

Stream Macroinvertebrate Response to Clearcut Logging

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Introduction

Why study response of stream invertebrates to watershed disturbances such as clearcut logging? Stream invertebrates can be excellent integrators of changes in such ecosystem phenomena as changes in the food base of ecosystems. For example, a number of invertebrate taxa appear to track changes in food resources (Hawkins et al. 1982; Fuller et al. 1986; Wallace and Gurtz 1986; Feminella and Hawkins 1995; Wallace and Webster 1996; Wallace et al. 1997; Jackson et al. 2007). Many taxa also exhibit substrate-specific as well as taxon-specific responses to physical alterations, such as sediment addition (Gurtz and Wallace 1984; Zweig and Rabeni 2001). Benthic invertebrates can also play important roles in many ecological processes (Wallace and Webster 1996), and in whole ecosystems, benthic invertebrates often display early and dramatic responses to manipulation (Reice and Wohlenberg 1993). Thus, assessment of benthic assemblages can be a valuable means to detect disturbance and long-term recovery from disturbance. Furthermore, knowledge of a change in the community structure of invertebrates offers an additional mechanism for detecting changes in ecological processes through time. Unfortunately, there have been few studies of the response to clearcut logging within the same stream over many years. Rather, such changes are occasionally inferred from examining multiple streams draining catchments that are in different stages of recovery.

Overview of Invertebrate Studies

Invertebrates in Big Hurricane Branch (BHB) draining Watershed (WS) 7 (clearcut) and Hugh White Creek (HWC) draining Watershed (WS) 14 (reference) were examined several times starting in 1977 immediately prior to the clearcut and following logging. During the original clearcut period, benthic samples were taken

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monthly from January 1977 through September 1978 (Gurtz and Wallace 1984). Three logging roads for access were constructed on the watershed between April and June 1976 and logging encompassed the period of January 1977 to June 1977 (see Swank and Webster, chapter 1, this volume). Most of the logging debris entering the stream channel was removed between August and October 1977. In 1982–83, five years following the initial logging, a series of seasonal (every 3 months) benthic samples were taken in each stream, BHB and HWC (Wallace et al. 1988). Between February 1993 and February 1994 both BHB and HWC were sampled bimonthly (every 2 months) for benthic invertebrates (Stone and Wallace 1998). Benthic samples were again collected bimonthly between February 2003 and December 2003 (Ely 2005; Ely and Wallace 2010). In the 1977–78 study, 4 samples were collected in bedrock outcrop, cobble riffle, pebble riffle, and sandy reach (depositional) areas of each stream reach (upper, middle, and lower) using a stratified random sampling procedure (Gurtz and Wallace 1984). In the 1982–83 and 1993–94 collecting periods, a similar stratified-random sampling procedure was used in which nine samples were collected from the upper, middle, and lower portion of each stream (Wallace et al. 1988). However, in these latter studies we limited substrate sampling to bedrock outcrop, cobble-pebble riffles, and depositional areas, that is, 3 substratum types. The 2003 study employed a similar sampling regime to the 1993–94 study; however, the bedrock outcrop habitat was further divided into areas with high moss cover and with low moss cover. During the original 1977–78 and 1982–83 studies, a Surber sampler was used for all collections. For the later studies, 225-cm² areas of bedrock were scraped into a 250- μ m mesh net; a Surber was used for cobble-riffle samples; and a 400-cm² stove pipe corer was used to sample depositional habitats. Between-year comparisons of benthic abundances were complicated for depositional habitats because the benthic corer greatly increased the recovery of small animals, especially collector-gatherer taxa.

For the 1993–94 and 2003 studies, we examined abundance, biomass, and secondary production for most taxa (Stone and Wallace 1998; Ely 2005), whereas the earlier studies had focused primarily on abundance and biomass. However, for some selected taxa in the 1977–78 study that showed especially strong responses to clearcutting, we also measured production (Gurtz and Wallace 1986; Wallace and Gurtz 1986). Production is the most comprehensive measure of the success of a population because it includes a composite of several features: abundance, biomass, growth, reproduction, survivorship, and generation time (Benke 1993). Productivity is most useful when assessing the impact of animals on their resources and energy flow through populations. An example is given below under the baetid mayfly responses in BHB to clearcutting and subsequent canopy regrowth of WS 7.

