EFFECTS OF A LABILE CARBON ADDITION ON A NORTH CAROLINA HEADWATER STREAM FOOD WEB

By

Heidi S. Wilcox

(Under the direction of Dr. J.B. Wallace)

ABSTRACT

We added dextrose during two eight-week periods (summer and autumn) to a headwater stream in North Carolina, U.S.A. Bacterial densities were significantly higher in the treatment reach during both additions. Increased microbial growth led to higher respiration rates on leaf disks and a three-fold increase in instantaneous growth rates of Chironomidae larvae. Collector-gatherer and predator abundance and biomass in bedrock habitats increased significantly during the summer addition. No functional feeding group in bedrock habitat increased in abundance during the autumn addition; however, shredder biomass increased significantly. In mixed substrates, shredder abundance and scraper biomass increased significantly during the autumn addition. All functional feeding groups assimilated isotopically distinct dextrose during additions. Assimilation of dextrose, measured by stable isotope analysis, and increases in insect abundance and biomass suggest that the added carbon was an important food resource, particularly for consumers of heterotrophic organisms and biofilm.

INDEX WORDS: Aquatic insects, organic enrichment, carbon isotopes, streams.

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DEDICATION

This thesis is dedicated to my parents and Mabel Stritmatter.

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CHAPTER 1

LITERATURE REVIEW

Dissolved organic matter (DOM) is the largest pool of organic carbon present in streams (Hobbie and Likens 1973, McDowell and Fisher 1976, Moeller et al., 1979). While much of the DOM present in running waters is refractory (Thurman 1985) and of limited importance biologically, smaller fractions of labile carbon are extremely important in heterotrophic energy pathways (Rounick and Winterbourn 1983, Hall and Meyer 1998).

Much of the DOM entering streams is in the form of dissolved organic carbon (DOC). DOC is vitally important in aquatic ecosystems and often regulates biotic processes such as bacterial production thereby influencing dissolved oxygen concentrations, food-web structure, and microbially mediated biogeochemical transformations (Wetzel 2001). It is a major source of organic matter in stream food webs and may comprise up to 98% of a stream's total organic matter inputs in extreme cases (Meyer 1994, Webster and Meyer 1997). Uptake of DOC by bacteria represents a significant energy pathway in many aquatic systems. The quantity and quality of DOC present in the water column determines microbial production, which forms the energy base for invertebrate food webs in many stream ecosystems (Bott et al., 1984; Bott and Kaplan, 1985; Findlay et al., 1993; Jones, 1995, Hall and Meyer 1998).

Sources of DOC

Slow leaching from depositional areas behind large woody debris dams, release from sediments in the stream channel mediated by microbial and chemical processes, and direct inputs from litter and soils of the floodplains represent the three primary sources for stream DOC inputs in low-gradient streams (Meyer 1990). Primary production occurring adjacent to stream channels is a particularly important source of stream DOC. While much of the DOC leached from vegetation is retained by soils adjacent to streams, riparian wetlands are an important contributor of DOC to streams (Cronan 1990, Fiebig et al., 1990). For example,sources of DOC in or near the stream channel allow concentrations of DOC to increase with distance from stream seeps despite near constant DOC concentration in entering groundwater and removal of DOC from the water column via biotic and abiotic processes (Kaplan et al. 1980, Wallace et al. 1982, Meyer 1990).

Abiotic and biotic utilization of DOC

DOC may be removed from the water column by abiotic and biotic processes including bacterial uptake (Meyer et al., 1987, Hall and Meyer 1998) and uptake by non-bacterial components which include absorption, flocculation, precipitation, and photochemical destruction (Meyer 1986, Sherr 1988, Wotton 1988). In smaller streams, processes within the streambed account for most DOC removal (Lock and Hynes, 1976). The large internal surface area of sediments promotes the colonization of bacterial biofims. As a result, rapid uptake by sediments alone is followed by microbial colonization within the sediments. Uptake by these microorganisms, assimilation of organic carbon into microbial biomass, and re-mineralization of DOC to CO_2 by community respiration all contribute to removal of DOC from the water column (Dahm

1981). The quantity and quality of carbon available often controls bacterial biomass. Additionally, the rate of bacterial uptake of DOC is dependent on numbers and types of bacteria present, temperature, and the chemical makeup of DOC present (Bott et al. 1984). Biofilms on surfaces within a stream have the ability to store and metabolize specific DOC fractions. In particular, highly labile fractions of DOC such as leaf leachate and simple sugars are taken up most rapidly, usually within 48-72 h (Lock and Hynes, 1976; Lush and Hynes, 1978; Dahm 1981). Studies have demonstrated differing rates of microbial utilization depending on the leaf species from which it was leached (Dahm 1981). Other studies have examined bacterial uptake as it relates to molecular weight fractions. Low molecular weight fractions, such as monosacharides, are typically most available to bacteria (Meyer et al. 1987; Fischer et al., 2002).

Higher trophic levels benefit directly from bacterial biomass produced by DOC uptake. Deposit-feeders such as chironomids and oligochaetes utilize bacterial biomass in the sediments (Rounick and Winterbourn 1983). As sediment bacteria are often associated with detritus particles, invertebrates feeding on this detritus therefore are omnivores, receiving energy from both the microbial and detrital sources (Meyer 1994). Hall and Meyer (1998) showed that bacterial carbon was more important for some insect taxa than others. Using an isotopic tracer, they found that invertebrates derive <10% to 100% of their carbon from bacteria. A positive relationship between fraction of carbon derived from bacteria and amount of amorphous detritus in invertebrate guts was found (Hall and Meyer 1998). As bacterial carbon consumed by invertebrates is mainly derived from amorphous detritus, differences in bacterial assimilation are related to feeding differences between taxa. Filterers such as *Wormaldia* (Trichoptera), scrapers

(*Stenonema*, Ephemeroptera), gatherers (Chironomidae, Diptera and copepods), and shredders (*Leuctra,* Plecoptera) all derived a significant proportion of their carbon from bacteria. Blackflies (Simulidae), capture bacteria directly from the water column (Fredeen 1964; Wotton 1988). Epilithon, derived from DOC and consisting of bacteria, algae, and other organisms in a mucopolysaccaride matrix attached to hard substrates, is another valuable food resource for stream organisms particularly for taxa within the collector-gatherer and scraper functional groups (Lock et al., 1984). Invertebrate predators ingest filterers and collector-gatherers that consume material derived from DOC. This predation provides high quality protein and serves to link the microbial and macroconsumer food webs. Thus, a measurable fraction of the total carbon intake of invertebrates can be linked to bacterial production, regardless of functional feeding group.

Finally, carbon availability can strongly affect nitrogen dynamics in streams. The quality and quantity of organic matter and the rate of organic mineralization in sediments has been shown to have important consequences for rates of nitrogen transformation (Seitzinger 1994, Jones et al. 1995, Currie 1999). Bernhardt and Likens (2001) found that DOC enrichment of a stream stimulated bacterial growth, leading to higher respiration and a corresponding increase in the assimilated demand for nitrogen. Recent lab studies have found that increasing DOC concentration and quality lead to reduced rates of nitrification due to a reduction in dissolved organic nitrogen (DIN) and higher assimilative demand for N by stream microbes (Strauss and Lamberti 2002).

Human impacts on DOC inputs to streams

Land use change, pulp mills, domestic and industrial wastewater, agriculture, and food processing industries all potentially increase imported organic material to a stream with important consequences for stream biota. Increased availability of carbon produced from these practices may encourage growth of nuisance bacteria or fungi, alter water chemistry, and impact higher trophic levels (Warren et al., 1964, Hedin 1989, Bernhardt and Likens 2001). The presence of abundant filamentous bacteria in a stream has been shown to cause mortality and reduced densities of some aquatic organisms (Lemly 1998), while increasing densities of other taxa able to exploit this new resource (Warren et al., 1964). Warren and others added sucrose to a stream in Oregon; this addition of a labile form of DOC led to growth of the slime bacteria *Sphaerotilus natans* corresponding increases in Chironomidae (Diptera) larvae and growth of higher trophic levels. Similarly, effluent from pulp and paper mills, a labile carbon source, was found to have a profound impact on chironomid assemblages in the paleolimnological analysis of core sediments of a boreal lake in Finland (Merilainen et al., 2001). Another common source of organic pollution in streams is manure from cattle grazing. An addition of cow manure to several California streams resulted in increases in pollution-tolerant taxa densities (del Rosario et al. 2002). Stable C isotope analysis revealed that the manure was an important food source for collector-gatherers in particular.

Land use changes lead to major changes in sediment, carbon, and nitrogen loadings to a stream (Howarth et al., 1996). The removal of riparian zones and the subsequent decrease in organic matter flow and resources deeply impact stream ecosystems and may alter macroinvertebrate community structure. Clear-cutting of a stream riparian zone has been found to reduce annual export of DOC and lower instream DOC concentrations (Meyer and Tate 1983). Lower DOC export was due in part to reduced inputs from throughfall and fresh litter leaching. More significantly, lower export rates were attributed to lower DOC inputs in subsurface water and less instream generation of DOC. Elimination of annual inputs of litter to a stream channel markedly decreased instream generation of DOC from leaf litter stored in the channel (Meyer et al.1998). DOC released by microbial breakdown of leaf litter, from chemical leaching, and that released via invertebrate feeding on decaying leaf matter all decreased in the litter-excluded stream. The lowering of available DOC in the water column and reduction in benthic POM (particulate organic matter) affected higher trophic levels that are dependent on DOC and associated microbial growth (Wallace et al. 1999).

Disruption and alteration of DOC inputs to streams ultimately may also negatively impact ocean ecosystems. Production and utilization of dissolved organic carbon in riverine systems influences the amount of carbon transported to the sea (Romankevich 1984). Fluvial transport has been estimated to deliver 17 x 10^{12} mol/year to the sea (Smith and Hollibaugh 1993). Large increases in the eutrophication of rivers and soil erosion due to deforestation and agricultural practices have contributed to the near doubling of this delivery and burial of organic carbon in coastal oceans over the last 200 years (Likens et al., 1981). In summary, human perturbations on land, including erosion and increased discharge of organic pollutants, contribute to changes in aquatic (marine and freshwater) organic carbon cycles that may ultimately affect the global organic carbon budget.

Conclusion

The importance of DOC in supporting and maintaining stream ecosystems has been well documented. Changes in DOC concentration through human alterations of the landscape and increases in organic pollutants may have a substantial impact upon biotic and abiotic factors within a stream ecosystem. Microbial abundance, determined by in-stream DOC concentration, has been found to be a particularly large component of stream food webs particularly in detrital based systems. DOC provides a food resource for aquatic organisms, impacts trophic interactions, and affects nutrient cycling and transport (Meyer 1990). Continued research on DOC and microbial growth will undoubtedly help to elucidate the central role of bacteria in food webs.

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CHAPTER 2

EFFECTS OF DEXTROSE ADDITION ON A HEADWATER STREAM FOOD WEB

Introduction

Dissolved organic carbon (DOC) is vitally important to the maintenance of aquatic ecosystems (Wetzel 2001). It is a major source of organic matter in stream food webs and may comprise up to 98% of a stream's total organic matter inputs in extreme cases (Myer 1994, Webster and Meyer 1997). While much of the dissolved organic matter present in running waters is refractory (Thurman 1985) and of limited importance biologically, smaller fractions of labile carbon are extremely important in heterotrophic energy pathways (Rounick and Winterbourn 1983, Hall and Meyer 1998). Bacteria and fungi are often limited by carbon quantity and quality in aquatic ecosystems (Bott et al., 1984; Findlay and Sobczak 2000; Kaplan and Newbold 2000). Higher trophic levels have been shown to benefit directly from bacterial biomass produced by labile DOC uptake (Hall and Meyer 1998). Microbes are consumed by flagellates and ciliates which in turn are grazed by macroinvertebrate consumers (Bott and Kaplan 1990; Carlough and Meyer 1990). The utilization of waste products, exudates, and decomposing consumers by microbes completes the "microbial loop" in small streams. Thus, carbon limitation (quantity and/or quality) may play a key role in the structuring of lotic food webs (Bott et al., 1984; Bott and Kaplan, 1985; Findlay et al., 1993; Jones, 1995).

Food web studies using isotopic tracer additions have found that invertebrates derive from <10 to 100% of their carbon from bacteria (Hall and Meyer 1998). Differences in bacterial assimilation are generally related to feeding differences between taxa. However, variety in food resources that invertebrates are able to consume may broaden traditional functional feeding groups (Mihuc and Minshall 1995). Filterers, collector-gatherers and shredders all derive a significant proportion of their carbon from bacteria (Hall and Meyer 1998). Epilithon, derived from DOC and consisting of bacteria, algae, and other organisms in a mucopolysaccaride matrix attached to hard substrates, is a valuable food resource for stream organisms particularly for taxa within the collector-gatherer and scraper functional groups (Lock et al., 1984). Finally, many invertebrate predators ingest primary consumers that consume significant amounts of material derived from DOC. Predation therefore provides high quality protein and serves to link the microbial and macroconsumer food webs. Thus, a measurable fraction of the total carbon intake of invertebrates can be linked to bacterial production, regardless of functional feeding group.

Anthropogenic activities may alter aquatic organic carbon cycles. Land use change, pulp mills, domestic and industrial wastewater, agriculture, and food processing industries all potentially increase imported organic material to a stream with great consequences for stream biota. Increased availability of carbon produced from these practices may encourage growth of nuisance bacteria or fungi, alter water chemistry, and impact higher trophic levels (Warren et al., 1964, Hedin 1989, Bernhardt and Likens 2001). Human inputs of labile forms of carbon into lotic systems occur through wastewater inputs from several industries including brewing and processing of meat, poultry, fruit, and potatoes (Eikelboom 1977, Strom and Jenkins 1984, ATV Working Group 2.6.1., 1989). Organic enrichment and subsequent increases in food resource availability may alter aquatic insect species composition and ultimately lead to increases in densities of tolerant taxa while decreasing those taxa sensitive to enrichment (Hynes 1960).

While earlier studies have added labile forms of carbon to streams (Warren et al., 1960; McDowell 1985; Hedin 1986; Bernhardt and Likens 2002), few have examined the responses of invertebrate consumers or the possibility of carbon limitation in extremely heterotrophic systems with large standing stocks of litter, such as low-order streams of the Southern Appalachian Mountains. Based on earlier findings, we hypothesized that the addition of a labile form of carbon to a forested headwater stream would elevate microbial abundance and activity and result in greater resource availability and higher macroinvertebrate growth rates. We expected gatherers, scrapers, and filterers (consumers of biofilm and associated heterotrophic organisms) to show the greatest response to treatment by assimilating more dextrose-derived carbon and having the largest increase in abundance and biomass. We predicted the impact of dextrose addition would be lower during autumn than summer due to lower ambient stream temperatures and the autumn pulse of leaf litter. This pulse of organic matter would increase available carbon and hence reduce the impact of the added labile carbon.

Study Site

The study was conducted in Jenny Branch (Watershed 4), a first-order stream located within a 4-hectare catchment at the Coweeta Hydrologic Laboratory in Macon

County, North Carolina, U.S.A. Coweeta is a 1625-ha drainage basin in the Blue Ridge Province of the southern Appalachian Mountains. The steep forested catchment (gradient ~30cm/m) is dominated by white and red oaks (*Quercus alba* L. and *Quercus rubra* L.), tulip poplar (*Liriodendron tulipifera* L.), and dogwood (*Cornus florida* L.). A dense understory of *Rhododendron maximum* L. shades the stream year-round, limiting primary productivity (Webster et al. 1983). The stream is strongly heterotrophic with litter inputs in a nearby stream of ~500 g ash-free dry mass (AFDM) $m^{-2} yr^{-1}$ (Wallace et al. 1995). The substrate consists of bedrock outcrop or mixed substrate (cobble and pebble, mixed with sand). The stream has had no human disturbance since the 1940s with the exception of a two-year period (1962-64) when the entire Coweeta basin was sprayed with DDT to control elm spanworm (*Ennomos subsignarius,* Hubner). Jenny Branch has never been manipulated experimentally. Stream pH in streams of the Coweeta basin range from 6.0 - 7.0. (Swank and Waide, 1987). The only vertebrates present in the stream are salamanders.

Methods

Experimental Design

An 80-m reach of the stream was divided into two 40-m sections. The upstream portion served as the reference section and received no treatment. During two experimental periods (August 8 – October 6, 2001 and November 8, 2001– January 10, 2002) a concentrated solution of dextrose (Corn Products International food grade dextrose; 250g/L) was added to the treatment reach from a holding tank at the 40-meter mark via a peristaltic pump (Watson and Marlow 504S). The pump was positioned over a small cascade to ensure full mixing in the water column within a short distance from the site of addition. The rate of dextrose addition to the stream was adjusted every three days to keep the downstream DOC concentration at 20 mg/L above the ambient concentration of ~ 1-2 mg/L. In order to reduce microbial growth, the holding tank for the solution was replaced weekly with an acid-washed tank filled with fresh dextrose solution.

