BENTHIC MACROINVERTEBRATES OF A SOUTHERN APPALACHIAN WILD AND SCENIC RIVER: PATTERNS IN ASSEMBLAGE STRUCTURE AND ECOLOGICAL PROCESSING

by

ERICA CHIAO

(Under the Direction of J. Bruce Wallace)

ABSTRACT

Many stream-dwelling aquatic macroinvertebrates are functionally adapted to utilize resources associated with the bottom of channels. Local stream bed sediments are important components of macroinvertebrate habitat. Distribution of macroinvertebrate fauna within stream benthos is highly influenced by this factor. This study was undertaken to: (a) examine the effects of fine sediments on benthic macroinvertebrate assemblage structure within streams of a southern Appalachian watershed; (b) gain insight into ecological function within these streams; and, (c) examine benthic macroinvertebrate community structure along a longitudinal continuum within the same watershed. Results from this study indicate that fine, deposited sediments (≤ 2mm) covering stream beds are affecting benthic macroinvertebrate communities at both the mesohabitat and reach scale within headwaters of the Chattooga River watershed. Sensitive invertebrate taxa (Ephemeroptera, Plecoptera, Trichoptera taxa) declined within study reaches with elevated sediments. Shredder abundance was significantly reduced within reaches where levels of fine sediments were higher, and fine sediments influenced the composition of shredder assemblages. Large-bodied cranefly larvae were more predominant in channels containing higher amounts of deposited sediments and they replaced stonefly shredders. Fine, deposited sediments prevented some taxa from exploiting coarse leaf litter. There was also evidence indicating that fine sediments could be having a negative impact on algal resources in these streams. Fine sediments had differential effects on the sampled habitats: (1) in cobble riffles, the number of EPT taxa declined with increased fine sediments; (2) in bedrock outcrops, total assemblage abundances and grazer abundances were negatively correlated to reach-scale amounts of fine, deposited sediments; and (3) in depositional habitats, the second most frequently collected taxon (specific taxon varied with stream channel) was positively correlated to levels of fine, deposited sediments. Macroinvertebrate communities along a continuum of the Chattooga River watershed followed some, but not all river continuum concept predictions. Local habitat conditions influenced the composition of reach-level benthic macroinvertebrate communities. Invertebrate communities occurring in geomorphically distinct habitats (riffles, bedrock outcrops, and depositional areas) had unique structural patterns.

INDEX WORDS: benthic macroinvertebrates, streams, sediments, river continuum concept, leaf breakdown, wild and scenic river

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DEDICATION

This is dedicated to my family, Dr. Randall (Toby) Schuh, Dr. Wallace and my friends. They encouraged me to succeed by believing that I would.

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I would like to thank Dr. Wallace for bearing with me through the process of generating this document, for encouraging me to continue with this work when I thought I would rather stop, and for being generous enough to share his time with me.

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CHAPTER 1

INTRODUCTION & LITERATURE REVIEW

Ecological function of lotic, freshwater systems is tightly linked to the structure of the communities they support (Cummins 1974). Within these communities, benthic macroinvertebrates fill lower and intermediate trophic levels and act out important ecosystem roles—they consume primary energetic resources, diversify the ways in which energetic resources can be used by other consumers (Ross and Wallace 1983, Hunter and Price 1992), and act as both prey and predators. Furthermore, benthic macroinvertebrates are primary linkages for horizontal and longitudinal energy transfers within systems (Vannote *et al*. 1980; Wallace *et al*. 1982, Junk *et al*. 1999).

Many stream-dwelling aquatic macroinvertebrates are functionally adapted to utilize resources associated with the bottom of channels (Cummins 1973, Merritt and Cummins 1996). Local stream bed sediments, water characteristics (e.g. velocity, discharge, chemical components, temperature) and organic matter standing crops are important components of macroinvertebrate habitat (Cummins 1984). Distribution of macroinvertebrate fauna within stream benthos is highly influenced by these factors (Cummins 1968, Allan 1975, Minshall 1985, Huryn and Wallace 1987, Wallace *et al*. 1995).

Sediment delivery to channels within pristine river systems is a natural process largely controlled by climate and parent geology. However, in much of the world, human society has supplanted nature as the controlling force over landscape ecosystems through the introduction of unnatural substances to the environment (i.e. many chemical compounds and synthetic materials) and the decoupling of natural processes from time (i.e. anthropogenic generation of naturally occurring materials over an unnaturally rapid timescale). The way humans use land has a great influence on stream channels and stream network qualities (Leopold 1994). By altering landscape attributes humans change hydrology, erosion rates, and water constituents (e.g. enrichment of surface waters with agricultural runoff) within a given watershed. These changes to streams have profound effects on stream organisms, which rely upon local conditions to provide them with suitable habitat for living, feeding, and propagating.

Under natural circumstances, fine sediments (generally acknowledged as those ≤ 2 mm in size) comprise at least a fraction of most stream beds, and their occurrence within stream substrates is due to both overland and within-channel delivery systems (Knighton 1996). In anthropogenically altered systems, fine sediments are deposited by the same mechanisms; however, the amounts of fine sediments that are available for delivery often change drastically. It is possible for fine sediments to enter systems in unnaturally excessive amounts. Excessive amounts of fine sediments within riverine systems alter the physical structure of benthic habitats, change the availability of organic resources and can interfere with faunal behaviors, especially when fine sediments are entrained (Schofield, Pringle and Meyer 2004).

The Chattooga River Watershed

The Chattooga River and its tributary waters flow within a 72,840 ha southern Appalachian drainage basin that is completely contained within the Blue Ridge physiographic province (Fig. 1.1). The Chattooga River was conferred Wild and Scenic status in 1974 by Congress, under the Wild and Scenic Rivers Act of 1968. The Wild and Scenic designation brought a great deal of attention to the Chattooga River Watershed, and there is widespread concern for the quality of its waters and scenic integrity of the area. Furthermore, the southern

Appalachian mountain range harbors one of the most diverse fish assemblages in the world, with 345 species (Walsh et al. 1995). The watershed is primarily forested (>92%). Upland forests are dominated by Virginia and shortleaf pine, and chestnut and scarlet oak. Streamside vegetation is primarily eastern hemlock, yellow poplar, and white pine. Rhododendron and mountain laurel generally form dense understories over and along stream channels. Approximately 70% of the watershed is under the stewardship of the U.S.D.A. Forest Service.

The Chattooga River watershed has experienced high levels of logging and logging-related activities, as well as other erosion-causing disturbances in the past. Sediments deposited into stream channels as a result of past erosion are likely still affecting the Chattooga River system. Currently, sediment is contributed to channels via various sources: roads, eroding banks and ditches, agricultural activity, timbering operations, beaver activity, and urban development (USEPA 1999). It has been estimated that greater than eighty percent of sediment production in the Chattooga River watershed is road-related (Van Lear 1995). There has been little tree harvesting within the last decade (C. Neihardt, US Forest Service *pers. comm.*).

The Chattooga River watershed is characterized by steep, rugged terrain. Its streams are heterogeneous in nature, generally shaded by riparian vegetation, contain sediments that vary greatly in size, and are characterized by the presence of three major habitats: cobble riffle, bedrock outcrop and depositional. Elevated levels of fine, inorganic sediments within stream reaches of the Chattooga River network put this system at risk of ecological impairment. Many stream reaches of the Chattooga River Watershed contain unnaturally high levels of fine, inorganic sediments (USEPA 1999).

Study Background

In 1999, the United States Environmental Protection Agency (USEPA) published the results of an assessment of water quality conditions undertaken in the Chattooga River Watershed (Rabun Co., GA; Macon Co. NC; Oconee Co., SC) (USEPA 1999). This assessment was performed as a result of a settlement agreement for a lawsuit over total maximum daily loads (TMDLs) in Georgia. Sampling for this assessment was done one time for each stream segment in the late summer and fall season. The study sampled and analyzed the benthic macroinvertebrate community, chemical constituents of the water column, and surveyed the habitat condition and channel morphology across the watershed. One conclusion reached upon examination of survey results was that the primary impact to water quality in the watershed is excessive sedimentation resulting from past and present land uses (primarily implicating agricultural, silvicultural, recreational and mining activities).

In response to USEPA (1999) findings, the USDA Forest Service (Southern Research Station) initiated a monitoring project in the Chattooga River watershed. Restoration of impacted sites is one goal of the USDA Forest Service.

Purpose of the Study

The purpose of this study is to: (a) examine the effects of fine sediments on benthic macroinvertebrate community structure within streams of a southern Appalachian watershed (Chapter 2), (b) gain some insight into ecological function within these streams (Chapter 3), (c) examine benthic macroinvertebrate community structure along a longitudinal continuum within the same watershed (Chapter 4) and (d) discuss management implications of study results (Chapter 5). The overarching goal of this study is to uncover basic information regarding sediment disturbance in streams and to provide ecological data for a specific region. Results from this study provide fairly detailed characterizations of a few stream reaches in the Chattooga River network to which results from future biological monitoring can be compared.

Patterns of benthic macroinvertebrate community structure in the context of geomorphic variation (i.e. stream-bed characteristics) were examined at reach and mesohabitat scales in Chapter 2. It was postulated that in comparison to less sedimented reaches, excessive or heavy sedimentation in some reaches should be reflected by differences in respective benthic macroinvertebrate community structures (i.e. taxonomic composition, diversity, trophic organization).

In Chapter 3, I evaluate benthic macroinvertebrate community structure of stream segments in context of reach position within the longitudinal profile of the Chattooga River system. Longitudinal differences in benthic macroinvertebrate communities within the river system are expected due to physical and energetic differences among reaches along a longitudinal river continuum (Vannote et al. 1980). Community structure of benthic invertebrates was also considered at the mesohabitat scale (e.g. the scale of an individual riffle, bedrock outcrop, or depositional area) in this study because understanding relationships between communities at this scale can be informative to the understanding of linkages between communities at a broader scale.

The influence of sedimentation on leaf breakdown is investigated in Chapter 4. If sedimentation within a reach is great enough to influence habitat attributes, then sedimentation may also affect rates of organic matter breakdown by bringing about changes in benthic invertebrate community structure, or simply by making leaflitter unavailable to invertebrates through physical burial. As an ecosystem-level process that integrates leaf litter supply, microbial activity, macroinvertebrate activity, and physical and chemical stream characteristics, leaf breakdown can be used to understand sediment impacts on stream function.

A summary of results and a discussion of federal laws governing land use and management are included in Chapter 5. As a National Wild and Scenic River that lies mostly within the boundaries of three separate National Forests, a number of federal statutes affect the administration of lands surrounding its waters.

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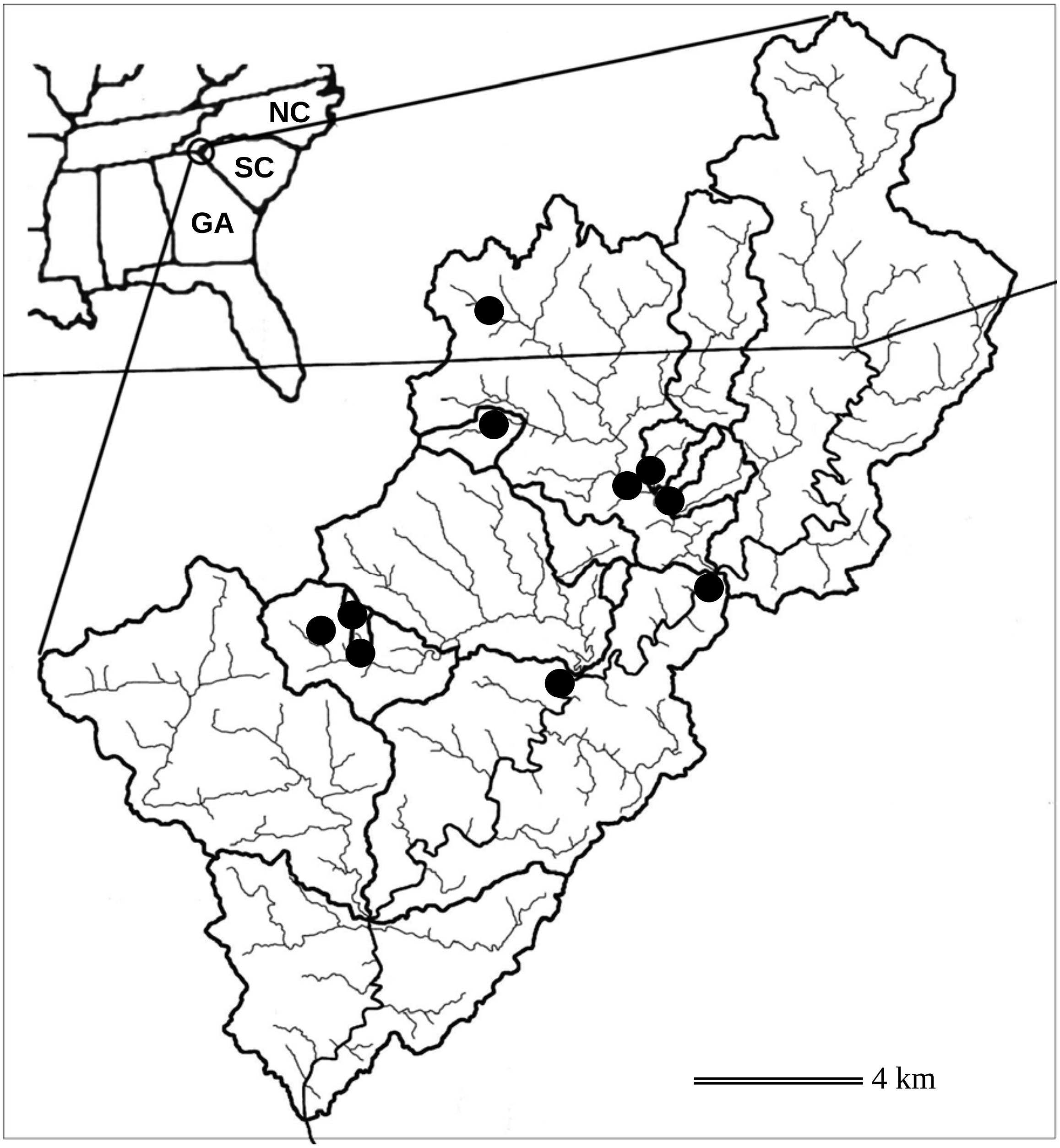
1.1. Map of Chattooga River watershed, USA: Georgia, North Carolina, South Carolina.


NC
SC
GA
4 km

CHAPTER 2

STREAM MACROINVERTEBRATE RESPONSE TO FINE, DEPOSITED SEDIMENTS AT MESOHABITAT AND REACH SCALES IN SOUTHERN APPALACHIAN STREAMS[1]

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[1] Chiao, E. and J.B. Wallace. To be submitted to *Freshwater Biology*.

ABSTRACT

1. The effects of fine deposited sediments ($\leq$ 2 mm) on macroinvertebrate communities were examined for seven tributaries (first order on 1:24 000 scale map) to the Wild and Scenic Chattooga River in Georgia, North Carolina, South Carolina, U.S.A. Macroinvertebrate community structure was characterized at two different scales (reach and mesohabitat) using various metrics.

2. At the reach scale, EPT richness and shredder density were negatively related to levels of fine, deposited sediments ($r^2 = 0.69$, $p = 0.02$; $r^2 = 0.63$, $p = 0.03$). Reach-level estimates of chlorophyll *a* were negatively related to sedimentation ($r^2 = 0.62$, $p = 0.04$). Other macroinvertebrate community metrics (total density, total richness, % dominant taxon, functional feeding group measures) and trophic variables (standing stock of BOM, small wood, leaves, FBOM, periphyton biomass) were not significantly related to reach-scale levels of fine, deposited sediments.

3. Analysis of community structure within discrete habitat types based on invertebrate density and biomass show distinct community types upon which sedimentation is likely having a differential effect. Riffle EPT richness was negatively related to *reach*-scale levels of deposited sediments ($r^2 = 0.69$, $p = 0.02$). Bedrock outcrop community density and gatherer density were negatively related to *reach*-scale amounts of fine, deposited sediments ($r^2 = 0.64$, $p = 0.03$; $r^2 = 0.57$, $p = 0.05$). In depositional habitats, the second most frequently collected taxon was positively related to levels of fine, deposited sediments within study reaches ($r^2 = 0.74$, $p = 0.01$).

4. Fine sediments covering stream beds affected benthic macroinvertebrate communities at both mesohabitat and reach scales. Our ability to detect these effects demonstrates that fine sediment accrual within patches on stream beds can lead to reach-level consequences.

Introduction

Channel substrate is perhaps the most important factor regulating benthic macroinvertebrate distribution (Hynes, 1970; Minshall, 1984). Benthic macroinvertebrates have been shown to exhibit preferences regarding sediment sizes (Allan, 1975; Minshall, 1984), and differences in bed sediments have been related to differences in benthic macroinvertebrate taxonomic and functional composition within habitats (Tebo, 1955; Gurtz and Wallace, 1984; Wallace *et al*., 1995; Zweig and Rabeni, 2001). On meso- and micro- habitat scales, geomorphology (i.e. stream-bed characteristics and their interaction with streamflow) has been shown to influence the distribution of benthic macroinvertebrates and to have effects on the retention, type, and delivery of organic matter (McAuliffe, 1984; Huryn and Wallace, 1987).

Accelerated erosion caused by many human activities leads to unnaturally high inputs of fine, inorganic sediments to stream channels (Knighton, 1998). Sediment inputs alter stream characteristics and negatively impact benthic macroinvertebrate habitat, feeding, respiration, and behavior (Lenat, 1981; Lemly, 1982; Mebane, 2001; Waters, 1995). Benthic invertebrate macrofauna are essential to ecosystem function: they occupy intermediate and lower positions of riverine foodwebs and act to transfer bottom-up and top-down effects (Minshall and Petersen, 1985; Hunter and Price, 1992). Significant alterations within these communities can result in impaired biological function of lotic systems. Due to energetic linkages in riverine ecosystems (Vannote *et al.*, 1980; Minshall *et al*., 1985; Junk, 1999), impacts to the benthic macroinvertebrate community in heavily sedimented reaches and patches may alter biological function elsewhere in the network.

Despite evidence that sedimentation leads to changes in community composition of benthic macroinvertebrates at the meso- and micro- habitat scales, how these local changes affect reach-scale community dynamics remains unclear. Mesoscale habitats are here considered as the hierarchical category between stream segments and individual substrate particles (*sensu* Huryn and Wallace 1987), and are characterized as riffle, bedrock outcrop, or depositional habitat.

The goal of this study was to provide descriptive analyses of benthic macroinvertebrate communities within headwater tributaries of the Wild and Scenic Chattooga River and to investigate the relationship between benthic macroinvertebrate community structure and fine, deposited sediments by: (1) quantifying fine, deposited sediments (as percent surface cover of stream beds) within study reaches; (2) describing macroinvertebrate communities at mesohabitat and reach-level scales, and; (3) quantifying relationships between fine, deposited sediments and benthic macroinvertebrate community attributes at both scales. We postulated that whole reach, habitat-weighted benthic macroinvertebrate communities would show similar responses to sediments as has been previously reported from single habitat types (e.g. Lenat, 1981; Lemly, 1982; Mebane, 2001; Zweig and Rabeni, 2001).

Methods

Study region

Study sites are located in the Chattooga River Watershed, a 730 km^2 basin located in the southern Appalachian Mountains of western North Carolina (Macon County), northeastern Georgia (Rabun County) and northwestern South Carolina (Oconee County) (Fig. 2.1). Residing in an area rich in natural beauty, the Chattooga River was granted Wild and Scenic River status in 1974. As one of the few remaining free-flowing, large rivers in the US, the Chattooga River and its tributary waters are an important resource. The area attracts many visitors, supports a large amount of recreational use, and its streams serve as the headwaters of municipal drinking water sources (USEPA, 1999).

The catchment lies entirely within the Blue Ridge physiographic region, and its land cover is predominantly forest (> 92%). Upland forests are dominated by Virginia and shortleaf pine, and chestnut and scarlet oak. Streamside canopy is primarily eastern hemlock, yellow poplar, and white pine. Rhododendron and mountain laurel form the principal riparian understory and grow close enough to many stream channels to provide year-long shading. Basin soils are classified as highly erodible and are derived from gneiss, mica-schist, quartz and granite. Timber harvesting began in the 1800's and was widespread within the entire watershed by the early twentieth century. Agriculture and mining for minerals has also occurred in some areas. Today, most of the basin is second growth, although old growth does exist in some areas (particularly on steep slopes). Currently, there are no active mines, and harvesting of trees from the area has ceased. The topography of the area is generally steep (elevations 300-1,500 meters). The watershed is mainly rural, with small pockets of agriculture and some urbanizing areas. A great number of unpaved logging roads carve through the watershed and contribute greatly to sedimentation of catchment channels (Van Lear et al., 1995) and altered hydrology of the area. Approximately 70 % of the watershed is publicly owned as National Forest (Chattahoochee National Forest, GA; Nantahala National Forest, NC; Sumpter National Forest, SC).

All study reaches are forested, except Roach Mill Creek site 2, where the stream runs through a private garden. Roach Mill Creek, site 2 is approximately 500 m downstream of Roach Mill Creek site 1.

Study design

Seven sites on six first order tributaries (based on a 1:24 000 scale map) of the Chattooga River were selected for this study (Fig. 2.1). Site selection was based on previous United States Environmental Protection Agency (USEPA) evaluations of basin waters (USEPA, 1999). Chosen sites reflected a range of impairment as reported by the USEPA (1999) (Table 1.1).

Sediments and other abiotic variables

One 100-m reach was sampled at each site whenever possible; however, natural or man-made features made it necessary to shorten some study reaches (e.g. houses, bedrock outcrops too large to scale). Wetted width was averaged from measurements taken every 20 m along the length of each study reach.

The stream bed of each reach was characterized by dividing reaches into discrete, 5m sections. Sections were simultaneously observed by two investigators who described each segment proportionately using five categories: bedrock, cobble, pebble, gravel and ≤ 2 mm. Observations were averaged over each reach to obtain whole reach estimates for the three most prevalent habitats: bedrock outcrop, cobble riffle, and depositional. Pebble and gravel occurred within either depositional, or riffle habitats and did not individually constitute habitats separate from bedrock outcrop, cobble riffle, or depositional. Results from both investigators were averaged for final estimates. Stream bed characterization was done one time during the study period. Depositional habitat was considered to be any area of stream bed covered with fine sediments; therefore the two categories, % depositional habitat and % reach covered in fine, deposited sediments are assigned identical values. Areas considered as depositional were patches of sand and silt that were often quite deep. These areas of the stream bed were not ephemeral patches and were not flushed out during rain events that occurred over the course of the study. It should be noted, however, that the study took place during a dry year.

Proportions of sediment sizes within riffle samples were visually estimated as macroinvertebrate sampling occurred. Sediments were categorized proportionately into the same five categories as above. Amounts of fine sediments were not measured within sampled bedrock outcrop and depositional habitats. Although some fine sediments are often trapped by aquatic mosses growing on bedrock outcrop habitats, we assumed bedrock habitat to be comprised of 100 % bedrock. Likewise, although depositional habitats trap some larger sediment, they are largely comprised by fine sediments, and we assumed they were comprised of 100 % fine sediments.

Temperature in each reach was measured every two hours over the course of two years (October 2000 – November 2002) using HOBO© temperature sensor and recording devices (Onset Computer Corporation, Bourne, MA, U.S.A.). Temperature data used in analyses were recorded during October 2000 – October 2001, but equipment failure at one site (Overflow Creek) necessitated inclusion of October 2001 – November 2002 temperature values at that site.

Slope was measured along the lengths of study reaches from riffle top to riffle top using an auto level and stadia rod.

Sampling methods

Macroinvertebrates. Seasonal benthic macroinvertebrate samples were collected from each site throughout one year: October 2000 – July 2001. Nine samples were taken from each stream reach per season. Three separate riffle, bedrock outcrop and depositional habitats were randomly located within each study reach for sampling on each sample date. A Surber sampler fitted with a

250 µm mesh net was used in riffles to obtain quantitative samples (riffle rocks were hand scrubbed with a brush and riffle sediments stirred to a depth of approximately 10 cm). A stove-pipe corer was used to delineate depositional samples and a dipper used to remove samples from within the corer into a bucket so that they could be elutriated and passed through a 250 µm mesh net. Bedrock outcrop habitats were sampled by scraping known areas (generally 100 cm^2) into a 250 µm mesh net. All samples were preserved in their entirety in 10 % formalin containing phloxine B (a protein dye that stains bright pink and used to simplify removal of macroinvertebrates from other sample components).

In the laboratory, preserved samples were washed into 1 mm and 250 µm nested sieves (to split the sample into two size fractions: coarse fraction, > 1 mm; fine fraction, 250 µm – 1 mm) that were placed over a graduated bucket to catch all rinse water and very fine particles. Benthic macroinvertebrates in both size fractions were separated by hand from organic matter with the aid of dissecting microscopes. When necessary, fine fractions were subsampled using a sample splitter (Waters, 1969), and macroinvertebrates were removed from complete subsample fractions until at least 100 individuals were counted.

Invertebrates were counted and measured using a dissecting microscope to the nearest mm. Insects, with the exception of Chironomidae (Insecta: Diptera), were identified to genus (instars too small to properly identify were taken to family-level) using insect keys (Merritt & Cummins, 1996; Wiggins, 1996). Chironomids were divided into Tanypodinae (predaceous) and non-Tanypodinae. Non-insect invertebrates were identified to order. Biomass was calculated using published length-weight regressions (Benke *et al*., 1999). Macroinvertebrate densities (no. individuals m^{-2}) and biomass were habitat weighted by multiplying measured values by the proportion of each habitat present in respective study reaches. Invertebrates were categorized according to functional feeding groups (FFGs) based on Merritt & Cummins (1996). North Carolina Biotic Index (Lenat, 1993) was calculated for each site, as well as various metrics considered to be responsive to habitat conditions. All reported macroinvertebrate assemblage attributes have been calculated seasonally and averaged to determine an annual value.

Trophic variables. Coarse (> 1 mm) and fine (250 µm – 1 mm) benthic organic matter (BOM: coarse = CBOM; fine = FBOM) standing crop was quantified from samples after macroinvertebrates were separated from organic matter. CBOM was further separated into the following categories: moss, leaves, and wood. FBOM was re-suspended in a known volume of water and subsampled with a syringe, then filtered onto glass fiber filters (Whatman® GF/F filters, pore size = 0.7µm, Whatman Inc., Clifton, NJ). Very fine benthic organic matter (particles < 250 µm, VFBOM) standing crop was subsampled with a syringe (re-suspended prior to collection by stirring) from the graduated bucket over which the sample had been washed and filtered onto pre-weighed and ashed glass fiber filters. All BOM was oven dried at 50 ºC for one week, weighed, subsampled if necessary (for CBOM) and then ashed at 500 ºC in a muffle furnace to determine ash-free dry mass (AFDM) of each sample. Chlorophyll *a* and biofilm biomass were estimated by randomly collecting sediment at five locations within each study reach per sampling date (however, sediments ≤ 10 cm were excluded from these collections). Sediment samples were put into sterile sample bags, placed on ice and kept frozen until processing. Biofilm and chlorophyll *a* laboratory protocols follow methods outlined by Steinman and Lamberti (1996). In the laboratory, biofilm was removed from sediment samples by scrubbing collected substrates in water with a stiff toothbrush. Using a syringe, a well-stirred subsample was removed for chlorophyll *a* estimates and the remainder (of known volume) filtered onto glass fiber filters, and processed following the same protocol used for FBOM (*see above*). Chlorophyll *a* samples were filtered onto glass fiber filters, rinsed with $MgCO_3$ to prevent chlorophyll degredation and frozen. Chlorophyll *a* was extracted in the dark using 90% acetone buffered by $MgCO_3$ and values were obtained fluorometrically. Surface area of biofilm substrates were measured by covering rocks with aluminum foil, weighing each unique piece and comparing weights to a pre-weighed piece of a known area.

Data analyses.

Distribution of all dependent and independent variables were checked for normality and transformed if necessary. Macroinvertebrate abundances were $\log_{10}(x + 1)$ transformed and all percentage data were arcsine square-root transformed prior to analyses. Macroinvertebrate densities (no. individuals m^{-2}) and biomass were habitat weighted by first multiplying values found for abundance and biomass within specific habitats (i.e. abundance / biomass per bedrock outcrop, depositional area, riffle sample) by the proportion of each habitat present in respective study reaches, then summing resulting products. All values listed in tables and used in analyses are annual averages. Simple linear regression was used to characterize relationships between sediments and biotic variables. All regressions were made using SigmaStat for Windows, Version 3.1, Copyright 2004 SPSS Inc. Non-metric multidimensional scaling (NMS) was used to examine differences among habitat assemblages based on biomass of taxa (PC-ORD Version 4, MjM Software Design, Glenden Beach, OR, U.S.A.).

Results

Fine, deposited sediments of study reaches and fine sediments within riffles

Levels of fine, deposited sediments differed significantly among reaches ($p < 0.001$; Fig 2.2a). The lowest amount of deposited sediment was observed in Overflow Creek, and Law Ground Creek contained the greatest amount of deposited sediment. Proportions of sediments ≤ 2 mm in sampled riffles were lowest in Overflow Creek and highest in Law Ground Creek (Fig. 2.2 *b*). One-half of all riffle ($n = 84$) samples contained between 5% and 28% fine sediments. Every study reach except Law Ground Creek had riffle samples containing no fine sediments; however, Overflow Creek had the most riffles without fines (7 out of 12 samples). Regression analysis between reach-level deposited, fine sediments and riffle fine sediments show a significant positive relationship ($r^2 = 0.74$, $p = 0.013$; Fig. 2.2 *c*).

Macroinvertebrate distribution among reaches

Annual average taxonomic richness ranged between 54 (Law Ground Creek) and 79 (Addie Creek) (Fig. 2.3 *a*), whereas total taxonomic richness (a count of all unique taxa found throughout the four seasons) ranged between 84 (Law Ground Creek) and 127 (Addie Creek) (Fig. 2.3 *b*). Mean annual EPT richness ranged between 26 (Law Ground Creek) and 44 (Addie Creek) (Fig. 2.3 *c*) and was negatively related to quantities of fine, deposited sediments within study reaches ($n = 28$, $r^2 = 0.45$, $p < 0.001$, Fig. 2.3).

Abundances ranged between 20,672 ind. m^{-2} (Law Ground Creek) and 43,095 ind. m^{-2} (Addie Creek). Gatherers (especially gathering Chironomidae and Oligochaeta) were the most abundant functional group, accounting for > 45 % of community abundance at each study reach. Functional attributes of communities, based upon comparisons of abundance and percent abundance, were similar across all study reaches (Figs. 2.5 and 2.6). However, some differences were observed. Scrapers were found in fewer numbers at Roach Mill Creek site 1 (Fig. 2.5 *c*). Scrapers accounted for significantly lower proportions of the community at Roach Mill site 1 than at other study sites (Fig. 2.6 *e*). Predators accounted for significantly lower proportions of community abundance at Roach Mill site 2 (Fig. 2.6 *b*). Shredder density was negatively related to levels of fine, deposited sediments ($n = 28$, $r^2 = 0.25$, $p = 0.007$, Fig. 2.7 *a*). Percent shredder contribution to community abundance was also negatively related to levels of fine, deposited sediments ($n = 28$, $r^2 = 0.17$, $p = 0.03$, Fig. 2.7 *b*).

Biomass was highest at Roach Mill site 2, the only non-forested study reach, and Law Ground Creek, the most heavily sedimented reach (Fig. 2.8 *a*). Biomass of functional groups did not vary significantly among study sites (Fig. 2.8 *b* - *f*). Percent gatherer contribution to community biomass was significantly elevated at Roach Mill Creek site 1 and significantly depressed at Law Ground Creek (Fig. 2.9 *d*). Otherwise, functional group percent biomass did not differ significantly among study sites. Shredder biomass and percent shredder contribution to community biomass were positively related to levels of fine, deposited sediments ($n = 28$, $r^2 = 0.19$, $p = 0.02$, Fig. 2.10 *a*; $n = 28$, $r^2 = 0.14$, $p = 0.053$, Fig. 2.10 *b*). Percent scraper biomass was weakly negatively related to levels of fine, deposited sediments ($n = 28$, $r^2 = 0.10$, $p = 0.055$, Fig. 2.10 *c*).

Macroinvertebrate distribution among mesohabitats

Taxonomic richness and EPT richness were greatest in riffle habitats. Taxonomic richness ranged between an average value of 50 for riffle habitats and 29 and 27 in bedrock outcrops and depositional habitats respectively. Average EPT richness was 29 in riffles, 13 in bedrock outcrops and 12 in depositional habitats.

Macroinvertebrate abundance was greatest on bedrock outcrops, intermediate in depositional habitats and lowest in cobble riffles (Fig. 2.11 *a*). Community structure varied among habitats when all pair-wise combinations were compared (Fig. 2.11 *c*). Filterer and scraper abundances were significantly lower in depositional areas, whereas gatherers were significantly more abundant in depositional areas. Predator abundance was lowest on bedrock outcrops and shredders were most abundant in cobble riffles.

Total macroinvertebrate biomass did not significantly differ among habitat types when all pair-wise combinations were compared (Fig. 2.11 *b*). However, there were differences in community structure (based on biomass estimates) among habitat types (Fig. 2.11 *d*). Gatherer biomass was lowest in cobble riffles, whereas scraper biomass was highest in cobble riffles. Predator biomass was greatest in depositional areas. Shredder biomass was lowest on bedrock outcrops.

Trophic variables

Measures of trophic resources were varied among reaches, but except for chlorophyll *a*, were not significantly different among sites (Fig. 2.12 *a – f*). Levels of chlorophyll *a* were negatively related to the amount of fine, deposited sediments within study reaches ($r^2 = 0.62$, $p = 0.04$). Total CBOM, FBOM, small wood, leaves, moss, FBOM and biofilm AFDM were not related to deposited sediments. Depositional habitats contained the greatest amounts of CBOM, small wood and leaves (Fig. 2.13). Moss was primarily found on bedrock outcrops, with none being present at depositional sites (Fig. 2.13).

Discussion

Impacts of sediment pollution to stream biota have been well documented (e.g. Waters, 1995), and it is not surprising that the dramatic changes to habitat brought about by fine sediments would alter the nature of biological communities within impacted patches (e.g. Tebo, 1955; Lenat, 1981; Lemly, 1982; Gurtz and Wallace, 1984; Wallace *et al*., 1995; Mebane, 2001; Zweig and Rabeni, 2001). Past studies, however, tend to focus on benthic macroinvertebrate response in one habitat at a time (e.g. riffles, glides, or sand patches), and sampled sites have generally contained either few fine sediments, or large amounts of fine sediments. The results from this study indicate that impacts of sedimentation to benthic community structure may be dramatic enough to detect even when examining community structure on a reach-level scale while choosing sample sites randomly within dominant habitat types and not based on presence or absence of fine sediments.

The positive relationship found between reach-scale levels of fine, deposited sediments and fine sediments found within sampled riffles (Fig. 2.2 *c*) of this study provides further evidence that visually judging deposited sediment as percent surface cover is an effective method of quantifying stream fine sediments, as suggested by Zweig and Rabeni (2001). Riffle habitats sampled for this study were all initially identified as being largely composed of variously sized cobbles and otherwise were randomly chosen. It was only upon closer inspection that evidence of interstitial infilling of larger sediments by sand could be measured. Because riffle habitats are areas of complex sediment composition, they are at greater risk of undergoing dramatic physical changes through fine sediment accrual (i.e. simplification through infilling) than either bedrock outcrop, or depositional habitats. In addition, although current velocity may be adequate within riffle areas to keep many fine sediments entrained, the boundary layer next to riffle sediments could allow for enough fine sediment accrual upon sediment surfaces to disturb benthic invertebrates (Lemly, 1982).

