LONG-TERM RESPONSE OF STREAM INVERTEBRATES TO CATCHMENT LOGGING

by

DAMON THOMAS ELY

(Under the Direction of J. Bruce Wallace)

ABSTRACT

As part of a long-term study of stream response to whole-catchment logging, we measured secondary production, organic matter standing crops, wood volume, and stormflow seston concentrations in a stream in its twenty-sixth year following whole-catchment logging (BHB) and a nearby reference (HWC). Annual secondary production was only slightly higher in BHB; no differences in habitat-weighted abundance or biomass occurred between streams. Resources were significantly lower in BHB, yet invertebrate biomass per unit organic matter standing crop was higher than the reference. We believe that BHB food quality is higher than HWC despite lower resource quantity, resulting in similar assemblage production between streams. Higher stormflow seston concentrations in BHB indicate less retentive capability, though wood volume did not differ between streams. Differences in food quality and resource retention suggest continued impairment of functional processes in BHB. Care should be taken in judging recovery from disturbance on invertebrate data alone.

INDEX WORDS: Secondary production, Benthic macroinvertebrates, Forest harvest, Disturbance, Southern Appalachians, Headwater streams

LONG-TERM RESPONSE OF STREAM INVERTEBRATES TO CATCHMENT LOGGING

by

DAMON THOMAS ELY

B.S., The University of Maine, 2002

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial
Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2005

LONG-TERM RESPONSE OF STREAM INVERTEBRATES TO CATCHMENT LOGGING

by

DAMON THOMAS ELY

Major Professor:	J. Bruce Wallace
Committee:	Darold Batzer Judy Meyer

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
May 2005

ACKNOWLEDGEMENTS

First and foremost I wish to thank my fiancée Amanda Rau for her significant contributions to this study in both the field and the laboratory. The quality of this work was considerably enhanced by her attention to detail and admirable work ethic, as well as our many stimulating conversations throughout these 2½ years. Dr. Wallace, what can I say? The experience of working in your laboratory and studying aquatic ecology under your direction has been both highly rewarding and enjoyable. I am honored to have had this opportunity and will follow your instruction in all of my endeavors. Thank you to my committee members Darold Batzer and Judith Meyer for their many helpful comments. Darold Batzer deserves special thanks for his enthusiasm and sense of humor when interacting with me and all other graduate students (it really, really helps), and for cheerfully answering all of my endless questions. To past and present members of the Wallace lab (Sally Entrekin, Wyatt Cross, Erica Chiao, Sue Eggert, and Angela Romito) I give my warmest thanks for your support and friendship. Wyatt – I couldn't imagine learning Coweeta taxa (and the ancient art of *gestalt*) without your help, and although you couldn't be there for the end, your earlier instruction improved my writing skills considerably. Erica – thanks for always lending an ear over these last few months and for your eternal optimism. Lastly, I must credit Alex Huryn as my inspiration to study freshwater ecology while working as an undergraduate in his laboratory, and I wish to personally thank him for his role in my graduate studies here in Georgia.

TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

Introduction

Invertebrate assemblages in headwater (i.e. first to third order) streams rely heavily upon heterotrophic resources for their growth and production (Hall et al. 2001; Benstead and Pringle 2004), and are structured to utilize allochthonous inputs efficiently (Vannote et al. 1980). The feeding activities and production of benthic consumers in these systems serve functional roles in the retention, transformation, and downstream export of energy (Cuffney et al. 1990; Wallace and Webster 1996; Wipfli and Gregovich 2002). These ecosystem services benefit larger river systems by preventing nutrient and detritus loading, while maintaining resource delivery to consumers (Meyer and Wallace 2001). The alteration of upland landscapes has the greatest potential to negatively impact important stream services due to the intimate association of headwater taxa with allochthonous resources (Wallace et al. 1999), and the primary position of these systems in the river network (Meyer and Wallace 2001).

Large-scale deforestation (i.e. clear-cut logging) is a significant alteration of the landscape, which disrupts the flow of energy and nutrients between terrestrial and aquatic systems. Headwater streams draining logged catchments typically display a shift in energy base from allochthonous (leaf litter) to autochthonous (periphyton) subsidies as a result of higher solar inputs and large reductions in leaf litter entering the stream (Hawkins et al. 1982; Webster et al. 1983; Sabater et al. 1998). Invertebrate assemblages often reflect these resource alterations with immediate shifts in the dominance of certain feeding guilds (e.g. increases in algae-scraping taxa, Gurtz and Wallace 1984) and overall increases in abundance, biomass, and production (Kedzierski and Smock 2001; Hernandez et al. 2005). Rapid re-growth of the aggrading forest may restore shading and litter inputs within five to ten years (Webster et al. 1983), however, throughout the various stages of forest succession, differences persist in the composition, quality, and availability of these new resources (Griffith and Perry 1991; Benfield et al. 2001).

Models of stream response to logging in the southern Appalachians predict minimal inputs of large, dam-forming woody debris, thus lowering the retention of organic matter, nutrients, and sediments (Hedin et al. 1988, Webster et al. 1992, Valett et al. 2002). Invertebrate assemblages are expected to be affected by these long-term resource alterations since secondary production, an estimate of consumer energy flow over time, fluctuates dramatically with resource quantity (Wallace et al. 1999) and quality (Cross 2004) in streams of this region. However, longitudinal studies of the response of stream macroinvertebrate communities to catchment logging are currently rare, and sorely needed to enhance our understanding of the effects of historical deforestation on current ecological processes.

This study is a long-term follow up investigation of the benthic invertebrate assemblages within a stream disturbed by logging 26 years prior and an undisturbed reference. To our knowledge, this study is the first to describe the response of an entire assemblage over such a length of time. The initial paired-catchment design of this ecosystem-level experiment was not replicated, employing one reference stream and one treatment stream. We realize the limitations associated with the inference potential of this design (Hurlbert 1984, 2004). Nonetheless, ecosystem-level experiments have advanced our understanding of complex systems and are valued for their realism and scale (Carpenter et al. 1995; Schindler 1998; Oksanen 2001, 2004). In addition, the current study benefits from a wealth of long-term data compiled by many researchers examining numerous aspects of both the terrestrial and aquatic responses to logging. We felt that these attributes, in combination with the high level of detail associated with assemblage production estimates, greatly increased the inference potential of this study.

The stream draining the logged catchment (hereafter referred to as the 'disturbed' stream) underwent the temporary shift to autochthonous resources (Webster et al. 1983) described earlier. Algae-scraping mayfly taxa increased considerably in abundance and production on bedrock surfaces during the first 21 months following logging (Wallace and Gurtz 1986), while leaf-shredding taxa suffered only moderate declines in abundance (Gurtz and Wallace 1984). With the return of forest subsidies and riparian shading, scrapers had declined considerably within five years after logging, while shredder abundance did not differ from the reference at this time (Wallace et al. 1988). Sixteen years following logging, annual secondary production was higher in all major habitats of the disturbed stream, and shredder contributions to habitat-weighted production were double that of the reference (Stone and Wallace 1998). Previous investigators suggest that larger proportions of high-quality, early-successional leaf litter input may have enhanced the production of benthic consumers (Stout et al. 1993; Stone and Wallace 1998). Other effects on the disturbed stream include faster wood (Golladay and Webster 1988) and leaf (Benfield et al. 2001) breakdown, fewer debris dams (Golladay et al. 1989), lower organic matter (OM) standing crops (Golladay et al. 1989; Stout et al. 1993), lower retention of seston during storms (Gurtz et al. 1980; Golladay et al. 1987), and higher stream nitrate concentrations (Swank et al. 2001).

Our main objectives in the current study were 1) to compare invertebrate production and functional structure in the disturbed and reference streams, 2) to determine if processes of energy and sediment retention remained impaired after twenty-six years of forest succession, and 3) to describe general patterns of the long-term response to logging disturbance by stream invertebrates. Secondary production takes into account many taxon-specific life history characteristics (e.g. growth, survivorship, generation time, etc.; Benke 1996), and provides a more ecologically meaningful measure of the functional structure and success of benthic assemblages than that of ‘snapshot’ measurements of abundance and biomass. Retentive capabilities were assessed by measurement of OM standing crops, seston concentrations in the water column during a large storm, and the volume of woody debris in both streams.

Study Sites

The study sites are high-gradient, first- and second-order mountain streams located within the confines of Coweeta Hydrologic Laboratory (Otto, North Carolina, USA). Coweeta streams typically display high habitat heterogeneity consisting of a mix of sand/pebble riffles and large bedrock-outcrops. The reference and disturbed streams were paired for study prior to logging because of their high degree of physical similarity (Table 1). Although quantitative pre-treatment data is lacking, the macroinvertebrate communities of both streams were observed to be similar before logging (Gurtz and Wallace 1984).

Hugh White Creek (HWC) drains the reference catchment 14 (C14) and has remained relatively undisturbed since selective logging during the early 1900's and the chestnut blight (*Endothia parasitica*), which affected the entire Coweeta basin during the 1930's. Vegetation on this catchment is a mixed hardwood assemblage dominated by oaks (*Quercus* sp.), hickory (*Carya* sp.), red maple (*Acer rubrum*), and yellow poplar (*Liriodendron tulipifera*). Riparian vegetation consists of birch (*Betula* sp.) and a dense understory of rhododendron (*Rhododendron maximum*) which provides year-round shading of the entire stream channel.

Big Hurricane Branch (BHB) drains the disturbed catchment 7 (C7), which was experimentally clearcut and cable logged in 1977. Forest removal was complete, with the exception of 16 ha on upper slopes and ridges. Logging activity began with the construction of three logging roads in spring 1976 and ended with the removal of all logging slash from the stream channel by October 1977. Record storms during the last two weeks of May 1976 introduced large amounts of sediment into the channel from the unfinished logging roads, which had not yet been stabilized by vegetative cover. Further details concerning the 1977 logging of BHB can be found in Elliott et al. (1997) and Swank et al. (2001).

Prior to logging activity, C7 forest composition did not differ from the reference. Recent forest inventories of C7 report more basal area of black locust (*Robinia pseudoacacia*), *L*. *tulipifera*, and *A*. *rubrum*, while oak and hickory species are distinctly lacking as compared to C14 (Elliott et al. 1997). Like the reference, the main channel of BHB is also heavily shaded year-round by a dense cover of rhododendron.

Methods

Field Collection

Benthic sampling began February 2003 and continued bimonthly through December 2003. Each stream was divided into upper, middle, and lower reaches (Table 1) and four habitats (depositional, riffle, mossy bedrock, and bare bedrock) were sampled within each reach (2 streams x 3 reaches x 4 habitats x 6 dates = 144 samples). Locations within reaches were chosen randomly beforehand and samples were taken at the first representative of each habitat encountered upstream. A stovepipe corer (area = 400 cm^2) was used to sample depositional habitats. All benthos within the corer was removed up to a depth of 10 cm and poured through a 250 μm mesh bag. Riffle samples were taken using a Surber sampler (0.093 m^2) with a 250 μm mesh. Bare and mossy bedrock samples were collected by scraping a 100 cm^2 area into a 250 μm mesh bag. All samples were fixed in the field using a 37% formalin solution containing Phloxine B dye to facilitate invertebrate sorting in the laboratory.

Estimates of current velocity (Gessner bag current meter, Gessner 1950), and substrate size class proportions (visual inspection) were made before collection of each sample. We used the modified Wentworth scale of substratum size classification and sizes were converted to a phi scale (negative log base 2). The median phi for each sample was then calculated (Cummins 1962).

Sample processing

In the laboratory, samples were poured through 1 mm and 250 μm nested sieves creating coarse and fine fractions, respectively. If the fine fraction contained >300 organisms, it was subsampled (≥ 1/64) using a sample splitter (Waters 1969); coarse fractions were never subsampled. Invertebrates were removed from organic matter by hand under a dissecting microscope at 15 x magnification.

All invertebrates were identified, counted, and measured to the nearest millimeter under a dissecting microscope at 15 x magnification. Most identification was made to the genus level using the keys of Merrit & Cummins (1996), Peckarsky et al. (1990), and Wiggins (1977). Midge larvae (Diptera: Chironomidae) were identified as either Tanypodinae or non-Tanypodinae. Non-insect taxa were identified to the ordinal level or higher. Individual taxa were assigned a functional feeding group based on Merritt and Cummins (1996), or studies of other Coweeta streams (Wallace et al. 1999; Stone and Wallace 1998).

Biomass [ash-free dry mass (AFDM)] was calculated using length-weight regressions obtained from Benke et al. (1999) and data from organisms in these and other Coweeta streams (Stone and Wallace, unpublished observations; J.B. Wallace, J. O'Hop, G.J. Lugthart, unpublished observations).

Secondary production (g AFDM m^{-2} yr^{-1}) for most taxa was calculated using the size-frequency method as outlined by Benke (1996). Cohort production intervals (CPIs) for individual taxa were obtained from Coweeta literature (Huryn and Wallace 1987; Stone and Wallace 1998; Wallace et al. 1999). Annual production of non-Tanypodinae midges was calculated using the community-level method (Huryn and Wallace 1986;

Huryn 1990). Production of all other taxa was estimated using production/biomass (P/B) ratios multiplied by mean annual biomass. An empirically derived P/B of 18 was used for Copepoda (O'Doherty 1998), and a P/B of 5 was used for Nematoda, Oligochaeta and Turbellaria (Benke et al. 1984). Rare taxa, which made up only a small portion of total biomass, were assigned theoretical P/B values of 5 and 10 for univoltine and bivoltine taxa, respectively (Lugthart and Wallace 1992). *Micrasema* (Trichoptera: Brachycentridae) abundance, biomass, and production was divided evenly between the gatherer and shredder functional groups. Crayfish (*Cambarus* spp.) and salamanders (*Desmognathus* and *Eurycea* spp.) were not considered in this study due to inadequate sampling procedures and the nocturnal activity of some organisms. Secondary production of each taxon was estimated within each habitat; habitat-weighted estimates for both streams were made by multiplying each habitat's production value by its respective proportion of total stream area (Table 1) and summing these four values. The percent area composition of habitat types was estimated for both streams by visual inspection of consecutive five meter segments of stream length for all study reaches.

Following invertebrate removal, all particulate matter was poured through nested 4 mm, 1 mm, and 250 μm sieves. Organic matter (OM) ≥ 4 mm was sorted to leaves, wood, moss, and miscellaneous coarse particulate organic matter (CPOM). All OM remaining on the 1 mm sieve was designated miscellaneous CPOM, and < 1 mm > 250 μm particles were considered fine particulate organic matter (FPOM). FPOM was undoubtedly underestimated because of this mesh size. All OM was dried for one week

(50 °C), weighed, subsampled, re-weighed, ashed (500 °C, 24 hour), and reweighed to obtain AFDM.

Among-year Comparisons

Differences in sample collection methods and variables measured among the study years prevented the direct comparison of invertebrate and organic matter data among all studies. The 1977 and 1982 studies measured only invertebrate abundance (the 1982 study considered only taxa from the orders Ephemeroptera, Plecoptera, Trichoptera, and Odonata [EPTO]) and all of the samples were taken using a Surber sampler. In 1993, a different sampling method was used within each habitat and the use of a stovepipe corer in depositional areas enhanced the recovery of small, early-instar taxa compared to previous studies. Comparisons among all study years were therefore restricted to the percent contribution of functional feeding groups of EPTO taxa to the total abundance of these taxa. Data from bare and mossy bedrock habitats in the current study were weighted and combined for comparison with bedrock-outcrop data from previous years.

Current benthic sampling methods and production calculations follow the methods of Stone and Wallace (1998), except for the creation of bare and mossy bedrock habitats. Direct quantitative comparisons of invertebrate and OM measurements between the 1993 and 2003 studies were thus possible.

