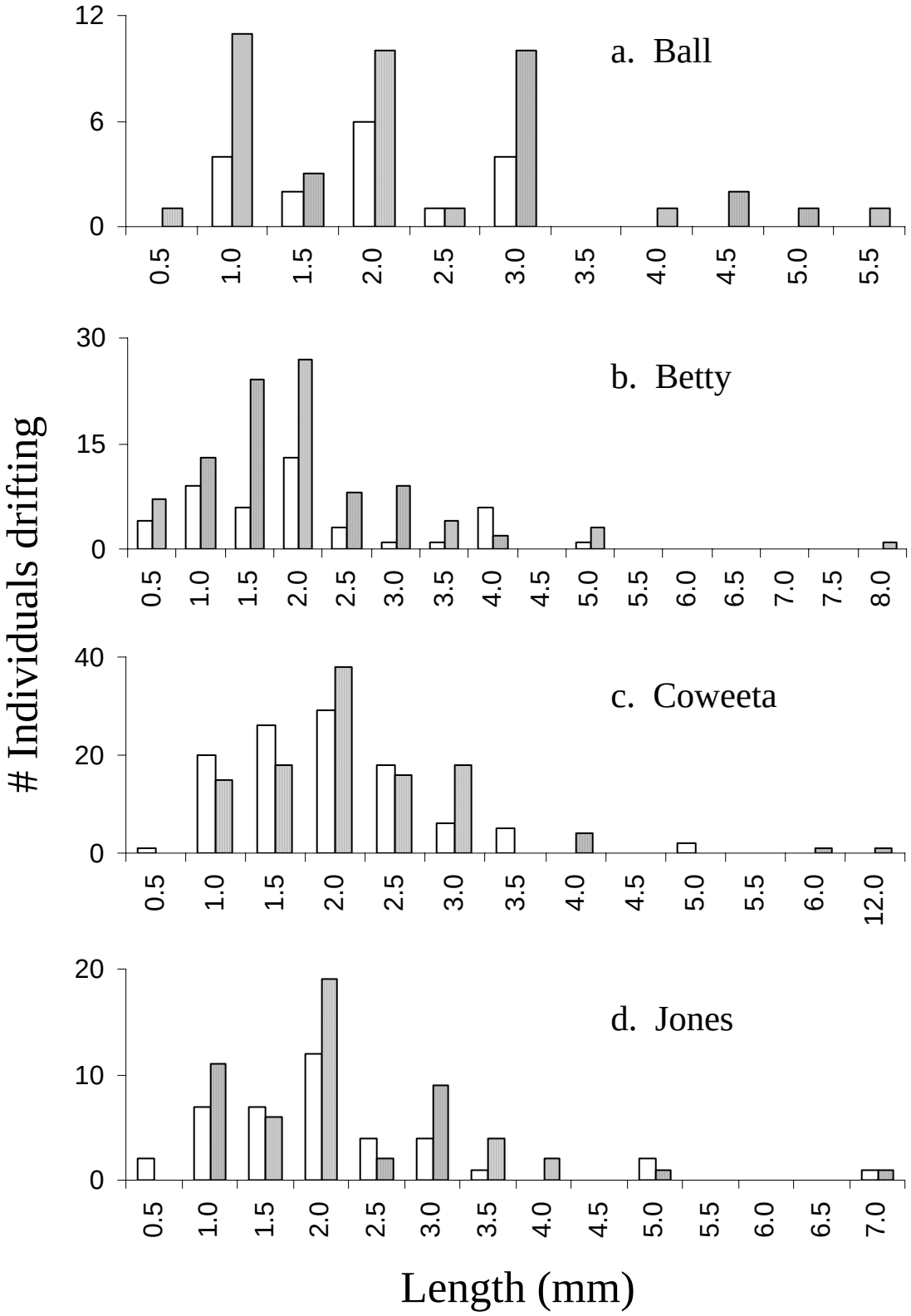

a. Ball
b. Betty
c. Coweeta
d. Jones
Individuals drifting
Length (mm)

Figure 5.5. Size frequency distributions for ephemeropteran drift in control (white bars) and exclusion (shaded bars) replicates, at (a) Ball, (b) Betty, (c) Coweeta, and (d) Jones. Each value represents sum across five replicates.

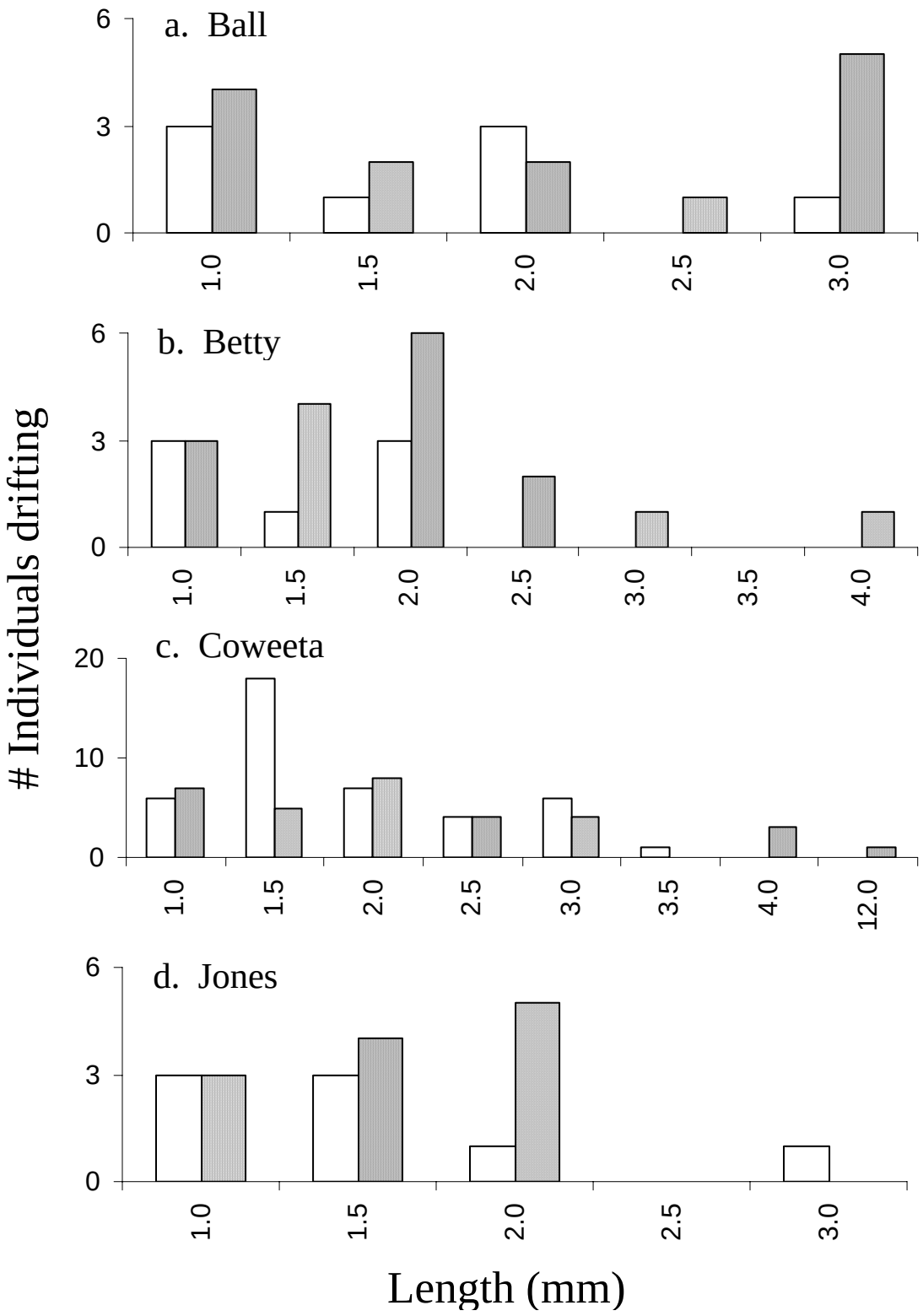

a. Ball
b. Betty
c. Coweeta
d. Jones
Individuals drifting
Length (mm)
6
3
0
20
10
1.0
1.5
2.0
2.5
3.0
3.5
4.0
12.0

Figure 5.6. Size frequency distributions for dipteran drift in control (white bars) and exclusion (shaded bars) replicates, at (a) Ball, (b) Betty, (c) Coweeta, and (d) Jones. Each value represents sum across five replicates.

