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# Response of *Baetis* Mayflies (Ephemeroptera) to Catchment Logging

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**ABSTRACT:** Following clear-cutting of a southern Appalachian hardwood catchment, standing stock densities and biomass of *Baetis* spp. increased in four stream substrate types (rock face, cobble riffle, pebble riffle and sandy reach) compared to those of a nearby undisturbed reference stream. *Baetis* production in the stream draining the clear-cut catchment averaged 17.6 X higher than that of the reference stream, and up to 27.6 X that of the reference stream in the more physically stable rock-face substrates. Food preferences and food-specific bioenergetic efficiencies were used to estimate the amount of food consumed and the amount of *Baetis* production attributable to each food category. Diatoms comprised the most important food in each stream. Analyses of gut contents of *Baetis* following logging indicate a significant increase in diatom consumption in the stream draining the clear-cut catchment. Diatom consumption in the reference stream (0.234 g ash-free dry mass [AFDM]/m<sup>2</sup>) and treatment stream (5.788 g AFDM/m<sup>2</sup>) comprised 9.0 and 7.4%, respectively, of the net primary production of each stream during the 1st year following the clear cut. These suggest that a similar proportion of net primary production was harvested by *Baetis* in each stream. Although the two *Baetis* populations consumed the same proportion of net primary production, *Baetis* in the clear-cut catchment stream had 1.2-2.0 X more diatoms in their guts while maintaining a standing stock biomass that exceeded that of the reference stream by 10-30 X, suggesting a much higher rate of periphyton harvesting in the clear-cut catchment. Sampling 4 and 5 years following the clear cut indicates significant declines in *Baetis* populations of the clear-cut stream that coincided with a 10-fold decrease in primary productivity. Although characterized by short; multivoltine life cycles and high fecundity, *Baetis* spp. comprise a minor component of the standing stock biomass in most headwater streams of the region. However, with disturbances such as clear-cutting, they respond quickly to exploit increases in autochthonous production, and assume major roles in energy processing. In contrast, larger, less fecund univoltine and semivoltine species lack the ability to respond quickly and exploit the relatively short-lived increases in primary production.

## INTRODUCTION

Changes in community structure and abundances of invertebrate taxa following logging have been documented (e.g., Woodall and Wallace, 1972; Newbold *et al.*, 1980; Murphy *et al.*, 1981; Gurtz and Wallace, 1984). However, studies of the influence of logging or other disturbance on secondary production are lacking (Benke, 1984). The resilience of stream ecosystems to disturbances may be greatly enhanced by species that have less specialized feeding habits, high fecundity and short generation times (Webster *et al.*, 1983). Ulfstrand (1975) pointed out that several groups of mayflies possess these characteristics.

Gurtz and Wallace (1984) observed that several mayfly taxa increased in abundance in a stream draining a clear-cut catchment compared to similar taxa in a nearby reference stream. Among mayfly taxa, *Baetis* spp. responded the most dramatically, with mean densities in the clear-cut catchment stream exceeding those of the reference

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stream by 20 X in 15 months immediately following logging. Conversely, there were no significant differences in densities between these streams during logging operations in the 1st 3 months of the study. However, differences in densities among populations do not necessarily reflect different levels of secondary production (Benke *et al.*, 1984; O'Hop *et al.*, 1984). Secondary production is a useful method for assessing function of aquatic insects and, when combined with food analysis, can provide insight into understanding responses of taxa to ecosystem level changes (Benke, 1984).

Surrounding forests exert important influences on headwater stream ecosystems (Hynes, 1975). Inputs of allochthonous organic matter (Fisher and Likens, 1973; Cummins, 1974; Vannote *et al.*, 1980; Webster *et al.*, 1983) and reduction of solar radiation reaching the stream (Ross, 1963; Vannote *et al.*, 1980; Webster *et al.*, 1983) are two very obvious influences of terrestrial vegetation on stream processes. Clear-cutting can alter thermal regimes (*e.g.*, Gray and Edington, 1969; Swift, 1983) and the nature and timing of inputs of plant production into the aquatic system (Webster *et al.*, 1983). Therefore, such disturbances can influence physical, chemical and biological characteristics of stream communities.

Our objective is to examine the effects of logging on the production of *Baetis* mayflies. We explore how changes in their productivity relate to, and are influenced by, changes in the physical, chemical and biological characteristics of the stream induced by clear-cutting the surrounding forest.