Storm Sampling

The Coweeta Hydrologic Laboratory experienced a storm on September 5-6, 2004 as a result of hurricane activity affecting the southeastern U.S. Stormflow was sampled in both streams over 22.5 hours, starting before the onset of precipitation and ending during a period of reduced rainfall and discharge mid-way through the storm. Stormflow grab samples were taken at the base of the lower reach in both streams at various time intervals depending on discharge. Plastic Nalgene© containers (1L) were held halfway in the water column to collect samples. Discharge was recorded from weirs already in place on both catchments.

Storm samples were brought back to the laboratory and filtered (pre-combusted Pall type A/E glass fiber filters) within 24 hr of collection. Filters were dried (55 °C, 24 hr), desiccated (24 hr), weighed, ashed (550 °C, 24 hr), rewetted to restore water of hydration, dried, desiccated, and reweighed. Organic seston (g AFDM L^{-1}) and inorganic seston (g ash L^{-1}) concentrations were determined by weight loss upon ashing and weight remaining, respectively.

Wood Volume

Estimates of wetted (within the channel and wet), bankfull (dry wood on banks), and overhanging (suspended above the channel) wood volume were made on May 15, 2004 using the line-intersect method (De Vries 1974) as modified by Wallace and Benke (1984). Within each reach of both streams, we placed a line perpendicular to the stream channel at five random, pre-determined locations. The diameters (≥1 mm) of all wood that intersected the line were measured with Vernier calipers to the nearest millimeter. Large wood was considered to have a diameter ≥10 cm, while small wood was <10 cm in diameter. A total of 15 measurements of each wood category were made per stream.

Statistical Analysis

Estimates of organic matter standing crops and invertebrate abundance, biomass, and production were converted to a m^{-2} basis. Significant differences between streams within each habitat for OM standing crops and invertebrate abundance and biomass were determined using a Student's *t*-test. Data failing normality was log(x+1) transformed to reduce heteroscedasticity (Zar 1984). Transformed data still failing normality was analyzed using a Mann-Whitney rank sum test. Differences among habitat-types were not statistically assessed as numerous Coweeta studies have already done so (Huryn and Wallace 1987; Gurtz and Wallace 1984; Stone 1995; Grubaugh et al. 1997; Wallace et al. 1999) and the emphasis of this study was on differences between streams.

Pearson correlation was used to compare FFG biomass with standing crops of organic matter and current velocity. Simple linear regression was used to compare total invertebrate biomass with standing crops of organic matter (minus wood) in riffle and depositional habitats. All statistical analyses were performed using SigmaStat (v. 2.03). Taxonomic similarity between streams within habitats was assessed using cluster analysis (PC-ORD v. 4.10) on log(x+1) transformed, habitat-specific abundance of 69 taxa. We used the Bray-Curtis distance measure (beta = -0.25) to calculate the amount of dissimilarity ($0 \leq x \leq 1$) between groups.

Results

EPTO comparisons among study years

The functional structure of the EPTO community in HWC has remained relatively stable over the last twenty-six years (Figure 1a, b, c, and d). This is not the case for BHB; most noticeable is the large scraper response in all habitats during logging, which subsides quickly and is followed by an increase in shredder dominance that peaks in 1993 and has since declined (Figure 1). Few differences are apparent between streams for filterer, gatherer, and predator categories among study years. Habitat-weighted EPTO assemblage structure in BHB during 2003 was more similar to reference conditions than in any previous year (Figure 1d).

Macroinvertebrate communities in 2003

Total habitat-weighted invertebrate abundance and biomass did not significantly differ between streams (Table 2a,b). No differences were found between streams for total habitat-specific abundance or biomass with the exception of the mossy bedrock habitat (Table 2a,b), where abundance in BHB was nearly twice that of the reference ($P < 0.05$). Predator biomass was approximately four times higher in the mossy bedrock habitats of BHB ($P < 0.001$) (Table 2b). Habitat-weighted scraper abundance was significantly higher in the disturbed stream, although habitat-weighted scraper biomass and production showed no large differences between streams (Table 2).

Invertebrate biomass showed numerous, strong relationships with current velocity and organic matter; few differences were apparent between streams (Table 3). Scrapers were positively correlated with current velocity and moss, and negatively correlated with all other OM types (Table 3). Shredders showed exactly the opposite trend as scrapers (Table 3), reflecting the strong habitat and resource preferences of these two feeding groups. Gatherers and predators were negatively related to current velocity and positively related to CPOM, FPOM, and total OM in both streams (Table 3). Filterers were positively associated with current velocity and moss and displayed negative relationships with all other OM types in both streams; however, few of these correlations were significant (Table 3).

Habitat-specific and habitat-weighted secondary production within both streams was estimated for a total of 69 taxa (see Appendix). Total habitat-weighted secondary production in BHB (10.1 g AFDM m^{-2} yr^{-1}) was only slightly higher than HWC (9.3 g AFDM m^{-2} yr^{-1}) (Table 2c). The trend of slightly higher annual production in BHB was consistent across all habitats and functional feeding groups (Table 2c). The only striking difference in secondary production between streams was found in the mossy bedrock habitat, where annual production was 1.6 times higher in BHB with considerable differences occurring in all FFGs except shredders (Table 2c). HWC had the greatest production in depositional > mossy bedrock > bare bedrock > riffle habitats, while the greatest production in BHB followed the order: mossy bedrock > depositional > bare bedrock > riffle (Table 2c). Secondary production during 2003 was 2.1 times higher in HWC and 1.2 times higher in BHB than in 1993 (Figure 2b).

Functional feeding group contributions to total secondary production displayed strong habitat-specific patterns in both streams (Table 2c). Briefly, high scraper contributions were found in the bare bedrock habitat; shredders were most dominant in depositional areas; gatherer production was highest in mossy bedrock and depositional habitats; filterers had large contributions in all habitats except depositional zones; and predator contributions were highest in riffle and depostional habitats (Table 2c). Proportional contributions of FFGs to annual habitat-weighted production were nearly identical between streams (Table 2c).

HWC contained only three taxa (*Anchytarsus*, *Habrophlebia*, *and Psilotreta*) not found in the disturbed stream, and BHB contained one unique taxon (*Taeniopteryx*) (see appendix). Within particular habitats, cluster analysis revealed little taxonomic difference between streams (1 to 4.8%, Figure 3). No habitat-specific differences were found in the mean number of taxa between streams (Table 2d).

Physical measurements

Due to weir repair on WS14 in the autumn, comparisons of stream discharge during 2003 were limited to the time period of January to early September (Table 1). Mean discharge during this period was very similar between streams (Table 1); the annual mean discharge for BHB during 2003 (24.7 L s^{-1}) was 1.4 times higher than the 29-year record reported in Gurtz and Wallace (1984). Habitat-specific current velocities were not different between streams (Table 4). Likewise, no difference in habitat-specific substrate size between streams was observed (Table 4).

Organic matter standing crops

Total habitat-weighted standing crop of OM was significantly higher in the reference stream (342 g AFDM m^{-2}) than the disturbed (171 g AFDM m^{-2}, $P < 0.01$) (Table 5). Lower organic matter standing crops (not including wood) were found at all times of the year in riffle and depositional habitats of BHB, with significant differences occurring during the October and December sampling dates (Figure 4a). Significant habitat-weighted differences (HWC > BHB) were found in the wood, CPOM, and FPOM categories, and appear to be driven by the depositional habitats (Table 5). Percent contributions of OM types were very similar between streams for depositional habitats and habitat-weighted standing crops (Figure 5d,e).

Organic matter standing crops in both streams were lowest in bare bedrock habitats, and highest in depositional areas (Table 5). Mossy bedrock and riffle OM standing crops were intermediate between depositional and bare bedrock habitats (Table 5). BHB mossy bedrock contained significantly more moss (38.2 g AFDM m^{-2}) than HWC (20.5 g AFDM m^{-2}, $P < 0.05$), which has been reported in all three previous studies (Gurtz and Wallace 1984; Wallace et al. 1988; Stone and Wallace 1998) and is believed to reflect pre-logging conditions. Compared to the 1993 study, OM standing crops in 2003 were 22% lower in BHB and almost 2.5 times higher in HWC (Figure 2a).

Storm transport of seston

Seston concentrations were similar in both streams just prior to rainfall, however, large differences in the amount of suspended organic and inorganic material were observed with rising discharge (Figure 6a,b). Maximum concentrations of particulate organic and inorganic matter in BHB were 1.7 and 56.5 times higher than in HWC, respectively. Total precipitation during the 22.5 hr sampling period was 4.45 cm.

Woody debris

We found no significant difference in wood volume between streams for any category (Figure 7a,b,c). In both streams, wood volume was highest in the bankfull category and lowest in the overhanging category (Figure 7).

Consumer-resource relations

Two lines of evidence prompted an analysis of the relationship between organic matter resources and invertebrate biomass. First, annual consumer production in BHB was very similar to HWC (Table 2) despite having half the amount of available resources (Table 5). Secondly, on each sampling date, organic matter standing crops were consistently lower in the riffle and depositional areas of BHB (Figure 4a), yet consumer abundance and biomass in these habitats displayed no consistent differences between streams (Figure 4b,c). These findings suggest that food quality is enhanced in the disturbed stream, which has been proposed by previous investigators. Regressions of organic matter (wood not included as a food source) with invertebrate biomass in riffle and depositional samples were highly significant for both streams (HWC: $r^2 = 0.61$, $P < 0.001$; BHB: $r^2 = 0.59$, $P < 0.001$) (Figure 8). The slope of the BHB regression was significantly greater than that of HWC (one-tailed Student's *t*-test, $P < 0.01$; see chapter 18 in Zar 1984).

Discussion

Long-term comparisons

Resource dynamics appear to be driving the BHB invertebrate assemblage response to the deforestation of C7. Abundance, biomass, and production of *Baetis* (Ephemeroptera: Baetidae) increased sharply immediately following logging, and the large quantities of diatoms found in their guts (Wallace and Gurtz 1986) imply that they were responding directly to the observed increase in primary production (Webster et al. 1983). The common leaf-shredding stonefly *Tallaperla* (Plecoptera: Peltoperlidae) decreased in abundance during this time (Gurtz and Wallace 1984) in conjunction with the 98% reduction in leaf litter inputs (Webster et al. 1992).

With regrowth of the forest, pre-disturbance levels of canopy shading and litter inputs to BHB were restored within 5-6 years (Webster et al. 1992). Scraper contributions to habitat-weighted EPTO abundance decreased from 40% to 16% during this time and have continued to decrease in the years since (Figure 1d). Shredder contributions to habitat-weighted EPTO abundance increased with return of the forest from 9% (1977), to 13% (1982), to 43% in 1993 (Figure 1d). The current study found BHB shredders contributing 28% to EPTO abundance, which resembles reference conditions (Figure 1d), suggesting the structural stabilization of this group over time.

No large differences between streams or among years were observed for relative abundances of EPTO filterers, gatherers, or predators in the twenty-six years since logging (Figure 1). The lack of a filterer response may be explained by substrate stability and mode of food acquisition. Filterers display strong preferences for bedrock-outcrop surfaces (Table 2), which are less prone to disturbance effects like sedimentation and scour than riffle or depositional areas (Gurtz and Wallace 1984). Furthermore, baseflow seston concentrations in BHB have remained similar to HWC since clearcutting (Golladay et al. 1987), and filter-feeding caddis flies catch much more suspended particulate matter than is ingested and select for higher quality food (Haefner and Wallace 1981). Thus, the substrate and resource preferences of filter-feeders may provide increased resistance to logging disturbance. Gatherers are ubiquitous in lotic systems (Table 2a), and their high consumption rates, low assimilation efficiencies, and short generations (Fisher and Gray 1983) may confer stability over time. Invertebrate predators are highly dependent upon the success of their prey and are expected to display similar contributions to community measures regardless of the relative changes observed in other functional feeding groups (Wallace et al. 1999). The high degree of proportional similarity of habitat-weighted EPTO functional feeding group composition between the disturbed stream in 2003 and all previous reference investigations suggest recovery of the disturbed EPTO assemblage in terms of functional structure (Figure 1).

Organic matter standing crop

Benthic organic matter storage following forest disturbance is predicted to be inefficient and therefore much lower than pre-disturbance conditions until the late stages of recovery (Odum 1969; Webster et al. 1992; Valett et al. 2002). Lower amounts of organic debris in logged streams are attributed to reductions in the number of debris dams (Silsbee and Larson 1983) and faster leaf breakdown rates due to greater inputs of early-successional “fast” leaf species, abrasion of leaf surfaces by high amounts of storm-transported sediment, and increased invertebrate feeding activity (Benfield et al. 2001). Lower OM standing crops were found in BHB after eight (Golladay et al. 1989) and eleven (Stout et al. 1993) years, but not after 16 years (Stone and Wallace 1998). Despite similar quantities of annual leaf input (J.R. Webster, unpublished data), we found significantly lower standing crops of almost all OM types in BHB twenty-six years after logging (Table 5). The proportional similarity of OM categories between streams (Figure 5) indicates that no single OM type was more affected than another by the processes that led to lower standing crops in BHB.

Reasons for the significantly higher standing crops of benthic OM found in BHB during the 1993 study remain unclear. Figure 2a shows that the difference between study years is mostly due to much higher OM standing crop in the reference stream during 2003. In their review of OM dynamics in Satellite Branch over a nine-year period, Wallace et al. (1997) suggested that Coweeta headwater streams may undergo multi-year cycles of OM accumulation and loss due to discharge variability, the stochastic nature of storms, and lateral deposition in the riparian zone. The lower standing crops in BHB during previous study years (Golladay et al. 1989; Stout et al. 1993) and the consistent trend of lower benthic OM in BHB on each sampling date during 2003 (Figure 4a) imply that BHB continues to store less OM than HWC and that the low OM in HWC in 1993 may have been anomalous.

Invertebrate assemblages in 2003

Estimates of habitat-specific and habitat-weighted secondary production and functional feeding group contributions during the current study (Table 2c) are within the range of previously reported values from other forested headwater streams in the southeastern United States (Huryn and Wallace 1987; Whiles and Wallace 1995; Wohl et al. 1995; Grubaugh et al. 1997). Few differences were observed between the reference and logged streams regarding habitat-specific and habitat-weighted abundance, biomass, and secondary production during 2003 (Table 2a,b,c). The much greater production in mossy bedrock surfaces of BHB was undoubtedly due to the higher amounts of moss found on these substrates (Table 5). Mosses are known to provide habitat and refugia for invertebrates (Korsu 2004) and support extremely high levels of production (Huryn and Wallace 1987). The between-stream similarities in FFG contributions to production in mossy bedrock surfaces imply that all feeding guilds responded equally to the “moss effect” with the possible exception of predators, which appear to have benefited disproportionately well in terms of biomass (Table 2b) from the increase in prey availability. In addition, the slightly higher habitat-weighted annual secondary production in BHB is mostly due to the mossy bedrock habitat and its greater density of moss, which is a fundamental, pre-disturbance difference between streams.

Total habitat-weighted production was only 835 mg m^{-2} yr^{-1} higher in the disturbed stream with nearly equal contributions by functional feeding groups between streams (Table 2c). This is different from 1993, when annual secondary production in BHB was almost twice that of HWC (Figure 2b) and shredder and filterer contributions to production were double and half that of the reference, respectively (Stone and

Wallace 1998). The high degree of similarity observed in current community measures (Table 2) and cluster analysis of taxon-specific abundance (Figure 3) imply that the functional structure of the BHB macroinvertebrate assemblage is nearly identical to reference conditions after 26 years of recovery from logging disturbance.