Results

Changes in Physical Properties and Resource Base

Stream invertebrates represent an important response variable to watershed disturbances, such as logging, because they respond both directly and indirectly to many

of the physical and biological disturbances associated with clearcut timber harvest. One of the most striking changes was increased solar radiation and within-stream primary production. In the early clearcutting stages of WS 7, there were reduced allochthonous litter inputs and a short-lived shift from an allochthonous to an autochthonous energy base (Webster et al. 1983; Wallace and Gurtz 1986; Wallace 1987; for a detailed account of changes in organic matter standing crop in BHB and HWC, see Webster et al., chapter 10, this volume). Dissolved organic matter and nutrient inputs from the terrestrial ecosystem were altered as a result of vegetation removal (Meyer and Tate 1983; Swank and Waide 1988). Stream thermal regimes were altered as a result of the removal of terrestrial vegetation (Swift 1983). Sediment inputs were increased as a result of road-building activities and increased soil disturbance (Gurtz et al. 1980; Webster et al. 1983; Gurtz and Wallace 1984). Increased runoff resulted from loss of terrestrial vegetation and lower evapotranspiration (Swank et al. 1982). With such a wide array of disturbances to both the energy base and physical environment, it is not surprising that stream invertebrate populations would exhibit strong responses to logging.

Invertebrate Response

Total benthic abundance of invertebrates increased in BHB as compared to HWC following logging, and most of this increase occurred in the moss-covered bedrock substrates (Gurtz and Wallace 1984). Much of this increase in abundance was attributable to the collector-gatherer (C/G) functional feeding group, especially baetid and *Ephemerella* spp. mayflies (Gurtz and Wallace 1984). However, subsequent work and gut analyses of the baetid mayflies showed large amounts of diatoms in their guts, suggesting that these animals were functioning more as scrapers than collector-gatherers in these two Coweeta streams (Wallace and Gurtz 1986). The failure of a significant habitat-weighted scraper response to the clearcutting of WS 7 reported by Gurtz and Wallace (1984) is undoubtedly attributable to the placement of baetid mayflies in the collector functional group rather than the scraper group.

We initially hypothesized that the shredder functional group would decline following clearcutting because of reduced litter inputs. Large reductions in litter inputs did occur as leaf-fall inputs to BHB declined from $259.2 \text{ g m}^{-2} \text{ y}^{-1}$ prior to logging to 4.2 g in 1978 and 1979 following logging, and annual lateral movement inputs declined from 178 g/linear m prior to logging to 38.6 g following logging (Webster and Waide 1982). Despite these large reductions in litter inputs to BHB, abundance of the shredder functional feeding group did not decline as expected (Gurtz and Wallace 1984). Although there was a large reduction in leaf litter inputs, no significant difference was found in leaf detritus in the cobble riffle habitats between BHB and HWC during the 21-month post-logging sampling period (Gurtz and Wallace 1984). Standing crop of leaf detritus only declined in sandy and pebble substrates of BHB, and much of the leaf material was buried in the substrate or retained in dams of woody debris. For a nearby Coweeta stream, where all terrestrial litter inputs were excluded from a headwater stream, it took 2 years to see significant reductions in shredder abundance and biomass (Wallace et al. 1997, 1999). Thus the 21-month post-logging sampling period, coupled with inputs from logging and

material retained in the channel may have been insufficient to produce a detectable "bottleneck" in shredder food resources. In other streams, increases in shredder taxa immediately following logging may occur when logging slash is not removed and detrital resources increase (Jackson et al. 2007). Reduced litterfall inputs to BHB did not persist for a long period due to the rather rapid plant succession on WS 7. For example, within 6 years following clearcutting, litter inputs to BHB were about 89% ($436 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$) of that of the reference stream HWC ($491 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$). However, the standing crop of large ($> 1 \text{ mm}$ diameter) benthic organic matter in BHB was only 58% of that of HWC; and fine organic matter ($< 1 \text{ mm}$ diameter) in BHB was 68% of HWC (Golladay et al. 1989). In a study on small tributary streams within WS 7 and WS 14, completed 9 to 10 years following clearcutting (1986–1987), litter inputs to BHB contained more fast-processing leaf species than those to HWC. Abundance, biomass, and production of the three dominant shredder taxa, *Tallaperla* (Plecoptera), *Pycnopsyche* (Trichoptera), and *Tipula* (Diptera), were all higher in the disturbed tributaries of BHB than in the reference tributaries of HWC (Stout et al. 1993). Stout et al. (1993) attributed the increased abundance, biomass, and production of these shredders to greater inputs of early successional species of litter, which were 7.5 times higher in BHB tributaries than in those of HWC. Production of shredder taxa was also 3.8 times higher in the main channel of BHB than in HWC 17 years following the clearcut (Stone and Wallace 1998). Twenty-six years after logging, shredder production was similar between streams; however, the annual standing crop of benthic detritus in BHB was only 49% of that in HWC (Ely 2005).