Reach-scale EPT richness was negatively related to levels of fine, deposited sediments within study reaches (Fig. 2.4). Total taxonomic richness tended to decline within study reaches as levels of sedimentation increased, and there was a difference in taxonomic richness of communities between reaches containing the greatest and lowest levels of fine sediments (Fig. 2.3 *a* - *c*). These findings corroborate results commonly reported for single habitat measures of total and EPT richness (Lenat, 1981; Lemly, 1982; Mebane, 2001; Zweig and Rabeni, 2001). However, of four metrics commonly reported as responsive to sedimentation (taxonomic richness, total density, EPT richness and EPT density), we found only EPT richness to be significantly (negatively) related to fine, deposited sediments. We did not choose sampling sites within each stream reach based on degree of sedimentation; rather sampling sites were chosen randomly within each stream for each habitat type. Therefore, the trends in macroinvertebrate metrics reflect the study reach as an integrated unit, rather than as sample sites stratified by the presence or absence of sedimentation. If sites had been chosen based upon the presence or absence of sedimentation, there would likely be even stronger relationships between macroinvertebrate community metrics and levels of fine, deposited sediments.

Although overall abundance did not vary significantly among study reaches, total biomass was greatly elevated at the most highly sedimented site (Law Ground Creek) and the most open site (Roach Mill Creek site 2; Fig. 2.8 *a*). This change reflects a structural and taxonomic shift, most notably in the shredder functional group. Shredder abundance and biomass exhibit opposite relationships with levels of fine, deposited sediments (Figs. 2.7 and 2.10 *a*, *b*). When shredder taxa are compared between Addie Creek (20 % surface of stream bed covered by fine sediments) and Law Ground Creek (60 % surface of stream bed covered by fine sediment), it is clear that there is a shift from numerous, smaller-bodied shredders (i.e. *Tallaperla* spp.) to fewer large-bodied shredders (i.e. *Pteronarcys* spp., *Tipula* spp.). Others have observed that excessive deposition of fine sediments within streams renders macroinvertebrate habitat unstable and leads to declines in shredder density (Reice, 1974; Lenat et al., 1981). Wallace *et al*. (1995) observed that plecopteran shredders did not track increased leaf litter abundances at debris dams formed from log additions to streams (which were characterized by elevated levels of sediments and slower current velocities), whereas trichopteran and dipteran shredders were able to exploit increased debris dam resources. This difference in response was attributed to differences in physiological capabilities of different taxa and to low levels of current velocity within debris dams (Wallace *et al*., 1995). In this study, dipteran individuals dominated the shredder functional group abundance and biomass in depositional habitats, whereas plecopteran shredders were rarely found. Therefore, the relative dominance of depositional patches within stream reaches will likely influence the density, biomass and identity of shredding taxa. However, larger-bodied shredder taxa (e.g. *Tipula* spp. and *Pteronarcys* spp.) are more common at Overflow Creek (19 % surface of stream bed covered by fine sediments) than at Addie Creek, and they did not replace smaller shredders; therefore the abundance of shredding individuals at Overflow and Addie Creeks is similar, whereas shredder biomass at Overflow Creek is greater than at Addie. This difference between shredding communities at the two sites with lowest levels of fine, deposited sediments makes it clear that sediments alone do not account for the presence of large-bodied shredders.

The differential responses of mesoscale macroinvertebrate communities to sedimentation suggest that the effects of fine sediments on macroinvertebrate communities are mediated by local factors (i.e. physical nature of habitats). In riffle and bedrock outcrops, macroinvertebrates are likely responding to physical impacts of entrained fine sediments (as direct abrasion, or through reduction of available habitat), or to a reduction in food resources (lowered amounts of primary production). Physical scour is likely to be especially important in bedrock outcrop habitats where relatively high current velocities (Fig. 2.14) may keep fine sediments entrained.

Within one exception, the stream reaches included in this study were all forested and heterogenous (Table 2.1). Although some reaches were quite obviously impacted by sediment pollution, all were structurally complex channels that contained numerous riffles, runs, debris dams, and were considered to be unaffected by organic pollution (USEPA, 1999). That reach-level relationships were found to exist between simple macroinvertebrate community metrics and fine sedimentation under these conditions is an indication of the influence that fine sediments exerts on these communities.

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Table 2.1. Study reach environmental variables.

	Addie	Overflow	Reed Mill	Martin-Finney	Law Ground	Roach Mill	Roach Mill 2
USEPA (1999) listing label	Reference	Reference	Threatened	Threatened	Impaired	Impaired	Impaired
Slope (%)	2.96	0.76	3.63	2.02	2.00	3.40	2.30
Average wetted width (m)	5.58	6.55	3.35	2.4	2.51	2.01	1.10
Reach length (m)	60	120	80	70	85	80	45
Catchment size (ha)	588	2,530	435	705	251	207	207
Average temperature (ºC)	10.46	10.91	11.17	11.22	11.47	11.35	12.24
% Deposited fine sediment	20	19	37	38	60	47	37
Riffle % fine sediment	8.58	5.00	18.33	17.72	31.25	13.33	23.75
% Bedrock outcrop	43	13	30	19	8	28	15
% Riffle	37	68	34	43	32	25	48
Chl *a* (mg m^{-2})	53.26	60.59	22.99	21.06	19.61	17.23	54.96
Biofilm biomass (g AFDM m^{-2})	43.49	81.15	89.97	51.14	56.27	110.45	75.03
Total CBOM (g AFDM m^{-2})	140.54	76.66	123.86	175.56	135.85	182.54	142.58
Total wood (g AFDM m^{-2})	39.43	20.76	62.73	89.84	28.27	47.51	39.11
Total leaves (g AFDM m^{-2})	6.77	9.94	49.17	56.21	7.11	23.95	11.71
Total FBOM (g AFDM m^{-2})	30.52	7.47	39.28	60.39	32.41	79.94	46.51

Figure 2.1. Map of study area. Circles represent reference sites, squares represent threatened sites and triangles represent threatened sites.

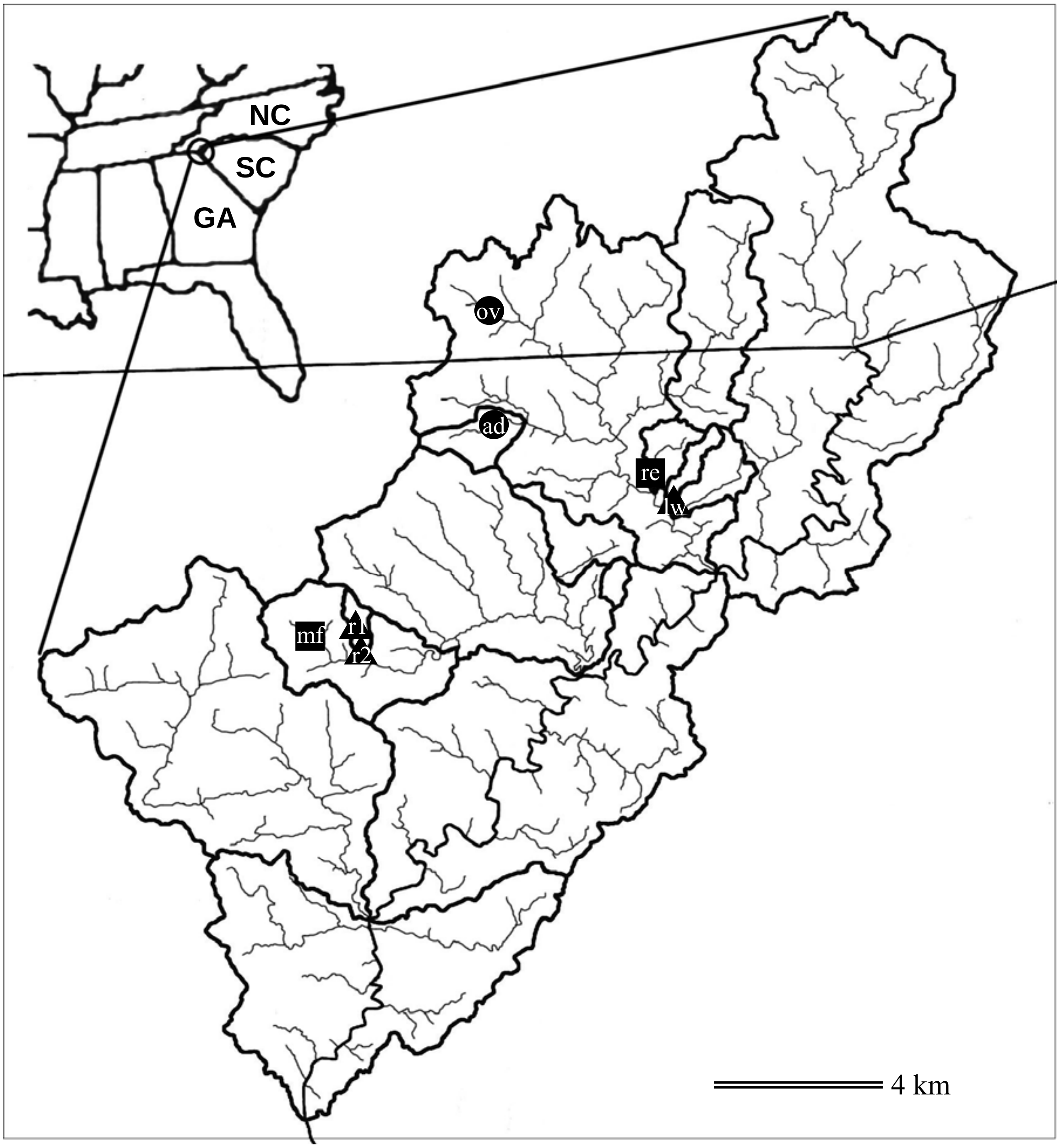

NC
SC
GA
ov
ad
re
lw
mf
r1
r2
4 km

Figure 2.2. Mean ± SE of deposited fine sediments within study reaches. Results of ANOVA are shown: reaches with different letters differ significantly in levels of fine, deposited sediments $p < 0.0001$ (*a*); levels of fine sediments within riffle samples (*b*); A simple linear regression between riffle fines and reach deposited fines, $y = 0.8089x - 9.4283$ (*c*). All proportional values have been asine square root transformed. For (*a*) and (*b*): AD = Addie Creek, OV = Overflow Creek, RE = Reed Mill Creek, MF = Martin-Finney Creek, R2 = Roach Mill Creek site 2, R1 = Roach Mill Creek site 1, LW = Law Ground Creek.

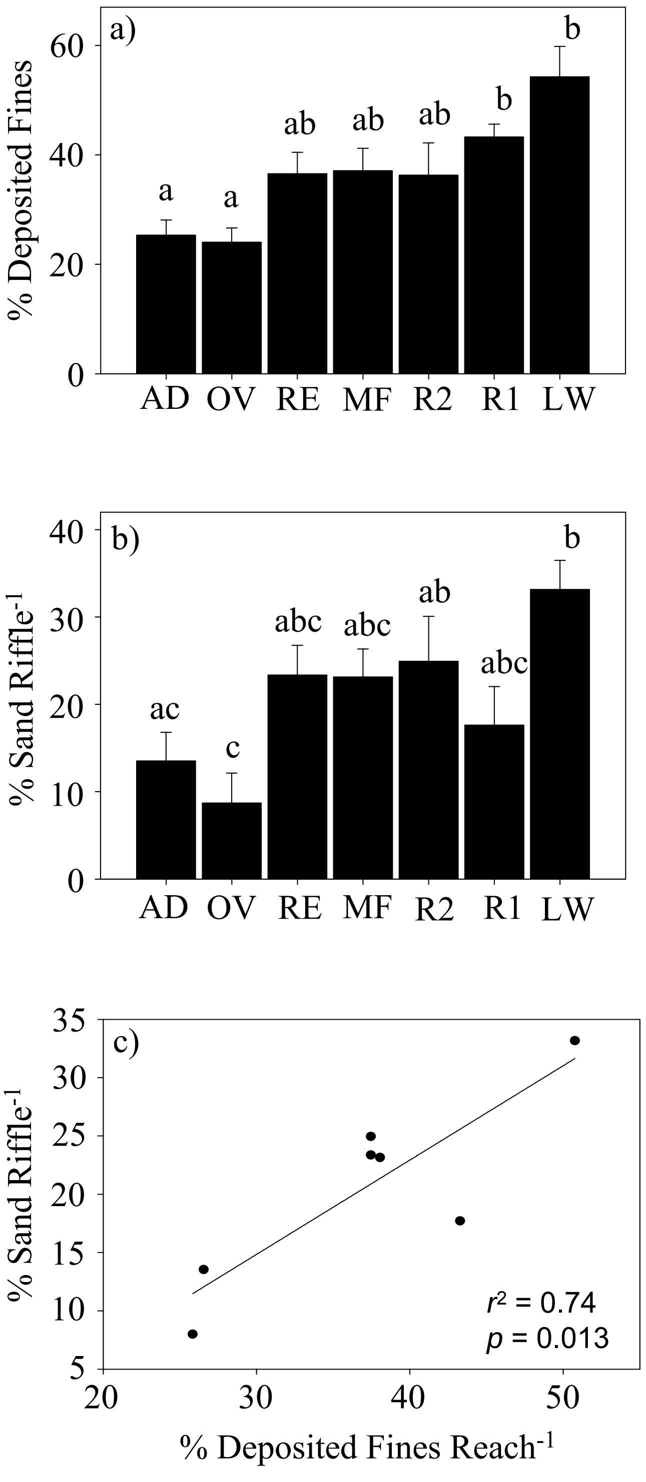
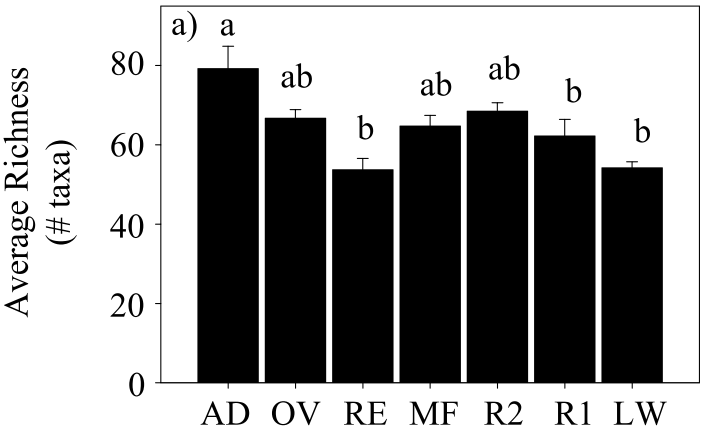
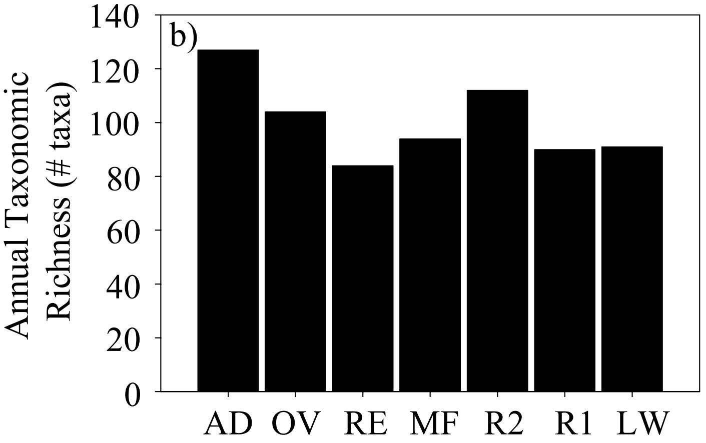

a)
% Deposited Fines
0
20
40
60
a
a
ab
ab
ab
b
b
AD
OV
RE
MF
R2
R1
LW
b)
% Sand Riffle^{-1}
0
10
20
30
40
ac
c
abc
abc
ab
abc
b
AD
OV
RE
MF
R2
R1
LW
c)
% Sand Riffle^{-1}
5
10
15
20
25
30
35
r^2 = 0.74
p = 0.013
20
30
40
50
% Deposited Fines Reach^{-1}

Figure 2.3. Mean and ± SE average taxonomic richness values (*a*). (b) Taxonomic richness = total number unique taxa found over the course of one year. (c) Mean and ± SE EPT taxa richness, *n* = 36. For list of site names, refer to figure 2.2.


a)
Average Richness (# taxa)
0
20
40
60
80
a
ab
b
ab
ab
b
b
AD
OV
RE
MF
R2
R1
LW


b)
Annual Taxonomic Richness (# taxa)
0
20
40
60
80
100
120
140
AD
OV
RE
MF
R2
R1
LW

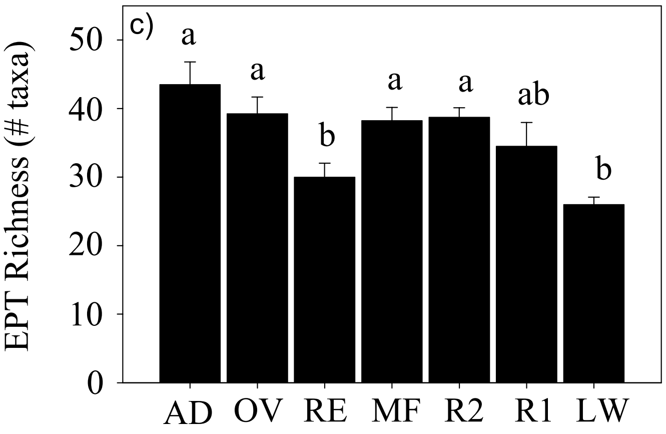
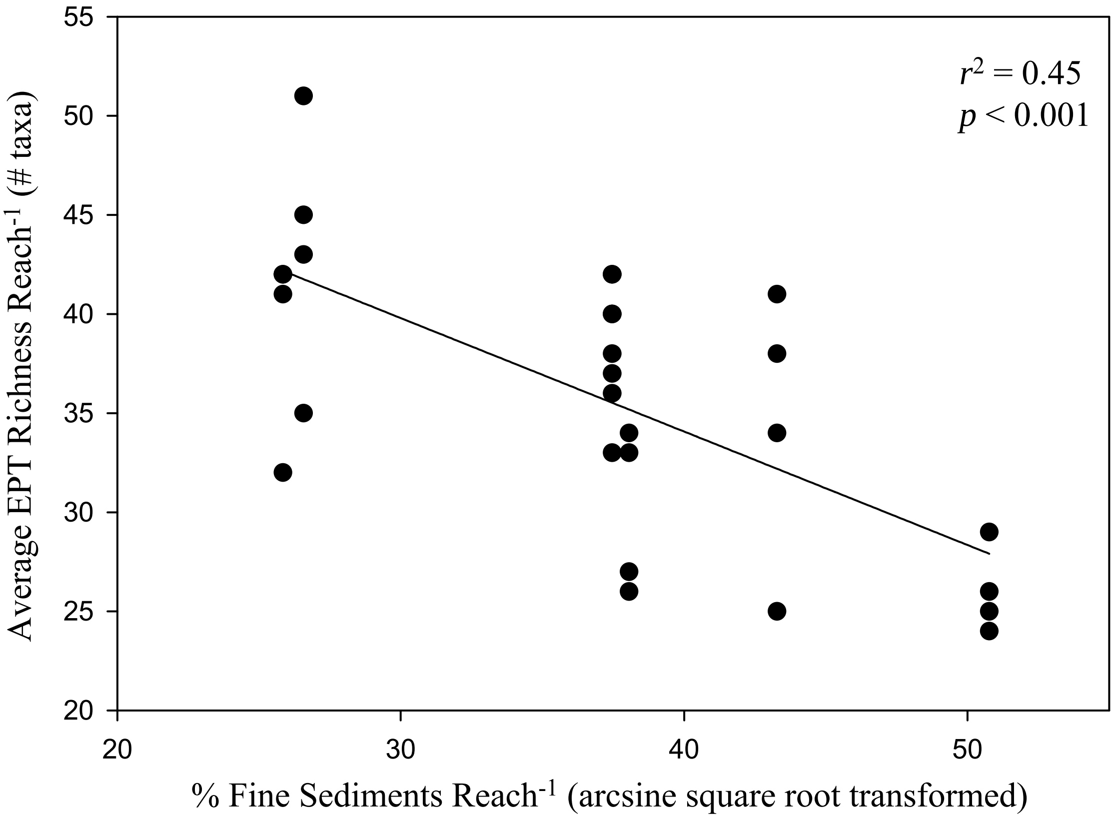

c)
EPT Richness (# taxa)
0
10
20
30
40
50
a
a
b
a
a
ab
b
AD
OV
RE
MF
R2
R1
LW

Figure 2.4. Linear regression between average EPT richness and reach-level fine, deposited sediments, *y* = -0.5724 + 56.966 (*n* = 28).



55
50
45
40
35
30
25
20
20
30
40
50
Average EPT Richness Reach^{-1} (# taxa)
% Fine Sediments Reach^{-1} (arcsine square root transformed)
$r^2 = 0.45$
$p < 0.001$

Figure 2.5. Mean ± SE macroinvertebrate total and functional group abundance values (habitat-weighted) for all study reaches. Asterisks (*) denote significantly different values (results of ANOVA). For study site names, refer to Fig. 2.2

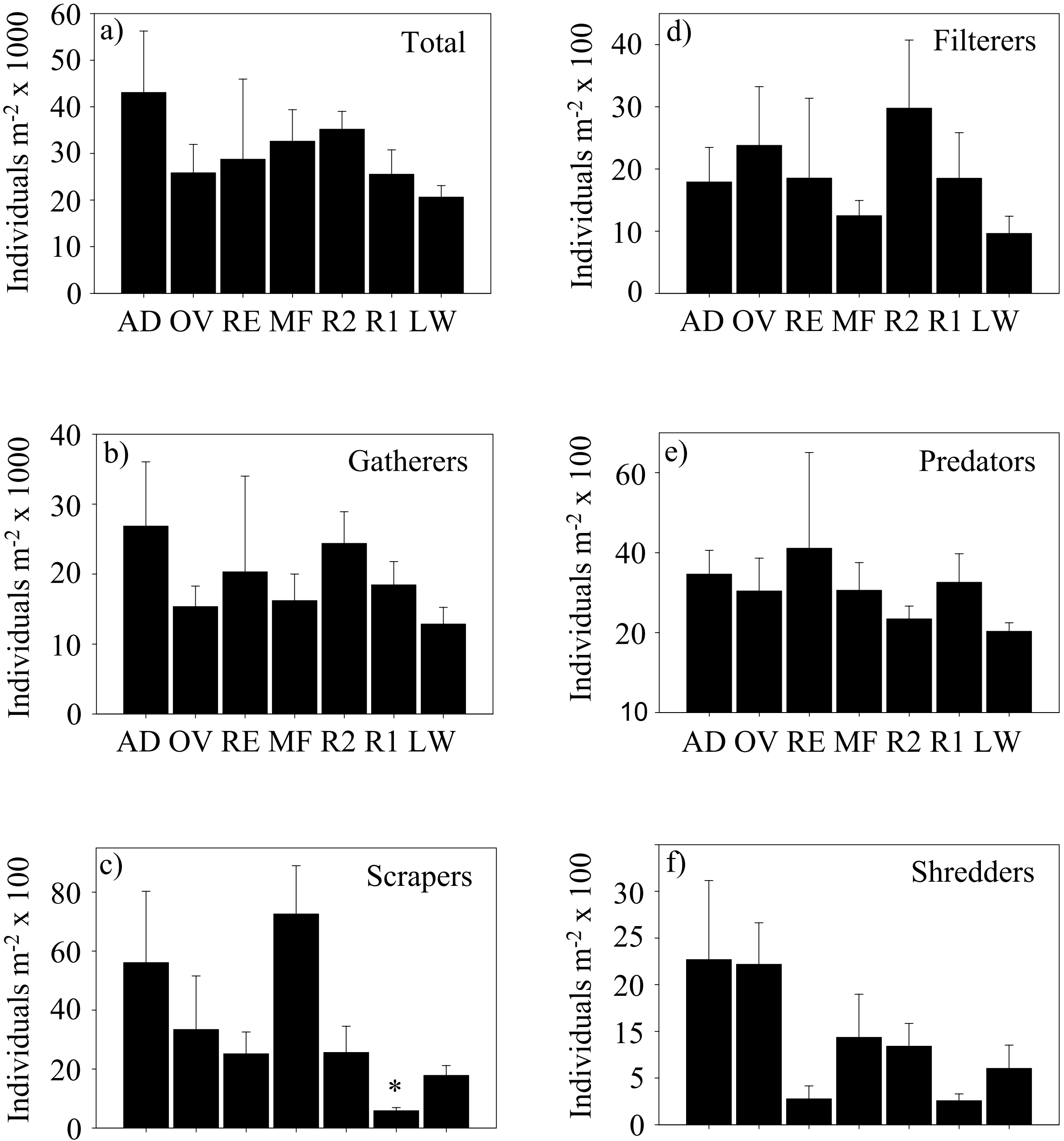
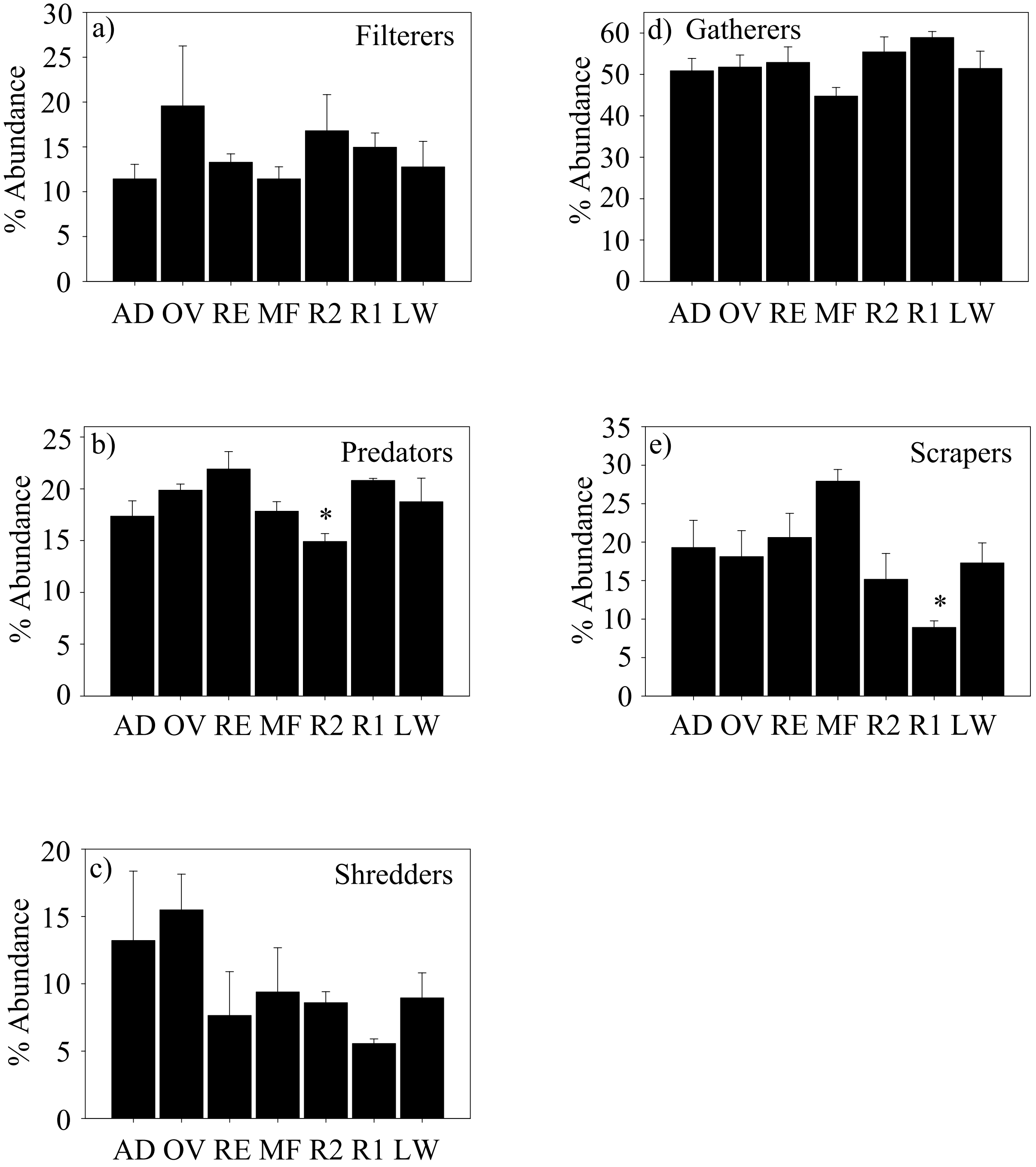
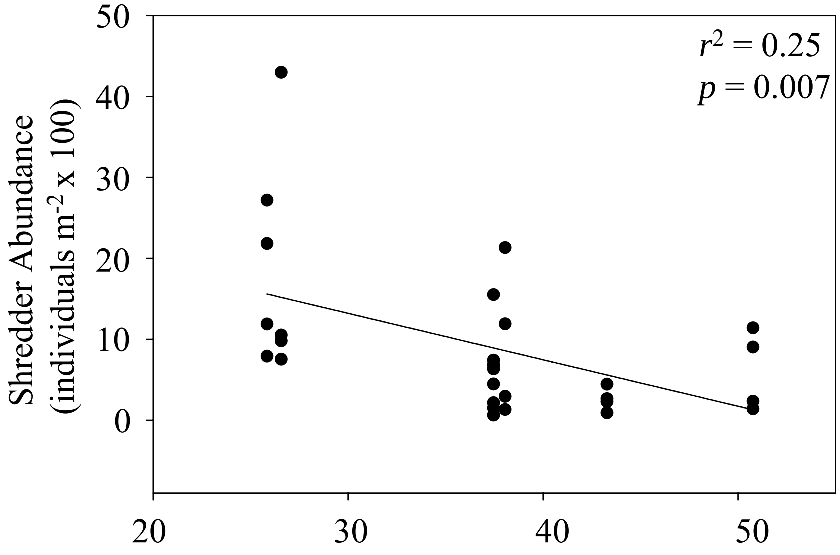

a)
Total
Individuals m-2 x 1000
60
50
40
30
20
10
0
AD OV RE MF R2 R1 LW
d)
Filterers
Individuals m-2 x 100
40
30
20
10
0
AD OV RE MF R2 R1 LW
b)
Gatherers
Individuals m-2 x 1000
40
30
20
10
0
AD OV RE MF R2 R1 LW
e)
Predators
Individuals m-2 x 100
60
40
20
10
AD OV RE MF R2 R1 LW
c)
Scrapers
Individuals m-2 x 100
80
60
40
20
0
*
AD OV RE MF R2 R1 LW
f)
Shredders
Individuals m-2 x 100
30
25
20
15
5
0
AD OV RE MF R2 R1 LW

Figure 2.6. Mean ± percent contribution (% abundance) of functional groups to total community abundance for each study reach (habitat-weighted annual averages). Asterisks (*) denote significantly different values (results of ANOVA). For study site names, refer to Fig. 2.2.



a)
Filterers
% Abundance
0
5
10
15
20
25
30
AD OV RE MF R2 R1 LW
d)
Gatherers
% Abundance
0
10
20
30
40
50
60
AD OV RE MF R2 R1 LW
b)
Predators
% Abundance
0
5
10
15
20
25
*
AD OV RE MF R2 R1 LW
e)
Scrapers
% Abundance
0
5
10
15
20
25
30
35
*
AD OV RE MF R2 R1 LW
c)
Shredders
% Abundance
0
5
10
15
20
AD OV RE MF R2 R1 LW

Figure 2.7. Relationships between reach-level fine, deposited sediments and shredder abundance, $y = -57.391x + 3042.5$ (*a*), and shredder contribution to total community biomass, $y = -0.3006x + 20.981$ (*b*). All % values have been arcsine square root transformed. For both regressions, $n = 28$.


$r^2 = 0.25$
$p = 0.007$
Shredder Abundance (individuals m^{-2} x 100)
50
40
30
20
10
0
20
30
40
50

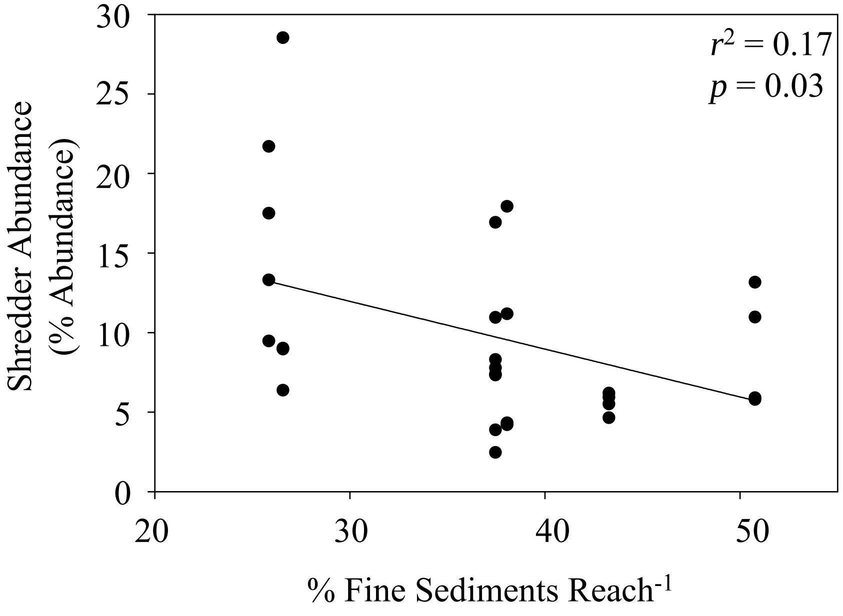

$r^2 = 0.17$
$p = 0.03$
Shredder Abundance (% Abundance)
30
25
20
15
10
5
0
20
30
40
50
% Fine Sediments $Reach^{-1}$

Figure 2.8. Mean ± SE macroinvertebrate total and functional group biomass values (habitat-weighted) for study reaches. Results of ANOVA shown, different letters denote significant differences. For study site names, refer to Fig. 2.2.