Stream flow was calculated three times per week by weighing the amount of flow captured in a large plastic bag at a weir immediately downstream of the experimental reach during the experimental period. Daily average stream flow was estimated by regression with discharge data obtained from a nearby Coweeta stream (WS 53). Weekly water samples were taken 5m above the dripper in the reference reach, and at 5, 20, and 40 meters downstream from the dextrose addition. All samples were filtered through precombusted Gelman A/E glass fiber filters, and stored in precombusted glass bottles at 4° C until analysis. DOC concentration was determined in duplicate using a Shimadzu TOC-5000A total organic carbon analyzer.

Bacterial Counts

Twenty-five non-glazed ceramic tiles (5.4 x 5.4 cm) were placed randomly in both treatment and non-treatment sections of the stream one week before each dextrose release began to allow for bacterial colonization. One day prior to the start of the addition and on four other bi-weekly sampling dates during each study period, replicate tiles (n=5) were removed from each reach at randomly selected meter marks along a gradient. Tiles were preserved in the field using 5% formalin solution and were processed within one month of collection. Biofilm was scraped from the tiles with a soft toothbrush and suspended material was sonicated for ~15 s. Subsamples were stained with acridine orange, filtered through a 0.22-μm pore size irgalan black stained nucleopore filters, and bacteria counted by epifluorescent microscopy at 1000X magnification (Hobbie et al. 1977). Ten fields with 10-50 bacterial cells were counted per slide (Kirchman et al. 1982). Average bacterial numbers for treatment and reference reaches were compared for each sampling date using 95% confidence intervals. This is a very conservative test for differences (Zar)

Leaf pack respiration

Rates of microbial respiration associated with decomposing red maple leaves were estimated from measurements of dissolved oxygen consumption. Leaf bags (1-mm mesh size) were deployed in the treatment (n = 5) and reference (n = 5) sections of WS 4 at the start of each experimental period. Each bag contained 10g of air-dried red maple leaves collected the previous year. These bags remained in the stream for the duration of dextrose addition. At the end of each treatment period (Summer experimental period = 53 days; autumn experimental period = 45 days), ten leaf discs were cut from each leaf bag using a cork borer and placed into glass chambers containing 29 ml of membrane-filtered (0.2 μm) stream water. Changes in dissolved oxygen were monitored every five minutes for 30 min. using oxygen microelectrodes (YSI model 5100 and model 58). All measurements were conducted in darkness at ambient stream temperature. For each stream reach an additional chamber containing only filtered stream water was monitored for use as a control and correction factor. After respiration rates were determined, leaf discs from chambers were dried, weighed, ashed at 500 °C and reweighed to obtain AFDM. Mean respiration rates (mg O_2 g^{-1} h^{-1}) in the treatment reach with values higher than the 95% confidence intervals of reference samples were considered to be significantly different.

Chironomidae Growth Rates

Chironomid growth rates were determined for non-Tanypodinae taxa (sensu Huryn and Wallace 1986). Growth rates were measured twice during each dextrose addition (August, September, and November, December 2001). Chironomids were obtained by collecting leaf litter from nearby Coweeta streams. Leaf litter was washed through a series of nested sieves with stream water. Chironomid larvae were removed from the sieve contents and specimens were measured and placed within one of three size classes: ≤ 1.5mm, 1.5-2.5mm, and 4.5+ mm. Each specimen was measured live to the nearest 0.1 mm with an ocular micrometer under a dissecting microscope. Each size class (25-70 chironomids) was then placed in a wedge-shaped growth chamber containing red maple leaves as a substrate (4-6 leaves collected from the reach in which the specimens were to be incubated). Three growth chambers (one containing each size class) were placed in both the treatment and reference sections of the stream and incubated for 7-15 days.

Estimates of the change in average larval biomass before and after incubation were used to calculate growth rates. Biomass (AFDM) was obtained using length-mass regressions derived from animals in nearby Coweeta streams (Benke et al. 1999). All individuals recovered in each size class were measured after incubation. Instantaneous growth rate coefficients (IGRs) (mg mg^{-1} d^{-1}) were calculated by the following equation:

$$\mathrm{IGR} = (\ln W_f - \ln W_i) / t$$

Where W_i and W_f are the intial and final larval AFDM observed during a period (t) in days (Romanovsky and Polischuk 1982). Huryn and Wallace (1986) describe the methods and growth chambers used to determine daily growth rates (g) in greater detail. Chironomidae growth rates in the dextrose addition and non-dextrose addition reaches were compared by Analysis of Covariance (ANCOVA) using the slope of the lines generated by regressing growth vs. initial size of non-tanypodinae Chironomids.

Stable isotope analysis

Stable isotope analysis was used to determine any shifts in the fraction of carbon assimilated from in-stream sources to that of the added labile carbon source (Peterson and Fry 1987, Hauer and Lamberti 1996). Dextrose is derived from C_4 plant material (corn) that has a $\delta^{13}C$ of ~ -10 ‰ and is easily distinguished from typical leaf-derived carbon at Coweeta (–28 ‰ to –25 ‰) and periphyton in small forest streams ($\delta^{13}C$ of ~30 ‰) (Smith and Epstein 1971;Hall and Meyer 1998; Findlay 1999).

Benthic samples of coarse particulate matter (CPOM) were collected by hand, dried at 50°C, and finely ground in a Spex ball mill. Fine particulate organic matter (FPOM) was elutriated from inorganic sediments, sieved through a 1-mm sieve, , and processed in the same manner as CPOM. Biofilm was scraped from submerged rocks in the stream, collected on Gelman A/E glass fiber filters, and dried. Microbial growth on rockfaces in the treatment reach (see results) was collected, dried, and processed in the same manner as CPOM.

Invertebrates were collected from representative habitats in the treatment and reference sections of Jenny Branch at the end of each addition (October 2001 and January 2002). Benthic samples were elutriated, poured over 1-mm and 250-μm nested sieves, and animals picked from debris. Invertebrates were all larvae or nymphs. Specimens were transported to the laboratory on ice and frozen. Later, invertebrates were thawed, cleaned of any detached detritus, and their gut contents removed by dissection. It was not feasible to remove the guts of chironomids because of their small size. After removing the guts, all animals were dried at 50°C. Individuals or ground subsamples of each consumer taxon were combined to form a single composite sample (~1 mg) for each reach. Samples were weighed using a microbalance and combusted in a Carlo Erba NA 1500 CHN analyzer coupled to a Finnigan Delta C mass spectrometer as a continuous flow system. The $\delta^{13}C$ for carbon was calculated according to the following equation:

$$\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is the ratio of ^{13}C: ^{12}C. Samples enriched with dextrose will have a higher $\delta^{13}C$ relative to the unenriched samples. Relative importance of the two carbon sources (leaf litter and dextrose) to the diet of each taxon was analyzed using a linear mixing model (Phillips and Gregg 2001). We used the $\delta^{13}C$ of microbial mats (see results) as a proxy for all microbial growth in mixing model calculations. Only $\delta^{13}C$ were entered into the mixing model; consumer $\delta^{13}C$ values were not corrected for trophic fractionation. Taxa in the treatment reach with $\delta^{13}C$ values higher than the 95% confidence intervals of reference samples were considered to be significantly labeled (i.e, assimilating dextrose).

Benthic Sampling

Random benthic samples were collected biweekly during summer (August, September, and October 2001) and autumn (November 2001 and December 2002) for a total of eight collection dates. Two methods were used for benthic sampling. Rockface habitats (bedrock outcrops) were sampled by scraping and brushing moss and associated particles from 15 x 15 cm areas into a 250µm mesh bag that was held flush to the rock surface. Mixed substrate habitats (gravel, sand) were sampled with a 400-cm^2 corer (Lugthart and Wallace 1992).

Organic matter in samples, including invertebrates and salamanders was elutriated from the inorganic substrate, passed through nested 1-mm and 250-µm sieves, and preserved in a 6-8% formalin solution containing Phloxine B dye to facilitate sorting. Animals were removed form the coarse particulate organic matter (CPOM) on the 1-mm sieve by hand picking under 15X magnification and preserved in 6-8% formalin. Material on the 250-µm sieve was subsampled (1/8- 1/64 of the whole sample) using a splitter (Waters 1969) following Lugthart and Wallace (1992). Invertebrates in the samples were then removed by hand, counted, identified to genus, and measured (total body length) under a dissecting microscope (15x) with a graduated stage. Larval chironomids were identified as being either Tanypodinae or non-Tanypodinae. Non-insect invertebrates were generally identified to order. Following invertebrate removal, CPOM and fine particulate organic matter (FPOM) in the samples were processed, weighed, ashed, and re-weighed to obtain ash-free dry mass (AFDM) estimates of benthic organic matter (Lugthart and Wallace 1992).

Biomass (AFDM) for all insect taxa and non-insect taxa was obtained using length-mass regressions (Benke et al. 1999). Taxa were assigned to functional feeding groups according to Merritt and Cummins (1984). Mean abundance and biomass for specific taxa, functional feeding groups, and total invertebrate community were estimated separately for mixed substrate and bedrock outcrop habitats. Insect abundance and biomass in the treatment and reference reaches were analyzed by ANCOVA to compare the slopes of lines generated by regressing abundance or biomass vs. time for each treatment period. Organic matter standing crops (g AFDM/m^2) for mixed substrate habitats and bedrock outcrops during the summer and autumn dextrose additions were compared using a two-way ANOVA.

Results

Physical and chemical characteristics

During the summer dextrose enrichment, stream flow ranged from 0.2 to 0.9 L/s, and water temperatures ranged between 11.6 and 17°C (Figure 1). Stream flow ranged from 0.4 to 1.0 L/s and temperatures ranged between 8.9°C and 11.7 during the autumn enrichment period. DOC concentrations in the reference section averaged 0.91 mg/L ± 0.14 (mean ± 1 SE, n = 12; range 0.41 – 1.07 mg C/L) throughout the experiment (Figure 2). Average concentration of DOC in the treatment reach during the summer addition period was 5.21 ± 1.80 mg /L (n = 6; range 0.42 – 25.46) (Figure 2). DOC concentration in the treatment reach was not markedly higher than the concentration in the reference reach until the 48th day of the dextrose addition. Mean concentrations of DOC decreased from the site of DOC addition (mean concentration 5-m from addition = 6.56 ± 3.77mg/L, 20-m = 6.21 ± 3.49 mg/L, 40-m = 2.64 ± 1.65 mg/L). Mean DOC concentration in the treatment section during the autumn study period was 10.9 ± 1.97 mg/L (n = 6; range 0.44 – 25.46 mg/L) (Figure 2). Again, DOC concentrations decreased with distance from the dripper. DOC concentrations in the treatment reach were greatly elevated above ambient concentration by the 18th day of the addition. DOC concentration in the treatment reach was highest on day 18 five meters from the dextrose addition site and then decreased on each subsequent sampling date. DOC concentrations were not elevated at sampling locations located further from the dextrose addition (20–m and 40–m). Average concentrations were 12.58 ± 4.24 mg/L at 5-m, 12.60 ± 1.02 mg/L at 20-m, and 6.69 ± 2.09 mg/L at 40-m (Figure 2).

Microbial responses

Tiles incubated for 59 days during the first period of enrichment showed large increases in bacterial numbers in the treatment section compared to the reference section (Figure 3). There was no clear pattern in bacterial numbers in relation to distance downstream from the dextrose addition. Average bacterial densities in the treatment reach during the first study period were nearly three times higher ($4.15 \pm 1.79 \times 10^{11}$ [mean ± 1 SE]) than in the reference section ($1.66 \pm 0.29 \times 10^{11}$). By the third sampling date (10 September 2001), treatment densities were above 95% confidence interval of the reference reach. During the second study period beginning on November 1st, bacterial densities in the treatment section ($2.42 \pm 0.23 \times 10^{11}$) were double those of the reference section ($1.08 \pm 0.11 \times 10^{11}$) (Figure 3). Treatment densities were significantly higher than those of the reference section on all sampling dates. Bacterial densities increased during both treatment periods despite a constant decrease in average daily water temperatures (Figure 1).

As early as one week into each study period, the response of the benthic microbial community was visible to the naked eye as growth on tiles. As the experiments continued, thick microbial "mats"developed, particularly in areas of higher velocity flow on bedrock outcrops. Microscopic examination of microbial mats revealed an abundance of non-sheathed bacteria and sheathed bacteria of the genus *Sphaerotilus* (Mulder and

Deinema 1981). The aquatic hyphomycete *Lemmoniera pseudofloscula* dominated the fungal community.

During the first dextrose addition, respiration rates of leaf disks taken from litter bags in the treatment section were nearly double (average rate – 0.17 $gO^2h^{-1}g^{-1}$AFDM) those of disks from litter bags in the reference section (average rate – 0.05 $O^2h^{-1}g^{-1}$AFDM) (Figure 4). Respiration rates during the second study period were on average lower than those during the summer experiment and there was no significant difference between leaf disk respiration rates in the treatment and reference reach (Figure 4).

Invertebrate response

Stable Isotope Analysis

Organisms collected within the treatment reach during both dextrose additions were significantly ^{13}C-enriched relative to CPOM and had shifted towards the signature of the added dextrose (mean δ^{13}C 10.6 ‰)(Figures 6). All organisms sampled from the reference reach had δ^{13}C values close to that of CPOM (Figure 6). Using a linear mixing model, several organisms were found to have >50% reliance on dextrose carbon, including the mayflies *Paraleptophlebia* sp. and *Stenonema* sp., plecopterans *Isoperla,*spp. *Leuctra* spp., *Tallaperla* spp., and *Sweltsa* sp., caddisflies *Fattigia* sp., and *Wormaldia* spp., and dipterans *Hexatoma* spp. and *Pseudolimnophila* spp. (Table 2). Non-Tanypodinae chironomids were the most strongly labeled during the first treatment (-14.2 ‰) and obtained the largest proportion of their carbon from dextrose (>80%) (Table 2). *Paraleptophlebia* sp. was the most enriched organism during the autumn addition (-15.5 ‰) and obtained > 70% of its carbon from dextrose (Table 2).

A large amount of variation in reliance on dextrose-derived carbon was observed within functional groups. While collector-gatherers in the treatment reach (non-Tanypodinae chironomids, *Paraleptophlebia,* and *Stenonema*) had isotopic signatures greatly shifted towards the signature of the added dextrose, oligochaetes in the treatment reach had $\delta^{13}C$ values near that found for most organisms in the reference reach during the summer addition (Table 2). The collector-gatherer mayfly *Stenonema* was significantly labeled during both additions. The average $\delta^{13}C$ for *Stenonema* shifted from – 26.2 to –15.8‰ during the two additions (Tables 2). Gatherers from the reference reach were not analyzed during the first treatment period, as it was not possible to collect an adequate number of organisms for analysis. All gatherers in the treatment reach sampled during autumn had $\delta^{13}C$ signatures shifted towards that of dextrose (Table 2). FPOM $\delta^{13}C$ collected from the treatment reach was significantly labeled and shifted towards the signature of dextrose during the summer experimental period (Figure 6). The isotopic signature of biofilm shifted from –27.2‰ in the reference to –25.7‰ in the treatment during the summer and was significantly labeled (Figure 6). Biofilm $\delta^{13}C$ was not significantly labeled during the autumn addition (Figure 6).

All shredder taxa in the treatment reach were significantly labeled during both addition periods (Table 2). Reference reach shredder $\delta^{13}C$ ranged from –27.6‰ to –25.1‰ (Table 2). Values in the treatment reach ranged from –23.2‰ to –16.8‰. *Leuctra* had the highest $\delta^{13}C$ value and reliance on dextrose-derived carbon in the treatment reach during both additions (Table 2). Composite CPOM $\delta^{13}C$ was significantly higher in the treatment reach than in the reference reach during the summer addition. CPOM however, was much less labeled than any of the shredders. Average CPOM $\delta^{13}C$ values in the treatment and reference reaches were not found to be significantly different from each other during the autumn addition (Figure 6).

During the summer enrichment the filterering caddisflies *Parapsyche* and *Diplectrona* both had significantly enriched $\delta^{13}C$ values in the treatment reach (Table 2). Average signatures ranged from –25.3‰ to –21.2‰ for *Parapsyche* and –25.7‰ to –21.0‰ for *Diplectrona* (Table 2). *Wormaldia* was the most enriched filterer (-16.9 ‰) at the end of the autumn addition (Table 2). As in the first treatment period, the filterers *Parapsyche* and *Diplectrona* were both highly labeled during the autumn addition. Average $\delta^{13}C$ for *Parapsyche* was –20.6‰ while *Diplectrona* $\delta^{13}C$ was –19.5‰ (Table 2).

All predators, with the exception of the salamander *Desmognathus,* were significantly labeled in the treatment reach during the summer addition (Table 2). Mean predator $\delta^{13}C$ ranged from –24.2‰ to –23.6‰ in the reference reach (Table 2). In the treatment reach their $\delta^{13}C$ ranged from –23.2‰ to –21.4‰. The predatory dipteran, *Pedicia* became the most isoptopically enriched, shifting from –23.8‰ to –21.4‰. Autumn enrichment predator $\delta^{13}C$ ranged between –18.2‰ for *Hexatoma* and –23.0‰ for the salamander *Eurycea* (Table 2). Reference $\delta^{13}C$ values ranged from –23.2‰ to –24.0‰ (Table 2). As in the first treatment period, predators were the least labeled of all the functional feeding groups.

