

Long-term functional group recovery of lotic macroinvertebrates from logging disturbance

Damon T. Ely and J. Bruce Wallace

Abstract: Clear-cut logging rapidly affects stream macroinvertebrates through substantial alteration of terrestrial-aquatic resource linkages; however, lesser known are the long-term influences of forest succession on benthic macroinvertebrate assemblages, which play key roles in stream ecosystem function. We compared secondary production and standing crops of detritus in two mountain headwater streams within Ceweeta Hydrologic Laboratory, North Carolina, USA, as part of a long-term, paired-watershed investigation of macroinvertebrate recovery from whole-catchment logging. Mean annual habitat-weighted abundance and biomass in the disturbed stream (catchment entirely logged 26 years prior) did not differ from that of the reference stream, and secondary production was only 0.8 g ash-free dry mass (AFDM)·m⁻²·year⁻¹ greater in the disturbed stream (disturbed, 10.1; reference, 9.3). Taxonomic composition, shredder-scraper ratios, and North Carolina biotic index scores were more similar between streams than in previous years. However, mean annual standing crops of benthic organic matter (BOM) were much lower in the disturbed stream (167 g AFDM·m⁻²) than in the reference stream (339 g AFDM·m⁻²), and the disturbed stream supported greater macroinvertebrate biomass per unit BOM. We suggest that despite similarities in macroinvertebrate structure and function, past logging activity continues to influence consumer-resource relationships in the disturbed stream through enhanced resource quality.

Résumé : La coupe forestière à blanc affecte rapidement les macroinvertébrés en modifiant de manière importante les liens entre les ressources terrestres et aquatiques; on connaît, cependant, moins bien les effets à long terme de la succession forestière sur les peuplements de macroinvertébrés benthiques qui jouent des rôles essentiels dans le fonctionnement des écosystèmes d'eau courante. Nous comparons la production secondaire et la biomasse du détritus dans deux cours d'eau d'amont de montagne au Ceweeta Hydrologic Laboratory, Caroline du Nord, É.-U., dans le cadre d'une étude à long terme de bassins hydrographiques appariés sur la récupération des macroinvertébrés de la coupe de bois sur l'ensemble du bassin versant. L'abondance et la biomasse moyennes annuelles pondérées en fonction de l'habitat dans le cours d'eau perturbé (bassin entièrement soumis à la coupe 26 ans auparavant) ne diffèrent pas de celles du cours d'eau témoin et la production secondaire dans le cours d'eau perturbé est supérieure de seulement 0,8 g de masse sèche sans les cendres (« AFDM »)·m⁻²·an⁻¹ dans le cours d'eau perturbé (perturbé, 10,1; témoin, 9,3). La composition taxonomique, les rapports déchiqueteurs-racleurs et les cotes de l'indice biotique de Caroline du Nord sont plus semblables dans les cours d'eau que durant les années antérieures. Cependant, les biomasses moyennes annuelles de matière organique benthique (« BOM ») sont de beaucoup inférieures dans le cours d'eau perturbé (167 g AFDM·m⁻²) que dans le cours d'eau témoin (339 g AFDM·m⁻²) et le cours d'eau perturbé soutient une plus grande biomasse de macroinvertébrés par unité de BOM. Nous croyons que, malgré les similarités dans la structure et la fonction des macroinvertébrés, les activités de coupe forestière du passé continuent à influencer les relations consommateurs-ressources dans le cours d'eau perturbé par la qualité accrue des ressources.

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Introduction

Stream ecosystem responses to the sudden removal of watershed vegetation (i.e., clear-cut logging) are well studied, and because of the widespread use of benthic fauna as bioindicators of anthropogenic disturbance, much attention is paid to influences on macroinvertebrate assemblages (e.g., Fuchs et al. 2003). Logging activities that do not leave

riparian vegetation (i.e., buffers) intact can induce a short-term shift in the energy base of streams from allochthonous sources of carbon to autochthonous in-stream production (Webster et al. 1983; Wallace and Gurtz 1986), which then declines with canopy regrowth during forest succession. These short-term changes are often reflected in macroinvertebrate assemblage structure as shifts in relative abundance and biomass among functional feeding groups (FFGs) (Wal-

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lace et al. 1988). However, little is known about the long-term (i.e., >10 years) influences of watershed logging on benthic macroinvertebrate assemblages, which play key roles as organic matter processors and intermediaries in aquatic food webs (Wallace and Webster 1996).

Long-term models of stream resource dynamics during forest succession predict reduced inputs of dam-forming wood, resulting in greater material transport and reduced retention of benthic organic matter (BOM) and inorganic nutrients until late successional stages (Webster et al. 1992; Valett et al. 2002). In addition, the quality of allochthonous detritus may change with the composition of the aggrading forest (Boring et al. 1981). Thus, in contrast to brief, pulse-type disturbances that can alter habitat structure and cause mass mortality, watershed logging represents a press-type disturbance (sensu Bender et al. 1984) to stream ecosystems with long-term consequences for the quantity, quality, and storage of resources.

