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Long-term comparisons of insect abundances in disturbed and undisturbed Appalachian headwater streams

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With 4 figures and 4 tables in the text

Introduction

Surrounding forests exert important influences on headwater stream ecosystems. Logging of forested catchments may produce long-term changes in physical, chemical, and biological characteristics of streams. Logging is known to produce changes in community structure and abundances of invertebrate taxa (e.g. WOODALL & WALLACE 1972, NEWBOLD et al. 1980, MURPHY et al. 1981, ROUNICK & WINTERBOURN 1982, GURTZ & WALLACE 1984) and may influence secondary production of invertebrates (O'HOP et al. 1984, WALLACE & GURTZ 1986). Our objective was to examine 5-year substrate-specific changes in invertebrate abundances and trophic structure in streams draining clear-cut and forested (reference) catchments.

Study sites

The two second order study streams are located within the confines of the Coweeta Hydrologic Laboratory (U. S. Forest Service) in the southern Appalachian Mountains of North Carolina, U.S.A. Hugh White Creek (HWC) drains catchment #14, a 61.1 ha forested watershed with mixed hardwood vegetation and a dense understory of rhododendron which shades the stream bed. Big Hurricane Branch (BHB) drains a 59.5 ha catchment (#7) which was a mature hardwood forest prior to 1977. In 1977, the catchment was clear-cut, and all streamside vegetation (primarily rhododendron) was removed. Logging of the BHB catchment caused many changes within the stream, including: higher maximum temperatures and increased diel fluctuations (SWIFT 1983); small but detectable increases in some stream nutrients (WEBSTER et al. 1983); increased organic and inorganic seston (GURTZ et al. 1980); shifts in the concentration and pattern of dissolved organic carbon export (MEYER & TATE 1983); reduction of leaf litter inputs and increased primary production in BHB thereby shifting the energy base from allochthony to autochthony (WEBSTER et al. 1983); and, subsequent changes among aquatic insect taxa and functional groups as collector-gatherers and scrapers increased while the dominant shredder declined (GURTZ & WALLACE 1984, WALLACE & GURTZ 1986). With regrowth of the forest and shading of the stream, leaf-litter inputs increased whereas autochthonous production greatly decreased by 1981—82 (WEBSTER et al. 1983).

Methods

Benthic samples were collected quarterly during March 1982 through January 1983 from each of four substrate types, which were defined by the predominant inorganic substrate particle size: 1. bedrock (exposed bedrock surfaces, outcrops, and large boulder surfaces); 2. cobble (primarily 64—256 mm diameter substrates); 3. pebble (primarily 16—64 mm diameter substrates); and 4. sand (primarily substrates <2 mm in diameter). In BHB, four samples were collected from each substrate type on each date vs. three samples from each substrate on each date for HWC (except in January 1982 when n = 4 in bedrock and sand of HWC). Sampling and ancillary measurements for current velocity, substrate particle size, and detritus, followed that described by GURTZ & WALLACE (1984). For the 1982—1983 samples, all macroinvertebrates were removed following methods of WALLACE et al. (1986) who used a sample splitter as described by WATERS (1969). Compared to the original study (GURTZ & WALLACE 1984), the sample splitter enhanced recovery of small, early

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instars, of insects resulting in overall higher abundances in both streams for all substrate types compared to the 1977—1978 samples (see also WALLACE et al. 1986). Therefore, direct comparisons of abundances with those obtained in the 1977—1978 period were not made.

Between-year comparisons were limited to each taxon's percentage contribution to total abundances and functional feeding group composition of the four orders considered (Ephemeroptera, Odonata, Plecoptera, and Trichoptera) using proportional similarity (PS) indices (e.g. WHITTAKER 1975). Functional feeding group assignments used in the present study follow those of GURTZ & WALLACE (1984) and MERRITT & CUMMINS (1984) except for baetid mayflies and *Amphinemura wui* (Plecoptera: Nemouridae), which were reassigned to scrapers (WALLACE & GURTZ 1986) and collector-gatherers (WALLACE & GURTZ, unpublished), respectively.

