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Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure

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SUMMARY

1. Changes in benthic invertebrate community structure following 16 years of forest succession after logging were examined by estimating benthic invertebrate abundance, biomass and secondary production in streams draining a forested reference and a recovering clear-cut catchment. Benthic invertebrate abundance was three times higher, and invertebrate biomass and production were two times higher in the disturbed stream.
2. Comparison of invertebrate community abundance 1, 5 and 16 years after clear-cutting indicated that the proportion of scrapers had decreased, whereas shredders had increased. Functional group percentage similarity indicated that the invertebrate community in the disturbed stream 16 years after clear-cutting was more similar to the reference than to that found earlier in the disturbed stream.
3. The five indices calculated from data collected over the past 16 years, as well as the abundance, biomass and production data collected during this study, proved to be of differing value in assessing recovery of the disturbed stream from logging. Percent dominant-taxon and EPT (Ephemeroptera, Plecoptera and Trichoptera) taxon richness failed to show any initial differences between reference and disturbed streams, indicating that these indices may not be useful for measuring recovery from logging. The percentage *Baetis* and shredder-scraper indices showed significant differences only during the 1977 study and suggest recovery (no difference between reference and disturbed) by 1982. The North Carolina Biotic Index showed continued differences during 1982 in the riffle and depositional habitats and recovery by 1993. Total macroinvertebrate abundance, biomass and production, as well as EPT abundance, indicated continued differences between the reference and disturbed streams in the 1993 study.

Introduction

Disturbance can have significant impacts on structure and function of stream macroinvertebrate communities and has become an important focus in stream ecology (see reviews by Resh *et al.* 1988; Niemi *et al.* 1990; Yount & Neimi, 1990). Bender, Case & Gilpin (1984) recognized two general types of disturbance, pulse and press, based on the nature and duration of their effects. Pulse disturbances are generally characterized as catastrophic events of relatively short duration, while press disturbances tend to be longer in duration.

Logging is a large-scale, press disturbance of the terrestrial ecosystem, which can have a significant impact on streams; for example, logging may change temperature regimes (Swift, 1983), flow regimes (Borman & Likens, 1979), primary production (Webster *et al.*, 1983; Duncan & Brusven, 1985; Noel, Martin & Federer, 1986) and organic matter dynamics (Webster 1983) and macroinvertebrate community structure (Newbold, Erman & Roby, 1980; Gurtz &Wallace, 1984; Noel *et al.*, 1986; Wallace, Gurtz & Smith-Cuffney, 1988). Since stream recovery is closely tied in to the long-term process of forest regrowth, studies examining recovery from logging should be continued over a long period of time.

Resh *et al.* (1988) discuss the difficulty of measuring the recovery of aquatic communities and stress the importance of choosing study and reference streams with similar hydrologic regimes and similar geomorphology. They also recommend using a wide range of measures, such as macroinvertebrate abundance, biomass, secondary production, taxon richness and functional diversity, to assess community recovery.

Other studies support the necessity of using a wide range of indices to gauge recovery, Lugthart &Wallace (1992) showed that abundance data overestimated the importance of small, numerically abundant organisms, which tend to dominate disturbed systems, while biomass overestimated the importance of large, slow-growing organisms. Benke *et al.* (1984) suggest production is a better indicator of an organism's role in the community, since it attempts to estimate energy flow through the system and takes into account differences in turnover rates among organisms.

During this study, benthic macroinvertebrate community structure and productivity, as well as benthic organic matter, were assessed in streams draining reference and disturbed catchments. The disturbed catchment was clear-cut 16 years previously and allowed to progress through forest succession. The four principal objectives of this study were:

1 to estimate benthic invertebrate community abundance, biomass, production and benthic organic matter in streams draining reference and logged catchments following 16 years of forest succession;
2 to identify changes in benthic community structure over the previous 16 years;
3 to determine the extent of recovery of the benthic community in the disturbed stream;
4 to evaluate the merits of five biotic assessment indices: taxon richness of the insect orders Ephemeroptera, Plecoptera, and Trichoptera (EPT);% dominant taxon; % *Baetis*, shredder/ scraper ratio; and, using the North Carolina Biotic Index (NCBI), assessment of the effects of and recovery from clear-cut logging.

Table 1 Physical characteristics of reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams at the Coweeta Hydrologic Laboratory

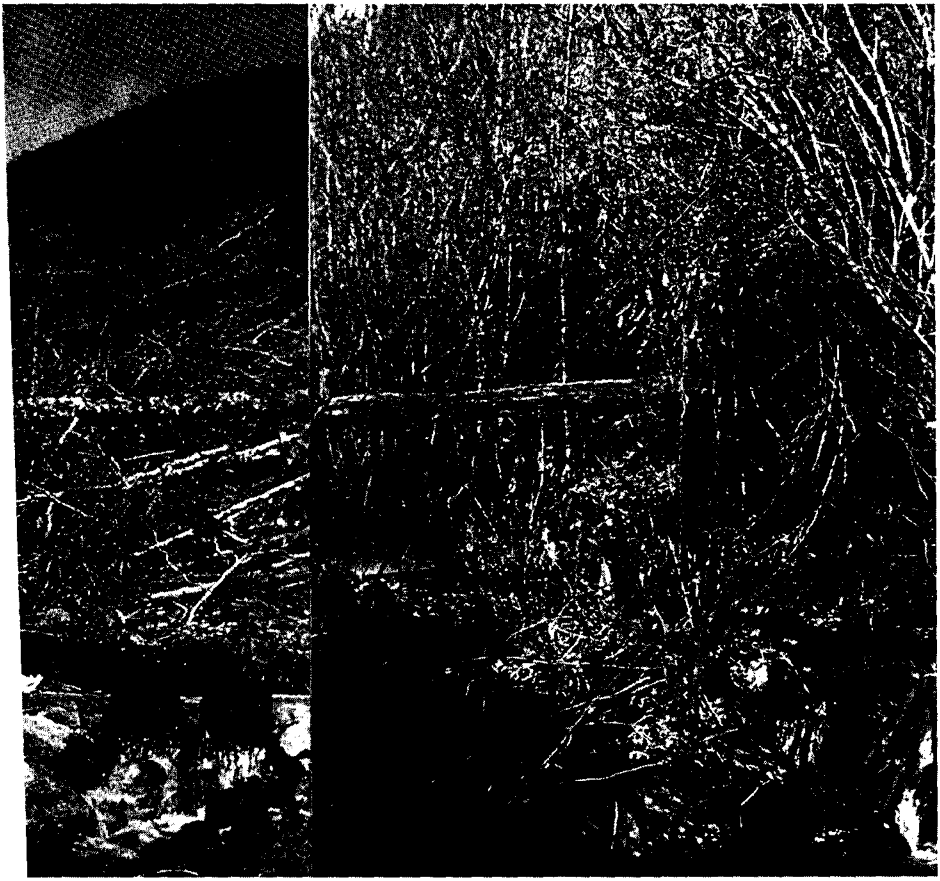
Catchment characteristics	Reference	Disturbed
Catchment area (ha)	61.1	59.5
Catchment orientation (aspect)	North-west	South
Main channel length (m)	1077.0	1225.0
Maximum channel elevation (m a.s.l.)	996.0	1060.0
Minimum channel elevation (m a.s.l.)	708.0	724.0
Mean annual discharge ($L s^{-1}$)	19.0	17.7
Temperature (°C)*		
Maximum	19.5	17.5
Minimum	0.5	2.0
Average	11.1	11.5
Annual degree days	4036.0	4189.0
% Habitat composition†		
Bedrock	36.5	16.8
Riffle	34.4	47.1
Depositional	29.1	36.1
Reach lengths and distance (m)‡		
Upper	380-426	889-955
Middle	265-298	485-525
Lower	37-122	159-252

*Average of daily stream temperatures during the present study. Supplied by the US Forest Service.
†Estimates of whole stream substratum composition from Gurtz &Wallace (1984).
‡Numbers indicate range of distances above the weir for each stream.

Study sites

The study sites are within the confines of the Coweeta Hydrologic Laboratory in Macon County, North Carolina, U.S.A. The reference and disturbed catchments are both drained by second-order streams which have similar physical features (Table 1). The catchments differ in aspect, with the reference catchment facing north-west and the disturbed catchment facing south. Streams draining each catchment, as all streams in the Coweeta Basin, are characterized by low nutrients (< 1 mg L^{-1}) and pH is generally between 6.5 and 6.9 (Swank & Waide, 1988).