As a group, collector-gatherers increased on all substrates except sand in BHB following logging as compared with the reference stream HWC. However, with exception of collector-gatherer chironomids (Diptera) on bedrock substrates and *Ephemerella* spp. mayflies on all substrates, much of the increase was attributable to baetid mayflies, which we now know were functioning more like scrapers than collector-gatherers (Wallace and Gurtz 1986). In 1993–94, production of collector-gatherers remained greater in all habitats of BHB than of HWC. These differences were most pronounced in the moss-covered bedrock habitats of BHB, where abundance exceeded HWC by 12 times and production of collector-gatherers exceeded those of HWC by 4.3 times (Stone and Wallace 1998). In 2003, abundance, biomass, and production of collector-gatherers were similar in all habitats of BHB and HWC except bedrock habitats with high moss cover, where all values were greater in BHB by 2- to 3-fold (Ely 2005).

The response of baetid mayflies to the clearcut were so striking, we measured abundance, biomass, production, and gut analyses of these mayflies in both streams (Wallace and Gurtz 1986). Mean standing stock abundance and biomass of baetids increased in all substrate types (bedrock, cobble riffle, pebble riffle, and sandy reach) of BHB compared to HWC, and baetids reached their peak in BHB about 12 to 21 months following logging (Wallace and Gurtz 1986). Habitat-weighted baetid production in BHB averaged 17 times that of the reference stream, HWC. Baetid production increased during logging and increased again following site preparation when logging slash was removed from the stream bed and riparian rhododendron was cut (figure 11.1). Abundance, biomass, and production were much greater in

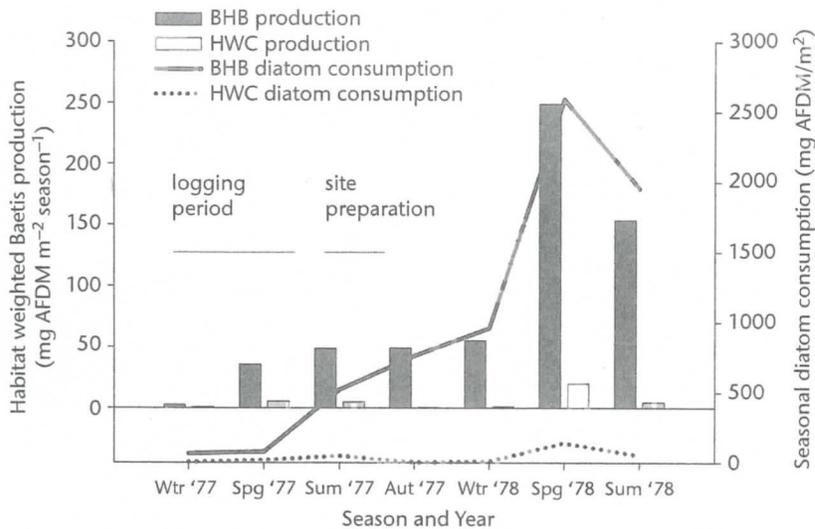


Figure 11.1 Habitat-weighted baetid mayfly production in Hugh White Creek (HWC) and Big Hurricane Branch (BHB) during successive seasons starting with the logging period of BHB (HWC was the reference stream). Note the large increase in baetid production following site preparation (removal of slash and riparian rhododendron) in BHB. Much of the increase in *Baetis* production was attributable to diatom consumption. *Baetis* consumption of diatoms was estimated based on the methods of Benke and Wallace (1980). Redrawn from the data of Wallace and Gurtz (1986).

BHB than HWC, and following site preparation, baetid guts examined from BHB contained more diatoms than those from HWC (figure 11.2). Increased diatoms in guts, as well as increased abundance and biomass of baetids in BHB, indicates a much greater rate of algal grazing by baetids in the clearcut stream. The large increased abundance and production of baetids and other scraper taxa are probably why Hains (1981) could not detect an increase in algal cells in BHB compared to HWC, despite measuring higher rates of primary productivity in BHB. In the more physically stable bedrock habitat, baetid production in BHB was almost 28 times that of HWC (Wallace and Gurtz 1986). Surprisingly, diatoms comprised the most important component of the baetid diets in each stream, even the heavily shaded reference stream. Estimated diatom consumption to account for baetid production was 25 times greater in BHB than HWC (5.788 versus 0.234 g AFDM/m²) (figure 11.2). Baetids obviously responded to changes in the energy base of headwater streams, that is, the shift from allochthonous energy resources to autochthonous resources immediately following logging (Hains 1981). However, the increase in primary productivity was short-lived (Webster et al. 1983), and baetid abundance continued to decline in 1982–83 (Wallace et al. 1988) and 1992–93 (Stone and Wallace 1998) with increased shading and terrestrial litter inputs. The high baetid production in BHB, 17 times that of HWC, observed in the first 21 months following logging, had declined to 3.4 times that of HWC by 1992–93 (Stone and Wallace