Results

Substrate parameters

The average standing crop of moss on the bedrock substrate of BHB was over 5 × that of the bedrock of HWC (Fig. 1). Thick moss in BHB also facilitated the retention of other detrital material. Miscellaneous detritus was more abundant on the bedrock of BHB than that of HWC. Moss was rare on the smaller substrates of both streams. Standing crops of leaf detritus were higher in the cobble and sandy reaches of HWC. Estimates of wood included only small woody debris, as large logs and debris dams, which exceed several kg $\cdot$ m^{-2} AFDM, were not sampled. Fine detritus (< 1 mm) was undoubtedly underestimated as 250 μm mesh nets were used in sampling.

Invertebrates: Between-year comparisons 1977—78 vs. 1982—83

The reference stream, HWC, had a higher functional similarity than that of the treatment stream, BHB, between 1977—78 and 1982—83 (Table 1). However, there were differences among substrates (range = 0.966 to 0.729) as cobble and bedrock of HWC had the highest 5-yr functional similarity whereas pebble substrates had the lowest between

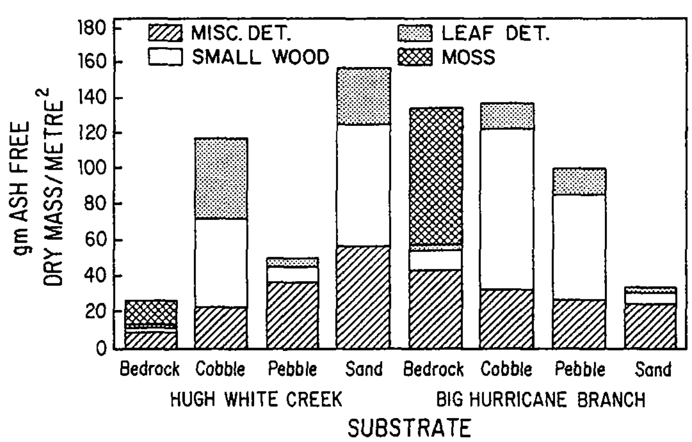

Fig. 1. Mean standing crop of benthic organic matter in benthic samples of 1982—83 by substrate and stream. Miscellaneous detritus includes fine particulate organic matter (< 1mm) and detritus (1—5 mm) of unknown origin. Mean current velocities (cm/s) at each site were as follows: HWC = 70.6 (Bedrock), 46.4 (Cobble), 31.7 (Pebble), and 14.5 (Sand); BHB = 67.7 (Bedrock), 45.7 (Cobble), 46 (Pebble), and 29.7 (Sand).

Table 1. Proportional similarity of functional feeding groups and abundances of individual taxa for various substrates in Hugh White Creek and Big Hurricane Branch (1977 – 1978 versus 1982 – 1983).

Substrate Type	Hugh White Creek		Big Hurricane Branch	
	Func./Grp.	Taxa	Func./Grp.	Taxa
Bedrock	0.950	0.865	0.788	0.674
Cobble	0.966	0.824	0.791	0.762
Pebble	0.775	0.717	0.729	0.625
Sand	0.854	0.708	0.866	0.724
Mean =	0.886	0.779	0.794	0.696

Table 2. Percent change in functional group abundances for various substrates in the two study streams between 1977 – 1978 and 1982 – 1983. A positive value indicates that the functional group increased by that percentage during the 5-yr period, whereas a negative (–) value indicates a decrease for that substrate type. (CG = collector-gatherers; SC = scrapers; SH = shredders; CF = collector-filterers; and PR = predators.)

Functional	Hugh White Creek					Big Hurricane Branch				
Group	Bedrock	Cobble	Pebble	Sand	Avg.	Bedrock	Cobble	Pebble	Sand	Avg.
CG	3.3	–2.7	–12.3	2.1	–2.4	13.2	21.0	19.2	3.8	14.3
SC	1.7	2.1	3.2	–1.2	1.5	–20.0	–14.9	–21.1	–10.7	–16.7
SH	–4.3	0.9	5.8	15.5	4.5	–1.3	–2.0	7.9	6.4	2.7
CF	–0.5	0.4	13.5	–11.7	0.4	6.7	–2.1	–3.0	3.3	1.2
PR	–1.0	–0.7	–10.2	–1.6	–3.4	1.3	–1.7	2.9	–2.7	–1.5
std. dev. =	2.9	1.8	11.0	9.8	3.1	12.5	13.0	15.0	6.9	11.1

year similarities in each stream. Overall changes in HWC are less pronounced than those of BHB among the 5-yr comparisons (Table 2). Although the larger substrates, bedrock and cobble, showed the smallest 5-yr changes in functional groups in HWC, sand fauna showed the smallest functional change in BHB. In BHB, large decreases in scrapers (—16.7 %), primarily baetids, and large increases in collector-gatherer taxa (+ 14.3 %), primarily *Ephemerella* spp. (*sensu lato*) and *Paraleptophlebia* sp., were the major 5-yr changes.