The reference catchment (C14), drained by Hugh White Creek, has been relatively undisturbed except for selective logging during the early 1900s and the chestnut blight [*Endothia parasitica* (Murrill) Anderson] during the 1930s. Current vegetation in the reference catchment is dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), yellow poplar (*Liriodendron*



following clear-cutting and removal of riparian rhododendron in late summer 1977. Note fallen
me log during winter of 1988, following 11 years of forest succession, showing dense coppice
I rhododendron.

tulipifera L.) and red maple (*Acer rubrum* L.). Riparian vegetation consists of birch (*Betula* sp.) and rhododendron (*Rhododendron maximum* L.), which forms a dense year-round understorey.

The disturbed catchment (C7), drained by Big Hurricane Branch, was clear-cut between January and June 1977, and logs were removed with a mobile cable system. All stems > 2.5 cm were clear-felled (including rhododendron along the stream bank) during summer and early autumn of 1977 (Fig. 1). Most logging slash' was cleared from the main channel, but pre-existing debris dams were not removed. Prior to cutting, the riparian and adjacent cove hardwood forest was dominated by hickories > red oak (*Quercus rubra* L.) > yellow-poplar (*L. tulipifera*) > black birch > rhododendron (Boring & Swank, 1986). Stem density (number of stems ha^{-1}) increased by twenty-four to forty-six times that of the pre-cut forest within the first year following clear-cutting, and by 1993 stem density remained six to nine times greater than that of the pre-cut forest (Elliott et al., 1997) (Fig. 1). The 17-year-old forest is still aggrading and by 1993, most of the stems (58% of the density and 12% of the basal area) were < 2.5-cm d.b.h., although there were c. 100 stems ha^{-1} in larger size classes (18- to 28-cm d.b.h.) (Elliott *et al.*, *1997*). Compared to the pre-cut forest, there was also a change in composition within the cove hardwood forest of the disturbed catchment. Although revegetation was rapid, forest composition has changed during succession with opportunistic species such as yellow poplar, black locust (*Robinia* pseudoacacia L.) and red maple increasing in abundance, while oaks and hickories have declined (Elliott et al., 1997). In 1993, the cove hardwood forest of the disturbed catchment was dominated by yellow poplar, black birch, rhododendron, black locust, eastern hemlock (*Tsuga cunadensis* (L.) Carriere), dogwood (*Cornus florida* L.), red maple and red oak (Elliott et *al., 1997*). The current canopy structure is characterized by extensive coppice growth resulting in heavy stream cover during summer. In addition, a number of early successional, shade-intolerant species' of herbaceous plants have declined since 1977.

Webster *ef al.* (1983) summarized early abiotic changes in the disturbed stream caused by clear-cutting. These changes included increases in stream discharge, stream temperature, organic seston, inorganic seston and some nutrients. Most of these changes were short-term and values were returning to near reference levels within 4 years, although some, such as storm-flow seston, remained high for longer periods (Webster ef *al.*, 1990).

Leaf litter inputs were only 1.6% of predisturbance levels during the first year following logging, but had increased to 50% of predisturbance levels by 1980. There was a difference in the quality of these inputs, however, which reflected changes in the species composition of the forest (Webster *ef al.*, 1983). During 1993-94, total leaf litter inputs to the reference and disturbed streams were almost identical, although the species of leaf litter continued to show differences (J. R. Webster, personal communication). Primary production rose sharply in the disturbed stream during the year following clear-cutting, but returned to near reference levels within 2 years (Webster et *al.*, 1983).

Removal of the canopy also caused significant changes in the macroinvertebrate community of the disturbed stream. During, and immediately after, clear-cutting, Gurtz & Wallace (1984) reported increases in scraper abundance, predominantly *Baetis* **spp.,** and decreases in the predominant shredder, *Tallaperla maria* (Needham & Smith) (Plecoptera: Peltoperlidae). Five years after clear-cutting, scraper abundance had decreased in all habitats, and collector abundance had increased (Wallace et *al., 1988).*

Materials and methods

Field collection

Nine samples were collected every 2 months from the main channel of each study stream beginning in February 1993 and ending in February 1994. Samples were collected from bedrock outcrops, riffles and depositional areas following a randomized block design. Streams were divided into upper, middle and lower reaches, and three samples, one from each habitat type, were collected from each stream reach on each collection date.

Bedrock outcrops were sampled by scraping a 225 cm^2 area and washing this material through a 250-µm-mesh bag held to the substratum. Riffles were sampled using a modified Surber sampler with a 250-pm-mesh net. Large cobbles were scrubbed with a brush to remove macroinvertebrates, and the substratum was disturbed to a depth of 10 cm when possible. Depositional areas were sampled using a coring device driven 10 cm into the substratum when possible. The contents of the corer were scooped out and poured through a 250-μm-mesh bag. All samples were preserved in the field with 7–8% formalin containing Phloxine B dye and returned to the laboratory for processing.

Prior to collecting each sample, current velocity was determined using a Gessner bag current meter (Gessner, 1950), and substratum composition was estimated by visual inspection. Substratum categories corresponded to the modified Wentworth scale: boulder > 256 mm, cobble 64-256 mm, pebble 16-64 mm, gravel 2-16 mm, and sand < 2 mm. Size classes were converted to a phi scale (negative log base 2), and the median phi for each sample was calculated (Cummins, 1962).

Sample processing

In the laboratory, each sample was elutriated to separate organisms and organic material from inorganic sediments and poured through l-mm and 250-μm nested sieves. Organisms were separated from organic material using a dissecting microscope at 15 X magnification. If the 250 urn-1 mm fraction contained > 300 organisms, it was subsampled (1/8–1 / 64 of total) using a sample splitter (Waters, 1969), followed by removal of organisms.

Organisms were identified, measured and counted using a dissecting microscope. Most insects were identified to genus using the keys of Brigham, Brigham & Gnilka, (1982), Merritt & Cummins (1984) and Wiggins (1977). Members of the family Chironomidae were identified as Tanypodinae or non-Tanypodinae. Most non-insect taxa were identified only to order. Each taxon was assigned to a functional feeding group based on Merritt & Cummins (1984) or studies of other Coweeta streams (Huryn & Wallace, 1987; Lugthart & Wallace, 1992).

Biomass [ash-free dry mass (AFDM)] for Collembola, Copepoda, Hydracarina and Nematoda was calculated using mean mass per individual determined from a sample of fifty individuals. Biomass for all other taxa was calculated using length-weight regressions derived from organisms in other Coweeta streams (Huryn, 1986; A.D. Huryn, unpublished observations; J. B. Wallace, J. O'Hop, G. J. Lughart, unpublished observations).

Secondary production (g AFDM m^{-2} yr^{-1}) for insect taxa with a distinct cohort structure was calculated using the size-frequency method (Hamilton, 1969) with a correction for the cohort production interval (Benke, 1979). Cohort production intervals were derived from size-frequency histograms or from studies of other Coweeta streams (Huryn & Wallace, 1987; Lugthart & Wallace, 1992). The community-level method of Huryn & Wallace (1986), modified by Huryn (1990), was used to calculate production of non-Tanypodinae chironomids. Production of the remaining taxa was calculated using production/biomass (P/B) ratios multiplied by the annual average biomass. A P/B of 18 was used for Copepoda (O'Doherty, 1988), and a P/B of 5 was used for Nematoda, Oligochaeta and Turbellaria (Benke *et al.*, *1984).*

After removal of all organisms in the laboratory, the remaining organic matter was poured through 4-mm, l-mm and 250-μm nested sieves. Organic matter > 4 mm was separated into leaves, wood, moss and miscellaneous (seeds, buds, unidentified material). Organic material l-4 mm was considered miscellaneous coarse particulate organic matter (CPOM), and material 250 μm–1 mm was considered fine particulate organic matter (FPOM). All organic matter was dried for 7 days at 50 °C and weighed. Subsamples were then weighed, ashed at 550 °C and reweighed to obtain AFDM.

Calculation of indices

Taxa used for calculation of indices were restricted to members of the orders Ephemeroptera, Plecoptera and Trichoptera (EPT). Monthly (1977), quarterly (1982), or bimonthly (1993) average abundances of EPT taxa were used to calculate: EPT taxa richness (total number of EPT taxa); % dominant taxon (most abundant taxon/ total abundance);% Baetis (*Baetis* abundance/ total abundance); and shredder-scraper ratio (shredder abundance/ scraper abundance).