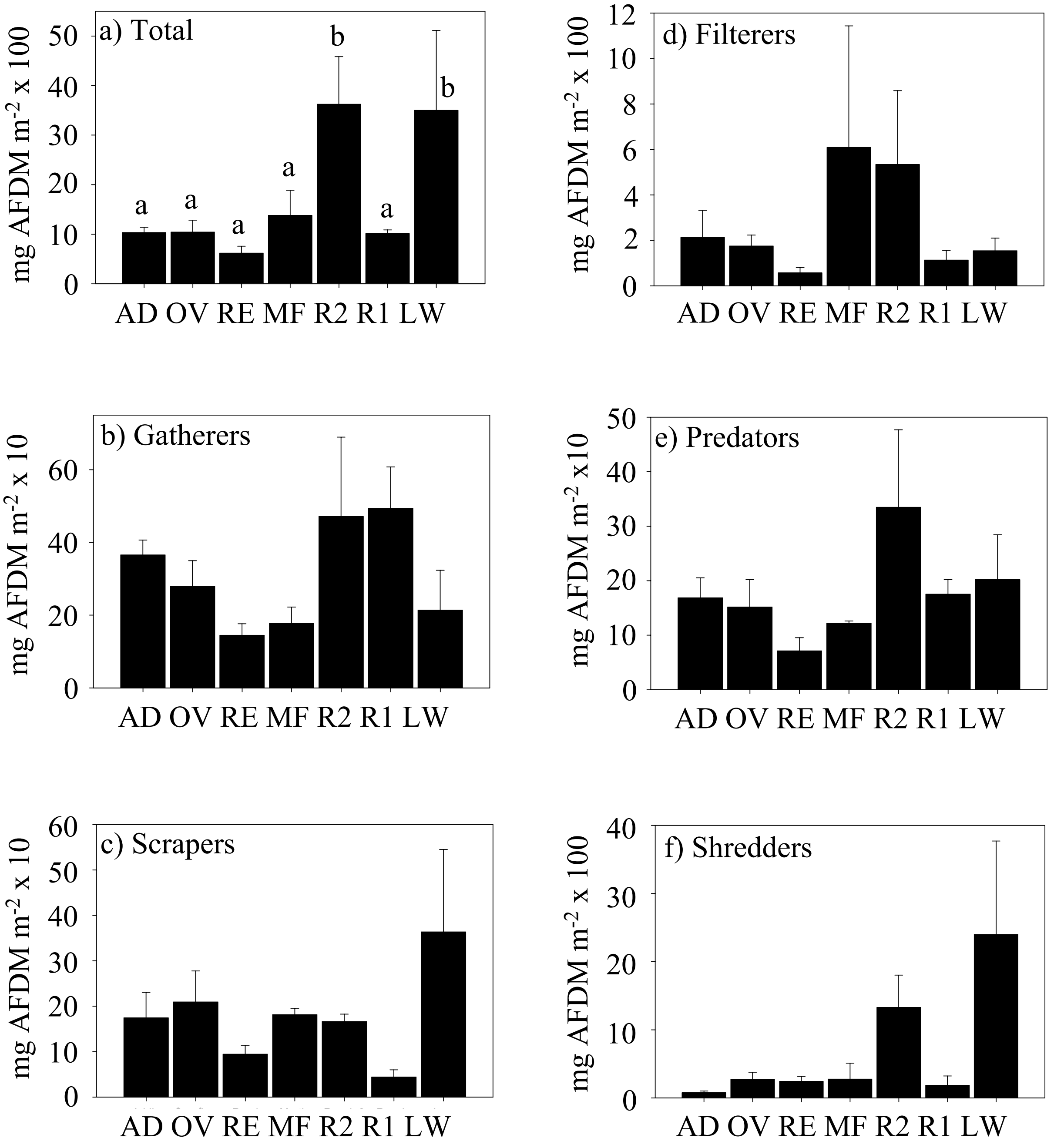
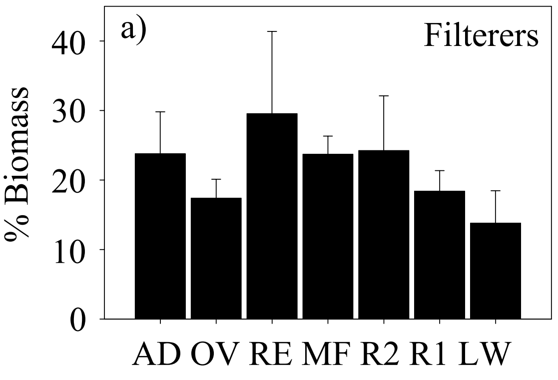
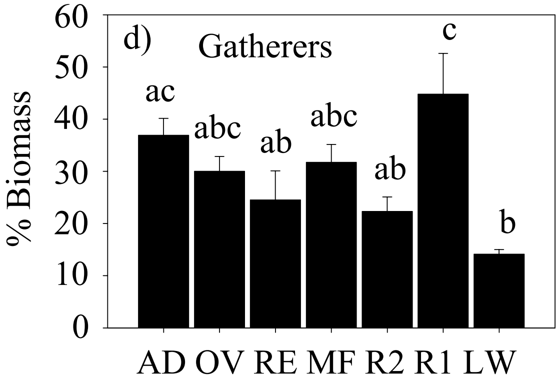
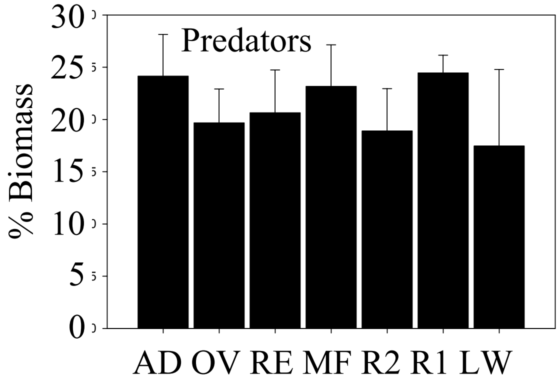
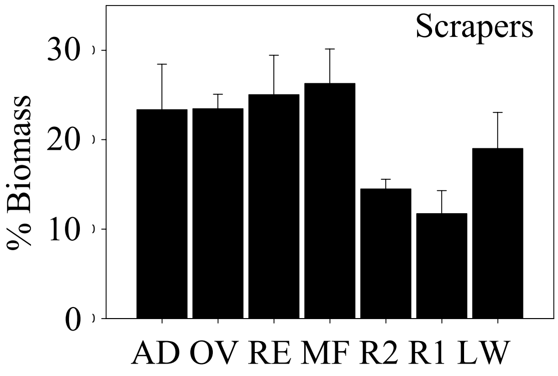

a) Total
mg AFDM m-2 x 100
0
10
20
30
40
50
a
a
a
a
b
a
b
AD OV RE MF R2 R1 LW
d) Filterers
mg AFDM m-2 x 100
0
2
4
6
8
10
12
AD OV RE MF R2 R1 LW
b) Gatherers
mg AFDM m-2 x 10
0
20
40
60
AD OV RE MF R2 R1 LW
e) Predators
mg AFDM m-2 x10
0
10
20
30
40
50
AD OV RE MF R2 R1 LW
c) Scrapers
mg AFDM m-2 x 10
0
10
20
30
40
50
60
AD OV RE MF R2 R1 LW
f) Shredders
mg AFDM m-2 x 100
0
10
20
30
40
AD OV RE MF R2 R1 LW

Figure 2.9. Mean ± percent contribution (% biomass) of functional groups to total community abundance for each study reach (habitat-weighted annual averages). For study site names, refer to Fig. 2.2.


a)
Filterers
% Biomass
0
10
20
30
40
AD OV RE MF R2 R1 LW


d)
Gatherers
% Biomass
0
10
20
30
40
50
60
ac
abc
ab
abc
ab
c
b
AD OV RE MF R2 R1 LW


Predators
% Biomass
0
5
10
15
20
25
30
AD OV RE MF R2 R1 LW


Scrapers
% Biomass
0
10
20
30
AD OV RE MF R2 R1 LW

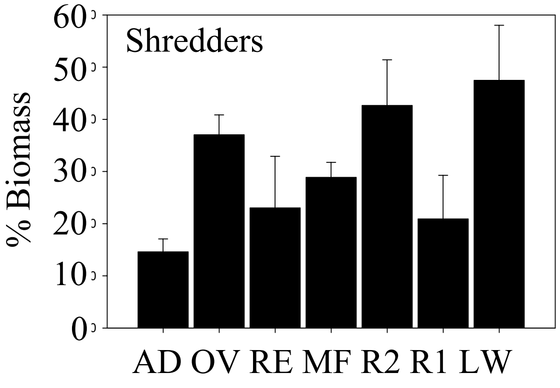

Shredders
% Biomass
0
10
20
30
40
50
60
AD OV RE MF R2 R1 LW

Figure 2.10. Relationships between shredder biomass and reach-level fine, deposited sediments, $y = 67.03x - 1800.3$ (*a*), percent shredder biomass and reach fines, $y = 0.77x + 2.08$ (*b*) and percent scraper biomass and reach fines, $y = -0.36x + 33.80$ (*c*). All proportional values were arcsine square root transformed before analysis. For all regressions, $n = 28$.

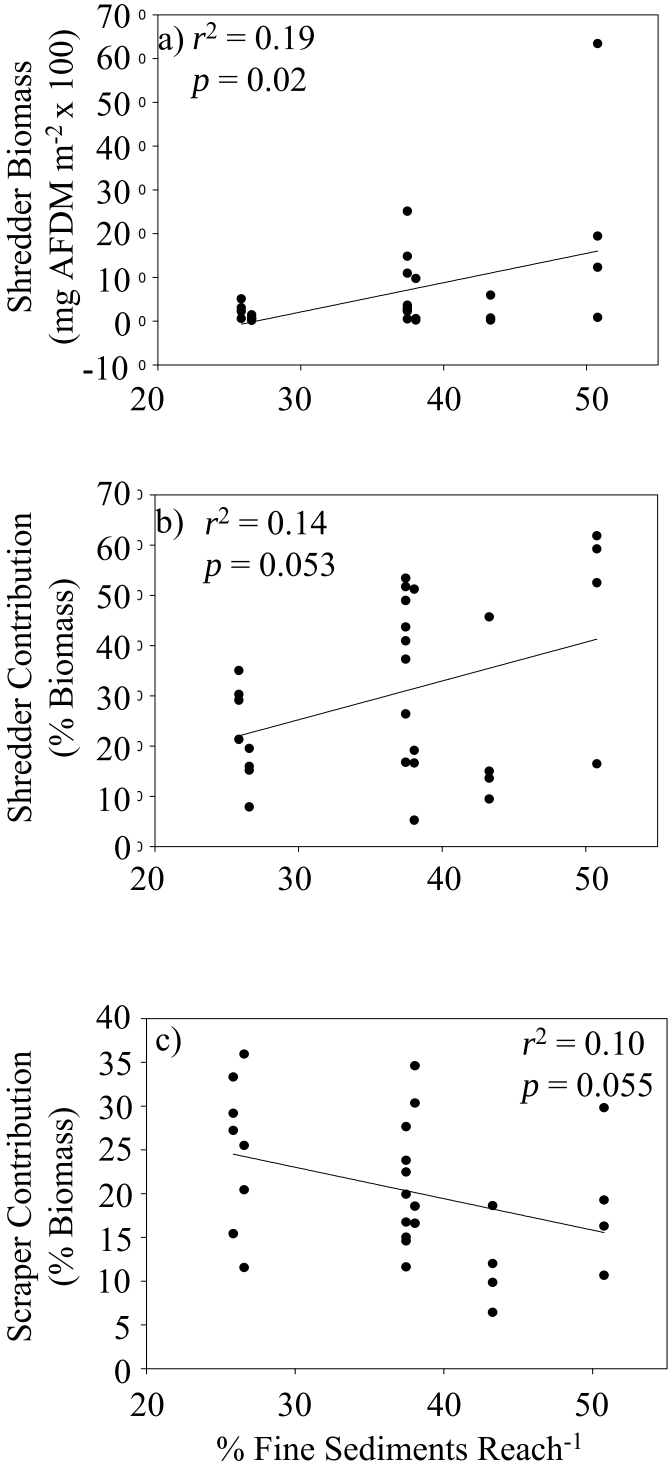

a) $r^2 = 0.19$
$p = 0.02$
Shredder Biomass
(mg AFDM m^{-2} x 100)
70
60
50
40
30
20
10
0
-10
20
30
40
50
b) $r^2 = 0.14$
$p = 0.053$
Shredder Contribution
(% Biomass)
70
60
50
40
30
20
10
0
20
30
40
50
c)
$r^2 = 0.10$
$p = 0.055$
Scraper Contribution
(% Biomass)
40
35
30
25
20
15
10
5
0
20
30
40
50
% Fine Sediments $Reach^{-1}$

Figure 2.11. Total macroinvertebrate community abundance for each habitat (*a*); total macroinvertebrate community biomass for each habitat (*b*); % contribution of functional groups to community abundance for each habitat type (*c*); % contribution of functional groups to community biomass for each habitat type (*d*). All values are annual averages, all proportional values were arcsine square root transformed before analysis. Different letters denote significant differences among habitat types (t-tests were used to test for differences between all pair combinations and Bonferroni correction applied; $\alpha = 0.017$). For all histograms: bedrock outcrop shown in black bars, cobble riffle shown in light grey bars, and depositional habitat shown in dark grey bars. For two histograms on left: F = filterers, G = gatherers, P = predators, C = scrapers, H = shredders.

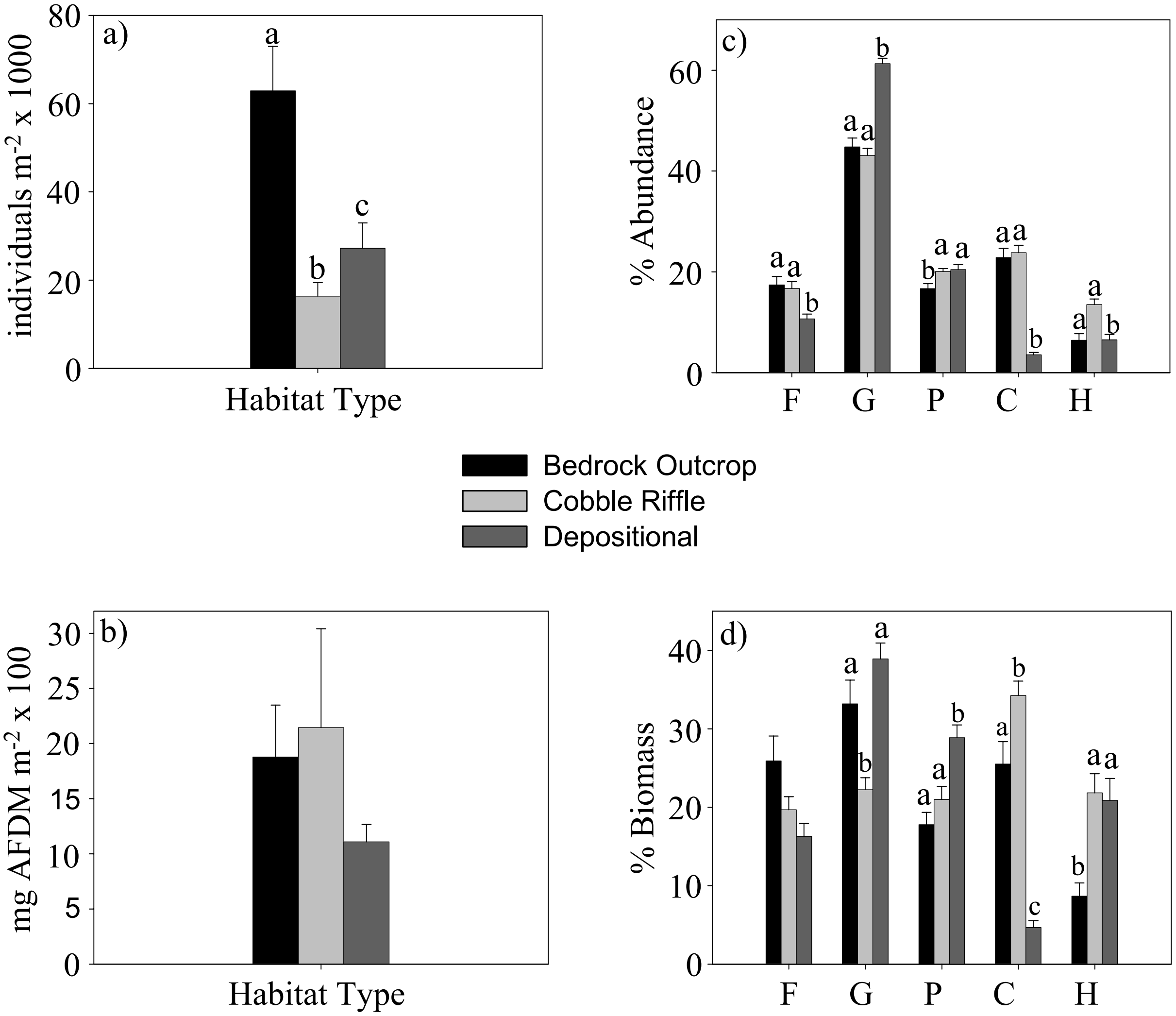

a)
individuals m^{-2} x 1000
0
20
40
60
80
a
b
c
Habitat Type
c)
% Abundance
0
20
40
60
a
a
b
a
a
b
b
a
a
a
a
b
a
a
b
F
G
P
C
H
Bedrock Outcrop
Cobble Riffle
Depositional
b)
mg AFDM m^{-2} x 100
0
5
10
15
20
25
30
Habitat Type
d)
% Biomass
0
10
20
30
40
a
b
a
a
a
b
a
b
c
b
a
a
F
G
P
C
H

Figure 2.12. Habitat-weighted annual average values for study reach trophic variables. All biomass values on Y-axes expressed in g AFDM m^{-2} x 100, unless otherwise indicated. Different letters denote significant differences. For study reach names, refer to Fig. 2.2.

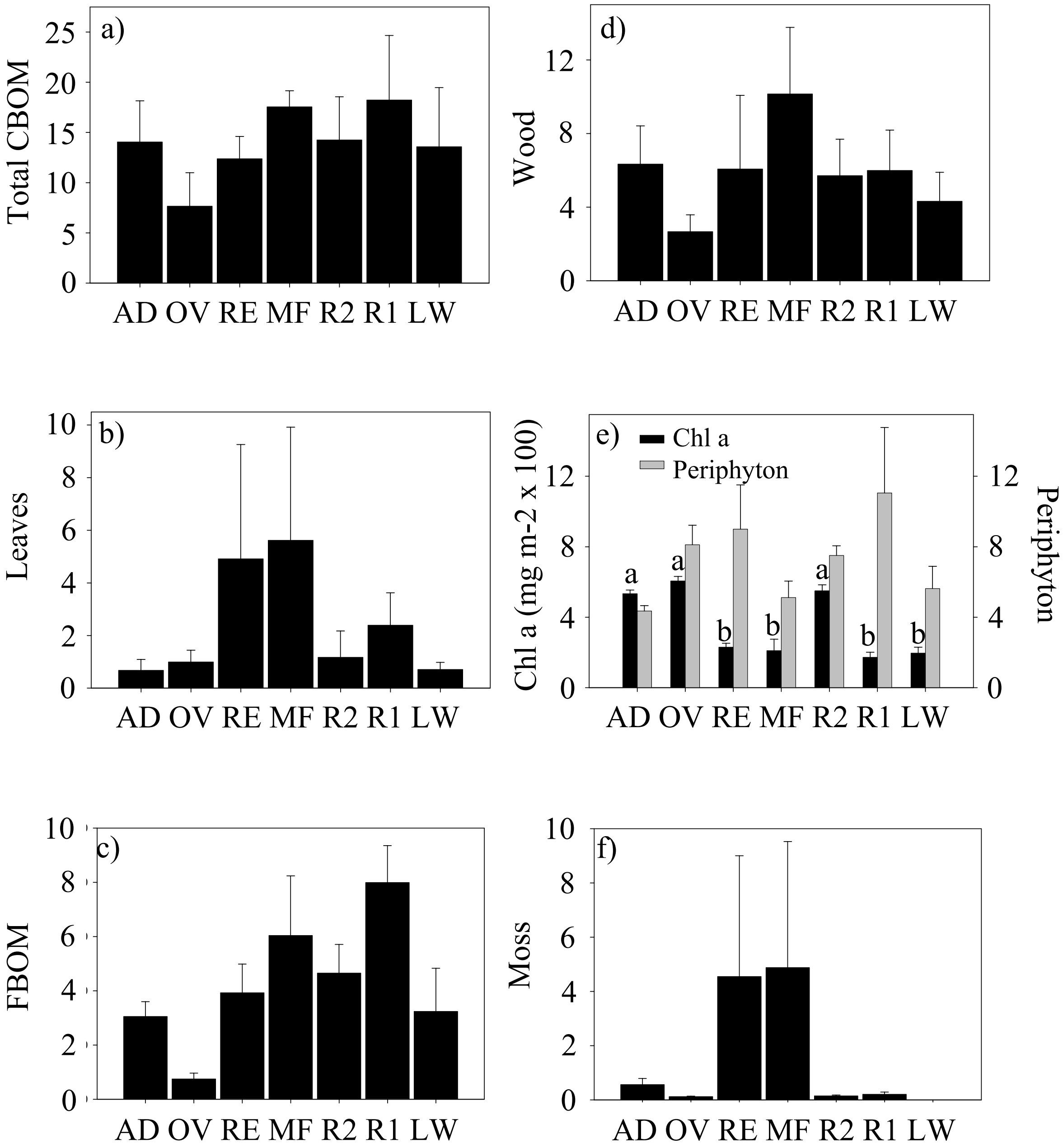
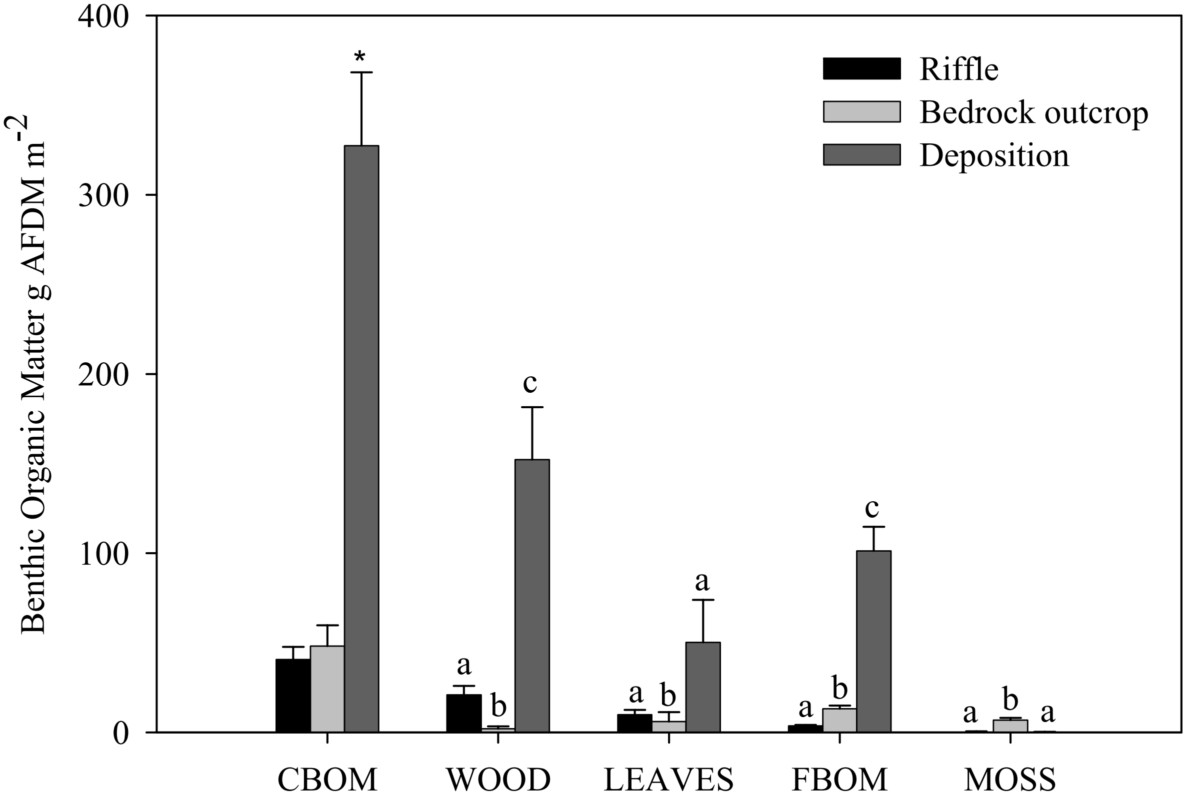

a)
Total CBOM
0
5
10
15
20
25
AD OV RE MF R2 R1 LW
d)
Wood
0
4
8
12
AD OV RE MF R2 R1 LW
b)
Leaves
0
2
4
6
8
10
AD OV RE MF R2 R1 LW
e)
Chl a
Periphyton
Chl a (mg m-2 x 100)
Periphyton
0
4
8
12
a
a
b
b
a
b
b
AD OV RE MF R2 R1 LW
c)
FBOM
0
2
4
6
8
10
AD OV RE MF R2 R1 LW
f)
Moss
0
2
4
6
8
10
AD OV RE MF R2 R1 LW

Figure 2.13. Trophic variables for each habitat type (annual averages). Different letters denote significantly different values among habitat types (t-tests were used to test for differences between all pair combinations and Bonferroni correction applied; $\alpha = 0.017$).



Benthic Organic Matter g AFDM m-2
0
100
200
300
400
Riffle
Bedrock outcrop
Deposition
*
a
b
c
a
b
a
a
b
c
a
b
a
CBOM
WOOD
LEAVES
FBOM
MOSS

CHAPTER 3

BENTHIC MACROINVERTEBRATE ASSEMBLAGE STRUCTURE ALONG AN APPALACHIAN WILD AND SCENIC RIVER CONTINUUM IN THE SOUTHEASTERN USA[1]

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[1] Chiao, E. and J.B. Wallace. To be submitted to *Freshwater Biology*.

ABSTRACT

1. Longitudinal trends in taxonomic richness, diversity, abundance and biomass of benthic macroinvertebrate communities were examined in cobble riffle, bedrock outcrop and depositional habitats at four study reaches within the Chattooga River watershed over the course of three seasons (winter, spring, summer) during one year. The continuum began at a small, forested tributary reach (259 ha basin) and continued into the main channel of the Chattooga River (34 213 ha basin).

2. Taxonomic richness decreased as catchment size of study reaches increased. At all sites, cobble riffle habitat supported the greatest number of macroinvertebrate taxa and depositional habitats the least.

3. Habitat-weighted macroinvertebrate abundance was greatest at the smallest study stream. With the exception of filterers, abundance of functional groups decreased as catchment size increased. Filtererer abundance increased with catchment size. Gatherers were the most abundant functional group, accounting for 62 - 80 % of habitat-weighted reach-scale communities. Relative contributions of functional groups to total abundance did not change significantly between endpoints of the continuum.

4. Habitat-weighted macroinvertebrate community biomass followed the same trends as habitat-weighted abundance. However, relative contribution of predators to community biomass declined as catchment size increased ($r^2 = 0.97$ $p = 0.02$). Habitat-weighted functional group biomass along the continuum matched some, but not all predictions of the River Continuum Concept. As predicted by the RCC, (1) relative dominance of scrapers peaked in a mid-size reach before decreasing in the downstream direction; (2) shredders declined in relative dominance in the downstream direction, although they contributed slightly more to total community biomass at

the second continuum site than at the first; and (3) the relative dominance of collectors increased downstream. Contrary to RCC predictions, relative biomass of predators decreased downstream, rather than remaining constant.

5. Benthic macroinvertebrate communities differed among habitat types. This result suggests that local distribution of habitat types (i.e. local lithology and geomorphology) greatly influences benthic macroinvertebrate community dynamics at the reach scale. Trends in benthic macroinvertebrate communities along the Chattooga River continuum are the result of predictable longitudinal physical gradients and local conditions (i.e. mesoscale geomorphology, aquatic plant growth, sedimentation).

Introduction

Changes imposed upon the landscape by humans often have unintended and far-reaching consequences. The interdependency of ecosystems and their components make it difficult to estimate the impacts of land uses on landscape and ecosystem attributes. Furthermore, even many well-intended activities (i.e. recreation) negatively impact natural areas. Unfortunately, allowing once-altered lands to recover some natural features may not be enough to fix enduring problems (Harding *et al*., 1998; Foster *et al*. 2003).

The watershed in which the Wild and Scenic Chattooga River and its tributary waters reside (Georgia, North Carolina, South Carolina; U.S.A.) was almost entirely logged during the late nineteenth and early twentieth centuries. Historically, agriculture and some mining for minerals were also practiced within watershed boundaries. Today, the basin is over ninety two percent forested, although there are areas of agricultural, commercial, urban, and residential land uses within the catchment. In 1997, the United States Environmental Protection Agency

(USEPA) assessed water quality within the Chattooga watershed in order to settle a lawsuit over Georgia Total Maximum Daily Loads. The resulting report concluded that excessive fine sediments are a major contaminant of Chattooga waters and implicated both past and present land uses as fundamental to the problem (USEPA, 1999). Sediments contributed to stream channels via logging roads and recreational activities (e.g. hiking, camping, white water rafting, all-terrain vehicle usage, and etc.) were of particular concern.

As human activities on the landscape continue to alter characteristics of natural systems, it becomes increasingly important to directly measure ecosystem attributes. Our ability to responsibly steward natural resources depends on this type of information. The objective of this study is to describe benthic macroinvertebrate community structure in context of reach position within a longitudinal profile of a Wild and Scenic River. Habitat-weighted estimates of abundance and biomass (*sensu* Huryn and Wallace, 1987) are used to characterize functional composition of benthic macroinvertebrate communities along the profile. We are interested in: (1) whether or not patterns in benthic community structure match predictions made for pristine river systems; and, (2) how understanding upstream-downstream relationships between macroinvertebrate communities within the Chattooga River network can inform watershed management decisions.

The River Continuum Concept (RCC, Vannote *et al*., 1980, Minshall *et al*., 1985*a*) proposes that benthic communities have evolved to maximize usage of energetic resources along longitudinal gradients of river networks. Based upon the fluvial geomorphic theory of energy equilibrium (Leopold and Maddock, 1953), the biotic and abiotic links proposed by the RCC are dependent upon the average condition of the river channel—a dynamic steady state that is likely altered by elevated long-term fine sediment loading in excessive amounts. According to the

RCC, benthic macroinvertebrate data resulting from sampling differently sized stream reaches along a longitudinal stream continuum should show benthic invertebrate community structure predictably changing to reflect physical and energetic differences among reaches. Many studies testing predictions of the RCC in forested North American streams have shown results generally concurrent with RCC predictions (e.g. Hawkins and Sedell, 1981; Minshall *et al*. 1983, Minshall *et al.* 1992, Grubaugh *et al*. 1996, Grubaugh *et al*. 1997). Deviations from RCC predictions may help evaluate impairment due to sedimentation along the Chattooga continuum. The RCC is an especially important conceptual framework to consider in the context of lotic freshwater conservation because it emphasizes the upstream-downstream and terrestrial linkages that characterize stream drainages.

Methods

Study region

The Chattooga River was conferred Wild and Scenic status in 1974 by Congress, under the Wild and Scenic Rivers Act of 1968 (WSRA). The Wild and Scenic designation brought a great deal of attention to the Chattooga River watershed, and there is widespread concern for the quality of its waters and scenic integrity of the area. Furthermore, the southern Appalachians harbor one of the most diverse fish assemblages in the world, with 345 species (Walsh et al. 1995). The Chattooga River watershed currently supports a high level of recreation, offering activities such as fishing, hiking and boating (especially white-water varieties). In addition to its Wild and Scenic status, the Chattooga River has the distinction of having been the setting for the film *Deliverance*. The notoriety bestowed upon the river and the surrounding forest by this classic movie helps to maintain the popularity of the watershed as a recreational destination.

The Chattooga River watershed is a 730 km^2 basin located in the southern Appalachian Mountains of western North Carolina (Macon County), northeastern Georgia (Rabun County) and northwestern South Carolina (Oconee County). The catchment lies entirely within the Blue Ridge physiographic region, and its land cover is predominantly forest (>92%). Upland forests are dominated by Virginia and shortleaf pine, and chestnut and scarlet oak. Streamside canopy is primarily eastern hemlock, yellow poplar, and white pine. Rhododendron and mountain laurel form the principle riparian understory and grow close enough to many stream channels to provide year-long shading. Basin soils are classified as highly erodible and are derived from gneiss, mica-schist, quartz and granite. Most of the watershed has been logged and agriculture and mineral mining have also occurred in some areas. Currently there are no active mines, and harvesting of trees from the area has ceased. The topography of the area is generally steep and rugged (elevations 300-1,500 meters). The watershed is mainly rural, with small pockets of agriculture and some urbanizing areas. A great number of unpaved former logging roads are found in the watershed and contribute greatly to sedimentation of catchment channels (Van Lear et al., 1995). Approximately 70 % of the watershed is publicly owned as National Forest (Chattahoochee NF, GA; Nantahala NF, NC; Sumpter NF, SC).

Study design

Four reaches along one longitudinal continuum of the Chattooga River were selected for this study (Fig. 3.1). Sites were sampled over the course of three seasons (winter, spring, summer) within one year. Three habitats were sampled at each site: depositional, riffle, and bedrock outcrop. At study site L3, bedrock outcrop habitat was not available, however large boulders that jutted out from the water column were present; because they represented a third habitat that approximated bedrock outcrop, they were sampled. Boulder outcrop differed from bedrock outcrop in that it did not support any growths of the aquatic macrophyte, *Podostemum* spp.

Sediments and other abiotic variables

Wetted width was averaged from measurements made every 20 m (average, four transects per site). At the first order stream reach, habitat distribution was assessed by dividing reaches into discrete, 5 m sections which were simultaneously observed by two investigators who described each segment proportionately using five categories: bedrock, cobble, pebble, gravel and < 2 mm. Observations were averaged between investigators and over the reach to obtain whole reach estimates for the three most prevalent habitats: bedrock outcrop, riffle, and depositional. Pebble and gravel occurred within either depositional, or riffle habitats and did not individually constitute habitats separate from bedrock outcrop, cobble riffle, or depositional. Habitat characterizations of reaches L2 – L4 were made by one observer. A tape measure was affixed at the upstream end of the study reach and allowed to float downstream so that the observer was able to walk alongside the tape and note the dominant channel substrate present at each meter mark. Characterizations were thus recorded along the length of the entire reach and averaged to obtain estimates for the dominant habitat types.

Temperature of each reach was measured every two hours over the course of one year using HOBO temperature sensor and recording devices (Onset Computer Corporation, Bourne, MA, U.S.A.). Slope was measured from riffle-top to riffle-top along study reaches using an auto-level and stadia rod.

Biotic sampling

Macroinvertebrates. Seasonal benthic macroinvertebrate samples were collected from each site from February 2001 to August 2001. Nine samples were taken from each stream reach per collection date. On each sampling date, three separate riffle, bedrock outcrop and depositional habitats were randomly located within each study reach for sampling. A Surber sampler fitted with a 250 µm mesh net was used in riffles to obtain quantitative samples (riffle rocks were hand scrubbed with a brush and sediments stirred to a depth of approximately 10 cm to dislodge any attached invertebrates). Depositional habitats were sampled using a stove-pipe corer to delineate a fixed area and a cup to remove the contents of the corer into a bucket so that they could be elutriated and collected into a 250 µm mesh net before preservation. Bedrock outcrop habitats were sampled by scraping known areas (generally 100 cm^2) into a 250 µm mesh net. All samples were preserved in their entirety in 10 % formalin. Depositional samples were elutriated (in the field) with bucket and a 250 µm mesh net before preservation.

In the laboratory, preserved samples were washed into two nested sieves (> 1mm, coarse fraction; 250 µm – 1 mm, fine fraction) that were placed over a graduated bucket to catch all (rinse) water and very fine particles. Benthic macroinvertebrates were picked out of organic matter from coarse and fine fractions with the aid of dissecting microscopes. When necessary, fine fractions were subsampled using a sample splitter (Waters, 1969) and macroinvertebrates were removed from whole subsample fractions until at least 100 individuals were found.

Invertebrates were counted, and measured to the nearest mm under dissecting microscopes. Insects, with the exception of Chironomidae (Insecta: Diptera), were identified to genus (instars too small to properly identify were taken to family-level) using insect keys (Merritt & Cummins, 1996; Wiggins, 1996). Chironomids were divided into Tanypodinae and non-Tanypodinae (a distinction that separates predatory midges, Tanypodinae, from midges belonging to other functional groups). Non-insect invertebrates were identified to order. Biomass estimates were obtained using published length-mass regression equations (Benke *et al*., 1999). Macroinvertebrate densities (no. individuals m^{-2}) and biomass were habitat weighted by multiplying found values by the proportion of each habitat present in respective study reaches and then summing products from individual habitats (Huyrn and Wallace, 1987). Invertebrates were categorized according to functional feeding groups (FFGs) based on Merritt & Cummins (1996).