Five-year comparisons of abundances of individual taxa in HWC corresponded with substrate particle size with bedrock > cobble > pebble > sand (Table 1). In the disturbed stream, BHB, PS of abundances of taxa over the 5-yr period was highest for: cobble > sand > bedrock > pebble. In the pebble substrate of BHB, baetid mayfly populations showed large 5-yr decreases, whereas *Ephemerella* spp., *Paraleptophlebia* sp., and *Leuctra* spp. increased in abundance. Faunal changes on bedrock substrates of BHB were primarily attributable to declines in baetids and *Amphinemura*, coupled with large increases in *Ephemerella* spp.

Substrate and stream differences 1982—1983

Total abundance was significantly greater in BHB than HWC for all substrates (Table 3). Shredders were the only functional group that did not differ significantly for any substrate between streams. Within each stream abundances were greater for bedrock > cobble > pebble > sand of each stream. Collector-filterers in HWC and collector-gatherers and scrapers in both streams followed this pattern of substrate preference. In BHB, predators (bedrock > cobble > sand > pebble) and collector filterers (bedrock > pebble > sand > cobble) showed alternate patterns of significant substrate preference.

Table 3. Between stream differences (1982–1983) in functional feeding group abundances of Ephemeroptera, Odonata, Plecoptera, and Trichoptera by substrate (t-test, log transformed data, * = P<0.05, ** = P<0.01, *** = P<0.001, all significant differences are BHB>HWC). Total organisms (individuals per m^2) are listed below for each substrate type.

Functional Feeding Group	Substrate Bedrock	Cobble	Pepple	Sand
Collector-gatherers	***	**	**	*
Scrapers	**	**	***	***
Shredders				
Collector-filterers	*			***
Predators	**			
Total Organisms	***	*	***	*
Hugh White Creek no. per m^2 =	5,078	2,016	1,097	607
Big Hurricane Branch no. per m^2 =	14,148	3,274	2,610	1,563

Predators in HWC and shredders in both streams showed no significant substrate preferences (one-way ANOVA, P > 0.05).

Highest between stream functional similarity occurred in the two extreme substrate types (bedrock PS = 0.747 and sand PS = 0.716). For bedrock, collector-gatherers (30.9 % in HWC and 48.5 % in BHB) and collector-filterers (29.4 % in BHB and 47.3 % in HWC) contributed most to between stream similarity. In sand substrates, collector-gatherers (30.2 % in HWC and 34.6 % in BHB) and shredders (26.1 % in BHB and 42.6 % in HWC) were the primary contributors. The average PS for abundances of functional feeding groups among substrates was higher in BHB (0.792) than HWC (0.702).

In 1982—83, the average PS for abundances of individual taxa among substrates in the BHB (0.578) was also higher than HWC (0.463) (Table 4). The higher values for BHB are primarily attributable to two mayfly taxa each of which contributed substantially to the substrate-specific abundances in each substrate, *Ephemerella* spp. (9.2 to 40.1 %) and baetids (5.8 to 19.1 %). In HWC, only peltoperlids (6.8 to 28.3 %), comprised > 5 % abundance in each substrate.

Functional group composition (as a percentage of substrate-specific abundances for a given substrate) generally displayed similar patterns in the two streams within the same substrate. As a percentage of abundance within each substrate, scrapers were more abundant on intermediate size substrates (cobble and pebble), whereas shredders

Table 4. Proportional similarity for functional feeding groups and abundances of individual taxa between substrates within each stream in 1982–1983.