A modified North Carolina Biotic Index (NCBI) was also calculated using the above insect orders. The NCBI is based on an extensive data set of benthic stream samples collected throughout North Carolina, and is designed to be specific to mountain, Piedmont or coastal ecoregions of the south-eastern United States (Lenat, 1993). The NCBI is calculated as:

$$\mathrm{NCBI} = \sum_{i=1}^{s} \frac{\mathrm{TV}}{}\, i\, \frac{N}{N_t}$$

Table 2 Annual averages for current velocity (Vel.) and substratum median phi (Mdϕ) in reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams during 1977–78, 1982–83 and 1993–94

		1977		1982		1993	
		Reference	Disturbed	Reference	Disturbed	Reference	Disturbed
Bedrock	Vel.	77.9	76.2	70.6	67.7	105.6	100.6
	Md ϕ	-8.0	-8.0			-8.0	-8.0
Riffle	Vel.	62.5	63.0	46.4	45.7	83.9	82.7
	Md ϕ	-6.5	-6.1			-4.8	4.9
Depositional	Vel.	31.2	36.1	14.5	29.7	21.7	30.5
	Md ϕ	-1.5	-1.4			0.0	0.0

Table 3 Annual average habitat-specific and habitat-weighted organic matter standing crop (g AFDM m^{-2}) in reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams. Groups within the same row that share the same letter are not significantly different by Tukey's multiple comparison technique ($P < 0.05$)

	Reference			Disturbed			Habitat-weighted	
Organic type	Bedrock	Riffle	Depositional	Bedrock	Riffle	Depositional	Reference	Disturbed
Moss	19.1[a]	0.0[b]	0.0[b]	93.3[c]	0.0[b]	0.0[b]	7.0[a]	15.7[b]
Leaves	0.3[a]	26.1[b]	65.5[b]	1.3[a]	42.2[b]	42.5[b]	28.2[a]	35.4”
Wood	0.1[a]	67.4[b]	133.P	2.8[c]	88.1[b]	181.7[b]	62.2[a]	107.6”
Misc. CPOM	5.5[a]	10.6[b]	51.9[c]	15.6[a,b]	12.7[a]	26.2[b]	20.8[a]	18.0[a]
FPOM	6.8[a]	9.0[a]	46.9[b]	32.0[a]	17.3[b]	77.5[c]	19.2[a]	41.5[b]
Total	31.8[a]	113.1[b]	298.0[c]	145.0[a,b]	160.3[a]	327.9[b]	137.4”	218.2[b]

where S is the number of taxa, TV’ is the tolerance value of the ith taxon, N^i is density of the ith taxon as abundance (numbers m-2), and N^t is total abundance of macroinvertebrates in the sample. Tolerance values range from 0 (highly intolerant taxa) to 10 (highly tolerant taxa).

Statistical analysis

For each study year, all data within a habitat or stream (for habitat-weighted data) were pooled across upper, middle and lower. stream reaches for analysis. Significant differences between habitat types, streams and study years for all measured values were determined using one-way ANOVA and Tukey's multiple comparison technique. All data failing normality tests were transformed using a log(x + 1) transformation. Transformed data still failing normality tests were compared using Kruskal–Wallis ANOVA on ranks and Dunn's multiple comparison technique. Statistical analyses were performed using SAS, SigmaStat and SysStat computer software.

Taxonomic and functional group relationships among the streams over the three study periods were examined using percentage similarity. A percentage similarity matrix (Brower & Zar, 1984) was constructed based on habitat-weighted abundance in reference and disturbed streams during all three study periods, and a dendrogram was generated using average linkage clustering (Anderburg, 1973).

Between-year comparisons were complicated by differences in sample collection and processing methods among the different studies. The 1977 and 1982 studies used a Surber sampler in the depositional habitat, whereas a coring device was used during the present study. The coring device increased recovery of macroinvertebrates and organic matter in the depositional habitats of both streams compared to the previous studies. The 1993 and the 1982 studies also used a sample splitter (Waters, 1969), which tended to increase recovery of small invertebrates compared to the 1977 study. This prevented direct comparison of macroinvertebrate abundance and organic matter standing crop across the three studies. Direct comparisons for macroinvertebrate abundance were only made between reference and disturbed streams within the same study, and between-year comparisons were limited to the percentage contribution of each functional group or organic matter type to the total. In addition, macroinvertebrate data from one of the two previous studies were limited to abundance of EPT taxa. Comparison of taxa and functional groups between years was therefore limited to EPT taxa only. Raw data for current velocity, substratum median phi and organic matter during the 1977 and 1982 studies were not available, precluding statistical analysis of these parameters across the three studies.

Results

Physical parameters and organic matter

Habitat current velocity and substratum particle size followed similar trends during all three study years (Table 2). Median phi values for riffle and depositional habitats during the 1993 study suggest that the present study sampled in riffle and depositional areas with slightly smaller substratum particle sizes than during the 1977 study.

During the present study, the disturbed stream had significantly higher habitat-weighted annual standing crop of moss, FPOM and total organic matter ($P < 0.05$) (Table 3). In contrast, habit&weighted annual standing crop of leaf detritus, wood and miscellaneous CPOM showed no significant difference between reference and disturbed streams during the present study Total organic matter standing crops were greatest in the depositional habitat of both streams followed by riffle and bedrock habitats (Table 3).

Habitat-weighted data demonstrated an overall slight increase in the percentage of leaf detritus in the disturbed stream from 1982 to 1993 (Fig. 2). Distribution of organic matter among the three habitats of the reference and disturbed streams during the present study was similar to that found during the 1982 study (Fig. 2). Between-year changes in the disturbed stream were greatest in the depositional habitat, where wood and leaf detritus increased and FPOM decreased (Fig. 2).

Macroinvertebrate abundance

Total habitat-weighted macroinvertebrate abundance was greater in the disturbed stream than in the reference stream ($P < 0.05$) (Table 4a). Collectors, predators and shredders were more abundant in the disturbed stream ($P < 0.05$), however, abundance of filterers and scrapers was not different between streams. Collectors were three times more abundant in the disturbed stream and accounted for 83% of habitat-weighted abundance (Table 4a and Appendix).

Total macroinvertebrate abundance was significantly different among habitat types in both reference and control streams during the present study (Table 4a). The reference stream had greatest macroinvertebrate abundance in the depositional > bedrock > riffle habitats, and the disturbed stream had greatest abundance in the bedrock > depositional > riffle habitats.

Macroinvertebrate community comparisons among study years were limited to abundance of EPT taxa. Functional group abundance in the disturbed stream showed the same trend across the previous 16 years in all habitats (Fig. 3). Shredder abundance, mainly *Tallaperla maria*, increased in the disturbed stream, while scraper abundance, predominantly *Baetis*, decreased. Functional group distribution in the reference stream during all three studies was very similar for the bedrock and riffle habitats and habitat-weighted data. The depositional habitat did show an increase in the percentage of shredders over time, but not as dramatic as that seen in the disturbed stream (Fig. 3). Percent similarity for functional groups and individual taxa indicated that the EPT taxa in the disturbed stream during the current study were distinctly different from that in the disturbed stream during the 1977-78 and 1982-83 studies (Fig. 4).

Macroinvertebrate biomass and production

Total habitat-weighted biomass was about twofold greater in the disturbed stream than in the reference ($P < 0.05$) (Table 4b). Biomass of collectors and shredders in the disturbed stream exceeded that of the reference ($P < 0.05$), while biomass for filterers, predators and scrapers was not significantly different between streams. The shredder functional group biomass showed the greatest difference between streams. Shredders represented 40% of community biomass in the disturbed stream and only 19% in the reference stream. The contribution of the remaining groups was similar between reference and disturbed streams.