Benthic macroinvertebrate assemblage structure and function are contingent upon the nature and relative availability of resources, and strong positive associations exist between detrital resource standing crops and secondary production in forested headwater streams (Wallace et al. 1999). The tight relationships between macroinvertebrate consumers and resource type and delivery are represented by the morphological and behavioral adaptations for food acquisition that describe macroinvertebrate FFGs (i.e., scrapers, shredders, collector-gatherers, collector-filterers, and predators; Cummins 1973). Shifts in the relative proportions of FFGs reflect changes in resource dynamics, and specific FFG ratios have been proposed as surrogates for various ecosystem attributes (Merritt et al. 2002). Thus, long-lasting, resource-related influences of forest succession on stream ecosystem condition could be evident in the relative amounts of biomass and production found among FFGs. However, extended temporal changes in forested headwater assemblages following logging are poorly understood, as most studies (with the exception of Stone and Wallace (1998), discussed below) either focus on short-term responses or compare multiple streams draining stands of different ages. Furthermore, long-term patterns in functional attributes of benthic macroinvertebrates within a particular stream ecosystem following logging are relatively unknown.

Recently, investigations of ecosystem function have been recommended to accompany traditional, structural-based metrics (i.e., species distribution and abundance) in the assessment of stream response to catchment disturbance (Young et al. 2008). Collective properties of ecosystems integrate environmental conditions with biological patterns, thus providing relative information on the status of a broad range of system attributes (Young et al. 2008). The elaboration of consumer biomass (i.e., secondary production) is an energetic function of stream ecosystems that reflects thermal regime, resource availability, and water quality and is a measure of the relative success of assemblages that takes into account numerous taxon-specific differences in life history (Huryn and Wallace 2000; Benke and Huryn 2006). Studies of secondary production have enhanced our understanding of the energetic relationships between streams and other watershed subsystems (e.g., lake outlets; Wotton 1988) and have illustrated ecosystem-level sensitivity to

changes in resource (Wallace et al. 1999) and nutrient (Cross et al. 2006) loading, as well as broad differences in land use (Shieh et al. 2003). Because macroinvertebrate assemblages in forested headwater streams rely mainly on allochthonous detritus to meet their energetic demands, investigations of secondary production coupled with a knowledge of benthic resource dynamics (i.e., inputs, standing stocks) are particularly effective tools in evaluating stream response and recovery following catchment-scale disturbances or anthropogenic alterations such as logging.

In the present study, we investigated benthic resource pools and annual whole-assemblage secondary production in a stream draining a previously logged (26 years prior) catchment and its paired reference as part of a long-term assessment of benthic macroinvertebrate recovery from logging disturbance; this paired-watershed study remains the longest-running investigation of stream ecosystem response to clear-cut logging in North America. We compared various structural attributes of macroinvertebrate assemblages (abundance, biomass, taxonomic composition, and biotic indices), mean annual secondary production of macroinvertebrate FFGs, and standing crops of detritus between the previously disturbed stream and its long-term reference to evaluate the current recovery status of the logged stream. We also compared our findings with those of previous investigations of these systems to gain perspective on the relative magnitudes and trends in resource availability and macroinvertebrate response.

Materials and methods

Study sites

The study sites are two perennial second-order streams within the Coweeta Hydrologic Laboratory (US Forest Service) in Macon County, North Carolina, USA. Coweeta is a 1625 ha drainage basin located in the Blue Ridge Physiographic Province of the southern Appalachian Mountains. The Coweeta basin receives 187 cm of precipitation annually and is drained by high-gradient headwater streams composed of bedrock-outcrop, riffle, and depositional habitats. Coweeta streams are highly heterotrophic: primary production is extremely low ($\sim 6 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), and terrestrial detrital inputs are $\sim 400 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (Webster et al. 1997).

The reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams were paired for study because of their many physical similarities (Table 1), and although quantitative pretreatment data are lacking, the macroinvertebrate communities of both streams were observed to be similar before logging (Gurtz and Wallace 1984). Prior to logging, both catchments were dominated by mixed hardwoods, including oaks (*Quercus* spp.), hickory (*Carya* spp.), red maple (*Acer rubrum* L.), and yellow poplar (*Liriodendron tulipifera* L.). After the 1977 cable logging of the entire catchment (except 16 ha on upper slopes and ridges), forest succession was allowed to progress undisturbed. Leaf area index (a measure of canopy cover) of the logged catchment (Elliott et al. 2002) and litter inputs to the disturbed stream (Webster et al. 1992) recovered within 10 years of deforestation. Recent forest inventories on the logged site report more basal area of black locust (*Robinia pseudoacacia* L.), *L. tulipifera*, and *A. rubrum* and a distinct lack of

Table 1. Physical characteristics of reference (Hugh White Creek) and disturbed (Big Hurricane Branch) streams located within the Coweeta Hydrologic Laboratory, North Carolina, USA.

	Reference	Disturbed
Catchment orientation	Northwest	South
Catchment area (ha)	61	59
Reach length (m)	1077	1225
Maximum channel elevation (m asl)	992	1077
Elevation at weir (m asl)	707	722
Mean annual temperature ($^{\circ}$ C)*	10.8	11.2
Mean discharge ($L \cdot s^{-1}$)†	29.9	27.7
Habitat composition		
Bare bedrock (%)	12.1	9.6
Mossy bedrock (%)	14.5	11.5
Riffle (%)	38.9	48.2
Depositional (%)	34.6	30.7

Note: asl, above sea level.

*10 February 2003 to 9 February 2004.

†1 January 2003 to 1 September 2003.

oak and hickory species (Elliott et al. 2002). A dense understory of rhododendron (*Rhododendron maximum* L.) provides year-round shading of both stream channels. Further details of the 1977 clear-cut were reported by Swank et al. (2001) and Elliott et al. (2002).