Stream retention

Compared to mature systems, recently disturbed ecosystems are characterized as “leaky” in terms of nutrient and energy retention (Odum 1969; Vitousek and Reiners 1975). Terrestrial systems suffer large particulate matter and nutrient losses after deforestation due to reduced transpiration, mineralization, and erosion (Bormann et al. 1974; Martin et al. 2000). Catchment 7 appears to conform to this pattern of loss. High amounts of sediment and organic matter were transported during storms immediately following logging (Gurtz et al. 1980) and the rate of sediment yield at the ponding basin of C7 was nearly 50% above pre-treatment levels during the subsequent fifteen years (Swank et al. 2001). Nutrient losses from the successional forest have led to elevated nitrate concentrations in BHB since just after the clearcut (Swank et al. 2001) to the present day (J.M. Vose, personal communication).

Aquatic systems draining logged catchments may experience lowered retentive capability for many years following terrestrial disturbance due to reduced inputs of dam-forming, large woody debris (Valett et al. 2002). In BHB, reduced benthic organic matter standing crops (Golladay et al. 1989), increased travel distance of leaf and wood surrogates (Webster et al. 1994), and higher storm export (Gurtz et al. 1980; Golladay et al. 1987) have all been attributed to a lack of large wood and debris dams. In the current study, concentrations of particulate material in transport during a storm were much higher in BHB than HWC (Figure 6), suggesting continued lowered retention in the disturbed stream. Higher concentrations of inorganics in transport during storms may have strong implications for sediment deposition and consequent habitat degradation (Reice et al. 1990) in both local and downstream reaches.

Storm transport can also have considerable control over resource export. In a 9-year study of three other Coweeta headwaters, Wallace et al. (1995) found that 63 - 77% of annual CPOM export occurred during the largest twenty storms. Higher transport during storms may explain the much lower OM standing crops found in BHB during 2003. However, we cannot attribute the observed lowered retentive capability of BHB to a lack of large woody debris since wood volume did not appear to be different between streams (Figure 7).

Consumer-resource relations

Terrestrial subsidies of detritus often dominate the trophic basis of primary consumer production in forested headwater stream communities (Hall et al. 2001, Benstead and Pringle 2004). This dependence arises from the fact that invertebrate consumers of detritus have no influence on the renewal rate of their resource (i.e. these are “donor-controlled” systems, Polis et al. 1997). Consequently, invertebrate communities display high sensitivity to differences in terrestrial composition and the associated variation in resource quantity and quality (Ross 1963; Woodall and Wallace 1972; Molles 1982; Silsbee and Larson 1983; Whiles and Wallace 1997; England and Rosemond 2004). The BHB invertebrate community is no exception, as we have seen opposing patterns in the response of scrapers (Wallace and Gurtz 1986) and shredders (Stout et al. 1993; Stone and Wallace 1998) to shifts in the energy base of this disturbed stream.

Other secondary production studies in low-order streams of the southeastern U.S. suggest benthic organic matter as limiting production (Lugthart and Wallace 1992; Wohl et al. 1995; Grubaugh et al. 1997). Wallace et al. (1999) report a strong positive relationship between litter standing crop and secondary production in Coweeta streams, and Hall et al. (2001) found the same relationship in two headwater streams within the Hubbard Brook Experimental Forest. Thus, the current amount of similarity between the BHB and HWC invertebrate assemblages (Table 2; Figure 3) is surprising given the strong correlations of FFG biomass with benthic organic matter (Table 3) and the reduced presence of this resource in the disturbed stream (Table 5, Figure 4).

We believe that resources in the disturbed stream are of a higher quality than those of the reference and are bioenergetically enhancing production of the invertebrate community, which has been suggested elsewhere (Stout et al. 1993; Stone and Wallace 1998). Our finding that BHB invertebrates have significantly higher biomass per unit available resource than HWC (Figure 8) supports this idea. We could hypothesize that BHB invertebrates are simply consuming more to achieve similar biomass and production, thereby depleting their resource. Yet, this would also imply that quantities of available benthic resources in both streams are equal at some point during the year, most likely during autumn leaf-fall, and then decline faster in the disturbed stream. We found significantly lower OM standing crops in BHB riffle and depositional habitats during October and December when litter inputs are greatest, implying that lower resource standing crops in the disturbed stream are probably the result of poor retention (Figure 6) instead of heightened invertebrate activity.

There is good reason to believe that resource quality is higher in BHB and is enhancing invertebrate growth as compared to the reference. Throughout the years since logging, early-successional litter inputs (Webster et al. 1983; Stout et al. 1993; Stone and Wallace 1998), leaf breakdown rates (Benfield et al. 2001), and nitrate concentrations (Swank and Vose 1997; J.M. Vose, pers. comm.) have been higher in BHB than either pre-disturbance levels or reference conditions. As compared to HWC, Stout et al. (1993) found greater shredder production in BHB tributaries when OM standing crops were lower, but contained significantly more high-quality, herbaceous litter. Leaves from early to mid-successional tree species contains higher concentrations of N and P (Boring et al. 1981) and lower lignin concentrations (Webster and Benfield 1986) than that of late-successional species, and have been shown to be preferred by detritivore shredders (Golladay et al. 1983; Benfield and Webster 1985). High nitrate concentrations in the water column can increase microbial biomass on leaf surfaces (Meyer and Johnson 1983; Suberkropp and Chauvet 1995), resulting in higher growth rates of both direct (*Tallaperla*, O’Hop et al. 1984) and indirect (filter-feeding caddis flies, Haefner and Wallace 1981) consumers. In a nearby Coweeta stream, nutrient enrichment significantly increased the quality of detrital resources, leading to higher secondary production of many taxa (Cross 2004). Alternatively, Hutchens et al. (1997) could not explain greater *Pycnopsyche* (Trichoptera: Limnephilidae) production in BHB by higher growth rates on fast-decaying leaves as these animals grew optimally on properly conditioned leaves, regardless of leaf species. However, the authors conditioned all experimental leaves in reference stream water at least two months before the caddis flies were allowed to feed (Hutchens et al. 1997), preventing any possible nitrate-enriched effects on microbial biomass, and subsequently invertebrate growth, during the conditioning period.

Long-term recovery from logging

Assessments of disturbance effects on ecosystems and the progress made towards recovery by these systems should employ a variety of indicators (Resh et al. 1988) with careful consideration of the endpoint each one represents (Kelly and Harwell 1990). We found that indicators of community-level endpoints (consumer functional structure) were almost identical between streams for all habitats and functional feeding groups, while indicators of ecosystem-level endpoints (organic matter storage and transport; consumer-resource relationships) suggest continued impairment of the disturbed stream as compared to the reference.

Data from a decade prior to this study reveal that the current similarity in secondary production between streams is largely due to much higher production in the reference during the current study year, while BHB production increased only slightly during this time (Figure 2b). Between-year comparisons of OM standing crop reveal a proportionally similar increase in benthic resources in HWC during this time, while only a small change in BHB resource quantity was observed (Figure 2a), emphasizing the resource limitations on production within these systems. Thus, the differences in growth and production between consumers in HWC and BHB observed in 1993 still exist in 2003, but are masked by the variation in resource availability. However, for the first time since logging, we observed high similarity between streams in contributions of *i)* benthic OM categories to habitat-weighted totals, *ii)* FFGs to habitat-weighted EPTO taxa abundance, and *iii)* FFGs to habitat-weighted production. Taken together, these results imply recovery of the functional structure of the BHB macroinvertebrate assemblage long before forest succession is complete.

Conclusions

The tight linkage between aquatic and terrestrial systems is well known (Hynes 1975), and there is increasing awareness of the legacies of past terrestrial disturbance that persist in associated aquatic systems (Harding et al. 1998, Wallace et al. 2001). Long-term analysis of Big Hurricane Branch following large-scale deforestation of the surrounding watershed has revealed a highly-resilient macroinvertebrate community that continues to be affected by the energetic (resource quality) and physical (resource retention) alterations wrought by the successional forest. Headwater streams are important sites of storage, transformation, and the downstream export of detritus (Meyer and Wallace 2001), all of which are vital ecosystem services (Baron et al. 2002) that may be altered for decades following a single logging event. In addition to local impairment, downstream communities dependent upon the quantity, quality, and timing of upstream subsidies (Cuffney et al. 1990; Rosi-Marshall and Wallace 2002; Wipfli and Gregovich 2002) may be affected by increased inputs of sediments and unprocessed organic material.

This study emphasizes the importance of viewing clearcut logging as a “press” disturbance (*sensu* Bender et al. 1984) that continues to influence aquatic systems long after the actual disturbance event. We expect complete recovery to occur only when the quality of detritus inputs, the storage of these inputs, and the regulation of nutrient flow from the surrounding forest return to pre-disturbance levels. Long-term considerations of these terrestrial influences on our waterways may better direct future land-use management.

We have shown how interactions among multiple stressors may produce similarities in invertebrate assemblages between reference and disturbed sites. To prevent misclassification, assessments of stream recovery from deforestation should focus on a range of functional processes (e.g. energy input, storage, transformation, and export) and caution should be taken in the common practice of judging recovery from invertebrate data alone (Hutchens et al. 2004; Fortino et al. 2004).

Literature Cited

Baron, J.S., N.L. Poff, P.L. Angermeier, C.N. Dahm, P.H. Gleick, N.G. Hairston, R.B. Jackson, C.A. Johnston, B.D. Richter, and A.D. Steinman. 2002. ESA Report: Meeting ecological and societal needs for freshwater. Ecological Applications 12: 1247-1260.

Bender, E.A., T.J. Case, and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65: 1-13.

Benfield, E.F. and J.R. Webster. 1985. Shredder abundance and leaf breakdown in an Appalachian Mountain stream. Freshwater Biology 15: 113-120.

Benfield, E.F., J.R. Webster, J.L. Tank, and J.J. Hutchens. 2001. Long-term patterns in leaf breakdown in streams in response to watershed logging. International Review of Hydrobiology 86: 467-474.

Benke, A.C. 1996. Secondary production of macroinvertebrates. Chapter 26 In: R. Hauer and G. Lamberti (eds.) *Methods in Stream Ecology*, Academic Press, NY.

Benke, A.C., A.D. Huryn, L.A. Smock, and J.B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18: 308-343.

Benke, A.C., T.C. Van Arsdall, D.M. Gillespie Jr, and F.K. Parish. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecological Monographs 54: 25-63.

Benstead, J.P. and C.M. Pringle. 2004. Deforestation alters the resource base and biomass of endemic stream insects in eastern Madagascar. Freshwater Biology 49: 490-501.

Boring, L.R., C.D. Monk, and W.T. Swank. 1981. Early regeneration of a clear-cut southern Appalachian forest. Ecology 62: 1244-1253.

Bormann, F.H., G.E. Likens, T.G. Siccama, R.S. Pierce, and J.S. Eaton. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. Ecological Monographs 44: 255-277.

Carpenter, S.R., S.W. Chisholm, C.J. Krebs, D.W. Schindler, and R.F. Wright. 1995. Ecosystem experiments. Science 269: 324-327.

Cross, W.F. 2004. Nutrient enrichment of a detritus-based stream ecosystem: effects on invertebrate community structure and function. PhD dissertation. University of Georgia, Athens, GA.

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

Cummins, K.W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. American Midland Naturalist 67: 477-504.

De Vries, P.G. 1974. Multi-stage line intersect sampling. Forest Science 20: 129-133.

Elliot, K.J., L.R. Boring, W.T. Swank, and B.R. Haines. 1997. Successional changes in plant species diversity and composition after clearcutting a Southern Appalachian watershed. Forest Ecology and Management 92: 67-85.

England, L.E. and A.D. Rosemond. 2004. Small reductions in forest cover weaken terrestrial-aquatic linkages in headwater streams. Freshwater Biology 49: 721-734.

Fisher, S.G. and L.J. Gray. 1983. Secondary production and organic-matter processing by collector macroinvertebrates in a desert stream. Ecology 64: 1217-1224.

Fortino, K., A.E. Hershey, and K.J. Goodman. 2004. Utility of biological monitoring for detection of timber harvest effects on stream and evaluation of Best Management Practices: a review. Journal of the North American Benthological Society 23: 634-646.

Gessner, F. 1950. Die ökologische Bedeutung der Stromungsgeschwindigkeit fliessendeer Gewasser und ihre Messung auf kleinstem Raum. Archive für Hydrobiologie 43: 159-165.

Golladay, S.W. and J.R. Webster. 1988. Effects of clear-cut logging on wood breakdown in Appalachian mountain streams. American Midland Naturalist 119: 143-155.

Golladay, S.W., J.R. Webster, and E.F. Benfield. 1983. Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. Holarctic Ecology 6: 157-162.

Golladay, S.W., J.R. Webster, and E.F. Benfield. 1987. Changes in stream morphology and storm transport of seston following watershed disturbance. Journal of the North American Benthological Society 6: 1-11.

Golladay, S.W., J.R. Webster, and E.F. Benfield. 1989. Changes in stream benthic organic matter following watershed disturbance. Holarctic Ecology 12: 96-105.

Griffith, M.B. and S.A. Perry. 1991. Leaf pack processing in two Appalachian mountain streams draining catchments with different management histories. Hydrobiologia 220: 247-254.

Grubaugh, J.W., J.B. Wallace, and E.S. Houston. 1997. Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. Freshwater Biology 37: 581-596.

Gurtz, M.E. and J.B. Wallace. 1984. Substrate-mediated response of stream invertebrates to disturbance. Ecology 65: 1556-1569.

Gurtz, M.E., J.R. Webster, and J.B. Wallace. 1980. Seston dynamics in southern Appalachian streams: effects of clear-cutting. Canadian Journal of Fisheries and Aquatic Sciences 37: 624-631.

Haefner, J.D. and J.B. Wallace. 1981. Production and potential seston utilization by *Parapsyche cardis* and *Diplectrona modesta* (Trichoptera: Hydropsychidae) in two streams draining contrasting southern Appalachian watersheds. Environmental Entomology 10: 433-441.

Hall, R.O., G.E. Likens, and H.M. Malcolm. 2001. Trophic basis of invertebrate production in 2 streams at the Hubbard Brook Experimental Forest. Journal of the North American Benthological Society 20: 432-447.

Harding, J.S., E.F. Benfield, P.V. Bolstad, G.S. Helfman, and E.B.D. Jones. 1998. Stream biodiversity: the ghost of land use past. Proceedings of the National Academy of Sciences 95: 14843-14847.

Hawkins, C.P., M.L. Murphy, and N.H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology 63: 1840-1856.

Hedin, L.O., M.S. Mayer, and G.E. Likens. 1988. The effect of deforestation on organic debris dams. Verhandlungen der Internationale Vereiningung für Theoretische und Angewandte Limnologie 23: 1135-1141.

Hernandez, O., R.W. Merritt, and M.S. Wipfli. 2005. Benthic invertebrate community structure is influenced by forest succession after clearcut logging in southeastern Alaska. Hydrobiologia 533: 45-59.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Hurlbert, S.H. 2004. On misinterpretations of pseudoreplication and related matters: a reply to Oksanen. Oikos 104: 591-597.

Huryn, A.D. 1990. Growth and voltinism of lotic midge larvae: patterns across an Appalachian mountain basin. Limnology and Oceanography 35: 339-351.

Huryn, A.D. and J.B. Wallace. 1986. A method for obtaining *in situ* growth rates of larval Chironomidae (Diptera) and its application to studies of secondary production. Limnology and Oceanography 31: 216-222.

Huryn, A.D. and J.B. Wallace. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. Ecology 68: 1932-1942.

Hutchens, J.J., D.P. Batzer, and E. Reese. 2004. Bioassessment of silvicultural impacts in streams and wetlands of the eastern United States. Water, Air, and Soil Pollution: Focus 4: 37:53

Hutchens, J.J., E.F. Benfield, and J.R. Webster. 1997. Diet and growth of a leaf-shredding caddisfly in southern Appalachian streams of contrasting disturbance history. Hydrobiologia 346: 193-201.