Total habitat-weighted production in the disturbed stream exceeded that of the reference stream by 1.9 X (Table 4c). Distribution of production among the functional groups also differed between streams. Filterers were the only functional group with higher production in the reference stream (31% of total) than the disturbed

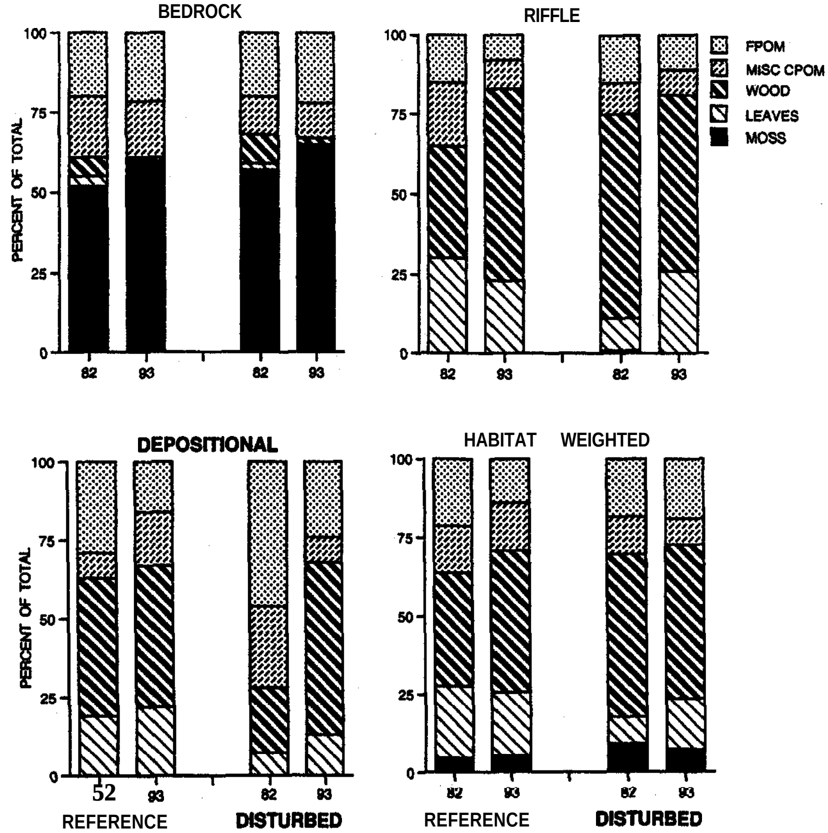


Fig. 2 Relative distribution of habitat-specific and habitat-weighted organic matter standing crops in reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams during 1982-83 and 1993-94.

stream where they constituted < 14% of total production. Shredders (35% of total) dominated production in the disturbed stream, whereas shredders represented < 18% of the total production in the reference stream (Table 4c).

Secondary production, as well as abundance and biomass of some groups (Table 4a–c), also differed among habitats. Secondary production of each functional group was greater in each habitat of the disturbed stream (Table 4c), thus higher habitat-weighted production of filterers in the reference stream is primarily a consequence of more than two times greater bedrock habitat availability (Table 1) in the reference stream. Total habitat-specific macroinvertebrate production was greatest in the bedrock habitat of both streams followed by depositional and riffle habitats (Table 4c). Macroinvertebrate biomass and production estimates were not available for the 1977 or 1982 studies.

Biotic indices

Total EPT taxon richness in the disturbed stream was slightly higher during the 1977 and 1982 study, and was equal to that of the reference stream during the present study (Table 5). However, taxon richness using habitat-specific abundance exhibited different trends in each habitat. Bedrock habitat taxon richness was significantly greater in the disturbed stream during the 1977 study, but showed no significant difference between streams during either the 1982 or 1993 studies. Taxon richness in the riffle and depositional habitats did not differ significantly between streams within individual study years, although some differences were detected among years, with the greatest richness in 1982 followed by 1977 and 1993 (Table 5).

The percentage dominant taxon index showed no significant difference for any habitat or stream during any study year ($P > 0.05$). Percent dominant taxon for the bedrock habitat was slightly higher, but not significant, in the reference stream during each study year. The disturbed stream exhibited higher percentage dominant taxon for riffle, depositional and habitat-weighted data during the 1977 and 1993 studies.

The percentage *Baetis* index for habitat-weighted data was significantly higher during the 1977 study but was not significantly different from the reference

Table 4 Habitat-specific and habitat-weighted annual average abundance (a, number m-2), biomass (b, mg AFDM m-2) and production (c, g AFDM m^{-2} yr^{-1}) for macroinvertebrate functional groups in reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams. Groups within the same row that share the same letter are not significantly different by Tukey's multiple comparison technique *(P < 0.05)*

	Reference			Disturbed			Habitat-weighted	
Organic type	Bedrock	Riffle	Depositional	Bedrock	Riffle	Reference	Disturbed	Depositional
(a) Abundance								
Shredders	429^{a}	834^{a}	1068^{a}	1958'	1557^{a}	2100"	754^{a}	1821^{b}
Collectors	9907^{a}	4882^{a}	18595^{b}	118494^{a}	10684^{b}	24757^{b}	10706'	33876^{b}
Filterers	1240^{a}	320^{a}	87^{b}	4288^{a}	399^{a}	198^{b}	588^{a}	980^{a}
Predators	1855"	1326^{a}	2187^{a}	13649^{a}	1160^{b}	1965^{b}	1770^{a}	3549^{b}
Scrapers	431'	518^{a,b}	226^{b}	1574^{a}	679^{a,b}	447^{b}	401^{a}	746'
Total	13862^{a,b}	7879^{a}	22163^{b}	139963^{a}	14479^{b}	29468^{b}	14220^{a}	40971^{b}
(b) Biomass								
Shredders	45^{a}	133^{a}	251"	307^{a}	610'	665'	135^{a}	579^{b}
Collectors	199^{a}	83^{a}	119"	758^{a}	98^{b}	186^{b}	136'	240^{b}
Filterers	453^{a}	82^{b}	22^{c}	628^{a}	96^{b}	50^{c}	200^{a}	169^{a}
Predators	56^{a}	116'	474^{b}	391^{a}	221^{a}	553^{b}	198^{a}	369"
Scrapers	46^{a}	91^{b}	15^{a}	65^{a,b}	93^{a,b}	47^{a}	53'	72'
Total	800^{a}	505^{a}	881'	2148^{a}	1117^{b}	1501^{b}	722^{a}	1429^{b}
(c) Production								
Shredders	360	869	1138	1852	2745	3621	761	2911
Collectors	1838	675	1097	7941	824	1485	1222	2258
Filterers	3190	450	109	4755	521	262	1351	1139
Predators	333	519	1321	2088	859	1813	684	1410
Scrapers	356	543	96	776	762	288	345	593
Total	6076	3056	3761	17412	5710	7468	4363	8311

stream in 1982 or 1993 (Table 6). Habitat-specific data also demonstrated a significantly higher percentage *Baetis* index in all habitats during the 1977 study, but showed no difference in any habitat during the 1982 or 1993 studies.

The only significant difference between the reference and disturbed streams for the shredder/scraper ratio was during the 1977 study, similar to the percentage *Baetis* index (Table 7). The shredder/scraper ratio did exhibit an increase in all habitats of the disturbed stream during each subsequent study, consistent with a decrease in scrapers and an increase in shredders.

The North Carolina Biotic Index, calculated using habitat-weighted abundance, was significantly different between reference and disturbed streams during the 1977 study *(P <* 0.05) but was not different between streams during the 1982 or 1993 studies (Table 8). The NCBI for the reference stream during the three studies was very similar and showed no significant difference among years. The NCBI for the disturbed stream showed more variation- among years and declined (higher biotic integrity) during each successive study following the clear-cutting; the only significant difference, however, was between the 1977 and 1993 studies (Table 8).

Annual average NCBI based on habitat-specific abundance suggested a difference in the relative recovery rates of the three habitats (Table 7 and Fig. 5). NCBI for the 1977 study revealed significant differences between streams for all three habitats. The bedrock habitat was not different between streams during the 1982 study, while riffle and depositional habitats were still different between streams. There were no significant differences between streams for any habitat during the 1993 study.