	Hugh White Creek Cobble	Pebble	Sand		Big Hurricane Branch Cobble	Pebble	Sand
			Functional Group				
Bedrock	0.640	0.646	0.515	Bedrock	0.789	0.778	0.745
Cobble		0.797	0.862	Cobble		0.893	0.721
Pepple			0.753	Pepple			0.823
Mean = 0.702				Mean = 0.792			
			Taxa				
Bedrock	0.449	0.361	0.252	Bedrock	0.519	0.570	0.488
Cobble		0.662	0.523	Cobble		0.751	0.611
Pepple			0.528	Pepple			0.528
Mean = 0.463				Mean = 0.578			

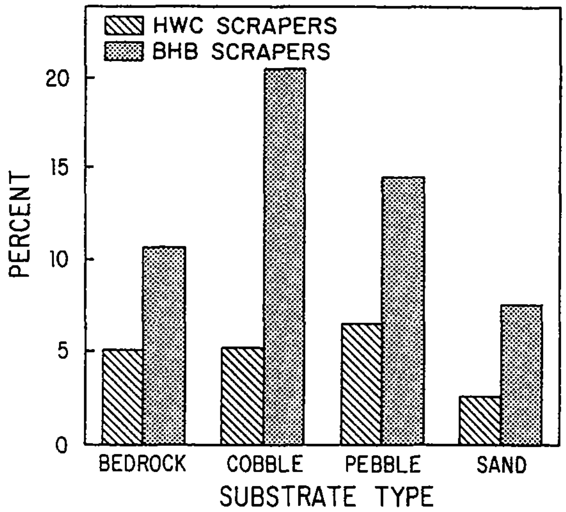

Fig. 2. Percent of total abundance composed of scrapers (2) for each substrate type in HWC and BHB in 1982—83.

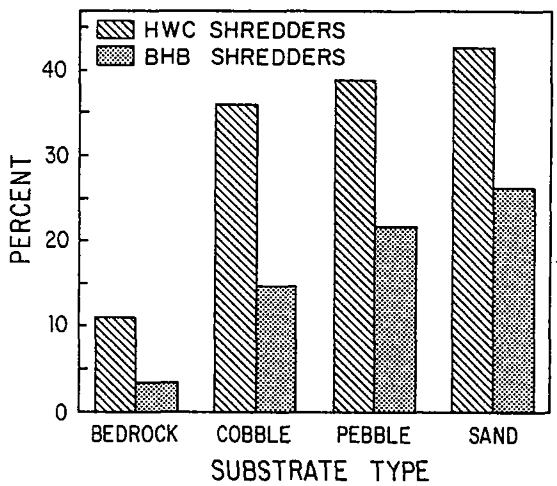

Fig. 3. Percent of total abundance composed of shredders for each substrate type in HWC and BHB in 1982—83.

followed: sand > pebble > cobble > bedrock in each stream, although the relative abundances differed greatly between streams (Figs. 2 and 3). Collector-gatherers were abundant and rather evenly distributed across all substrates in both streams. Predators constituted their largest proportional abundances in the sand and cobble substrates of each stream. Filterfeeders constituted their greatest proportional abundance on bedrock substrates of each stream (Fig. 4). Most collector-filterer food on the bedrock consists of invertebrate drift caught in catchnets by *Parapsyche* (Trichoptera: Hydropsychidae), hence, the low apparent abundances of predators on the Bedrock actually reflect a shift in

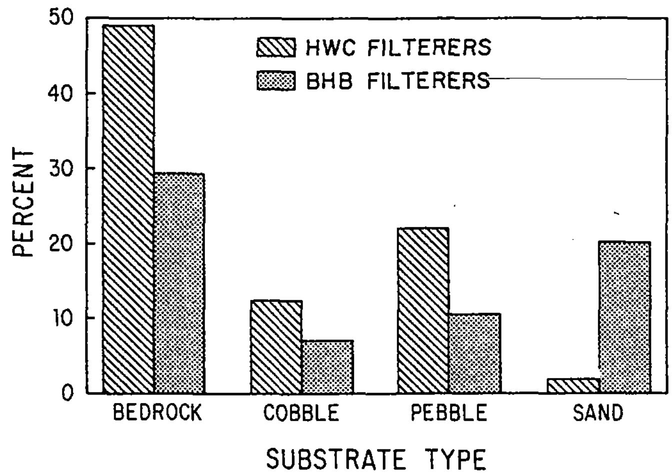

Fig. 4. Percent of total abundance composed of collectors-filterers for each substrate type in HWC and BHB in 1982—83.

the mode of food acquisition by predators in the high current velocity of the bedrock habitat.