Hynes, H.B. 1975. The stream and its valley. Verhandlungen der Internationale Vereiningung für Theoretische und Angewandte Limnologie 19: 1-15.

Kedzierski, W.M. and L.A. Smock. 2001. Effects of logging on macroinvertebrate production in a sand-bottomed, low-gradient stream. Freshwater Biology 46: 821-833.

Kelly, J.R. and M.A. Harwell. 1990. Indicators of ecosystem recovery. Environmental Management 14: 527-545.

Korsu, K. 2004. Response of benthic invertebrates to disturbance from stream restoration: the importance of bryophytes. Hydrobiologia 523: 37-45.

Lugthart, G.J. and J.B. Wallace. 1992. Effects of disturbance on benthic functional structure and production in mountain streams. Journal of the North American Benthological Society 11: 138-164.

Martin, C.W., J.W. Hornbeck, G.E. Likens, and D.C. Buso. 2000. Impacts of intensive harvesting on hydrology and nutrient dynamics of northern hardwood forests. Canadian Journal of Fisheries and Aquatic Sciences 57: 19-29.

Merritt, R.W. and K.W. Cummins (eds.). 1996. An introduction to the aquatic insects of North America, 3rd edn. Kendall / Hunt, Dubuque, IA.

Meyer, J.L. and C. Johnson. 1983. The influence of elevated nitrate concentration on rate of leaf decomposition in a stream. Freshwater Biology 13: 177-183.

Meyer, J.L. and J.B. Wallace. 2001. Lost linkages and lotic ecology: rediscovering small streams. In: Ecology: Achievement and Challenge. 41st Symposium of the

British Ecological Society (eds. M.C. Press, N.J. Huntly, S. Levin), pp. 295-317. Cambridge University Press, Cambridge, UK.

Molles, M.C. 1982. Trichopteran communities of streams associated with aspen and conifer forests: long-term structural change. Ecology 63: 1-6.

O'Doherty, E.C. 1988. The ecology of meiofauna in an Appalachian headwater stream. PhD Dissertation. University of Georgia, Athens, GA.

O'Hop, J.B. Wallace, and J.D. Haefner. 1984. Production of a stream shredder, *Peltoperla maria* (Plecoptera: Peltoperlidae) in disturbed and undisturbed hardwood catchments. Freshwater Biology 14: 13-21.

Oksanen L. 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? Oikos 94: 27-38.

Oksanen, L. 2004. The devil lies in details: reply to Stuart Hurlbert. Oikos 104:598-605.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164: 262-270.

Peckarsky, B.L., P. Fraissinet, M.A. Penton, and D.J. Conklin, Jr. 1990. Freshwater macroinvertebrates of Northeastern North America. Cornell University Press, Ithaca, NY. 442 pp.

Polis, G.A., W.B. Anderson, and R.D. Holt. 1997. Toward and integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28: 289-316.

Reice, S.R., R.C. Wissmar, and R.J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environmental Management 14: 647-659.

Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G. W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace, and R.C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7: 433-455.

Rosi-Marshall, E.J. and J.B. Wallace. 2002. Invertebrate food webs along a stream resource gradient. Freshwater Biology 47: 129-141.

Ross, H.H. 1963. Stream communities and terrestrial biomes. Archiv für Hydrobiologie 59: 235-242.

Sabater, S., A. Butturini, I. Muñoz, A. Romani, J. Wray, and F. Sabater. 1998. Effects of removal of riparian vegetation on algae and heterotrophs in a Mediterranean stream. Journal of Aquatic Ecosystem Stress and Recovery 6: 129-140.

Schindler, D.W. 1998. Replication versus realism: the need for ecosystem-scale experiments. Ecosystems 1: 323-334.

Silsbee, D.G. and G.L. Larson. 1983. A comparison of streams in logged and unlogged areas of Great Smoky Mountain National Park. Hydrobiologia 102: 99-111.

Stone, M.K. 1995. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. MS Thesis. University of Georgia, Athens, GA.

Stone, M.K. and J.B. Wallace. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. Freshwater Biology 39: 151-169.

Stout, B.M., E.F. Benfield, and J.R. Webster. 1993. Effects of a forest disturbance on shredder production in southern Appalachian headwater streams. Freshwater Biology 29: 59-69.

Suberkropp, K. and E. Chauvet. 1995. Regulation of leaf breakdown by fungi in streams: influences of water chemistry. Ecology 76: 1433-1445.

Swank, W.T. and J.M. Vose. 1997. Long-term nitrogen dynamics of Coweeta forested watersheds in the southeastern United States of America. Global Biogeochemical Cycles 11: 657-671.

Swank, W.T., J.M. Vose, and K. J. Elliot. 2001. Long-term hydrologic and water quality responses following commercial clearcutting of mixed hardwoods on a southern Appalachian catchment. Forest Ecology and management 143: 163-178.

Valett, H.M., C.L. Crenshaw, and P.F. Wagner. 2002. Stream nutrient uptake, forest succession, and biogeochemical theory. Ecology 83: 2888-2901.

Vitousek, P.M. and W.A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. Bioscience 25: 379-381.

Wallace, J.B. and A.C. Benke. 1984. Quantification of wood habitat in sub-tropical coastal-plain streams. Canadian Journal of Fisheries and Aquatic Sciences 41: 1643-1652.

Wallace, J.B. and M.E. Gurtz. 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment Logging. American Midland Naturalist 115: 25-41.

Wallace, J.B. and J.R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology 41: 115-139.

Wallace, J.B., J.R. Webster, S.L. Eggert, J.L. Meyer, and E.R. Siler. 2001. Large woody debris in a headwater stream: long-term legacies of forest disturbance. International Review of Hydrobiology 86: 501-513.

Wallace, J.B., M.E. Gurtz, and F. Smith-Cuffney. 1988. Long-term comparisons of insect abundances in disturbed and undisturbed Appalachian headwater streams. Verhandlungen der Internationale Vereiningung für Theoretische und Angewandte Limnologie 23: 1224-1231.

Wallace, J.B., M.R. Whiles, S. Eggert, T.F. Cuffney, G.J. Lugthart, and K. Chung. 1995. Long-term dynamics of coarse particulate organic matter in three Appalachian Mountain streams. Journal of the North American Benthological Society 14: 217-232.

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

Wallace, J.B., T.F. Cuffney, S.L. Eggert, and M.R. Whiles. 1997. Stream organic matter inputs, storage, and export for Satellite Branch at Coweeta Hydrologic Laboratory, North Carolina, USA. Journal of the North American Benthological Society 16: 67:74.

Waters, T.F. 1969. Subsampler for dividing large samples of stream invertebrate drift. Limnology and Oceanography 14: 813-815.

Webster, J.R., A.P. Covich, J.L. Tank, and T.V. Crockett. 1994. Retention of coarse organic particles in streams in the southern Appalachian Mountains. Journal of the North American Benthological Society 13: 140-150.

Webster, J.R. and E.F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17: 567-594.

Webster, J.R., M.E. Gurtz, J.J. Hains, J.L. Meyer, W.T. Swank, J.B. Waide, and J.B. Wallace. 1983. Stability of Stream Ecosystems. In: Stream Ecology (eds J.R. Barnes and G.W. Minshall), pp. 355-395. Plenum Press, New York, USA.

Webster, J.R., S.W. Golladay, E.F. Benfield, J.L. Meyer, W.T. Swank, and J.B. Wallace. 1992. Catchment disturbance and stream response: an overview of stream research at Coweeta Hydrologic Laboratory. In: River Conservation and Management (eds. P.J. Boon, P. Calow and G.E. Petts), pp. 231-253. Wiley and Sons, Chichester.

Whiles, M.R. and J.B. Wallace. 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrologic extremes. Canadian Journal of Fisheries and Aquatic Sciences 52: 2402-2422.

Whiles, M.R. and J.B. Wallace. 1997. Leaf litter decomposition and macroinvertebrate communities in headwater streams draining pine and hard wood catchments. Hydrobiologia 353: 107-119.

Wiggins, G.B. 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press, Toronto.

Wipfli, M.S. and D.P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology 47: 957-969.

Wohl, D.L., J.B. Wallace, and J.L. Meyer. 1995. Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (U.S.A.). Freshwater Biology 34: 447-464.

Woodall, W.R. and J.B. Wallace. 1972. The benthic fauna in four small southern Appalachian streams. American Midland Naturalist 88: 393-407.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Table 1. Physical characteristics of Hugh White Creek (HWC) and Big Hurricane Branch (BHB) at Coweeta Hydrologic Laboratory during 2003.

	HWC	BHB
Catchment orientation	Northwest	South
Catchment area (ha)*	61.1	59.5
Main channel length (m)*	1077	1225
Maximum channel elevation (m asl)*	996	1060
Minimum channel elevation (m asl)*	708	724
Maximum discharge (L/s) †	128.9	105.0
Minimum discharge (L/s) †	12.8	13.7
Mean discharge (L/s) †	29.9	27.7
Reach lengths ‡		
Lower	0-150	0-430
Middle	150-300	450-800
Upper	310-500	810-1050
%Habitat Composition		
Bare Bedrock	12.1	9.6
Mossy Bedrock	14.5	11.5
Riffle	38.9	48.2
Depositional	34.6	30.7

* from Gurtz and Wallace (1984)

† data from 1/1/03-9/1/03

‡ meters above weir

Table 2. Mean annual habitat-specific and habitat-weighted (a) abundance (number m^{-2}), (b) biomass (mg AFDM m^{-2}), and (c) production (mg AFDM m^{-2} yr^{-1}) for invertebrate functional feeding groups and (d) mean annual number of taxa within each habitat in reference (HWC) and disturbed (BHB) streams during 2003. Data failing normality was log(x+1) transformed. Significant differences between streams were determined using a t-test (α = 0.05). Transformed data still failing normality was analyzed using a Mann-Whitney Rank Sum test. * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001

	Bare Bedrock		**Mossy Bedrock**		**Riffle**		**Depositional**		**Weighted**	
	HWC	**BHB**	**HWC**	**BHB**	**HWC**	**BHB**	**HWC**	**BHB**	**HWC**	**BHB**
(a) Abundance										
Scrapers	1039	1506	1378 *	2956	495	511	389	622	653 *	922
Shredders	336	342	703	1592	625	839	3980	3519	1764	1701
Gatherers	5886	4819	32042 *	62431	6177	7432	106324	97329	44556	41104
Filterers	972	2611	4189	5385	331	429	171	547	913	1245
Predators	911	939	4261 **	12394	1156	921	6893	6710	3564	4020
Total	9144	10217	42572 *	84757	8785	10131	117757	108727	51449	48990
(b) Biomass										
Scrapers	330	267	69	246	35	46	23	7	71	78
Shredders	38	115	76	90	79	229	1486	1466	561	582
Gatherers	78	83	346	948	71	69	600	570	295	325
Filterers	190	425	1182	1537	184	172	42	76	281	324
Predators	239	35	86 ***	343	176	263	928	1460	431	618
Total	876	925	1759	3164	545	780	3079	3580	1639	1927
(c) Production										
Scrapers	2005	1637	513	1377	206	319	173	93	457	498
Shredders	130	229	309	376	369	939	7260	7387	2717	2786
Gatherers	636	585	3307	7787	538	519	4838	4324	2440	2530
Filterers	1549	2806	9676	11843	977	1117	226	458	2050	2310
Predators	807	148	356	1538	718	818	3420	4569	1612	1988
Total	5126	5405	14161	22921	2808	3713	15917	16831	9276	10111
(d) # of taxa	13	14	17	18	26	26	25	27	----	----
(min/max)	(5,24)	(6,25)	(13,22)	(14,24)	(17,31)	(19,40)	(12,39)	(16,37)		

Table 3. Pearson correlation coefficients (r) for correlations of macroinvertebrate biomass with current velocity (CV) and different organic matter types. All data were log(x+1) transformed prior to analysis. N = 72; NS = non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; CPOM = coarse particulate organic matter; FPOM = fine particulate organic matter.

		CV	Moss	Wood	Leaves	CPOM	FPOM	Tot. OM
Scraper	HWC	.514***	.204 ^{NS}	-.347**	-.282*	-.354**	-.436***	-.445***
	BHB	.652***	.367**	-.560***	-.428***	-.464***	-.486***	-.490***
Shredder	HWC	-.695***	-.298*	.606***	.677***	.633***	.743***	.823***
	BHB	-.605***	-.316**	.529***	.453***	.607***	.682***	.743***
Gatherer	HWC	-.597***	.076 ^{NS}	.397***	.462***	.443***	.774***	.762***
	BHB	-.427***	.264*	.036 ^{NS}	.132 ^{NS}	.354**	.686***	.629***
Filterer	HWC	.545***	.479***	-.226 ^{NS}	-.192 ^{NS}	-.154 ^{NS}	-.095 ^{NS}	-.124 ^{NS}
	BHB	.461***	.33**	-.396***	-.22 ^{NS}	-.218 ^{NS}	-.191 ^{NS}	-.207 ^{NS}
Predator	HWC	-.609***	-.359**	.581***	.478***	.496***	.622***	.678***
	BHB	-.578***	-.036 ^{NS}	.367**	.212 ^{NS}	.447***	.779***	.779***
Total	HWC	-.483***	.004 ^{NS}	.340**	.464***	.423***	.640***	.673***
	BHB	-.377**	.212 ^{NS}	.055 ^{NS}	.121 ^{NS}	.360**	.638***	.557***

Table 4. Annual mean current velocity (Vel., cm/s) and substrate median phi (Med. Φ) in Hugh White Creek (reference) and Big Hurricane Branch (disturbed) during 2003. Values within a row that share the same letter are not significantly different by a Student's t-test ($\alpha = 0.05$).

Habitat		Reference	Disturbed
Bare Bedrock	Vel.	78.7^a	73.6^a
	Med. Φ	-8.0^a	-8.0^a
Mossy Bedrock	Vel.	82.7^a	84.0^a
	Med. Φ	-8.0^a	-8.0^a
Riffle	Vel.	55.4^a	56.0^a
	Med. Φ	-4.88^a	-4.74^a
Depositional	Vel.	< 15	< 15
	Med. Φ	-3.31^a	-2.05^a

Table 5. Mean annual habitat-specific and habitat-weighted organic matter standing crops (g AFDM m^{-2}) in reference (HWC) and disturbed (BHB) streams. Data failing normality was log(x+1) transformed. Significant differences between streams were determined using a t-test (α = 0.05). Transformed data still failing normality was analyzed using a Mann-Whitney Rank Sum test. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Misc. CPOM = miscellaneous coarse particulate organic matter (≥1 mm, unknown origin); FPOM = fine particulate organic matter (< 1 mm).

	Bare Bedrock		**Mossy Bedrock**		**Riffle**		**Depositional**		**Weighted**	
	HWC	**BHB**	**HWC**	**BHB**	**HWC**	**BHB**	**HWC**	**BHB**	**HWC**	**BHB**
Moss	1.4	1.3	20.5 *	38.2	0.1	0.0	0.0	0.1	3.2	4.5
Wood	3.0	12.2	2.4	1.5	15.8	51.7	370.5 *	155.1	135.1 *	73.9
Leaves	2.9	3.2	2.5	1.6	9.0	9.5	118.1	54.9	45.1	21.9
Misc. CPOM	3.5	3.0	8.6	7.7	10.6	7.8	232.3 **	88.0	86.2 ***	31.9
FPOM	4.4	6.5	20.9	24.6	8.5	9.4	188.9 *	100.3	72.2 *	38.8
Total	**15.2**	**26.2**	**54.8**	**73.7**	**44.0**	**78.4**	**910.0 ****	**398.3**	**341.8 ****	**171.1**

Figure 1. Percent contribution of functional feeding group taxa from Ephemeroptera, Plecoptera, Trichoptera, and Odonata (EPTO) insect orders to total EPTO abundance. Data are compared within (a) bedrock, (b) riffle, (c) depositional, and (d) habitat-weighted categories for 1977, 1982, 1993, and 2003 in Hugh White Creek (reference) and Big Hurricane Branch (BHB). 2003 bedrock data combined from bare and mossy bedrock habitats.