Discussion

Effects of succession *on the macroinvertebrate community*

Logging may affect stream communities by changing the stream from an allochthonous energy base to an autochthonous energy base. The two distinct trends in macroinvertebrate abundance in the disturbed stream over the previous 16 years, a decrease in scrapers and

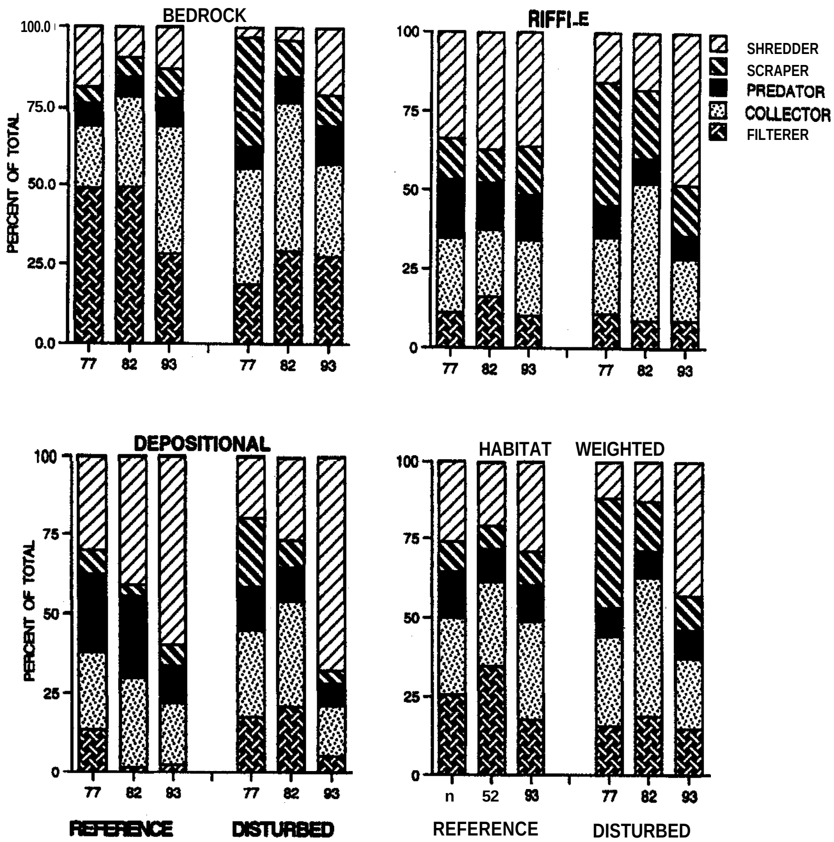


Fig. 3 Relative contribution of functional groups of Ephemeroptera, Plecoptera and Trichoptera to habitat-specific and habitat-weighted abundance in reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams during 1977-78, 1982-83 and 1993-94.

Table 5 Annual average habitat-specific and total EPT taxon richness in reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams during 1977–78, 1982–83 and 1993-94. Averages within the same row that share the same letter are not significantly different by ANOVA (P c 0.05)

	1977		1982		1993	
	Reference	Disturbed	Reference	Disturbed	Reference	Disturbed
Bedrock	11.0^{a}	13.2^{b}	14.5^{b,c}	17.0^{c}	11.9^{a,b}	12.6^{b}
Riffle	18.7^{a,b}	19.4^{a,b}	21.5^{a}	22.5^{a}	18.6^{b}	17.1^{b}
Depositional	13.5^{a}	14.2^{a}	12.0^{a}	17.0^{a}	13.1’	14.9^{a}
Total taxa	28.0	32.0	27.0	32.0	27.0	27.0

an increase in shredders, may be explained based on changing energy resources. Prior to clear-cutting in 1976, allochthonous inputs supplied > 99% of the organic matter entering the disturbed stream. Immediately following clear-cutting, however, autochthonous inputs exceeded allochthonous inputs (Webster *et al.*, 1983). During the 1977 study, primary production in the disturbed steam was 8.9 mg C m^{-2} h^{-1}, about thirty times greater than in the reference, however, primary production dropped to 0.9 mg C m^{-2} h^{-1} within 2 years because of canopy regrowth (Webster *et al.*, 1983).

The response by scrapers has mirrored the sharp increase and successive decline in primary productivity over the previous 16 years. Scrapers accounted for 40% of habitat-weighted EPT abundance during the 1977 study but only 16% and 10.7% during the 1982 and 1993 studies, respectively (Fig. 3). Wallace & Gurtz (1986) reported sharp increases in abundance and production of *Baefis,* a scraper, coinciding with the increased primary production immediately following clear-cutting of the catchment. Production of *Baetis in* the disturbed stream during the present study was only 24% of that found by Wallace & Gurtz (1986) in the year following clear-cutting. In contrast, production of

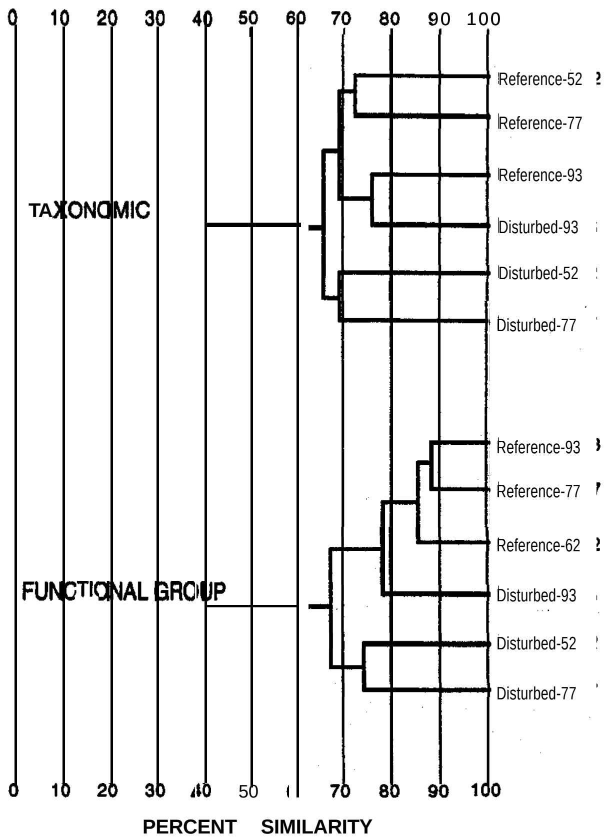


Fig. 4 Percent similarities between reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams based on habitat-weighted abundance of Ephemeroptera, Plecoptera and Trichoptera during 1977–78, 1982–83 and 1993-94.

Baetis in the reference stream during the present study was very similar to that found earlier by Wallace & Gurtz (1986). Diatoms were an important food source for *Baetis* in the disturbed stream during the year following logging (Wallace & Gurtz, 1986), and reduced production of *Baetis* thereafter was probably because of decreased primary production following canopy regrowth.

The second trend after clear-cutting, a marked drop and gradual increase in shredder abundance, is in response to the return of allochthonous inputs. Leaf detritus is the main source of energy in forested headwater streams. As the forest canopy has regrown the proportion of leaf detritus in the disturbed stream has increased from 9% of total standing crop in 1982 to 16% of total in 1993 (Fig. 2). The standing crop of leaf detritus in the main channel of the disturbed stream was lower than that in the reference during 1983-84 (Golladay, Webster & Benfield, 1989), as well as in the first-order tributaries of the disturbed stream during 1986-87 (Stout, Benfield & Webster, 1993). The standing crop of leaf detritus measured in the reference and disturbed streams during this study did not differ significantly (Table 3).

Although total leaf litter inputs into both streams were almost identical, litter inputs to the disturbed stream contained a larger proportion of early successional and herbaceous litter (J.R. Webster, personal communication). Stout *et al.* (1993) reported that the standing crop of leaf detritus from early successional tree species was 7.5 times higher in the first-order tributaries of the disturbed stream. The leaves of tree species that dominate early successional forests are more quickly conditioned and decompose more rapidly than those from trees dominating more mature forests (Webster & Benfield, 1986; Boring, Monk & Swank, 1988). Early successional leaves may represent a better food resource for shredders (Stout *et al.*, 1993) and demons&ate that forest succession may affect the quality, as well as, the quantity, of food resources for stream macroinvertebrates. Shredders accounted for only 9% and 13% of habitat-weighted EPT abundance during the 1977 and 1982 studies, respectively, while accounting for 43% of habitat-weighted EPT abundance during the present study (Fig. 3). The disturbed stream also supported higher shredder biomass and production during the present study, suggesting a higher quantity and/or quality of food resources. Shredder biomass and production were 3.8 times higher in the disturbed stream, and shredders there contributed twice as much to community biomass and production (Table 3b & c). Stout et *al.* (1993) also found that first-order tributaries of the disturbed stream had higher shredder biomass and production than those of the reference. In the present study, *Tallaperla* production was 3.9 times greater in the disturbed stream and accounted for 50% of shredder production and 17% of total macroinvertebrate production in the disturbed stream, vs. 48% of shredder production and only 8.5% of total community production in the reference. This is in sharp contrast to the first year following clear-cutting, when there was a significant decline in abundance of *Tallaperla* in the disturbed stream compared to the reference (Gurtz & Wallace, 1984).