Discussion

Despite the magnitude of the initial disturbance, the average proportional similarity for abundances of individual taxa among substrates within the same stream (PS = 0.520) was slightly less than the same substrates in different streams (PS = 0.575), which emphasizes the importance of considering substrate in the sampling regime. Local geomorphology has been shown to influence both abundances and secondary production of functional groups in another Coweeta stream through its influence on resource delivery (collector-filterers), retention (shredders) and substrate maintenance (scrapers) (Huryn & Wallace 1987). Coweeta streams have localized areas which may favor transport or deposition. For example bedrock substrates are typically shallow, high velocity, habitats, which favor entrainment of organic matter. In Coweeta streams, filterfeeders constitute a large portion (47 % in HWC and 29 % in BHB [Fig. 4]) of the fauna of bedrock substrates. For smaller substrates, there was an inverse relationship between filter-feeder abundances and detrital accumulations indicating their reliance on entrained rather than retained materials (cf. Figs. 1 und 4, HWC pebble and BHB sand). In BHB, thick moss on bedrock substrates also retained large amounts of organic matter (Fig. 1), which enhanced abundances of collector-gatherers (48 % in BHB vs 31 % in HWC). Sand substrates of HWC resembled pool habitats with lower current velocity, more small wood, leaf, and miscellaneous detritus than the sand habitat in BHB. Despite these between stream differences, shredders constituted their highest proportional abundances in smaller substrates of both streams, although relative abundances were higher in HWC (Fig. 3). In both streams, scrapers tend to reach their greatest proportional abundances on intermediate size substrates (cobble and pebble) which are free of moss.

The larger substrates, bedrock and cobble, of HWC had greater 5-year functional group and individual taxa similarities than the pebble or sand substrates (Table 1), which suggests that biological stability in HWC is closely linked to substrate stability. This pattern was not evident in BHB, the disturbed stream, as the sand substrates had the highest functional PS and 2nd-highest PS for taxa. In 1977—78, scrapers constituted a much smaller proportion of sand substrates than any other substrate in BHB, whereas relative abundances of collector-gatherers were high. Thus, compared with other substrates, sand changed proportionally less in BHB over the 5-yr period.

Only sand substrate in HWC had lower 5-yr PS for functional groups and individual taxa than the corresponding substrate in BHB; however, this result must be viewed with some caution. Ancillary measurements of detritus and mean current velocity at sample locations also differed most for the sand substrate of HWC between the 5-yr period and were most similar for bedrock and cobble. This phenomenon may be an artifact of substrate recognition by personnel as different individuals sampled during the two studies.

The most consistent and dramatic shift in either stream was the decline in scrapers from 30 to 13.3 % of the total population in BHB, primarily attributable to baetid mayflies. Despite this decline, the absolute abundances of baetids in BHB remained greater than that of HWC. Baetid abundances averaged 1356 m^{-2} across all substrates in BHB in the period of autumn 1977 through summer 1978 (Wallace & Gurtz 1986) versus 471 m^{-2} in 1982—83, whereas populations in HWC remained similar (mean, 1977—78 = 31 m^{-2}; 1982—83 = 39 m^{-2}). The decline in scrapers is consistent with subsiding autochthonous production. With regrowth of the forest and shading of the stream, leaf-litter inputs had recovered to 60 % of pre-logging levels by 1982—83 (Webster, per. comm.) whereas autochthonous production had decreased by 10 × compared to 1977—78 levels (Webster et al. 1983).

Despite the decline in scraper abundances and the shift in energy inputs, there was no evidence that the fauna of BHB was converging toward that of HWC either taxonomically or functionally by 1982—83. Between-stream PS of taxa abundances for bedrock, cobble, pebble, and sand substrates averaged 0.579 in 1977—78 versus 0.575 in 1982—83. Similarly, between-stream functional group PS averaged 0.686 (range = 0.628 to 0.787) for the four substrates in 1977—78 versus 0.695 (range = 0.647 to 0.747) in 1982—83. Catchment disturbances, such as logging, alter both the physical environment and energy inputs to streams. Such disturbances may alter physical characteristics, such as retention, for decades (e.g. Likens & Bilby 1982). Thus, to document the return of the biota to some predisturbance configuration may require extremely long-term studies.

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