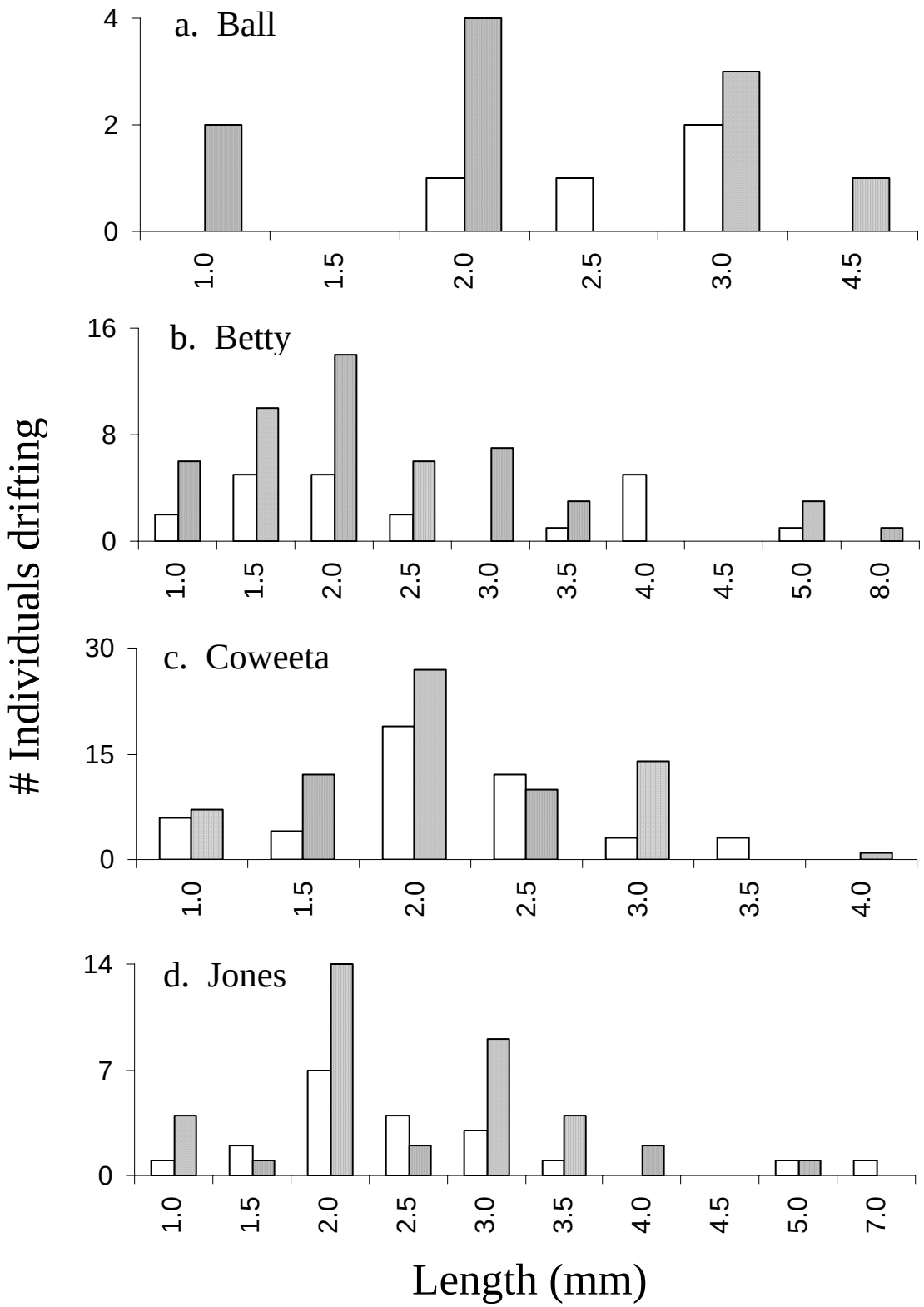

a. Ball
4
2
0
1.0
1.5
2.0
2.5
3.0
4.5
b. Betty
16
8
0
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
8.0
c. Coweeta
30
15
0
1.0
1.5
2.0
2.5
3.0
3.5
4.0
d. Jones
14
7
0
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
7.0
Individuals drifting
Length (mm)

Figure 5.7. Total, ephemeropteran (E), and dipteran (D) drift abundance in control (white bars) and electric exclusion (shaded bars) replicates, at (a) Ball, (b) Betty, (c) Coweeta, and (d) Jones. Values represent mean (n = 5) + 1 SE.

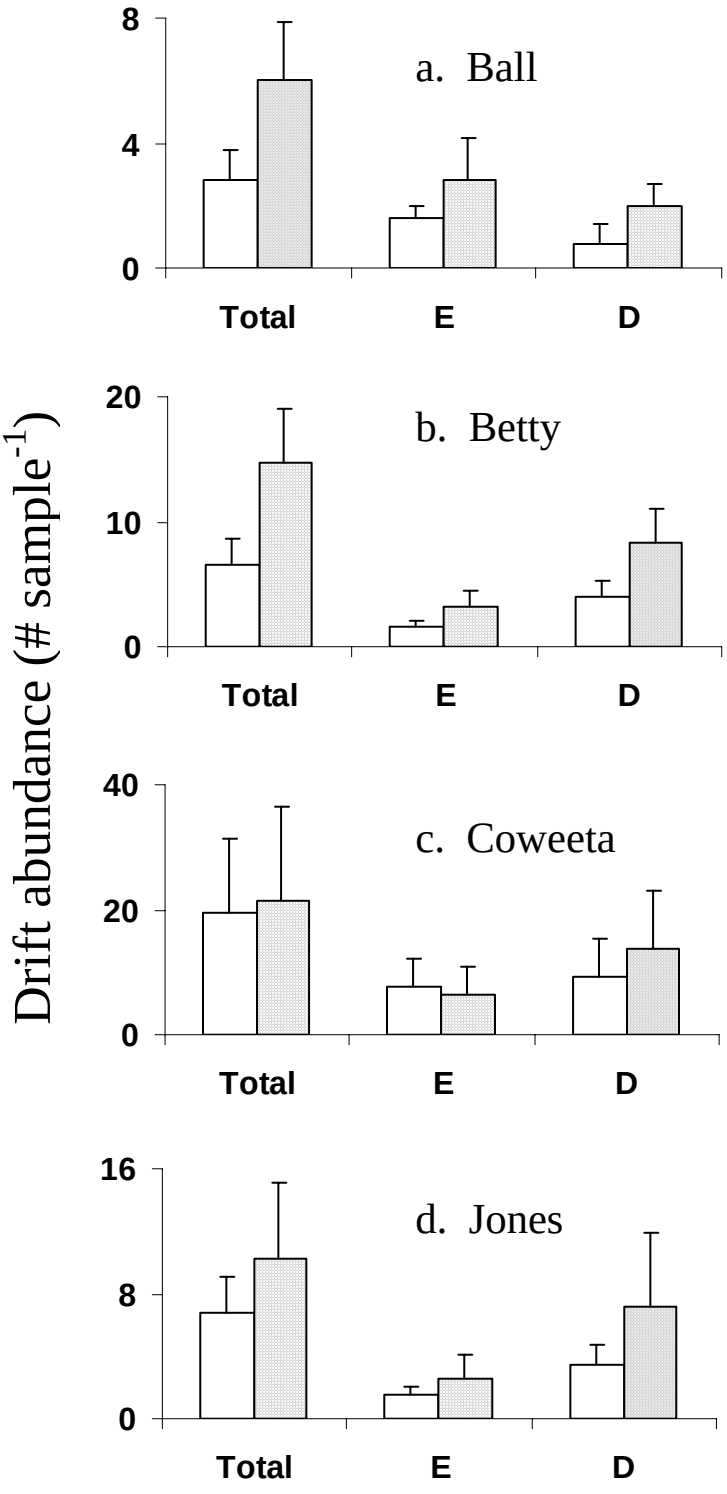

Drift abundance (# sample-1)
a. Ball
b. Betty
c. Coweeta
d. Jones
Total
E
D
0
4
8
10
20
40
16

Figure 5.8. Total, ephemeropteran (E), and dipteran (D) drift biomass in control (white bars) and electric exclusion (shaded bars) replicates, at (a) Ball, (b) Betty, (c) Coweeta, and (d) Jones. Large individuals (> 5 mm) were omitted from these values (total = 6 individuals across 40 replicates). Values represent mean (n = 5) + 1 SE. * indicates paired t-test with $P < 0.05$.