Trophic variables. Coarse (> 1 mm) and fine (250 µm – 1 mm) benthic organic matter (BOM: coarse, CBOM; fine, FBOM) standing crop was quantified from samples after macroinvertebrates were removed. CBOM was further separated into moss, leaves or wood. FBOM was re-suspended in a known volume of water and subsampled with a syringe, then filtered onto pre-weighed and ashed glass fiber filters (Whatman® GF/F filters, pore size = 0.7µm, Whatman Inc., Clifton, NJ). Very fine benthic organic matter (particles < 250 µm, VFBOM) standing crop was subsampled with a syringe (re-suspended prior to collection by stirring) from the graduated bucket over which the sample had been washed (*see macroinvertebrate methods above*) and filtered onto glass fiber filters. All BOM was oven dried at 50 ºC for one week, weighed, subsampled if necessary and then ashed at 500 ºC in a muffle furnace to determine ash-free dry mass (AFDM) of each sample. Biofilm biomass was estimated by randomly collecting cobbles at five locations within each study reach per sampling date. Biofilm samples were collected into bags, placed on ice and kept frozen until processing. In the laboratory, biofilm was removed from cobbles by scrubbing them in water. A known volume was filtered onto glass fiber filters and processed following same protocol used for FBOM.

Data analyses

Distribution of all dependent and independent variables were checked for normality and transformed if necessary. Macroinvertebrate abundances were $\log_{10}(x + 1)$ transformed when necessary. All percentage data were arcsine square-root transformed prior to analyses. Average habitat-weighted values from different habitats within one reach from a given season are summed to obtain whole reach values (Huryn and Wallace, 1987). All values listed in tables and used in analyses are annual averages, unless otherwise noted. Simple linear regression was used to examine relationships between macroinvertebrate assemblage attributes and catchment sizes. All regressions were made using SigmaStat for Windows, Version 3.1, Copyright 2004 SPSS Inc.

Results

Physical variables. Physical differences among study reaches are summarized in Table 3.1. Drainage areas ranged between 259 and 34,213 ha. L2 was the steepest channel and L4 the least steep. Average width ranged between 5.58 and 56.1 m. In-stream temperatures were highest at L4 and lowest at L1. Depositional habitat was most prevalent at L3. Cobble riffles made up most of the channel area at L2. Bedrock outcrop habitat was highest at L1.

Benthic organic matter and biofilm standing crops. Total benthic organic matter (BOM) standing crop decreased between continuum endpoints (Table 3.5). This pattern held for both coarse

(CBOM) and fine (FBOM) organic matter fractions. However, VBOM is much lower at L2 than any other study reach (Table 3.5). BOM standing crop was positively related to invertebrate biomass in depositional habitats across sites (n = 54; $r^2 = 0.20$, $p < 0.001$) as well as to invertebrate abundances in bedrock outcrop habitats across sites (n = 54; $r^2 = 0.40$, $p < 0.001$). Biofilm standing crop increased between L1 and L3 and decreased between L3 and L4 (Table 3.5).

Taxonomic composition. Over the course of one year, a total of 115 taxa were collected from the four study sites, mean taxonomic richness per site ranged from 38 to 72 (Table 3.2). Richness was greatest at the smallest study reach, Addie Creek (L1). Cobble riffle habitats supported greater taxonomic richness than did bedrock outcrop and depositional habitats at every sampling station. Taxonomic richness was lowest on bedrock outcrops at each site. There is a trend towards declining richness in cobble riffles along the continuum.

Shannon diversity index was highest at L1 and lower downstream (Table 3.2). Riffle habitats supported the highest diversity at all sites except L1, where bedrock outcrop habitat diversity was higher. Riffle diversity remained consistent among all sites, whereas diversity of bedrock outcrop and depositional communities declined between L1 and the other reaches.

Abundance. Annual habitat-weighted total abundance declined as catchment size increased, although the trend was not statistically significant (Table 3.3). Bedrock outcrop habitats at all sites except L3 supported slightly higher densities of invertebrates than did depositional habitats; abundances were lowest in cobble riffles, except at L3. Abundances were greatest at L1 in all habitats (Table 3.3). Densities in cobble riffles remained fairly consistent among sites, whereas densities in bedrock outcrops and depositional habitats declined between L1 and the other study reaches. Depositional and riffle abundances were lowest at L2 and bedrock outcrop density was lowest at L3.

No statistically significant longitudinal trends were found between macroinvertebrate density and catchment size. Scraper, shredder, gatherer and predator densities declined between L1 and downstream reaches. Filterer abundance exhibited no general trend. Gatherers were the most abundant functional group at all sites (Table 3.3). Percent abundance of shredders and predators to total abundance decreased downstream (Table 3.3). Percent abundance of other functional groups exhibited no trend.

Biomass. Although abundance was lower in downstream sites, reach-scale macroinvertebrate biomass was not. Biomass decreased from L1 to L2, did not differ between L2 and L3, and increased from L3 to L4 (Table 3.4). In general, bedrock outcrop habitats supported the greatest biomass; however, depositional biomass was greater than bedrock outcrop biomass at L1 (Table 3.4). Patterns in mean macroinvertebrate biomass for individual habitat types were roughly similar to those of macroinvertebrate abundance. Biomass on bedrock outcrops did not differ between L1 and L4 and was significantly lower at L2 and L3. Biomass decreased downstream in depositional habitats, and remained somewhat consistent in riffle habitats (Table 3.4).

No functional group was consistently highest in biomass across study sites (Table 3.4). Biomass of scrapers, shredders, gatherers, and predators declined downstream, whereas filterer biomass increased. L3 had the lowest biomass values for all groups except gatherers (Table 3.4).

Relative biomass of scrapers and peaked at L2 before declining further downstream (Table 3.4). Relative biomass of gatherers did not change between continuum endpoints, but was highest at L3 (Table 3.4). Relative biomass of filterers increased downstream, whereas relative biomass of predators declined downstream and was negatively related to catchment size (r^2 = 0.97, p = 0.02, n = 12).

Habitat-specific relative biomass. A negative significant relationship was found between percent shredder biomass and catchment area in bedrock outcrop habitat (r^2 = 0.94, p = 0.04; Fig. 3.2). Percent biomass of filterers was positively related to catchment area in bedrock outcrop habitat (r^2 = 0.92, p = 0.04; Fig. 3.2). Otherwise, percent functional group biomass was not related to catchment size within habitats. Non-metric multidimensional scaling (NMS) placed samples into macroinvertebrate assemblage space along three axes (stress = 17.67). The three axes together explained 57 % of variation in the data (axis 1 r^2 = 0.21; axis 2 r^2 = 0.23; axis 3 r^2 = 0.13). Samples grouped according to habitat, with some overlap between cobble riffle and bedrock outcrop samples (Fig. 3.3). Velocity was significantly related to axis 1 (r = 0.74, $p < 0.05$). Coarse benthic organic matter (CBOM) was significantly related to axis 2 (r = - 0.48, $p < 0.05$). Fine benthic organic matter (FBOM) was significantly related to axis 2 (r = - 0.50, $p < 0.05$).

Discussion

Results from this study support the RCC tenet that the functional characteristics of stream macroinvertebrate communities reflect the mean conditions of their respective channels according to their positions along a longitudinal continuum, and in general, macroinvertebrate community structure of sequential continuum reaches can be anticipated based on equally predictable physical changes along the longitudinal continuum (Vannote *et al*., 1980). However, not all predictions of the RCC were met, and localized patterns in geomorphology had a strong influence on reach-scale community structure along the Chattooga River continuum.

The RCC predicts that taxonomic richness should increase with stream size until a maximum is reached in mid-sized streams, after which taxonomic richness should again decline (Vannote *et al*., 1980; Minshall *et al*. 1983; Minshall *et al*. 1985*b*). Contrary to expectations, macroinvertebrate taxonomic richness along the study continuum was highest in the smallest site (L1, Table 2), a first order stream reach according to a 1:24 000 scale map. However, when mean wetted width, catchment area and daily average temperature are compared to study sites along another southern Appalachian stream continuum, L1 is more similar to second and fourth order reaches (Grubaugh *et al*., 1996; Grubaugh *et al*., 1997). Therefore, even though L1 is a first order stream on a 1:24000 scale map, it is not the true beginning of the longitudinal continuum; macroinvertebrate taxonomic richness is likely lower in reaches upstream of L1. Hansen (2001) estimated that 1:24 000 scale topographic maps of the Chattooga River watershed show only 21% of the entire stream network (ephemeral, intermittent and perennial channels), so tributaries upstream of L1 are not indicated on maps of that scale. Taxonomic richness at the lower study stations of the Chattooga River continuum are low compared to values reported by Grubaugh *et al*. (1996) for catchments of similar size along the Little Tennessee River continuum. Differences in downstream community richness between the two continua are likely due to differences in amounts of aquatic macrophytes present within riffle habitats. At L3 and L4, some cobbles within riffle habitats supported growth of the macrophyte, *Podostemum* spp.; however, the plant growth was sparse and could not be described as substantially covering any riffle substrates. A sizeable proportion of riffles within downstream reaches of the Little Tennessee continuum were composed of cobble covered by *Podostemum ceratophyllum* (Grubaugh *et al.* 1996). The plant-covered cobble creates a more heterogeneous riffle habitat and the higher taxonomic richness within the Little Tennessee can be at least partially attributed to this additional environmental complexity (Minshall *et al*., 1985*b*; Heino *et al*., 2003, Hutchens *et al*., 2004).

Predictions of the RCC relating to macroinvertebrate community structure were expressed in terms of the relative dominance of individual functional groups, and those authors anticipated that measurements of relative dominance would be derived from biomass estimates (Vannote *et al*., 1980). Many subsequent studies, however, have compared patterns in macroinvertebrate community structures based on abundance data along river continua to predictions of the RCC. Although Grubaugh *et al*. (1996) observed that using abundance data to test predictions of the RCC is inappropriate and could be misleading, it is still useful to draw comparisons among studies when possible. Patterns of benthic macroinvertebrate abundance along the Chattooga River continuum largely conformed to results from previous studies within North America. In four different states, grazers did not exhibit a pattern predicted by the RCC; shredders decreased in percent abundance in the downstream direction; collectors increased in relative contribution downstream; and percent abundance of predators was inconsistent amongst longitudinal sites (Minshall *et al*. 1983). Collectors along these four continua were the most abundant functional group. Grazers were next in abundance, except in the headwater streams, where shredders were more abundant than grazers. The results from the Chattooga River continuum echo these generalized results, diverging only in the predator functional group, which clearly decreases in abundance and percent abundance along the Chattooga River continuum. Similar patterns of percent abundances of benthic macroinvertebrate functional groups were found along the Little Tennessee River continuum (Grubaugh *et al*. 1996). No significant correlations exist between macroinvertebrate abundances or percent abundances and catchment size in this study.

In general, reach-scale habitat-weighted biomass was lower in larger catchments (Table 3.4). This trend conflicts with the pattern observed along the Little Tennessee continuum where total biomass increased dramatically downstream (Grubaugh *et al*. 1996). The high downstream biomass values underpinned many of the significant correlations found between functional group biomass and catchment size in the Little Tennessee (Grubaugh *et al*., 1996). Downstream growth of *Podostemum ceratophyllum* in the Little Tennessee was likely responsible for the high macroinvertebrate biomass found there. In contrast, macroinvertebrate biomass did not increase greatly in downstream reaches of the Chattooga River continuum, where *Podostemum* spp. is much less prevalent than in the Little Tennessee. Similarly, macroinvertebrate abundance and biomass was lowest in boulder/bedrock outcrop habitat of L3, which was the only site where bedrock/boulder outcrops did not support *Podostemum* spp. A strong negative relationship was found between percent biomass of predators and increasing catchment size ($r^2 = 0.92$, $p = 0.02$). This trend, also reported by Grubaugh *et al*. (1996), may simply be an artifact of functional group categorization, which does not account for the predatory nature of important downstream invertebrates (e.g. members of the trichopteran family, Hydropsychidae) which capitalize on animal tissue, but are categorized as filterers. Hence, predator biomass may not have declined as much as indicated.

Biomass and percent biomass of gatherers along the Chattooga River continuum also follow the pattern reported for gatherers from the Little Tennessee River continuum (Grubaugh *et al*., 1996). Benthic organic matter standing crops in depositional habitats may influence biomass of gatherer invertebrates, which was related to BOM standing crop in depositional habitats ($r^2 = 0.20$, $p < 0.001$).

Examination of benthic macroinvertebrate community dynamics within different habitat types revealed two things: (1) local geomorphology exerted a strong influence on the structure of macroinvertebrate communities in the Chattooga continuum, as samples clustered according to habitat type when analyzed with NMS (Fig. 3.3); (2) patterns in assemblage structure along the continuum followed trends in assemblage structure in bedrock outcrops and riffles (based on annual means of percent biomass) (Fig. 3.2). This implies that patterns of macroinvertebrate community structure along a gradient are dependent upon distribution of habitat along the gradient.

The importance of substrata to reach-scale macroinvertebrate community structure can be demonstrated by comparing habitat distributions and reach-scale habitat-weighted macroinvertebrate community structure in the Chattooga and Little Tennessee rivers (Grubaugh *et al*., 1996 & 1997). Sites for comparison were chosen based on similarity in catchment size (Tables 3.1, 3.6). An additional comparison is drawn between the most downstream reaches of both studies despite the disparity in size between the two catchments (Tables 3.1, 3.6).

Reach-scale, habitat-weighted estimates of biomass reflect the relative proportions of each habitat type within the stream reach as well as the amount of macroinvertebrate biomass supported by each habitat. When Chattooga River benthic macroinvertebrate data are habitat-weighted according to Little Tennessee River habitat distributions (for each site respectively), differences in total community biomass and functional groups between rivers result when (1) habitat distributions are substantially different between the two different reaches; or (2) habitats support different macroinvertebrate assemblages. For example, only slight differences result when biomass for site Chattooga L1 is habitat-weighted according to Little Tennessee S-3 substrate distributions (Fig. 3.4 *a – f*, leftmost comparison on each graph) because the distribution is similar between the two sites (Fig. 3.5 *a – c*).

When habitat-weighted biomass was calculated for Chattooga L4 according to habitat distributions of both Chattooga L4 and Little Tennessee R-1, differences in biomass estimates show the influence of bedrock outcrop habitat on community structure (Fig. 3.4 *d*, third comparison from left). There is a lack of bedrock outcrop habitat at Little Tennessee R-1 (Fig. 3.5 *a - c*), and because of this, filterer biomass and total biomass are reduced (Fig. 3.4 *d*, third comparison from left and Fig. 3.4 *a*, third comparison from left). Biomass at Chattooga L4 is often higher than it is at Little Tennessee R-1 in this comparison (Fig. 3.4 *a – f*, third comparison from left on all graphs). This is because depositional and riffle habitats supported enough shredder and predator biomass so that the increases in these habitats (at Little Tennessee R-1) more than made up for the loss of bedrock outcrop (Fig. 3.5). Depositional habitat was especially important to shredder biomass at Chattooga L4, and this is reflected by the increased shredder biomass at the Little Tennessee R-1 comparison, where depositional habitat was more available (Fig. 3.4 *f*, third comparison from right and Fig. 3.5 *a*).

When Little Tennessee macroinvertebrate data collected downstream of S-3 was used with habitat distributions from both Chattooga and Little Tennessee sites, Little Tennessee biomass was invariably higher (Fig. 3.6 *a- f*). These differences are a result of less riffle and depositional habitats in the Little Tennessee. Comparison between Little Tennessee R-3 and Chattooga L4 illustrates the effects of less bedrock outcrop habitat, but similar depositional habitat (Fig. 3.5 *a – c*). Lowered biomass is a result of the importance of bedrock outcrop at the Little Tennessee R-3 site to all but shredder functional groups. Depositional habitat was important to shredder biomass in the Little Tennessee R-3 reach and this was reflected in the relatively small change in biomass (Fig. 3.6. *f*, rightmost comparison).

Sediment distribution within channels is an important factor that regulates benthic macroinvertebrate distribution (Cummins and Lauff, 1968; Hynes, 1970; Allan, 1975; Minshall, 1984; Waters, 1984). Differences in bed sediments have been related to differences in benthic macroinvertebrate taxonomic and functional composition within habitats (Tebo, 1955; Gurtz and Wallace, 1984; Huryn and Wallace, 1987; Lugthart and Wallace, 1992; Wallace *et al*., 1995; Zweig and Rabeni, 2001; Roy *et al*., 2003). Although the RCC has proven useful as a general ecosystem model, deviations from the predicted nature of stream networks along longitudinal continua must be expected due to regional variations in climate and geology and local variations in network structure, geomorphology and canopy cover (Minshall *et al*., 1983; Naiman *et al*., 1987; Montgomery, 1999; Brussock and Brown, 1991). Results from this study reinforce this qualification of the RCC and underscore the importance of local geomorphology to reach-scale community structure.

Mesoscale invertebrate communities occurring in geomorphically discrete habitats (i.e. riffles, bedrock outcrops, and depositional areas) exhibit unique structural patterns. These structural patterns are suited to exploit distinct, site-specific physical characteristics. Reach-level communities are composites of these mesoscale communities (Huryn and Wallace 1987). Bedrock outcrop and cobble riffle contributions to reach-scale communities of the Chattooga continuum were largely responsible for driving the patterns in macroinvertebrate community functional structure that conformed to predictions made by the RCC. Depositional communities tended to be dominated by gatherers at all sites. This observation has important management implications, especially in regard to the issue of sedimentation, because it allows one to predict the effects of increased fine sediment deposition to these stream channels.

Dramatic sedimentation due to catchment logging has been observed to accumulate first within channel features lowest in gradient: sandy-gravel areas > pebble riffles > cobble riffles > bedrock outcrops (Gurtz and Wallace, 1984). Sandy gravel areas and pebble riffles are less frequently found than cobble riffles, bedrock outcrops or depositional areas within many reaches of the Chattooga. It is evident that fine sediment deposition has already covered many of these channel features. Continued deposition of fine sediments within Chattooga channels could eventually simplify the heterogeneous nature of cobble riffle habitats and increase the extent of depositional habitat (i.e. cover riffle habitat entirely). If this were to happen, reach-scale community structure would change and become more similar to that of depositional habitats. If severe enough, sedimentation could dramatically change the structure and functional attributes of reach-scale benthic macroinvertebrate communities through habitat simplification. It is unlikely that bedrock outcrops would ever be smothered by fine sediments; however, these areas could be affected by scour, and the entrainment of inorganic particles in excessive quantities could interfere with filter-feeding or respiration of macroinvertebrates.

Benthic macroinvertebrates sampled along a longitudinal continuum of the Chattooga River conform to expectations of a naturally functioning corridor. However, these results also reinforce the the USEPA (1999) conclusion that elevated levels of fine sediments pose a threat to the sustained integrity of many stream segments within the Chattooga basin. Because stream segments exist within a network, there is connectivity between upstream and downstream reaches. Sediments generated in the headwaters will eventually be transported to downstream reaches. Therefore, these downstream reaches cannot be protected unless upstream reaches are also protected. Although the Chattooga and the West Fork Chattooga Rivers are protected under the WSRA 1968, the restriction of certain land use activities only extends along the main river corridors and up to one-quarter mile on each side of the rivers. Headwaters of the Chattooga River and West Fork Chattooga River must be considered as part of these Wild and Scenic Rivers and should be similarly protected so that these systems can retain their “Wild” status. Natural ecological function is implicit in the *wild* designation. Without preservation of the overall river network, the Wild and Scenic Chattooga and Wild and Scenic West Fork Chattooga Rivers are at risk of becoming neither Scenic nor Wild.

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Table 3.1. Physical parameters of sampling reaches along study continuum.

	Drainage area (ha)	Slope (%)	Average width (m)	Average temperature (ºC)	Bedrock outcrop (%)	Boulder outcrop (%)	Cobble riffle (%)	Depositional (%)
Addie Creek (L-1)	259	2.96	5.58	10.5	43	-	37	20
West Fork Creek (L-2)	12 533	3.23	22.93	11.2	35	-	47	18
Chattooga River at Low Water Bridge (L-3)	32 688	0.00	34.70	-	-	26	34	40
Chattooga River at Earl’s Ford (L-4)	34 213	0.75	56.1	17.7	27	-	44	29

Table 3.2. Macroinvertebrate taxonomic richness and diversity scores (*H*, Shannon diversity index). All values are annual averages: for habitat types, *n* = 9 and for sampling stations, *n* = 3.

	L-1	L-2	L-3	L-4
Taxonomic richness by habitat type (average)				
Bedrock outcrop	56	34	8	28
Cobble riffle	81	55	49	45
Depositional areas	61	36	23	30
Average annual taxonomic richness by sampling station	72	45	38	38
Annual average diversity by sampling station	2.50	1.90	1.57	1.94
Diversity by habitat type				
Bedrock outcrop	2.67	1.95	1.37	2.13
Cobble riffle	2.62	2.45	2.55	2.55
Depositional areas	2.21	1.29	0.80	1.51

Table 3.3. Average annual abundances for habitat assemblages ($n = 9$), sampling stations ($n = 3$), and functional groups ($n = 3$). Values in four left columns are annual averages (no. m^{-2}) values in four right columns are percentage values. Habitat-specific values are not habitat-weighted. Results of ANOVA for abundance within habitats along continuum, by sampling station and by functional group and % functional group shown. Values not sharing common letters are significantly different, $p < 0.001$.

	Abundance (individuals m^{-2})				Percent			
	L-1	L-2	L-3	L-4	L-1	L-2	L-3	L-4
By habitat type								
Bedrock outcrop/boulder outcrop	44 981^{a}	23 005^{b}	411^{c}	21 187^{b}	-	-	-	-
Cobble riffle	11 286^{a}	8 765^{b}	9 682^{b}	9 922^{b}	-	-	-	-
Depositional areas	37 139^{a}	15 326^{b}	17 593^{b}	23 428^{ab}	-	-	-	-
By sampling station (habitat-weighted)	30 945^{a}	14 930^{b}	10 612^{c}	16 914^{b}	-	-	-	-
By functional group (habitat-weighted)								
Filterers	1 608^{a}	2 144^{b}	499^{c}	2 037^{b}	5^{a}	14^{b}	5^{a}	12^{b}
Gatherers	19 111^{a}	9 702^{b}	8 451^{b}	11 789^{b}	62^{a}	65^{a}	80^{a}	70^{a}
Predators	3 136^{a}	1 152^{b}	761^{ab}	1 056^{b}	10^{a}	8^{a}	7^{ab}	6^{b}
Scrapers	4 358^{a}	1 784^{b}	791^{c}	1 879^{b}	14^{a}	12^{a}	8^{b}	11^{a}
Shredders	2 299^{a}	89^{b}	9^{c}	7^{c}	7^{a}	1^{b}	0.1^{c}	0.04^{c}

Table 3.4. Average annual biomass (mg AFDM m^{-2}) for habitat assemblages ($n = 9$), sampling stations ($n = 3$), and functional groups ($n = 3$). Values in four left columns are annual averages (no. m^{-2}) values in four right columns are percentage values. Habitat-specific values are not habitat-weighted. Results of ANOVA for biomass within habitats along continuum, by sampling station and by functional group and % functional group shown. Values not sharing common letters are significantly different, $p < 0.001$.

	Biomass (mg AFDM m^{-2})				Percent			
	L-1	L-2	L-3	L-4	L-1	L-2	L-3	L-4
By habitat type								
Bedrock outcrop/boulder outcrop	1 068^{a}	662^{b}	11^{c}	1 330^{a}	-	-	-	-
Cobble riffle	469^{a}	461^{a}	298^{b}	482^{a}	-	-	-	-
Depositional areas	1 570^{a}	178^{b}	533^{c}	218^{b}	-	-	-	-
By sampling station (habitat-weighted)	947^{a}	481^{b}	323^{b}	638^{c}	-	-	-	-
By functional group (habitat-weighted)								
Filterers	97^{a}	84^{a}	51^{a}	290^{b}	10^{a}	18^{a}	16^{a}	46^{b}
Gatherers	349^{a}	99^{b}	193^{ab}	162^{ab}	37^{a}	21^{a}	60^{b}	25^{a}
Predators	247^{a}	103^{b}	40^{c}	58^{c}	26^{a}	21^{a}	12^{b}	9^{b}
Scrapers	181^{a}	147^{a}	33^{b}	93^{c}	19^{a}	31^{b}	10^{a}	15^{a}
Shredders	63^{a}	43^{a}	2^{b}	27^{c}	7^{a}	9^{a}	1^{b}	4^{b}

Table 3.5. Longitudinal trends in benthic organic matter standing crop (BOM: > 1 mm = coarse fraction, CBOM; < 1 mm > 250 µm = fine fraction, FBOM; < 250 µm = very fine fraction, VFBOM), all values are habitat-weighted and averaged across all seasons (*n* = 3). Results of ANOVA shown. Values not sharing common letters are significantly different, $p < 0.001$

	BOM (g m^{-2})	CBOM (g m^{-2})	FBOM (g m^{-2})	VFBOM (g m^{-2})	Periphyton (mg cm^{-2})
Addie Creek (L-1)	50.48^{a}	37.21^{a}	8.7^{a}	4.57^{a}	4.48^{a}
West Fork Creek (L-2)	67.27^{a}	49.97^{a}	16.91^{b}	0.39^{b}	7.71^{ab}
Chattooga River at Low Water Bridge (L-3)	45.63^{a}	34.83^{a}	7.79^{a}	3.01^{a}	13.37^{b}
Chattooga River at Earl’s Ford (L-4)	23.17^{b}	16.95^{b}	2.91^{c}	3.31^{a}	5.43^{a}

Table 3.6. Catchment sizes for Ball Creek – Coweeta Creek – Little Tennessee River continuum study sites being compared to Chattooga River continuum sites.

Site	Drainage Area (ha)
S-3	119
R-1	36 260
R-3	112 900
L1	259
L3	32 688
L4	34 213

Figure 3.1. Map of study sites. Numbers correspond to position along continuum, 1 is most upstream study reach and 4 is most downstream reach.

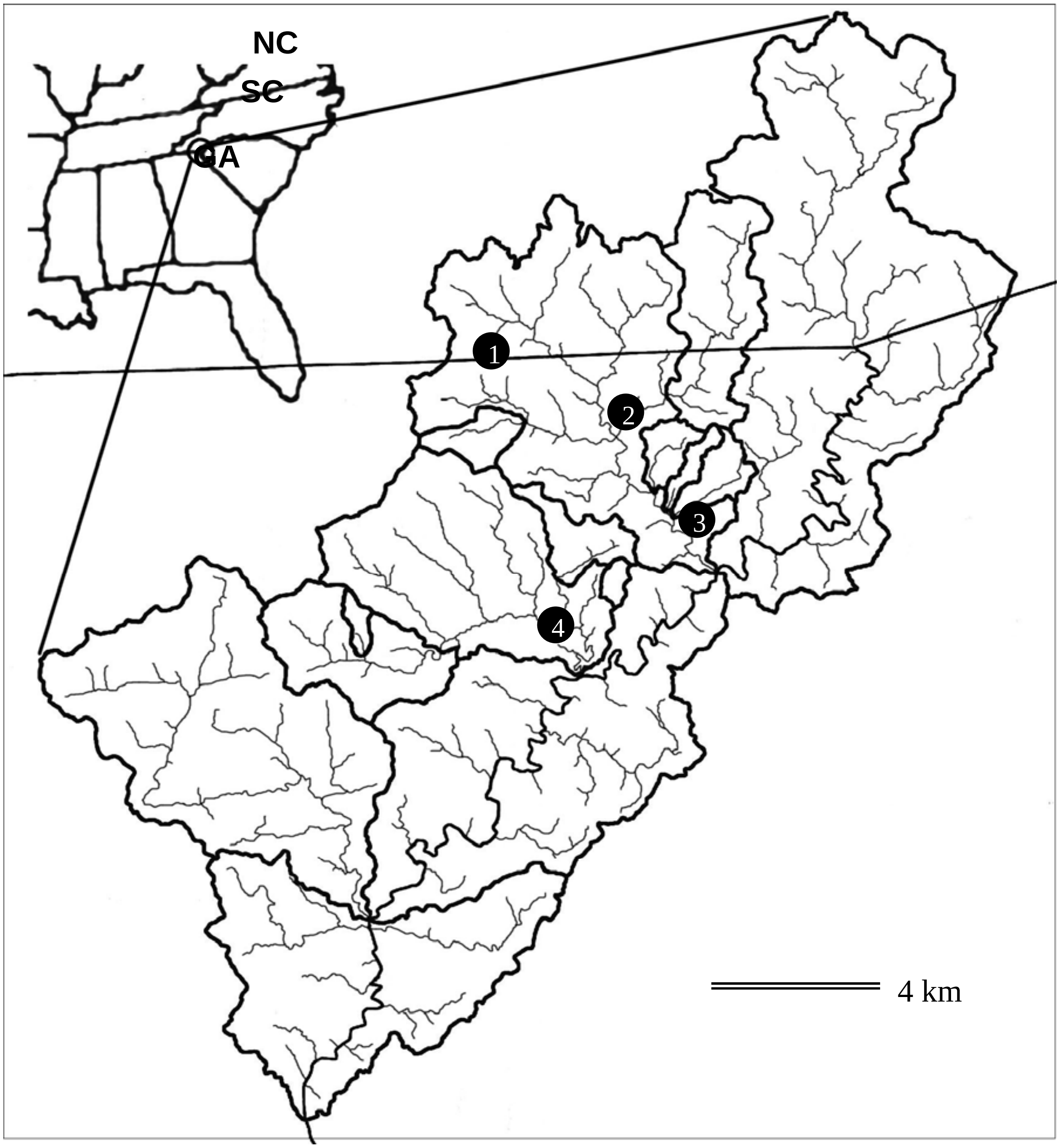
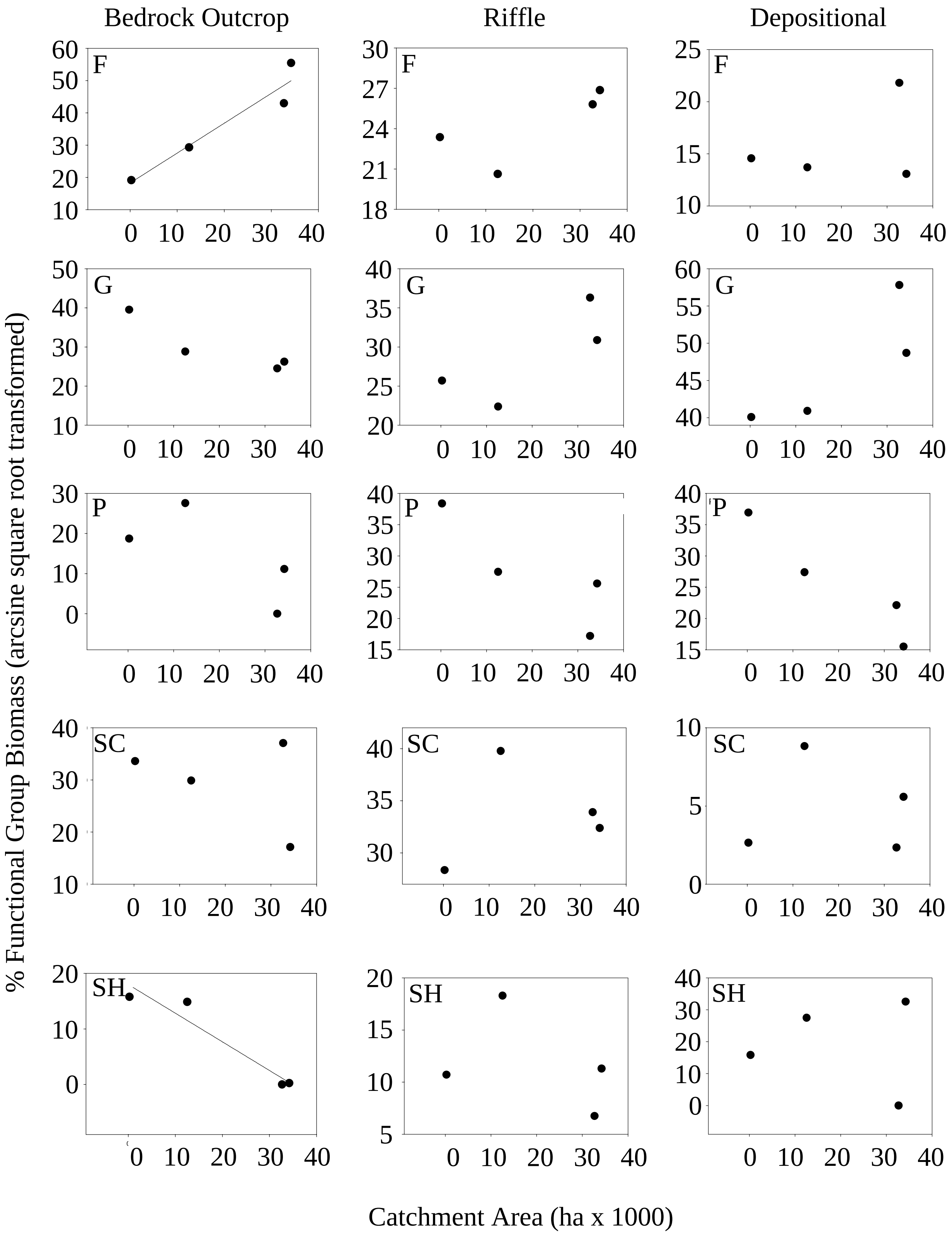

NC
SC
GA
1
2
3
4
4 km

Figure 3.2. Annual mean relative contributions of functional groups to community structure within individual habitats. F = filterers; G = gatherers; P = predators; SC = scrapers and; SH = shredders. For relationship between mean fitlerer % biomass and catchment area in bedrock outcrop habitats: $r^2 = 0.92$; $p = 0.04$; $y = 0.0009x + 18.275$. For relationship between mean shredder % biomass in bedrock outcrop habitats: $r^2 = .93$; $p = 0.04$; $y = -0.0005x + 17.984$.



Bedrock Outcrop
Riffle
Depositional
F
G
P
SC
SH
60
50
40
30
20
10
0
5
15
18
21
24
25
27
35
45
55
0 10 20 30 40
% Functional Group Biomass (arcsine square root transformed)
Catchment Area (ha x 1000)

Figure 3.3. Non-metric multidimensional scaling (NMS) ordination of samples in macroinvertebrate assemblage space. Only first two (of three) axes shown. Velocity was significantly related to axis 1 ($r = 0.74$, $p < 0.05$). Coarse benthic organic matter (CBOM) was significantly related to axis 2 ($r = - 0.48$, $p < 0.05$). Fine benthic organic matter (FBOM) was significantly related to axis 2 ($r = - 0.50$, $p < 0.05$).