Previous investigations of macroinvertebrate response to logging in this system have revealed two major patterns: a sudden increase in scraper production associated with a temporary period of high algal growth (Wallace and Gurtz 1986), and a delayed, long-term increase in shredder production following the return of leaf inputs (Stone and Wallace 1998). Sixteen years after logging, Stone and Wallace (1998) were the first to compare whole-assemblage secondary production rates between these streams. Macroinvertebrate abundance, biomass, and production were all greater in the disturbed stream at that time, yet no compositional differences were found between assemblages using multiple biotic indices (Stone and Wallace 1998).

We are aware of the statistical limitations associated with this unreplicated design (Hurlbert 1984). Nonetheless, as with previous investigations of this system, we adhere to the tradition of the paired-watershed approach (Bormann and Likens 1979), which has advanced our understanding of large, complex systems (Schindler 1998).

Benthic sampling

Benthic sampling for the current study began in February 2003 and continued every other month through December 2003. Four habitats (bare bedrock, moss-covered bedrock, riffle, and depositional areas), each within upper, middle, and lower sections of both streams (i.e., $n = 3$ per habitat; Table 1), were sampled randomly on each date. A stovepipe corer (area = 400 cm²) was used to sample depositional habitats. All benthos within the corer was removed up to a depth of 10 cm and poured through a 250 μ m mesh bag. Riffle samples were collected using a Surber sampler (0.093 m²) with a 250 μ m mesh net. Bare and moss-covered bedrock habitats were scraped (100 cm²) with a dull knife and then scrubbed with a nylon brush into a 250 μ m mesh

bag. All samples were preserved in the field using a 37% formalin solution containing Phloxine B dye to facilitate invertebrate sorting in the laboratory.

Current velocity (Gessner bag current meter; Gessner 1950) and substrate size class proportions (visual inspection) were measured prior to collecting each sample. We used the Wentworth scale of substratum size classification, and sizes were converted to a phi scale (negative log base 2); the median φ for each sample was then calculated (Cummins 1962). The US Forest Service provided mean daily discharge and temperature for both streams (available online: http://coweeta.uga.edu/ecology/ecology_data.html).

Sample processing and secondary production

In the laboratory, samples were poured through 1 mm and 250 μ m nested sieves creating coarse and fine fractions, respectively. Invertebrates were removed from benthic material by hand under a dissecting microscope at 15 \times magnification. All invertebrates were then identified and counted, and their lengths were measured to the nearest millimetre. Most identification was to genus using the keys of Merritt and Cummins (1996) and Wiggins (1977). Midge larvae (Diptera: Chironomidae) were identified as either Tanypodinae (predaceous) or non-Tanypodinae (non-predaceous); non-insect taxa were identified to order. Each taxon was assigned a FFG according to Merritt and Cummins (1996), Stone and Wallace (1998), and Wallace et al. (1999).

Macroinvertebrate biomass (ash-free dry mass, AFDM) was calculated using length-weight regressions from Benke et al. (1999). Cohort production intervals for each taxon were obtained from previous studies (Stone and Wallace 1998; Wallace et al. 1999). Secondary production (g AFDM·m⁻²·year⁻¹) for most taxa was calculated using the size-frequency method as outlined by Benke and Huryn (2006). An empirically derived production-to-biomass ratio ($P:B$) of 18 was used for Copepoda (see Wallace et al. 1999), and a $P:B$ of 5 was used for Nematoda, Oligochaeta, and Turbellaria (Benke et al. 1984). Rare taxa were assigned $P:B$ values of 5 and 10 for univoltine and bivoltine taxa, respectively (Lughart and Wallace 1992); production for these taxa was calculated by multiplying $P:B$ by mean annual biomass. *Micrasema* (Trichoptera: Brachycentridae) abundance, biomass, and production were divided evenly between the gatherer and shredder functional groups (Wallace et al. 1999). Secondary production of each taxon (with the exception of crayfish (*Cambarus* spp.) and salamanders (*Desmognathus* and *Eurycea* spp.), which were not considered because of inadequate sampling procedures and the increased nocturnal activity of some organisms) was estimated within each habitat. We calculated habitat-weighted values of macroinvertebrate abundance, biomass, and production by summing habitat-specific areal values multiplied by the proportion of total reach length occupied by each habitat type (Table 1). To estimate habitat proportions, we visually inspected each consecutive 5 m segment of both stream reaches.

Benthic organic matter

To determine BOM composition and biomass, samples were poured (following invertebrate removal) through 4.75 mm, 1 mm, and 250 μ m sieves. Organic matter \geq

4.75 mm was sorted to leaves, wood, and miscellaneous coarse benthic organic matter (CBOM). All organic matter ≥ 1 mm was designated miscellaneous CBOM, and particles smaller than 1 mm but larger than 250 μm were considered fine benthic organic matter (FBOM). The AFDM of all OM types was calculated as the difference between dried (50 °C, 7 days) and ashed (500 °C, 24 h) mass.

Among-year invertebrate comparisons

Differences in sample collection methods and variables measured among the study years prevented the direct comparison of macroinvertebrate and BOM data among studies. The 1977 (Gurtz and Wallace 1984) and 1982 (Wallace et al. 1988) studies used a Surber sampler in both riffle and depositional habitats and quantified only invertebrate abundance. Furthermore, the 1982 study considered taxa only from the orders Ephemeroptera, Plecoptera, and Trichoptera (EPT). In 1993, a different sampling method was used for each habitat, and the use of a stovetube corer in depositional areas enhanced the recovery of small, early-instar taxa compared with previous studies (Stone and Wallace 1998).