Total abundance and biomass

Total invertebrate abundance in bedrock habitats did not significantly increase during the first dextrose addition. Invertebrate biomass did show a small but significant increase in bedrock habitats in the treatment reach (Table 3). During the second dextrose addition, total invertebrate abundance in bedrock habitats of the treatment reach was 5X higher than in the reference reach. There were no significant differences in total invertebrate abundance or biomass between the two reaches during either dextrose addition period in mixed-substrate habitats (Table 3 and 4).

Functional group response

Response to the dextrose addition varied among functional-feeding groups (Table 3 and 4 and Appendix). Total gatherer abundance and biomass increased in the bedrock habitats of the treatment reach during the first addition. Average collector-gatherer abundance in the treatment reach was 3X higher than in the reference while collector-gatherer biomass in the treatment reach was 5X higher than in the reference. Scraper biomass showed a weak but significant increase during the autumn addition. No other functional group's total abundance or biomass differed significantly between the treatment and reference reaches during the first or the second addition period in bedrock habitats.

In mixed-substrate habitats there was no difference in any functional feeding group's abundance or biomass during the summer dextrose addition (Table 3). During the autumn addition total scraper biomass significantly increased in the treatment reach and was 3X higher than the reference reach (Table 4). No other functional group showed a significant response to treatment in mixed substrate habitats.

Response of individual taxa

In bedrock habitats, individual taxa within the collector-gatherer functional feeding group showed the greatest response to treatment during the summer addition (Table 3). Average non-tanypod Chironomidae densities increased by a factor of three in the treatment reach. Average nematode densities and biomass in the treatment reach were 8X higher than in the reference reach. *Serratella* (Ephemeroptera) abundance increased 17-fold and had 5X greater biomass. Non-tanypod Chironomidae (6X higher) and Ceratopogonidae (Diptera) (400X higher) both increased in abundance during the second experimental period in bedrock habitats (Table 4).

In the mixed-substrate habitat during the summer dextrose addition the caddisfly *Lepidostoma*, *Tipula* (Diptera), and non-tanypod Chironomidae abundances in the treatment reach were twice that of the reference reach. Only *Lepidostoma* showed a significant increase in biomass (2X higher in the treatment reach) during the first addition. During the autumn addition in the mixed-substrate habitats of the dextrose reach non-tanypod Chironomidae abundance increased significantly and was twice that of the treatment reach. No other taxa showed a significant response to the treatment.

Chironomid Growth

Growth rates were not significantly correlated with temperature in the reference reach ($r^2 = 0.001$, $P = 0.923$) or in the treatment reach ($r^2 = 0.007$, $P = 0.803$). Chironomid growth rates were significantly higher in the treatment than in the reference reach (ANCOVA F = 26.01, df = 1,20, $p<0.0001$; Table 1 and Figure 5). Average growth rates in the treatment reach were >2X higher than in the reference reach. Smaller size classes in both the treatment and reference reaches had consistently higher growth rates than the larger size classes (Figure 5). Average lengths of larvae in all size classes increased. Negative growth rates in August were an artifact of limited recovery of individuals. The recovery of individuals from the growth chambers ranged from 11% to

84% of the organisms originally introduced to the growth chambers. There were no significant differences in mortality rates between the two reaches.

Organic matter

Total standing crop of CPOM in the mixed substrate habitat of Jenny Branch was significantly lower during the summer experimental period (285 gAFDM/m^2) than in the autumn (745 gAFDM/m^2). There was no significant difference in total CPOM between the reference and treatment reach (Table 5). There was no significant difference in total FPOM between the reference and in the treatment reaches or between seasons in mixed substrate or rockface habitats (Table 5).

Discussion

The results of these experiments indicate that the Jenny Branch food web is limited by carbon quality. The addition of a labile form of DOC resulted in a large response by the benthic microbial community. Increases in microbial growth resulted in higher leaf disk respiration rates during the summer dextrose release and allowed incubated chironomids to grow at a faster rate in the treatment reach. Assimilation of dextrose, increases in insect abundance and biomass, and the alteration of 13C signatures suggest that the added carbon was an important food resource despite high ambient standing stock of leaf litter present in the autumn. This is particularly apparent for consumers of biofilm and heterotrophic organisms.

DOC removal from water column

Sediments and sediment-bound organisms rapidly removed added DOC from the water column in the experimental reach (Fig. 2 and 3). DOC was removed from the water column throughout the summer and autumn addition periods, indicating that Jenny Branch, like other streams to which DOC has been added, has a great capacity for processing added labile DOC (McDowell 1985; Meyer et al. 1988; Hedin 1989). The lack of elevation of DOC concentration above ambient levels until day 48 of the summer dextrose addition is further evidence of the large capacity for uptake of labile carbon by Jenny Branch. Conservative tracer experiments conducted in headwater streams of the Appalachians have shown extensive and rapid penetration of the sediments by infiltrating water (Munn and Meyer 1988); prolonged contact between the water and sediments may have increased the rate that DOC was removed from the water column during the experimental periods. The rate at which surface waters enter sediments has been linked to the rate at which DOC may be removed from the water column (Meyer 1990). Published rates of uptake of added labile DOC in North Carolina streams, geomorphically similar to Jenny Branch, are considerably higher than rates found in streams in other areas of North America (Meyer 1990). Additionally, several studies have indicated that higher concentrations of DOC are linked to higher rates of removal of DOC from the water column (McDowell 1985; Meyer et al. 1988). It seems plausible therefore, that DOC removal rates in Jenny Branch were elevated due to increased DOC loading.

Effects of dextrose addition on microbial community

Carbon inputs to Coweeta streams are likely to be much more refractory than dextrose. The experimental addition of a labile form of carbon represented a large and sudden increase in a biologically available energy source. Rapid uptake of DOC by sediments is associated with uptake by microbes, which are responsible for the majority of DOC removal from the water column (Dahm 1981). The addition of labile carbon led to higher bacterial densities during both dextrose addition periods, reflecting the importance of sediment-bound organisms in determining quantity and quality of DOC present in a stream through selective consumption of specific fractions of DOC (Findlay et al.1993; Volk et al. 1997). In a lowland German stream, monosaccharides (such as dextrose) were retained more effectively by the sediments than other sugars, and bacterial production was strongly correlated with DOC retention within sediments (Fischer et al., 2002).

Metabolic activity of bacteria is often determined by the concentration and composition of DOC present in a system (Kaplan and Bott 1989; Baker et al. 1999). Higher respiration rates observed during the summer addition were the result of increased microbial activity in the treatment reach. Temperature can influence heterotrophic respiration; therefore, lower ambient stream temperature most likely led to lower densities of bacteria and decreased leaf pack respiration rates during the autumn dextrose addition (Sinsabaugh 1997). The addition of labile carbon in earlier studies has resulted in growth of the slime bacterium *Sphaerotilus natans* (Warren 1964; Hedin 1989). Microscopic examination of the microbial growth present in Jenny Branch revealed it to consist of a complex of bacterial cells and the fungus *Lemmoniera*. While microbial growth in other studies was mainly associated with sediments, growth in Jenny Branch was concentrated in high-velocity bedrock habitats. Bacterial densities were not significantly higher in the treatment reach until the 3rd sampling date; however, the first signs of microbial growth within the treatment reach were observed within one week of the dextrose addition and copious growth was evident on bedrock outcrops by the 23rd day of addition (H.S. Wilcox; personal observation). Extracellular polymers have been found to diffuse DOC into biofilms where it can be stored and utilized by microbes (Freeman and Lock 1995; Fiebig 1997). Dense microbial growth in rockface habitats suggest high uptake of added DOC by fungi and bacteria located in the epilithon.

Assimilation and use of dextrose-derived carbon by invertebrates

The number of trophic transfers between bacterial production and macroinvertebrates can be numerous (Allen 1995). Dextrose-derived carbon may have been assimilated by macroinvertebrates via several pathways including direct consumption of bacterial cells by filterers (Simuliidae), selective grazing of biofilms, consumption of particle and leaf associated bacteria, and via the metazoan food web. Likely primary consumers of microbial production resulting from the addition of dextrose include protists, and micro-metazoans. In particular, ciliates and flagellates often exert significant grazing pressure on benthic bacteria (Bott and Kaplan 1990). These protists increased in density during the autumn dextrose addition (J. Norman, unpublished data). Increases in numbers of protists represented a possible increase in food resources for the next trophic level (metazoans). Meiofauna, including copepods, oligochaetes, and nematodes, grow rapidly and may be consumed in great numbers by larger invertebrate consumers. Consumption of these meiofauna by macroinvertebrates represents an alternative means for dextrose carbon assimilation.

In general, collector-gatherers derived the highest portion of their carbon from added dextrose (average % from dextrose carbon was 66%). Relatively small body size and the ability to feed on fine particles (< 1 mm) in depositional areas and on substrate surfaces likely led to the high contribution of dextrose carbon to the $\delta^{13}C$ of this trophic group. *Stenonema* (Ephemeroptera) were highly enriched and had $\delta^{13}C$ values considerably higher than FPOM or biofilm. This suggests that *Stenonema* were selectively feeding on highly enriched particles within the biofilm or even on the fungus *Lemonniera* itself. Hall and Meyer (1998) found no evidence that typical stream hyphomycetes were significantly labeled above background levels during their ^{13}C-acetate release, as the concentrations added were much lower than those added to Jenny Branch. Results of stable isotope analysis in this study indicate that the fungus *Lemonniera* was highly enriched. Invertebrates are able to directly consume DOC absorbed by biofilms, thus bypassing the bacterial intermediate (Hershey et al 1996; Wotton 1996). Consumption of biofilms containing *Lemonniera* and direct consumption of dextrose derived DOC may have allowed *Stenonema* to remain highly labeled despite lower bacterial growth present in Jenny Branch during the autumn addition.

Other functional groups were not as uniformly labeled. Broad differences in the relative contribution of dextrose carbon seen within the shredder and predator functional groups can perhaps be traced to differential consumption of bacterial cells and exopolymers or prey type consumed. Hall and Meyer (1998) found that many of the same shredder taxa highly labeled in our study (*Leuctra* and *Tallaperla*) derived a larger portion of their carbon from bacteria than other taxa in the same functional group (Table 6). All shredders sampled in their study derived a portion of their carbon from the added dextrose. *Leuctra*, although classified as a shredder (Merritt and Cummins 1996), has been found to be primarily a collector in early instars that relies heavily on FPOM and organic matter, particularly in bedrock habitats (Dobson and Hildrew 1992). Higher quality of FPOM in bedrock habitats in the treatment reach of Jenny Branch during the additions most probably contributed to the high labeling observed for *Leuctra.* Bacterial carbon may consist of a large amount of bacterial exopolymers (Hall and Meyer 1998). High biomass of these exopolymers found in streams may play a large role in supporting invertebrate production (Couch et al., 1996). Our values of the fraction of carbon derived from added dextrose and by proxy, microbial growth, for the same species are similar to the percentages found by Hall and Meyer (1998) (Table 6) who suggested that exopolymers may represent a more important carbon source than the bacterial cells themselves.

Some predators obtained >50% of their carbon from dextrose during the autumn addition (*Isoperla, Sweltsa,* and *Hexatoma*), suggesting that despite a relatively short experimental period, dextrose-derived carbon was reaching higher trophic levels. *Isoperla, Sweltsa,* and *Hexatoma* were presumably more enriched then other predators because they fed mostly on highly labeled Chironomidae (Merritt and Cummins 1996). Other predators analyzed (e.g. *Cordulegaster, Lanthus*, *Beloneuria*) are considered to be generalists, not concentrating their feeding on any organisms in particular.

Contrary to our expectations, filterers were not as highly labeled as collector-gatherers. The exception was *Wormaldia* (δ^{13}C of -16.98 ‰ during autumn addition). Functional feeding groups are based on feeding mode. Filter-feeders often do not fit neatly into such classification schemes. Although *Parapsyche, Diplectrona*, and *Wormaldia* have roughly the same body size and cohort production interval (~ 300 days), the three taxa feed on very different types of food. The net built by *Wormaldia* has a smaller mesh size (< 1 μm) than either *Parapsyche* or *Diplectrona,* allowing it to filter bacterial-sized particles from the water column (Wallace and Malas 1976). The ability to filter bacteria-sized particles contributed to the high enrichment of *Wormaldia* during

Hall and Meyer's 1998 sodium acetate addition. In contrast, gut analyses by Benke and Wallace (1980) have shown that *Parapsyche* ingests a higher proportion of animal matter than *Diplectrona* and animal matter is most significant for growth and production.. The type of food captured by each taxon may explain the higher labeling of *Wormaldia* and possibly the small differences observed in $\delta^{13}C$ between *Parapsyche* and *Diplectrona* at the end of the autumn addition.

Assimilation of dextrose by all functional feeding groups suggests that the added carbon was an important food resource during both dextrose additions. Fast growing chironomids with high turnover rates (~ 8 days at 15ºC at Coweeta; Huryn and Wallace 1986) were highly labeled; however, many taxa that assimilated a large proportion of dextrose carbon are slow developing taxa. The degree to which an organism was labeled by the $\delta^{13}C$ of dextrose in our experiment was a function of turnover of carbon and diet. Consumer $\delta^{13}C$ integrate prey $\delta^{13}C$ over relatively long periods of time depending on body size and growth rate (Finlay 2001). Organisms with faster carbon turnover rates such as Chironomidae were more highly labeled at the end of the dextrose addition having been exposed to the dextrose-derived carbon for a large proportion of their lifecycle. Chironomids may have been less labeled during the second addition due to lower availability of microbes as a food resource. Some invertebrates sampled in a nearby Coweeta stream were found not to have equilibrated with their food at the end of a 3-week period (Hall and Meyer 1998). Consequently, slower-growing, larger bodied taxa may not have turned over enough of their carbon during the additions to accrue a large proportion of enriched carbon. Increases in labeling observed at higher trophic levels by the end of the second addition period imply that all animals would be even more highly labeled with a longer period of enrichment. However, one must be cautious in interpreting these results because any insects with cohort production intervals greater than 60 d may have incorporated dextrose-derived carbon during both addition periods and therefore be disproportionately labeled in the second addition.

Impact of dextrose addition on invertebrate abundance and biomass

Higher trophic levels in Jenny Branch directly benefited from the microbial biomass produced by DOC uptake. Increased microbial activity in the treatment led to greater food resource availability for chironomid larvae. Huryn (1990) found that the substrate in growth chambers had no influence on growth and that larvae fed predominately on fine organic material entering the incubation chambers. It is likely then that the high microbial content associated with FPOM in the treatment reach may have led to higher growth rates. Consequently, insect production in Jenny Branch may be limited by organic matter quality.

Few taxa exhibited significant changes in density or biomass. While collector-gatherers (Nematoda, *Serratella,* and Chironomidae) increased in abundance during the summer addition, scraper and filterer densities did not increase, contrary to our hypothesis. There were no significant changes in filterer biomass during either addition. Chironomids, which are known to utilize bacterial biomass in sediments and are typically tolerant to organic enrichment (Rounick and Winterbourn 1983), were the only taxon to respond to the labile carbon with increases in abundance during both dextrose additions in both habitats sampled. Increases in Chironomidae abundance are typical of results seen in other experimental additions of organic matter to stream ecosystems. Warren and others (1964) found that the addition of sucrose to a stream resulted in increases in

Tendepedidae (Diptera) larvae. More recently, the addition of manure to streams in California dramatically increased Chironomidae densities (del Rosario et al., 2002). Observed increases of insect biomass were most probably due to the increased availability of microbes as food resource for collector-gatherer and shredder insects, while carnivorous insects benefited indirectly.

In this study, a greater number of taxa in the bedrock habitats responded to the addition of labile carbon. Differential responses of invertebrates to experimental treatment have been linked to the type of substrate in which they exist (Gurtz and Wallace 1984). The moss associated with bedrock habitats traps particles and aids in biological stability. Additionally, high flow rates in bedrock habitats contribute to high delivery rates of DOC. Many of the dominant rockface groups (collector-gatherers, filterers, and predators) are less dependent on CPOM and rely heavily on organic matter and FPOM trapped within moss. During this study, bedrock outcrops were heavily covered with microbial growth and enriched FPOM. Although FPOM quantity did not increase significantly during either addition, the quality of organic matter present in rockface habitats may have been greater in the treatment reach. This increase in FPOM quality may have allowed some taxa to increase in densities and biomass during a relatively short experimental time.

The fact that nearly all organisms sampled assimilated the dextrose, but fewer taxa exhibited significant changes in density or biomass, suggests that length of enrichment and sampling effort may not have been sufficient to accurately gauge effects of enrichment on insect communities in Jenny Branch. In a longer-term study, alterations in seston quality and substrate composition led to decreased invertebrate diversity, particularly for collector-filterers and scraper taxa (Mayack and Waterhouse 1983). Our study revealed no significant relationship between changes in insect abundance or biomass vs. treatment $\delta^{13}C$ values of taxa (Linear regression $p > 0.05$). Insects sampled for stable isotope analysis were pooled from mixed-substrate habitats and bedrock outcrops. A clearer relationship between benthic data and $\delta^{13}C$ probably would have emerged had samples from each habitat been collected and analyzed separately. The results of this study point to the need for further research on microhabitat differences in stable isotope signatures (see Findlay et al., 2002).