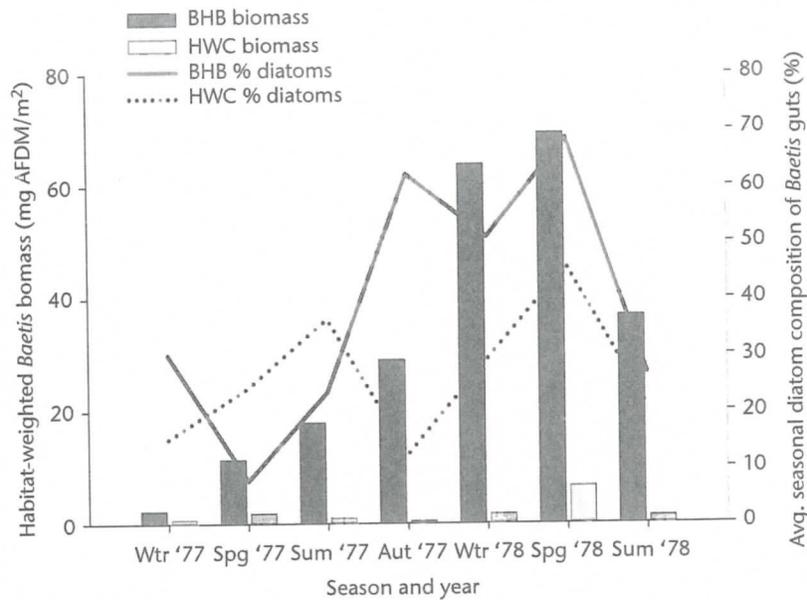


Figure 11.2 Seasonal habitat-weighted baetid biomass in Big Hurricane Branch (BHB), which drains the clearcut watershed, and Hugh White Creek (HWC), which drains the reference stream. The logging and site preparation times for BHB are noted in figure 11.1. Note that following site preparation, baetid populations in BHB contained more diatoms in their guts, despite much higher biomass (and abundance) than in the reference stream HWC, indicating much greater consumption of diatoms in the clearcut stream. Percent diatoms in baetid guts based on projected area of gut contents. Data are from Wallace and Gurtz (1986).

1998). By 2003, mean annual habitat-weighted baetid production was nearly equal between streams (Ely 2005).

Immediately following logging, filter-feeding invertebrates declined significantly in the depositional substrates of BHB compared to the reference stream, HWC. Hydropsychid caddisflies dominated abundance and production of filterers in both BHB and HWC and displayed distinct substrate preferences with bedrock outcrops > riffles > depositional areas (Gurtz and Wallace 1986). The same substrate-specific trends for filterers existed 17 years (Stone and Wallace 1998) and 26 years later (Ely 2005) in each stream.

During the initial clearcut, the abundance of invertebrate predators on bedrock substrates increased significantly in BHB and decreased significantly in depositional areas compared to HWC (Gurtz and Wallace 1984). In 1993–94, invertebrate predator production in BHB exceeded that of HWC for all habitats and was greatest for the bedrock outcrop habitats; that is, bedrock outcrop (6.3 x) > riffle (1.7 x) > depositional (1.4 x) (Stone and Wallace 1998). Undoubtedly, the greater predator production in BHB was related to the approximately 2 times greater overall production in BHB than was found in HWC during that study. Other studies at Coweeta have found evidence that production of invertebrate predators is closely linked to

prey production (Wallace et al. 1997, 1999). Thus the greater abundance of prey in BHB may have reduced food limitation on predatory invertebrates. In 2003, predator production in BHB was only 1.2 times that in HWC, reflecting the similarity in whole-assembly production between BHB (10.1 g AFDM m⁻² yr⁻¹) and HWC (9.3 g AFDM m⁻² yr⁻¹) during that study (Ely 2005).

Synthesis

Benthic Biotic Indices Following Logging

Disturbance may be considered to be the movement of the community away from a nominal value or behavior (Yount and Niemi 1990); and recovery, as directional movement toward some state resembling the predisturbance state. Biological indices are often used to evaluate the impact of disturbance on stream communities. The choice of indices, sampling methods, sampling locations, and reference streams may all affect the ability to determine the level of recovery (Niemi et al. 1993). Preferably, indices should show a definitive trend between reference and disturbed streams compared to initial conditions. There should also be relatively little variation of the index in the reference stream over the same period (Fortino et al. 2004).