Higher biomass and production in the disturbed stream was not limited to the shredder functional group. All functional groups, with the exception of filterers, had higher biomass and production in the disturbed stream, although not all differences were

Table 6 Annual average percentage *Baetis* (*Buefis* abundance/total abundance) in reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams during 1977–78, 1982–83 and 1993-94. Averages within the same row that share the same letter are not significantly different by Kruskal–Wallis ANOVA on ranks (*P* < 0.05)

	1977		1982		1993	
	Reference	Disturbed	Reference	Disturbed	Reference	Disturbed
Bedrock	3.7^a	28.9^b	7.9^a	$10.3^{a,b}$	8.1^a	8.9^a
Riffle	3.1^a	35.3^b	4.1^a	$14.4^{a,b}$	5.3^a	$16.9^{a,b}$
Depositional	1.7^a	26.9^b	1.0^a	$5.8^{a,b}$	1.8^a	1.8^a
Habitat-weighted	3.0”	32.5^b	$5.1^{a,b}$	$11.8^{a,b}$	6.0^a	9.5^a

Table 7 Annual average shredder-scraper indices in reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams during 1977–78, 1982–83 and 1993-94. Averages within the same row that share the same letter are not significantly different by Kruskal-Wallis ANOVA on ranks (P < 0.05)

	1977		1982		1993	
	Reference	Disturbed	Reference	Disturbed	Reference	Disturbed
Bedrock	5.06^a	0.18^b	1.81a	0.60a	3.34^a	5.10’
Riffle	2.87^a	0.34^b	4.73^a	0.90^a	2.35^a	8.38^a
Depositional	5.75”	0.49^b	28.83’	3.16’	7.51^a	20.03’
Habitat-weighted	3.19’	0.33^b	3.27^a	0.81^a	2.68”	8.00’

Table 8 Annual average modiied NCBI scores based on habitat-specific and habitat-weighted macroinvertebrate abundance in reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams during 1977–78, 1982–83 and 1993-94. Averages within the same row that share the same letter are not significantly different by ANOVA (*P* c 0.05)

	1977		1982		1993	
	Reference	Disturbed	Reference	Disturbed	Reference	Disturbed
Bedrock	1.38^a	2.75^b	$1.81^{a,b}$	$2.06^{a,b}$	1.71^a	1.80’
Riffle	1.60”	2.96^b	1.72^a	2.21^b	1.74^a	2.18”
Depositional	1.57^a	2.68^b	1.48^a	1.85^b	1.69’	1.69^a
Habitat-weighted	1.48^a	2.88^b	1.71^a	$2.09^{a,b}$	1.68’	1.90^a

significant. Higher habitat-weighted filterer biomass and production in the reference stream was a result of much greater availability of bedrock substratum in this stream (Table 1).

Even with regrowth of the forest canopy and decreased primary productivity, scraper production was still 1.7 times greater in the disturbed stream. Scraper biomass, however, was only 1.4 times greater than that of the reference and did not differ significantly between streams, indicating higher overall scraper growth (i.e. production/biomass [P/B]) in the disturbed stream. The higher scraper P/B in the disturbed stream was due primarily to production of *Baefis, which* was 3.4 times that of the reference stream.

A similar quantity of leaf litter inputs, albeit of higher quality, may not adequately explain the much greater secondary production of all functional groups in the disturbed stream. In a nearby Coweeta stream, leaflitter exclusion resulted in decreased abundance and biomass of shredders, collectors and predators (Wallace et *al.*, 1997). However, compared to a nearby reference stream, litter exclusion increased microbial activity on woody debris (Tank & Webster, 1998) and inorganic substrata (Hall & Meyer, 1998) and was accompanied by a slight increase in algal growth without loss of forest canopy (J. L. Meyer, S. L. Eggert & J. B. Wallace, unpublished observations). Furthermore, based on chironomid growth rates, the quality of FPOM has been maintained compared to a reference stream (M. Golladay, J. L. Meyer & J. B. Wallace, unpublished data). Therefore, in the absence of leaves, other substrata in these nutrient-poor streams now appear to be important nutrient sinks

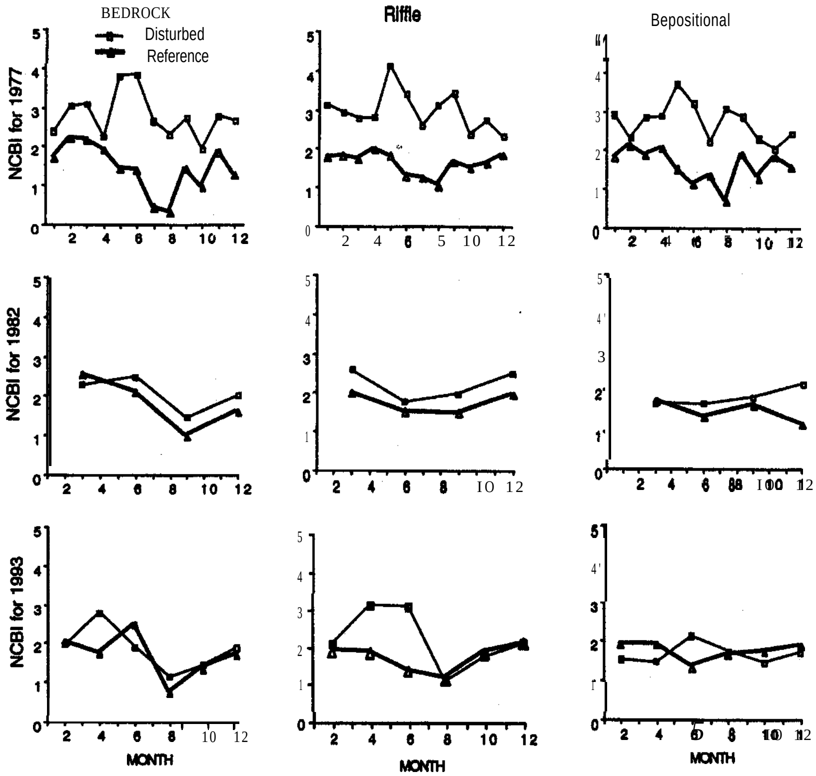


Fig. 5 Modified North Carolina Biotic Index (NCBI) values for benthic invertebrates in reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams for bedrock, riffle and depositional habitats during the 1977-78 (top row), 1982-83 (middle row) and 1993-94 (bottom row).

Table 9 Summary of indices in reference and disturbed streams during 1977–78, 1982–83 and 1993-94. Numbers represent ratio of disturbed stream to reference stream (index value of disturbed/index value of reference), not actual index values. Asterisk (*) indicates a significant difference (P<0.05) between index values in reference and disturbed streams.

	Bedrock			Riffle			Depositional			Habitat-weighted		
Index	77	82	93	77	82	93	77	82	93	77	82	93
Total abundance	–	–	10.10	–	–	1.84*	–	–	1.33	–	–	2.88*
Total biomass	–	–	2.67	–	–	2.21*	–	–	1.70*	–	–	1.98*
Total production	–	–	2.87	–	–	1.87	–	–	1.99	–	–	1.90
EPT abundance*	5.28*	2.74*	2.65*	1.79*	1.92	1.39	1.32	2.54"	1.73	2.99*	1.83*	1.59*
EPT taxon richness	1.20*	1.17	1.06	1.04	1.05	0.92	1.05	1.40	1.14	1.14	1.18	1.00
% Dominant taxon	0.80	0.86	0.87	1.59	0.86	1.27	1.12	0.72	1.27	1.14	0.74	1.15
% *Baetis*	7.81"	1.30	1.10	11.39*	3.51	3.19	15.8*	5.80	1.00	10.8*	2.31	1.58
Shredder-scraper	0.03*	0.33	1.53	0.12*	0.19	3.59	0.09*	0.11	2.67	0.10"	0.25	2.98
NCBI	1.99*	1.14	1.05	1.85*	1.28*	1.25	1.71*	1.25*	1.00	1.95*	1.22	1.13

*Significant difference based on t-test between disturbed and reference streams within the same year only.

which enhanced other food resources in the exclusion stream compared to a nearby reference stream. Another study of a southern Appalachian catchment has shown that the uptake of elements in streams is strongly affected by standing stock of benthic organic matter, such as leaves (Mulholland *et al., 1985).*

Annual average standing crop of leaf detritus did not differ significantly between reference and disturbed streams during the present study; however, there was a difference in seasonal standing crops. The standing crop of leaf litter in the disturbed stream exceeded that of the reference during early and late autumn. During subsequent periods, however, leaf standing crops in the reference stream exceeded those in the disturbed stream (1.5, 2.6, 4.1, 5.3 times higher in January, March, May and July, respectively; J.R. Webster, unpublished data), indicating faster processing of leaf detritus in the disturbed stream. Rapid processing of litter in the disturbed stream was also noted in 1986 (Benfield *et al.*, 1991) as well as in 1991, when decomposition of chestnut oak was about 2.6 times faster in the disturbed stream (E.F. Benfield & J.J. Hutchens, personal communication).