In conclusion, dextrose addition affected aquatic insects in Jenny Branch differently depending on their functional feeding group, microhabitat, diet, and turnover time. This study is among the first to examine the effects of a labile carbon addition on higher trophic levels in a heterotophic system. In this experiment, added labile carbon was taken up by microbes and was an important food resource for macroinvertebrates during the entire experimental period. All insects relied to some degree on the dextrose-derived carbon, demonstrating the strong linkage between bacteria and macroinvertebrates in heterotrophic food webs. Increases in the amount of organic matter present in streams can be the result of natural processes, but frequently are caused or accelerated by human activities. In this study, the short-term addition of labile carbon led to increased microbial and macroinvertebate productivity. Longer-term increases in carbon inputs may lead to changes in community structure that could impact overall stream ecosystem health. The addition of labile carbon to aquatic ecosystems via organic pollution may affect the quantity and quality of basal resources, resulting in effects that can seen at all trophic levels.

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CHAPTER 3

SUMMARY AND CONCLUSIONS

In this thesis I have examined some of the roles that carbon quality limitation may play in headwater stream food webs. The addition of a labile form of carbon (dextrose) to Jenny Branch enabled me to approximate some of the effects of carbon altering anthropogenic activities (food processing, wastewater treatment, pulp mill effluent) on stream ecosystems. Prior to this research, few studies had examined the responses of invertebrate consumers or the possibility of carbon limitation in extremely heterotrophic systems with large standing stocks of litter, such as the low-order streams found at Coweeta Hydrologic Laboratory in North Carolina.

During two experimental periods (August 8th – October 6th 2001 and November 8th 2001– January 10th 2002) a concentrated solution of dextrose (Corn Products International food grade dextrose; 250g/L) was added to the treatment reach from a holding tank at the forty-meter mark of an eighty-meter reach via a peristaltic pump. Throughout both addition periods average DOC concentration in the reference reach was ~ 1.0 mg/L. Average concentration of DOC in the treatment reach during the first addition period was 5.21 ± 1.80 mg /L (n = 6; range 0.42 – 25.46). Mean DOC concentration in the treatment section during the second study period was 10.9 ± 1.97 mg/L (n = 6; range 0.44 – 25.46 mg/L) (Chapter 2). Mean concentrations of DOC decreased from the site of DOC addition during both additions. DOC was removed from the water column throughout the summer and autumn addition periods, indicating that Jenny Branch, like other streams to which DOC has been added, has a great capacity for processing added labile DOC. DOC concentration in the treatment reach was not markedly higher than the concentration in the reference reach until the 48th day of the dextrose addition due to increased abiotic and biotic uptake. Additionally, DOC removal rates in Jenny Branch may have been elevated due to increased DOC loading.

The experimental addition of a labile form of carbon represented a large increase in a biologically available energy source. Consequently, the elevation of DOC concentration in stream led to large increases in bacterial numbers in the treatment section compared to the reference section. Average bacterial densities in the treatment reach during the first study period (August to October 2001) were nearly three times higher ($4.15 \times 10^{11} \pm 1.79 \times 10^{11}$ [mean ± 1 SE]) than in the reference section ($1.66 \times 10^{11} \pm 2.91 \times 10^{10}$). During the second study period beginning on November 1st, bacterial densities in the treatment section ($2.42 \times 10^{11} \pm 2.26 \times 10^{10}$) were double those of the reference section ($1.08 \times 10^{11} \pm 1.09 \times 10^{10}$). Bacterial densities increased during both treatment periods despite a constant decrease in average daily water temperatures. Thick microbial "mats" developed, particularly in areas of higher velocity flow on bedrock outcrops. Microscopic examination of microbial mats revealed an abundance of non-sheathed bacteria, sheathed bacteria of the genus *Sphaerotilus* (Mulder and Deinema 1981), and predominantly, the aquatic hyphomycete *Lemmoniera pseudofloscula* (V. Gulis and K. Suberkropp, personal communication).

Metabolic activity of bacteria is often determined by the concentration and composition of DOC present in a system (Kaplan and Bott 1989; Baker et al. 1999).

Therefore, higher respiration rates observed in the treatment reach during the summer addition were the result of increased microbial activity. However, it is worth noting that respiration rates on the whole were not remarkably high when compared to published rates for benthic microbial respiration in the Appalachian region (Hill et al., 2002). Temperature may influence heterotrophic respiration; consequently, lower ambient stream temperature most likely led to lower densities of bacteria and decreased leaf pack respiration rates during the autumn dextrose addition (Sinsabaugh 1997). While microbial growth in other studies where a labile form of carbon was added was mainly associated with sediments, growth in Jenny Branch was concentrated in high-velocity bedrock habitats.

Assimilation of dextrose by all functional feeding groups suggests that the added carbon was an important food resource during both dextrose additions. In general, collector-gatherers derived the highest portion of their carbon from added dextrose (average % dextrose carbon = 66%). High labeling of *Stenonema* during both dextrose additions suggests that this taxon was selectively feeding on highly enriched particles within the biofilm or even on the fungus *Lemonniera* itself. Although Hall and Meyer (1998) found no evidence that typical stream hyphomycetes were significantly labeled above background levels during their ^{13}C-acetate release, results of stable isotope analysis in this study indicate that the fungus *Lemonniera* was highly enriched. Organisms that directly ingested *Lemonniera* would have assimilated a large proportion of dextrose-derived carbon. Other functional groups were not as uniformly labeled as collector-gatherers. Wide differences in the relative contribution of dextrose carbon seen within the shredder and predator functional groups can perhaps be traced to differential consumption of bacterial cells and exopolymers resulting from the addition of labile carbon or type prey consumed. *Leuctra*, although classified as a shredder, has been found in early instars to be primarily a collector that relies heavily on FPOM and organic matter, particularly in bedrock habitats (Dobson and Hildrew 1992). All shredders sampled in their study derived a portion of their carbon from the added dextrose. This finding supports the analogy that microorganisms on a leaf are like peanut butter on a cracker, with some of the nourishment coming from the peanut butter (Cummins 1974). Predators found to have a >50% contribution of dextrose carbon during the autumn addition (*Isoperla, Sweltsa,* and *Hexatoma*) are evidence that, despite a relatively short experimental period, dextrose-derived carbon was reaching higher trophic levels.

Higher trophic levels in Jenny Branch directly benefited from the microbial biomass produced by DOC uptake. Increased microbial density in the treatment reach led to greater food resource availability for chironomid larvae. It is likely then that the high microbial content associated with FPOM in the treatment reach may have also contributed to higher growth rates. While collector-gatherers (Nematoda, *Serratella,* and Chironomidae) increased in abundance during the summer addition, scraper and filterer densities did not increase, contrary to our hypothesis. There were no significant changes in filterer density or biomass during either addition. Chironomids, typically tolerant to organic enrichment, were the only taxon to respond to the labile carbon with increases in abundance during both dextrose additions in both habitats sampled. The fact that nearly all organisms sampled assimilated the dextrose but fewer taxa exhibited significant changes in density or biomass suggests that the length of the enrichment and sampling effort may not have been sufficient to accurately gauge the effects of the enrichment on insect communities present in Jenny Branch. Additionally, the design of the experiments described in this thesis required us to employ methods of statistical analysis that are extremely conservative. The patchy nature of benthic habitats and organisms associated with them leads to difficulties in uncovering patterns in changes of macroinvertebrate densities during the dextrose addition. For example, copepods were found to have increased dramatically in rockface habitats in the treatment reach, but this difference was obscured due to the fact that copepods did not consistently increase over the time of the experiment.

Our study revealed no significant relationship between insect abundance and biomass and shifts observed between reference and treatment $\delta^{13}C$ values of taxa (Linear regression $p > 0.05$). Insects sampled for stable isotope analysis were pooled from mixed-substrate habitats and bedrock outcrops. We believe that a clearer relationship between benthic data and $\delta^{13}C$ would have emerged had samples from each habitat been analyzed separately. The results of this study point to the need for research of microhabitat differences in stable isotope signatures (see Findlay et al., 2002).

In conclusion, dextrose addition affected aquatic insects in Jenny Branch differently depending on their functional feeding group, diet, and turnover time. This study is among the first to examine the effects on a labile carbon addition on higher trophic levels in a heterotophic system. In this experiment, added labile carbon was taken up by microbes and was an important food resource for macroinvertebrates during the entire experimental period. All insects relied to some degree on the dextrose-derived carbon, demonstrating the strong linkage between bacteria and macroinvertebrates in heterotrophic food webs. These effects were observed during both dextrose additions suggesting that stream ecosystems are sensitive to this type of pollution throughout the year. Increases in the amount of organic matter present in streams can be the result of natural processes, but frequently are caused or accelerated by human activities. The addition of labile carbon to aquatic ecosystems via organic pollution may affect the quantity and quality of basal resources, resulting in effects that are seen at all trophic levels. These changes may negatively impact overall stream ecosystem health.

An important goal of further research is to fully understand the effects of organic pollution on stream food webs. The work attempted in this thesis is a step towards this goal but clearly there are limitations to whole-ecosystems manipulations that are not longer in length. Future directions for research in this area might include long-term multi-stream comparisons of carbon quality and quantity limitation with a focus on microhabitat differences in impacts of this limitation on stream food webs. Research such as that described in this thesis will continue to illuminate of the importance of microbial linkages in aquatic food webs.

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Table 1. Size and temperature-specific growth data used to derive chironomid growth rates and regression equations used in this study. Li - Average initial length rounded to the nearest 0.5 mm; Mi and Mf - average initial and final mass (ug) of individuals placed ingrowth chambers; ni and nf - initial and final numbers of individuals observed; t - number of days incubated; g - daily growth rate; T - average stream temperature.

	Treatment	*Li*	*Mi*	*ni*	*Mf*	*nf*	*t*	*g*	*T*
August	Sugar	1	0.001	40	0.005	13	9	0.162	15.96
August	Sugar	2	0.004	93	0.008	19	9	0.061	15.96
August	Sugar	3	0.012	27	0.018	13	9	0.044	15.96
August	No sugar	1	0.001	49	0.003	7	9	0.101	15.96
August	No sugar	2	0.004	47	0.004	14	9	-0.008	15.96
August	No sugar	3	0.127	26	0.009	3	9	-0.003	15.96
September	Sugar	1	0.001	36	0.002	20	7	0.114	15.61
September	Sugar	2	0.004	18	0.007	9	7	0.071	15.61
September	Sugar	3	0.014	21	0.015	13	7	0.014	15.61
September	No sugar	1	0.001	50	0.001	10	7	0.066	15.61
September	No sugar	2	0.003	19	0.003	16	7	0.010	15.61
September	No sugar	3	0.126	19	0.013	9	7	0.004	15.61
November	Sugar	1	0.001	50	0.006	12	15	0.106	11.19
November	Sugar	2	0.004	48	0.009	7	15	0.061	11.19
November	Sugar	3	0.015	14	0.036	7	15	0.059	11.19
November	No sugar	1	0.001	49	0.004	15	15	0.084	11.19
November	No sugar	2	0.003	49	0.006	7	15	0.048	11.19
November	No sugar	3	0.015	14	0.020	8	15	0.017	11.19
December	Sugar	1	0.001	49	0.002	14	10	0.122	6.97
December	Sugar	2	0.003	27	0.006	11	10	0.067	6.97
December	Sugar	3	0.011	17	0.014	5	10	0.021	6.97
December	No sugar	1	0.001	48	0.001	10	10	0.046	6.97
December	No sugar	2	0.003	49	0.004	11	10	0.011	6.97
December	No sugar	3	0.013	16	0.014	7	10	0.004	6.97

Table 2. Two-source linear mixing model results for taxa collected from the treatment and reference reaches of Jenny Branch at the end of the summer (August- October 2001) and autumn (November 2001- January 2002) dextrose addition periods.Standard errors for all taxa were < 2%. Three letter acronyms for taxa are used in all stable isotope bi-plots. Bold type indicates taxa with > 50% reliance on dextrose carbon in the treatment reach. Asterisks indicate taxa in the treatment reach with 13C values higher than the 95% confidence intervals of reference samples.

		SUMMER							**AUTUMN**						
						Source contribution							**Source contribution**		
		δ13C				**Treatment**			**δ13C**				**Treatment**		
Functional Group	**Taxon**	**Ref**	**n**	**Treat**	**n**	**CPOM**	**Dextrose**		**Ref**	**n**	**Treat**	**n**	**CPOM**	**Dextrose**	
Collector-Gatherers	Oligochaeta (OLI)	…	…	-22.6	3	62%	38%		…	…	…	…	…	…	
	Paraleptophlebia spp. (PAL)	…	…	-16.0	3	22%	78%		-25.9	2	-15.5	3	26%	74%	*
	Chironomidae (NON-TAN)	…	…	-14.2	2	11%	89%		-27.0	2	-18.8	2	46%	54%	*
	Stenonema sp. (STE)	-25.9	3	-15.8	3	21%	79%	*	-26.6	3	-15.9	2	28%	73%	*
Shredders	*Leuctra spp.* (LEU)	-24.6	3	-18.1	2	35%	65%	*	-25.3	2	-16.8	2	34%	66%	*
	Tallaperla spp. (TAL)	-25.1	2	-19.0	3	40%	60%	*	-26.5	3	-21.1	3	61%	39%	*
	Fattigia spp. (FAT)	-26.6	2	-18.8	3	39%	61%	*	-26.0	3	…	…	…	…	
	Pycnopsyche spp. (PYC)	…	…	…	…	…	…		-27.6	3	-23.2	3	74%	20%	*
	Lepidostoma spp. (LEP)	-26.3	3	…	…	…	…		…	…	…	…	…	…	
	Psilotreta spp. (PSI)	…	…	-23.4	3	67%	33%		…	…	…	…	…	…	
	Tipula spp. (TIP)	-26.4	3	-22.4	3	61%	39%	*	-26.6	3	-20.4	3	56%	44%	*
Filterers	*Diplectrona spp.* (DIP)	-25.3	2	-21.0	3	52%	48%	*	-25.0	2	-19.5	3	51%	49%	*
	Parapsyche sp. (PAP)	-25.7	3	-21.2	3	53%	47%	*	-25.2	2	-20.6	3	57%	43%	*
	Wormaldia spp. (WOR)	…	…	…	…	…	…		-25.7	2	-17.0	2	35%	**65%**	*
Predators	*Cordulagaster spp.* (COR)	-24.2	2	-22.5	3	61%	39%	*	-24.2	2	-20.1	3	55%	45%	
	Lanthus spp. (LAN)	-23.6	3	-21.6	3	56%	44%	*	-23.6	3	-21.9	3	66%	34%	
	Beloneuria sp . (BEL)	-24.0	2	-22.8	3	63%	37%	*	-24.5	3	-19.7	3	52%	48%	*
	Hexatoma spp. (b) (HEX)	-23.9	3	-21.9	3	58%	42%	*	-24.5	2	-18.2	3	42%	58%	*
	Pedicia spp. (PED)	-23.8	3	-21.4	3	55%	45%	*	…	…	…	…	…	…	
	Desmognathus sp.(DES)	-23.7	2	-23.3	3	66%	34%		-23.0	3	-20.7	3	58%	42%	*
	Isoperla spp. (ISO)	…	…	…	…	…	…		-25.1	2	-18.9	2	47%	53%	*
	Rhyacophila spp. (RHY)	…	…	…	…	…	…		-24.4	3	-20.9	3	59%	41%	*

Table 3. Analysis of covariance of probability of no change in abundance and biomass of functional groups and specific tax between the non-dextrose and dextrose reaches of Jenny Branch during the first treatment period from August to October 2001.