Taxonomic diversity usually decreases with disturbance and increases with recovery. However, based on observations from BHB, clearcut harvesting may result in a somewhat different scenario. Immediately after clearcutting, EPT (Ephemeroptera, Plecoptera, and Trichoptera) taxa increased in the disturbed stream compared with the reference. Increased insolation, primary productivity, 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, for example, *Pteronarcys* (Plecoptera) and *Hydropsyche* (Trichoptera), colonized the disturbed stream without significant loss of headwater EPT taxa (Gurtz 1981). Following catchment logging of a low-gradient Virginia stream, more invertebrate taxa were also found in a logged reach versus a nearby forested reach (Kedzierski and Smock 2001).

Clearcutting caused shifts in the predominance of certain taxa in the disturbed stream, but few taxa were lost from the community. Habitat-weighted EPT indices of taxa richness and abundance show subsequent declines in BHB as forest succession, that is, recovery, progressed. Taxa richness may thus be more appropriate for detecting such disturbances as organic pollution and toxic chemicals, which result in the loss of sensitive species, rather than disturbances that only cause shifts in relative abundance. However, Martel et al. (2007) found declining richness in larger streams (\geq third order) when basin-wide logging intensity increased, suggesting that cumulative impacts of logging may result in different invertebrate responses in downstream reaches than in smaller headwaters and thus require alternative bio-monitoring techniques.

Among the indices used by Stone and Wallace (1998), the percentage *Baetis* index, shredder-scraper index, and the North Carolina Biotic Index (NCBI; Lenat 1993) showed the greatest ability to detect differences between the clearcut and

reference streams through time. During the initial study, the percentage *Baetis* index indicated differences between reference and disturbed streams 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). There was a trend of decreasing percentage *Baetis* index in the disturbed stream during the 1982, 1993, and 2003 studies, while the reference stream was relatively constant. The trend of decreasing *Baetis* following clearcutting of WS 7 indicated that differences between reference and disturbed streams in 1982, 1993, and 2003 were insignificant. The reduction of *Baetis* populations was correlated with increased shading of the stream by riparian vegetation during succession. The percentage *Baetis* index measured was one of the major long-term trends identified by Stone and Wallace (1998), along with decreasing abundance of scrapers in response to forest succession and the return to an allochthonous energy base.

The shredder-scaper index also showed a significant difference between reference and disturbed streams only during the first five years following clearcutting. The index was extremely low in the disturbed stream during 1977, indicating lower shredder and higher scraper abundance, and though still low in 1982, had increased over the 5-year period. In contrast, by 1993 the shredder-scaper index in BHB far surpassed that of HWC, indicating a community dominated by shredders with relatively few scrapers. By 2003, the shredder-scaper ratio in BHB had lowered and was more similar between streams than in any previous year (Ely 2005). The reference stream shredder-scaper index was relatively constant over the 4 study periods, although the depositional habitat did show some variation. This index combines the two distinct trends in macroinvertebrate abundance identified by Stone and Wallace (1998) compared to 1977 and 1982, namely, increasing shredders and decreasing scrapers. Thus, there were ongoing changes in functional structure of the benthic community in the clearcut stream between 1977 and 1993, with apparent recovery by 2003 (Ely 2005).

The relative rate of recovery also differed among habitats with most rapid recovery in the more physically stable habitat, moss-covered bedrock. However, a slower rate of recovery of biotic indices in the riffle and deposition habitats (Stone and Wallace 1998) suggests that these two habitats may be more sensitive indicators of long-term recovery than moss-covered bedrock habitats (Stone and Wallace 1998). The different rate of recovery of biotic indices among habitats also emphasizes the need for sampling regimes that cover all major habitats when assessing rates of recovery.

As pointed out by others (e.g., Karr 1994; Stone and Wallace 1998), biotic indices vary according to the nature and type of disturbance, that is, pulse versus press (sensu Bender et al. 1984). A number of studies have demonstrated the fallacy of relying on only one index for all disturbances (Karr 1994; Stone and Wallace 1996); multimetric monitoring, predictive modeling, or both approaches are recommended (Fortino et al. 2004). Treatment of a nearby Coweeta stream with an insecticide resulted in similar trends for both EPT taxa richness and the NCBI (Wallace et al. 1996). However, the clearcutting of WS 7 resulted in increased EPT taxa richness and the movement of downstream taxa into the upstream clearcut reach, without

corresponding loss of upstream taxa (Stone and Wallace 1998). Contrary to taxa richness, the NCBI incorporates both tolerance and relative abundance of taxa and appears to be more sensitive for measuring subtle changes following logging as the average NCBI in the disturbed stream showed gradual decline (lower score = more sensitive species) from 1977 to 2003. During this same 26-year period, the NCBI of the reference stream, HWC, remained virtually unchanged (Stone and Wallace 1998; Ely 2005).