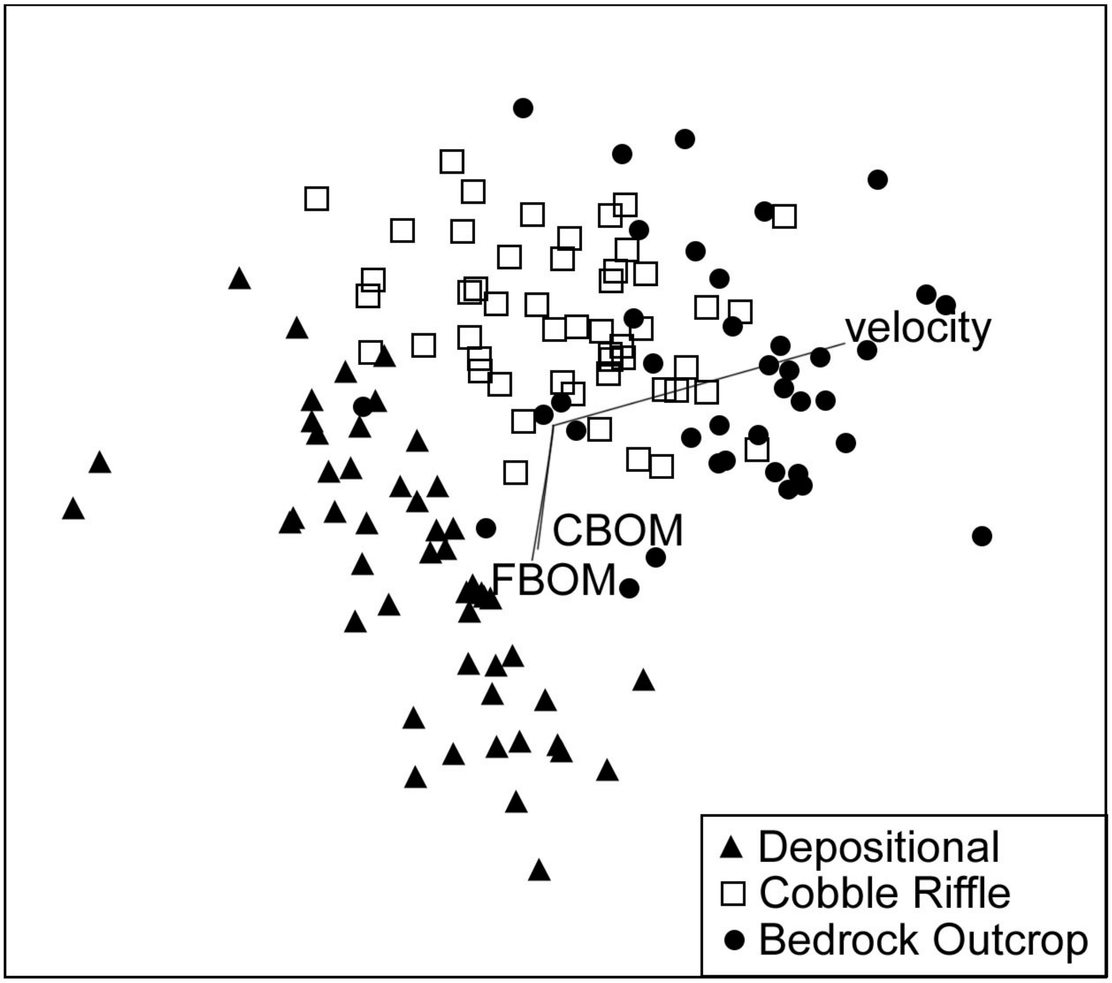

velocity
CBOM
FBOM
▲ Depositional
☐ Cobble Riffle
● Bedrock Outcrop

Figure 3.4. Biomass values on Y-axis (mg AFDM m^{-2} x 100). Chattooga River continuum benthic macroinvertebrate habitat data weighted according to distributions of bedrock outcrop, depositional and riffle habitats within the Chattooga River continuum (left, black column of each comparison) and the Little Tennessee River continuum (right, grey column of each comparison). Bars represent standard error.

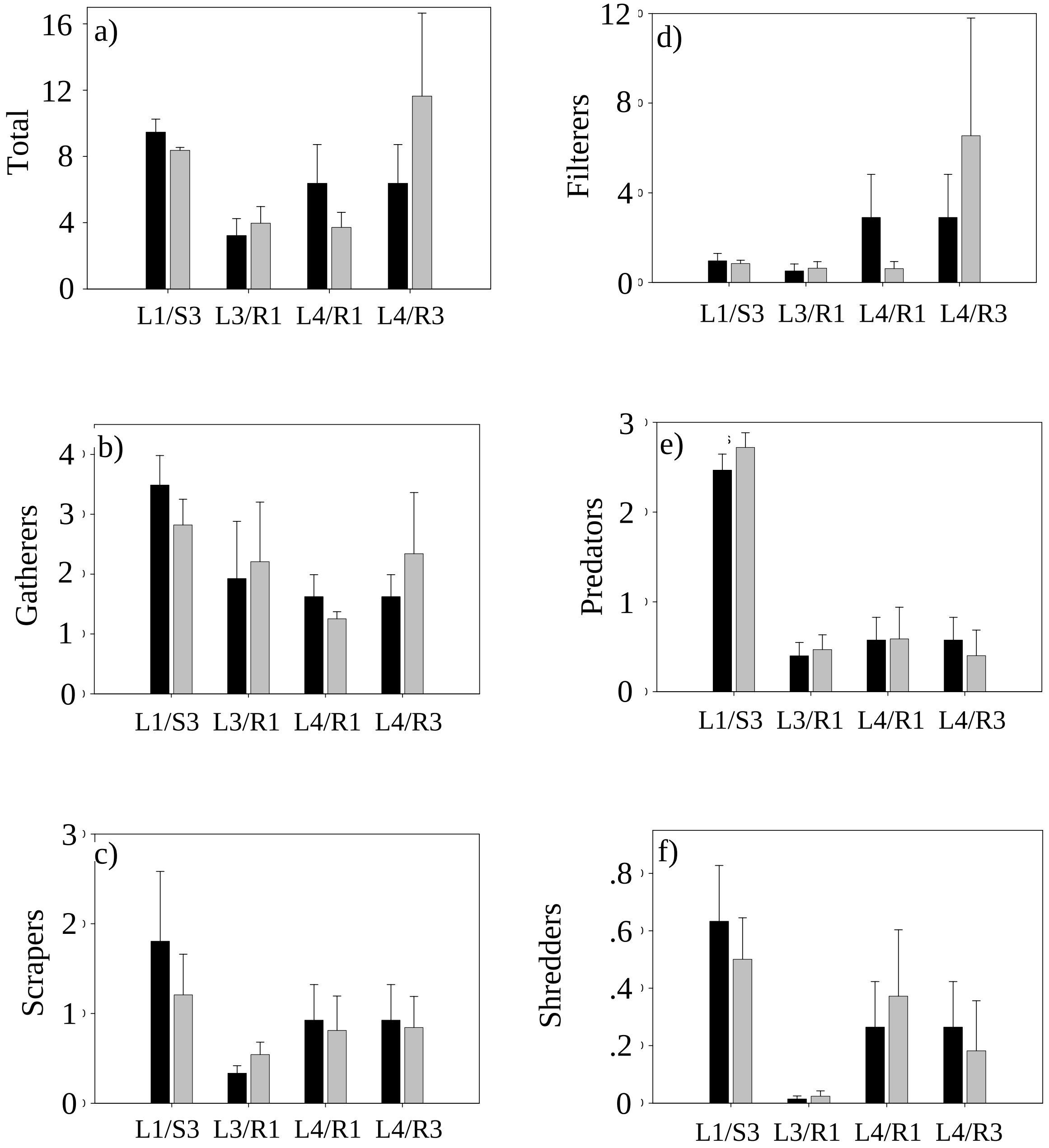

a)
Total
0
4
8
12
16
L1/S3
L3/R1
L4/R1
L4/R3
b)
Gatherers
0
1
2
3
4
L1/S3
L3/R1
L4/R1
L4/R3
c)
Scrapers
0
1
2
3
L1/S3
L3/R1
L4/R1
L4/R3
d)
Filterers
0
4
8
12
L1/S3
L3/R1
L4/R1
L4/R3
e)
Predators
0
1
2
3
L1/S3
L3/R1
L4/R1
L4/R3
f)
Shredders
0
.2
.4
.6
.8
L1/S3
L3/R1
L4/R1
L4/R3

Figure 3.5. A comparison of habitat distributions between the Chattooga and Little Tennessee River continua. Chattooga proportions are shown on the left side of each comparison, in black and Little Tennessee proportions are shown on the right side of each comparison, in grey.

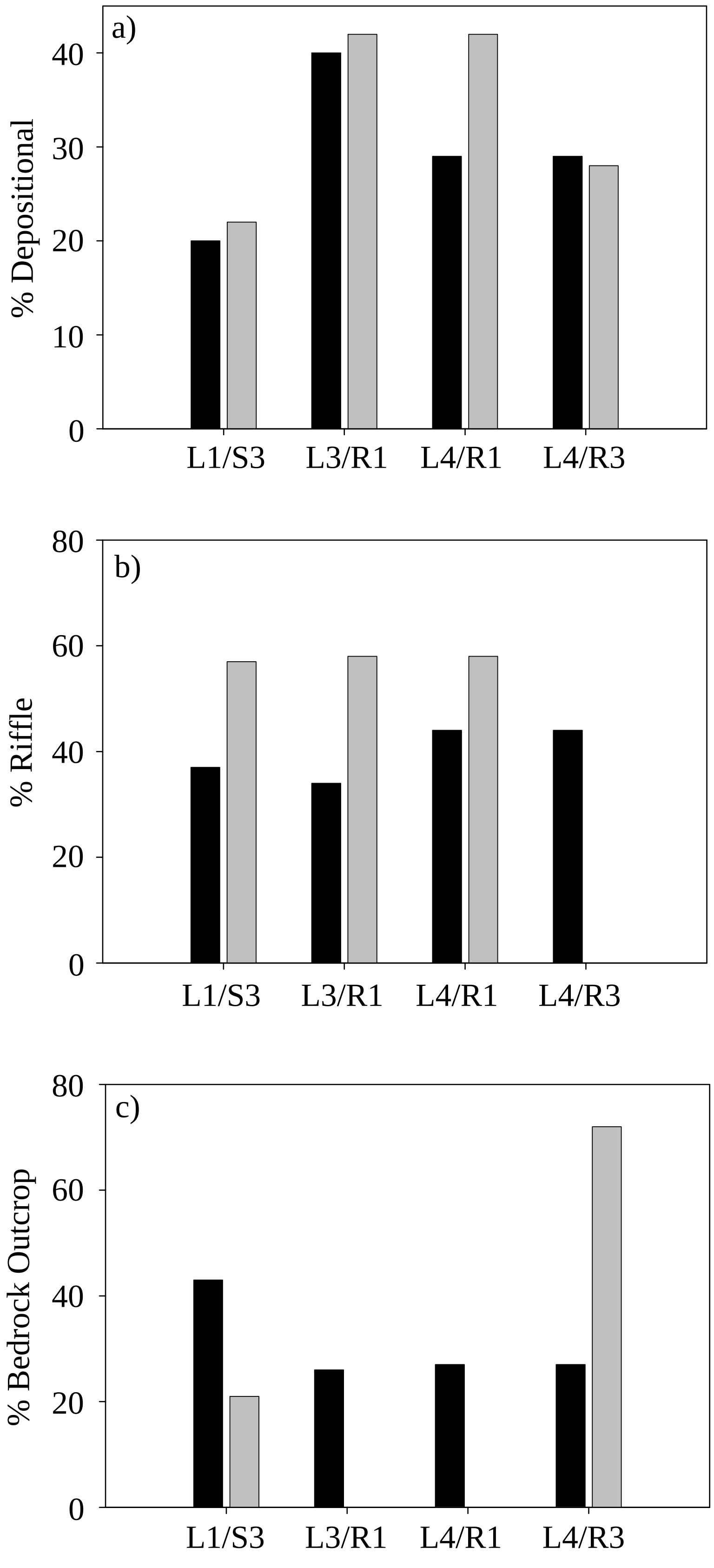
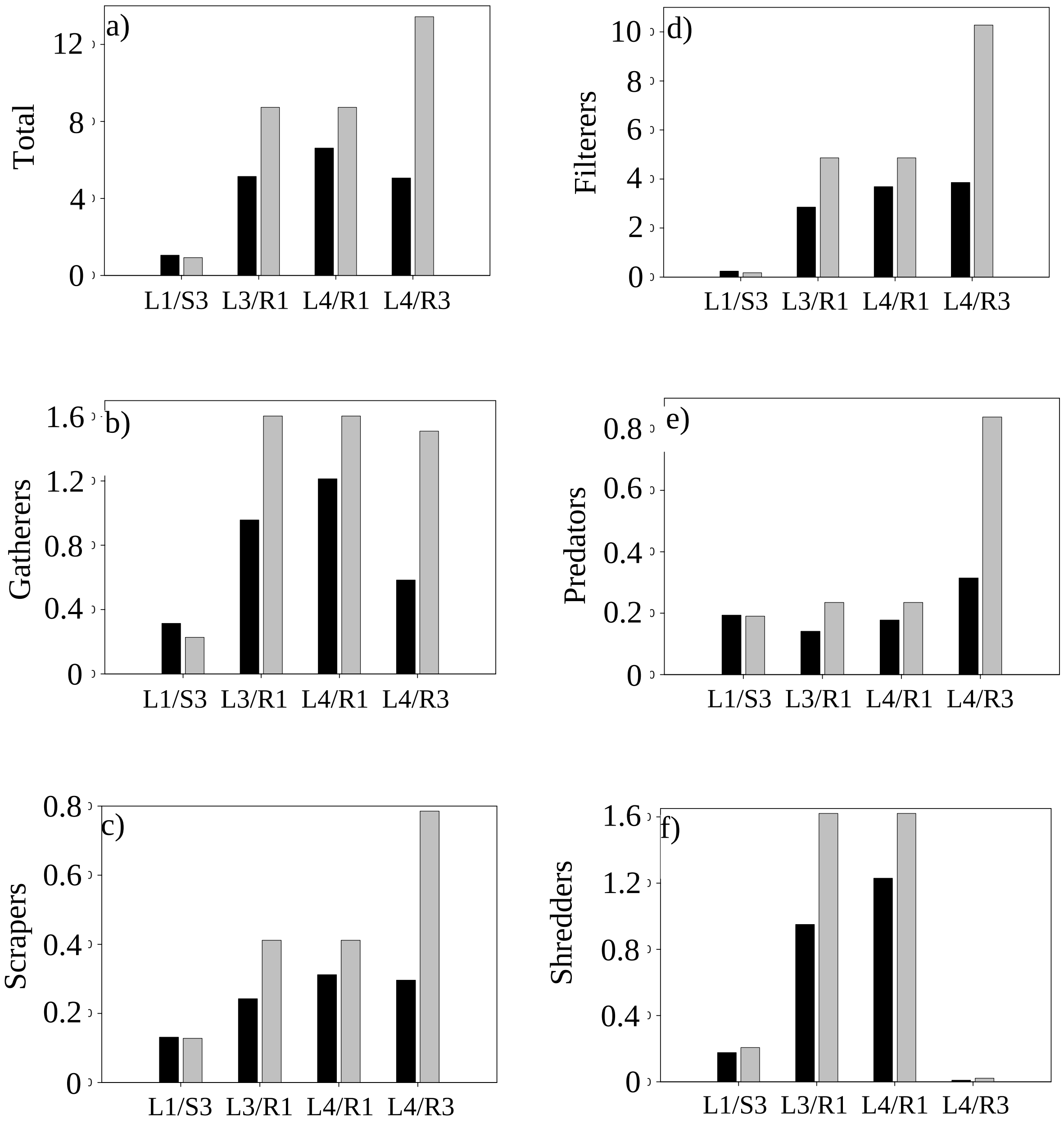

a)
% Depositional
0
10
20
30
40
L1/S3
L3/R1
L4/R1
L4/R3
b)
% Riffle
0
20
40
60
80
L1/S3
L3/R1
L4/R1
L4/R3
c)
% Bedrock Outcrop
0
20
40
60
80
L1/S3
L3/R1
L4/R1
L4/R3

Figure 3.6. Biomass values on Y-axis (mg AFDM m^{-2} x 1000). Little Tennessee River continuum benthic macroinvertebrate data habitat-weighted according to distributions of bedrock outcrop, depositional and riffle habitats within the Chattooga River continuum (left, black column of each comparison) and the Little Tennessee River continuum (right, grey column of each comparison). Limited access to data necessitated the use of annual averages and associated error could not be calculated.


a)
Total
0
4
8
12
L1/S3
L3/R1
L4/R1
L4/R3
d)
Filterers
0
2
4
6
8
10
L1/S3
L3/R1
L4/R1
L4/R3
b)
Gatherers
0
0.4
0.8
1.2
1.6
L1/S3
L3/R1
L4/R1
L4/R3
e)
Predators
0
0.2
0.4
0.6
0.8
L1/S3
L3/R1
L4/R1
L4/R3
c)
Scrapers
0
0.2
0.4
0.6
0.8
L1/S3
L3/R1
L4/R1
L4/R3
f)
Shredders
0
0.4
0.8
1.2
1.6
L1/S3
L3/R1
L4/R1
L4/R3

CHAPTER 4

EFFECTS OF FINE SEDIMENTS ON LEAF BREAKDOWN RATES IN FOUR SOUTHERN APPALACHIAN HEADWATER TRIBUTARIES OF A WILD AND SCENIC RIVER[1]

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ABSTRACT

1. Rates of leaf breakdown (red maple, *Acer rubrum* L.) were used to assess effects of deposited fine sediments (≤ 2 mm) on ecosystem function in four headwater tributaries to the Wild and Scenic Chattooga River. The four streams represent a gradient of fine deposited sediments (from 20 to 60% of study reach bed covered by fine sediments) and have been previously labeled by the United States Environmental Protection Agency as reference (1 stream) and impaired (3 streams).

2. Leaf breakdown was not related to levels of fine, deposited sediments within study streams. However, leaf breakdown was positively related to shredder biomass. The % contribution of shredding cranefly larvae *Tipula* spp. to overall shredder biomass leaf bag^{-1} was positively related to levels of fine, deposited sediments within reaches. The plecopteran, *Tallaperla* spp. dominated the shredder assemblage biomass within leaf bags of the reference stream (> 60% shredder biomass leaf bag^{-1}). At all other sites, *Tipula* spp. accounted for > 50% of shredder biomass leaf bag^{-1}.

3. Differences in shredder assemblages between reference and impaired reaches suggest that fine, deposited sediments influence leaf breakdown by preventing some taxa from exploiting coarse leaf litter. High levels of shredder biomass within leaf bags in impaired reaches were likely due to the introduction of stable sources of food to these streams. Artificially maintained food resources were important within impaired reaches because natural inputs of leaf litter were reduced—either due to deforestation and longitudinal disconnection, or because leaves were readily entrained and exported due to simplification in channel bedform.

Introduction

As active sites of deposition, retention and transformation of leaf matter, forested headwater streams are crucial components of river networks. Inputs of allochthonous organic matter to these reaches underpin complex trophic interactions (Meyer and Wallace, 2001) whose effects extend downstream (Vannote *et al*., 1980, Minshall *et al*., 1985). Various consumers depend upon particulate organic matter (POM) processed from leaves within headwater streams. The conversion of coarse leaf matter into finer organic particles (Webster *et al*., 1999) that are more easily transported allows this resource to be used by many downstream filtering and gathering consumers (Cummins and Klug, 1979). Disturbances that interrupt natural ecological function within headwater streams will likely have a detrimental effect on downstream reaches due to close associations among these network components (Meyer and Wallace, 2001).

Fine, inorganic sediments are ubiquitous pollutants within river systems because of landscape alterations that lead to changes in natural sedimentation regimes (Knighton, 1998). Accelerated rates of fine sedimentation result from many landscape modifications (e.g. logging, road building, agricultural practices, building construction and etc.); as much as two billion tons of fine sediments end up in stream channels per year (Berg 1979 *in* Waters, 1996). Elevated quantities of fine sediments deposited within stream channels alter characteristics of benthic habitat (Wallace *et al*., 1995) and potentially influence macroinvertebrate community structure as well as ecosystem function (Reice, 1974; Lenat *et al*., 1981; Sponseller & Benfield, 2001).

Since 1974 the Chattooga River and its West Fork have been federally protected under the Wild and Scenic Rivers Act of 1968. In the late 1990's, concern over water quality in the Chattooga River watershed led interested parties to sue the United States Envrionmental Protection Agency (USEPA) over issues relating to Total Maximum Daily Loads (TMDLs). To meet requirements set by the settlement of this lawsuit, the USEPA initiated an assessment of the waters within the Chattooga River watershed. The physical and biological data from the survey led the USEPA to conclude that many of the Chattooga River tributaries were either impaired or threatened by excessive levels of fine (≤ 2 mm), deposited sediments (USEPA 1999). Altered hydrology, in-stream erosion, and forest roads were implicated as the main sources of these sediments.

A major aim of the Wild and Scenic Rivers Act of 1968 is to preserve the natural integrity of rivers of outstanding and remarkable value. The protection afforded to designated rivers is chiefly accomplished by limiting activities on federal lands adjacent to such water bodies (to one quarter of a mile on each side of the river) and by preventing the obstruction of free flowing waters (i.e. no dam building). It is important to recognize that protecting only the main channel of these river networks will likely prove ineffective in preserving river health (*sensu* Meyer, 1997). Rather, it is important to monitor and protect all components of stream networks in order to guard river integrity.

The objective of this study was to use the process of leaf breakdown to assess the impact of fine, deposited sediments on ecosystem function in four headwater tributaries of the Chattooga River. We postulated that as levels of fine, deposited sediments increased in stream reaches, rates of leaf breakdown would decrease. We further hypothesized that fine sediments would depress leaf breakdown rates either through the direct burial of leaves, which would make the resource unavailable to shredding macroinvertebrates, or by otherwise altering macroinvertebrate habitat (e.g. infilling of larger bed sediments, decreasing current velocity) which could lead to changes in benthic macroinvertebrate community structure and taxonomic identities of the assemblages associated with leaf breakdown.

Methods

Study sites. The Chattooga River Watershed is a 730 km^2 basin located in the southern Appalachian Mountains of western North Carolina (Macon County), northeastern Georgia (Rabun County) and northwestern South Carolina (Oconee County). As one of the few remaining free-flowing, large rivers in the US, the Chattooga River and its tributary waters are an important natural resource. The area attracts many visitors, supports a large amount of recreational use and its streams serve as the headwaters of municipal drinking water sources (USEPA 1999).

The catchment lies entirely within the Blue Ridge physiographic region, and its land cover is predominantly forest (> 92%). Upland forests are dominated by Virginia and shortleaf pine, and chestnut and scarlet oak. Streamside canopy is primarily eastern hemlock, yellow poplar, and white pine. Rhododendron and mountain laurel form the principle riparian understory and grow close enough to many small stream channels to provide year-long shading. Basin soils are classified as highly erodible and are derived from gneiss, mica-schist, quartz and granite. Timber harvesting began in the 1800's and was widespread within the entire watershed by the early twentieth century. Agriculture and mineral mining has also occurred in some areas. Today, most of the watershed is second growth, although old growth does exist in some areas (particularly on steep slopes). Currently, there are no active mines, and harvesting of trees from the area has ceased. The topography of the area is generally steep (elevations 300-1,500 meters). The watershed is mainly rural, with small pockets of agriculture and urbanizing areas. A great number of unpaved logging roads dissect the watershed and contribute to sedimentation of catchment channels (Van Lear et al., 1995) and altered hydrology of the area.

Four tributaries to the Chattooga River were chosen as study streams based on designations reported by the USEPA (1999). One stream, in very good condition, was chosen as a reference site and three impaired streams were chosen as study reaches (Fig. 4.1). All study reaches are forested, except Roach 2 (Table 4.1), where the stream runs through a private garden. Roach 2 is approximately 500 m downstream of Roach 1.

Study reach characterization. The stream bed of each study reach was characterized by dividing reaches into discrete, 5m sections which were simultaneously observed by two investigators who described each segment proportionately using five categories: bedrock, cobble, pebble, gravel and ≤ 2 mm. Observations were averaged over each reach to obtain whole reach estimates for the three most prevalent habitats: bedrock outcrop, cobble riffle, and depositional. Pebble and gravel occurred within either depositional, or riffle habitats and did not individually constitute habitats separate from bedrock outcrop, cobble riffle, or depositional. Results from both investigators were averaged for final estimates. Stream bed characterization was done one time during the study period. Depositional habitat was considered to be any area of stream bed covered with fine sediments; therefore the two categories, % depositional habitat and % reach covered in fine, deposited sediments are assigned identical values. Areas considered as depositional were patches of sand and silt that were often quite deep. These areas of the stream bed were not ephemeral patches and were not flushed out during rain events that occurred over the course of the study. It should be noted, however, that the study took place during a dry year.

Temperature of each reach was measured every two hours over the course of the study using HOBO© temperature sensor and recording devices (Onset Computer Corporation, Bourne, MA, U.S.A.). HOBOS were secured so that they remained submersed within the water column.

Slope was measured along the length of study reaches in the upstream direction from riffle top to riffle top using an auto level and stadia rod. Width was measured as bankfull width every 15 m along the study reach and averaged to obtain mean value.

Litter bags. Red maple (*Acer rubrum* L.) leaves collected soon after abscission, were air-dried, and approximately 15 g (± 0.02 g) were placed into drawstring plastic mesh bags (25 x 35 cm pecan bags, Cady Industries Inc., Memphis, TN) with openings measuring 5 mm. Sites within reaches used for placement of leaf-bags were chosen according to flow conditions by the use of Statzner hemispheres (hemisphere # 6; 1.999 g cm^{-3}, 142.6 g). Flow conditions were consistent between all leaf-bag placement sites, and these areas were generally pebble-gravel runs. On December 9, 2001, thirty-six bags were placed into each stream and anchored into bed sediments (using 9 inch gutter nails) in groups of four. Five leaf bags were carried into the field and back to the laboratory in order to assess leaf material lost due to handling. Four bags were retrieved from each stream on each date of collection according to the following schedule: days 8, 22, 56, 123, 185, 225, 260, 323, and 385. At time of leaf bag retrieval, current velocity was measured directly over collected bags. Leaf bags were carefully collected into a 250 µm net before transferring to a pollination bag so that all inorganic sediments associated with each bag (those sediments within and on top of leaf bags) were simultaneously preserved. Ice was used to preserve collected materials until they could be processed in the laboratory.

Laboratory processing. Litter bag contents were emptied into nested sieves and rinsed under running water. All components of leaf bags over 250 µm were retained for further processing. Macroinvertebrates were separated from inorganic and organic materials and preserved in 10 % formalin containing phloxine B (a protein dye used to highlight macroinvertebrates and simplify removal from surrounding matter). Leaf litter ≥ 5 mm (used to measure ash-free dry mass (AFDM) remaining) was placed into paper bags and oven dried at 60 ºC to constant weight. A subsample of dried leaves from each bag was used to determine AFDM by ashing in a muffle furnace at 500 ºC (Benfield, 1996). All sediments associated with each leaf bag were oven dried at 60 ºC for one week and then weighed. After obtaining total dry weight, a subsample was removed and separated into > 2 mm and < 2 mm size fractions by sifting. Each fraction was then ashed at 500 ºC to obtain AFDM.

Macroinvertebrates. Benthic macroinvertebrates were identified to genus using insect keys (Merritt & Cummins, 1996; Wiggins, 1996). Chironomids were divided into Tanypodinae (predaceous) and non-Tanypodinae. Non-insect invertebrates were identified to order. Early instar insects were identified to family when they were too small for positive identifications to be made. All macroinvertebrates were counted and measured to the nearest mm in order to estimate biomass using published length-weight regressions (Benke *et al*., 1999). When necessary, fine fractions (≥ 250 µm) were subsampled using a sample splitter (Waters, 1969), and macroinvertebrates were removed from complete subsample fractions to a minimum of 100 individuals.

Analysis. Slopes of regression lines fitted to leaf mass loss over time were compared using analysis of covariance (ANCOVA). Least squares means student’s t-test was used to identify differences between leaf breakdown among sites. Macroinvertebrate community metrics were compared using the Kruskal-Wallis test, and pairwise comparisons were made using Dunn’s test. Relationships between leaf breakdown rates and shredder biomass were analyzed using linear regression ($\alpha = 0.05$ for statistical significance). Non-metric multidimensional scaling (NMS) was used to examine differences among leaf bag macroinvertebrate assemblages based on biomass of taxa (PC-ORD Version 4, MjM Software Design, Glenden Beach, OR, U.S.A.). Resultant ordination axes were then regressed (simple linear regression) with levels of fine, deposited sediments in study reaches to determine if sedimentation accounted for any separation of leaf bag assemblages within the ordination space.

Results

Study reach characterization

Slopes ranged from 2.0 to 3.4 % (Table 4.1). Areas of stream beds covered by fine, deposited sediments ranged between 20 and 60 %. Riffle habitat ranged between 25 and 48 % and bedrock outcrop habitat ranged from 8 to 43 %. Annual mean temperature ranged from 10.5 to 12.2 ºC and was highest in the study reach running through a private garden and old field (Roach 2; Table 4.1). Slope and fine, deposited sediments were not correlated.

Macroinvertebrates

Average leaf bag taxonomic richness ranged from 21 to 24 taxa (Fig. 4.2 *a*). Mean Ephemeroptera, Plecoptera, Trichoptera (EPT) richness ranged between 12 and 14 taxa (Fig. 4.2 *b*). Shredder richness ranged from 4 to 6 taxa, and it was significantly lower in the reference stream than in two of the impaired reaches (Kruskal-Wallis and Dunn test, $P = 0.006$; Fig. 4.2, *c*).

Total macroinvertebrate biomass averaged between 54 and 843 mg AFDM leaf bag^{-1} and was significantly higher at Roach 2, the only non-forested study reach (Kruskal-Wallis and Dunn test, *P* < 0.001; Fig. 4.2 *d*). Macroinvertebrate biomass was not related to number of days leaf bags were in streams. Mean EPT biomass ranged from 25 to 98 mg AFDM leaf bag^{-1}, and mean shredder biomass ranged from 23 to 774 mg AFDM leaf bag^{-1}. Shredder biomass was significantly higher at Roach 2 than at any other study reach (Kruskal-Wallis and Dunn test, *P* < 0.001; Fig. 4.2 *f*). There was no relation between shredder biomass and length of time leaf bags were in streams.

Shredder taxa were similar among sites, however assemblage structure differed greatly between reference and impaired study reaches (Fig. 4.3). At all impaired sites, the dipteran shredder, *Tipula* spp. dominated shredder assemblages (Fig. 4.4), whereas the plecopteran shredder, *Tallaperla* spp. accounted for 60 % of mean shredder biomass leaf bag^{-1} in the reference reach (Fig. 4.4). Contribution of Pteronarcys spp. biomass to shredder assemblage biomass was higher in reference leaf bags than in leaf bags of impaired sites.

NMS of leaf bag macroinvertebrate assemblages (based on biomass estimates) resulted in a final configuration arranged along two axes which together explained 63% of the variation in biomass of leaf bag macroinvertebrate assemblages (axis 1 $r^2 = 0.19$, axis 2 $r^2 = 0.44$; final stress = 16.02; Fig. 4.5). Symbols represent individual leaf bag assemblages, which tended to cluster based on site identity. *Tallaperla* spp. biomass is negatively related to axis 1 ($r^2 = 0.30$, $p < 0.05$) and *Tipula* spp. biomass is positively related to axis 2 ($r^2 = 0.59$, $p < 0.05$). NMS axis 1 is positively related to reach-scale levels of fine, deposited sediments ($r^2 = 0.25$, $p < 0.001$).

Leaf litter processing

Processing coefficients (*k* values) for leaf bags ranged from 0.007 to 0.03 d^{-1} (Fig. 4). Leaf breakdown rates among sites differed significantly among study reaches (*F* < 0.001; Fig. 4.6).

Leaf breakdown rates and shredder biomass were significantly related ($r^2 = 0.93$, $p = 0.03$; Fig. 4.7). Levels of fine, deposited sediments within study reaches and shredder biomass leaf bag^{-1} were not related; however, levels of fine deposited sediments within study reaches were positively related to the amounts of shredder biomass attributed to dipteran shredder, *Tipula* spp ($r^2 = 0.95$, $p = 0.025$). Fine, deposited sediments associated with individual leaf bags were not related to leaf breakdown rates.

Discussion

The breakdown of leaf material is mediated by many factors; however, the feeding activities of some benthic macroinvertebrate (shredders) are especially important to the reduction of coarse leaf materials (CPOM) to fine particles (FPOM) (Cummins and Klug, 1979; Wallace *et al*., 1982). Leaf breakdown has been observed to occur more quickly in streams where invertebrate shredder taxonomic richness and biomass is higher (Huryn *et al*., 2002); leaf processing rates may also increase with increased shredder densities (Benfield & Webster, 1985); and reductions in invertebrate shredders have resulted in significantly depressed leaf-litter processing rates (Wallace *et al*., 1986; Cuffney *et al*. 1990).

Accumulation of deposited, fine sediments may bury leaves making them unavailable to microbes and macroinvertebrates and result in slower breakdown rates (Herbst 1980, Webster and Waide 1982). Excessive deposition of fine sediments within streams may also render macroinvertebrate habitat unstable, leading to a decline in shredder density and depressed rates of leaf processing (Reice, 1974; Lenat *et al*., 1981). Furthermore, in southern Appalachian streams leaf breakdown rate and shredder density and biomass are positively related to mean substrate particle size at site of leaf bag placement (Sponseller and Benfield, 2001).

In this study, leaf breakdown rate was predicted to decrease with increasing levels of fine, deposited sediments within study reaches, and shredder biomass was expected to decline along this gradient. The results of this study did not support these predictions; there was no relationship between levels of reach-scale fine, deposited sediments and leaf breakdown rate, and there was no relationship between reach fine sediments and shredder biomass.

Despite the lack of correlation between these ecosystem attributes, there is evidence that fine sediments are having an effect upon macroinvertebrate communities within these streams when individual taxa are examined. Increases in reach-scale levels of fine, deposited sediments were accompanied by taxonomic changes within the leaf bag shredder assemblages.

Leaf bag shredder taxa were similar among streams (Fig. 4.2); however, there were dramatic changes in percent contribution of individual taxa towards total shredder biomass that exhibited strong trends with increased levels of reach-scale fine sediments (Figs. 4.2, 4.3). Stonefly shredders, *Tallaperla* spp. contributed the greatest amount of biomass to the shredder assemblage at only the reference reach, where levels of fine, deposited sediments were estimated to cover 20 % of the stream bed. Large-bodied cranefly larvae dominated the leaf bag shredder assemblages in all other streams, where the stream beds were estimated to be ≥ 37 % fine, deposited sediments. In addition, percent contribution of *Tipula* spp. biomass to total shredder biomass was positively related to levels of fine, deposited sediments within study reaches (Fig. 6). Wallace *et al*. (1995) observed that plecopteran shredders did not track increased leaf litter abundances at debris dams (characterized by lowered current velocity and increased amounts of silt and sand) formed from log additions to streams, whereas trichopteran and dipteran shredders were able to exploit increased debris dam resources. This difference in response was attributed to differences in physiological capabilities and low levels of current velocity within debris dams

(Wallace *et al*., 1995). Deposited sediments are also likely to be important regarding patch-specific dynamics (Reice, 1974). In this study, trichopteran shredders did not increase within more heavily sedimented reaches; however, percent biomass of another stonefly shredder, *Pteronarcys* spp. was lower in leaf bags placed into all impaired streams (compared to the reference reach). The simultaneous decline of *Tallaperla spp.* and *Pteronarcys spp*. provides evidence that there is some physiological and/or morpho-behavioral constraint preventing these plecopteran groups from tracking resources within leaf bags, as suggested by Wallace *et al*. (1995). Fine sediments, especially silt, can interfere with the function of unprotected gill surfaces—perhaps by coating gills. The majority of *Tallaperla* spp. and *Pteronarcys* spp. gills are located on the thoracic body segments—in close proximity to their mouthparts. As these animals feed on coarse leaf matter, their ability to burrow into sandy sediments is likely constricted by the burial of their gills by sand and silt.

Only shredder biomass was related to an increasing rate of leaf breakdown (Fig. 5). Taxonomic richness of the shredder assemblage within leaf bags was not related to rates of leaf breakdown. Experimental as well as ecosystem-level evidence shows increases in taxonomic richness resulting in increased leaf processing rates (Jonsson and Malmqvist, 2000; Jonsson *et al*., 2001; Huryn *et al*., 2002). In our study differences in feeding rates between *Tallaperla* spp. and *Tipula* spp. are driving differences in leaf processing within leaf bags. Feeding activities of *Tallaperla* spp. break leaves down more slowly than feeding activities of *Tipula* spp. because *Tallaperla* spp. skeletonize leaves, whereas *Tipula* spp. remove large portions of leaves as they feed (Wallace *et al*., 1970). Hence higher biomass of *Tipula* spp. accelerated leaf breakdown rate.