The rapid processing of leaf litter in the disturbed stream would reduce leaf surface area available for microbial colonization, thereby enhancing nutrient availability, algae and microbes associated with other detritus and inorganic substrata. This may allow increased production by microbial populations as well as stream algae in late winter and early spring before the leaf canopy develops. The authors of the present study suggest this increased nutrient availability may have also contributed to the higher secondary production of macroinvertebrates found in the disturbed stream.

As the forest around the disturbed stream continues to mature, the quantity, quality and timing of leaf litter inputs into the disturbed stream should approach that of the reference. Production of all functional groups will probably decrease with time due to the replacement of herbaceous leaf material with more resistant species, such as oak and hickory. Furthermore, the large surface area available for microbial colonization of more resistant leaf species may decrease nutrient availability to microbes and algae on non-leaf substrata, including FPOM, woody debris and mineral particles. Thus, the overall quality of food available to invertebrates may decrease with forest succession. Recovery is further complicated by the gradual reduction of woody debris sufficiently large to form stable dams. As inputs of wood will have been reduced for many decades during forest succession, overall stream retentiveness will be reduced (e.g. Hedin, Mayer & Likens, 1988; Webster et al., 1992). Increased inputs of woody debris as the forest matures should mark the last stage of stream recovery. Thus, the full recovery of stream biota depends upon more than a simple recovery in the quantity of leaf litter inputs.

Biotic indices and stream recovery

Disturbance may be considered as movement of the community away from a nominal value or behaviour (Yount & Niemi, 1990), and recovery as directional movement towards some state resembling the predisturbance state. The choice of indices, sampling methods, sampling locations and reference streams may all affect the ability to determine the level of recovery (Niemi, Detenbeck & Perry, 1993). The most de&-able indices should show a definitive trend starting with a significant difference between reference and disturbed streams initially, to no difference at some later point. In addition, there should be relatively little variation of the index in the reference stream over the same period.

Generally, taxonomic diversity decreases with disturbance and increases with recovery, however, immediately after clear-cutting, EPT taxa increased in the disturbed stream compared with the reference. Increased insolation, primary productivity (see above) and altered thermal regimes (Swift, 1983) occurred in the disturbed stream, which made it more similar to downstream reaches. Several taxa normally confined to larger downstream reaches, e.g. *Pteronarcys* (Plecoptera) and' *Hydropsyche* (Trichoptera), colonized the disturbed stream without significant loss of headwater EPT taxa. Habitat-weighted EPT indices of taxon richness and abundance show subsequent declines in the disturbed stream with forest regrowth. These EPT indices suggest lower biotic integrity as succession, i.e. recovery, proceeded. Clear-cutting caused shifts in the predominance of certain taxa in the disturbed stream, but few taxa were lost from the community. Taxon richness may thus be more appropriate for detecting disturbances such as a organic pollution and toxic chemicals, which result in the loss of sensitive species, rather than disturbances that only cause shifts in relative abundance. Likewise, the percentage dominant taxon for the disturbed stream was of little value because *this* shifted from *Baetis in* 1977 to *Serratella* in 1982, and *Leuctra in 1993 with little* difference in contribution to overall percentages among years.

Among the indices considered in the present study, the percentage *Baetis* index, shredder-scraper index, and the NCBI, show the greatest ability to detect differences between the clear-cut and reference streams through time (Table 9). The percentage *Baetis* index indicated differences between reference and disturbed streams during the initial study in all habitats followed by decreases in all habitats during subsequent years. Others have also noted a large increase *in Baetis in* streams draining deforested catchments (Newbold *et al.*, 1980; Noel et *al.*, 1986; Anderson, 1992; Reed, Campbell&Bailey, 1994). There was a trend of decreasing percentage *Baetis* index in the disturbed stream duringthe 1982 and 1993 studies, while the reference stream was relatively constant. There was no significant difference between reference and disturbed streams in 1982 or 1993. The percentage *Baefis* index measured one of the major trends identified during this study that of decreasing scrapers in response to a return to an allochthonous energy base.

The shredder-scraper index also showed a significant difference between reference and disturbed streams only during 1977. The index was extremely low in the disturbed stream during 1977 and 1982 indicating lower shredder and higher scraper abundance. However, during 1993 the shredder-scraper index was very high, indicating a community dominated by shredders with relatively few scrapers. The reference stream shredder-scraper index was relatively constant over the three study periods, although the depositional habitat did show some variation. This index combines the two distinct trends in macroinvertebrate abundance identified during this study, increasing shredders and decreasing scrapers, and indicates differences in the functional structure of the reference and disturbed streams.

The relative rate of recovery also differed among habitats. Bedrock, the most stable habitat, recovered more quickly than riffle and depositional areas. Moss-covered bedrock at Coweeta has also been shown to display larger proportional changes than other habitats upon exposure to toxicants, although it also recovered more quickly (Wallace, Grubaugh & Whiles, 1996). Riffle and depositional habitats may be more sensitive indicators of long-term recovery, suggesting that sampling regimes should incorporate multiple habitats whenever possible.

The results of the present study indicate that biotic indices vary with the nature of the disturbance, i.e. pulse vs. press (sensu Bender *et al.*, 1984), demonstrating the pitfalls of relying solely on one index for all disturbances (see -also Karr, 1991); for example, insecticidal manipulation of a nearby Coweeta stream resulted in similar trends for both EPT taxon richness and NCBI (Wallace *et al., 1996).* The NCBI incorporates both tolerance and relative abundance of taxa, and appears to be more sensitive for measuring subtle changes following logging. Unlike taxon richness and percentage dominant taxon, annual average NCBI in the disturbed stream showed gradual decline through time. In contrast, the reference stream remained virtually unchanged.

Secondary production may be one of the most sensitive indicators of the status of stream recovery because logging can cause major changes in the energy base, nutrient dynamics, light levels and temperature of streams. In New England, abundance of stream macroinvertebrates in 2- and 3-year-old clearcuts was two to four times greater than streams draining uncut reference catchments (Noel *et al., 1986).* Noel *et al.* attributed increased abundance primarily to higher periphyton and stream temperatures in streams draining logged catchments. Such shifts in the food base may be accompanied by large increases in scraper secondary production (e.g. Wallace & Gurtz, 1986). Because production estimates energy flow through the system and takes into account differences in turnover rates among organisms (Benke *et al.*, 1984), an index based on the scraper/shredder ratio of production through time would undoubtedly be more valuable for clear-cutting than one based only on abundance. However, total secondary production may increase following clear-cutting from potentially enhanced food quality Higher productivity should not necessarily be equated with improved biological conditions. Enhanced nutrient levels may also increase secondary productivity (Krueger & Waters, 1983). Results of the present study also suggest that increases in total secondary productivity may be much more prolonged than the relatively short-term (5-year) increase in the EPT index noted above for the disturbed stream. In contrast, total secondary production may be more appropriate for detecting disturbances such as toxic chemicals (Lugthart & Wallace, 1992; Wallace *et al.*, 1996) and sedimentation (Waters, 1984, 1995). As pointed out elsewhere (Karr, 1991), expense and time involved with data analyses are important considerations in biomonitoring programmes. Although secondary production would be a desirable method of assessing long-term similarity in ecosystem processes such as energy flow between disturbed and reference streams, production measurements may not be feasible as a widely used index because of the time and effort necessary for measurement.