		Bedrock outcrops				Mixed substrates			
Functional group and taxon	Order	F Ratio abundance	Probability, abundance	F Ratio biomass	Probability, biomass	F Ratio abundance	Probability, abundance	F Ratio biomass	Probability, biomass
Scrapers									
Epeorus sp.	E	0.006	0.941	0.071	0.793	…	…	…	…
Baetis sp.	E	1.815	0.193	1.815	0.193	0.292	0.593	1.172	0.287
Ectopria sp.	C	1.74	0.202	0.754	0.396	4.591	0.041	4.983	0.034
Hydroptila	T	0.383	0.543	0.383	0.543	0.236	0.631	0.292	0.593
Psilotreta	T	0.172	0.683	0.205	0.655	0.002	0.966	0.342	0.563
Nymphomyiidae	D	1.158	0.295	1.04	0.32	1.778	0.195	1.778	0.193
Thaumalea	D	…	…	…	…	…	…	…	…
Total Scrapers		2.59	0.123	0.883	0.359	0.001	0.973	2.183	0.151

Table 3. Continued

Shredders									
Tallaperla spp.	P	0.032	0.861	0.479	0.497	7.99	0.009	3.835	0.06
Leuctra spp.	P	0.059	0.811	0.144	0.709	1.673	0.207	2.688	0.112
Lepdidostoma spp.	T	1.523	0.231	0.238	0.631	**11.898**	**0.002**	**8.01**	**0.009**
Pycnopsyche spp.	T	0.323	0.576	0.323	0.576	0.045	0.834	0.119	0.733
Fattigia pele	T	…	…	…	…	0.024	0.878	0.224	0.64
Tipula spp.	D	0	1	0.015	0.904	**6.788**	**0.015**	4.168	0.051
Limonia	D	0.383	0.543	0.383	0.543	0.053	0.82	0.071	0.792
Molophilus	D	…	…	…	…	0.429	0.518	0.178	0.677
Cambarus spp.		…	…	…	…	0.996	0.327	0.9	0.351
Total Shredder		1.134	0.3	0.648	0.43	8.004	0.009	0.775	0.386

Table 3. continued

Gatherers									
Collembola	NI	2.873	0.116	4.203	0.054	2.809	0.105	4.38	0.046
Nematoda	NI	**5.532**	**0.029**	**5.77**	**0.026**	4.151	0.051	5.826	0.023
Oligochaeta	NI	4.304	0.051	**5.222**	**0.033**	0.021	0.887	0.132	0.719
Copepoda	NI	0.381	0.544	0.381	0.544	0.004	0.953	0.004	0.953
Paraleptophlebia spp.	E	1.336	0.261	3.585	0.073	2.043	0.164	3.223	0.083
Habroleptophlebia spp.	E	…	…	…	…	0.39	0.538	0.39	0.538
Stenonema sp.	E	0.486	0.494	1.404	0.25	…	…	…	…
Serratella sp.	E	**12.95**	**0.002**	**4.731**	**0.042**	12.95	0.002	4.418	0.045
Amphinemura	P	1.517	0.232	2.142	0.159	0.39	0.538	1.297	0.264
Elmidae (L)	C	3.003	0.099	2.037	0.169	0.626	0.435	0.274	0.605
Elmidae (A)	C	0.218	0.646	0.0003	0.987	1.778	0.173	1.778	0.193
Lype diversa	T	0.383	0.543	0.383	0.543	0.01	0.923	0.18	0.675
Ormosia	D	…	…	…	…	0.256	0.617	0.26	0.614
Sciaridae	D	1.653	0.213	1.653	0.213	0.015	0.904	0.972	0.333
Chironomidae (**)	D	**10.341**	**0.004**	3.573	0.073	**10.341**	**0.004**	0.075	0.786
Total Gatherer		**10.572**	**0.004**	**19.486**	**0.0003**	1.811	0.189	0.616	0.439

Table 3. continued

Filterers									
Cladocera	NI	0.739	0.4	1.008	0.328	0.001	0.983	0.0004	0.985
Diplectrona	T	…	…	…	…	0.549	0.465	1.231	0.277
Parapsyche cardis	T	0.041	0.841	1.064	0.315	0.745	0.396	0.13	0.721
Wormaldia	T	0.025	0.876	0.704	0.411	1.856	0.184	2.068	0.162
Simulidae	D	0.012	0.915	0.17	0.685	…	…	…	…
Total filterers		0.903	0.353	1.587	0.222	0.153	0.7	0.463	0.502

Table 3. continued

Inverterbate predators									
Acari	NI	1.229	0.281	0.624	0.439	0.02	0.889	0.02	0.889
Turbellaria	NI	0.033	0.858	0.337	0.568	0.029	0.867	0.048	0.757
Lanthus sp.	O	1.353	0.213	1.653	0.213	10.162	0.004	5.42	0.027
Cordulegaster sp.	O	0.383	0.543	0.383	0.543	11.386	0.002	4.683	0.039
Beloneuria sp.	P	0.305	0.587	0.395	0.537	0.289	0.595	0.737	0.398
Isoperla spp.	P	1.069	0.314	1.022	0.059	0.588	0.45	0.045	0.834
Sweltsa lateralis	P	0.049	0.827	0.308	0.585	0.328	0.571	0.328	0.571
Rhyacophila spp.	T	0.987	0.332	0.103	0.751	1.643	0.21	0.449	0.508
Pseudogoera sp.	T	0.068	0.797	0.424	0.523	0.04	0.843	0.14	0.711
Tanypodinae	D	0.869	0.362	2.185	0.155	0.493	0.489	0.333	0.569
Ceratopogonidae	D	2.242	0.15	1.66	0.212	1.031	0.319	0.447	0.509
Anchytarsus	D	1.351	0.259	2.666	0.118	3.461	0.073	3.35	0.078
Rabdomastix	D	1.815	0.193	1.815	0.193	1.454	0.238	0.093	0.763
Hexatoma spp.	D	0.849	0.524	1.234	0.295	0.39	0.738	0.517	0.728
Dicranota spp.	D	1.589	0.222	1.775	0.198	0.676	0.418	0.041	0.842
Pedicia sp.	D	…	…	…	…	1.482	0.234	1.8	0.192

Table 3. continued

Total Invertebrate		2.911	0.103	**4.376**	**0.049**	1.695	0.204	0.845	0.366
Vertebrate predators									
Desmognathus	NI	…	…	…	…	0.047	0.83	0.048	0.829
Eurycea	NI	1.815	0.193	1.815	0.193	2.038	0.165	1.357	0.254

Table 4. Analysis of covariance of probability of no change in abundance and biomass of functional groups and specific taxa between the non-dextrose and dextrose reaches of Jenny Branch during the second treatment period from November 2001 to January 2002. Ellipses (…) indicate taxa not present.

		Bedrock outcrops				Mixed substrates			
Functional group and taxon	Order	F Ratio	Probability abundance	F Ratio	Probability, biomass	F Ratio	Probability, abundance	F Ratio	Probability, biomass
Scrapers									
Epeorus sp.	E	0.272	0.608	0.272	0.608	…	…	…	…
Baetis sp.	E	0.243	0.628	0.243	0.628	0	0.998	0.031	0.863
Ectopria sp.	C	3.717	0.068	3.473	0.077	1.793	0.194	1.773	0.194
Hydroptila	T	0.272	0.608	0.272	0.608	1.293	0.265	0.995	0.327
Psilotreta	T	1.011	0.327	0.566	0.461	0.013	0.91	0.361	0.553
Nymphomyiidae	D	1.874	0.186	0.458	0.507	0.671	0.42	0.316	0.578
Total Scrapers		0.489	0.492	0.658	0.427	0.26	0.614	**4.402**	**0.045**

Table 4. continued

Shredders									
Tallaperla spp.	P	2.166	0.09	**7.501**	**0.013**	0.24	0.628	0.289	0.595
Leuctra spp.	P	0.483	0.495	1.335	0.262	1.795	0.191	1.039	0.317
Lepidostoma spp.	T	0.002	0.97	0.198	0.661	1.067	0.31	1.033	0.318
Pycnopsyche spp.	T	1.908	0.327	1.908	0.183	0.03	0.863	0	0.994
Fattigia pele	T	…	…	…	…	1.095	0.304	0.819	0.373
Anchytarsus	C	0.513	0.482	0.364	0.533	0.002	0.965	0.126	0.726
Tipula spp.	D	0.272	0.608	0.272	0.608	2.368	0.135	0.103	0.751
Limonia	D	0.06	0.809	0.078	0.783	4.007	0.055	4.069	0.053
Molophilus	D	0.452	0.509	0.031	0.861	0.047	0.83	0.44	0.513
Cambarus spp.		…	…	…	…	2.362	0.136	1.526	0.227
Total Shredder		1.61	0.219	**8.64**	**0.008**	**4.481**	**0.043**	0.467	0.5

Table 4. continued

Gatherers									
Collembola	NI	0.04	0.844	0.007	0.934	0.002	0.463	13.396	0.0004
Nematoda	NI	0.262	0.614	0.012	0.913	2.756	0.108	1.979	0.171
Oligochaeta	NI	0.34	0.566	0.022	0.884	0.742	0.396	1.205	0.282
Copepoda	NI	0.0002	0.989	0.001	0.972	0.364	0.551	0.48	0.494
Paraleptophlebia spp.	E	0.85	0.368	1.23	0.281	0.265	0.611	0	0.999
Stenonema sp.	E	…	…	…	…	0.227	0.638	0.015	0.905
Serratella sp.	E	0.652	0.419	0.508	0.484	0.245	0.625	0.024	0.88
Amphinemura	P	0.037	0.849	0.015	0.905	0.017	0.898	0.181	0.671
Elmidae (L)	C	0.002	0.964	0.29	0.596	0.851	0.364	1.291	0.266
Elmidae (A)	C	1.374	0.255	0.798	0.383	…	…	…	…
Dixa	D	1.922	0.181	2.286	0.146	1.961	0.172	0.619	0.438
Sciaridae	D	1.908	0.183	1.908	0.183	0.362	0.552	0.708	0.407
Chironomidae	D	**6.857**	**0.017**	1.242	0.278	**9.167**	**0.005**	2.903	0.1
Total Gatherer		0.538	0.472	3.353	0.082	0.225	0.639	3.706	0.064

Table 4. continued

Filterers									
Cladocera	NI	2.109	0.162	2.027	0.17	1.657	0.209	1.216	0.28
Diplectrona	T	…	…	…	…	0.006	0.938	0.003	0.961
Parapsyche cardis	T	0.022	0.883	1.956	0.177	1.773	0.194	1.773	0.194
Wormaldia	T	4.244	0.052	2.921	0.103	0.248	0.623	0.95	0.338
Simulidae	D	0.665	0.425	0.234	0.634	0.608	0.442	0.4	0.533
Total filterers		0.041	0.842	0.126	0.726	1.79	0.192	0.48	0.494

Table 4. continued

Inverterbate predators									
Acari	NI	0.341	0.566	2.274	0.147	2.987	0.095	2.808	0.105
Turbellaria	NI	10.422	0.004	8.01	0.01	1.864	0.183	1.864	0.183
Lanthus sp.	O	…	…	…	…	1.792	0.191	3.596	0.068
Cordulegaster sp.	O	…	…	…	…	0.783	0.384	2.011	0.167
Beloneuria sp.	P	0.184	0.673	0.362	0.554	2.892	0.1	3.466	0.073
Isoperla spp.	P	0.122	0.731	0.147	0.706	2.096	0.159	2.508	0.125
Sweltsa lateralis	P	…	…	…	…	0.648	0.428	1.039	0.317
Rhyacophila spp.	T	0.079	0.782	0.001	0.977	0.028	0.869	0.381	0.542
Pseudogoera sp.	T	1.039	0.32	3.189	0.089	0.08	0.78	0.116	0.736
Tanypodinae	D	4.253	0.052	3.168	0.072	1.076	0.308	1.652	0.209
Ceratopogonidae	D	**5.731**	**0.027**	0.535	0.473	0.256	0.617	0.194	0.663
Hexatoma spp.	D	0.444	0.526	0.57	0.474	0.165	0.726	0.34	0.662
Dicranota spp.	D	0.096	0.759	0.546	0.469	2.721	0.11	1.541	0.225
Pedicia sp.	D	1.326	0.263	0.553	0.466	0.146	0.705	0.176	0.678
Empiidae	D	1.626	0.217	0.392	0.538	0.004	0.951	0.001	0.973
Rabdomastix	D	…	…	…	…	0.101	0.754	0.022	0.883

Table 4. continued

Pelecorhynchida	D	0.32	0.578	1.908	0.183	0.278	0.602	0.0008	0.978
Total invertebrate predators		1.289	0.27	2.823	0.109	1.027	0.32	0.448	0.509
Total Invertebrate		**8.005**	**0.01**	4.099	0.057	1.089	0.306	0.338	0.566
Vertebrate predators									
Desmognathus	NI	…	…	…	…	0.557	0.462	0.473	0.497
Eurycea	NI	0.272	0.608	0.272	0.608	0.248	0.623	0.248	0.623

Table 5. Organic matter standing crops (g AFDM/m2) for mixed substrate and bedrock outcrop habitats in the summer (August to October 2001) and autumn (November 2001 to January 2002) in the treatment and reference reaches of Jenny Branch (WS 4).

Habitat	Treatment, Summer	Reference, Summer	Treatment, Autumn	Reference, Autumn
Mixed substrates				
Total FPOM	712.3a	471.6a	712.9a	440.2a
Total CPOM	437.0a	244.5a	995.0b	875.3b
Bedrock outcrop				
Total FPOM	14.7a	13.5a	12.7a	13.8a

Note: Values within a category in each stream that are followed by the same letter are not significantly different ($p > 0.05$, Two-way ANOVA and Tukey's Test).

Table 6. Fraction of invertebrate carbon derived from a) bacteria) and b) dextrose for 19 taxa in four functional feeding groups during July and December in WS 53 (Hall and Meyer 1998) and during October and January in Jenny Branch (WS 4). Numbers in parentheses are standard errors of the mean. Entries with ellipses (…) indicate taxa for which no data were available.

Functional feeding group	Insect order	Taxon	Jenny Branch, October-01	WS 53, July-94	Jenny Branch, January-02	WS 53, December-94
Shredders	Plecoptera	*Leuctra* spp.	0.65 (0.01)	0.77 (0.21)	0.66 (0.04)	1.15 (0.26)
	Plecotpera	*Tallaperla* spp.	0.59 (0.04)	0.38 (0.18)	0.39 (0.03)	0.31 (0.11)
	Trichoptera	*Fattigia pele*	0.61 (0.01)	…		0.15 (0.03)
	Trichoptera	*Lepidostoma*spp.	…	0.11 (0.08)		0.25 (0.11)
	Trichoptera	*Pycnopsyche* spp.	…	…	0.26 (0.02)	1.13 (0.28)
	Diptera	*Tipula spp.*	0.39 (0.02)	0.19 (0.06)	0.44 (0.02)	0.10 (0.10)
Gatherers	Ephmeroptera	*Paraleptophlebia* spp.	0.78 (0.01)	…	0.74 (0.02)	2.35 (0.81)
	Plecoptera	*Amphinemura* spp.	…	…		1.15 (0.26)
	Diptera	*Chironomidae*	0.89 (0.02)	0.34 (0.09)	0.54 (0.02)	…
		Oligochaete	0.38 (0.01)	…	…	0.32 (0.20)
Filterers	Trichoptera	*Diplectrona* spp.	0.48 (0.02)	…	0.49 (0.02)	0.53 (0.19)
	Trichoptera	*Parapsyche cardis*	0.47 (0.01)	…	0.43 (0.02)	0.52 (0.14)
	Trichoptera	*Wormaldia* spp.	…	10.8 (4.22)	0.65 (0.03)	13.1 (2.63)
Scrapers	Ephemeroptera	*Stenonema* spp.	0.79 (0.01)		0.72 (0.02)	4.72 (0.90)

Figure 1. Discharge (Q) data for Jenny Branch from July 31, 2001 to January 1, 2002. The solid line represents average daily Q obtained by regression (r-squared = 0.56) with data from a nearby stream WS 53. The line with circles indicates water column temperatures in degrees Celsius.

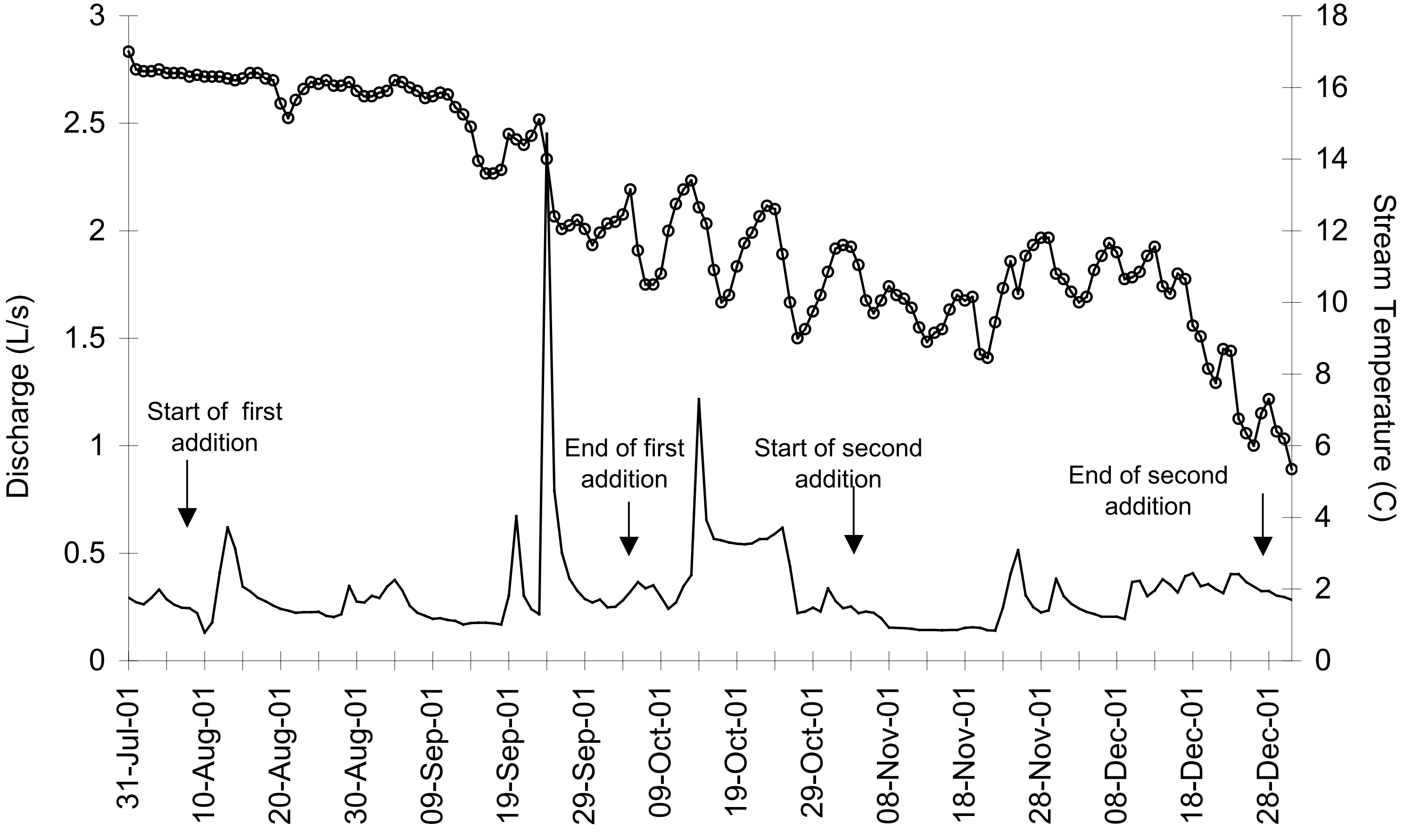

Discharge (L/s)
Stream Temperature (C)
0
0.5
1
1.5
2
2.5
3
0
2
4
6
8
10
12
14
16
18
31-Jul-01
10-Aug-01
20-Aug-01
30-Aug-01
09-Sep-01
19-Sep-01
29-Sep-01
09-Oct-01
19-Oct-01
29-Oct-01
08-Nov-01
18-Nov-01
28-Nov-01
08-Dec-01
18-Dec-01
28-Dec-01
Start of first addition
End of first addition
Start of second addition
End of second addition

Figure 2. Water column DOC concentrations on (A) seven sampling dates during the summer dextrose addition (August to October 2001) and (B) six sampling dates during the autumn dextrose addition (November 2001 to January 2002).