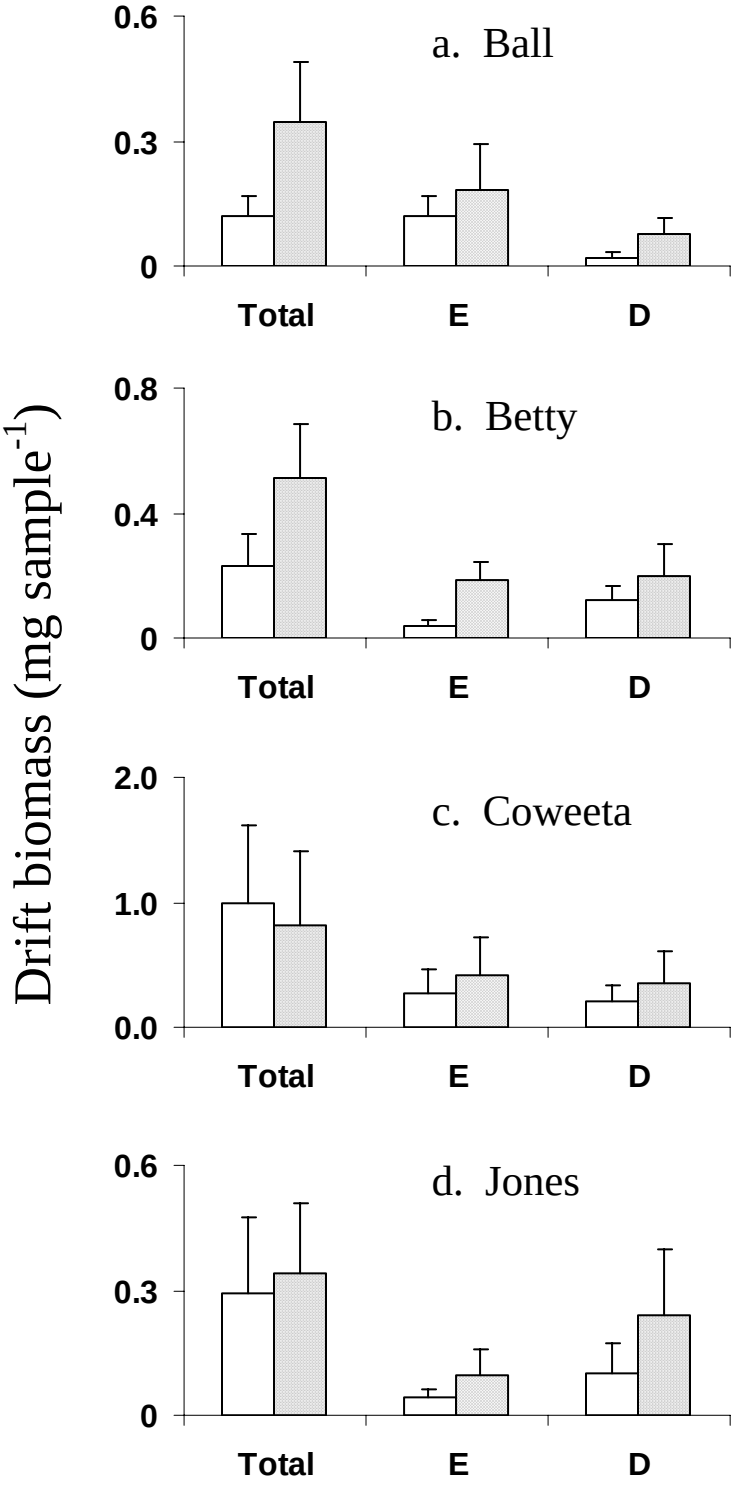

Drift biomass (mg sample-1)
a. Ball
0.6
0.3
0
Total
E
D
b. Betty
0.8
0.4
0
Total
E
D
c. Coweeta
2.0
1.0
0.0
Total
E
D
d. Jones
0.6
0.3
0
Total
E
D

Figure 5.9. Abundance (a) and biomass (b) of common insect taxa collected on control (white bars) and electric exclusion (shaded bars) tiles after 40 days, averaged across all five sites. Values represent mean (n = 46) + 1 SE. * indicates paired t-test with $P < 0.05$. CHI = Chironomidae, HYD = Hydropsychidae, HEP = Heptageniidae, BAE = Baetidae, TIP = Tipulidae.

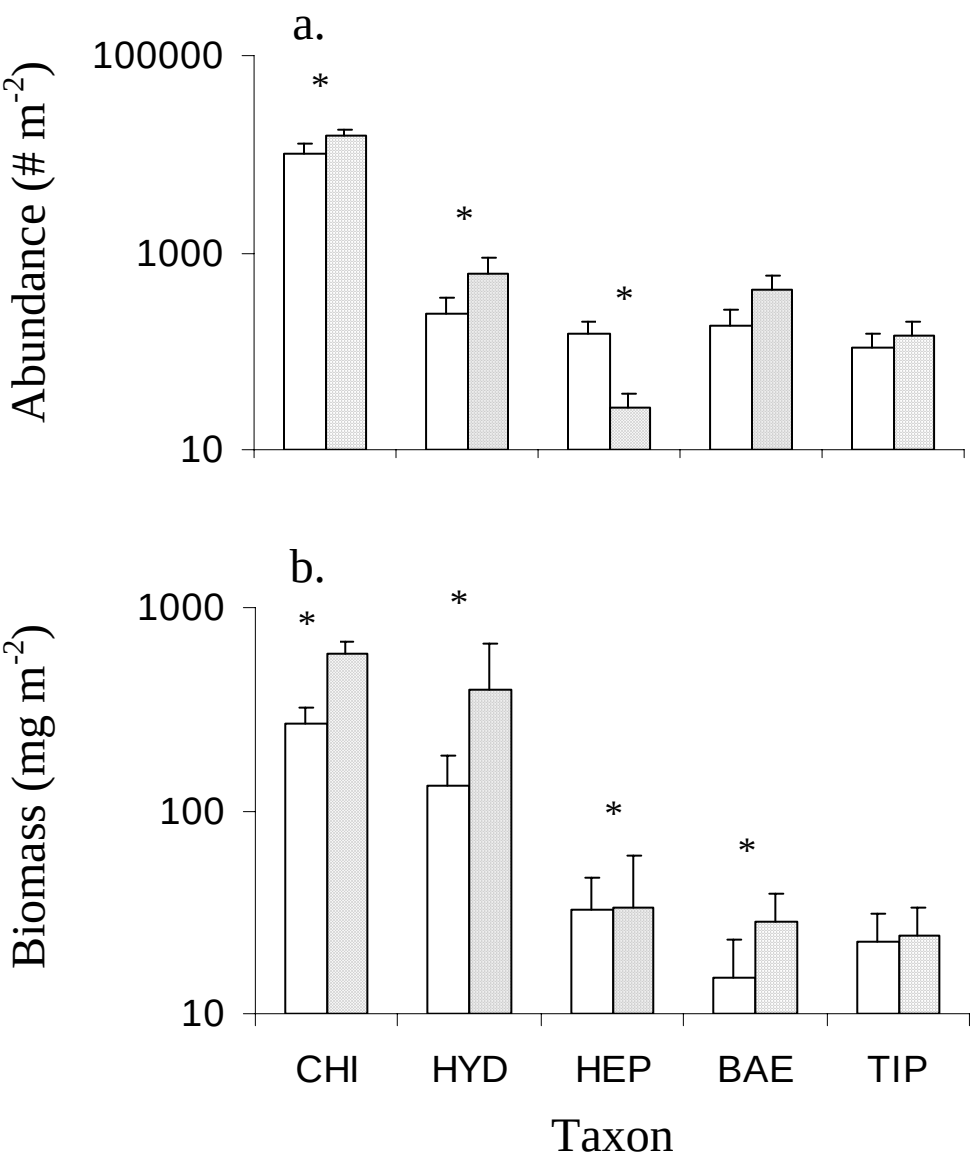
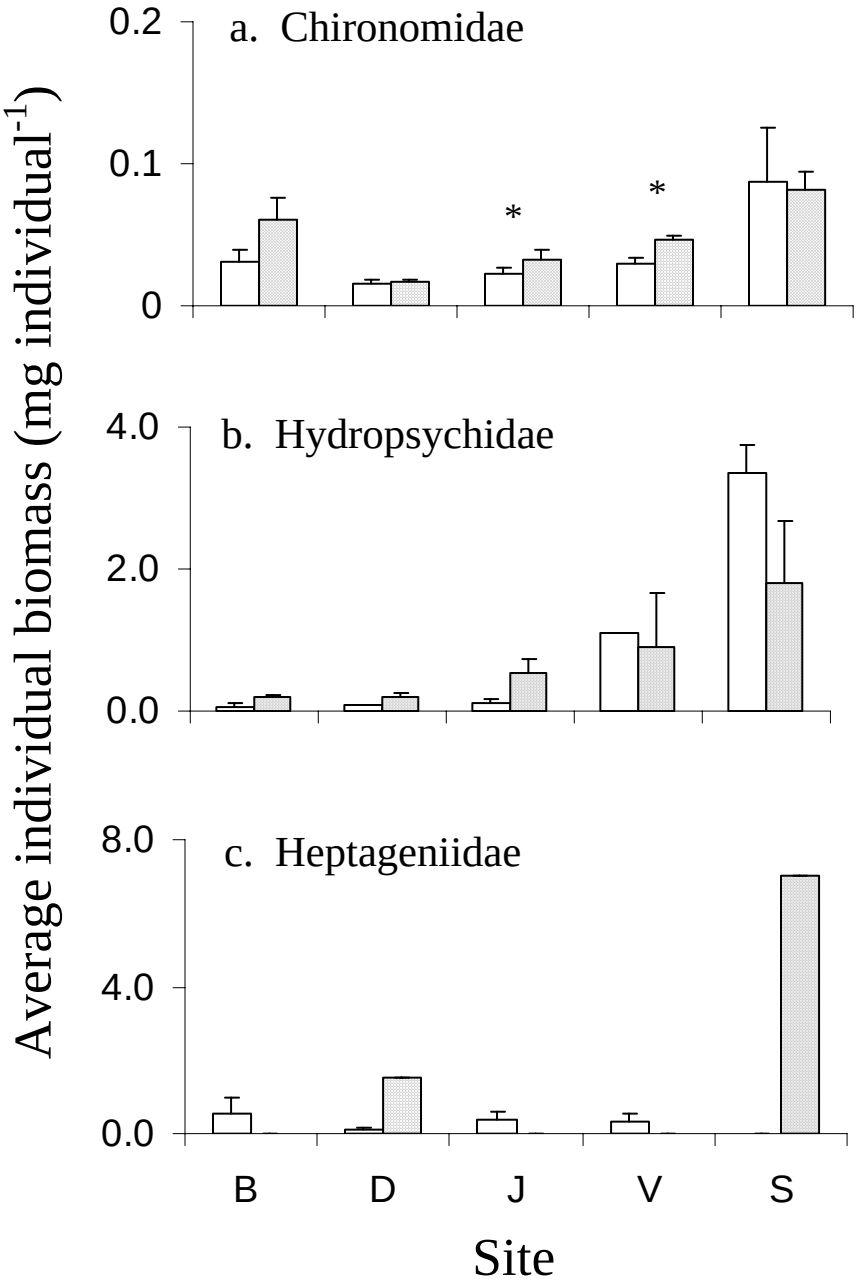
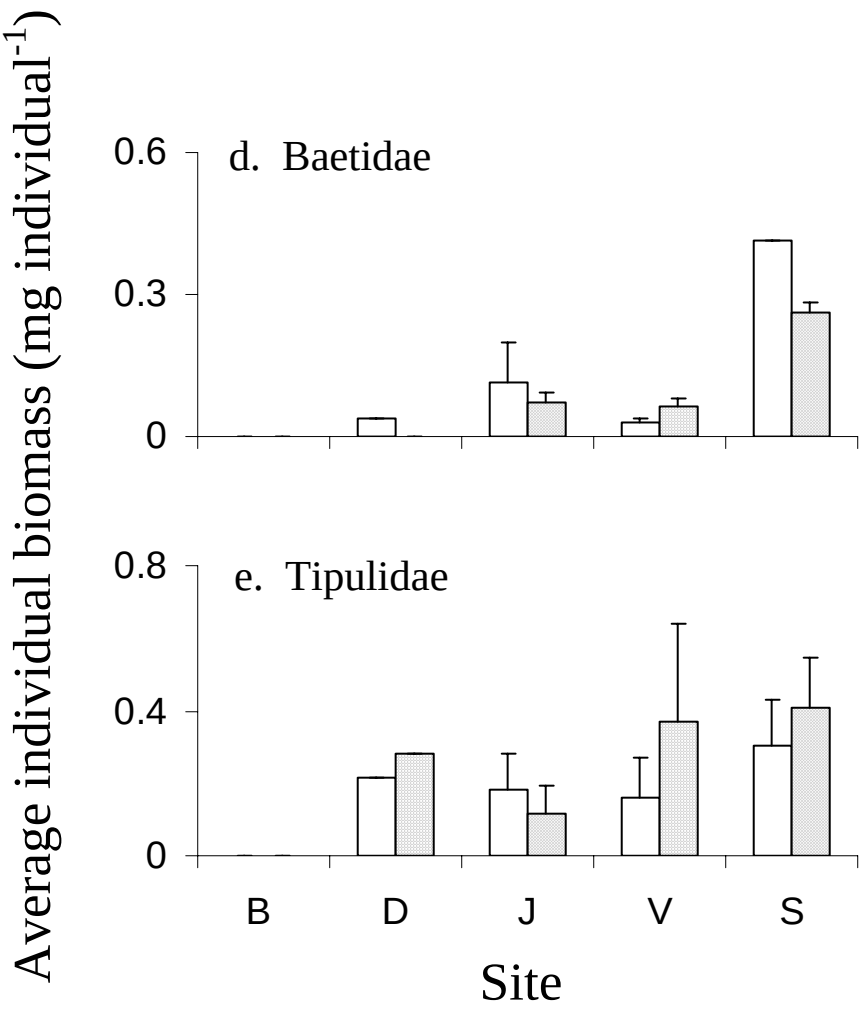