To assess taxonomic similarity between EPT assemblages, we calculated a single Bray–Curtis index score using mean annual taxon-specific abundance for each study year as

$$\text{BC} = \frac{\sum_{i=1}^S |y_{id} - y_{ir}|}{\sum_{i=1}^S (y_{id} + y_{ir})}$$

where BC is the Bray–Curtis distance between the reference and disturbed streams, y_{id} is the abundance of taxon i at the disturbed stream d , y_{ir} is the abundance of taxon i at the reference stream r , and S is the total number of EPT taxa present at the disturbed and reference sites (Krebs 1999). The BC index coefficient attains a maximum value of 1 for two sites that are entirely different and a minimum value of 0 for two sites with identical assemblages.

We used two biotic indices found by Stone and Wallace (1998) to have the greatest ability to detect differences between assemblages in logged and unlogged streams. The shredder–scraper ratio (shredder abundance/scraper abundance) and the North Carolina biotic index (NCBI; Lenat 1993; also described in detail in Stone and Wallace 1998) were calculated using EPT abundance for qualitative comparison with the previous three studies.

Statistical analyses

To account for seasonally driven patterns, paired t tests ($\alpha = 0.05$) on habitat-weighted means from upper, middle, and lower reaches on each sampling date ($n = 6$) were used to detect significant differences between streams for mean annual BOM standing crop, mean annual macroinvertebrate abundance and biomass, shredder–scraper ratios, and NCBI scores. Mean habitat-specific current velocities were compared using a paired t test ($n = 6$), and differences in mean habitat-specific substrate median φ values were evaluated with a t test ($n = 6$). To examine seasonal patterns of primary resource standing crops (leaves + CBOM + FBOM) between streams, we conducted t tests on each sampling

date using mean habitat-weighted values from upper, middle, and lower reaches ($n = 3$ per stream). To examine the relationship between consumers and benthic resource availability, we used linear regression of invertebrate biomass with primary BOM resource standing crop from individual Surber and core samples in riffle and depositional habitats, respectively, collected on all dates ($n = 36$ per stream).

To address changes in resource availability in both streams over the decade between 1993 and the current study, habitat-weighted mean annual standing crops of primary BOM resources were calculated for both streams in both studies and were compared using two-way analysis of variance (ANOVA) on mean values from each sampling date ($n = 6$ for both streams in both study years) with year and stream as main effects. Tukey's honestly significant difference (HSD) was used as a post-hoc multiple comparison test following significant ANOVA results. Data failing normality tests were $\log(x + 1)$ -transformed. All statistical analyses were performed using SigmaStat (version 3.11, Systat Software Inc., Chicago, Illinois).

Results

Physical measurements

Because of weir repair in autumn, comparisons of stream discharge during 2003 were limited to January through early September. Mean discharge was slightly higher in the reference stream (Table 1); hydrographs from both streams displayed nearly identical patterns (data not shown). Mean annual temperatures were also similar between streams (reference, 10.8 °C; disturbed, 11.2 °C; Table 1); however, the annual temperature range in the disturbed stream (12.1 °C) was less than in the reference stream (16.2 °C) and resulted in 164 more (or 4.2% greater) degree-days above 0 °C accumulated in the disturbed stream. Habitat-specific current velocities and substrate sizes did not differ between streams for any habitat (paired t test, $P > 0.05$, $n = 6$).

Invertebrate assemblages

Annual habitat-weighted means of total macroinvertebrate abundance and biomass did not differ between streams (Table 2). Likewise, we found no differences in abundance or biomass comparisons within any FFG between streams (Table 2).

Habitat-weighted secondary production within both streams was estimated for a total of 70 taxa. Annual macroinvertebrate production was similar between the disturbed (10.1 g AFDM·m $^{-2}$ ·year $^{-1}$) and reference (9.3 g AFDM·m $^{-2}$ ·year $^{-1}$) streams, with nearly identical contributions by all FFGs (Table 2). In both streams, production was greatest for shredders and least for scrapers (Table 2).

Biotic indices indicated similar assemblage composition between streams. Using abundance of EPT taxa, no differences between NCBI scores (reference, 1.59; disturbed, 1.72; paired t test, $P = 0.19$, $n = 6$) or shredder–scraper ratios (reference, 3.97; disturbed, 4.82; paired t test, $P = 0.78$, $n = 6$) were found between streams. The reference assemblage included three taxa (*Anchytarsus*, *Habrophlebia*, and *Psilotreta*) not found in the disturbed stream, whereas the disturbed assemblage had only one unique taxon (*Taeniopteryx*). Taxonomic dissimilarity calculated using

Table 2. Mean annual habitat-weighted abundance (number·m⁻² ± standard error, SE), biomass (mg ash-free dry mass·m⁻² ± SE), and secondary production (mg ash-free dry mass·m⁻²·year⁻¹) of macroinvertebrate functional feeding groups (FFG) in reference and disturbed streams.

FFG	Abundance		Biomass		Production	
	Reference	Disturbed	Reference	Disturbed	Reference	Disturbed
Scrapers	653±218	922±95	71±17	78±23	457	498
Shredders	1 764±460	1 701±358	561±196	582±144	2717	2 786
Gatherers	44 556±4530	41 104±3701	295±57	325±62	2440	2 530
Filterers	913±422	1 245±525	281±82	324±64	2050	2 310
Predators	3 574±321	4 020±591	432±105	618±106	1612	1 988
Total	51 460±5093	48 990±3998	1639±326	1927±212	9276	10 111

Note: No significant differences in abundance or biomass were found between streams within any FFG category or for total amounts (paired *t* test, $\alpha = 0.05$, $n = 6$).

the BC distance was 0.55 in 1977, 0.48 in 1982, 0.28 in 1993, and 0.19 in 2003 for an overall decline of 65% over the 26-year period.