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Appendix

Habitat-specific macroinvertebrate annual average **abundance (A; no. m^{-2}), biomass (B; mg AFDM m^{-2}) and production (P; mg AFDM m^{-2} yr^{-1})** for **bedrock,** riffle and depositional habitats **in the reference (REF, Hugh White Creek) and disturbed (DIST, Big Hurricane Branch)** streams during February **1993–February** 1994. Annual **means are based on $n = 21$ for each habitat.**

Taxa	Order	CPI	Stream	Bedrock A	Bedrock B	Bedrock P	Riffle A	Riffle B	Riffle P	Depositional A	Depositional B	Depositional P
Scrapers												
Baetis	E	120	REF	194	5	125	108	3	78	54	1	24
			DIST	818	16	531	353	15	340	44	2	48
Epeorus	E	340	REF	28	30	182	169	54	324	10	2	10
			DIST	6	17	102	76	44	266	23	7	41
Stenonema	E	340	REF	0	0	0	25	7	35	20	5	23
			DIST	0	0	0	33	19	95	19	23	116
Ectopria	C	365	REF	13	4	10	35	20	76	2	3	13
			DIST	0	0	0	7	4	16	7	2	10
Optioservus (larva)	C	365	REF	91	5	25	119	5	23	107	5	24
			DIST	467	17	79	157	7	29	307	12	62
Promoresia (larva)	C	365	REF	174	12	52	2	< 1	1	0	0	0
			DIST	0	0	0	0	0	0	2	0	0
Neophylax	T	213	REF	85	1	14	44	1	7	29	< 1	3
			DIST	76	1	11	34	2	15	33	1	11
Others*			REF	21	1	0	18	1	< 1	2	< 1	0
			DIST	33	3	0	16	1	1	14		0
Scraper sum			REF	431	46	356	518	91	543	226	15	96
			DIST	1574	65	776	679	93	762	447	47	288
Shredders												
Leuctra	P	340	REF	59	1	9	254	8	53	692	14	93
			DIST	835	20	152	623	11	87	1226	23	182
Tallaperla	P	540	REF	249	26	244	553	75	556	264	105	297
			DIST	952	216	1459	845	401	1634	566	214	1174
Pteronarcys	P	548	REF	0	0	0	1	< 1	Cl	0	0	0
			DIST	0	0	0	1	30	76	0	0	0
Pycnopsyche	T	275	REF	2	1	9	1	< 1	2	6	40	325
			DIST	4	5	49	30	14	109	74	94	637
Fattigia	T	664	REF	2	< 1	1	0	0	0	23	26	60
			DIST	0	0	0	6	2	4	20	56	128
Micrasema (1/2)†	T	229	REF	103	16	96	10	1	3	1	Cl	< 1
			DIST	28	6	38	0	0	0	2	Cl	2
Tipula	D	310	REF	0	0	0	2	45	249	1	52	301
			DIST	13	12	63	36	149	818	27	236	1298
Molophilus	D	365	REF	2	0	< 1	1	< 1	1	54	11	48
			DIST	6	3	12	10	2	7	93	30	134
Others‡			REF	12	< 1	1	13	3	4	29	3	15
			DIST	121	45	80	8	2	10	92	13	65
Shredder sum			REF	429	45	360	834	133	869	1068	251	1138
			DIST	1958	307	1852	1557	610	2745	2100	665	3621
Gatherers												
Serratella	E	330	REF	1091	130	1073	291	22	212	119	12	104
			DIST	2077	325	2100	321	34	306	102	13	89
Paraleptophlebia	E	340	REF	15	1	6	126	12	68	79	8	45
			DIST	87	7	44	42	4	22	107	8	50
Ameletus	E	330	REF	0	0	0	12	7	36	5	1	7
			DIST	0	0	0	0	0	0	0	0	0
Amphinemura	P	300	REF	141	2	14	74	3	19	112	5	27
			DIST	401	17	103	184	8	52	80	4	15

Appendix Cont.

Taxa	Order	CPI	Stream	Bedrock A	Bedrock B	Bedrock P	Riffle A	Riffle B	Riffle P	Depositional A	Depositional B	Depositional P
Micrasema (1/2)†	T	229	REF	103	16	96	10	1	3	1	<1	<1
			DIST	28	6	38	0	0	0	2	<1	2
Lype	T	332	REF	0	0	0	27	1	9	13	1	3
			DIST	2	C l	1	64	2	12	175	27	144
Chironomidae	D		REF	7292	34	541	2276	13	194	9554	46	622
			DIST	78048	308	5120	4715	26	273	11082	56	681
Antocha	D	260	REF	176	11	80	15	1	4	18	<1	2
			DIST	78	6	34	4	C l	1	0	0	0
Oligochaeta			REF	337	3	17	804	19	97	2020	36	182
			DIST	27932	76	380	1565	14	72	3000	60	300
Copepoda			REF	133	<1	2.3	690	1	12	3990	4	72
			DIST	4664	5	84	2997	3	54	8104	8	146
Others§			REF	619	2	8	558	4	20	2685	6	34
			DIST	5177	7	36	793	6	33	2105	10	57
Gatherer sum			REF	9907	199	1838	4882	83	675	18595	119	1097
			DIST	118494	758	7941	10684	98	824	24757	186	1485
Filterers												
Parapsyche	T	332	REF	911	435	3060	54	44	224	4	11	61
			DIST	1621	535	4062	76	46	232	42	11	58
Diplectrona	T	332	REF	36	2	8	91	28	144	23	9	25
			DIST	660	63	285	140	40	208	83	32	158
Dolophilodes	T	269	REF	2	C l	3	84	7	63	13	1	8
			DIST	171	11	93	61	6	46	28	2	15
Siuliidae	D	180	REF	281	16	118	73	1	12	46	1	15
			DIST	1833	19	315	100	3	32	43	1	9
Others+			REF	11	C l	<1	18	2	8	0	0	0
			DIST	2	C l	1	22	1	3	2	4	23
Filterer sum			REF	1240	453	3190	320	82	450	87	22	109
			DIST	4288	628	4755	399	96	521	198	50	262
Predators												
Cordulegaster	0	1140	REF	0	0	0	1	0	<1	12	278	473
			DIST	2	<1	<1	5	53	90	5	265	451
Lanthus	0	660	REF	2	C l	C l	4	13	28	6	77	192
			DIST	4	28	69	6	35	93	37	113	320
Sweltsa	P	630	REF	2	0	<1	69	9	42	42	10	47
			DIST	8	0	C l	33	5	25	64	4	29
Isoperla	P	300	REF	130	32	195	82	6	52	60	4	17
			DIST	708	90	630	87	11	79	48	3	37
Malirekus .	P	340	REF	11	1	4	27	25	138	11	Cl	<1
			DIST	2	1	3	18	40	222	4	2	10
Beloneuria	P	660	REF	2	<1	1	15	25	55	5	3	5
			DIST	4	1	2	6	21	33	7	2	3
Rhyacophila	T	340	REF	162	11	62	128	8	43	65	3	17
			DIST	355	53	302	81	11	60	36	5	31
Dicranota	D	310	REF	40	1	5	78	4	23	150	7	46
			DIST	510	16	126	70	3	17	89	2	13
Hexatoma	D	365	REF	23	1	8	22	4	26	108	25	168
			DIST	53	7	47	44	17	118	163	83	569
Rhabdomastix	D	365	REF	0	0	0	1	1	6	4	4	22
			DIST	0	0	0	1	<1	2	19	11	53
Palpomyia	D	365	REF	38	4	19	159	14	69	665	46	253
			DIST	368	50	207	a2	7	32	265	26	114

Appendix Cont.

Taxa	Order	CPI	Stream	Bedrock A	Bedrock B	Bedrock P	Riffle A	Riffle B	Riffle P	Depositional A	Depositional B	Depositional P
Pelecorynchidae	D	365	REF	0	0	0	0	0	0	2	4	19
			DIST	0	0	0	0	0	0	5	15	76
Empididae	D	340	REF	153	3	21	16	1	7	63	2	10
			DIST	571	30	122	41	2	13	86	2	19
Turbellaria			REF	37	< 1	2	127	3	17	335	7	34
			DIST	2782	93	467	361	14	71	446	13	66
Hydracarina			REF	1230	3	16	507	1	7	458	1	6
			DIST	8157	22	109	321	1	4	631	2	8
Others**			REF	25	< 1	2	93	1	6	202	3	13
			DIST	126	1	4	5	< 1	C l	62	5	24
Predator sum			REF	1855	56	333	1326	116	519	2187	474	1321
			DIST	13649	391	2088	1160	221	859	1965	553	1813

*Other scrapers: *Glossosoma* (T), *Oulimnius* (C, adult), *Optioservus* (C, adult), *Blephariceru* (D).
†*Micrasema* production was split between shredders and gatherers.
‡Other shredders: *Taeniopteryx* (P), *Anchytarsus* (C), *Lepidostoma* (T), *Psilotreta* (T), *Limonia* (D), *Leptotarsus* (D).
§Other gatherers: Collembola, *Ephemera* (E), *Drunella* (E), *Sciara* (D), Nymphomyiidae (D), Ostracoda, Ampbipoda, Isopoda.
¶Other filterers: Isonychiu (E), *Dixu* (D).
**Other predators: Tanypodinae (D), *Pediciu* (D), *N. Pediciu* (D), Dolichopodidae (D), Hirudinea.