a.
100000
1000
10
Abundance (# m-2)
*
*
*
b.
1000
100
10
Biomass (mg m-2)
*
*
*
*
CHI
HYD
HEP
BAE
TIP
Taxon

Figure 5.10. Average individual biomass of (a) Chironomidae, (b) Hydropsychidae, (c) Heptageniidae, (d) Baetidae, and (e) Tipulidae in control (white bars) and electric exclusion (shaded bars) treatments at each of the five tile experiment sites (B = Ball, D = Davidson, J = Jones, V = Beaverdam, S = Sweeten). Average individual biomass was calculated by dividing biomass by abundance; replicates in which individuals of a given taxa were not collected were not included in these averages. Values represent mean (n = 2 – 5) + 1 SE; bars without SE lines indicate that average individual biomass was based on one individual. * indicates paired t-test with $P < 0.05$.


a. Chironomidae
0.2
0.1
0
*
*
b. Hydropsychidae
4.0
2.0
0.0
c. Heptageniidae
8.0
4.0
0.0
B
D
J
V
S
Site
Average individual biomass (mg individual-1)


Average individual biomass (mg individual-1)
d. Baetidae
0.6
0.3
0
e. Tipulidae
0.8
0.4
0
B
D
J
V
S
Site

CHAPTER 6

CONCLUSIONS

Macroconsumers (fishes and crayfishes) significantly affected benthic community structure and/or function in southern Appalachian streams. Across a range of experiments, exclusion of these organisms consistently altered biotic response variables, including insect biomass, algal accrual, and fungal biomass. However, specific responses to macroconsumer exclusion differed among experiments, indicating that the relative strength and outcome of these top-down interactions was variable and depended upon factors such as season, sediment regime, substrate type, and macroconsumer identity (Peckarsky 1985, Rosemond et al. 1998, Gelwick 2000).

Crayfish played a significant role in the breakdown of rhododendron leaves during both summer and autumn, even though rhododendron is considered a low quality food (Chapter 2). Although sculpins (as well as crayfish) could have indirectly affected rhododendron breakdown via effects on insect shredders or predators (Short and Holomuzki 1992, Malmqvist 1993), there were not significant differences in insect biomass between control and exclusion treatments. Thus crayfish exerted a direct effect, accelerating rhododendron decay via shredding. Even at the relatively low density found in Lower Ball Creek (2 m^{-2}), crayfish were able to affect an ecosystem process such as leaf decay. The threatened status of many crayfish species in the United States makes this finding especially relevant. Even small alterations in crayfish assemblages, whether via loss of native species and/or introduction of exotic species, may have significant repercussions for ecosystem function.

Simultaneous manipulation of macroconsumers and sediment (Chapter 3) indicated that small yet environmentally realistic increases in bedload transport and deposition directly and indirectly

affected algal and detrital-based benthic communities. Throughout the world, anthropogenic sedimentation poses a significant threat to freshwater ecosystems. Sediment addition experiments demonstrated that increases in bedload can directly affect biota in both algal and detrital-based food webs in an otherwise undeveloped (e.g., hydrologically unaltered, unpolluted) southern Appalachian stream. Perhaps more important, elevated bedload can alter the outcome of species interactions. Macroconsumers reduced total insect biomass on tiles, but this macroconsumer effect disappeared with daily sediment addition. These indirect effects of sedimentation are examined less frequently than direct biotic responses, but our results suggest that alteration of top-down effects may be an important aspect of bedload increases. However, this sediment-mediated reduction of top-down forces may be substrate dependent, as macroconsumers had minimal effects on leaf pack insect assemblages regardless of sediment regime.

The influence of watershed development on top-down interactions was more complex. Macroconsumers consistently affected lower trophic levels in streams representing a range of human watershed disturbances, despite physical, chemical, and biological differences between study sites. These results indicate that macroconsumers can be important top-down interactors in southern Appalachian streams, and this role is not necessarily eliminated by in-stream changes associated with human development.

This finding may seem somewhat contradictory to results from the sediment addition experiment, where sedimentation eliminated macroconsumer effects on insect assemblages. In-stream sedimentation increased with watershed development, yet macroconsumer effects were not eliminated. Although certain changes associated with watershed land use may tend to decrease the strength of top-down interactions (e.g., shifts in macroconsumer assemblages, sedimentation), these reductions may be offset by other concurrent changes (e.g., increased light and nutrients availability, compositional shifts in insect assemblages). Thus, human modification of the landscape can influence the spatial and temporal variability of top-down interactions via multiple, potentially conflicting, pathways.