Benthic organic matter

Mean annual habitat-weighted standing crops of BOM were two times higher in the reference stream (339 g AFDM·m⁻²) than in the disturbed stream (167 g AFDM·m⁻²; paired *t* test, $P = 0.028$, $n = 6$) (Table 3). Greater amounts of all BOM types were found in the reference stream, but the relative contribution of each BOM type to total standing crop was similar between streams (Table 3). Primary resource standing crops in the disturbed stream were significantly lower than in the reference stream ($P < 0.05$, *t* test, $n = 3$) on all dates except August and displayed diminished seasonal peaks during spring and autumn (Fig. 1).

Consumer–resource relationships

Benthic macroinvertebrate biomass was positively related to the quantity of primary BOM resources in both streams (reference, $r^2 = 0.59$, $P < 0.001$; disturbed, $r^2 = 0.62$, $P < 0.001$; $n = 36$) (Fig. 2). The slope of this relationship was greater in the disturbed stream (0.405) than in the reference stream (0.272; *t* test of slopes, $P = 0.035$; Zar 1999).

Both benthic resources and secondary production doubled in the reference stream from 1993 to 2003, whereas in the disturbed stream, OM standing crop and secondary production slightly decreased and increased over the decade, respectively (Table 4). The combined mean annual standing crop of leaves, CBOM, and FBOM was similar between streams in 1993, and OM standing crop in the disturbed stream during 2003 was not different from that found in 1993 (Tukey's HSD, $P > 0.05$; Table 4). BOM resources in the reference stream during 2003 were greater than in 1993 (Tukey's HSD, $P = 0.004$) and were also greater than those found in the disturbed stream in either year (two-way ANOVA, year × site interaction, $P = 0.004$; Table 4).

Discussion

Macroinvertebrate assemblage comparisons

The structure and function of the macroinvertebrate assemblages in these two streams were more similar in this study than in any previous investigation. Though we cannot compare annual production statistically, total annual habitat-weighted production in the current study was only 9%

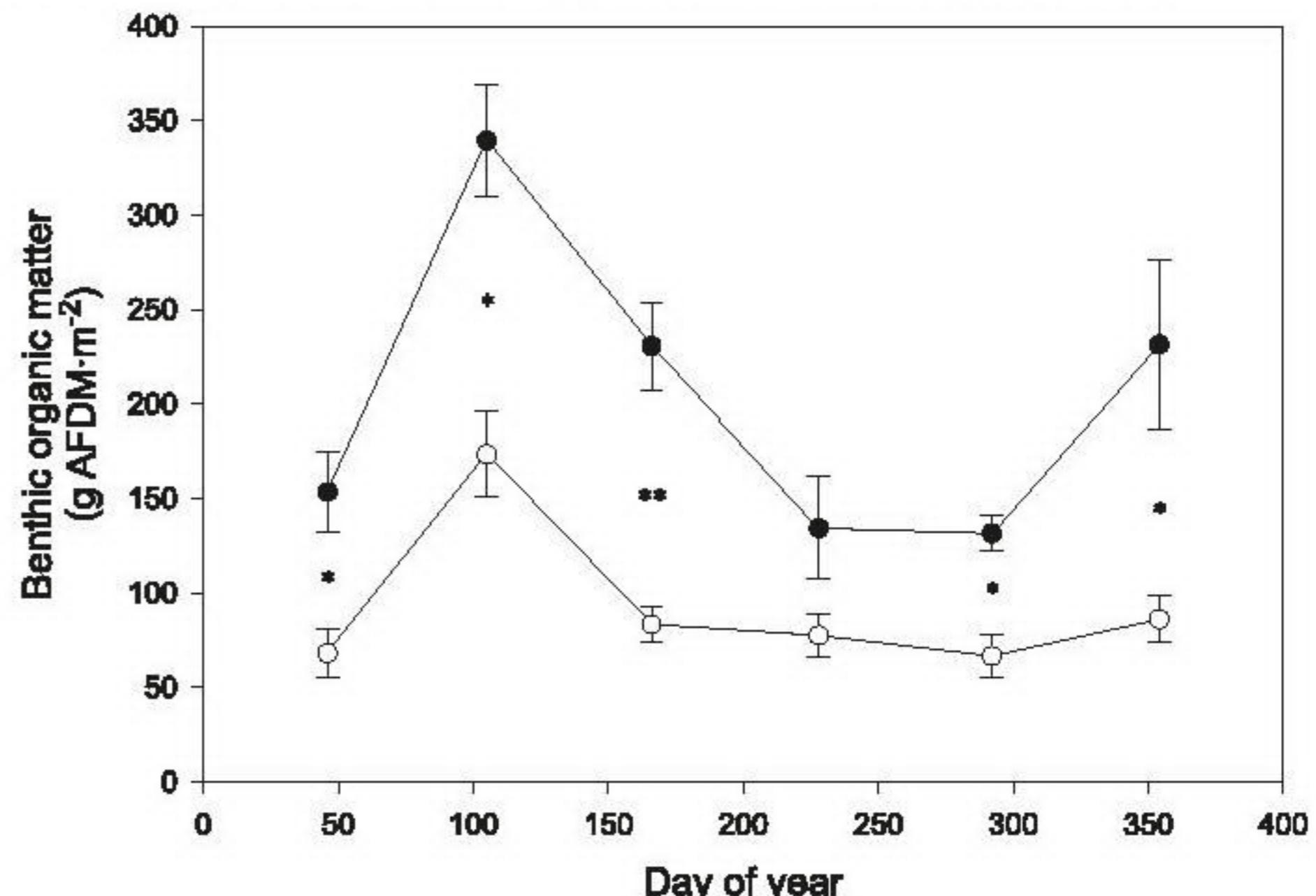
Table 3. Mean annual habitat-weighted benthic organic matter (BOM) standing crops (g ash-free dry mass·m⁻² ± standard error, SE) in reference and disturbed streams.