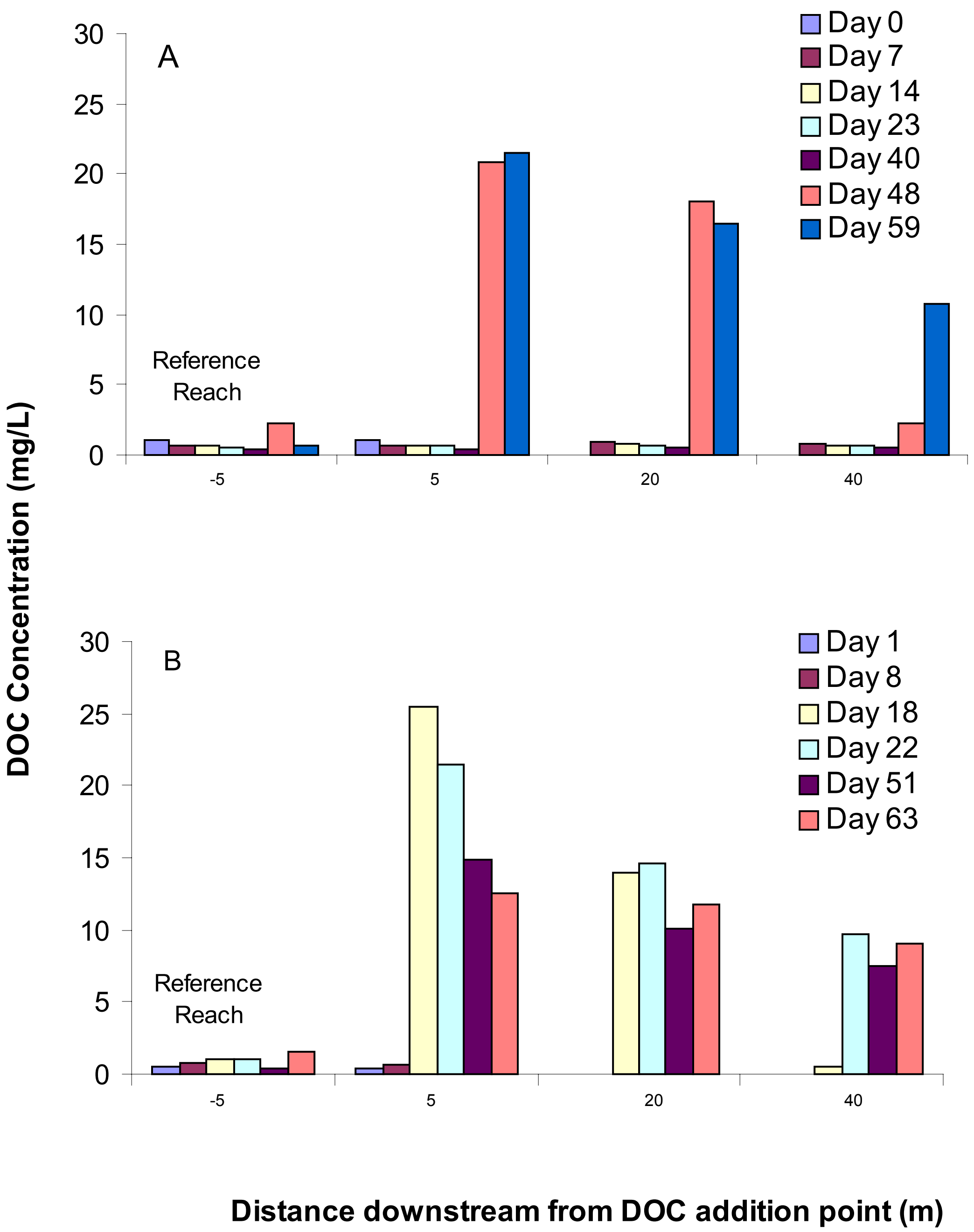

A
B
30
25
20
15
10
5
0
Day 0
Day 7
Day 14
Day 23
Day 40
Day 48
Day 59
Day 1
Day 8
Day 18
Day 22
Day 51
Day 63
Reference Reach
-5
5
20
40
DOC Concentration (mg/L)
Distance downstream from DOC addition point (m)

Figure 3. Average bacterial densities collected from ceramic tiles in the treatment and reference reaches of Jenny Branch during both dextrose additions. The line with solid markers represents the treatment reach while the line with open markers represents the reference reach. Error bars represent 95% confidence intervals based on duplicate samples.

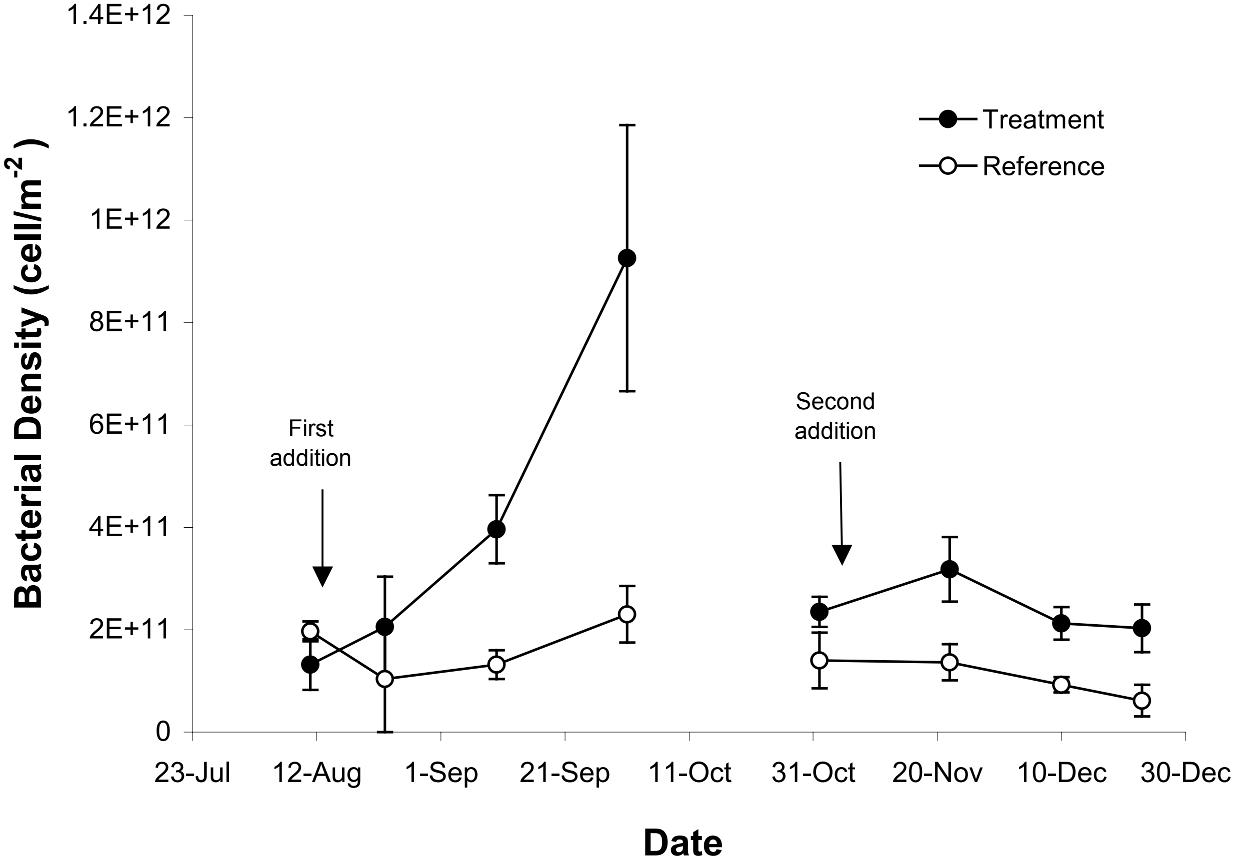

1.4E+12
1.2E+12
1E+12
8E+11
6E+11
4E+11
2E+11
0
Bacterial Density (cell/m^{-2})
Treatment
Reference
First addition
Second addition
23-Jul
12-Aug
1-Sep
21-Sep
11-Oct
31-Oct
20-Nov
10-Dec
30-Dec
Date

Figure 4. Leaf disk respiration rates for disks incubated in the treatment and reference reaches of Jenny Branch during the summer dextrose addition (August to October 2001) and during the autumn dextrose addition (November 2001 to January 2002). Error bars represent 95% confidence intervals. Hatched columns represent average respiration rates in the treatment reach while the white columns represent average rates in the reference reach.

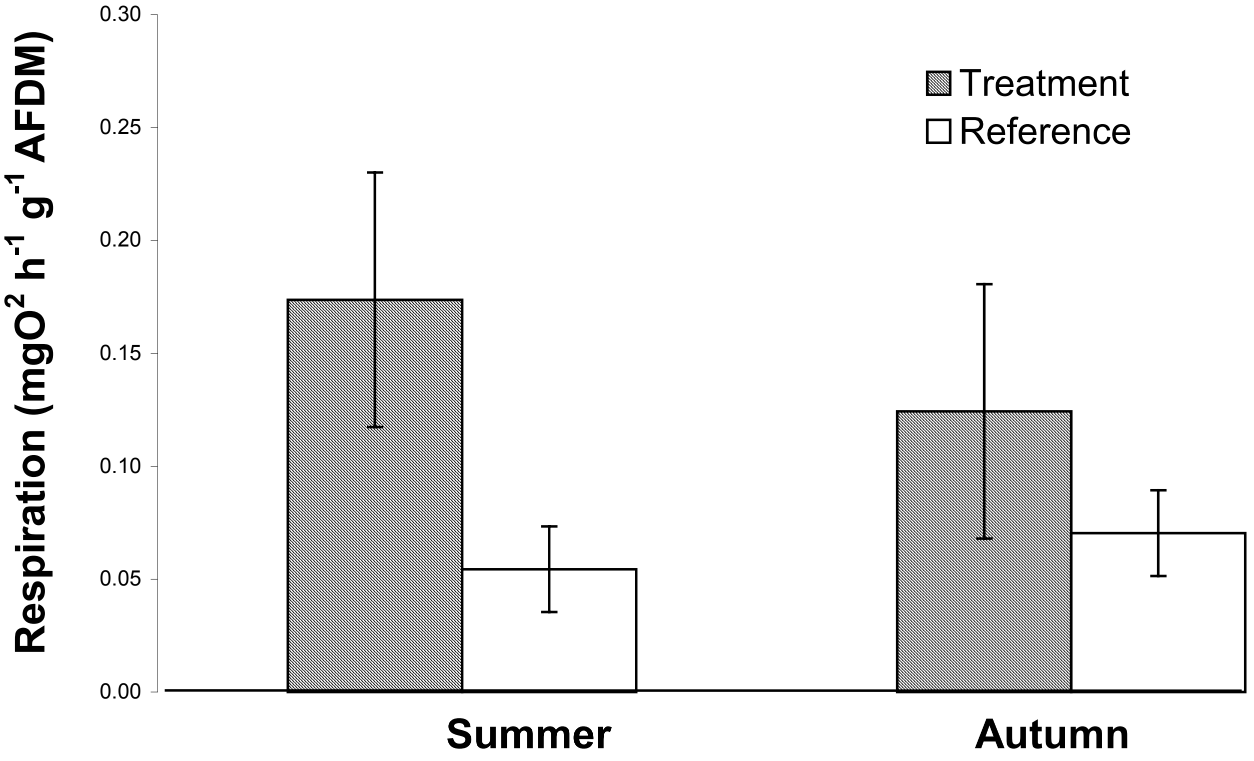

Respiration (mgO2 h-1 g-1 AFDM)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
▨ Treatment
☐ Reference
Summer
Autumn

Figure 5. Instantaneous growth rates for Chironomidae incubated in Jenny Branch during (A) August, (B) September, (C) October, and (D) December of 2001. Solid circles represent daily growth in the treatment reach while open circles represent those incubated in the reference reach. Size class 1 = Chironomids with initial length ≤ 1.5 mm, size class 2 = 1.5-2.5mm, and size class 3 = 4.5^+ mm.