Although many studies have examined the direct effects of watershed disturbance and associated in-stream changes, few have considered the repercussions of these changes for species interactions (Paul and Meyer 2001). Results presented here suggest that the influence of watershed disturbance on macroconsumer effects probably will be complex. Examination of this issue will greatly improve our understanding of stream ecosystems in a human-modified world, given: (1) the potential importance of top-down interactions in determining stream structure and function, and (2) the prevalence of anthropogenic watershed disturbance.

The electric exclusion technique is a useful tool for assessing macroconsumer effects, as it avoids the artifacts associated with traditional cage experiments. However, insects can be adversely affected by the electric current, at least in terms of initial drift abundance and biomass. Although insects collected on tiles generally were not adversely affected, the electric exclusion technique should be used wisely. In areas where insect assemblages are composed of large, potentially susceptible taxa (e.g., heptageniid mayflies), the minimum voltages necessary to exclude macroconsumers should be employed. In addition, consistency of voltages and amperages both within and across sites is an important consideration, especially as one moves into cross-site comparisons.

FUTURE RESEARCH DIRECTIONS

The exclusion experiments detailed here represent a first step towards understanding spatial and temporal variability of stream macroconsumer influence in the southern Appalachians. In many respects, these exclusion experiments serve as hypothesis-generation tools: by examining benthic community responses to macroconsumer exclusion, well-thought out, testable hypotheses about the specific mechanisms driving these responses can be developed. As a result, these experiments suggest many possibilities for future research.

- Macroconsumer (especially crayfish) effects on unconditioned versus pre-conditioned rhododendron leaf decay: In Chapter 2, we were surprised to find that

pre-conditioned rhododendron leaves were shredded by crayfish, even when other leaves were available. However, other studies have shown that crayfish had little effect on unconditioned rhododendron leaves (Powell 2001). Conducting macroconsumer exclusion experiments that use leaves pre-conditioned for varying amounts of time (e.g., 0 – 60 days), to examine how much pre-conditioning is necessary for increased palatability to crayfish. Experiments such as this would provide greater insight into the role of crayfishes in stream dynamics, an area about which relatively little is known.

- Simultaneous examination of top-down versus bottom-up effects: The relative strength of top-down (i.e., consumer-controlled) and bottom-up (i.e., resource-controlled) forces in structuring ecosystem dynamics has been the subject of much debate in ecology (e.g., Power 1992, Hunter and Price 1992). By placing nutrient diffusing substrates in macroconsumer access and exclusion treatments, one could conduct an elegant experiment assessing the relative importance of macroconsumers versus nutrients in southern Appalachian streams, as well as interactions between the two. Conducting these experiments in multiple streams varying in watershed development, to assess how the strength of top-down versus bottom-up influence changes with human modification.
- Examination of the effects of individual macroconsumers: One shortcoming of this electric exclusion technique is that it is not macroconsumer specific (i.e., fishes and crayfishes are both excluded). As a result, isolating which macroconsumers are driving different responses is difficult. These questions are crucial, however, in determining how stream systems will respond to loss and/or addition of species (e.g., loss of crayfishes with habitat degradation). These issues could be addressed by combining electric exclusion experiments with traditional cage enclosure/exclosure experiments, or by modifying the electric exclusion technique to create electric

enclosures. For example, larger PVC frames (~ 1 m^{-2}) with copper wire loops placed closer together (i.e., a few inches apart, close to the actual frame) may be able to enclose crayfishes and/or sculpins within the given area, at least over relatively short time periods. Again, this method would eliminate the artifacts associated with traditional cage experiments (e.g., increased sedimentation), and would allow examination of the relative influence of individual macroconsumer taxa.

- Further examination of land use-associated changes: In Chapter 3, we examined the influence stream sedimentation on the outcome of top-down interactions; in Chapter 4, we broadened our experimental scope to include the myriad physical, chemical, and biological alterations associated with anthropogenic watershed disturbance. To get a better understanding of interactions between macroconsumer effects and *specific* anthropogenic changes, combining macroconsumer exclusion experiments with controlled manipulations of isolated land use-associated alterations (e.g., increased nutrient *or* increased light) would be useful. These manipulations could be done in situ or in artificial stream systems, and would allow determination of the land use-associated changes most significant to top-down interactions.
- Examination of trophic versus non-trophic interactions: In our electric exclusion experiments, assessing whether macroconsumer influence results from trophic or non-trophic interactions is difficult. Extensive examination of macroconsumer gut contents and/or stable isotope analysis can be used to examine these questions (e.g., see March 2000), although gut content analysis may have limited usefulness in crayfish-dominated systems (i.e., due to pulverization of food items in crayfish guts). In addition, crayfish feeding preference tests may be useful for determining trophic relationships.
- Examination of scale effects: Several studies have shown that the scale at which exclusion experiments are conducted can significantly influence experimental results

(e.g., Englund 1997). Using the electric exclusion technique, it should be possible to exclude macroconsumers from different sized areas (e.g., 0.25 m^2 – entire reaches), allowing comparison of macroconsumer effects across multiple scales.

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APPENDIX A

Abundance (# pack^{-1}) and biomass (mg pack^{-1}) of insect shredders and predators in the rhododendron decay experiment (Chapter 2). Values are averages over 3 days (days 20, 32, and 44 during the summer experiment; days 20, 35, and 56 during the autumn experiment). Each summer value represents mean of five replicates, while each autumn value represents mean of four replicates. Standard error is given in parentheses.

SUMMER				
	Abundance (# pack^{-1})		**Biomass (mg pack^{-1})**	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Shredders				
Tallaperla	9.20 (3.56)	6.13 (3.31)	5.115 (1.317)	3.098 (1.698)
Pteronarcys	1.67 (0.50)	0.67 (0.18)	10.075 (3.447)	13.210 (9.772)
Leuctra	9.53 (1.89)	6.40 (2.69)	1.791 (0.411)	1.210 (0.591)
Taeniopteryx	0	0.067 (0.067)	0	0.002 (0.002)
Nemouridae	0	0.067 (0.067)	0	0.003 (0.003)
Lepidostoma	6.87 (1.52)	10.00 (2.92)	4.568 (1.583)	6.517 (1.938)
Oligostomis	0.067 (0.067)	0	0.069 (0.069)	0
Elmidae	0.067 (0.067)	0	0.007 (0.007)	0
Predators				
Ceratopogonidae	1.40 (0.04)	2.07 (0.063)	0.104 (0.041)	0.138 (0.019)
Tanypodinae	9.67 (1.30)	10.80 (2.02)	0.370 (0.114)	0.728 (0.178)
Empididae	0.40 (0.12)	0.47 (0.13)	0.020 (0.007)	0.020 (0.010)
Atherix	0.87 (0.13)	0.67 (0.35)	0.670 (0.319)	0.410 (0.232)
Dicranota	0.13 (0.08)	0.27 (0.07)	0.081 (0.052)	0.114 (0.033)
Perlidae	0.33 (0.15)	0.33 (0.15)	0.733 (0.477)	0.180 (0.110)
Perlodidae	2.00 (0.46)	1.53 (0.53)	1.633 (0.437)	1.350 (0.429)
Corydalidae	0.067 (0.067)	0.067 (0.067)	0.009 (0.009)	0.053 (0.053)
Rhyacophila	0.067 (0.067)	0	0.006 (0.006)	0

AUTUMN

	Abundance (# pack^{-1})		Biomass (mg pack^{-1})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Shredders				
Tallaperla	1.08 (0.42)	0.58 (0.34)	1.980 (0.667)	1.054 (0.650)
Pteronarcys	0.25 (0.16)	0.08 (0.08)	2.059 (1.262)	0.482 (0.482)
Leuctra	0.58 (0.58)	0	0.011 (0.011)	0
Taeniopteryx	3.42 (0.76)	7.42 (1.18)	0.871 (0.201)	1.246 (0.172)
Nemouridae	0	0.08 (0.08)	0	0.040 (0.040)
Capniidae	1.00 (0.36)	0.50 (0.32)	0.099 (0.024)	0.037 (0.028)
Lepidostoma	0.17 (0.17)	0.58 (0.39)	0.012 (0.012)	0.084 (0.050)
Limnephilidae	0.08 (0.08)	0	0.013 (0.013)	0
Elmidae	0.08 (0.08)	0	0.047 (0.047)	0
Leptotarsus	0.67 (0.27)	0.83 (0.42)	1.511 (0.879)	2.103 (1.233)
Predators				
Ceratopogonidae	0.50 (0.29)	0.50 (0.15)	0.109 (0.064)	0.117 (0.035)
Tanypodinae	6.83 (1.58)	14.83 (1.39)	0.127 (0.033)	0.249 (0.026)
Empididae	0.50 (0.17)	0.25 (0.16)	0.020 (0.014)	0.004 (0.003)
Atherix	0.25 (0.16)	0.33 (0.19)	0.881 (0.742)	0.195 (0.115)
Dicranota	0.17 (0.10)	0.08 (0.08)	0.005 (0.004)	0.003 (0.002)
Perlidae	0.17 (0.10)	0.08 (0.08)	0.115 (0.080)	0.045 (0.040)
Perlodidae	0.33 (0.14)	0.17 (0.10)	0.916 (0.606)	0.010 (0.005)
Rhyacophila	0.33 (0.24)	0.70 (0.22)	0.053 (0.050)	0.109 (0.052)
Hemiptera	0	0.08 (0.08)	0	0.006 (0.005)

APPENDIX B

Day 40 insect abundance (# m^{-2}) and biomass (mg m^{-2}) from the tile sediment addition experiment (Chapter 3). Each ambient sediment value represents mean of five replicates; each sediment addition value represents mean of four replicates. Standard error is given in parentheses.