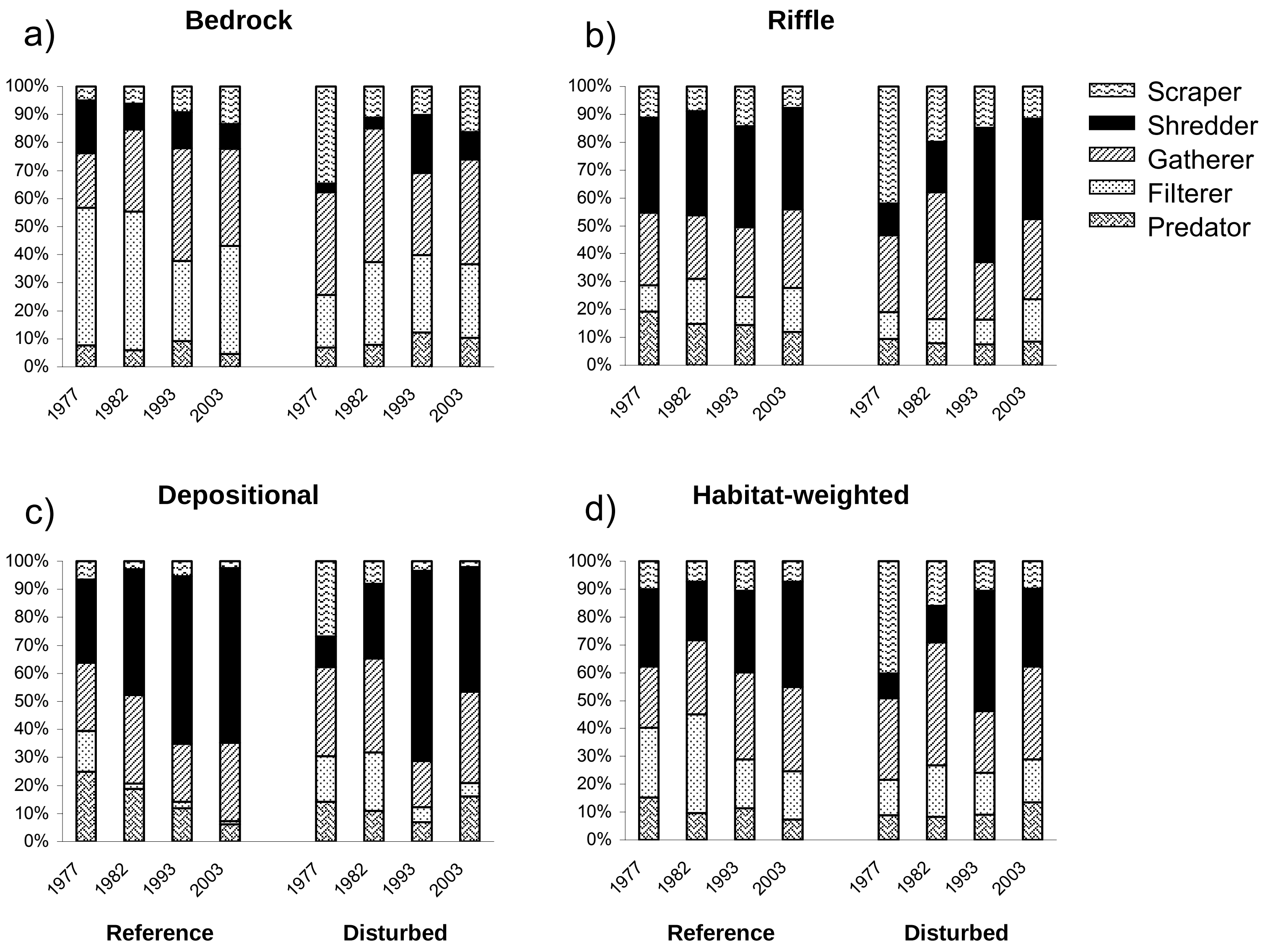
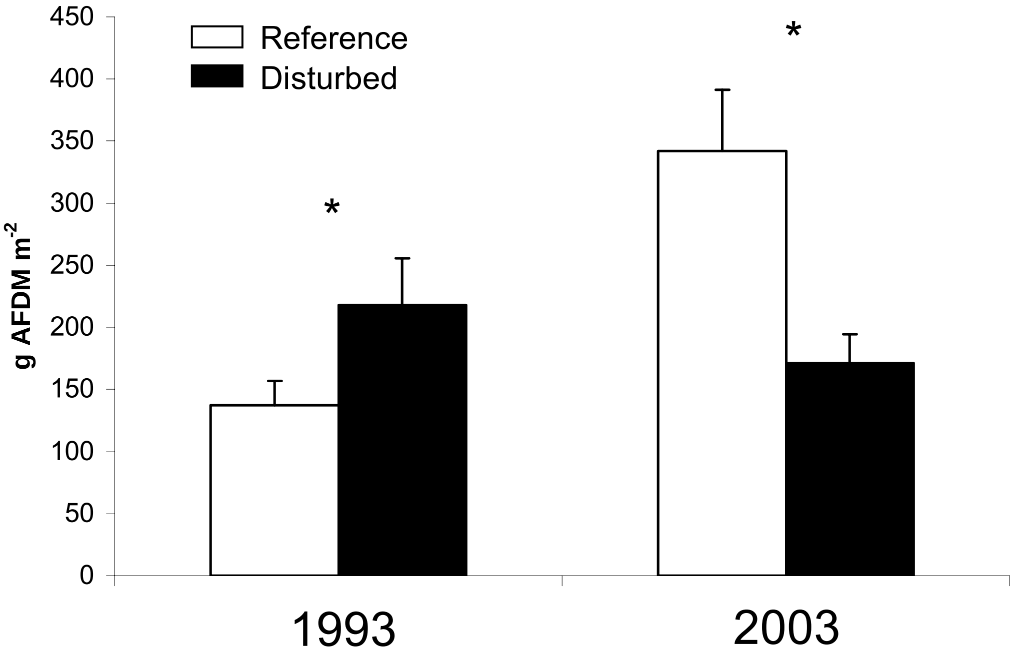

a)
Bedrock
b)
Riffle
c)
Depositional
d)
Habitat-weighted
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1977
1982
1993
2003
Reference
Disturbed
Scraper
Shredder
Gatherer
Filterer
Predator

Figure 2. Mean annual weighted (a) organic matter standing crops (g AFDM m^{-2}), and (b) secondary production (g AFDM m^{-2} yr^{-1}) in Hugh White Creek (reference) and Big Hurricane Branch (disturbed) during 1993 and 2003. 1993 data re-created from Stone and Wallace (1998). * $P < 0.05$, N = 18.

a) **Habitat-weighted Annual OM Standing Crops**



b) **Habitat-weighted Annual Secondary Production**

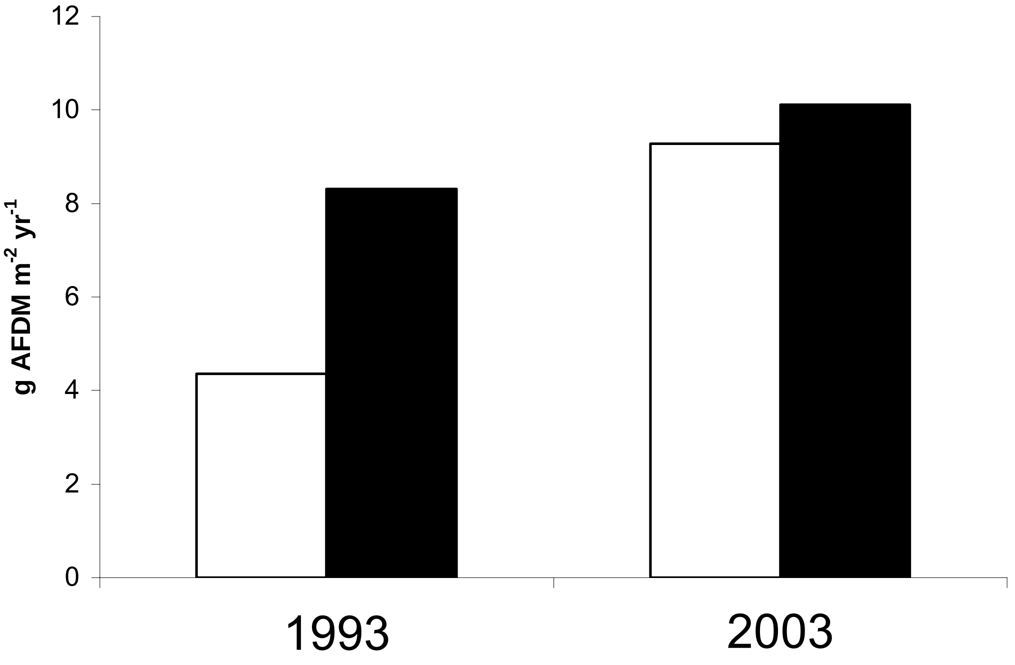


Figure 3. Cluster analysis dendrogram of mean annual habitat-specific abundance data for 69 taxa in Hugh White Creek (reference) and Big Hurricane Branch (disturbed). The objective function is a measure of dissimilarity between groups (Sorensen distance measure, $0 \leq x \leq 1$, beta = -0.25). Dist = disturbed stream, Ref = reference stream, BB = bare bedrock, BM = mossy bedrock, Rif = Riffle, Dep = depositional habitat.

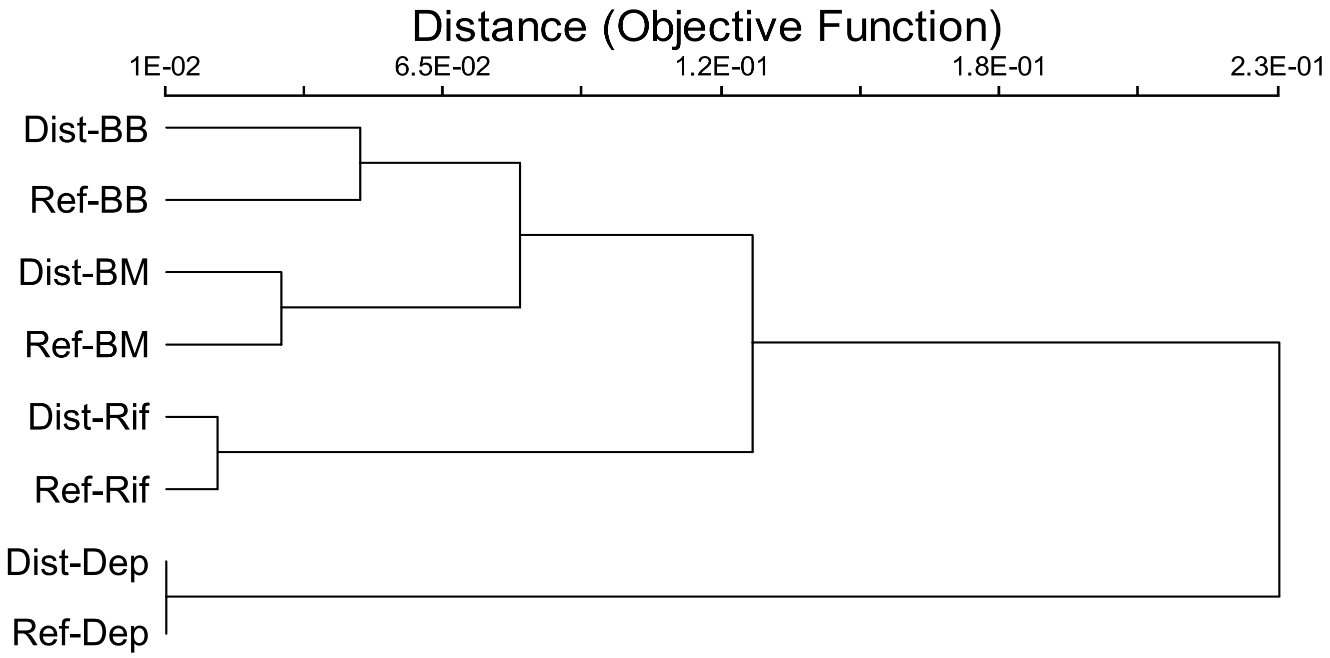

Distance (Objective Function)
1E-02
6.5E-02
1.2E-01
1.8E-01
2.3E-01
Dist-BB
Ref-BB
Dist-BM
Ref-BM
Dist-Rif
Ref-Rif
Dist-Dep
Ref-Dep

Figure 4. Mean habitat-weighted (a) organic matter standing crop (g AFDM m^{-2}), (b) invertebrate abundance (number m^{-2}), and (c) invertebrate biomass (mg AFDM m^{-2}) in Hugh White Creek (reference) and Big Hurricane Branch (disturbed) in bimonthly samples during 2003. Data are from riffle and depositional habitats only. Organic matter standing crop does not include wood. Significant differences between streams within similar months were determined by a *t*-test. * $P < 0.05$, N = 3.

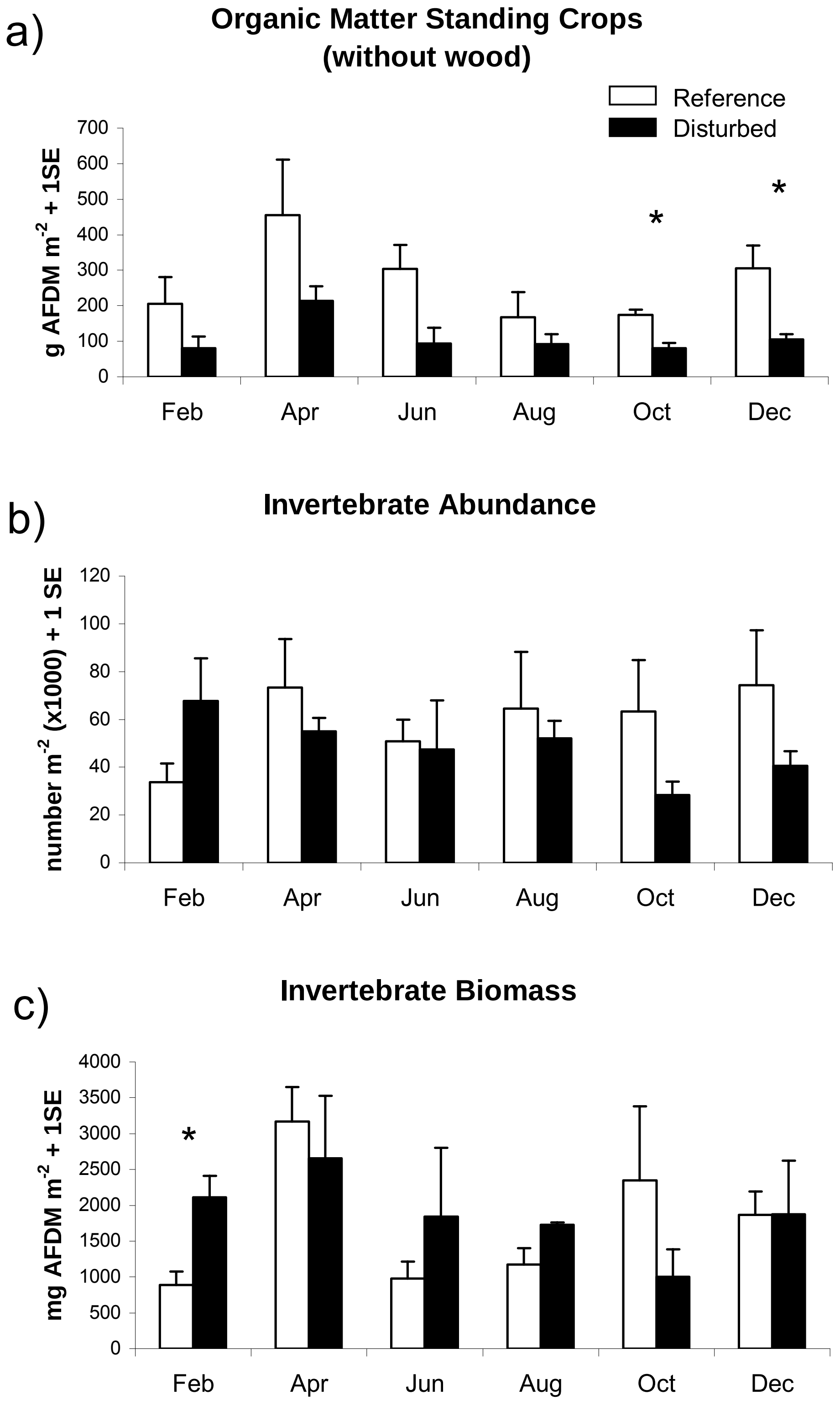

a)
Organic Matter Standing Crops
(without wood)
Reference
Disturbed
g AFDM m-2 + 1SE
0
100
200
300
400
500
600
700
*
*
Feb
Apr
Jun
Aug
Oct
Dec
b)
Invertebrate Abundance
number m-2 (x1000) + 1 SE
0
20
40
60
80
100
120
Feb
Apr
Jun
Aug
Oct
Dec
c)
Invertebrate Biomass
mg AFDM m-2 + 1SE
0
500
1000
1500
2000
2500
3000
3500
4000
*
Feb
Apr
Jun
Aug
Oct
Dec

Figure 5. Percent contributions of various organic matter types to (a) bare bedrock, (b) mossy bedrock, (c) riffle, (d) depositional, and (e) habitat-weighted totals in Hugh White Creek and Big Hurricane Branch during 2003.