Leaves in leaf bags in the study streams may have represented important and stable food resources, particularly in impaired reaches. Leaf breakdown rates were most elevated in the study reach containing the highest level of fine, deposited sediments and the reach with least canopy cover—the two most impacted reaches. This pattern suggests that the proliferation of shredder biomass within these streams may be limited by leaf inputs or by limited leaf retention. Shredder biomass and production can be determined by leaf litter availability (Wallace *et al*., 1997 & 1999). The nonforested reach included in this study was located approximately 500 m downstream of a forested study reach on the same stream (Roach 1 = forested; Roach 2 = unforested), and export of leaf resources from upstream, could be expected to support shredders immediately downstream (Sponseller and Benfield, 2001); however, intervening factors in the forms of residential activities and private water diversion and detainment (for a private trout pond) between the two study reaches likely broke continuity between them and prevented inputs of leaves to Roach 2 from Roach 1.

Alternatively, physical breakdown may account for some of the elevated processing rate at Roach 2. Due to its narrowness, it is possible that elevated current velocities within Roach 2 broke leaves down more quickly without the assistance of invertebrate processing. Although Statzner hemispheres were used to find areas of similar flow for leaf bag location, rain events may have led to higher current velocities in the narrower channel. In addition, warmer water temperatures of this open reach may have enhanced microbial conditioning and softening of leaf litter, and made it easier for actions of water currents to break leaves down. Our study design did not allow us to assess abiotic *versus* biotic roles in leaf breakdown, so it is impossible to say what portion of leaf breakdown at Roach 2 could be attributed to physical factors. However, the open canopy and narrowness of the Roach 2 channel makes it likely that physical factors and microbes figure more importantly in leaf breakdown at this site. Transport of fine particles out of Roach 2 is also likely to be enhanced due to elevated current velocity.

The absence of relationships between levels of fine, deposited sediments and leaf breakdown rates within reaches of this study may be attributed to a) changes in taxonomic identity within shredder assemblages and b) creation of artificial resource patches with the addition of leaf bags into impaired study reaches. These data suggest that to gauge leaf processing more accurately, it is important to carefully choose sites for leaf bag placement. An effort was made to place all leaf bags into similar physical environments within study reaches; however in order to obtain leaf breakdown rates that reflect actual study reach conditions, it would be more expedient to place leaf bags into areas of study reaches so that they are distributed amongst sites that together accurately represent the availability of different streambed conditions. Sponseller and Benfield (2001) likewise hypothesized that they were unable to predict shredder abundances with reach-scale sediment size characteristics due to patchiness in habitat types within streams and the failure to place leaf bags into sites that were representative of their study reaches.

The relationships between reach-scale levels of deposited, fine sediments, taxonomic alterations within leaf bag shredder assemblages and differences in leaf bag processing rates provide evidence that fine sediments are influencing ecosystem function in headwater tributaries of the Chattooga River watershed. Simplification of stream bedform due to excessive deposition of fine sediments may be reducing coarse organic matter retention within Chattooga tributary streams, and riparian activities around these headwater tributaries are likely reducing water quality and causing disruptions in network continuity. These consequences of human activities upon the landscape underscore the importance of monitoring and managing freshwater resources from the perspective of entire watersheds in order to protect rivers.

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Table 4.1. Study reach characteristics.

Site Name	Canopy	Drainage Area (ha)	Slope (%)	Width (m)	*V* (cm s^{-1})	Max ºC	Mean ºC	Min ºC	% Fines	% Riffle	% Bedrock
Addie	forested	560	3.0	5.58	37	18.2	10.5	0.29	20	37	43
Roach 1	forested	80	3.4	2.00	33	19.4	11.4	0.29	47	25	28
Roach 2	open	80	2.3	1.28	33	20.6	12.2	0.73	37	48	15
Law	forested	251	2.0	2.51	35	20.6	11.5	0.29	60	32	8

Figure 4.1. Map of study sites. Chattooga River watershed: Georgia, North Carolina, South Carolina. Circle represents reference sites and triangles represent impaired sites.

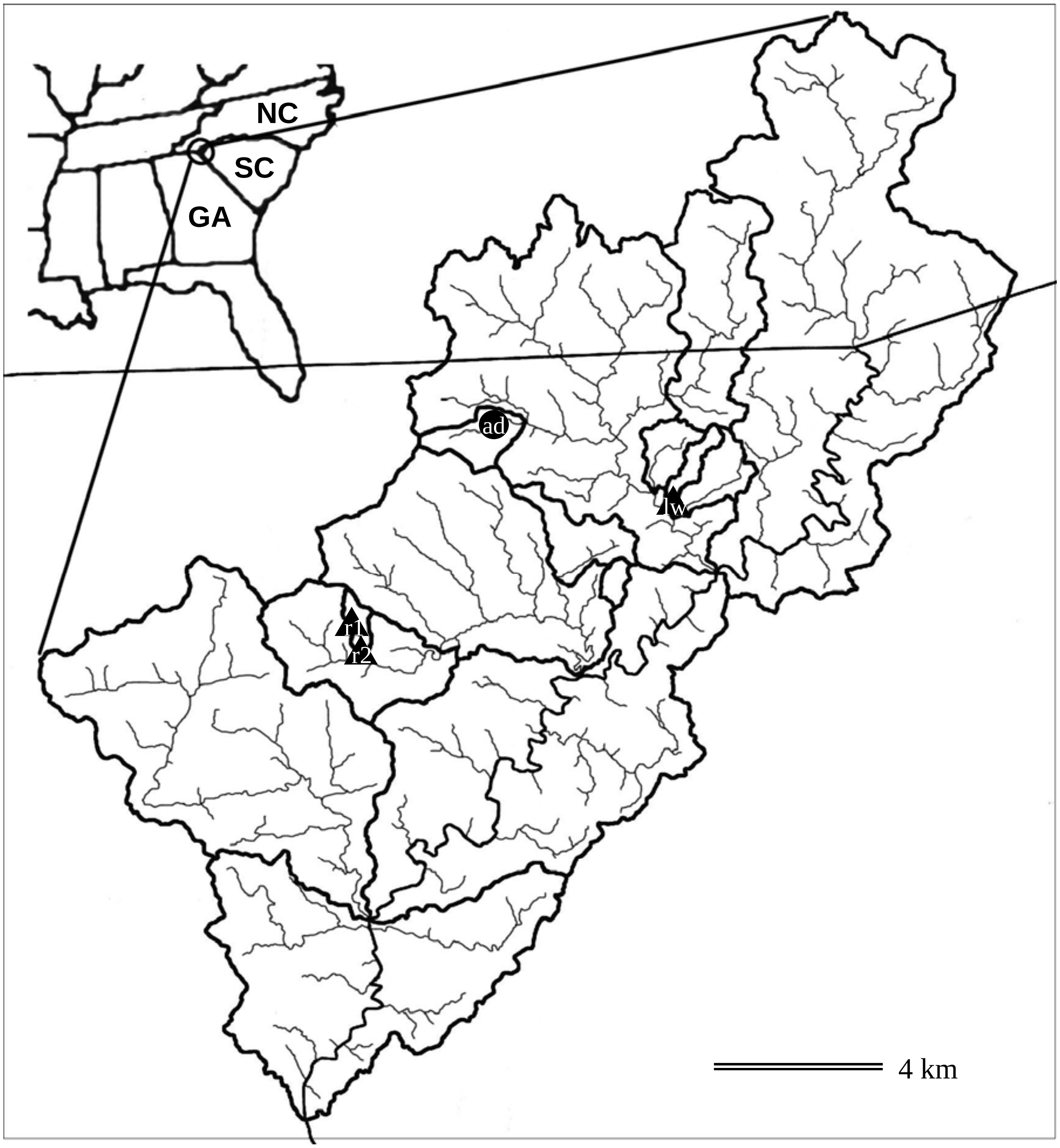

NC
SC
GA
ad
lw
r1
r2
4 km

Figure 4.2. Leaf bag macroinvertebrate assemblage attributes. Bars represent standard error. Different letters denote significant differences.

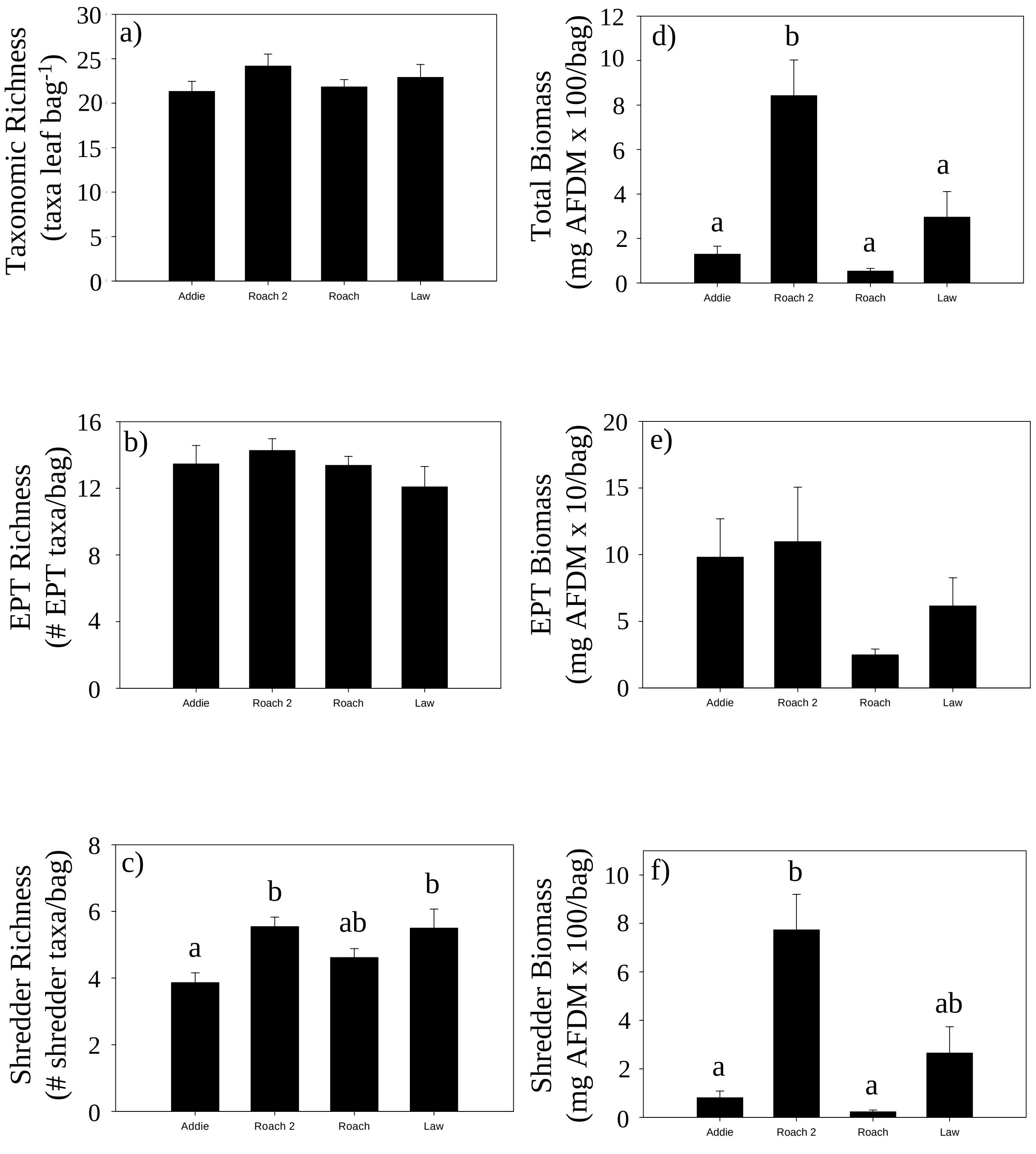
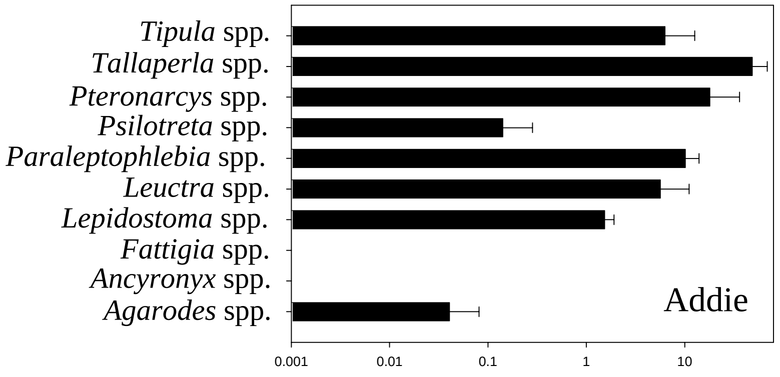
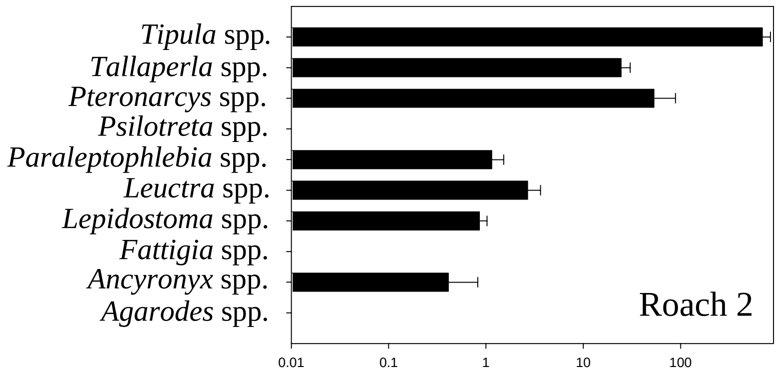
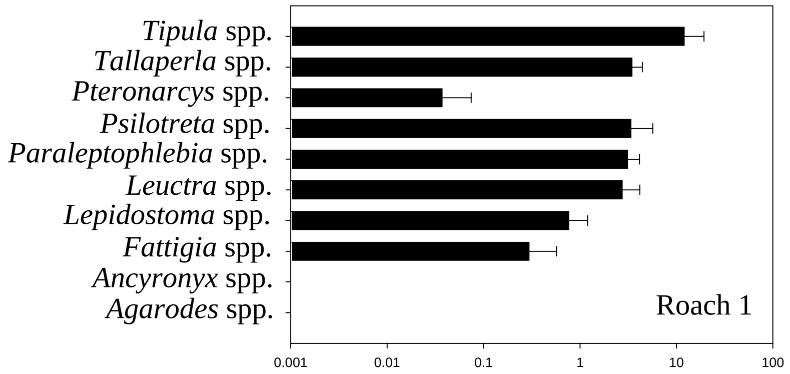

a)
Taxonomic Richness
(taxa leaf bag^{-1})
0
5
10
15
20
25
30
Addie
Roach 2
Roach
Law
d)
Total Biomass
(mg AFDM x 100/bag)
0
2
4
6
8
10
12
a
b
a
a
Addie
Roach 2
Roach
Law
b)
EPT Richness
(# EPT taxa/bag)
0
4
8
12
16
Addie
Roach 2
Roach
Law
e)
EPT Biomass
(mg AFDM x 10/bag)
0
5
10
15
20
Addie
Roach 2
Roach
Law
c)
Shredder Richness
(# shredder taxa/bag)
0
2
4
6
8
a
b
ab
b
Addie
Roach 2
Roach
Law
f)
Shredder Biomass
(mg AFDM x 100/bag)
0
2
4
6
8
10
a
b
a
ab
Addie
Roach 2
Roach
Law

Figure 4.3. Leaf bag shredder biomass; ten most common taxa shown.


Tipula spp.
Tallaperla spp.
Pteronarcys spp.
Psilotreta spp.
Paraleptophlebia spp.
Leuctra spp.
Lepidostoma spp.
Fattigia spp.
Ancyronyx spp.
Agarodes spp.
Addie
0.001
0.01
0.1
1
10


Tipula spp.
Tallaperla spp.
Pteronarcys spp.
Psilotreta spp.
Paraleptophlebia spp.
Leuctra spp.
Lepidostoma spp.
Fattigia spp.
Ancyronyx spp.
Agarodes spp.
Roach 2
0.01
0.1
1
10
100


Tipula spp.
Tallaperla spp.
Pteronarcys spp.
Psilotreta spp.
Paraleptophlebia spp.
Leuctra spp.
Lepidostoma spp.
Fattigia spp.
Ancyronyx spp.
Agarodes spp.
Roach 1
0.001
0.01
0.1
1
10
100

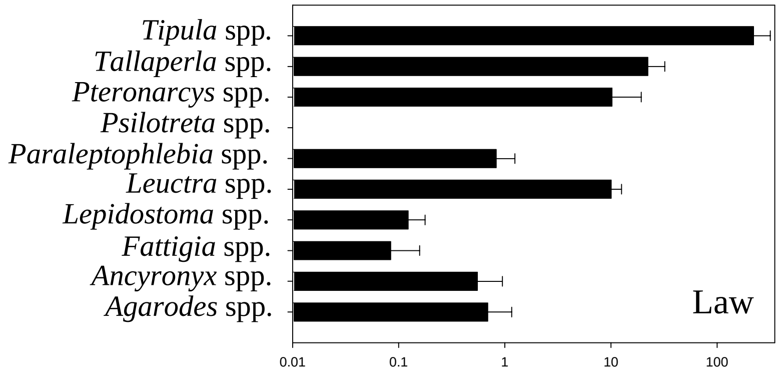

Tipula spp.
Tallaperla spp.
Pteronarcys spp.
Psilotreta spp.
Paraleptophlebia spp.
Leuctra spp.
Lepidostoma spp.
Fattigia spp.
Ancyronyx spp.
Agarodes spp.
Law
0.01
0.1
1
10
100

Figure 4.4. Percent contribution of shredders, *Tallaperla* spp. and *Tipula* spp. to total shredder biomass.

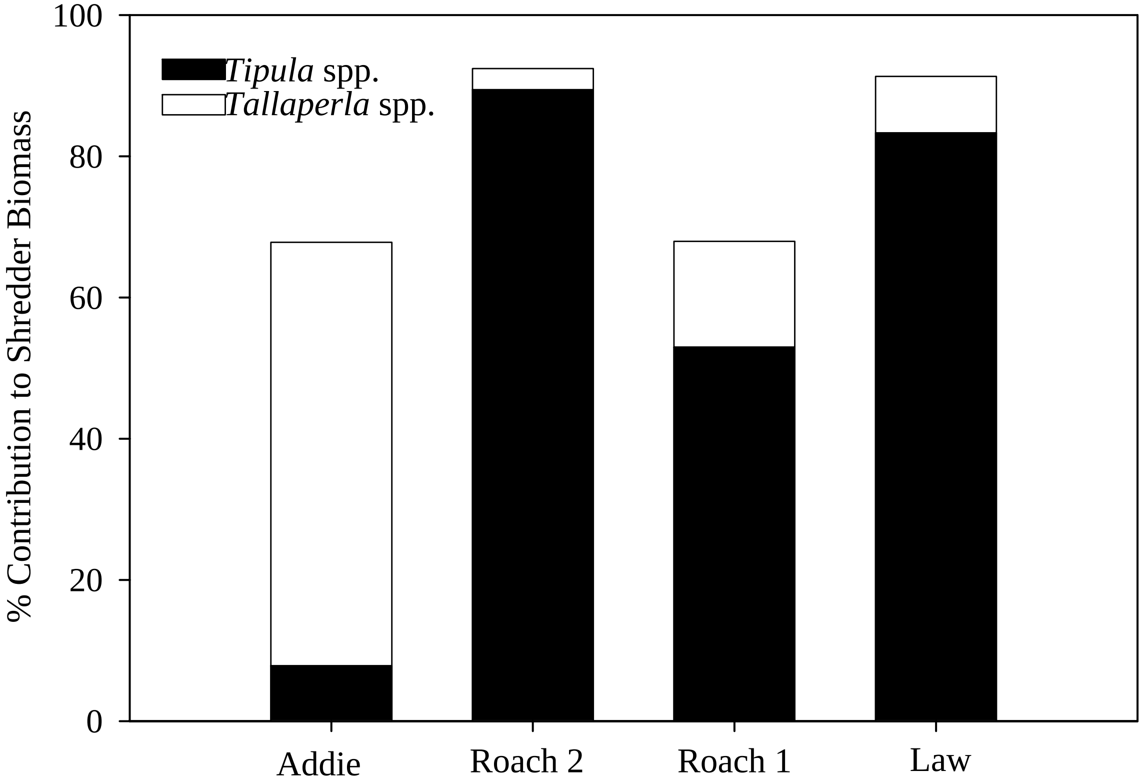

% Contribution to Shredder Biomass
100
80
60
40
20
0
Tipula spp.
Tallaperla spp.
Addie
Roach 2
Roach 1
Law

Figure 4.5. Non-metric multidimensional scaling (NMS) ordination of leaf bags in macroinvertebrate assemblage space. *Tallaperla* spp. biomass was negatively related to Axis 1 ($r^2 = 0.30$, $p < 0.05$). Deposited fine sediments were positively related to Axis 1 ($r^2 = 0.25$, $p < 0.001$). *Tipula* spp. Biomass was positively related to Axis 2 ($r^2 = 0.59$, $p < 0.05$).

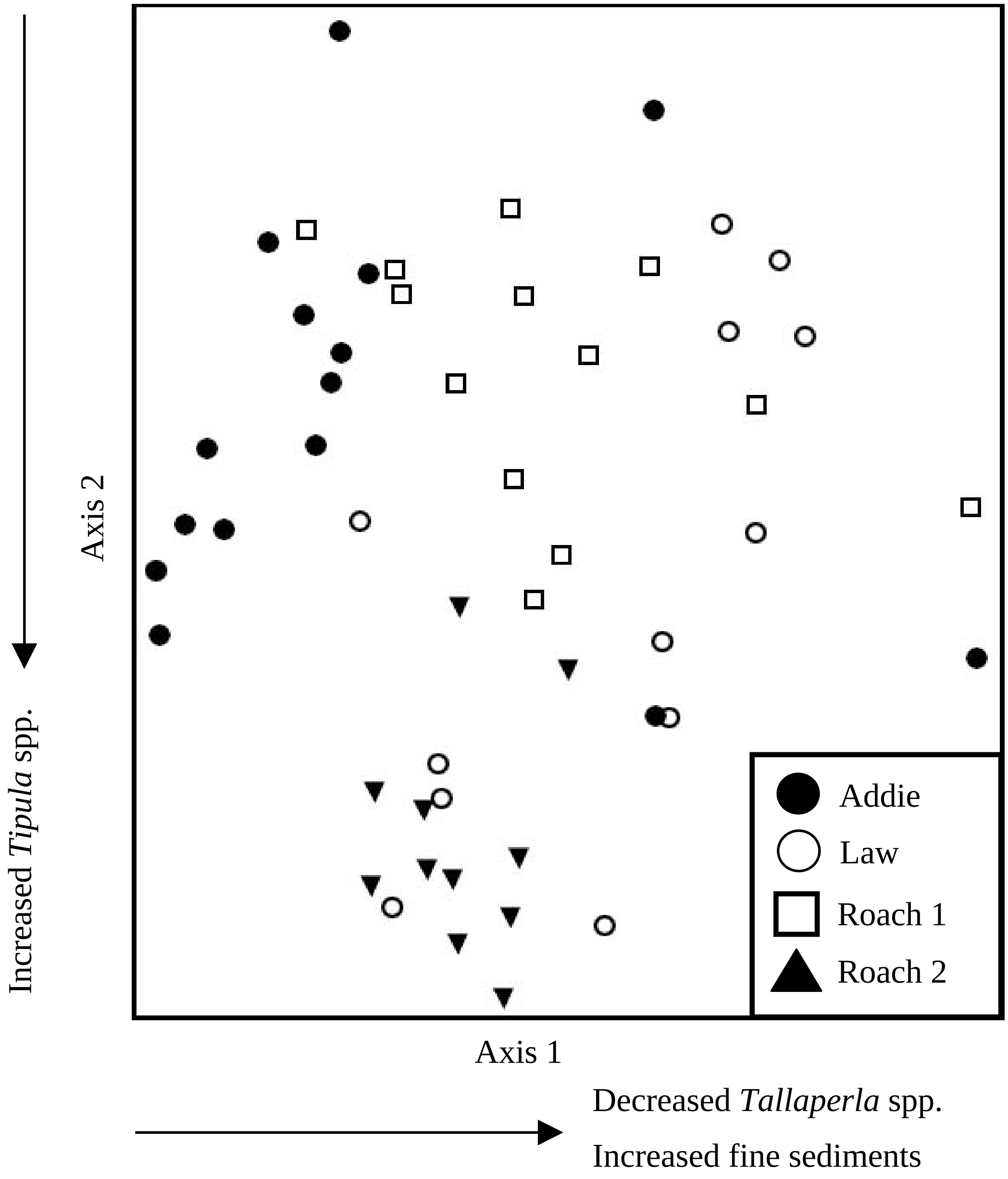

Axis 2
Increased *Tipula* spp.
Axis 1
Decreased *Tallaperla* spp.
Increased fine sediments
● Addie
○ Law
□ Roach 1
▲ Roach 2

Figure 4.6. Mean leaf bag processing coefficients. Processing coefficients varied significantly among reaches (*F* < 0.001). ANCOVA used to detect differences between reaches. Different letters denote significant differences.

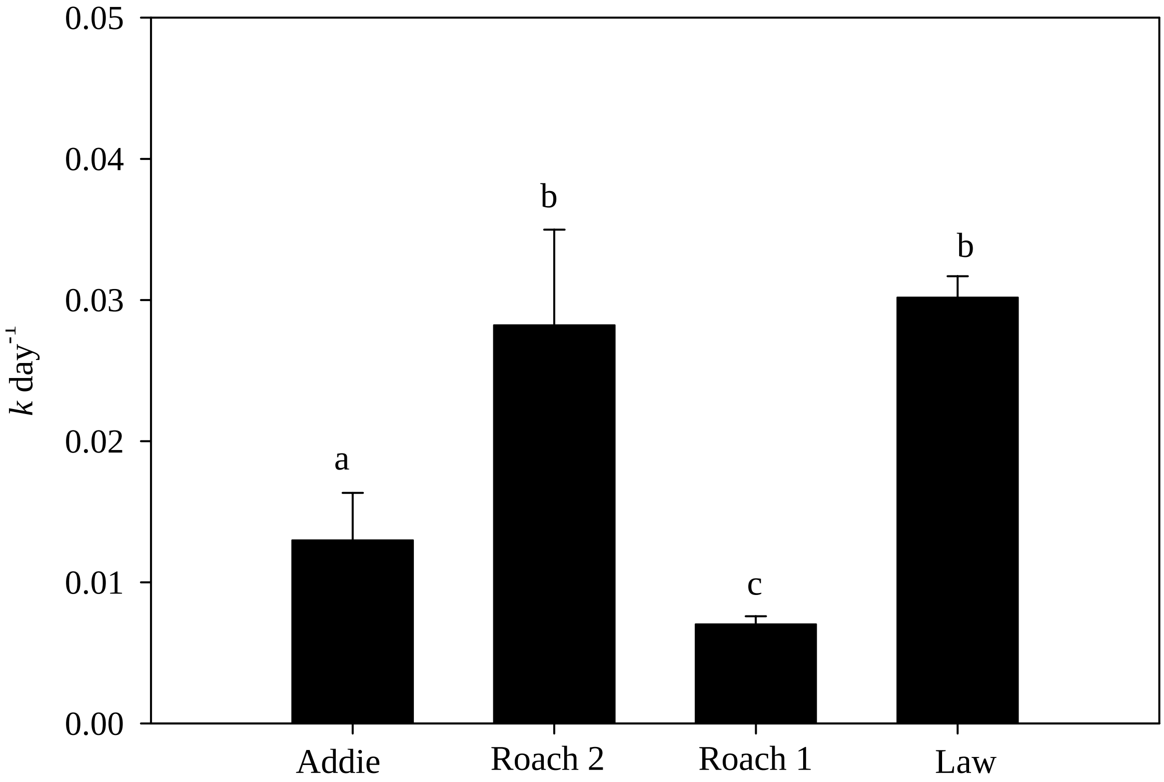

0.05
0.04
0.03
0.02
0.01
0.00
k day^{-1}
a
b
c
b
Addie
Roach 2
Roach 1
Law

Figure 4.7. Relationship between leaf breakdown rate and shredder biomass.

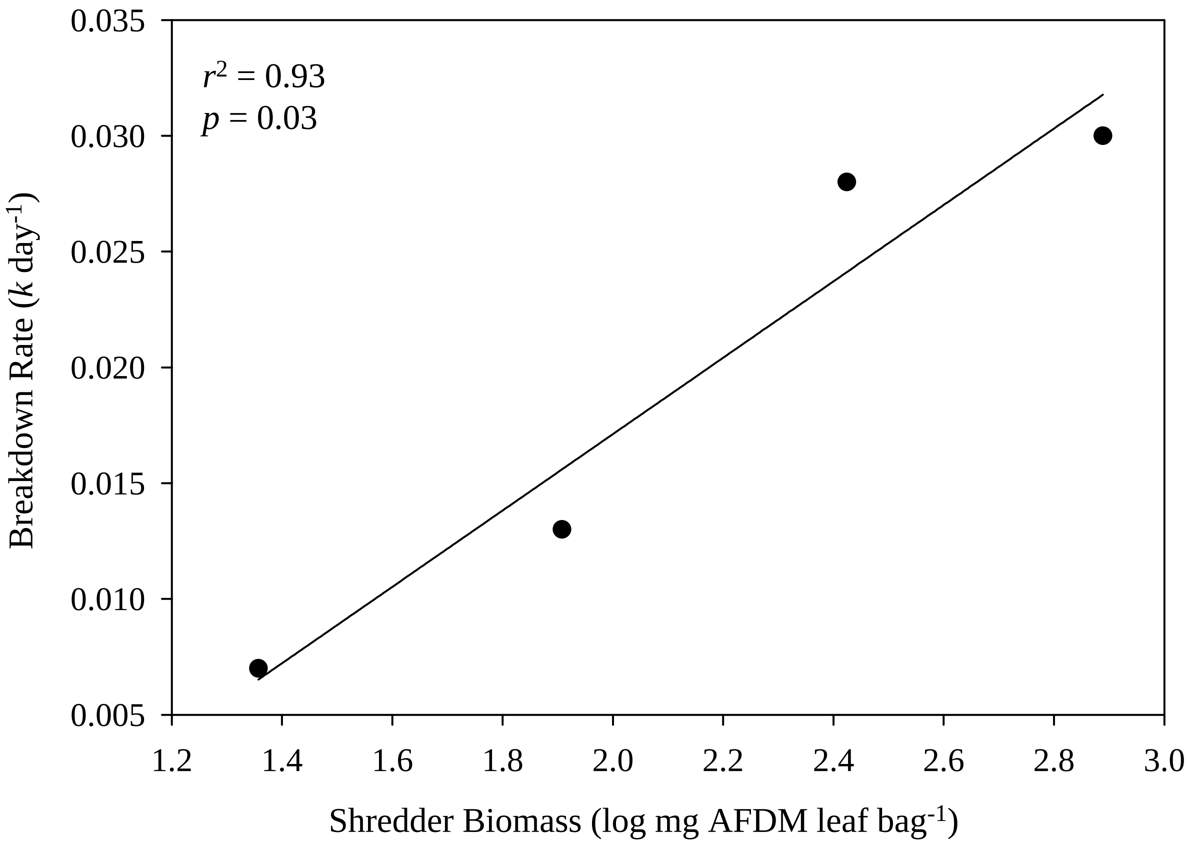
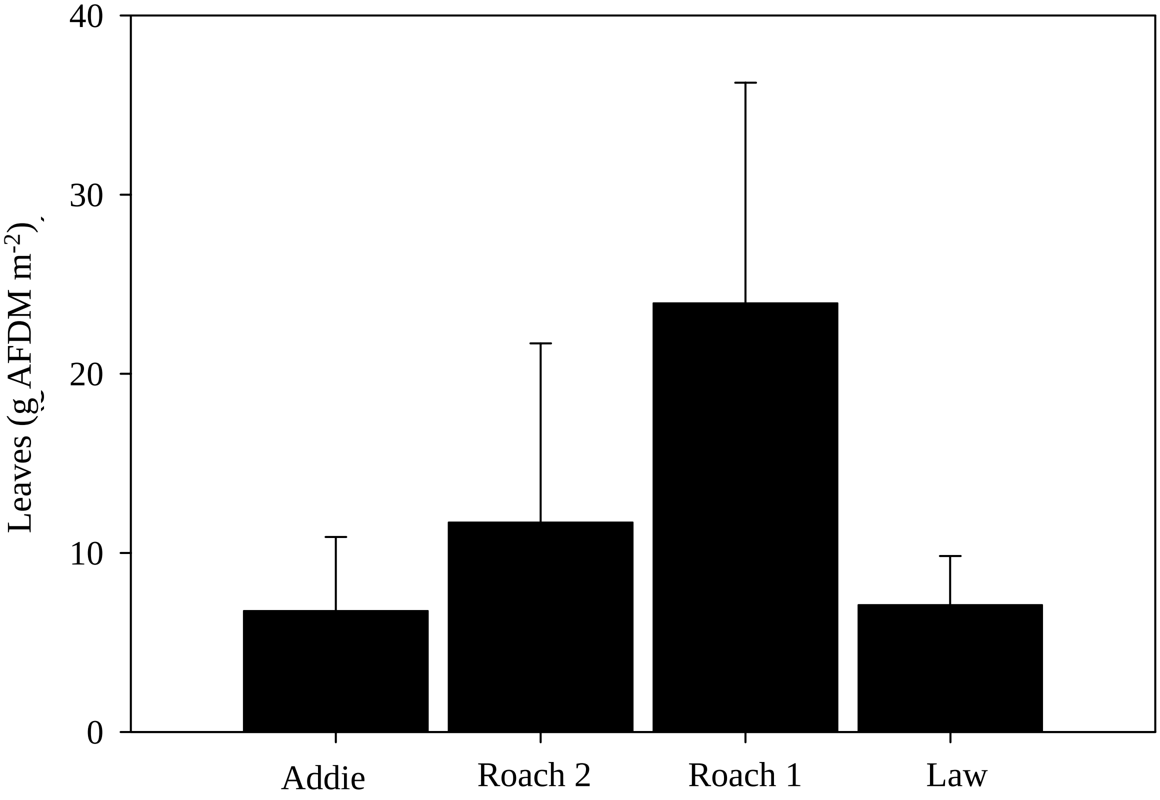

$r^2 = 0.93$
$p = 0.03$
0.035
0.030
0.025
0.020
0.015
0.010
0.005
Breakdown Rate (k day-1)
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
Shredder Biomass (log mg AFDM leaf bag-1)

Figure 4.8. Study reach leaf standing crops. Bars represent standard error.



40
30
20
10
0
Leaves (g AFDM m-2)
Addie
Roach 2
Roach 1
Law

CHAPTER 5

CONCLUSIONS

Processes within stream ecosystems (and stream ecosystems themselves) are complex emergent properties resulting from nested hierarchies of interacting biotic and abiotic elements. Ecologists have for some time recognized that riverine ecosystems are dependent upon the landscapes within which they reside (e.g. Hynes 1975) and that the distribution of some stream-dwelling insects is likely controlled by the nature of surrounding forests (Ross 1963). Freshwater systems are web-like entities made up of an enormous number of components, and they are intensely complex, with ill-defined boundaries—properties that make both study and conservation of these resources challenging and perplexing work. This study was undertaken to characterize benthic macroinvertebrate assemblage structure within channels of the Chattooga River network (Chapters 2 and 3), and to determine if there are effects of fine, deposited sediments on benthic invertebrate assemblages (Chapter 2) and on functional attributes of benthic invertebrate assemblages (Chapter 4).