AMBIENT SEDIMENT TREATMENT

	Abundance (# m^{-2})		Biomass (mg m^{-2})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Simuliidae	0	17.8 (17.7)	0	0.6 (0.6)
Chironomidae (non-Tanypodinae)	657.8 (144.7)	1226.7 (347.5)	27.5 (9.9)	81.9 (18.2)
Chironomidae (Tanypodinae)	355.6 (140.3)	320.0 (82.3)	4.8 (1.9)	4.4 (1.5)
Leptophlebiidae	35.6 (21.7)	17.8 (17.7)	5.1 (3.4)	1.6 (1.6)
Heptageniidae	88.9 (39.7)	88.9 (28.1)	53.1 (48.6)[1]	1.4 (0.5)
Ephemeroptera	17.8 (17.7)	0	0.1 (0.1)	0
Pteronarcys	35.6 (35.5)	0	1446.6 (1444.0)[2]	0
Isoperla	0	71.1 (17.7)	0	102.7 (46.1)
Leuctra	35.6 (35.5)	0	18.4 (18.4)	0
Plecoptera	17.8 (17.7)	0	0.2 (0.2)	0
Brachycentridae	17.8 (17.7)	0	0.1 (0.1)	0
Hydropsychidae	35.6 (21.7)	284.4 (90.5)	2.1 (2.0)	54.3 (16.3)
Rhyacophila	17.8 (17.7)	17.8 (17.7)	0.6 (0.6)	1.7 (1.7)

SEDIMENT ADDITION TREATMENT

	Abundance (# m^{-2})		Biomass (mg m^{-2})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Simuliidae	22.2 (22.2)	0	0.1 (0.1)	0
Chironomidae (non-Tanypodinae)	666.7 (147.4)	911.1 (272.5)	25.0 (6.5)	41.3 (14.0)
Chironomidae (Tanypodinae)	244.5 (127.6)	177.8 (72.6)	3.0 (0.8)	5.7 (4.3)
Ceratopogonidae	66.7 (66.7)	66.7 (66.7)	5.4 (5.4)	5.0 (5.0)
Leptophlebiidae	0	22.2 (22.2)	0	1.2 (1.2)
Heptageniidae	88.9 (51.3)	22.2 (22.2)	26.0 (17.5)	0.7 (0.7)
Ephemeroptera	44.5 (44.5)	44.5 (44.5)	1.9 (1.9)	1.1 (1.1)
Acroneuria	66.7 (42.6)	0	8.3 (5.1)	0
Leuctra	22.2 (22.2)	88.9 (36.3)	10.1 (10.1)	27.6 (9.7)
Plecoptera	22.2 (22.2)	0	0.4 (0.4)	0
Hydropsychidae	155.6 (75.9)	288.9 (260.1)	19.5 (13.7)	25.8 (23.8)
Rhyacophila	44.5 (44.5)	44.5 (25.7)	1.9 (1.9)	1.0 (0.7)

[1] With 1 large individual from a single replicate omitted, biomass = 3.8 (2.3).
[2] With 2 large individuals from a single replicate omitted,biomass = 0.

APPENDIX C

Day 56 insect abundance (# pack^{-1}) and biomass (mg pack^{-1}) from the leaf pack sediment addition experiment (Chapter 3). Each value represents mean of five replicates. Standard error is given in parentheses.

AMBIENT SEDIMENT TREATMENT

	Abundance (# pack^{-1})		Biomass (mg pack^{-1})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Simuliidae	4.8 (2.0)	9.6 (4.5)	0.036 (0.020)	0.120 (0.070)
Chironomidae (non-Tanypodinae)	82.4 (20.1)	113.4 (16.3)	1.687 (0.455)	2.284 (0.516)
Chironomidae (Tanypodinae)	18.2 (5.6)	39.8 (4.0)	0.199 (0.038)	0.386 (0.032)
Ceratopogonidae	2.6 (1.2)	4.2 (1.6)	0.737 (0.301)	1.132 (0.359)
Atherix	1.0 (0.6)	0.2 (0.2)	3.868 (1.613)	0.880 (0.878)
Empididae	0.8 (0.6)	0.2 (0.2)	0.009 (0.006)	0.011 (0.011)
Dicranota	1.6 (0.9)	1.4 (0.7)	0.024 (0.011)	0.014 (0.006)
Leptotarsus	0.4 (0.2)	1.4 (0.8)	8.595 (6.124)	7.054 (4.329)
Leptophlebiidae	0.6 (0.2)	0	0.486 (0.236)	0
Ephemerellidae	15.2 (7.2)	17.4 (4.0)	0.222 (0.112)	0.263 (0.041)
Baetidae	0	0.2 (0.2)	0	0.001 (0.001)
Heptageniidae	3.8 (2.4)	1.6 (1.2)	3.994 (3.276)	0.094 (0.083)
Ephemeroptera	0	3.6 (3.6)	0	0.030 (0.030)
Perlidae	0.2 (0.2)	00	0.939 (0.937)	0
Perlodidae	0.6 (0.4)	0.4 (0.4)	3.677 (2.622)	0.446 (0.446)
Pteronarcys	0.2 (0.2)	0.2 (0.2)	2.424 (2.420)	3.875 (3.869)
Leuctra	1.8 (0.6)	0.4 (0.2)	0.325 (0.118)	0.102 (0.063)
Peltoperlidae	2.6 (1.3)	0.4 (0.4)	8.209 (4.603)	0.820 (0.818)
Taeniopteryx	1.4 (0.8)	2.0 (1.3)	1.136 (0.763)	1.173 (0.836)
Plecoptera	16.0 (7.0)	21.2 (2.9)	0.235 (0.063)	0.268 (0.047)
Lepidostoma	1.2 (0.6)	0.4 (0.4)	0.206 (0.120)	0.174 (0.173)
Limnephilidae	0.2 (0.2)	0	0.686 (0.684)	0
Hydropsychidae	1.0 (0.3)	1.0 (0.5)	1.283 (0.620)	1.116 (0.622)
Rhyacophila	3.2 (0.4)	3.4 (1.3)	1.129 (0.073)	1.008 (0.318)
Trichoptera	2.2 (1.0)	5.4 (2.2)	0.016 (0.006)	0.044 (0.015)
Elmidae	0.6 (0.4)	1.0 (0.8)	0.057 (0.054)	0.010 (0.009)
Odonata	0	0.2 (0.2)	0	0.005 (0.005)
Hemiptera	0	0.2 (0.2)	0	0.002 (0.002)

SEDIMENT ADDITION TREATMENT

Taxon	Abundance (# pack^{-1})		Biomass (mg pack^{-1})	
	Control	***Exclusion***	***Control***	***Exclusion***
Simuliidae	8.2 (2.6)	4.6 (1.9)	0.127 (0.052)	0.080 (0.033)
Chironomidae (non-Tanypodinae)	99.0 (13.5)	109.8 (18.2)	1.769 (0.282)	2.634 (0.418)
Chironomidae (Tanypodinae)	31.4 (5.7)	26.8 (5.6)	0.436 (0.124)	0.274 (0.053)
Ceratopogonidae	3.4 (0.9)	2.6 (1.4)	0.913 (0.194)	0.884 (0.388)
Atherix	0	0.2 (0.2)	0	0.173 (0.173)
Empididae	0.4 (0.2)	0.4 (0.2)	0.018 (0.011)	0.007 (0.006)
Dicranota	1.8 (0.9)	1.4 (0.4)	0.038 (0.017)	0.036 (0.011)
Leptotarsus	1.2 (0.4)	0.8 (0.8)	10.241 (3.933	12.891 (12.869)
Leptophlebiidae	2.2 (0.6)	0	1.712 (0.516)	0
Ephemerellidae	16.0 (3.6)	11.2 (3.5)	0.220 (0.039)	0.287 (0.145)
Baetidae	0.6 (0.6)	0	0.026 (0.026)	0
Heptageniidae	3.0 (0.9)	1.8 (0.7)	2.774 (1.139)	0.356 (0.287)
Perlodidae	0.8 (0.6)	1.0 (1.0)	0.062 (0.039)	0.125 (0.125)
Pteronarcys	0.8 (0.2)	0.2 (0.2)	55.942 (33.962)[1]	4.305 (4.297)
Leuctra	2.0 (1.3)	0.4 (0.2)	0.326 (0.242)	0.097 (0.071)
Peltoperlidae	1.4 (0.5)	0.8 (0.4)	4.528 (2.005)	2.119 (0.940)
Taeniopteryx	3.8 (1.5)	1.0 (0.3)	2.905 (1.375)	0.492 (0.215)
Chloroperlidae	0.2 (0.2)	0	0.171 (0.171)	0
Capniidae	0.2 (0.2)	0	0.061 (0.060)	0
Plecoptera	13.2 (1.6)	11.8 (2.5)	0.161 (0.028)	0.141 (0.028)
Lepidostoma	0	0.4 (0.2)	0	0.193 (0.172)
Limnephilidae	0.2 (0.2)	0.4 (0.2)	0.503 (0.503)	0.804 (0.665)
Hydropsychidae	1.6 (0.5)	1.2 (0.6)	0.752 (0.440)	1.404 (0.806)
Rhyacophila	5.2 (1.9)	3.4 (0.9)	1.285 (0.429)	1.638 (0.469)
Brachycentridae	0	0.2 (0.2)	0	0.022 (0.022)
Trichoptera	2.2 (0.4)	2.6 (1.2)	0.013 (0.002)	0.016 (0.007)
Elmidae	0.2 (0.2)	0.6 (0.4)	0.112 (0.112)	0.155 (0.153)

[1] With 1 large individual from a single replicate omitted, biomass = 23.021 (11.082).