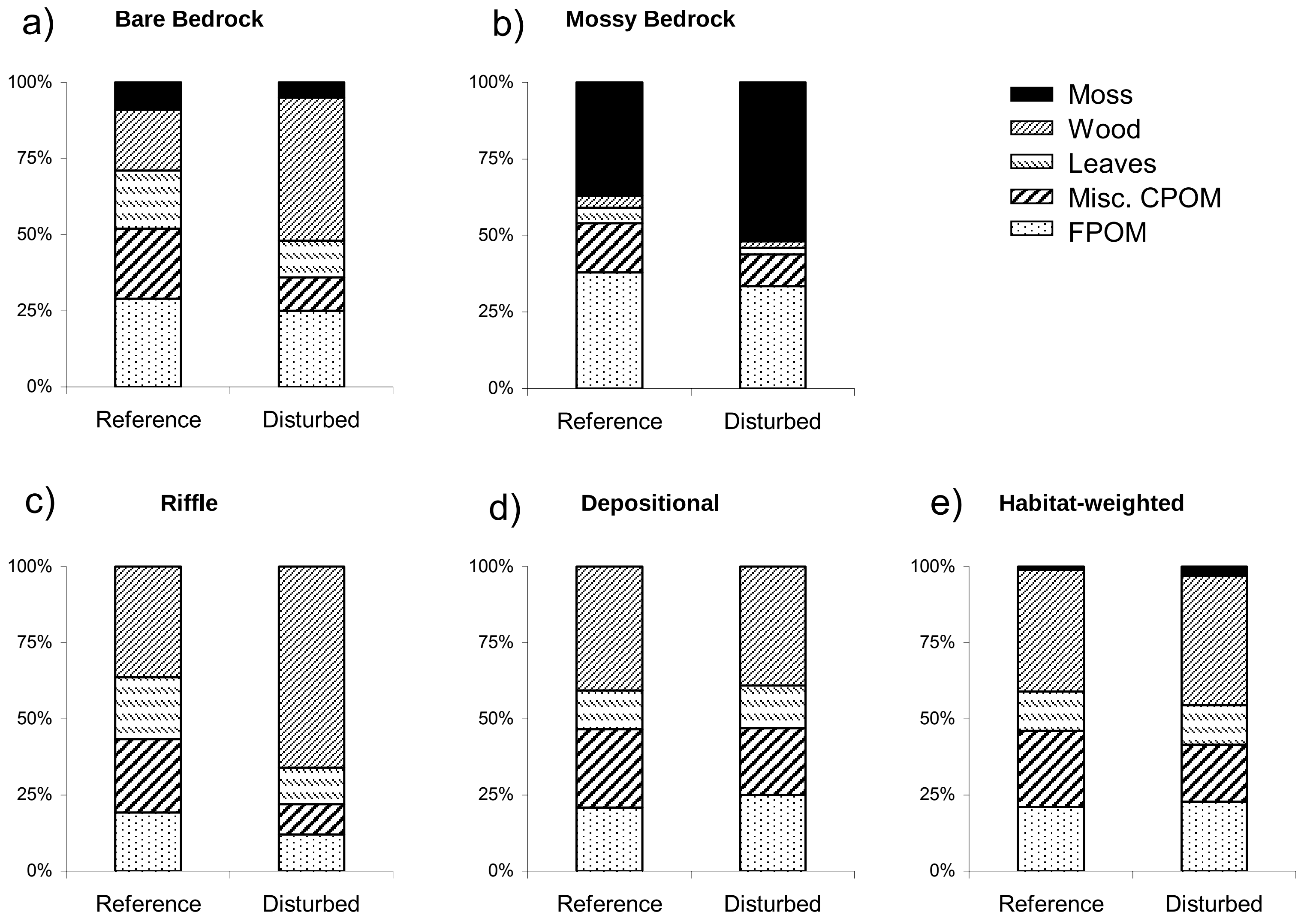
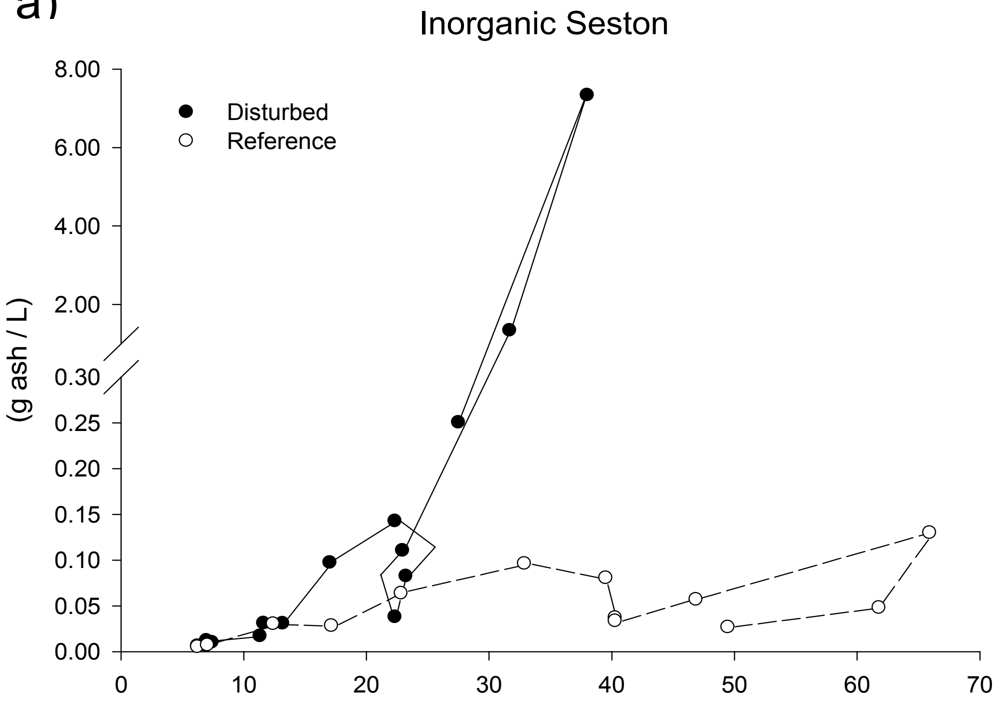

a)
Bare Bedrock
b)
Mossy Bedrock
c)
Riffle
d)
Depositional
e)
Habitat-weighted
100%
75%
50%
25%
0%
Reference
Disturbed
■ Moss
▨ Wood
▤ Leaves
▧ Misc. CPOM
⬚ FPOM

Figure 6. Concentrations of (a) inorganic (g ash L^{-1}) and (b) organic (g AFDM L^{-1}) seston versus discharge (L s^{-1}) in Hugh White Creek (reference) and Big Hurricane Branch (disturbed) during a large storm on 5-6 September, 2004. Lines connect consecutive samples taken over time within each stream.

a)


Inorganic Seston
Disturbed
Reference
(g ash / L)
8.00
6.00
4.00
2.00
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
10
20
30
40
50
60
70

b)

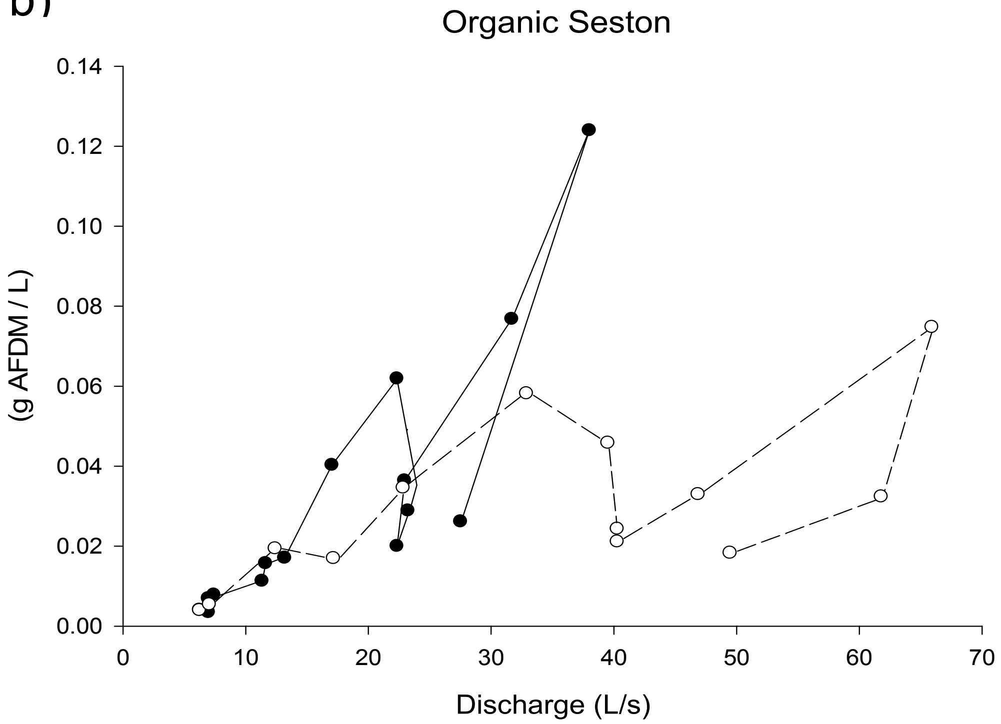

Organic Seston
(g AFDM / L)
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0
10
20
30
40
50
60
70
Discharge (L/s)

Figure 7. Volume (m^3 m^{-2}) of wood in (a) bankfull, (b) wetted, and (c) overhanging categories in Hugh White Creek (reference) and Big Hurricane Branch (disturbed). Measurements were made using the line-intersect method. Values are shown with one standard error. N = 15.

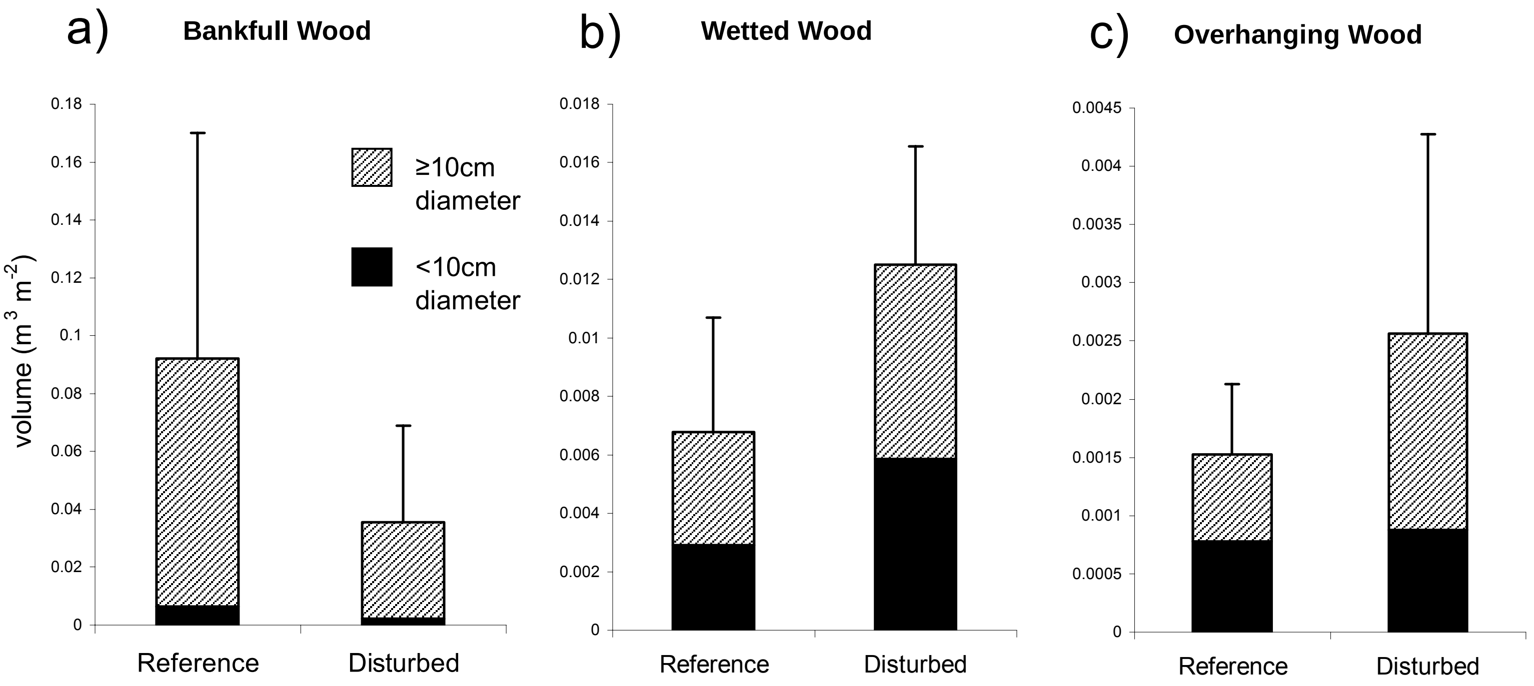
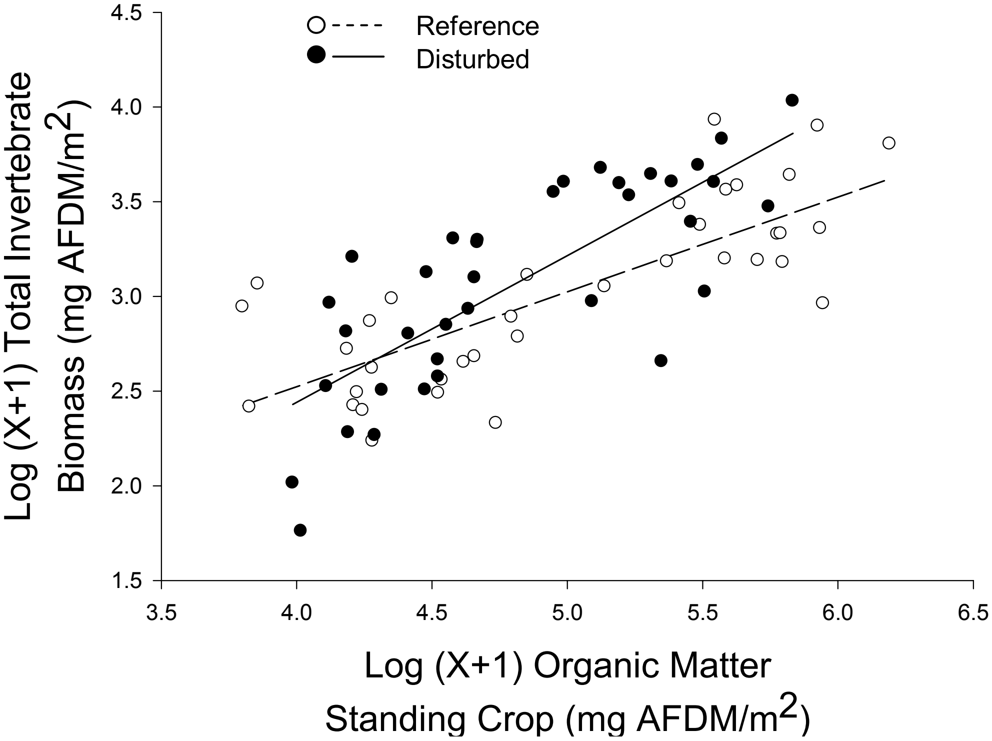
a)
Bankfull Wood
b)
Wetted Wood
c)
Overhanging Wood
volume (m^3 m^{-2})
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
▨ ≥10cm diameter
■ <10cm diameter
0.018
0.016
0.014
0.012
0.01
0.008
0.006
0.004
0.002
0
0.0045
0.004
0.0035
0.003
0.0025
0.002
0.0015
0.001
0.0005
0
Reference
Disturbed
Reference
Disturbed
Reference
Disturbed