The five indices calculated from data collected over the past 26 years, as well as the abundance, biomass, and production data collected during the two most recent studies, proved to be of differing value in assessing recovery of the disturbed stream from logging. Percent dominant taxon and EPT 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 some recovery (no difference between reference and disturbed) by 1982. The NCBI showed continued differences during 1982 in the riffle and depositional habitats and recovery by 1993. Comparisons of total macroinvertebrate abundance, biomass and production, and EPT abundance, indicated continued differences between the reference and disturbed streams in 1993 and apparent recovery by 2003 (Ely 2005). Thus, while benthic community composition had recovered by 1993 (i.e., similar NCBI scores between reference and disturbed streams), the much greater production in BHB than HWC implies that functional processes remained different between these streams.

Although total secondary production converged by 2003, these similarities reflect changes in the reference stream and underscore the role of detrital resources in the functioning of these headwater stream ecosystems. Macroinvertebrate production in HWC more than doubled from 1993 to 2003 simultaneous with a doubling of standing crop of detritus (Ely 2005). In BHB, neither secondary production nor detrital standing crops changed substantially during this time (Ely 2005). Positive relationships between secondary production and resource standing crops in low-order streams have been observed at Coweeta (Wallace et al. 1997, 1999) and elsewhere (Grubaugh et al. 1997; Hall et al. 2001). Similarly, the standing crop of benthic organic matter was a strong predictor of macroinvertebrate biomass in both streams during 2003 (Ely 2005). Thus, the BHB assemblage in 2003 elaborated biomass at a similar rate to HWC despite having only half the available detrital resources, indicating continued differences in consumer-resource relationships most likely related to differences in leaf type (i.e., greater inputs of early successional species to BHB) and the ongoing nutrient enrichment of BHB (Swank et al. 2001). However, we caution that a standing crop of food resources does not necessarily measure inputs, fluxes, and utilization of organic matter through the system. These findings suggest that long-term patterns in the input and retention of allochthonous resources following logging are important to the recovery of macroinvertebrate structure and function. Furthermore, these complex consumer-resource relationships may not necessarily be reflected in biotic index scores. In addition

to sediment and changes in stream flow, logging can cause major changes in the energy base, nutrient dynamics, light levels, and temperature of streams. In New England, abundances of stream macroinvertebrates in 2-year and 3-year clearcuts were 2–4 times greater than in streams draining uncut reference catchments (Noel et al. 1986). Noel et al. (1986) attributed increased abundance primarily to higher periphyton and stream temperatures in streams draining logged catchments. Similar results were found in British Columbia, where invertebrate abundance and biomass were greater in recently (≤ 5 years) logged boreal streams than in either reference streams or streams draining sites logged 20–25 years earlier, which did not differ (Fuchs et al. 2003). Using multivariate techniques, Fuchs et al. (2003) related the positive invertebrate response in the recently logged streams to higher chlorophyll *a* biomass and lower canopy cover than the reference and older logged streams. Such shifts in the food base may be accompanied by large increases in scraper secondary production as previously observed for BHB (Wallace and Gurtz 1986 and figures 11.1, 11.2). Increases in secondary production may occur following clearcutting because of increased food quality due to elevated primary production (Webster et al. 1983) and somewhat altered thermal regimes. Furthermore, the associated decrease in leaf detritus immediately following clearcutting may also increase nutrient availability to periphyton because this reduces the competition between leaf-associated microbes and periphyton for limited nutrients (Tank and Webster 1998). During the first 5 years after logging, there was elevated nutrient export from WS 7 (Swank 1988), which would also have enhanced both primary production and microbial activity on detritus. Secondary production can be an ancillary estimate of energy flow through the system and considers differences in turnover rates among organisms (Benke et al. 1984). Long-term assessment of secondary production for such groups as shredders and scrapers, rather than abundance measures, would undoubtedly change our assessment of benthic recovery from logging since our results indicate that increased secondary production persists for longer time spans than do changes in major biotic indices in BHB (Stone and Wallace 1998). However, higher levels of secondary production should not necessarily be equated with improved biological conditions. For example, elevated nutrients (Krueger and Waters 1983; Cross et al. 2006, 2007) and severe organic pollution may result in the exceptionally high productivity of a few taxa (Benke 1993). While production is a valuable tool for assessing changes in energy flow and assimilation in the benthic fauna, the expense and time associated with production studies are probably unfeasible for many biomonitoring programs.