BOM type	Reference	Disturbed	P value*
Wood	135±25	74±15	0.039
Leaves	45±15	22±7	0.075
CBOM	86±20	32±7	0.010
FBOM	72±11	39±10	0.023
Total	339±69	167±27	0.028

Note: CBOM, coarse BOM; FBOM, fine BOM.

*Paired *t* test, $n = 6$.

Fig. 1. Mean habitat-weighted benthic organic matter (leaves and coarse and fine fractions of benthic organic matter only) on each sample date in reference (solid circles) and logging-disturbed (open circles) streams. Points are means ± standard error (SE). *, $P \leq 0.05$; **, $P \leq 0.01$; *t* test, $n = 3$. AFDM, ash-free dry mass.



greater in the disturbed stream compared with the 190% greater annual production (vs. the reference) found 10 years prior (Stone and Wallace 1998). Production of each FFG in 2003 differed by only 3%–13% between streams, except for predators, which had 23% greater production in the disturbed stream. Although greater predator production was mostly due to differences on bedrock outcrops, predators contributed similarly to total production in both the reference (17%) and the disturbed (20%) streams. Because secondary production accounts for taxon-specific characteristics such as life span, survivorship, and fecundity (Huryn

Fig. 2. Linear regressions of macroinvertebrate biomass and benthic organic matter resources (wood not included; riffle and depositional habitats only) in reference (solid circles, continuous line; $r^2 = 0.59$, $P < 0.001$, $n = 36$) and disturbed (open circles, broken line; $r^2 = 0.62$, $P < 0.001$, $n = 36$) streams. Slopes are significantly different (t test, $P = 0.035$). AFDM, ash-free dry mass.

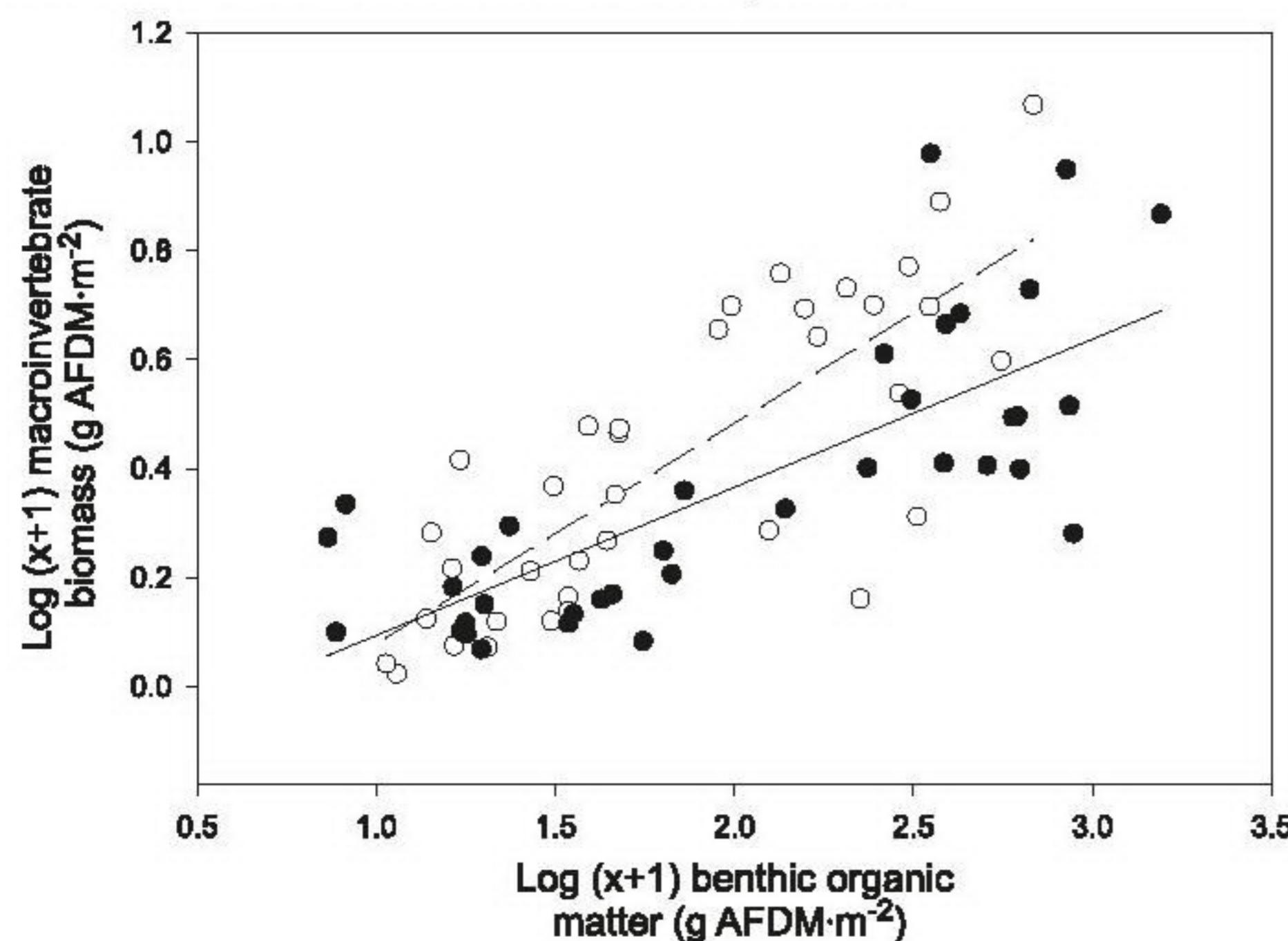


Table 4. Mean annual habitat-weighted benthic organic matter (BOM) standing crops (leaves, coarse BOM, and fine BOM only) and secondary production in reference and disturbed streams in 1993 and 2003.