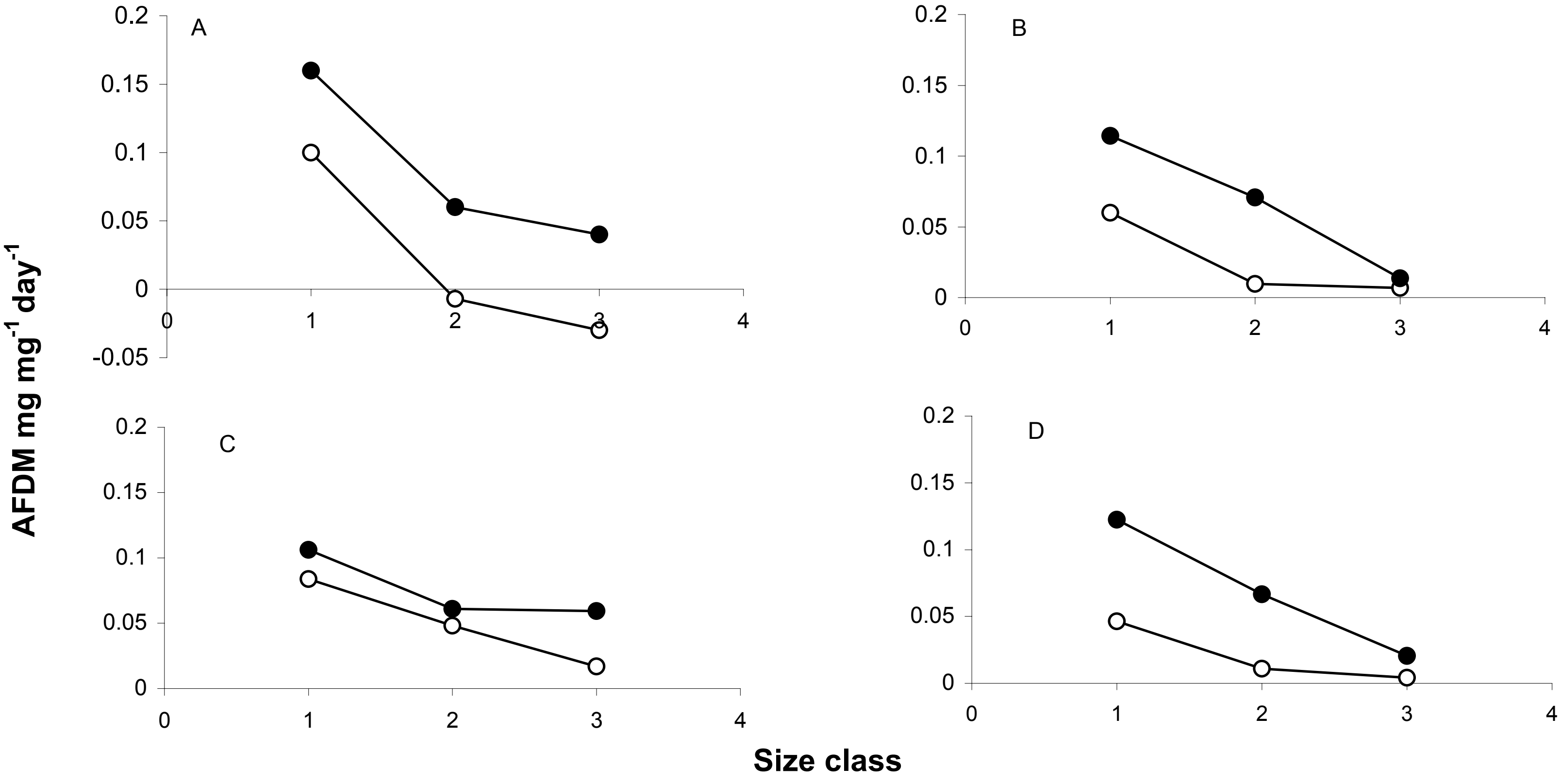
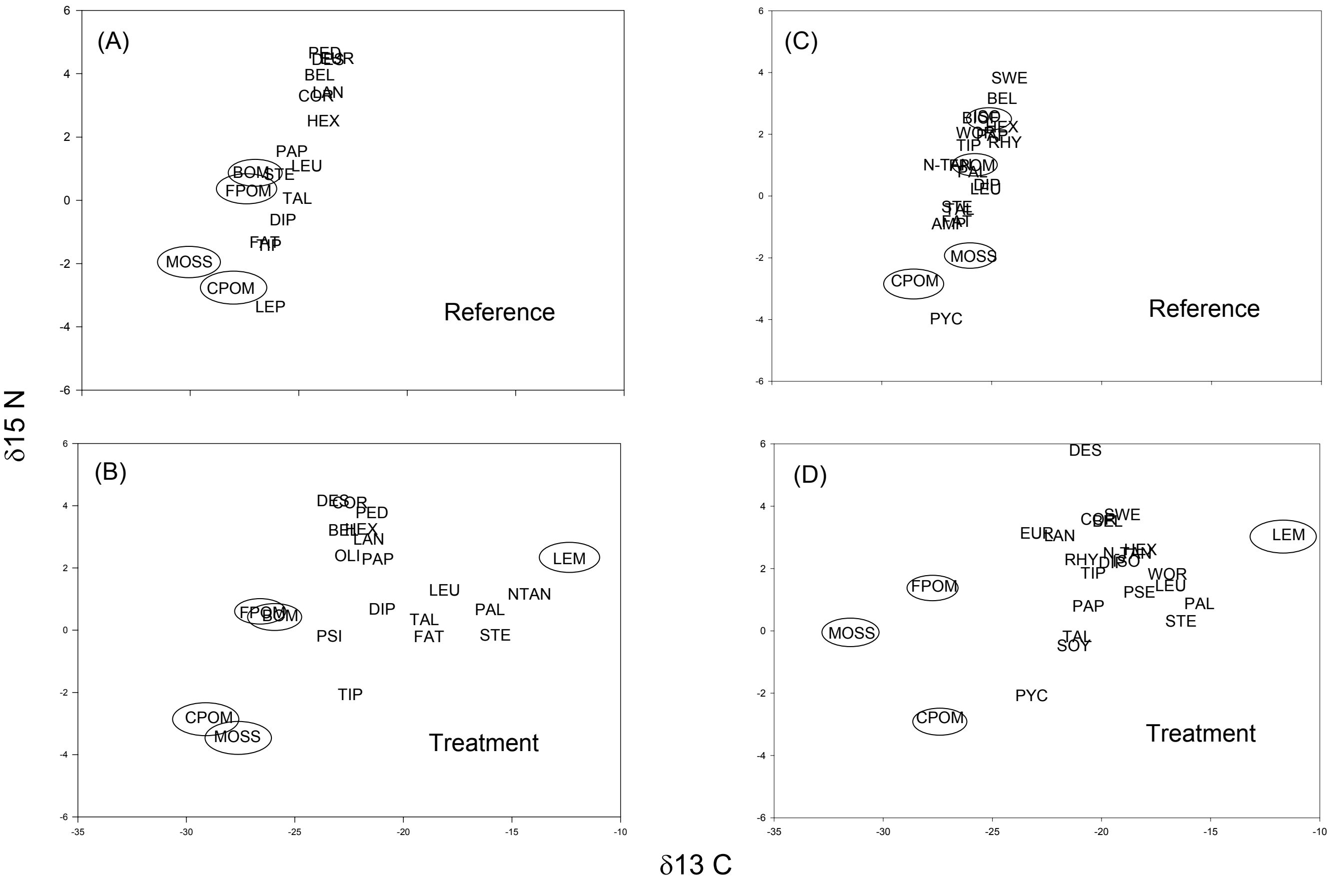

A
B
C
D
0.2
0.15
0.1
0.05
0
-0.05
0
1
2
3
4
AFDM mg mg^{-1} day^{-1}
Size class

Figure 6. Mean $\delta^{13}C$ and $\delta^{15}N$ values of taxa collected in the reference and treatment reaches of Jenny Branch showing how each taxon assimilated the introduced dextrose during the (A and B) first addition experiment from August to October 2001 and (C and D) the second addition form November 2001 to January 2002, Values are based on insects collected downstream of the dextrose addition and comparable locations from the reference reach. Circled values represent basal resources.


(A)
PED
DES
BEL
LAN
COR
HEX
PAP
LEU
BOM
STE
FPOM
TAL
DIP
FAT
TIP
MOSS
CPOM
LEP
Reference
(C)
SWE
BEL
BIO
ISO
HEX
WOR
PAL
RHY
TIP
N-TAN
FPOM
PAL
DIP
LEU
STE
TAL
FAT
AMP
MOSS
CPOM
PYC
Reference
(B)
DES
COR
PED
BEL
HEX
LAN
OLI
PAP
LEM
LEU
NTAN
DIP
PAL
FPOM
BOM
TAL
PSI
FAT
STE
TIP
CPOM
MOSS
Treatment
(D)
DES
COR
SWE
BEL
EUR
LAN
LEM
N-TAN
HEX
RHY
DIP
ISO
TIP
WOR
FPOM
LEU
PSE
PAP
PAL
STE
MOSS
TAL
SOY
PYC
CPOM
Treatment
6
4
2
0
-2
-4
-6
-35
-30
-25
-20
-15
-10
δ15 N
δ13 C

APPENDIX

Abundance, A (individuals/m2), and mean annual standing stock biomass, B (mgAFDM/m2) for major taxa in each functional feeding group found in the mixed substrate and moss-covered bedrock substrate of WS4 Jenny Branch (T = dextrose enrichment; R = no dextrose enrichment). Order = noninsects (NI), or insect orders, where C = Coleoptera, D = Diptera, E = Ephemeroptera, O = Odonata, P = Plecoptera, and T = Trichoptera. CPI = cohort production interval in days.

				Mixed substrate		Bedrock substrate	
Taxon	Order	Reach	Date	A	B	A	B
Scrapers							
Baetis sp.	E	R	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	50	0	0	0
			10/1/01	0	0	0	0
			11/1/01	0	0	0	0
			11/22/01	0	0	0	0
			12/10/01	100	14	0	0
			12/23/01	0	0	0	0
		T	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	0	0	0	0
			10/1/01	67	3	29	1
			11/1/01	0	0	0	0
			11/22/01	0	0	44	11
			12/10/01	0	0	0	0
			12/23/01	25	6	0	0
Epeorus sp.	E	R	8/11/01	0	0	0	0
			8/23/01	0	0	15	0
			9/11/01	0	0	39	0
			10/1/01	0	0	15	17
			11/1/01	1440	553	353	59
			11/22/01	1061	168	880	384
			12/10/01	325	155	0	0
			12/23/01	1439	738	0	0
		T	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	0	0	769	126

Appendix. Scrapers continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			10/1/01	0	0	0	0
			11/1/01	1078	736	0	0
			11/22/01	1125	1205	0	0
			12/10/01	791	607	44	51
			12/23/01	641	2208	0	0
Ectopria	C	R	8/11/01	13	6	0	0
			8/23/01	73	11	29	8
			9/11/01	0	0	15	2
			10/1/01	0	0	0	0
			11/1/01	0	0	0	0
			11/22/01	453	695	0	0
			12/10/01	500	362	0	0
			12/23/01	1125	1205	89	11
		T	8/11/01	0	0	59	69
			8/23/01	0	0	0	0
			9/11/01	6	3	0	0
			10/1/01	19	6	74	18
			11/1/01	0	0	89	85
			11/22/01	0	0	0	0
			12/10/01	0	0	0	0
			12/23/01	345	155	0	0
Elmidae	C	R	8/11/01	133	1	1066	36
			8/23/01	40	0	119	3
			9/11/01	300	1	182	6
			10/1/01	155	2	155	7
			11/1/01	334	74	44	1
			11/22/01	0	0	220	6
			12/10/01	0	0	754	1
			12/23/01	0	0	133	4
		T	8/11/01	133	1	30	0
			8/23/01	340	5	222	8
			9/11/01	13	0	68	2
			10/1/01	79	3	652	16
			11/1/01	0	0	0	0

Appendix. Scrapers continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			11/22/01	494	31	0	3
			12/10/01	400	12	44	4
			12/23/01	0	0	44	5
Other scrapers		R	8/11/01	0	0	15	0
			8/23/01	0	0	653	19
			9/11/01	0	0	29	1
			10/1/01	57	1	105	3
			11/1/01	284	1	613	3
			11/22/02	800	8	927	5
			12/10/02	1600	8	818	5
			12/23/02	0	0	88	2
		T	8/11/01	13	2	0	0
			8/23/01	0	0	223	25
			9/11/01	100	17	0	0
			10/1/01	13	2	15	0
			11/1/01	0	0	756	6
			11/22/02	0	0	1135	12
			12/10/02	1200	71	886	15
			12/23/02	25	4	900	5
Total scrapers		R	8/11/01	583	26	3241	108
			8/23/01	449	44	2446	91
			9/11/01	1400	6	797	26
			10/1/01	847	9	1204	83
			11/1/01	618	75	657	5
			11/22/01	800	8	1147	11
			12/10/01	1700	23	1572	6
			12/23/01	0	0	310	17
		T	8/11/01	582	10	266	207
			8/23/01	1358	20	2318	94
			9/11/01	475	79	2511	385
			10/1/01	973	55	2486	104
			11/1/01	0	0	845	91
			11/22/01	494	31	1179	25
			12/10/01	1600	83	974	71
			12/23/01	395	165	944	10

Appendix. Shredders continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
Shredders							
Leuctra spp.	P	R	8/11/01	316	8	3197	126
			8/23/01	607	88	89	2
			9/11/01	291	11	384	26
			10/1/01	202	6	316	13
			11/1/01	50	6	0	0
			11/22/01	0	0	132	16
			12/10/01	2425	27	0	0
			12/23/01	985	22	183	16
		T	8/11/01	3755	276	177	6
			8/23/01	1650	210	672	20
			9/11/01	1250	37	133	12
			10/1/01	75	10	1153	129
			11/1/01	266	61	266	26
			11/22/01	495	1	178	10
			12/10/01	800	46	1464	14
			12/23/01	25	6	628	7
Tallaperla spp.	P	R	8/11/01	50	29	88	7
			8/23/01	291	16	799	91
			9/11/01	1907	229	1313	188
			10/1/01	2723	117	2367	293
			11/1/01	793	43	274	11
			11/22/01	1719	412	837	22
			12/10/01	2000	874	1354	169
			12/23/01	1750	169	494	47
		T	8/11/01	1114	46	266	16
			8/23/01	25	11	176	65
			9/11/01	25	25	3050	2009
			10/1/01	1090	96	1140	329
			11/1/01	125	98	1649	908
			11/22/01	1140	179	246	191
			12/10/01	250	213	2044	142
			12/23/01	50	161	812	355

Appendix. Shredders continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
Lepidostoma spp.	T	R	8/11/01	3525	15	0	0
			8/23/01	75	37	0	0
			9/11/01	50	8	222	15
			10/1/01	175	53	178	1
			11/1/01	75	56	0	0
			11/22/01	761	51	71	0
			12/10/01	1225	122	88	4
			12/23/01	100	15	0	0
		T	8/11/01	50	15	0	0
			8/23/01	25	10	0	0
			9/11/01	1832	74	44	9
			10/1/01	568	54	0	0
			11/1/01	75	43	0	0
			11/22/01	881	51	0	0
			12/10/01	4200	256	0	0
			12/23/01	595	48	0	0
Pycnopsyche sp.	T	R	8/11/01	50	0	0	0
			8/23/01	0	0	0	0
			9/11/01	275	155	89	40
			10/1/01	25	11	0	0
			11/1/01	150	234	0	0
			11/22/01	914	109	0	0
			12/10/01	200	370	0	0
			12/23/01	325	62	0	0
		T	8/11/01	0	197	0	0
			8/23/01	75	348	0	0
			9/11/01	25	11	0	0
			10/1/01	100	491	0	0
			11/1/01	50	85	89	3
			11/22/01	278	107	0	0
			12/10/01	650	52	0	0
			12/23/01	25	3	0	0
Fattigia pele	T	R	8/11/01	150	111	0	0
			8/23/01	150	74	0	0

Appendix. Shredders continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			9/11/01	200	177	0	0
			10/1/01	441	138	0	0
			11/1/01	225	406	0	0
			11/22/01	275	462	0	0
			12/10/01	250	392	0	0
			12/23/01	175	124	0	0
		T	8/11/01	425	226	0	0
			8/23/01	0	0	0	0
			9/11/01	125	86	0	0
			10/1/01	516	224	0	0
			11/1/01	25	29	0	0
			11/22/01	100	140	0	0
			12/10/01	150	215	0	0
			12/23/01	150	109	0	0
Tipula sp.	D	R	8/11/01	416	537	44	78
			8/23/01	25	69	0	0
			9/11/01	175	719	0	0
			10/1/01	25	883	0	0
			11/1/01	75	1024	0	0
			11/22/01	0	0	0	0
			12/10/01	300	2260	44	148
			12/23/01	25	5	0	0
		T	8/11/01	25	69	44	148
			8/23/01	900	546	0	0
			9/11/01	150	1067	0	0
			10/1/01	841	1490	0	0
			11/1/01	1383	1069	0	0
			11/22/01	100	442	0	0
			12/10/01	850	1554	0	0
			12/23/01	75	455	0	0
Other shredders		R	8/11/01	300	494	1421	12
			8/23/01	125	1118	267	41
			9/11/01	1040	753	245	29
			10/1/01	479	139	102	3

Appendix. Shredders continued.

Taxon	Order	Reach	Date	Mixed substrates A	Mixed substrates B	Bedrock substrates A	Bedrock substrates B
			11/1/01	125	46	0	0
			11/22/01	279	114	177	6
			12/10/01	275	393	113	1
			12/23/01	25	88	0	0
		T	8/11/01	25	8	44	3
			8/23/01	1000	163	445	3
			9/11/01	1450	970	176	2
			10/1/01	707	43	177	4
			11/1/01	757	987	266	18
			11/22/01	441	1332	0	0
			12/10/01	300	2406	532	67
			12/23/01	50	42	0	0
Total shredders		R	8/11/01	1332	1194	4750	223
			8/23/01	1223	1375	1155	133
			9/11/01	5720	2119	2253	298
			10/1/01	4463	1349	2963	309
			11/1/01	1493	1801	274	11
			11/22/01	4068	1149	1217	44
			12/10/01	9650	4573	1599	323
			12/23/01	3880	516	677	63
		T	8/11/01	8869	965	531	173
			8/23/01	3725	1315	1293	88
			9/11/01	3075	2204	3403	2033
			10/1/01	3504	2408	2470	462
			11/1/01	2681	2385	2270	955
			11/22/01	3315	2252	424	202
			12/10/01	4225	4609	4040	223
			12/23/01	475	791	1440	362
Gatherers							
Paraleptophlebia sp.	E	R	8/11/01	0	0	0	0
			8/23/01	266	8	0	0
			9/11/01	400	2	915	18
			10/1/01	0	0	0	0
			11/1/01	0	0	382	92
			11/22/01	776	20	221	12

Appendix. Gatherers continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			12/10/01	950	83	44	1
			12/23/01	370	20	50	0
		T	8/11/01	0	0	0	0
			8/23/01	0	0	1691	18
			9/11/01	300	28	2583	50
			10/1/01	1599	216	1880	54
			11/1/01	25	2	0	0
			11/22/01	0	0	1144	98
			12/10/01	700	171	352	44
			12/23/01	320	70	0	0
Serratella sp.	E	R	8/11/01	0	0	0	0
			8/23/01	0	0	44	0
			9/11/01	0	0	0	0
			10/1/01	620	6	328	13
			11/1/01	284	3	0	0
			11/22/01	0	0	133	12
			12/10/01	75	18	132	33
			12/23/01	0	0	94	24
		T	8/11/01	0	0	400	10
			8/23/01	0	0	494	5
			9/11/01	0	0	1298	58
			10/1/01	0	0	4295	286
			11/1/01	0	0	0	0
			11/22/01	0	0	888	68
			12/10/01	0	0	0	0
			12/23/01	0	0	44	48
Stenonema sp.	E	R	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	0	0	237	3
			10/1/01	0	0	50	3
			11/1/01	0	0	0	0
			11/22/01	0	0	0	0
			12/10/01	25	10	0	0
			12/23/01	25	44	0	0

Appendix. Gatherers continued.