Figure 8. Linear regression of organic matter standing crop with macroinvertebrate biomass for reference (HWC; $r^2 = 0.61$, $P < 0.001$) and disturbed (BHB; $r^2 = 0.59$, $P < 0.001$) streams in 2003. Only data from riffle and depositional habitats were used; organic matter standing crop does not include wood. The slope of the BHB regression line is significantly greater than that of HWC (Students *t*-test, N = 72, $P = 0.01$).


4.5
4.0
3.5
3.0
2.5
2.0
1.5
3.5
4.0
4.5
5.0
5.5
6.0
6.5
Reference
Disturbed
Log (X+1) Total Invertebrate Biomass (mg AFDM/m2)
Log (X+1) Organic Matter Standing Crop (mg AFDM/m2)

Appendix 1a. Habitat-specific and habitat-weighted macroinvertebrate annual mean abundance (A; no./m^2), biomass (B; mg AFDM/m^2), and production (P; mg AFDM m^{-2} yr^{-1}) in Hugh White Creek (HWC) and Big Hurricane Branch (BHB) during 2003. Annual means are based on N = 18.

SCRAPERS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Baetis	E	120	A	738.9	1005.6	688.9	1388.9	85.7	193.2	111.1	101.4	261.1	380.5
			B	31.8	45.2	23.4	20.1	7.2	7.7	5.1	4.1	11.8	11.6
			P	572.0	719.2	338.9	434.4	82.5	100.6	83.6	80.4	179.5	192.2
Blepharicera	D	170	A	27.8	5.6	0.0	0.0	0.0	0.0	0.0	0.0	3.4	0.5
			B	28.5	0.3	0.0	0.0	0.0	0.0	0.0	0.0	3.5	0.0
			P	171.2	2.1	0.0	0.0	0.0	0.0	0.0	0.0	20.7	0.2
Ectopria	C	365	A	55.6	11.1	116.7	0.0	32.4	5.4	4.2	1.4	37.7	4.1
			B	25.0	0.2	31.8	0.0	15.5	4.0	3.7	0.2	15.0	2.0
			P	100.2	0.7	127.4	0.0	59.5	15.9	14.7	0.7	58.9	7.9
Elmid A.	C	-	A	5.6	50.0	55.6	88.9	45.6	20.4	2.8	19.4	27.5	30.8
			B	0.2	7.7	6.3	14.3	4.3	1.4	1.4	0.8	3.1	3.3
			P	-	-	-	-	-	-	-	-	-	-
Elmid L.	C	365	A	94.4	105.6	438.9	827.8	287.5	217.0	238.9	454.2	269.8	349.4
			B	0.7	1.2	4.4	7.7	2.6	2.0	1.1	2.2	2.1	2.7
			P	3.3	5.9	23.0	45.7	15.7	13.5	5.4	9.1	11.7	15.1
Epeorus	E	340	A	111.1	133.3	5.6	127.8	16.9	65.6	31.9	1.4	31.9	59.5
			B	243.7	191.3	1.5	187.0	4.8	30.2	11.6	0.0	35.6	54.5
			P	1157.5	752.5	9.2	729.2	41.7	184.0	69.3	0.1	181.6	244.8
Glossosoma	T	192	A	0.0	11.1	0.0	0.0	4.8	0.0	0.0	0.0	1.9	1.1
			B	0.0	4.0	0.0	0.0	0.3	0.0	0.0	0.0	0.1	0.4
			P	0.0	30.2	0.0	0.0	2.4	0.0	0.0	0.0	1.0	2.9

Appendix 1a. Continued

SCRAPERS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Neophylax	T	213	A	5.6	183.3	72.2	522.2	22.2	8.9	0.0	44.4	19.8	95.6
			B	0.0	17.5	1.1	17.0	0.3	0.6	0.0	0.2	0.3	4.0
			P	0.4	126.5	14.4	167.3	4.1	5.4	0.0	2.2	3.7	34.7
Scraper Sum			A	1038.9	1505.6	1377.8	2955.6	495.1	510.6	388.9	622.2	653.1	921.6
			B	330.1	267.5	68.6	246.2	35.0	45.9	22.8	7.5	71.4	78.4
			P	2004.6	1637.1	512.9	1376.6	205.9	319.4	173.0	92.5	457.1	497.8

Appendix 1b. Habitat-specific and habitat-weighted macroinvertebrate annual mean abundance (A; no./m^2), biomass (B; mg AFDM/m^2), and production (P; mg AFDM m^{-2} yr^{-1}) in Hugh White Creek (HWC) and Big Hurricane Branch (BHB) during 2003. Annual means are based on N = 18.

SHREDDERS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Anchytarsus	C	1095	A	0.0	0.0	0.0	0.0	7.8	0.0	48.6	0.0	19.9	0.0
			B	0.0	0.0	0.0	0.0	0.1	0.0	29.4	0.0	10.2	0.0
			P	0.0	0.0	0.0	0.0	0.2	0.0	37.5	0.0	13.0	0.0
Fattigia	T	664	A	0.0	0.0	0.0	0.0	0.0	7.9	40.3	69.4	13.9	25.1
			B	0.0	0.0	0.0	0.0	0.0	25.2	52.4	113.6	18.1	47.0
			P	0.0	0.0	0.0	0.0	0.0	51.2	129.0	222.9	44.6	93.1
Lepidostoma	T	246	A	11.1	0.0	0.0	16.7	4.8	1.2	325.0	313.9	115.7	98.9
			B	0.0	0.0	0.0	0.1	0.0	0.1	11.4	18.4	4.0	5.7
			P	0.4	0.0	0.0	0.6	0.2	0.6	92.7	167.9	32.2	51.9
Leptotarsus	D	365	A	0.0	0.0	0.0	0.0	0.6	0.0	48.6	5.6	17.1	1.7
			B	0.0	0.0	0.0	0.0	27.4	0.0	910.3	68.4	325.7	21.0
			P	0.0	0.0	0.0	0.0	137.1	0.0	4035.5	342.1	1449.8	105.0
Leuctra	P	340	A	38.9	138.9	111.1	744.4	379.8	660.8	2497.2	2156.9	1033.0	1079.6
			B	0.8	1.6	3.5	13.2	7.6	8.4	47.0	28.6	19.8	14.5
			P	2.7	7.6	10.1	79.7	53.1	58.7	372.6	296.9	151.4	129.3
Micrasema	T	229	A	63.9	25.0	158.3	347.2	0.0	0.6	0.7	0.0	30.9	42.6
			B	2.7	1.1	13.1	27.3	0.0	0.0	0.4	0.0	2.3	3.2
			P	16.1	6.6	78.7	163.7	0.0	0.1	2.1	0.0	14.1	19.5
Molophilus	D	365	A	5.6	0.0	0.0	0.0	0.6	13.2	341.7	456.9	119.1	146.7
			B	4.1	0.0	0.0	0.0	0.2	4.6	109.9	154.2	38.6	49.6
			P	16.5	0.0	0.0	0.0	0.8	18.5	510.4	556.3	178.9	179.7

Appendix 1b. Continued.

SHREDDERS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Psilotreta	T	335	A	0.0	0.0	0.0	0.0	0.6	0.0	6.9	0.0	2.6	0.0
			B	0.0	0.0	0.0	0.0	0.1	0.0	5.2	0.0	1.8	0.0
			P	0.0	0.0	0.0	0.0	0.7	0.0	25.9	0.0	9.2	0.0
Pycnopsyche	T	275	A	0.0	0.0	0.0	0.0	1.2	7.3	443.1	200.0	153.8	64.9
			B	0.0	0.0	0.0	0.0	6.7	44.4	155.9	783.3	56.6	261.9
			P	0.0	0.0	0.0	0.0	50.6	332.8	1303.5	4692.2	470.7	1600.9
Taeniopteryx	P	365	A	0.0	66.7	0.0	188.9	0.0	1.2	0.0	0.6	0.0	28.9
			B	0.0	0.9	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.4
			P	0.0	2.6	0.0	7.5	0.0	0.1	0.0	0.1	0.0	1.2
Tallaperla	P	540	A	216.7	111.1	433.3	294.4	229.9	145.7	222.2	304.2	255.6	208.1
			B	30.7	111.1	59.1	46.9	37.2	96.9	72.8	255.0	52.0	141.1
			P	94.0	212.0	220.3	124.7	126.7	204.0	251.3	862.3	179.7	397.7
Tipula	D	310	A	0.0	0.0	0.0	0.0	0.0	1.2	5.6	10.9	1.9	3.9
			B	0.0	0.0	0.0	0.0	0.0	49.7	90.9	44.7	31.5	37.7
			P	0.0	0.0	0.0	0.0	0.0	273.3	500.0	245.9	173.0	207.2
Shredder Sum			A	336.1	341.7	702.8	1591.7	625.3	839.2	3979.9	3518.5	1763.5	1700.5
			B	38.4	114.7	75.7	90.2	79.4	229.4	1485.6	1466.4	560.6	582.1
			P	129.7	228.8	309.1	376.2	369.3	939.4	7260.5	7386.6	2716.7	2785.7

Appendix 1c. Habitat-specific and habitat-weighted macroinvertebrate annual mean abundance (A; no./m^2), biomass (B; mg AFDM/m^2), and production (P; mg AFDM m^{-2} yr^{-1}) in Hugh White Creek (HWC) and Big Hurricane Branch (BHB) during 2003. Annual means are based on N = 18.

COLLECTOR-GATHERERS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Ameletus	E	330	A	0.0	0.0	0.0	0.0	1.2	0.6	5.6	0.0	2.4	0.3
			B	0.0	0.0	0.0	0.0	1.0	0.4	1.0	0.0	0.7	0.2
			P	0.0	0.0	0.0	0.0	5.1	2.1	4.8	0.0	3.7	1.0
Amphinemura	P	300	A	516.7	277.8	1400.0	2144.4	74.8	90.3	219.4	213.9	370.6	382.5
			B	10.4	4.9	28.0	33.3	2.7	4.8	14.9	5.9	11.6	8.4
			P	86.4	25.4	234.9	391.0	18.4	26.6	126.6	44.2	95.5	73.8
Antocha	D	260	A	105.6	27.8	16.7	66.7	4.8	0.6	0.0	0.0	17.1	10.6
			B	4.1	1.3	2.7	1.8	0.2	0.2	0.0	0.0	1.0	0.4
			P	20.4	6.6	13.6	9.2	1.2	0.9	0.0	0.0	4.9	2.1
Collembola	-	-	A	144.4	238.9	161.1	105.6	43.1	215.3	350.0	1040.3	178.7	458.2
			B	3.1	5.8	3.7	2.1	0.8	4.1	7.0	22.1	3.7	9.5
			P	15.7	29.0	18.7	10.3	4.0	20.4	35.0	110.4	18.3	47.7
Copepoda	-	-	A	294.4	605.6	950.0	6650.0	1221.1	1492.6	40773.6	40600.0	14757.3	14006.5
			B	0.3	0.6	1.0	6.7	1.2	1.5	40.8	40.6	14.8	14.0
			P	5.3	10.9	17.1	119.7	22.0	26.9	733.9	730.8	265.6	252.1
Eurylophylla	E	365	A	0.0	0.0	0.0	0.0	0.0	0.0	8.3	2.8	2.9	0.9
			B	0.0	0.0	0.0	0.0	0.0	0.0	6.9	3.4	2.4	1.0
			P	0.0	0.0	0.0	0.0	0.0	0.0	34.6	16.8	12.0	5.2
Habrophlebia	E	340	A	0.0	0.0	0.0	0.0	2.4	0.0	94.4	0.0	33.6	0.0
			B	0.0	0.0	0.0	0.0	0.2	0.0	11.2	0.0	4.0	0.0
			P	0.0	0.0	0.0	0.0	0.8	0.0	50.5	0.0	17.8	0.0

Appendix 1c. Continued.

COLLECTOR-GATHERERS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Lype	T	332	A	33.3	0.0	11.1	0.0	14.4	19.9	11.1	113.9	15.1	44.6
			B	0.4	0.0	0.0	0.0	1.9	2.5	2.5	14.1	1.6	5.5
			P	2.1	0.0	0.1	0.0	11.4	14.1	13.6	67.2	9.4	27.4
Micrasema	T	229	A	63.9	25.0	158.3	347.2	0.0	0.6	0.7	0.0	30.9	42.6
			B	2.7	1.1	13.1	27.3	0.0	0.0	0.4	0.0	2.3	3.2
			P	16.1	6.6	78.7	163.7	0.0	0.1	2.1	0.0	14.1	19.5
Nematoda	-	-	A	111.1	122.2	3266.7	1888.9	659.4	405.3	15306.9	13077.8	6040.5	4439.2
			B	0.2	0.2	5.0	2.3	0.8	0.5	18.0	16.8	7.3	5.7
			P	0.8	0.8	25.2	11.3	3.8	2.6	90.0	84.1	36.4	28.4
Nematomorpha	-	-	A	316.7	5.6	0.0	0.0	340.9	63.4	2302.8	809.7	968.0	279.7
			B	0.2	0.0	0.0	0.0	0.4	0.1	2.6	1.0	1.1	0.4
			P	1.2	0.1	0.0	0.0	2.0	0.5	13.1	5.2	5.5	1.9
Non-Tany	D	-	A	3555.6	2633.3	22055.6	38766.7	2138.6	3436.0	32762.5	25706.9	15798.1	14259.2
			B	9.9	9.1	81.0	165.9	11.7	12.8	152.0	102.5	70.1	57.6
			P	235.8	158.0	1447.9	1919.6	162.7	192.6	1861.0	1249.4	945.9	712.3
Nymphomyiidae	D	-	A	327.8	111.1	922.2	322.2	248.7	38.8	88.9	45.8	301.1	80.5
			B	2.5	0.7	6.4	2.7	1.6	0.3	0.5	0.2	2.0	0.6
			P	12.3	3.7	32.2	13.3	8.1	1.4	2.3	1.2	10.1	2.9
Oligochaete	-	-	A	127.8	277.8	1566.7	7977.8	1018.4	1072.8	12130.6	12558.3	4837.0	5316.6
			B	0.4	0.7	5.3	14.2	15.4	5.3	235.2	238.5	88.2	77.5
			P	2.0	3.6	26.4	71.2	77.2	26.7	1176.0	1192.3	441.1	387.4
Ostracoda	-	-	A	33.3	5.6	22.2	100.0	26.3	37.6	788.9	1104.2	290.5	369.1
			B	0.0	0.0	0.0	0.1	0.0	0.1	1.1	1.5	0.4	0.5
			P	0.2	0.0	0.2	0.7	0.2	0.3	5.4	7.5	2.0	2.5

Appendix 1c. Continued.