	BOM (g AFDM·m ⁻²)		Secondary production (g AFDM·m ⁻² ·year ⁻¹)	
	1993	2003	1993	2003
Reference	99.5a	203.5b	4.4	9.3
Disturbed	137.3a	92.6a	8.3	10.1

Note: Values in the BOM category that share a letter are not significantly different (two-way analysis of variance (ANOVA); Tukey's honestly significant difference (HSD); $\alpha = 0.05$; $n = 6$). BOM data for 1993 are from M.K. Stone (Georgia Perimeter College, Science Department, Dunwoody, Georgia 30338, USA, unpublished data).

AFDM, ash-free dry mass.

and Wallace 2000), similar secondary production between streams suggests that the activity and success of the disturbed assemblage has converged with the reference assemblage over the 26-year period.

Biotic indices also imply convergence in species composition. Bray–Curtis dissimilarity, which considers both the richness and evenness of the assemblage, consistently declined with each investigation. Likewise, NCBI scores became increasingly similar since logging. The NCBI incorporates tolerance values (i.e., higher scores indicate a greater proportion of taxa tolerant to disturbed conditions; Lenat 1993) into a measure of diversity. The steady decline of this score in the disturbed stream since logging (Stone and Wallace 1998; present study) suggests that logging influences have consistently lessened over time, allowing more sensitive taxa to persist. Decreases in NCBI scores are also associated with the recovery of leaf decomposition, organic matter dynamics, and secondary production (Wallace et al. 1996); thus the consistent decline in NCBI scores is indicative of the ongoing functional recovery of this system.

Changes in the shredder–scraper ratio since logging re-

flect shifts in stream energy base and indicate a nonlinear recovery trajectory of the dominant detritivores. During 26 years, the EPT-based shredder–scraper ratio was consistently between 2.7 and 4.0 in the reference stream. In the disturbed stream, the ratio was 0.33 and 0.81 in 1977 and 1982, respectively, due to the immediate rise and subsequent decline in algae-scraping mayflies (Wallace and Gurtz 1986; Wallace et al. 1988). Sixteen years following logging, scraper abundance was similar but shredder densities were much higher in the disturbed stream, where the habitat-weighted shredder–scraper ratio was 8.0 (Stone and Wallace 1998). In the current study, no differences in abundance or biomass were found for shredders or scrapers and shredder–scraper ratios were more similar than any previous year, differing only 0.8 between streams. However, although these assemblage-based assessments suggest recovery of various ecosystem dynamics (e.g., primary production, decomposition, and species interactions), the increased similarities in these assemblages compared with a decade before were due to changes in the reference assemblage. We contend that OM dynamics explain these changes and indicate continued differences in consumer–resource relationships not apparent from macroinvertebrate data alone.

Benthic organic matter storage

From 1993 to 2003, BOM doubled in the reference stream but did not change appreciably in the disturbed stream. In the 4-year period preceding both studies, mean annual precipitation was 17% greater than the long-term (72 years) mean at Coweeta before 1993 and 16% lower before 2003 (Coweeta Long Term Ecological Research: <http://coweeta.ecology.uga.edu>). Wet and dry periods often drive BOM depletion and accumulation, respectively (Wallace et al. 1995; 1997), and may explain the increase in BOM that we observed in the reference stream. Further, the lack of change in BOM standing crops in the disturbed stream despite differences in precipitation patterns suggests an impairment of retentive ability.

We suspect a decreased ability to retain particulate materials in the disturbed stream from our observations of lower OM standing crops throughout the year, despite equivalent annual inputs (J.R. Webster, Virginia Tech, Department of Biology, Blacksburg, Virginia, unpublished data). BOM standing crops were consistently lower in the disturbed stream on almost all sampling dates and did not display the peak in late autumn found in the reference stream during this study, a pattern also observed by Golladay et al. (1989). Greater macroinvertebrate ingestion is most likely not the cause of lower BOM in the disturbed stream because (i) this would lead to higher rates of production, and (ii) increases in ingestion would be unreasonably high to mask the autumnal pulse of OM inputs. We also observed similar contributions of each OM type to total standing crops in both streams (i.e., indiscriminate export), suggesting reduced physical retention. Fewer debris dams have been reported for the disturbed stream previously (Golladay et al. 1989), but current inventories of debris dams and measurements of particulate OM retention are needed.