Forest-Stream Linkages and Clearcutting

Linkages between stream invertebrates and the surrounding forest include both physical and biotic influences. For example, the forest shades the stream, thus modulating stream temperature (Ross 1963), reducing light availability and within-stream autochthonous production, and providing the allochthonous organic detritus that fuels the microbial community and energy base of the

invertebrate community (Wallace et al. 1997, 1999). In contrast, clearcutting reduces allochthonous inputs and increases solar inputs and primary production of streams. The invertebrate community responds to the large-scale shifts in the energy base of the stream following clearcutting accordingly (Haefner and Wallace 1981; Gurtz and Wallace 1984; Wallace and Gurtz 1986). The results of these Coweeta studies emphasize the strong linkages between the forest and headwater streams. The change in energy base immediately following the clearcutting of WS 7 and the subsequent shift in composition of invertebrate assemblages toward short-lived taxa, such as grazing baetid mayflies, demonstrates the close linkage between the surrounding forest and the stream. Elevated summer temperatures, with increased solar input, coupled with increased primary production (Hains 1981) resulted in a headwater stream more typical of downstream reaches. Several taxa that are more typical of downstream areas, such as baetids, *Ephemerella* spp. mayflies, and *Hydropsyche* spp. caddisflies, increased in BHB immediately following clearcutting. Interestingly, Edington and Hildrew (1973) noted that *Hydropsyche* spp. from downstream reaches appeared in a United Kingdom headwater stream following clearcutting; whereas the only hydropterygine genus in their study stream prior to logging was *Diplectrona*. Edington and Hildrew's research strongly suggests that different bioenergetic efficiencies in response to changing stream temperatures influenced the ability of *Hydropsyche* to persist within the cooler headwater reaches.

Furthermore, we suspect that our estimates of baetid production are extremely conservative, since differences in growth rates in BHB and HWC were based only on growth rates at various temperatures taken from the European literature and did not take in account differences in food quality or quantity (Wallace and Gurtz 1986). Subsequent studies on the Ogeechee River in southeastern Georgia (Benke and Jacobi 1994) and even in tundra streams in Alaska (A. D. Huryn, personal communication) suggest considerably higher growth rates than we used for BHB and HWC. In future studies, it would be desirable to use field growth chambers (e.g., Huryn and Wallace 1986) to obtain growth rates for selected invertebrates in disturbed and undisturbed streams.

Based on the studies of forest disturbance and aquatic invertebrate productivity from the Coweeta manipulations, it appears that in most cases forest disturbance increases overall invertebrate productivity (Stone and Wallace 1998; Kedzierski and Smock 2001). However, few studies have actually examined the productivity of benthic assemblages following logging but instead infer higher production rates from increased abundance (Nislow and Lowe 2006), biomass (e.g., Fuchs et al. 2003), or increased emergence rates (Banks et al. 2007). Furthermore, productivity should not always be considered the best measure of response to disturbance. For example, some of the highest measures of lotic invertebrate production are associated with excessive organic pollution, such as the heavy organic enrichment of a castle mote in Wales (Benke 1993). Likewise, higher biological diversity may not necessarily be a measure of enhanced habitat quality if there has been invasion by exotic species, such as the influx of downstream species into the headwaters of BHB, as a result of altered physical attributes and energy inputs. Exotic species can induce large changes in aquatic communities (e.g., Huryn 1998). Conservation

should strive to preserve the original inhabitants of a given habitat rather than focus on taxa diversity and productivity.

Conclusions

This clearcut was not "typical" as required by recent regulations in most regions of the United States, as there was no riparian zone set aside. Even riparian *Rhododendron* spp., which provide year-round shading of the stream, was cut following logging. If a riparian management zone had been established, the invertebrate response would probably be less pronounced than was observed from several aspects. Unforeseen natural events also increased the magnitude of the study. For example, shortly following road building on WS 7, an exceptionally large storm in the last two weeks of May 1976 resulted in large amounts of sediment entering BHB. This sediment input was greatest where access roads crossed BHB in its middle and upper portions. There was a large increase in inorganic and organic seston in BHB compared to the reference stream HWC (Gurtz et al. 1980). Accumulated sediments in the stream channel were greatest in low-gradient, sandy-gravel reaches > pebble riffles > cobble riffles and least in the steep gradient moss-covered bedrock substrates (Gurtz and Wallace 1984). Furthermore, BHB substrates in the sandy-gravel, pebble, and cobble habitats contained significantly higher proportions of sand than did those of the reference stream HWC (Gurtz and Wallace 1984). Thus, it is questionable that even riparian zone protection would have provided adequate protection to elevated sediment loading from road building in WS 7. Sedimentation associated with the exceptional April 1976 rainfall, which coincided with recent road construction, may have overwhelmed the capacity of the riparian zone to protect BHB at the stream crossings.