#### STUDY SITES

The study was conducted at the Coweeta Hydrologic Laboratory (U.S. Forest Service) in western North Carolina. Big Hurricane Branch (BHB) drains a 61.1-ha catchment that was clear-cut during January to June 1977. Site preparation (= clear-felling of all remaining trees) was completed in October 1977. Prior to logging, the dominant vegetation was oak-hickory, and rhododendron formed a rather dense understory along the main stream channel. Rhododendron was cut and removed from the stream margin of BHB during site preparation.

Hugh White Creek (HWC) drains a 59.5-ha catchment. The HWC catchment vegetation is dominated by oak-hickory with rhododendron forming a dense understory along most of the stream margin and resembles BHB catchment prior to logging. Both BHB and HWC are second-order streams. BHB has a mean annual discharge of 17.7 L/sec, while that of HWC is 19.5 L/sec. The substrate in both streams ranges from steep exposed bedrock to short, low-gradient, sandy reaches. HWC catchment has a northwestern aspect, while that of BHB is southern. Webster *et al.* (1983), Meyer and Tate (1983) and Gurtz and Wallace (1984) provide more complete site descriptions.

#### MATERIALS AND METHODS

*Sampling* — Monthly Surber samples (0.09 m<sup>2</sup>; 0.30-mm mesh opening) were taken from January 1977 to September 1978 using a stratified random sampling scheme. In most months, four monthly samples were taken from each of four substrate types in BHB: rock face (moss-covered boulders and outcrops), cobble riffle, pebble riffle and sand (predominantly sand and gravel size substrate). In HWC, three samples were collected monthly from each of the above substrate types. A total of 569 Surber samples were collected in the two streams. Gurtz and Wallace (1984) provided a more complete description of field sampling and laboratory procedures used to process samples. Weighted mean densities were obtained for each stream based on the proportional area of each stream occupied by each substrate type (Gurtz and Wallace, 1984). *Baetis* densities reported here exceed those reported by Gurtz and Wallace (1984), which were derived from log-transformed data. Arithmetic mean abundances are used here because our objective was to measure biomass and estimate production in each stream. Seasonal means were calculated using individual samples for each substrate type.

*Baetis biomass.*—Lengths of *Baetis* spp. were measured to the nearest 0.1 mm using a stereomicroscope equipped with an ocular micrometer. Mean biomass (ash-free dry mass [AFDM]) was estimated for each specimen based on length-weight regressions (see below). Specimens used for these regressions were oven-dried at 50 C for 24 hr, desiccated 24 hr, weighed, ashed at 500 C for 1 hr and reweighed to obtain AFDM. All weights (to nearest  $\mu\text{g}$ ) were obtained with a Cahn microbalance.

*Growth rates.*—Growth rates used in production estimates were derived from *Baetis* growth rates reported in the literature. These rates were expressed as a function of stream temperature. Using data reported by Humpesch (1979), we regressed the field growth rates (% length/day) on temperatures for each cohort of two *Baetis* species which inhabit streams with annual temperature regimes (1.5-21 C) similar to ours (0.5-20.5 C). The resulting growth model for *Baetis rhodani* Pictet was:

$$Y = 0.629e^{(0.0873T)} \quad (n = 23, r^2 = 0.76, P < 0.001) \quad (1)$$

and for *Baetis lutheri* Müller-Liebenau:

$$Y = 0.680e^{(0.088T)} \quad (n = 11, r^2 = 0.89, P < 0.001) \quad (2)$$

where: Y = growth rate (% length/day) and T = temperature (C). There was no significant difference ( $P > 0.5$ ) in field growth rates between these two species (Zar, 1974, analysis of covariance). Therefore, we combined (1) and (2) to form a common regression equation (3) (see Zar, 1974):

$$Y \text{ (% length/day)} = 0.655e^{(0.0875 T)} \quad (3)$$

The values for growth rates above are in length, and insects add proportionally more mass per unit time than per unit increase in length. *Baetis* from BHB and HWC were individually measured and weighed, and the following relationship (4) between weight and length was derived:

$$Y = 0.0075L^{2.423} \quad (n = 94, r^2 = 0.94, P < 0.001) \quad (4)$$

where Y = body mass (mg AFDM) and L = length (mm). Equation 4 indicates logarithmic increase in AFDM is 2.423 times higher than ln increase in length. Or, based on the  $18.8\% \pm 3.0$  ( $\bar{x} \pm 95\%$  CI) ash content of our specimens, dry mass increases  $2.88 \pm 0.07$  times greater than unit increase in length, which is reasonably close to the 2.98 value suggested by Humpesch (1979). The value of 2.423 (AFDM/length) was used to convert growth in length (3) at various temperatures to growth in weight as follows:

$$G \text{ (AFDM %/day)} = G \text{ (length %/day [equation 3])} \cdot 2.423 \text{ (AFDM/length)} \quad (5)$$