Benthic macroinvertebrate communities are important components of stream systems because they participate in many ecosystem processes (e.g. nutrient cycling, leaf litter breakdown) and act as longitudinal and horizontal trophic links along stream networks and within river basins (Vannote *et al*. 1980, Wallace *et al*. 1982, Junk *et al*. 1999). Benthic macroinvertebrates are important to many stream processes (Wallace and Webster 1996) and are responsive to environmental changes. Thus, benthic macroinvertebrates are ideal organisms to study in order to gain insight into the effects of disturbances on stream systems (Resh *et al*.

1996). Stream invertebrates respond to dramatic sediment loading due to catchment logging (Tebo 1955, Gurtz and Wallace 1984). Many studies have shown benthic invertebrates to be responsive to changes in habitat due to fine sediment addition (Lenat 1981, Lemly 1982, Waters 1984, Mebane 2001, Zweig and Rabeni 2001). This study examined the effects of fine sediments on benthic macroinvertebrate assemblages within stream mesohabitats, and stream reaches.

Results from this study indicate that fine, deposited sediments (≤ 2mm) covering stream beds are affecting benthic macroinvertebrate communities at both the mesohabitat and reach scale within headwaters of the Chattooga River watershed. Sensitive invertebrate taxa (Ephemeroptera, Plecoptera, Trichoptera—EPT taxa) declined within study reaches where sedimentation was elevated. Shredder abundance was significantly reduced within reaches where levels of fine sediments were higher, and fine sediments influenced the composition of shredder assemblages. Large-bodied cranefly larvae were more predominant in channels containing higher amounts of deposited sediments and they replaced stonefly shredders. Fine, deposited sediments may be influencing leaf breakdown by preventing some taxa from exploiting coarse leaf litter. There was also some evidence indicating that fine sediments could be having a negative impact on algal resources in these streams. Fine sediments had differential effects on the sampled habitats: (1) in cobble riffles, the number of EPT taxa declined as levels of fine sediments within channels increased; (2) in bedrock outcrops, total assemblage abundances and grazer abundances were negatively correlated to reach-scale amounts of fine, deposited sediments; and (3) in depositional habitats, the second most frequently collected taxon (specific taxon varied with stream channel) was positively correlated to levels of fine, deposited sediments within study reaches.

I found that elevated levels of fine sediments are having a detrimental effect on headwater streams within the Chattooga River watershed. However, it was not clear from this study that larger stream segments were being affected by fine, deposited sediments in the same way. By conducting the longitudinal study (Chapter 3) I was able to compare patterns in the macroinvertebrate community structure of the Chattooga River continuum to a predictive model (River Continuum Concept, RCC) of stream—river function (Vannote *et al*. 1980, Minshall *et al*. 1985).

Macroinvertebrate communities within the Chattooga River watershed largely followed tenets of the RCC regarding longitudinal changes. They were also very similar to patterns found within another southern Appalachian continuum (Grubaugh *et al*. 1996). Local habitat conditions (i.e. mesoscale, *sensu* Huryn and Wallace 1987) influenced the composition of reach-level benthic macroinvertebrate communities. Mesoscale invertebrate communities occurring in geomorphically distinct habitats (riffles, bedrock outcrops, and depositional areas) had unique structural patterns, and reach-level communities were composites of these mesoscale communities. In the Chattooga River continuum, bedrock outcrop and cobble riffle availability at the reach scale were largely responsible for driving the observed patterns in assemblage structure. Depositional assemblages tended to be dominated by gatherers at all sites. This observation has important management implications, especially in regard to sedimentation, because it allows one to predict the effects of increased fine sediment deposition to these stream channels.

Elevated deposition of fine sediments within Chattooga channels could, over time, simplify the heterogeneous nature of cobble riffle habitats and increase the extent of depositional habitat. If this were to happen, it should be expected that reach-scale communities would become more similar to those found in depositional habitats in proportion to depositional habitat increase (due to sedimentation) within a given stream segment. If severe enough, sedimentation could dramatically change the structure and functional attributes of benthic macroinvertebrate communities through habitat simplification. As high-relief channel forms, it is unlikely that bedrock outcrops would ever be smothered by fine sediments; however, these areas could be affected by scour, and the entrainment of inorganic particles in excessive quantities could interfere with filter feeding behaviors or respiration of macroinvertebrates.

Strategies for protecting the Chattooga River network against sustained sedimentation must address land use activities within the entire basin—the area over which sediments are generated and introduced to stream channels. Due to the connectivity of the waters, impacts to both physical stream habitats and stream biota are propagated downstream. Protecting only portions of the river will not prevent its eventual degradation.

A number of federal statutes govern water quality issues within the Chattooga River watershed. The land within the watershed is primarily owned by the United States Department of Agriculture Forest Service (USFS, approximately 70 %). Under the National Forest Management Act (NFMA), the USFS is responsible for protecting habitat for fishes and wildlife within forest land. The USFS is further charged with protecting renewable resources within forested areas. The main channel of the Chattooga River, together with the West Fork Chattooga River has been conferred Wild and Scenic status. The National Wild and Scenic Rivers Act (WSRA) mandates that water quality of protected rivers must be maintained. Finally, the federal Clean Water Act (CWA) requires the assessment of all waters, the establishment of water quality standards, and prohibits further water quality degradation. The CWA requires that for all water bodies listed as impaired, limits to identified pollutants are set (Total Maximum Daily Load, TMDL). TMDLs are quantitative limits set on pollutants with the intention of improving water quality so that impaired waters can achieve acceptable standards. For waters that require TMDLs, all pollution sources are identified. Point sources are discrete entities discharging pollutants into waters. Non-point source pollutants (e.g. sediments) are generated over areas that cannot be treated as single entities and easily regulated. Non-point source pollution is a complex issue, both from a technological standpoint (e.g. quantification and control), as well as a political standpoint (e.g. enforcement, regulation). Strategies for implementing TMDLs involve the reduction of both types of polluters; however, it is much simpler to regulate point sources. States, territories and authorized tribes are responsible for reporting impaired waters to the USEPA and for developing USEPA approved TMDLs. Implementation plans that seem reasonable in their potential for reducing pollution are included in approved TMDLs. TMDL implementation usually involves a number of private and public entities as well as regulatory and non-regulatory approaches to pollution reduction. Because the aim of a TMDL is to bring total pollution under some established benchmark, point source polluters can be restricted to discharging levels of pollutants that compensate for uncontrolled non-point source pollution. This strategy can be a powerful incentive for point source polluters to back non-regulatory and incentive-based approaches to controlling pollution within a watershed.

Although the CWA is our most promising vehicle for water quality protection, the effectiveness of TMDLs is obstructed by a number of challenges. For example: (1) The CWA requires that seasonal variation in pollution loads and a margin of safety be included in TMDLs. In creating such criteria, many assumptions have to be made and lead to the discredit of TMDLs—although ideally they are based on the best knowledge available. The development of quantitative limits to pollutants requires a great deal of data. This data does not always exist. (2)

River networks do not conform to political boundaries. The control of pollutants within watersheds necessitates the orchestration of any number of responsible authorities and stakeholders. The Chattooga River watershed is contained within three different states, so comprehensive protection of the Chattooga River network requires cooperation between each of these authorities. (3) The only way to know whether or not a TMDL has been effective is to monitor impaired waters. Such monitoring programs are time, personnel, and money intensive. This is a limitation that often prevents them from being able to effectively address general problems, such as sedimentation.

Much of the sediment being deposited into Chattooga channels are the result of the presence of the extensive network of logging roads within the watershed. These roads provide fine sediments, and they also transport run-off from rain events quickly into stream channels, which elevates in-stream erosion. An effective way to reduce sedimentation would be to close some roads and allow vegetation to grow over them. As a highly popular recreational area, it is unlikely that people who are interested in the area will ever allow access to be so regulated. Increased public awareness of Wild and Scenic Rivers may help to protect them (i.e. public insistence on compliance with WSRA statutes); however, increased recreation and continued access to all areas of these watersheds may exacerbate other types of pollution problems (i.e. erosion and sedimentation from forest roads). Research and outreach (with the aim of providing the public with information regarding conservation issues) will be crucial to conservation efforts in the Chattooga River watershed.

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Appendix A. Abundance and biomass data. Mean annual abundance (A, no./m-2) and biomass (B, mg AFDM/m-2) of taxa in each functional feeding group in bedrock outcrop, cobble riffle, and depositional habitats in study streams (AD = Addie Creek, LW = Law Ground Creek, RO = Roach Mill Creek, OV = Overflow Creek, MF = Martin-Finney Creek, RE = Reed Mill Creek). Insect orders are as follows: C = Coleoptera, D = Diptera, E = Ephemeroptera, P = Plecoptera, O = Odonata, T = Trichoptera, and NI = non-insect.

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Scrapers								
Ameletus sp.	E	AD	2008	13	18	11	33	<1
		LW	0	0	106	1	0	0
		RO	0	0	13	2	0	0
		R2	0	0	1	1	0	0
		OV	0	0	11	4	0	0
		MF	18	<1	1	1	0	0
		RE	0	0	0	0	0	0
Baetis sp.	E	AD	1860	23	248	4	63	2
		LW	225	2	707	15	8	<1
		RO	379	4	111	1	0	0
		R2	4096	63	725	19	180	<1
		OV	579	18	315	16	23	1
		MF	809	6	906	16	72	1
		RE	1098	18	260	6	29	<1
Baetidae	E	AD	307	2	23	<1	-	-
		LW	108	<1	0	0	-	-
		RO	0	0	0	0	-	-
		R2	0	0	1	<1	-	-
		OV	0	0	3	<1	-	-
		MF	0	0	0	0	-	-
		RE	0	0	0	0	-	-
Cinygmula sp.	E	AD	-	-	32	2	0	0
		LW	-	-	42	1	0	0
		RO	-	-	1	0	0	0
		R2	-	-	1	1	0	0
		OV	-	-	67	11	0	0
		MF	-	-	18	1	2	<1
		RE	-	-	0	0	0	0

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Drunella sp.	E	AD	18	1	160	20	-	-
		LW	8	<1	0	0	-	-
		RO	0	0	7	<1	-	-
		R2	46	4	27	8	-	-
		OV	8	<1	17	2	-	-
		MF	0	0	22	3	-	-
		RE	0	0	10	4	-	-
Epeorus sp.	E	AD	33	127	244	22	2	<1
		LW	64	33	1322	129	0	0
		RO	75	51	234	20	44	1
		R2	0	0	432	59	180	4
		OV	0	0	723	121	0	0
		MF	0	0	337	76	0	0
		RE	54	29	488	90	0	0
Heptageniidae	E	AD	-	-	19	<1	0	0
		LW	-	-	86	1	0	0
		RO	-	-	9	<1	17	<1
		R2	-	-	59	1	75	1
		OV	-	-	22	<1	33	1
		MF	-	-	60	1	100	1
		RE	-	-	30	6	27	<1
Rhithrogenia sp.	E	AD	-	-	4	11	-	-
		LW	-	-	17	494	-	-
		RO	-	-	0	0	-	-
		R2	-	-	1	1	-	-
		OV	-	-	0	0	-	-
		MF	-	-	0	0	-	-
		RE	-	-	0	0	-	-

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Stenacron sp.	E	AD	-	-	6	2	-	-
		LW	-	-	0	0	-	-
		RO	-	-	0	0	-	-
		R2	-	-	1	<1	-	-
		OV	-	-	3	1	-	-
		MF	-	-	0	0	-	-
		RE	-	-	0	0	-	-
Stenonema sp.	E	AD	0	0	182	21	19	1
		LW	8	<1	1035	251	6	13
		RO	83	2	114	67	0	0
		R2	0	0	387	124	305	5
		OV	0	0	515	64	0	0
		MF	164	2	291	64	25	8
		RE	8	<1	248	21	2	1
Diura sp.	P	AD	-	-	1	2	-	-
		LW	-	-	0	0	-	-
		RO	-	-	0	0	-	-
		R2	-	-	0	0	-	-
		OV	-	-	0	0	-	-
		MF	-	-	0	0	-	-
		RE	-	-	0	0	-	-
Ectopria sp.	C	AD	8	<1	76	22	0	0
		LW	133	12	150	85	0	0
		RO	46	4	53	11	4	1
		R2	13	1	37	44	19	<1
		OV	0	0	85	23	17	<1
		MF	158	7	130	35	6	<1
		RE	88	9	46	16	2	4

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Optioservus sp.	C	AD	67	<1	162	5	17	<1
		LW	420	3	2202	48	56	<1
		RO	88	1	71	2	8	2
		R2	196	4	179	8	102	8
		OV	0	0	237	3	152	5
		MF	97	3	286	15	19	2
		RE	125	0	252	7	133	4
Stenelmis sp.	C	AD	-	-	0	0	0	0
		LW	-	-	0	0	0	0
		RO	-	-	0	0	0	0
		R2	-	-	17	1	18	1
		OV	-	-	0	0	0	0
		MF	-	-	0	0	0	0
		RE	-	-	21	<1	0	0
Promoresia sp.	C	AD	6714	153	123	1	65	3
		LW	967	14	74	<1	21	<1
		RO	171	4	0	0	0	0
		R2	3014	65	44	1	36	<1
		OV	12117	291	48	1	66	2
		MF	21853	438	3447	6	44	1
		RE	4066	54	13	<1	413	1
Apatania sp.	T	AD	8	<1	7	<1	0	0
		LW	0	0	0	0	0	0
		RO	0	0	0	0	0	0
		R2	435	33	6	<1	4	<1
		OV	118	8	74	3	0	0
		MF	0	0	52	2	0	0
		RE	13	1	0	0	0	0

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Glossosoma sp.	T	AD	-	-	28	1	-	-
		LW	-	-	8	<1	-	-
		RO	-	-	14	<1	-	-
		R2	-	-	185	22	-	-
		OV	-	-	72	9	-	-
		MF	-	-	94	6	-	-
		RE	-	-	122	3	-	-
Goera sp.	T	AD	42	39	0	0	0	0
		LW	0	0	0	0	0	0
		RO	0	0	0	0	0	0
		R2	18	20	11	9	0	0
		OV	0	0	3	3	0	0
		MF	0	0	3	<1	2	<1
		RE	0	0	4	<1	0	0
Glossosoma sp.	T	AD	0	0	28	1	0	0
		LW	0	0	8	<1	0	0
		RO	67	1	14	<1	2	<1
		R2	83	1	185	22	8	<1
		OV	8	<1	72	9	0	0
		MF	0	0	94	6	6	<1
		RE	0	0	122	3	0	0
Hydroptila sp.	T	AD	0	0	0	0	-	-
		LW	0	0	0	0	-	-
		RO	0	0	0	0	-	-
		R2	257	48	24	4	-	-
		OV	150	25	8	<1	-	-
		MF	0	0	0	0	-	-
		RE	0	0	0	0	-	-

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Neophylax sp.	T	AD	33	<1	15	<1	0	0
		LW	0	0	50	1	6	<1
		RO	167	1	6	<1	183	1
		R2	0	0	24	4	0	0
		OV	0	0	16	1	0	0
		MF	283	2	60	6	17	<1
		RE	147	1	32	1	0	0
Total Scrapers		AD	11099	358	1374	125	199	5
		LW	1934	64	5807	1025	97	13
		RO	1075	66	645	103	258	4
		R2	8157	239	2345	328	928	18
		OV	12981	343	2288	270	291	10
		MF	23383	459	5801	237	292	14
		RE	5599	112	1648	157	606	10
Shredders								
Leuctridae	P	AD	0	0	49	2	258	10
		LW	8	1	475	19	50	<1
		RO	0	3	26	4	0	1
		R2	579	10	530	4	194	3
		OV	56	2	203	14	1021	4
		MF	100	7	234	11	993	4
		RE	17	0	228	4	120	4
Leuctra sp.	P	AD	0	0	41	2	35	<1
		LW	31	<1	508	22	12	<1
		RO	171	5	133	6	15	<1
		R2	133	4	436	20	89	1
		OV	158	4	226	12	10	<1
		MF	174	6	197	13	36	<1
		RE	0	0	108	9	3	<1

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Nemoura sp.	P	AD	-	-	69	1	0	0
		LW	-	-	0	0	0	0
		RO	-	-	0	0	0	0
		R2	-	-	0	0	0	0
		OV	-	-	1	1	0	0
		MF	-	-	9	<1	11	<1
		RE	-	-	7	<1	0	0
Ostrocerca sp.	P	AD	-	-	1	<1	-	-
		LW	-	-	206	10	-	-
		RO	-	-	0	0	-	-
		R2	-	-	0	0	-	-
		OV	-	-	0	0	-	-
		MF	-	-	0	0	-	-
		RE	-	-	0	0	-	-
Pteronarcys sp.	P	AD	23	24	2	15	0	0
		LW	0	0	256	6086	8	2
		RO	0	0	14	3	0	0
		R2	0	0	15	453	1	<1
		OV	2923	50	22	230	35	6
		MF	267	72	98	4	30	11
		RE	100	6	79	260	24	1
Tallaperla sp.	P	AD	684	69	2904	7	17	<1
		LW	0	0	180	257	2	<1
		RO	83	10	59	9	0	0
		R2	0	0	38	13	7	<1
		OV	2572	164	233	18	0	0
		MF	383	6	91	2	8	<1
		RE	17	<1	12	1	0	0

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Ancyronyx sp.	C	AD	0	0	0	0	2	11
		LW	0	0	61	13	6	3
		RO	25	1	2	0	0	0
		R2	75	1	17	3	19	3
		OV	17	6	1	0	0	0
		MF	79	10	19	3	0	0
		RE	0	0	2	1	2	<1
Molophilus sp.	D	AD	458	12	0	0	31	6
		LW	0	0	8	6	8	4
		RO	0	0	0	0	6	<1
		R2	0	0	1	<1	0	0
		OV	8	<1	0	0	0	0
		MF	0	0	0	0	17	<1
		RE	0	0	0	0	8	5
Tipula sp.	D	AD	473	18	12	2	4	9
		LW	0	0	44	720	19	298
		RO	125	6	5	0	46	301
		R2	13	0	27	1204	39	1392
		OV	3	71	1	0	11	71
		MF	17	7	6	9	6	616
		RE	0	0	2	1	65	87
Agarodes sp.	T	AD	-	-	2	4	0	0
		LW	-	-	0	0	2	<1
		RO	-	-	0	0	0	0
		R2	-	-	0	0	8	<1
		OV	-	-	0	0	0	0
		MF	-	-	0	0	0	0
		RE	-	-	0	0	0	0

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Fattigia sp.	T	AD	-	-	0	0	6	29
		LW	-	-	0	0	2	<1
		RO	-	-	0	0	6	3
		R2	-	-	15	<1	15	60
		OV	-	-	0	0	0	0
		MF	-	-	0	0	0	0
		RE	-	-	0	0	7	3
Heteroplectron sp.	T	AD	-	-	0	0	83	50
		LW	-	-	0	0	0	0
		RO	-	-	0	0	0	0
		R2	-	-	0	0	3	1
		OV	-	-	0	0	0	0
		MF	-	-	1	<1	2	<1
		RE	-	-	0	0	0	0
Hydatopsyche sp.	T	AD	-	-	0	0	6	3
		LW	-	-	8	9	21	28
		RO	-	-	0	0	6	24
		R2	-	-	0	0	18	27
		OV	-	-	0	0	23	150
		MF	-	-	0	0	15	4
		RE	-	-	0	0	13	200
Lepidostoma sp.	T	AD	-	-	19	<1	21	3
		LW	-	-	10	1	4	<1
		RO	-	-	1	<1	19	5
		R2	-	-	35	0	11	0
		OV	-	-	21	<1	4	0
		MF	-	-	5	<1	0	0
		RE	-	-	5	<1	0	0

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Pycnopsyche sp.	T	AD	-	-	49	2	-	-
		LW	-	-	475	19	-	-
		RO	-	-	26	4	-	-
		R2	-	-	530	4	-	-
		OV	-	-	203	14	-	-
		MF	-	-	234	11	-	-
		RE	-	-	228	4	-	-
Psilotreta sp.	T	AD	8	2	8	0	38	13
		LW	0	0	0	0	0	0
		RO	13	1	0	0	46	39
		R2	0	0	0	0	2	<1
		OV	0	0	0	0	5	10
		MF	0	0	0	0	0	0
		RE	0	0	0	0	0	0
Total Shredders		AD	1647	124	3155	36	502	134
		LW	39	1	2231	7161	135	336
		RO	417	26	265	26	144	373
		R2	1488	1488	1488	1488	1488	1488
		OV	5737	296	911	289	1111	241
		MF	1019	106	895	52	1118	635
		RE	133	6	671	280	242	300
Collector-gatherers								
Acerpenna sp.	E	AD	467	11	148	5	4	<1
		LW	58	4	139	28	0	0
		RO	17	13	5	1	0	0
		R2	223	24	103	7	0	0
		OV	50	7	24	5	83	<1
		MF	165	17	42	6	91	<1
		RE	167	4	17	4	0	0

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Baetisca sp.	E	AD	-	-	0	0	0	0
		LW	-	-	0	0	0	0
		RO	-	-	0	0	0	0
		R2	-	-	112	6	0	0
		OV	-	-	1	<1	0	0
		MF	-	-	0	0	50	2
		RE	-	-	0	0	0	0
Ephemerella sp.	E	AD	150	30	1	0	-	-
		LW	0	0	33	3	-	-
		RO	167	31	0	0	-	-
		R2	25	96	33	70	-	-
		OV	30	1	0	0	-	-
		MF	0	0	5	1	-	-
		RE	45	2	0	0	-	-
Ephemera sp.	E	AD	8	4	10	<1	954	368
		LW	33	12	4	<1	88	58
		RO	0	0	15	<1	519	628
		R2	333	120	351	200	15	11
		OV	13	2	107	10	508	195
		MF	0	0	14	1	581	45
		RE	0	0	13	4	156	27
Eurylophella sp.	E	AD	755	35	1	1	13	3
		LW	0	1	0	0	8	1
		RO	333	3	81	2	15	1
		R2	40	27	7	5	17	9
		OV	75	8	14	1	65	5
		MF	108	62	14	1	3	0
		RE	8	2	0	0	6	1

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Habrophlebia sp.	E	AD	-	-	0	0	160	9
		LW	-	-	0	0	0	0
		RO	-	-	1	<1	83	14
		R2	-	-	1	<1	0	0
		OV	-	-	0	0	13	<1
		MF	-	-	15	<1	0	0
		RE	-	-	7	<1	0	0
Paraleptophlebia sp.	E	AD	937	48	585	21	219	19
		LW	0	0	129	9	8	0
		RO	313	12	512	18	110	14
		R2	0	0	140	4	83	0
		OV	167	5	988	31	304	1
		MF	13	2	118	1	33	0
		RE	17	2	46	1	0	0
Serratella sp.	E	AD	1752	237	181	26	4	1
		LW	275	85	782	223	10	<1
		RO	375	123	265	33	2	<1
		R2	4604	1101	522	134	54	3
		OV	781	334	496	85	169	2
		MF	1243	338	870	55	2	1
		RE	432	145	58	11	0	0
Amphinemura sp.	P	AD	92	<1	8	<1	0	0
		LW	17	<1	517	40	4	0
		RO	158	2	52	4	100	0
		R2	107	1	53	<1	33	0
		OV	390	17	72	2	2	0
		MF	433	11	248	1	2	1
		RE	138	3	41	<1	83	0

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Antocha sp.	D	AD	0	0	3	<1	-	-
		LW	283	4	29	7	-	-
		RO	8	0	0	0	-	-
		R2	348	13	75	4	-	-
		OV	0	0	82	3	-	-
		MF	67	<1	136	1	-	-
		RE	17	<1	9	<1	-	-
Chironomidae (non-Tanypodinae)	D	AD	12624	35	1904	5	11617	38
		LW	3089	9	9906	65	3589	15
		RO	29879	91	1227	5	7821	31
		R2	42611	126	4729	12	20739	54
		OV	28260	70	3939	13	11569	25
		MF	20384	17	6373	7	7856	21
		RE	4497	4	939	4	17561	30
Lype sp.	T	AD	-	-	0	0	15	1
		LW	-	-	16	<1	0	0
		RO	-	-	10	<1	0	0
		R2	-	-	29	<1	2	<1
		OV	-	-	31	2	11	1
		MF	-	-	19	1	0	0
		RE	-	-	12	<1	0	0
Micrasema sp.	T	AD	203	5	8	<1	0	0
		LW	0	0	50	1	0	0
		RO	42	5	2	<1	0	0
		R2	213	5	3	1	2	<1
		OV	83	2	0	0	0	0
		MF	627	12	127	<1	17	<1
		RE	0	0	0	0	13	<1

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Copepoda	NI	AD	33	<1	64	<1	4215	2
		LW	83	<1	2200	1	3358	2
		RO	150	<1	254	<1	2547	1
		R2	390	<1	276	<1	939	<1
		OV	321	<1	122	<1	1595	1
		MF	704	1	250	<1	1290	<1
		RE	157	<1	111	<1	9597	5
Entomobryidae	NI	AD	0	0	29	1	0	0
		LW	42	1	104	1	8	<1
		RO	458	9	45	1	52	1
		R2	0	0	8	<1	2	<1
		OV	8	0	1	<1	0	0
		MF	0	0	1	<1	0	0
		RE	8	<1	4	<1	0	0
Nematoda	NI	AD	2413	3	47	<1	3052	3
		LW	8	<1	167	<1	299	1
		RO	3400	4	22	<1	806	1
		R2	1909	2	158	<1	2457	3
		OV	3158	4	38	<1	799	1
		MF	3131	6	908	<1	637	1
		RE	480	<1	20	<1	4419	5
Oligochaeta	NI	AD	28148	80	316	14	4344	92
		LW	1517	2	3451	40	3231	8
		RO	4788	5	163	2	1700	116
		R2	5171	9	3118	19	4332	154
		OV	11991	23	1322	10	1530	16
		MF	9090	25	1062	4	935	25
		RE	2616	7	346	14	12221	112

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Total C-gatherers		AD	47582	487	3305	72	24596	538
		LW	5406	118	17526	416	10603	85
		RO	40088	298	2653	65	13755	807
		R2	55974	1525	9718	463	28673	233
		OV	45327	473	7235	162	16649	248
		MF	35965	490	10201	80	11496	96
		RE	8581	169	1622	38	44057	180
Filterer-gatherers								
Isonychia sp.	E	AD	8	<1	1	<1	0	0
		LW	42	<1	225	4	0	0
		RO	0	0	11	1	8	<1
		R2	0	0	7	7	0	0
		OV	67	3	73	1	0	0
		MF	0	0	0	0	3	<1
		RE	0	0	34	<1	0	0
Dixa sp.	D	AD	0	0	13	<1	17	<1
		LW	25	1	317	25	0	0
		RO	17	<1	8	<1	2	<1
		R2	13	<1	16	<1	4	<1
		OV	67	3	0	0	0	0
		MF	0	0	1	<1	0	0
		RE	0	0	0	0	0	0
Simuliidae	D	AD	947	36	114	8	2	0
		LW	333	6	879	78	4	0
		RO	1 754	56	373	29	22	2
		R2	2159	65	308	341	232	0
		OV	1718	132	1007	91	2	0
		MF	2533	61	240	9	9	0
		RE	755	17	115	3	23	0

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Arctopsyche sp.	T	AD	653	291	11	39	0	0
		LW	0	2	0	0	0	0
		RO	654	138	3	1	2	<1
		R2	0	0	3	1	4	<1
		OV	42	16	1	<1	0	0
		MF	138	2988	0	0	0	0
		RE	242	22	2	1	0	0
Brachycentridae	T	AD	-	-	4	<1	-	-
		LW	-	-	0	0	-	-
		RO	-	-	0	0	-	-
		R2	-	-	0	0	-	-
		OV	-	-	0	0	-	-
		MF	-	-	0	0	-	-
		RE	-	-	0	0	-	-
Cheumatopsyche sp.	T	AD	0	0	0	0	-	-
		LW	0	0	0	0	-	-
		RO	17	5	0	0	-	-
		R2	33	4	27	3	-	-
		OV	8	1	91	17	-	-
		MF	167	2	9	1	-	-
		RE	17	<1	0	0	-	-
Chimera sp.	T	AD	0	0	0	0	-	-
		LW	0	0	0	0	-	-
		RO	17	<1	0	0	-	-
		R2	283	10	1	<1	-	-
		OV	0	0	0	0	-	-
		MF	0	0	0	0	-	-
		RE	0	0	0	0	-	-

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Diplectrona sp.	T	AD	27	9	409	38	0	0
		LW	142	16	394	151	2	6
		RO	1000	43	364	37	2	<1
		R2	1308	117	286	29	94	120
		OV	550	43	229	57	2	0
		MF	282	16	43	5	0	0
		RE	2038	44	542	52	2	2
Dolophilodes sp.	T	AD	120	1	92	13	0	0
		LW	0	0	16	8	0	0
		RO	133	2	81	7	0	0
		R2	50	65	95	19	30	2
		OV	0	0	102	4	17	4
		MF	75	49	40	9	0	0
		RE	0	0	8	<1	0	0
Hydropsychidae	T	AD	838	12	56	16	-	-
		LW	64	22	167	45	-	-
		RO	200	112	89	22	-	-
		R2	1608	400	337	102	-	-
		OV	192	67	31	9	-	-
		MF	430	108	41	5	-	-
		RE	355	140	70	10	-	-
Hydropsyche sp.	T	AD	308	30	40	9	0	0
		LW	100	33	184	60	4	4
		RO	25	24	26	3	0	0
		R2	5499	1419	317	39	387	20
		OV	308	98	17	11	2	1
		MF	571	80	33	3	2	1
		RE	0	0	0	0	0	0

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Phylocentropus sp.	T	AD	-	-	0	0	50	30
		LW	-	-	0	0	0	0
		RO	-	-	7	1	40	13
		R2	-	-	1	<1	9	12
		OV	-	-	1	<1	0	0
		MF	-	-	0	0	92	78
		RE	-	-	0	0	2	<1
Sphaeridae	NI	AD	-	-	0	0	797	49
		LW	-	-	83	2	416	140
		RO	-	-	1	<1	751	29
		R2	-	-	0	0	790	145
		OV	-	-	1	<1	262	20
		MF	-	-	0	0	95	6
		RE	-	-	8	1	517	20
Polycentropus sp.	T	AD	-	-	0	0	-	-
		LW	-	-	0	0	-	-
		RO	-	-	0	0	-	-
		R2	-	-	0	0	-	-
		OV	-	-	7	1	-	-
		MF	-	-	1	<1	-	-
		RE	-	-	0	0	-	-
Total F-collectors		AD	2902	378	739	123	866	79
		LW	706	81	2265	374	426	150
		RO	2063	380	962	100	827	45
		R2	10953	2080	1396	541	1550	300
		OV	2951	364	1561	193	285	25
		MF	4195	3304	408	32	201	85
		RE	3406	223	779	68	544	22

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Predators								
Boyeria sp.	O	AD	-	-	2	1	2	2
		LW	-	-	1	<1	0	0
		RO	-	-	0	0	0	0
		R2	-	-	0	0	0	0
		OV	-	-	0	0	0	0
		MF	-	-	0	0	0	0
		RE	-	-	0	0	0	0
Cordulegaster sp.	O	AD	0	0	3	30	52	105
		LW	0	0	0	0	0	0
		RO	0	0	3	<1	63	73
		R2	8	13	11	44	9	15
		OV	0	0	0	0	18	72
		MF	0	0	0	0	8	2
		RE	0	0	1	3	15	3
Gomphus sp.	O	AD	-	-	2	<1	6	6
		LW	-	-	1	3	0	0
		RO	-	-	1	<1	10	9
		R2	-	-	1	1	8	24
		OV	-	-	16	<1	15	14
		MF	-	-	6	1	6	6
		RE	-	-	1	<1	0	0
Lanthus sp.	O	AD	-	-	1	1	10	147
		LW	-	-	0	0	2	0
		RO	-	-	0	0	0	0
		R2	-	-	1	3	1	53
		OV	-	-	4	24	0	0
		MF	-	-	0	0	2	1
		RE	-	-	0	0	0	0

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Acroneuria sp.	P	AD	0	0	16	46	0	0
		LW	0	0	91	422	0	0
		RO	25	1	35	14	0	0
		R2	0	0	39	316	15	<1
		OV	0	0	61	45	17	<1
		MF	42	15	38	24	0	0
		RE	0	0	26	3	0	0
Agnetina sp.	P	AD	33	<1	26	2	0	0
		LW	0	0	0	0	0	0
		RO	246	4	134	3	0	0
		R2	0	0	39	3	12	<1
		OV	0	0	5	<1	0	0
		MF	164	2	32	<1	8	<1
		RE	0	0	7	<1	0	0
Beloneuria sp.	P	AD	-	-	23	21	0	0
		LW	-	-	50	41	0	0
		RO	-	-	6	13	2	36
		R2	-	-	14	69	0	0
		OV	-	-	5	1	0	0
		MF	-	-	4	34	0	0
		RE	-	-	4	2	0	0
Haploperla sp.	P	AD	-	-	8	1	23	8
		LW	-	-	18	10	0	0
		RO	-	-	8	1	15	5
		R2	-	-	110	2	99	0
		OV	-	-	26	1	1017	6
		MF	-	-	31	<1	117	1
		RE	-	-	17	1	27	<1

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Isoperla sp.	P	AD	100	40	6	4	0	0
		LW	0	0	67	4	0	0
		RO	246	26	82	5	0	0
		R2	379	20	60	7	17	<1
		OV	700	67	28	11	0	0
		MF	863	97	162	2	0	0
		RE	499	13	24	2	0	0
Atherix sp.	D	AD	31	2	9	<1	0	0
		LW	0	0	0	0	0	0
		RO	67	49	4	1	0	0
		R2	8	6	2	1	1	<1
		OV	50	47	3	1	0	0
		MF	113	59	8	3	0	0
		RE	54	7	3	1	0	0
Atrichopogon sp.	D	AD	-	-	0	0	-	-
		LW	-	-	0	0	-	-
		RO	-	-	0	0	-	-
		R2	-	-	22	<1	-	-
		OV	-	-	0	0	-	-
		MF	-	-	0	0	-	-
		RE	-	-	0	0	-	-
Ceratopogonidae	D	AD	594	17	65	4	2317	82
		LW	67	0	139	14	692	18
		RO	300	11	97	4	2733	77
		R2	1924	71	112	6	748	54
		OV	617	30	70	5	1074	33
		MF	8	1	36	5	949	22
		RE	25	2	46	3	3406	63

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Chelifera sp.	D	AD	169	3	16	<1	35	<1
		LW	83	1	7	<1	0	0
		RO	163	2	1	<1	0	0
		R2	481	6	93	<1	47	<1
		OV	742	16	54	2	0	0
		MF	444	4	366	<1	0	0
		RE	58	<1	9	<1	0	0
Dicranota sp.	D	AD	172	7	13	1	8	6
		LW	17	1	122	4	2	<1
		RO	138	1	19	<1	0	0
		R2	138	7	38	2	0	0
		OV	520	48	28	1	2	<1
		MF	50	3	17	1	0	0
		RE	17	5	2	0	0	0
Hemerodromia sp.	D	AD	-	-	0	0	25	<1
		LW	-	-	0	0	0	0
		RO	-	-	1	<1	17	<1
		R2	-	-	0	0	0	0
		OV	-	-	1	<1	0	0
		MF	-	-	0	0	0	0
		RE	-	-	0	0	0	0
Hexatoma sp.	D	AD	0	0	17	11	323	204
		LW	0	0	0	2	33	8
		RO	0	0	13	6	136	60
		R2	0	0	4	3	47	52
		OV	52	1	37	8	67	47
		MF	0	0	0	0	13	2
		RE	13	<1	1	1	460	31

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Limnophila sp.	D	AD	-	-	0	0	0	0
		LW	-	-	8	1	2	5
		RO	-	-	0	0	25	30
		R2	-	-	1	<1	13	14
		OV	-	-	7	0	8	7
		MF	-	-	0	0	0	0
		RE	-	-	1	<1	0	0
Chironomidae (Tanypodinae)	D	AD	258	1	143	1	2098	15
		LW	114	<1	99	1	178	<1
		RO	133	<1	57	1	781	2
		R2	821	3	182	1	245	4
		OV	375	1	132	1	1028	2
		MF	78	<1	43	<1	131	<1
		RE	0	0	12	<1	529	1
Rhyacophila sp.	T	AD	292	5	424	15	53	1
		LW	208	3	628	35	13	<1
		RO	600	22	88	2	0	0
		R2	238	45	115	17	19	<1
		OV	110	1	176	5	0	0
		MF	292	8	186	3	8	<1
		RE	56	<1	34	1	13	<1
Acari	NI	AD	2144	29	384	8	392	5
		LW	1742	23	2930	38	120	4
		RO	2196	33	214	2	99	1
		R2	1748	20	880	11	248	1
		OV	4558	79	723	9	325	9
		MF	6209	137	993	5	79	2
		RE	4569	59	355	4	611	8

Appendix A (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Total Predators		AD	3794	104	1156	147	5346	581
		LW	2231	28	4159	575	1042	35
		RO	4113	147	762	52	3880	293
		R2	5745	191	1724	487	1531	218
		OV	7724	290	1374	114	3570	190
		MF	8261	327	1923	78	1321	35
		RE	5290	85	542	19	5062	106

Appendix B. Abundance and biomass data. Mean annual abundance (A, no./m-2) and biomass (B, mg AFDM/m-2) of taxa in each functional feeding group in bedrock outcrop, cobble riffle, and depositional habitats in study streams. Insect orders are as follows: C = Coleoptera, D = Diptera, E = Ephemeroptera, P = Plecoptera, O = Odonata, T = Trichoptera, and NI = non-insect.