APPENDIX D

Insect abundance (# m^{-2}) and biomass (mg m^{-2}) data for Upper Davidson River, Jones Creek, Beaverdam Creek, and Sweeten Creek (Chapter 4). For Jones Creek and Sweeten Creek, each value represents mean of five replicates; for Upper Davidson River and Beaverdam Creek, each value represents mean of four replicates. Standard error is given in parentheses. See Appendix B for Ball Creek data (ambient sediment values).

UPPER DAVIDSON RIVER, day 40

	Abundance (# m^{-2})		Biomass (mg m^{-2})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Chironomidae (non-Tanypodinae)	10178 (3141)	1690 (4073)	167.0 (83.7)	271.0 (87.3)
Chironomidae (Tanypodinae)	1051 (353)	1411 (434)	25.5 (7.0)	60.7 (19.5)
Ceratopogonidae	229 (132)	0	5.9 (4.0)	0
Antocha	22 (22)	22 (22)	4.8 (4.8)	6.2 (6.2)
Serratella	0	89 (63)	0	52.7 (41.1)
Baetidae	111 (111)	0	4.3 (4.3)	0
Heptageniidae	373 (213)	22 (22)	16.6 (6.4)	33.4 (33.4)[1]
Ephemeroptera	444 (257)	2367 (351)	3.1 (1.8)	18.2 (3.8)
Perlidae	0	67 (67)	0	25.2 (25.2)
Peltoperlidae	22 (22)	0	7.6 (7.6)	0
Hydropsychidae	367 (367)	1589 (1559)	28.2 (28.2)	223.9 (216.1)
Rhyacophila	0	244 (244)	0	23.5 (23.5)
Dolophilodes	0	22 (22)	0	17.5 (17.5)
Trichoptera	462 (191)	589 (360)	2.8 (1.1)	3.5 (2.2)

[1] With 1 large individual from a single replicate omitted, biomass = 0.

JONES CREEK, day 15

	Abundance (# m^{-2})		Biomass (mg m^{-2})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Chironomidae (non-Tanypodinae)	2756 (226)	2773 (851)	65.0 (10.5)	65.9 (16.7)
Chironomidae (Tanypodinae)	2187 (353)	907 (403)	22.2 (4.8)	8.8 (3.7)
Simuliidae	53 (36)	142 (121)	2.1 (1.9)	8.2 (8.1)
Antocha	53 (36)	89 (28)	0.4 (0.3)	18.6 (15.4)
Ceratopogonidae	0	36 (36)	0	10.1 (10.1)
Ephemerellidae	0	18 (18)	0	0.4 (0.4)
Baetidae	942 (407)	605 (375)	112.2 (44.3)	104.4 (54.2)
Heptageniidae	178 (74)	71 (33)	91.1 (54.9)	1.2 (0.7)
Leptophlebiidae	18 (18)	18 (18)	0.2 (0.2)	3.5 (3.5)
Ephemeroptera	107 (33)	0	0.7 (0.2)	0
Leuctra	0	18 (18)	0	1.0 (1.0)
Perlidae	53 (22)	0	160.0 (92.0)	0
Hydropsychidae	178 (49)	125 (45)	46.5 (33.6)	13.8 (7.3)
Rhyacophila	18 (18)	0	1.0 (1.0)	0
Trichoptera	18 (18)	53 (53)	0.1 (0.1)	0.3 (0.3)

JONES CREEK, day 40

	Abundance (# m^{-2})		Biomass (mg m^{-2})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Chironomidae (non-Tanypodinae)	14578 (4385)	17351 (4379)	341.7 (96.9)	605.1 (95.8)
Chironomidae (Tanypodinae)	10080 (4248)	6524 (2103)	59.9 (20.0)	64.4 (20.8)
Simuliidae	356 (355)	107 (107)	2.0 (2.0)	3.7 (3.7)
Antocha	53 (36)	231 (107)	11.4 (9.7)	12.1 (5.5)
Atherix	36 (22)	18 (18)	5.8 (4.4)	1.2 (1.2)
Ephemerellidae	0	196 (174)	0	3.4 (2.2)
Baetidae	391 (241)	1013 (652)	41.8 (34.1)	57.5 (36.3)
Heptageniidae	71 (33)	0	28.5 (17.1)	0
Ephemeroptera	533 (259)	622 (332)	3.7 (1.8)	8.4 (6.1)
Acroneuria	18 (18)	0	47.7 (47.6)	0
Leuctra	18 (18)	0	4.0 (4.0)	0
Chloroperlidae	36 (36)	0	12.0 (12.0)	0
Plecoptera	356 (259)	267 (178)	3.2 (2.3)	2.4 (1.6)
Hydropsychidae	622 (411)	427 (165)	111.1 (101.9)	193.4 (100.3)
Philopotamidae	0	36 (36)	0	83.1 (82.9)
Glossosomatidae	18 (18)	0	3.8 (3.7)	0
Rhyacophila	0	36 (22)	0	11.4 (7.1)
Trichoptera	284 (262)	178 (109)	1.9 (1.5)	5.2 (3.5)
Gomphidae	0	18 (18)	0	141.4 (141.2)
Psephenus	0	18 (18)	0	76.3 (76.2)
Elmidae	0	18 (18)	0	15.6 (15.5)

BEAVERDAM CREEK, day 40

	Abundance (# m^{-2})		Biomass (mg m^{-2})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Chironomidae (non-Tanypodinae)	5867 (2266)	20298 (5794)	118.2 (50.3)	919.2 (235)
Chironomidae (Tanypodinae)	378 (233)	1587 (265)	52.0 (9.1)	51.2 (6.6)
Empididae	22 (22)	322 (147)	4.1 (4.1)	25.8 (10.1)
Antocha	222 (147)	178 (150)	25.6 (17.2)	28.6 (16.5)
Paraleptophlebia	111 (111)	22 (22)	86.7 (86.7)	10.2 (10.2)
Baetidae	422 (293)	1062 (191)	11.4 (7.0)	73.8 (31.9)
Baetisca	22 (22)	273 (160)	3.7 (3.7)	67.6 (47.5)
Serratella	22 (22)	22 (22)	6.5 (6.5)	17.0 (17.0)
Heptageniidae	289 (105)	0	67.0 (51.7)	0
Ephemeroptera	111 (111)	947 (333)	0.8 (0.8)	7.2 (2.4)
Hydropsychidae	22 (22)	189 (161)	24.4 (24.4)	56.7 (35.8)
Glossosomatidae	133 (133)	0	21.1 (21.1)	0
Goera	89 (36)	44 (44)	50.8 (25.9)	13.5 (13.5)
Psephenus	178 (96)	0	10.6 (4.1)	0
Coleoptera	0	22 (22)	0	4.2 (4.2)
Lepidoptera	0	22 (22)	0	1.3 (1.3)

SWEETEN CREEK, day 35

	Abundance (# m^{-2})		Biomass (mg m^{-2})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Chironomidae (non-Tanypodinae)	4018 (1347)	2551 (610)	136.7 (30.8)	230.3 (83.1)
Chironomidae (Tanypodinae)	236 (214)	613 (270)	21.5 (19.4)	78.5 (7.5)
Empididae	18 (18)	147 (146)	3.3 (3.3)	19.2 (19.2)
Antocha	640 (365)	271 (211)	122.2 (108.6)	61.9 (43.1)
Baetis	0	813 (77)	0	136.6 (34.1)
Hydropsychidae	627 (331)	591 (268)	580.8 (353.2)	724.7 (172.6)

SWEETEN CREEK, day 40

	Abundance (# m^{-2})		Biomass (mg m^{-2})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Chironomidae (non-Tanypodinae)	5800 (1485)	14667 (11013)	433.1 (171.8)	777.9 (118.9)
Chironomidae (Tanypodinae)	596 (156)	1156 (290)	73.9 (15.3)	127.7 (44.9)
Empididae	0	89 (89)	0	16.4 (16.3)
Antocha	258 (126)	276 (191)	68.4 (30.3)	71.0 (32.2)
Baetis	36 (36)	53 (36)	14.7 (14.7)	13.6 (8.7)
Stenonema	0	18 (18)	0	124.6 (124.4)[1]
Hydropsychidae	142 (66)	658 (493)	450.4 (189.7)	1337.7 (1267.6)
Boyeria	18 (18)	18 (18)	421.6 (420.9)[1]	421.6 (420.9)[1]

[1] With 1 large individual from a single replicate omitted, biomass = 0.