COLLECTOR-GATHERERS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Paraleptophlebia	E	340	A	33.3	83.3	183.3	66.7	180.7	254.3	377.8	834.7	231.8	394.5
			B	8.6	0.7	1.9	4.8	8.9	16.5	34.3	64.6	16.6	28.4
			P	51.6	4.4	11.3	29.0	80.6	91.4	209.9	443.2	111.9	183.9
Sciara	D	365	A	33.3	0.0	183.3	5.6	180.7	8.4	377.8	162.5	231.8	54.6
			B	0.0	0.0	0.0	0.4	0.2	0.7	26.5	7.9	9.3	2.8
			P	0.0	0.0	0.0	2.0	1.2	3.4	132.8	39.4	46.4	14.0
Serratella	E	330	A	211.1	305.6	1277.8	3944.4	154.3	229.2	20.8	495.8	278.2	745.6
			B	34.7	37.0	197.9	686.0	12.1	10.0	3.2	14.4	38.7	91.7
			P	180.5	229.1	1398.2	5043.4	84.8	59.2	28.6	116.9	267.5	666.4
Soyedina	P	300	A	5.6	66.7	50.0	44.4	28.1	52.1	704.2	543.1	262.5	203.3
			B	0.7	0.5	0.4	0.3	0.3	1.6	5.0	4.3	2.0	2.2
			P	5.2	3.3	2.5	2.2	1.5	12.2	35.0	38.4	13.7	18.2
Stenonema	E	340	A	5.6	33.3	0.0	0.0	18.7	13.8	155.6	22.2	61.8	16.7
			B	0.1	20.7	0.0	0.0	11.7	7.6	43.8	35.5	19.7	16.6
			P	0.3	103.7	0.0	0.0	52.9	38.1	283.1	177.6	118.6	82.8
Gatherer Sum			A	5919.4	4819.4	32225.0	62430.6	6356.5	7431.6	106479.9	97331.9	44709.9	41105.1
			B	78.3	83.4	346.4	947.9	71.3	69.0	606.9	573.2	297.5	326.2
			P	635.9	585.1	3306.8	7786.6	538.0	519.3	4838.2	4324.5	2440.3	2529.6

Appendix 1d. Habitat-specific and habitat-weighted macroinvertebrate annual mean abundance (A; no./m^2), biomass (B; mg AFDM/m^2), and production (P; mg AFDM m^{-2} yr^{-1}) in Hugh White Creek (HWC) and Big Hurricane Branch (BHB) during 2003. Annual means are based on N = 18.

COLLECTOR-FILTERERS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Diplectrona	T	332	A	377.8	266.7	1550.0	1972.2	220.2	266.1	43.1	316.7	371.2	477.9
			B	9.8	11.1	63.9	122.2	84.2	101.9	22.5	65.9	51.1	84.5
			P	48.9	74.4	542.0	975.9	470.8	626.3	112.7	404.6	307.1	545.5
Dixa	D	365	A	22.2	72.2	0.0	16.7	10.8	37.7	34.7	94.4	18.9	56.0
			B	0.0	0.7	0.0	0.3	0.0	0.5	0.3	1.0	0.1	0.7
			P	0.1	3.5	0.0	1.4	0.1	2.6	1.3	4.9	0.5	3.3
Dolophilodes	T	269	A	11.1	11.1	22.2	11.1	7.2	19.7	6.9	1.4	9.8	12.3
			B	0.2	0.3	1.1	7.1	0.8	0.5	4.3	0.7	2.0	1.3
			P	1.4	2.5	8.6	56.7	6.3	4.0	34.0	5.7	15.6	10.4
Isonychia	E	110	A	0.0	0.0	0.0	0.0	2.4	0.0	0.0	1.4	0.9	0.4
			B	0.0	0.0	0.0	0.0	52.2	0.0	0.0	0.6	20.3	0.2
			P	0.0	0.0	0.0	0.0	260.8	0.0	0.0	3.0	101.7	0.9
Parapsyche	T	332	A	294.4	350.0	2100.0	2540.7	36.1	63.3	6.9	1.4	356.6	356.7
			B	172.2	278.4	1103.9	1383.6	39.7	65.9	2.3	0.2	197.2	217.7
			P	1421.5	1409.7	9002.8	10632.0	204.8	454.0	12.4	1.1	1561.6	1577.2
Polycentropus	T	332	A	0.0	0.0	0.0	0.0	0.0	0.0	6.9	1.4	2.4	0.4
			B	0.0	0.0	0.0	0.0	0.0	0.0	5.3	3.1	1.8	1.0
			P	0.0	0.0	0.0	0.0	0.0	0.0	26.4	15.5	9.1	4.8
Simuliidae	D	180	A	266.7	1894.4	516.7	833.3	54.6	41.9	0.0	22.2	128.5	304.7
			B	7.9	134.4	13.3	23.7	6.8	3.2	0.0	0.1	5.5	17.2
			P	77.0	1314.5	122.3	176.2	34.6	30.1	0.0	0.0	40.5	161.0

Appendix 1d. Continued.

COLLECTOR-FILTERERS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Sphaeridae	-	-	A	0.0	16.7	0.0	11.1	0.0	0.0	72.2	108.3	25.0	36.1
			B	0.0	0.3	0.0	0.2	0.0	0.0	7.8	4.7	2.7	1.5
			P	0.0	1.4	0.0	1.0	0.0	0.0	38.8	23.6	13.4	7.5
Filterer Sum			A	972.2	2611.1	4188.9	5385.1	331.2	428.6	170.8	547.2	913.3	1244.5
			B	190.0	425.2	1182.2	1537.0	183.6	172.1	42.3	76.2	280.6	323.9
			P	1548.9	2806.0	9675.7	11843.1	977.4	1117.0	225.6	458.4	2049.6	2310.5

Appendix 1e. Habitat-specific and habitat-weighted macroinvertebrate annual mean abundance (A; no./m^2), biomass (B; mg AFDM/m^2), and production (P; mg AFDM m^{-2} yr^{-1}) in Hugh White Creek (HWC) and Big Hurricane Branch (BHB) during 2003. Annual means are based on N = 18.

PREDATORS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Acari	-	-	A	705.6	516.7	3311.1	8761.1	598.0	312.2	2059.7	1816.7	1511.4	1765.3
			B	1.9	1.4	8.8	23.3	1.6	0.8	5.5	4.8	4.0	4.7
			P	9.4	6.9	44.0	116.5	8.0	4.2	27.4	24.2	20.1	23.5
Beloneuria	P	660	A	0.0	5.6	0.0	0.0	9.7	2.4	9.7	1.4	7.1	2.1
			B	0.0	1.0	0.0	0.0	67.5	36.9	47.8	0.6	42.9	18.1
			P	0.0	3.0	0.0	0.0	202.6	110.7	143.4	1.7	128.6	54.2
Ceratopogonidae	D	365	A	16.7	16.7	72.2	100.0	129.8	78.5	1747.2	1852.8	667.6	619.7
			B	1.9	1.4	3.4	14.0	13.6	6.4	136.6	90.8	53.3	32.7
			P	9.7	6.8	17.0	70.0	61.2	33.4	594.1	487.5	233.1	174.5
Cordulegaster	O	1140	A	0.0	0.0	5.6	0.0	0.6	1.2	31.9	34.7	12.1	11.2
			B	0.0	0.0	4.4	0.0	3.7	68.2	141.8	382.9	51.2	150.4
			P	0.0	0.0	6.7	0.0	5.6	102.3	238.3	426.8	85.6	180.3
Dicranota	D	310	A	5.6	44.4	138.9	588.9	23.5	35.9	15.3	13.9	35.3	93.6
			B	0.1	2.4	2.9	25.2	4.2	2.1	8.9	5.3	5.2	5.8
			P	0.5	6.5	14.3	139.9	35.5	7.0	44.7	26.5	31.4	28.2
Empididae	D	340	A	22.2	16.7	94.4	188.9	1.8	4.8	1.4	183.3	17.6	81.9
			B	0.6	0.1	0.6	8.8	0.0	0.0	0.2	4.0	0.2	2.3
			P	2.8	0.3	3.1	44.2	0.0	0.1	1.1	19.8	1.2	11.3
Glutops	D	365	A	0.0	0.0	0.0	0.0	0.0	0.6	2.8	11.1	1.0	3.7
			B	0.0	0.0	0.0	0.0	0.0	5.2	34.4	80.0	11.9	27.1
			P	0.0	0.0	0.0	0.0	0.0	26.1	171.8	400.0	59.4	135.4

Appendix 1e. Continued.

PREDATORS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Hexatoma A	D	365	A	0.0	0.0	0.0	0.0	6.1	17.4	200.0	231.9	71.6	79.6
			B	0.0	0.0	0.0	0.0	1.8	1.9	63.9	36.5	22.8	12.1
			P	0.0	0.0	0.0	0.0	9.0	9.4	421.8	201.2	149.5	66.3
Hexatoma B	D	365	A	0.0	0.0	0.0	0.0	25.1	6.7	100.0	147.2	44.4	48.4
			B	0.0	0.0	0.0	0.0	1.6	1.4	21.8	29.4	8.2	9.7
			P	0.0	0.0	0.0	0.0	8.0	6.8	83.4	112.1	32.0	37.7
Hexatoma C	D	365	A	0.0	0.0	0.0	0.0	24.8	33.7	15.3	108.3	14.9	49.5
			B	0.0	0.0	0.0	0.0	26.8	30.7	41.8	112.3	24.9	49.3
			P	0.0	0.0	0.0	0.0	124.9	145.8	159.7	295.1	104.0	160.9
Hexatoma E	D	365	A	0.0	0.0	0.0	0.0	1.2	0.0	12.5	2.8	4.8	0.9
			B	0.0	0.0	0.0	0.0	0.5	0.0	14.0	1.8	5.1	0.5
			P	0.0	0.0	0.0	0.0	3.1	0.0	84.2	10.6	30.4	3.3
Isoperla	P	300	A	50.0	177.8	311.1	1333.3	98.6	63.5	265.3	891.7	181.4	474.7
			B	7.1	17.4	27.0	182.7	3.3	5.8	9.4	38.7	9.3	37.3
			P	27.0	69.3	110.6	770.4	26.8	24.8	51.5	212.9	47.6	172.5
Lanthus	O	660	A	11.1	5.6	0.0	16.7	2.4	18.2	43.1	200.0	17.2	72.6
			B	151.8	0.1	0.0	9.1	3.8	64.5	186.3	414.6	84.3	159.4
			P	379.5	0.1	0.0	22.7	9.6	161.4	535.0	1174.2	234.8	440.9
Malirekus	P	340	A	16.7	5.6	0.0	5.6	14.5	6.0	1.4	90.3	8.2	31.8
			B	61.4	5.1	0.0	0.4	30.7	1.1	0.7	1.8	19.6	1.6
			P	306.9	25.3	0.0	2.1	142.6	5.5	3.5	8.8	93.9	8.0
n.r. *Pedicia*	D	340	A	0.0	5.6	0.0	0.0	0.0	0.6	8.3	5.6	2.9	2.5
			B	0.0	1.8	0.0	0.0	0.0	0.1	13.0	1.1	4.5	0.5
			P	0.0	9.1	0.0	0.0	0.0	0.3	64.9	5.6	22.4	2.7

Appendix 1e. Continued.

PREDATORS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Pedicia	D	365	A	0.0	0.0	5.6	0.0	0.0	3.0	4.2	6.9	2.2	3.6
			B	0.0	0.0	0.2	0.0	0.0	0.3	10.0	80.3	3.5	24.8
			P	0.0	0.0	1.0	0.0	0.0	1.4	49.9	401.5	17.4	123.9
Pseudogoera	T	660	A	0.0	0.0	16.7	16.7	0.0	0.0	0.0	0.0	2.4	1.9
			B	0.0	0.0	0.8	1.6	0.0	0.0	0.0	0.0	0.1	0.2
			P	0.0	0.0	2.0	4.0	0.0	0.0	0.0	0.0	0.3	0.5
Pseudolimnophila	D	365	A	0.0	0.0	0.0	0.0	5.4	1.2	188.9	52.8	67.5	16.8
			B	0.0	0.0	0.0	0.0	2.3	1.8	92.6	37.3	32.9	12.3
			P	0.0	0.0	0.0	0.0	9.1	7.1	318.1	112.4	113.6	37.9
Rhabdomastix	D	365	A	0.0	0.0	0.0	0.0	0.6	2.4	65.3	218.1	22.8	68.1
			B	0.0	0.0	0.0	0.0	1.8	5.6	43.4	98.7	15.7	33.0
			P	0.0	0.0	0.0	0.0	9.2	27.8	217.0	452.9	78.7	152.4
Rhaphium	D	300	A	0.0	0.0	0.0	0.0	0.0	0.0	2.8	5.6	1.0	1.7
			B	0.0	0.0	0.0	0.0	0.0	0.0	3.3	1.5	1.1	0.5
			P	0.0	0.0	0.0	0.0	0.0	0.0	16.4	7.4	5.7	2.3
Rhyacophila	T	340	A	44.4	27.8	94.4	433.3	23.5	49.3	26.4	102.8	37.4	107.8
			B	13.8	0.2	36.2	59.8	5.7	14.7	1.6	5.6	9.7	15.7
			P	69.1	0.8	148.2	282.0	37.5	79.3	8.2	28.1	47.3	79.3
Sweltsa	P	630	A	0.0	5.6	0.0	16.7	56.3	75.4	75.0	19.4	47.9	44.8
			B	0.0	0.0	0.0	0.8	5.2	6.5	29.6	4.8	12.3	4.7
			P	0.0	0.1	0.0	2.3	16.1	17.9	56.6	16.8	25.9	14.1
Tanypodinae	D	-	A	27.8	16.7	172.2	300.0	57.5	20.9	1413.9	79.2	540.0	70.5
			B	0.1	0.0	0.5	0.4	0.2	0.1	7.7	0.9	2.8	0.3
			P	0.3	0.1	2.4	1.8	1.3	0.4	38.7	4.5	14.3	1.8

Appendix 1e. Continued.

PREDATORS:				Bare Bedrock		Mossy Bedrock		Riffle		Depositional		Habitat-Weighted	
Taxa	Order	CPI		HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
Turbellaria	-	-	A	11.1	94.4	38.9	633.3	76.7	187.4	634.7	638.9	256.5	368.4
			B	0.4	3.9	1.4	16.4	1.5	9.2	18.0	27.7	7.1	15.2
			P	1.9	19.5	6.8	82.2	7.6	46.2	90.1	138.5	35.3	76.1
Predator Sum			A	911.1	938.9	4261.1	12394.4	1156.2	921.4	6925.0	6715.3	3575.1	4021.2
			B	238.9	34.6	86.2	342.6	176.0	263.3	932.2	1461.2	432.6	618.2
			P	806.9	147.9	356.1	1538.1	717.6	817.8	3419.7	4568.9	1612.4	1987.9