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Scrapers								
Ameletus sp.	E	L1	11	<1	24	14	44	<1
		L2	0	0	0	0	0	0
		L3	0	0	0	0	0	0
		L4	0	0	0	0	0	0
Baetis sp.	E	L1	-	-	299	3	84	2
		L2	-	-	853	17	50	1
		L3	-	-	1206	28	37	<1
		L4	-	-	1918	35	31	<1
Cinygmula sp.	E	L1	-	-	43	3	-	-
		L2	-	-	5	<1	-	-
		L3	-	-	1	<1	-	-
		L4	-	-	4	<1	-	-
Drunella sp.	E	L1	11	<1	208	23	0	0
		L2	7	0	30	39	0	0
		L3	0	0	19	6	2	<1
		L4	40	35	59	8	2	<1
Epeorus sp.	E	L1	44	169	127	25	3	<1
		L2	13	63	177	28	0	0
		L3	0	0	10	4	0	0
		L4	7	8	10	6	0	0
Heptageniidae	E	L1	89	1	15	<1	-	-
		L2	107	1	0	0	-	-
		L3	0	0	32	<1	-	-
		L4	0	0	0	0	-	-

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Stenacron sp.	E	L1	-	-	9	1	0	0
		L2	-	-	24	1	3	<1
		L3	-	-	4	<1	0	0
		L4	-	-	5	<1	0	0
Rhithrogenia sp.	E	L1	-	-	2	14	-	-
		L2	-	-	10	7	-	-
		L3	-	-	1	0	-	-
		L4	-	-	0	0	-	-
Stenonema sp.	E	L1	0	0	109	18	25	1
		L2	7	<1	327	30	27	<1
		L3	0	0	215	22	30	<1
		L4	53	1	759	78	4	1
Ectopria sp.	C	L1	11	<1	27	<1	0	0
		L2	13	2	170	69	11	3
		L3	0	0	40	13	0	0
		L4	7	6	52	16	0	0
Optioservus sp.	C	L1	0	0	205	6	0	0
		L2	0	0	128	4	42	2
		L3	0	0	548	17	5	<1
		L4	67	2	320	13	25	2
Promoresia sp.	C	L1	5 815	127	147	1	22	<1
		L2	293	13	20	1	29	<1
		L3	0	0	560	19	3	<1
		L4	313	7	183	10	7	<1
Apatania sp.	T	L1	11	1	0	<1	-	-
		L2	7	1	7	1	-	-
		L3	0	0	0	0	-	-
		L4	0	0	6	<1	-	-

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Goera sp.	T	L1	56	<1	0	0	-	-
		L2	0	0	3	<1	-	-
		L3	0	0	1	2	-	-
		L4	0	0	1	<1	-	-
Glossosoma sp.	T	L1	-	-	31	0	-	-
		L2	-	-	33	3	-	-
		L3	-	-	69	3	-	-
		L4	-	-	15	4	-	-
Neophylax sp.	T	L1	44	<1	19	<1	-	-
		L2	0	0	0	0	-	-
		L3	0	0	1	<1	-	-
		L4	0	0	1	<1	-	-
Total Scrapers		L1	6 093	297	1265	109	179	3
		L2	447	79	1788	201	161	5
		L3	0	0	2707	114	77	0
		L4	487	59	3331	169	68	3
Shredders								
Leuctra sp.	P	L1	-	-	64	3	344	13
		L2	-	-	134	11	82	0
		L3	-	-	29	2	0	0
		L4	-	-	0	0	0	0
Ostrocerca sp.	P	L1	-	-	1	<1	-	-
		L2	-	-	0	0	-	-
		L3	-	-	0	0	-	-
		L4	-	-	0	0	-	-
Pteronarcys sp.	P	L1	-	-	0	0	-	-
		L2	-	-	1	20	-	-
		L3	-	-	0	0	-	-
		L4	-	-	1	6	-	-

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Tallaperla sp.	P	L1	857	59	3855	6	22	0
		L2	7	<1	1	1	0	0
		L3	0	0	0	0	0	0
		L4	0	0	0	0	0	0
Ancyronyx sp.	C	L1	-	-	0	0	3	15
		L2	-	-	0	0	0	0
		L3	-	-	1	3	0	0
		L4	-	-	0	0	0	0
Molophilus sp.	D	L1	611	16	-	-	42	8
		L2	0	0	-	-	70	6
		L3	0	0	-	-	3	1
		L4	0	0	-	-	0	0
Tipula sp.	D	L1	11	1	0	0	3	12
		L2	7	26	0	0	3	17
		L3	0	0	0	0	0	0
		L4	0	0	14	1	2	76
Agarodes sp.	T	L1	-	-	2	5	-	-
		L2	-	-	0	0	-	-
		L3	-	-	0	0	-	-
		L4	-	-	0	0	-	-
Fattigia sp.	T	L1	-	-	-	-	38	8
		L2	-	-	-	-	0	0
		L3	-	-	-	-	0	0
		L4	-	-	-	-	0	0
Hydatopsyche sp.	T	L1	-	-	-	-	8	4
		L2	-	-	-	-	7	5
		L3	-	-	-	-	0	0
		L4	-	-	-	-	0	0

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Lepidostoma sp.	T	L1	44	<1	21	<1	28	4
		L2	0	0	3	0	0	0
		L3	0	0	2	1	0	0
		L4	7	<1	10	2	0	0
Psilotreta sp.	T	L1	11	3	10	<1	47	15
		L2	0	0	0	0	0	0
		L3	0	0	0	0	0	0
		L4	0	0	0	0	0	0
Pycnopsyche sp.	T	L1	-	-	1	1	-	-
		L2	-	-	0	0	-	-
		L3	-	-	0	0	-	-
		L4	-	-	0	0	-	-
Total Shredders		L1	1535	78	3954	16	489	67
		L2	13	26	138	32	155	24
		L3	0	0	32	5	3	1
		L4	7	0	24	9	2	76
Collector-gatherers								
Acerpenna sp.	E	L1	100	3	148	6	6	0
		L2	60	4	7	1	0	0
		L3	0	0	1	0	0	0
		L4	40	1	59	5	0	0
Ephemerella sp.	E	L1	200	4	1	<1	0	0
		L2	40	11	44	9	25	3
		L3	0	0	83	14	0	0
		L4	73	64	98	37	3	1
Ephemera sp.	E	L1	11	5	11	<1	1246	477
		L2	0	0	2	<1	0	0
		L3	0	0	0	0	0	0
		L4	0	0	0	0	2	<1

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Eurylophella sp.	E	L1	1007	8	1	1	11	4
		L2	0	0	34	3	59	10
		L3	0	0	11	1	25	10
		L4	0	0	1	<1	2	1
Habrophlebia sp.	E	L1	-	-	-	-	192	12
		L2	-	-	-	-	0	0
		L3	-	-	-	-	0	0
		L4	-	-	-	-	0	0
Paraleptophlebia sp.	E	L1	782	45	474	17	267	23
		L2	0	0	47	6	13	<1
		L3	0	0	22	0	0	0
		L4	0	0	26	1	13	<1
Serratella sp.	E	L1	2302	304	202	34	3	2
		L2	187	62	23	4	5	1
		L3	0	0	136	36	0	0
		L4	440	109	134	41	3	2
Amphinemura sp.	P	L1	78	1	10	<1	-	-
		L2	60	0	1	<1	-	-
		L3	0	0	47	<1	-	-
		L4	0	0	0	0	-	-
Antocha sp.	D	L1	0	0	4	<1	0	0
		L2	237	4	467	12	6	1
		L3	0	0	283	16	0	0
		L4	173	1	119	3	0	0
Chironomidae (non-Tanypodinae)	D	L1	9847	33	1992	6	13031	45
		L2	11257	33	3442	17	10686	32
		L3	160	0	2959	14	14664	213
		L4	7027	17	2821	9	10562	47

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Lype sp.	T	L1	-	-	-	-	19	2
		L2	-	-	-	-	0	0
		L3	-	-	-	-	0	0
		L4	-	-	-	-	0	0
Micrasema sp.	T	L1	-	-	0	0	0	0
		L2	-	-	18	1	2	0
		L3	-	-	251	16	0	0
		L4	-	-	306	12	70	1
Copepoda	NI	L1	0	0	79	<1	4814	<1
		L2	40	<1	50	<1	510	1
		L3	0	0	6	<1	212	<1
		L4	0	0	15	<1	393	<1
Entomobryidae	NI	L1	0	0	12	<1	0	0
		L2	0	0	7	<1	0	0
		L3	7	<1	0	0	13	<1
		L4	0	0	0	0	2	<1
Nematoda	NI	L1	2170	3	53	<1	3711	4
		L2	127	<1	54	<1	480	1
		L3	0	0	84	<1	519	1
		L4	258	<1	37	<1	527	1
Oligochaeta	NI	L1	9250	15	337	17	4937	81
		L2	1707	2	914	8	2038	32
		L3	0	0	399	1	1100	72
		L4	1014	2	580	18	4832	52
Total C-gatherers		L1	25747	420	3123	47	28023	634
		L2	13714	116	5088	56	13819	79
		L3	167	0	4146	63	16534	295
		L4	9026	194	4063	85	16406	103

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Filterer-gatherers								
Isonychia sp.	E	L1	11	<1	0	0	0	0
		L2	0	0	88	2	168	2
		L3	7	<1	26	1	0	0
		L4	0	0	332	54	50	<1
Dixa sp.	D	L1	-	-	5	<1	-	-
		L2	-	-	0	0	-	-
		L3	-	-	0	0	-	-
		L4	-	-	0	0	-	-
Simuliidae	D	L1	963	19	57	6	0	0
		L2	4586	35	338	3	92	<1
		L3	180	5	629	9	51	<1
		L4	2625	31	587	6	10	<1
Arctopsyche sp.	T	L1	631	71	11	48	-	-
		L2	0	0	0	0	-	-
		L3	0	0	0	0	-	-
		L4	0	0	0	0	-	-
Brachycentrus sp.	T	L1	-	-	0	0	0	0
		L2	-	-	4	1	2	<1
		L3	-	-	6	7	0	0
		L4	-	-	0	0	0	0
Cheumatopsyche sp.	T	L1	0	0	0	0	-	-
		L2	7	<1	7	3	-	-
		L3	0	0	123	10	-	-
		L4	80	4	40	6	-	-
Diplectrona sp.	T	L1	11	6	12	6	-	-
		L2	0	0	0	0	-	-
		L3	0	0	0	0	-	-
		L4	0	0	0	0	-	-

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Dolophilodes sp.	T	L1	160	1	90	7	-	-
		L2	20	13	55	17	-	-
		L3	0	0	0	0	-	-
		L4	0	0	0	0	-	-
Hydropsyche sp.	T	L1	56	24	11	7	0	0
		L2	1362	118	191	32	2	<1
		L3	7	0	170	25	2	<1
		L4	3616	1035	304	46	3	<1
Polycentropodidae	T	L1	-	-	-	-	3	<1
		L2	-	-	-	-	0	0
		L3	-	-	-	-	0	0
		L4	-	-	-	-	0	0
Phylocentropus sp.	T	L1	-	-	-	-	67	40
		L2	-	-	-	-	2	<1
		L3	-	-	-	-	27	66
		L4	-	-	-	-	2	<1
Nyctiophylax sp.	T	L1	-	-	1	1	-	-
		L2	-	-	0	0	-	-
		L3	-	-	29	1	-	-
		L4	-	-	0	0	-	-
Sphaeridae	NI	L1	-	-	0	0	1015	59
		L2	-	-	0	0	83	6
		L3	-	-	1	<1	253	21
		L4	-	-	11	1	174	11
Total F-gatherers		L1	869	101	188	74	1085	99
		L2	1389	131	682	58	348	8
		L3	13	0	984	54	332	87
		L4	3696	1039	1274	112	239	11

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Predators								
Cordulegaster sp.	O	L1	-	-	4	41	67	140
		L2	-	-	0	0	0	0
		L3	-	-	0	0	0	0
		L4	-	-	0	0	0	0
Gomphus sp.	O	L1	-	-	2	<1	8	8
		L2	-	-	1	1	0	0
		L3	-	-	1	1	7	22
		L4	-	-	0	0	0	0
Lanthus sp.	O	L1	-	-	1	1	8	117
		L2	-	-	1	<1	2	7
		L3	-	-	0	0	0	0
		L4	-	-	0	0	0	0
Agnetina sp.	P	L1	44	1	15	2	-	-
		L2	67	1	44	1	-	-
		L3	0	0	50	4	-	-
		L4	87	1	103	2	-	-
Beloneuria sp.	P	L1	0	0	27	28	-	-
		L2	0	0	7	1	-	-
		L3	0	0	6	3	-	-
		L4	67	40	11	6	-	-
Haploperla sp.	P	L1	-	-	11	1	31	10
		L2	-	-	0	0	0	0
		L3	-	-	0	0	0	0
		L4	-	-	0	0	0	0
Isoperla sp.	P	L1	-	-	6	5	-	-
		L2	-	-	58	8	-	-
		L3	-	-	3	1	-	-
		L4	-	-	2	0	-	-

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Atrichopogon sp.	D	L1	156	1	-	-	0	0
		L2	0	0	-	-	0	0
		L3	0	0	-	-	0	0
		L4	0	0	-	-	3	<1
Atherix sp.	D	L1	11	<1	0	0	-	-
		L2	7	4	1	<1	-	-
		L3	0	0	0	0	-	-
		L4	7	4	0	0	-	-
Ceratopogonidae	D	L1	567	14	53	4	2706	86
		L2	13	1	31	4	361	16
		L3	0	0	27	1	299	41
		L4	40	0	15	1	293	12
Chelifera sp.	D	L1	226	4	21	<1	47	1
		L2	242	3	37	1	68	0
		L3	0	0	1	<1	0	0
		L4	24	1	1	<1	0	0
Dicranota sp.	D	L1	207	9	7	<1	11	8
		L2	0	0	0	0	53	<1
		L3	0	0	0	0	2	<1
		L4	0	0	0	0	0	0
Empididae	D	L1	-	-	0	0	-	-
		L2	-	-	1	<1	-	-
		L3	-	-	4	<1	-	-
		L4	-	-	0	0	-	-
Hemerodromia sp.	D	L1	0	0	0	0	0	0
		L2	136	3	44	1	47	1
		L3	0	0	53	1	0	0
		L4	138	1	29	1	13	<1

Appendix B (cont.)

			Bedrock Outcrop		Cobble Riffle		Depositional	
Functional group or taxon	Order	Site	A	B	A	B	A	B
Hexatoma sp.	D	L1	-	-	23	14	423	267
		L2	-	-	1	1	3	4
		L3	-	-	0	0	2	2
		L4	-	-	1	2	0	0
Chironomidae (non-Tanypodinae)	D	L1	133	1	123	1	2150	19
		L2	133	1	70	1	185	<1
		L3	0	0	172	1	258	2
		L4	27	<1	188	2	262	2
Rhyacophila sp.	T	L1	-	-	319	19	70	2
		L2	-	-	11	1	0	0
		L3	-	-	48	0	0	0
		L4	-	-	1	1	7	<1
Acari	NI	L1	1415	21	345	4	334	4
		L2	1123	14	705	9	165	2
		L3	0	0	1235	16	107	1
		L4	765	10	1136	14	80	1
Total Predators		L1	2759	50	957	119	5854	662
		L2	1722	27	1013	28	883	31
		L3	0	0	1599	29	674	68
		L4	1154	56	1489	30	658	14

Appendix C. Abundance and biomass data. Mean annual abundance (A, no./m-2) and biomass (B, mg AFDM/m-2) of taxa in leaf bags. Insect orders are as follows: C =Coleoptera, D = Diptera, E = Ephemeroptera, P = Plecoptera, O = Odonata, T = Trichoptera, and NI = non-insect.

Functional group or taxon	Order	Site	Date	A	B
Scrapers					
Ameletus sp.	E	AD	17-Dec-01	2	1
			5-Jan-02	1	1
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	5	<1
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
Baetis sp.	E	AD	17-Dec-01	26	1
			5-Jan-02	23	1
			5-Feb-02	8	<1
			11-Jun-02	4	0
		LW	17-Dec-01	0	<1
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	4	<1
			5-Jan-02	2	<1
			5-Feb-02	5	<1
			11-Jun-02	1	<1
		R2	17-Dec-01	0	0
			5-Jan-02	5	<1
			5-Feb-02	2	<1

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Epeorus sp.	E	AD	17-Dec-01	1	<1
			5-Jan-02	1	<1
			5-Feb-02	2	<1
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
Diura sp.	P	AD	17-Dec-01	1	<1
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Ectopria sp.	C	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	<1	<1
			5-Jan-02	0	0
			5-Feb-02	0	0
Promoresia sp.	C	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	<1	<1
			11-Jun-02	1	0
		LW	17-Dec-01	0	0
			5-Jan-02	<1	<1
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	2	<1
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	2	<1

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Goera sp.	T	AD	17-Dec-01	2	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
Total Scrapers		AD	17-Dec-01	32	2
			5-Jan-02	25	2
			5-Feb-02	10	0
			11-Jun-02	5	<1
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	8	<1
			5-Jan-02	2	0
			5-Feb-02	5	0
			11-Jun-02	2	0
		R2	17-Dec-01	0	0
			5-Jan-02	5	<1
			5-Feb-02	4	<1

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Shredders					
Leuctra sp.	P	AD	17-Dec-01	1	0
			5-Jan-02	1	0
			5-Feb-02	24	1
			11-Jun-02	1401	8
		LW	17-Dec-01	60	0
			5-Jan-02	136	8
			5-Feb-02	321	14
		RO	17-Dec-01	2	0
			5-Jan-02	29	2
			5-Feb-02	88	9
			11-Jun-02	2	1
		R2	17-Dec-01	7	0
			5-Jan-02	101	5
			5-Feb-02	33	3
Pteronarcys sp.	P	AD	17-Dec-01	0	0
			5-Jan-02	1	<1
			5-Feb-02	2	68
			11-Jun-02	0	<1
		LW	17-Dec-01	<1	<1
			5-Jan-02	6	1
			5-Feb-02	11	30
		RO	17-Dec-01	0	0
			5-Jan-02	2	<1
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	58
			5-Jan-02	1	113
			5-Feb-02	10	4

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Tallaperla sp.	P	AD	17-Dec-01	4	5
			5-Jan-02	17	27
			5-Feb-02	82	151
			11-Jun-02	0	0
		LW	17-Dec-01	2	3
			5-Jan-02	0	0
			5-Feb-02	28	67
		RO	17-Dec-01	3	3
			5-Jan-02	2	5
			5-Feb-02	5	0
			11-Jun-02	3	6
		R2	17-Dec-01	7	26
			5-Jan-02	2	5
			5-Feb-02	20	38
Ancyronyx sp.	C	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	<1	1
			5-Feb-02	<1	1
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	1	2
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Molophilus sp.	D	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	<1	1
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
Tipula sp.	D	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	1	0
		LW	17-Dec-01	0	0
			5-Jan-02	1	168
			5-Feb-02	2	495
		RO	17-Dec-01	0	0
			5-Jan-02	0	13
			5-Feb-02	0	0
			11-Jun-02	5	52
		R2	17-Dec-01	3	495
			5-Jan-02	4	779
			5-Feb-02	3	824

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Agarodes sp.	T	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	<1	1
		LW	17-Dec-01	1	0
			5-Jan-02	<1	1
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
Fattigia sp.	T	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	1	<1
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	<1	1
			11-Jun-02	1	<1
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Lepidostoma sp.	T	AD	17-Dec-01	13	1
			5-Jan-02	27	2
			5-Feb-02	23	3
			11-Jun-02	3	0
		LW	17-Dec-01	2	0
			5-Jan-02	2	0
			5-Feb-02	11	0
		RO	17-Dec-01	13	0
			5-Jan-02	30	0
			5-Feb-02	4	0
			11-Jun-02	5	4
		R2	17-Dec-01	48	0
			5-Jan-02	106	1
			5-Feb-02	43	1
Psilotreta sp.	T	AD	17-Dec-01	0	1
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	4
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	1	4
			5-Jan-02	0	0
			5-Feb-02	1	9
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Pycnopsyche sp.	T	AD	17-Dec-01	2	<1
			5-Jan-02	2	1
			5-Feb-02	<1	1
			11-Jun-02	1	<1
		LW	17-Dec-01	7	3
			5-Jan-02	2	1
			5-Feb-02	6	4
		RO	17-Dec-01	1	<1
			5-Jan-02	1	1
			5-Feb-02	1	1
			11-Jun-02	1	<1
		R2	17-Dec-01	1	<1
			5-Jan-02	4	2
			5-Feb-02	1	1
Total Shredders		AD	17-Dec-01	20	6
			5-Jan-02	49	30
			5-Feb-02	130	223
			11-Jun-02	1406	9
		LW	17-Dec-01	71	11
			5-Jan-02	147	180
			5-Feb-02	379	612
		RO	17-Dec-01	19	8
			5-Jan-02	65	21
			5-Feb-02	100	21
			11-Jun-02	15	63
		R2	17-Dec-01	66	580
			5-Jan-02	218	906
			5-Feb-02	109	871

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Collector-gatherers					
Acerpenna sp.	E	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	<1	<1
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
Ephemera sp.	E	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	1
		LW	17-Dec-01	2	0
			5-Jan-02	1	2
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	4	7
			11-Jun-02	4	4
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	1	<1

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Eurylophella sp.	E	AD	17-Dec-01	0	0
			5-Jan-02	1	1
			5-Feb-02	0	0
			11-Jun-02	128	0
		LW	17-Dec-01	0	<1
			5-Jan-02	0	0
			5-Feb-02	2	5
		RO	17-Dec-01	1	<1
			5-Jan-02	1	<1
			5-Feb-02	<1	<1
			11-Jun-02	1	1
		R2	17-Dec-01	5	3
			5-Jan-02	2	1
			5-Feb-02	2	2
Habrophlebia sp.	E	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	1	<1
			5-Jan-02	1	<1
			5-Feb-02	0	0
		RO	17-Dec-01	<1	<1
			5-Jan-02	1	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	<1	<1
			5-Jan-02	0	0
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Paraleptophlebia sp.	E	AD	17-Dec-01	9	3
			5-Jan-02	27	9
			5-Feb-02	20	10
			11-Jun-02	307	120
		LW	17-Dec-01	1	1
			5-Jan-02	1	1
			5-Feb-02	10	2
		RO	17-Dec-01	15	1
			5-Jan-02	51	3
			5-Feb-02	22	6
			11-Jun-02	16	4
		R2	17-Dec-01	6	2
			5-Jan-02	11	1
			5-Feb-02	3	<1
Stenonema sp.	E	AD	17-Dec-01	2	3
			5-Jan-02	1	2
			5-Feb-02	1	3
			11-Jun-02	0	1
		LW	17-Dec-01	1	1
			5-Jan-02	0	1
			5-Feb-02	7	5
		RO	17-Dec-01	1	1
			5-Jan-02	0	0
			5-Feb-02	1	1
			11-Jun-02	1	3
		R2	17-Dec-01	9	6
			5-Jan-02	5	3
			5-Feb-02	5	1

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Amphinemura sp.	P	AD	17-Dec-01	2	<1
			5-Jan-02	5	<1
			5-Feb-02	5	1
			11-Jun-02	0	<1
		LW	17-Dec-01	4	<1
			5-Jan-02	8	<1
			5-Feb-02	105	12
		RO	17-Dec-01	5	<1
			5-Jan-02	30	<1
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	12	<1
			5-Feb-02	0	0
Antocha sp.	D	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	1	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Chironomidae (non-Tanypodinae)	D	AD	17-Dec-01	120	<1
			5-Jan-02	276	1
			5-Feb-02	250	1
			11-Jun-02	5068	2
		LW	17-Dec-01	667	1
			5-Jan-02	723	3
			5-Feb-02	892	6
		RO	17-Dec-01	786	1
			5-Jan-02	832	3
			5-Feb-02	941	3
			11-Jun-02	317	2
		R2	17-Dec-01	1785	4
			5-Jan-02	1781	5
			5-Feb-02	635	2
Lype sp.	T	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Micrasema sp.	T	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	<1	<1
			11-Jun-02	0	0
		R2	17-Dec-01	<1	<1
			5-Jan-02	0	0
			5-Feb-02	<1	<1
Copepoda	NI	AD	17-Dec-01	15	<1
			5-Jan-02	10	<1
			5-Feb-02	12	<1
			11-Jun-02	820	<1
		LW	17-Dec-01	209	<1
			5-Jan-02	307	<1
			5-Feb-02	441	<1
		RO	17-Dec-01	20	<1
			5-Jan-02	20	<1
			5-Feb-02	172	<1
			11-Jun-02	161	<1
		R2	17-Dec-01	93	<1
			5-Jan-02	64	<1
			5-Feb-02	15	<1

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Entomobryidae	NI	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	1	<1
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	1	<1
		RO	17-Dec-01	0	0
			5-Jan-02	3	<1
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	9	<1
Nematoda	NI	AD	17-Dec-01	1	<1
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	3	<1
		LW	17-Dec-01	55	<1
			5-Jan-02	29	<1
			5-Feb-02	2	<1
		RO	17-Dec-01	<1	<1
			5-Jan-02	0	0
			5-Feb-02	<1	<1
			11-Jun-02	0	0
		R2	17-Dec-01	10	<1
			5-Jan-02	9	<1
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Oligochaeta	NI	AD	17-Dec-01	4	<1
			5-Jan-02	3	<1
			5-Feb-02	6	<1
			11-Jun-02	0	<1
		LW	17-Dec-01	87	<1
			5-Jan-02	203	5
			5-Feb-02	0	0
		RO	17-Dec-01	4	<1
			5-Jan-02	84	<1
			5-Feb-02	0	11
			11-Jun-02	0	0
		R2	17-Dec-01	82	<1
			5-Jan-02	380	2
			5-Feb-02	39	<1
Total C-gatherers		AD	17-Dec-01	153	5
			5-Jan-02	321	12
			5-Feb-02	293	14
			11-Jun-02	6327	124
		LW	17-Dec-01	1026	3
			5-Jan-02	1272	12
			5-Feb-02	1460	30
		RO	17-Dec-01	831	3
			5-Jan-02	1020	6
			5-Feb-02	1140	29
			11-Jun-02	499	13
		R2	17-Dec-01	1989	16
			5-Jan-02	2264	12
			5-Feb-02	708	5

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Filterer-gatherers					
Isonychia sp.	E	AD	17-Dec-01	0	0
			5-Jan-02	1	<1
			5-Feb-02	3	<1
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	4	<1
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
Dixa sp.	D	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	1	<1
		RO	17-Dec-01	8	<1
			5-Jan-02	6	<1
			5-Feb-02	0	<1
			11-Jun-02	0	0
		R2	17-Dec-01	<1	<1
			5-Jan-02	3	<1
			5-Feb-02	21	<1

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Simuliidae	D	AD	17-Dec-01	<1	<1
			5-Jan-02	9	<1
			5-Feb-02	22	1
			11-Jun-02	0	<1
		LW	17-Dec-01	2	<1
			5-Jan-02	0	0
			5-Feb-02	1	<1
		RO	17-Dec-01	35	<1
			5-Jan-02	32	1
			5-Feb-02	0	0
			11-Jun-02	2	<1
		R2	17-Dec-01	10	<1
			5-Jan-02	26	1
			5-Feb-02	1	<1
Dolophilodes sp.	T	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	1	1
			5-Jan-02	0	0
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Diplectrona sp.	T	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	2	1
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	1	<1
			5-Feb-02	7	8
		RO	17-Dec-01	5	1
			5-Jan-02	5	4
			5-Feb-02	<1	<1
			11-Jun-02	23	4
		R2	17-Dec-01	5	1
			5-Jan-02	12	4
			5-Feb-02	3	2
Hydropsyche sp.	T	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	<1	<1
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	4	1

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Phylocentropus sp.	T	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	1	<1
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	1	1
		RO	17-Dec-01	0	0
			5-Jan-02	9	<1
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	2	<1
			5-Feb-02	0	0
Sphaeridae	NI	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	1	1
		LW	17-Dec-01	13	0
			5-Jan-02	8	0
			5-Feb-02	2	<1
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	3	<1
			11-Jun-02	0	0
		R2	17-Dec-01	3	<1
			5-Jan-02	14	1
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Total F-gatherers		AD	17-Dec-01	0	0
			5-Jan-02	10	<1
			5-Feb-02	27	2
			11-Jun-02	1	1
		LW	17-Dec-01	15	<1
			5-Jan-02	8	<1
			5-Feb-02	16	9
		RO	17-Dec-01	48	1
			5-Jan-02	52	5
			5-Feb-02	3	<1
			11-Jun-02	25	4
		R2	17-Dec-01	19	2
			5-Jan-02	56	6
			5-Feb-02	29	3
Predators					
Cordulegaster sp.	O	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	1	<1
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	<1	<1
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	2	1
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Lanthus sp.	O	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	<1	1
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
Acroneuria sp.	P	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	2	<1
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	<1	<1
		RO	17-Dec-01	0	0
			5-Jan-02	<1	<1
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	<1	<1
			5-Jan-02	1	18
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Agnetina sp.	P	AD	17-Dec-01	7	<1
			5-Jan-02	14	1
			5-Feb-02	10	2
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	18	<1
			5-Jan-02	32	<1
			5-Feb-02	0	0
			11-Jun-02	2	<1
		R2	17-Dec-01	1	<1
			5-Jan-02	7	<1
			5-Feb-02	0	0
Diploperla sp.	P	AD	17-Dec-01	1	<1
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	4	1
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	16	4
			5-Jan-02	0	0
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Haploperla sp.	P	AD	17-Dec-01	0	0
			5-Jan-02	3	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	7	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	6	2
			5-Jan-02	0	0
			5-Feb-02	0	0
Isoperla sp.	P	AD	17-Dec-01	1	1
			5-Jan-02	15	3
			5-Feb-02	26	10
			11-Jun-02	0	0
		LW	17-Dec-01	3	<1
			5-Jan-02	0	<1
			5-Feb-02	20	6
		RO	17-Dec-01	0	0
			5-Jan-02	39	1
			5-Feb-02	10	1
			11-Jun-02	4	1
		R2	17-Dec-01	11	1
			5-Jan-02	44	6
			5-Feb-02	26	8

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Ceratopogonidae	D	AD	17-Dec-01	0	0
			5-Jan-02	1	<1
			5-Feb-02	2	1
			11-Jun-02	25	1
		LW	17-Dec-01	7	<1
			5-Jan-02	7	1
			5-Feb-02	19	6
		RO	17-Dec-01	1	<1
			5-Jan-02	5	1
			5-Feb-02	35	7
			11-Jun-02	43	5
		R2	17-Dec-01	3	1
			5-Jan-02	11	4
			5-Feb-02	6	1
Chelifera sp.	D	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	1	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	3	0
			5-Jan-02	0	0
			5-Feb-02	3	0
			11-Jun-02	2	0
		R2	17-Dec-01	0	0
			5-Jan-02	7	0
			5-Feb-02	1	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Dicranota sp.	D	AD	17-Dec-01	0	0
			5-Jan-02	3	<1
			5-Feb-02	6	<1
			11-Jun-02	43	<1
		LW	17-Dec-01	3	<1
			5-Jan-02	5	<1
			5-Feb-02	26	4
		RO	17-Dec-01	4	<1
			5-Jan-02	3	<1
			5-Feb-02	0	0
			11-Jun-02	2	<1
		R2	17-Dec-01	1	<1
			5-Jan-02	10	<1
			5-Feb-02	2	<1
Hemerodromia sp.	D	AD	17-Dec-01	<1	<1
			5-Jan-02	1	<1
			5-Feb-02	<1	<1
			11-Jun-02	0	0
		LW	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	0	0

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Hexatoma sp.	D	AD	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	1	0
			11-Jun-02	2	1
		LW	17-Dec-01	0	0
			5-Jan-02	1	5
			5-Feb-02	1	0
		RO	17-Dec-01	0	0
			5-Jan-02	0	1
			5-Feb-02	0	0
			11-Jun-02	4	4
		R2	17-Dec-01	0	0
			5-Jan-02	0	0
			5-Feb-02	2	0
Chironomidae (Tanypodinae)	D	AD	17-Dec-01	7	<1
			5-Jan-02	24	<1
			5-Feb-02	2	<1
			11-Jun-02	1939	<1
		LW	17-Dec-01	10	<1
			5-Jan-02	23	<1
			5-Feb-02	4	<1
		RO	17-Dec-01	3	<1
			5-Jan-02	55	<1
			5-Feb-02	36	<1
			11-Jun-02	49	2
		R2	17-Dec-01	16	<1
			5-Jan-02	23	<1
			5-Feb-02	1	<1

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Rhyacophila sp.	T	AD	17-Dec-01	1	0
			5-Jan-02	4	0
			5-Feb-02	6	1
			11-Jun-02	0	0
		LW	17-Dec-01	3	1
			5-Jan-02	0	0
			5-Feb-02	7	3
		RO	17-Dec-01	7	1
			5-Jan-02	2	0
			5-Feb-02	0	0
			11-Jun-02	0	0
		R2	17-Dec-01	0	0
			5-Jan-02	1	0
			5-Feb-02	2	1
Acari	NI	AD	17-Dec-01	6	<1
			5-Jan-02	12	<1
			5-Feb-02	37	<1
			11-Jun-02	650	<1
		LW	17-Dec-01	13	<1
			5-Jan-02	4	<1
			5-Feb-02	66	1
		RO	17-Dec-01	18	<1
			5-Jan-02	32	<1
			5-Feb-02	14	<1
			11-Jun-02	8	<1
		R2	17-Dec-01	9	<1
			5-Jan-02	19	<1
			5-Feb-02	15	<1

Appendix C (cont.)

Functional group or taxon	Order	Site	Date	A	B
Total Predators		AD	17-Dec-01	22	1
			5-Jan-02	77	4
			5-Feb-02	90	13
			11-Jun-02	2661	3
		LW	17-Dec-01	40	1
			5-Jan-02	40	7
			5-Feb-02	142	20
		RO	17-Dec-01	66	2
			5-Jan-02	168	3
			5-Feb-02	99	9
			11-Jun-02	112	12
		R2	17-Dec-01	62	8
			5-Jan-02	123	29
			5-Feb-02	53	10