Taxon	Order	Reach	Date	Mixed substrates A	Mixed substrates B	Bedrock substrates A	Bedrock substrates B
		T	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	0	0	44	8
			10/1/01	0	0	266	13
			11/1/01	25	10	0	0
			11/22/01	25	10	0	0
			12/10/01	0	0	0	0
			12/23/01	50	91	0	0
Amphinemura sp.	P	R	8/11/01	0	0	44	2
			8/23/01	200	1	1201	51
			9/11/01	0	0	1117	41
			10/1/01	0	0	189	5
			11/1/01	0	0	177	27
			11/22/01	0	0	132	19
			12/10/01	0	0	44	13
			12/23/01	25	1	133	27
		T	8/11/01	0	0	177	20
			8/23/01	0	0	799	36
			9/11/01	0	0	574	64
			10/1/01	0	0	2239	202
			11/1/01	0	0	88	26
			11/22/01	0	0	220	93
			12/10/01	50	15	572	265
			12/23/01	0	0	812	21
Lype diversa	T	R	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	25	3	0	0
			10/1/01	0	0	0	0
			11/1/01	0	0	0	0
			11/22/01	0	0	0	0
			12/10/01	175	23	0	0
			12/23/01	0	0	0	0
		T	8/11/01	50	4	0	0
			8/23/01	0	0	267	4

Appendix. Gatherers continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			9/11/01	0	0	0	0
			10/1/01	75	4	0	0
			11/1/01	25	6	0	0
			11/22/01	0	0	0	0
			12/10/01	0	0	0	0
			12/23/01	0	0	0	0
Chironomidae	D	R	8/11/01	89650	68	21123	46
(Non-Tanypodinae)			8/23/01	23651	62	11194	17
			9/11/01	30775	114	25962	34
			10/1/01	48536	71	30574	21
			11/1/01	30468	52	14140	19
			11/22/01	76627	198	9856	11
			12/10/01	103125	268	12728	45
			12/23/01	35346	54	20379	43
		T	8/11/01	69709	87	6925	8
			8/23/01	70629	145	46622	114
			9/11/01	119561	231	76798	267
			10/1/01	172076	545	129947	191
			11/1/01	47044	167	62853	82
			11/22/01	67995	247	71923	338
			12/10/01	108860	702	76119	120
			12/23/01	192125	723	171985	459
Copepoda	NI	R	8/11/01	45910	46	178	0
			8/23/01	17315	17	799	1
			9/11/01	19814	20	1660	2
			10/1/01	32184	32	443	0
			11/1/01	19152	19	1772	2
			11/22/01	22610	23	178	0
			12/10/01	102400	102	530	1
			12/23/01	20930	21	3827	4
		T	8/11/01	33175	33	17405	17
			8/23/01	101322	101	10456	10
			9/11/01	49050	49	6341	6
			10/1/01	45785	46	29786	30

Appendix. Gatherers continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			11/1/01	43106	43	13042	13
			11/22/01	36800	37	15025	15
			12/10/01	79200	79	16288	16
			12/23/01	104756	105	14512	15
Nematoda	NI	R	8/11/01	62545	60	399	0
			8/23/01	46499	58	932	1
			9/11/01	39401	43	2412	2
			10/1/01	21914	17	294	0
			11/1/01	15448	12	222	0
			11/22/01	17738	13	265	0
			12/10/01	29600	22	472	0
			12/23/01	9828	7	1207	1
		T	8/11/01	118569	150	4795	4
			8/23/01	131313	131	3434	3
			9/11/01	64875	62	8826	7
			10/1/01	24759	19	16277	12
			11/1/01	80532	61	2562	2
			11/22/01	29874	23	2354	2
			12/10/01	29600	22	6252	5
			12/23/01	30400	23	1964	1
Oligochaeta	NI	R	8/11/01	1874	40	132	1
			8/23/01	3125	230	0	0
			9/11/01	2550	452	355	1
			10/1/01	1373	105	3440	12
			11/1/01	275	68	88	0
			11/22/01	254	20	0	0
			12/10/01	4175	165	1062	4
			12/23/01	75	1	0	0
		T	8/11/01	6366	177	44	0
			8/23/01	1676	36	0	0
			9/11/01	1575	50	177	1
			10/1/01	1779	1005	44	1
			11/1/01	3754	24	355	2
			11/22/01	2074	31	712	7

Appendix. Gatherers continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			12/10/01	1809	83	44	0
			12/23/01	1715	165	538	8
Other gatherers		R	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	0	0	0	0
			10/1/01	320	2	0	0
			11/1/01	0	0	0	0
			11/22/01	0	0	0	0
			12/10/01	0	0	0	0
			12/23/01	0	0	0	0
		T	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	0	0	0	0
			10/1/01	25	1	0	0
			11/1/01	0	0	0	0
			11/22/01	0	0	0	0
			12/10/01	0	0	0	0
			12/23/01	0	0	0	0
Total gatherers		R	8/11/01	199979	215	21876	50
			8/23/01	91056	377	14170	70
			9/11/01	92965	633	32658	100
			10/1/01	104947	233	35318	55
			11/1/01	65627	154	16781	140
			11/22/01	118005	274	10785	55
			12/10/01	240525	691	15012	97
			12/23/01	66599	148	25690	99
		T	8/11/01	277721	452	29746	60
			8/23/01	406387	813	63763	190
			9/11/01	185509	419	96641	461
			10/1/01	144651	1435	184734	788
			11/1/01	174511	314	78900	125
			11/22/01	136768	347	92266	622
			12/10/01	220219	1073	99627	450
			12/23/01	329366	1177	189855	554

Appendix. Filterers continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
Filterers							
Diplectrona spp.	T	R	8/11/01	25	2	0	0
			8/23/01	200	1	0	0
			9/11/01	848	70	162	20
			10/1/01	429	23	0	0
			11/1/01	0	0	0	0
			11/22/01	273	7	0	0
			12/10/01	100	17	0	0
			12/23/01	25	10	0	0
		T	8/11/01	1166	176	0	0
			8/23/01	25	5	886	76
			9/11/01	350	166	44	4
			10/1/01	633	17	0	0
			11/1/01	500	117	0	0
			11/22/01	228	6	0	0
			12/10/01	750	63	0	0
			12/23/01	150	39	0	0
Parapsyche cardis	T	R	8/11/01	75	10	10168	827
			8/23/01	316	30	1423	122
			9/11/01	25	1	1725	150
			10/1/01	177	2	828	127
			11/1/01	0	0	400	168
			11/22/01	0	0	310	278
			12/10/01	0	0	472	142
			12/23/01	25	14	1195	487
		T	8/11/01	100	18	888	123
			8/23/01	2233	54	6196	459
			9/11/01	25	8	2583	864
			10/1/01	0	0	2212	1076
			11/1/01	0	0	751	565
			11/22/01	0	0	352	168
			12/10/01	0	0	1719	1113
			12/23/01	0	0	928	1271

Appendix. Filterers continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
Wormaldia spp.	T	R	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	0	0	0	0
			10/1/01	0	0	138	11
			11/1/01	0	0	0	0
			11/22/01	0	0	44	0
			12/10/01	0	0	207	28
			12/23/01	0	0	228	24
		T	8/11/01	0	0	0	0
			8/23/01	0	0	316	1
			9/11/01	50	4	0	0
			10/1/01	25	4	1066	5
			11/1/01	0	0	1068	73
			11/22/01	25	2	25	8
			12/10/01	0	0	531	77
			12/23/01	0	0	0	0
Other filterers		R	8/11/01	0	0	0	0
			8/23/01	0	0	88	7
			9/11/01	0	0	237	0
			10/1/01	0	0	0	0
			11/1/01	0	0	178	0
			11/22/01	100	2	44	0
			12/10/01	825	17	59	0
			12/23/01	225	1	188	6
		T	8/11/01	0	0	0	0
			8/23/01	0	0	316	1
			9/11/01	400	3	0	0
			10/1/01	0	0	0	0
			11/1/01	0	0	0	0
			11/22/01	0	0	44	2
			12/10/01	50	5	399	2
			12/23/01	0	0	178	3
Total filterers		R	8/11/01	100	13	10168	827
			8/23/01	516	30	1511	129

Appendix. Filterers continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			9/11/01	873	71	2124	170
			10/1/01	606	25	966	139
			11/1/01	0	0	578	169
			11/22/01	373	10	398	279
			12/10/01	925	34	738	170
			12/23/01	275	25	1611	517
		T	8/11/01	1266	194	888	123
			8/23/01	2258	60	7714	538
			9/11/01	825	180	2627	868
			10/1/01	658	21	3278	1081
			11/1/01	500	117	1819	638
			11/22/01	253	8	421	178
			12/10/01	800	69	2649	1192
			12/23/01	150	39	1106	1274
Predators							
Cordulegaster sp.	O	R	8/11/01	50	392	0	0
			8/23/01	316	350	0	0
			9/11/01	50	276	0	0
			10/1/01	1219	554	0	0
			11/1/01	75	1425	0	0
			11/22/01	25	11	0	0
			12/10/01	50	21	0	0
			12/23/01	25	11	0	0
		T	8/11/01	466	253	0	0
			8/23/01	608	229	25	120
			9/11/01	25	20	0	0
			10/1/01	50	1874	0	0
			11/1/01	0	0	0	0
			11/22/01	25	69	0	0
			12/10/01	125	114	0	0
			12/23/01	0	0	0	0
Lanthus sp.	O	R	8/11/01	225	526	44	45
			8/23/01	1688	220	0	0
			9/11/01	625	942	0	0

Appendix. Predators continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			10/1/01	1679	296	0	0
			11/1/01	100	113	0	0
			11/22/01	229	17	0	0
			12/10/01	325	1235	0	0
			12/23/01	125	1567	0	0
		T	8/11/01	682	404	0	0
			8/23/01	300	1146	0	0
			9/11/01	150	164	0	0
			10/1/01	175	334	0	0
			11/1/01	125	610	0	0
			11/22/01	75	284	0	0
			12/10/01	100	286	0	0
			12/23/01	0	0	0	0
Sweltsa sp.	P	R	8/11/01	0	0	0	0
			8/23/01	0	0	177	35
			9/11/01	200	25	0	0
			10/1/01	0	0	0	0
			11/1/01	0	0	0	0
			11/22/01	0	0	0	0
			12/10/01	850	132	0	0
			12/23/01	0	0	0	0
		T	8/11/01	0	0	0	0
			8/23/01	0	0	222	8
			9/11/01	0	0	44	2
			10/1/01	0	0	0	0
			11/1/01	25	20	0	0
			11/22/01	0	0	0	0
			12/10/01	0	0	0	0
			12/23/01	25	7	0	0
Beloneuria sp.	P	R	8/11/01	0	0	44	18
			8/23/01	133	8	222	89
			9/11/01	25	10	44	18
			10/1/01	320	18	398	8
			11/1/01	25	138	0	0

Appendix. Predators continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			11/22/01	50	100	0	0
			12/10/01	0	0	0	0
			12/23/01	0	0	0	0
		T	8/11/01	0	0	44	8
			8/23/01	0	0	445	25
			9/11/01	0	0	222	86
			10/1/01	291	118	88	42
			11/1/01	50	112	44	8
			11/22/01	25	73	0	0
			12/10/01	400	1936	44	8
			12/23/01	75	865	88	26
Isoperla spp.	P	R	8/11/01	425	6	6127	821
			8/23/01	139	21	43154	7939
			9/11/01	1425	126	1712	66
			10/1/01	817	8	189	5
			11/1/01	525	23	89	1
			11/22/01	937	78	266	15
			12/10/01	4900	532	132	11
			12/23/01	965	53	461	28
		T	8/11/01	3191	121	177	4
			8/23/01	1866	19	533	25
			9/11/01	500	28	1867	132
			10/1/01	582	29	310	85
			11/1/01	874	54	0	0
			11/22/01	2079	238	1422	61
			12/10/01	1700	98	1079	59
			12/23/01	4050	60	0	0
Ryacophila spp.	T	R	8/11/01	391	19	0	0
			8/23/01	759	10	132	6
			9/11/01	1966	86	133	16
			10/1/01	606	54	88	28
			11/1/01	450	3	222	28
			11/22/01	150	45	133	1

Appendix. Predators continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			12/23/01	275	3	222	26
		T	8/11/01	1725	57	0	0
			8/23/01	4608	70	1694	43
			9/11/01	450	28	986	20
			10/1/01	525	138	221	83
			11/1/01	100	198	1112	55
			11/22/01	75	412	178	2
			12/10/01	990	78	133	6
			12/23/01	825	12	760	74
Pseudogoera sp.	T	R	8/11/01	0	0	1510	39
			8/23/01	133	3	133	0
			9/11/01	0	0	326	0
			10/1/01	320	0	322	0
			11/1/01	1293	33	44	0
			11/22/01	825	1	133	0
			12/10/01	400	1	132	6
			12/23/01	624	6	178	2
		T	8/11/01	50	4	133	3
			8/23/01	0	0	0	0
			9/11/01	75	1	115	0
			10/1/01	260	0	710	1
			11/1/01	425	4	622	6
			11/22/01	50	1	0	0
			12/10/01	1200	21	0	0
			12/23/01	0	0	0	0
Ceratopogonidae	D	R	8/11/01	7820	137	488	6
			8/23/01	2653	66	0	0
			9/11/01	1907	191	89	3
			10/1/01	2432	171	88	3
			11/1/01	2951	254	0	0
			11/22/01	1332	173	0	0
			12/10/01	4250	330	0	0
			12/23/01	919	33	0	0
		T	8/11/01	7428	244	0	0

Appendix. Predators continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			8/23/01	11799	665	133	21
			9/11/01	10950	1079	0	0
			10/1/01	8027	501	355	41
			11/1/01	10777	683	44	7
			11/22/01	7656	594	44	9
			12/10/01	10600	794	44	9
			12/23/01	7025	597	356	0
Hexatoma spp.	D	R	8/11/01	2761	189	0	0
			8/23/01	525	48	25	8
			9/11/01	866	525	0	0
			10/1/01	1679	973	0	0
			11/1/01	809	637	44	3
			11/22/01	600	52	0	0
			12/10/01	4750	918	0	0
			12/23/01	75	12	118	4
		T	8/11/01	1123	53	0	0
			8/23/01	1225	95	0	0
			9/11/01	2350	238	178	4
			10/1/01	566	145	0	0
			11/1/01	1790	237	88	15
			11/22/02	886	189	89	11
			12/10/02	1100	219	89	11
			12/23/02	375	106	947	20
nr. *Pedicia* sp.	D	R	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	266	9	0	0
			10/1/01	0	0	0	0
			11/1/01	25	13	0	0
			11/22/01	0	0	0	0
			12/10/01	825	80	0	0
			12/23/01	75	26	178	6
		T	8/11/01	0	0	0	0
			8/23/01	0	0	0	0
			9/11/01	25	8	0	0

Appendix. Predators continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			10/1/01	291	27	0	0
			11/1/01	25	8	44	4
			11/22/01	75	229	0	0
			12/10/01	0	0	133	23
			12/23/01	850	92	0	0
Acari	NI	R	8/11/01	18114	48	888	2
			8/23/01	10472	18	1532	7
			9/11/01	8802	23	8262	22
			10/1/01	18021	48	3492	9
			11/1/01	7156	19	725	2
			11/22/01	11528	31	1100	3
			12/10/01	27600	73	1311	3
			12/23/01	8991	24	812	2
		T	8/11/01	12921	34	32945	88
			8/23/01	35779	95	6952	18
			9/11/01	24650	66	4888	13
			10/1/01	18097	48	14434	38
			11/1/01	22646	60	4222	11
			11/22/01	11112	30	9242	25
			12/10/01	15200	40	3343	9
			12/23/01	11200	30	756	2
Other invertebrate predators		R	8/11/01	2737	216	1446	25
			8/23/01	133	2	291	9
			9/11/01	791	94	88	0
			10/1/01	749	150	50	0
			11/1/01	575	589	142	0
			11/22/01	2729	20	44	0
			12/10/01	5625	50	148	2
			12/23/01	0	0	228	1
		T	8/11/01	1707	387	0	0
			8/23/01	4440	463	222	1
			9/11/01	750	470	842	12
			10/1/01	832	720	974	26
			11/1/01	2649	230	578	62

Appendix. Predators continued.

				Mixed substrates		Bedrock substrates	
Taxon	Order	Reach	Date	A	B	A	B
			11/22/01	2271	221	177	6
			12/10/01	75	65	221	21
			12/23/01	4200	33	0	0
Total invertebrate predators		R	8/11/01	32523	1532	10572	964
			8/23/01	16951	745	45641	8086
			9/11/01	16923	2306	10654	126
			10/1/01	27842	2272	4671	56
			11/1/01	13984	3247	1222	32
			11/22/01	18405	526	1676	19
			12/10/01	51975	3429	1929	30
			12/23/01	12074	1733	2079	66
		T	8/11/01	29293	1557	33299	103
			8/23/01	60625	2781	10404	265
			9/11/01	39925	2101	8964	265
			10/1/01	29696	3936	17180	330
			11/1/01	39486	2217	7067	164
			11/22/01	24329	2339	11152	114
			12/10/01	31490	3653	5944	154
			12/23/01	28625	1802	1604	101
Salamanders		R	8/11/01	50	760	0	0
			8/23/01	0	0	0	0
			9/11/01	25	203	0	0
			10/1/01	50	271	0	0
			11/1/01	25	435	0	0
			11/22/01	50	1304	0	0
			12/10/01	0	0	89	722
			12/23/01	0	0	0	0
		T	8/11/01	25	368	0	0
			8/23/01	0	0	0	0
			9/11/01	25	509	0	0
			10/1/01	0	0	44	284
			11/1/01	25	785	0	0
			11/22/01	0	0	0	0
			12/10/01	50	870	0	0
			12/23/01	0	0	0	0