*Stream temperature.*—Stream temperature was measured continuously with a recording thermograph in BHB throughout the study period. To derive HWC temperature, temperature in HWC and BHB was measured hourly for 24 hr once a month for the period of June 1977 to May 1978. The resulting mean daily temperatures in BHB were regressed with those from HWC, with the following relationship: Temperature (C) HWC =  $-4.130 + 1.187 \cdot \text{temp. (C) BHB}$  ( $r^2 = 0.994$ ,  $n = 12$ ,  $P < 0.001$ ). Mean daily temperatures obtained from the recording thermograph in BHB were used in the above equation to obtain mean temperatures for HWC. These mean daily temperatures were combined with growth equations to estimate daily growth rates for *Baetis* nymphs in each stream.

*Production.*—Overlapping cohorts of *Baetis* species preclude using conventional production methods, which rely on the ability to distinguish individual cohorts. The presence of at least three *Baetis* species, tentatively identified as *B. tricaudatus* Dodds, *B. intercalaris* McDunnough and *B. amplus* (Traver) based on the key of Morihara and McCafferty (1979), compounded the problem of cohort identification. Furthermore, delayed hatching of *Baetis* eggs (e.g., Elliott, 1972; Brittain, 1982) may have added to the problem of distinguishing cohorts. To provide monthly estimates of production we used the product of monthly growth rates (%/d), mean biomass between sampling intervals, and days to obtain monthly production estimates:

$$P = G \cdot ([B_o + B_t]/2) \cdot t$$

where  $G$  is the daily growth rate,  $B_0$  is biomass at the start of time interval,  $B_t$  is the biomass at the end of the interval and  $t$  is the length of the interval in days. For the last interval, September to October 1978, we used the September biomass. This method allows a reasonable estimate of the temporal distribution of production. The latter was an important criterion since our objective was to assess the production response of *Baetis* spp. during and immediately following logging. Continuous recruitment and rapid increase in *Baetis* spp. densities following logging precluded use of instantaneous growth methods from field data because mean individual biomass actually decreased between many sample dates. The latter was often true of larger individuals between sample dates as well. Although the size frequency method (Waters and Hokestrom, 1980) does not require recognizable cohorts, it does not allow a mechanism for the temporal assessment of production.

*Food analysis.*—Food consumed by *Baetis* spp. was analyzed in each stream (BHB and HWC) using a modification of Cummins' (1973) membrane filter technique. Individual particles found in the foreguts were outlined on paper using a compound microscope (300X magnification). Projected areas of food particles from random microscope fields were measured with a Hewlett-Packard 9864A digitizer interfaced with an HP9825A desktop computer. Relative areas of particles in six food types (fine amorphous detritus of unknown origin, vascular plant detritus, animal material, fungal hyphae, filamentous algae and diatoms) were used as an index of food in the guts. Because of difficulty in extracting gut contents from small nymphs, mean sizes of animals used for food analysis were larger than the average size comprising the standing stock. However, there was no significant difference between head widths of specimens selected from BHB and HWC for gut analysis: BHB,  $\bar{x}$  head width = 0.75 mm  $\pm$  0.047 (95% CI) (range = 0.37-1.12 mm,  $n$  = 100); HWC,  $\bar{x}$  head width = 0.80 mm  $\pm$  0.10 (95% CI) (range = 0.30-1.2 mm,  $n$  = 56). Gut contents of nymphs from rock face, cobble riffle and pebble riffle substrates from each stream were analyzed seasonally from winter 1977 to summer 1978. In samples taken during some seasons, numbers of medium to large nymphs were insufficient to allow analyses from all the above substrates. Gut analyses were not performed upon nymphs from sand substrates due to their rarity. Projected areas of each food type were used to compare *Baetis* feeding habits between streams and were combined with available literature on bioenergetic efficiencies to estimate the trophic basis of production (Benke and Wallace, 1980).