Lower BOM standing crops in the disturbed stream may also be due to enhanced microbial decomposition under elevated nutrient concentrations. Nitrate-N concentrations have

been 3–10 times higher in the disturbed stream than in the reference stream since deforestation (Swank et al. 2001), and mean annual nitrate-N concentration in the disturbed stream during the current study year ($114 \mu\text{g}\cdot\text{L}^{-1}$) was almost 12 times that of the reference stream ($10 \mu\text{g}\cdot\text{L}^{-1}$; J.D. Knoepp, USDA Forest Service, Coweeta Hydrologic Laboratory, Otto, North Carolina, unpublished data). Nutrient enrichment positively affects microbial biomass (Meyer and Johnson 1983) and breakdown rates of leaf litter (Greenwood et al. 2007), and microbial growth may be further enhanced by the high N and P content of early-successional leaf litter (Boring et al. 1981). Enhanced microbial activity was suggested by Benfield et al. (2001) as partly responsible for faster leaf breakdown rates found in the disturbed stream. Thus, the lower amounts of BOM that we observed are probably due to a combination of reduced physical retention, a greater proportion of early-successional leaf litter, and increased microbial activity due to nutrient enrichment.

Consumer–resource relationships

Because of the energetic dependence of headwater macroinvertebrate assemblages on allochthonous inputs, secondary production increases with detritus standing crops in temperate, forested streams (Wallace et al. 1999). Comparing the 1993 and 2003 studies, this relationship appears to be true within each of our study streams: secondary production in the reference stream increased twofold along with a doubling of BOM, whereas in the disturbed stream, neither BOM nor secondary production changed appreciably. Furthermore, we found strong positive associations between macroinvertebrate biomass and BOM standing crop in both streams. However, in both of these analyses, there appears to be greater resource-use efficiency in the disturbed stream (see also Greenwood et al. 2007). In 1993, secondary production in the disturbed stream was double that of the reference stream despite similar BOM quantities, and currently, abundance, biomass, and production in the disturbed stream are similar to those in the reference stream despite half the amount of BOM. Additionally, there is currently greater macroinvertebrate biomass per unit BOM standing crop in the disturbed stream.

Resource quality may be germane to consumer–resource relationships in both streams, as the quantities of litter entering the streams appear to be in excess of macroinvertebrate requirements. Using rough estimates of macroinvertebrate assimilation efficiency (AE) of leaf detritus and net production efficiency (from Benke and Wallace 1997), the amount of ingestion required to support observed shredder, gatherer, and filter-feeder production was between 19%–21% of OM inputs in either stream (D.T. Ely, unpublished data). Although this is an extremely coarse evaluation, these values are similar to calculations of ingestion in headwater streams elsewhere (Rosi-Marshall and Wallace 2002). Although export, respiration, and burial may all be significant pathways of resource loss, calculated annual ingestion was only about 33% and 77% of the mean annual standing crop of BOM resources in the reference and disturbed streams, respectively. These findings suggest that a specific subset of high-quality BOM is driving the observed relationships between BOM and macroinvertebrate biomass and growth.

The notion of a higher-quality subset of the OM pool is consistent with concepts of proper conditioning and the palatability of resources, which are microbially mediated phenomena. Because neither individual body sizes (biomass/abundance) nor assemblage growth rates (production/biomass) differ between streams, we hypothesize that macroinvertebrates in the disturbed stream display comparable growth despite lower resource abundance because these resource pools contain a larger subset of high quality OM that is more easily assimilated by detritivores. If higher nutrient concentrations have increased microbial biomass, as found in similar streams (Meyer and Johnson 1983), then greater macroinvertebrate AE of microbe-rich OM is logical. Invertebrate AE is much higher for microorganisms than for detritus (Cummins and Klug 1979), and greater microbial abundance in the disturbed stream should increase the size of the palatable resource pool in addition to providing some of the carbon responsible for comparable production to the reference stream. Hutchens et al. (1997) measured the AE of *Pycnopsyche*, a predominant leaf-shredding caddisfly, on leaves from both streams and found that AE depended only on leaf conditioning time, regardless of stream identity. However, both the laboratory and field experiments in that study used leaves conditioned in the reference stream only, which prevented any effect due to differences in microbial colonization. Determining the AE of consumers on substrates conditioned in their respective streams should be a future priority and may show that nutrient enrichment can counteract reductions in BOM retention imposed by forest succession by lowering macroinvertebrate dependence on resource quantity, as found in an experimental nutrient enrichment study in a nearby stream (Cross et al. 2006; Greenwood et al. 2007).

We caution against the sole use of macroinvertebrate metrics in the assessment of lotic recovery from large-scale disturbances because such events can influence numerous structural and functional attributes of terrestrial and aquatic systems for decades. Although we have not directly shown that consumer–resource relationships remain impaired in the third decade since logging, the disturbed stream displays many characteristics that suggest enhanced resource quality. We measured only one of many stream ecosystem processes that may be influenced by forest succession. A more thorough understanding of both the recovery of benthic macroinvertebrates from logging disturbance and their role in the recovery of the system as a whole may be achieved via the simultaneous measurement of energy- and nutrient-related functions such as ecosystem metabolism, nutrient uptake, organismal growth rates, and litter decomposition, in addition to secondary production.

Finally, macroinvertebrate dependence on allochthonous resources may limit the application of general successional theory to stream assemblages, a topic that receives continued attention (Milner et al. 2008). Whereas forest succession is an autogenic process characterized by interacting, self-organized mechanisms of facilitation, inhibition, and tolerance (Connell and Slatyer 1977), lotic consumer recovery in donor-controlled systems (sensu Polis et al. 1997) is largely an allogegenic function more dependent on interactions across system boundaries than within the assemblage. To better understand the recovery process of logged stream ecosys-

tems, future studies should focus on the role of forest succession in determining inputs, retention, resource quality and quantity, and how these variables interact to influence the structure and function of macroinvertebrate assemblages.

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