APPENDIX E

Abundance (# sample^{-1}) and biomass (mg sample^{-1}) of drifting insects at Ball Creek, Betty Creek, Coweeta Creek, and Jones Creek (Chapter 5). Each value represents mean of five replicates. Standard error is given in parentheses. Biomass values < 0.005 mg sample^{-1} are listed as 0.

BALL CREEK

Taxon	Abundance (# sample^{-1})		Biomass (mg sample^{-1})	
	Control	***Exclusion***	***Control***	***Exclusion***
Chironomidae	0.80 (0.58)	0.40 (0.24)	0.02 (0.02)	0
Simuliidae	0	1.00 (0.45)	0	0.04 (0.02)
Tipulidae	0	0.60 (0.40)	0	0.03 (0.03)
Hydropsychidae	0	0.20 (0.20)	0	0
Rhyacophilidae	0.20 (0.20)	0	0.03 (0.03)	0
Baetidae	1.60 (0.40)	2.40 (0.98)	0.05 (0.03)	0.14 (0.07)
Ephemerellidae	0	0.20 (0.20)	0	0.04 (0.04)
Heptageniidae	0	0.20 (0.20)	0	0.01 (0.01)
Leuctridae	0	0.60 (0.24)	0	0.10 (0.06)
Perlodidae	0	0.20 (0.20)	0	0.03 (0.03)
Veliidae	0.20 (0.20)	0	0.02 (0.02)	0
Elmidae	0	0.20 (0.20)	0	0.01 (0.01)
TOTAL – all insects	2.80 (0.97)	6.00 (1.89)	0.12 (0.05)	0.40 (0.16)
TOTAL – Ephemeroptera	1.60 (0.40)	2.80 (1.35)	0.05 (0.03)	0.18 (0.11)
TOTAL – Diptera	0.80 (0.58)	2.00 (0.71)	0.02 (0.02)	0.08 (0.04)
TOTAL – Plecoptera	0	0.80 (0.37)	0	0.13 (0.08)
TOTAL – Trichoptera	0.20 (0.20)	0.20 (0.20)	0.03 (0.03)	0

BETTY CREEK

	Abundance (# sample^{-1})		Biomass (mg sample^{-1})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Chironomidae	2.40 (0.93)	6.00 (1.92)	0.10 (0.05)	0.23 (0.11)
Simuliidae	1.00 (0.45)	1.80 (0.80)	0.02 (0.01)	0.04 (0.03)
Tipulidae	0.40 (0.40)	0.40 (0.24)	0	0.02 (0.02)
Ceratopogonidae	0.20 (0.20)	0.20 (0.20)	0	0
Hydropsychidae	0.40 (0.24)	2.40 (0.81)	0.01 (0.01)	0.07 (0.04)
Polycentropodidae	0.20 (0.20)	0	0.02 (0.02)	0
Baetidae	0.80 (0.37)	3.00 (1.14)	0.02 (0.02)	0.16 (0.06)
Ephemerellidae	0.60 (0.24)	0	0.01 (0.00)	0
Heptageniidae	0.20 (0.20)	0.20 (0.20)	0.01 (0.01)	0.03 (0.03)
Leuctridae	0.20 (0.20)	0	0.02 (0.02)	0
Perlidae	0.20 (0.20)	0	0.01 (0.01)	0
Cucurlionidae	0	0.20 (0.20)	0	na
Veliidae	0	0.20 (0.20)	0	0.05 (0.05)
Lepidoptera	0	0.40 (0.24)	0	0.01 (0.00)
TOTAL – all insects	6.60 (1.96)	14.80 (4.20)	0.23 (0.10)	0.59 (0.19)
TOTAL – Ephemeroptera	1.60 (0.51)	3.20 (1.24)	0.04 (0.02)	0.19 (0.06)
TOTAL – Diptera	4.00 (1.26)	8.40 (2.61)	0.12 (0.05)	0.28 (0.13)
TOTAL – Plecoptera	0.40 (0.24)	0	0.04 (0.02)	0
TOTAL – Trichoptera	0.60 (0.40)	2.40 (0.81)	0.03 (0.02)	0.07 (0.04)

COWEETA CREEK

	Abundance (# sample^{-1})		Biomass (mg sample^{-1})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Chironomidae	3.60 (2.87)	7.00 (3.75)	0.05 (0.04)	0.08 (0.05)
Simuliidae	5.40 (3.23)	6.20 (4.97)	0.16 (0.10)	0.21 (0.16)
Tipulidae	0.20 (0.20)	0.40 (0.40)	0	0
Blephariceridae	0	0.20 (0.20)	0	0.05 (0.05)
Hydropsychidae	0.60 (0.24)	0.20 (0.20)	0.01 (0.01)	0
Brachycentridae	0.40 (0.24)	0.40 (0.40)	0.31 (0.19)	0.27 (0.27)
Rhyacophildae	0.40 (0.40)	0	0.04 (0.04)	0
Baetidae	6.80 (4.19)	6.00 (4.28)	0.26 (0.18)	0.41 (0.30)
Ephemerellidae	0.80 (0.37)	0.20 (0.20)	0.02 (0.01)	0.01 (0.01)
Isonychiidae	0	0.20 (0.20)	0	1.19 (1.19)
Leuctridae	0.20 (0.20)	0.20 (0.20)	0.01 (0.01)	0.01 (0.01)
Perlidae	0.20 (0.20)	0	0.01 (0.01)	0
Perlodidae	0.20 (0.20)	0	0.01 (0.01)	0
Peltoperlidae	0.20 (0.20)	0	0.10 (0.10)	0
Corydalidae	0.20 (0.20)	0	0.01 (0.01)	0
Elmidae	0.20 (0.20)	0.60 (0.60)	0.01 (0.01)	0.04 (0.04)
Lepidoptera	0.20 (0.20)	0	0	0
TOTAL – all insects	19.60 (11.88)	21.60 (14.87)	0.99 (0.63)	2.28 (2.05)
TOTAL – Ephemeroptera	7.60 (4.52)	6.40 (4.43)	0.28 (0.19)	1.61 (1.48)
TOTAL – Diptera	9.20 (6.07)	13.80 (9.30)	0.20 (0.14)	0.35 (0.26)
TOTAL – Plecoptera	0.80 (0.49)	0.20 (0.20)	0.13 (0.11)	0.01 (0.01)
TOTAL – Trichoptera	1.40 (0.75)	0.60 (0.60)	0.36 (0.22)	0.27 (0.27)

JONES CREEK

	Abundance (# sample^{-1})		Biomass (mg sample^{-1})	
Taxon	***Control***	***Exclusion***	***Control***	***Exclusion***
Chironomidae	1.60 (0.75)	4.80 (2.98)	0.05 (0.03)	0.12 (0.07)
Simuliidae	1.40 (0.93)	2.20 (1.56)	0.04 (0.04)	0.12 (0.09)
Tipulidae	0	0.20 (0.20)	0	0
Empididae	0.20 (0.20)	0	0.01 (0.01)	0
Ceratopogonidae	0.20 (0.20)	0	0.06 (0.06)	0
Hydropsychidae	1.40 (0.60)	0.20 (0.20)	0.13 (0.10)	0
Brachycentridae	0.20 (0.20)	0	0	0
Philopotamidae	0	0.20 (0.20)	0	0.13 (0.13)
Baetidae	0.80 (0.37)	2.60 (1.43)	0.02 (0.01)	0.09 (0.07)
Ephemerellidae	0.40 (0.24)	0	0	0
Heptageniidae	0.20 (0.20)	0	0	0
Leptophlebiidae	0.20 (0.20)	0	0.02 (0.02)	0
Elmidae	0.20 (0.20)	0	0.02 (0.02)	0
TOTAL – all insects	6.80 (2.26)	10.20 (4.91)	0.35 (0.17)	0.47 (0.26)
TOTAL – Ephemeroptera	1.60 (0.51)	2.60 (1.43)	0.04 (0.02)	0.09 (0.07)
TOTAL – Diptera	3.40 (1.36)	7.20 (4.73)	0.16 (0.07)	0.24 (0.16)
TOTAL – Plecoptera	0	0	0	0
TOTAL – Trichoptera	1.60 (0.68)	0.40 (0.24)	0.13 (0.10)	0.14 (0.13)