Under normal conditions adequate riparian zones may have resulted in different results than those we observed for benthic macroinvertebrates. First, because of greater shading of the stream, there would not have been a large increase in primary production and stream temperature increases (Swift 1983) would not have been as prominent. Thus, the observed shift from an allochthonous to an autochthonous energy base of the invertebrate assemblage would have been reduced. Second, a larger source of allochthonous detritus to the stream bed would have been maintained, and the energy base of the stream would not have shifted from allochthonous detritus to autochthonous primary production as was observed by Webster et al. (1983). Finally, although most sediment input to the stream was associated with road building, a riparian management zone would have reduced fine-sediment input. Even a modest riparian buffer width (3 m) in association with moderate-intensity harvesting (42% basal area removed) has been shown to mitigate changes in canopy cover, temperature, water chemistry, fine-sediment input, and litter input with little change in macroinvertebrate assemblage structure (Kreutzweiser et al. 2005). In summary, the establishment of a riparian management zone would undoubtedly have reduced some of the major changes observed in invertebrate assemblage (i.e., increases in grazers such as baetids and the influx of taxa from downstream areas)

and lessened the impact of sediments on fauna of the lower-gradient depositional zones (Quinn et al. 2004).

Another factor that should be considered is that BHB is a high-gradient, erosional stream with a diverse array of substrates ranging from depositional zones to extremely steep, moss-covered, bedrock outcrops. Clearcutting of low-gradient streams, such as those of the southeastern Coastal Plain, may yield somewhat different results. For example, Kedzierski and Smock (2001) studied the response of invertebrates to logging in a low-gradient, soft-bottomed stream in Virginia and found several points of contrast from high-gradient streams that had been logged. First, there was increased macrophyte production in logged reaches of low-gradient streams compared to increased periphyton production in the rocky reaches of high-gradient streams. Second, the abundant macrophytes resulted in much higher productivity among collectors, filterers, and predators in the logged reaches, whereas scrapers were the least affected. Thirdly, macrophytes appear to be a key factor in influencing invertebrate response to logging in low-gradient streams (Kedzierski and Smock 2001). Thus, geomorphology and landscape must be considered as important variables when assessing the response of invertebrates to watershed disturbances such as clearcutting.

Invariably, in long-term studies one confronts several decisions in field sampling for benthic invertebrates with regard to sampling methods, taxonomic considerations, and differences in sampling frequency over several decades. As improved and more efficient sampling methods evolve, for example, use of benthic corer and a laboratory sample splitter for more efficient recovery of small organisms, we should always strive for the most effective methods. Unfortunately, this may result in values for abundance, biomass, and production that are not directly comparable with earlier studies; however, it will give a better picture of the current conditions. In the last 25 years, more effective and complete keys to benthic invertebrates, especially the aquatic insects, have been developed (e.g., Merritt et al. 2008). Long-term storage of representative specimens from earlier studies and adequate institutional museum space and resources for maintaining specimens are required to assess potential changes in taxonomy. Finally, the resources available to conduct a given project will vary among studies, and researchers must decide the most appropriate methods and sampling regimes to best coincide with both the short- and long-term objectives of a given study.

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Long-Term Response of a Forest Watershed Ecosystem

CLEARCUTTING IN THE
SOUTHERN APPALACHIANS

EDITED BY
Wayne T. Swank
Jackson R. Webster

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Our North American forests are no longer the wild areas of past centuries; they are an economic and ecological resource undergoing changes from both natural and management disturbances. A watershed-scale and long-term perspective of forest ecosystem responses is requisite to understanding and predicting cause and effect relationships. This book synthesizes interdisciplinary studies conducted over thirty years, to evaluate responses of a clear-cut, cable-logged watershed at the Coweeta Hydrologic Laboratory in the Nantahala Mountain Range of western North Carolina. This research was the result of collaboration among Forest Service and university researchers on the most studied watershed in the Lab's 78-year history. During the experiment, a variety of natural disturbances occurred: two record floods, two record droughts, a major hurricane, a blizzard of the century, major forest diseases, and insect infestations. These disturbances provided a unique opportunity to study how they altered the recovery of the forest ecosystem. This book also shows that some long-term forest trends cannot be forecast from short-term findings, which could lead to incorrect conclusions of cause and effect relationships and natural resource management decisions.

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