## RESULTS

*Baetis* densities, biomass and growth rates.—During the initial logging period (winter 1977) on the BHB catchment, *Baetis* spp. densities in BHB were about 3X those of HWC (Table 1). Excluding one slight decline (winter 1978) in the rock face and cobble riffle substrates, densities of *Baetis* increased steadily in BHB during the following seasons and reached a maximum in spring 1978. Mean densities of *Baetis* exceeded 7000 per  $m^2$  on the rock face substrates of BHB during this period (Table 1). The maximum density of *Baetis* in HWC was 119.6 per  $m^2$  on the cobble riffle substrates during the spring of 1978. For the last 5 seasons, summer 1977 through summer 1978, densities of *Baetis* on all substrates in BHB significantly exceeded those of HWC ( $P < 0.05$ , Gurtz and Wallace, 1984). The ratios of densities (BHB/HWC) on each substrate for the entire study were: rock face = 46.7; cobble riffle = 15.3; pebble riffle = 17.0, and sand = 14.2.

Dramatic increases in *Baetis* biomass occurred in BHB following logging. Most of the increase in *Baetis* biomass was associated with the larger and more physically stable substrates. The average standing stock biomass for the rock face and cobble riffle habitat of BHB exceeded those of all other habitats (Table 2). There was no significant difference in *Baetis* biomass between the rock face and cobble riffle habitats in BHB (ANOVA  $P > 0.05$ ). Lowest *Baetis* biomass in BHB was in the sandy reach habitats; however, *Baetis* biomass in this habitat was significantly higher than that of any habitat

TABLE 1.—Standing stock densities (number per m<sup>2</sup>,  $\bar{x} \pm se$ ) of *Baetis* spp. in Hugh White Creek (HWC) and Big Hurricane Branch (BHB) for each of four substrate types. Logging operations were initiated on the Big Hurricane Branch catchment in winter (January) 1977 (see text)

Season	Substrate and stream							
	Rock face		Cobble riffle		Pebble riffle		Sand	
	HWC <sup>1</sup>	BHB <sup>2</sup>	HWC	BHB	HWC	BHB	HWC	BHB
winter 1977	16.9 ± 7.0	51.1 ± 21.0	12.3 ± 4.4	39.5 ± 8.5	3.1 ± 1.9	20.6 ± 6.8	4.6 ± 2.2	14.4 ± 2.8
spring 1977	37.1 ± 11.0	493.4 ± 235.0	41.9 ± 6.8	356.1 ± 140.1	17.9 ± 6.2	140.8 ± 47.3	6.0 ± 2.6	57.4 ± 22.5
summer 1977	45.5 ± 14.1	967.0 ± 316.1	37.1 ± 9.3	247.6 ± 63.9	14.4 ± 4.0	140.8 ± 48.3	1.2 ± 1.2	83.4 ± 45.1
autumn 1977	33.5 ± 16.9	1428.1 ± 561.8	7.2 ± 2.5	697.0 ± 88.5	6.0 ± 2.6	219.8 ± 56.2	1.2 ± 1.2	153.4 ± 25.7
winter 1978	44.3 ± 12.0	1155.2 ± 352.1	14.4 ± 4.4	662.9 ± 208.9	12.0 ± 4.5	388.4 ± 108.9	8.4 ± 3.5	62.8 ± 27.9
spring 1978	16.9 ± 9.9	7014.7 ± 4376.0	119.6 ± 26.6	2026.4 ± 425.9	56.2 ± 25.0	967.9 ± 179.3	17.9 ± 7.2	257.5 ± 50.6
summer 1978	47.0 ± 21.6	3730.7 ± 738.4	76.6 ± 11.8	807.3 ± 178.8	22.7 ± 6.8	434.2 ± 64.1	16.7 ± 7.8	178.5 ± 66.2
all seasons	45.4 ± 6.1	2120.3 ± 678.5	45.2 ± 6.5	691.0 ± 98.8	19.4 ± 4.3	330.4 ± 44.7	8.1 ± 1.8	115.3 ± 16.9

<sup>1</sup>HWC n = 9 for all seasons and each substrate except as follows: winter 1977, n = 7 for all substrates

<sup>2</sup>BHB n = 12 for all seasons and each substrate except as follows: winter 1978, n = 10; rock face spring 1977, n = 11; and, pebble riffle, autumn 1977, n = 10

TABLE 2.— Standing stock biomass (mg AFDM/m<sup>2</sup>,  $\bar{x} \pm \text{se}$ ) of *Beatis* spp. in Hugh White Creek (HWC) and Big Hurricane Branch (BHB) for four substrate types. The 1st 3 months of the study correspond to the initial logging period on the BHB catchment

Period	Substrate and stream							
	Rock face		Cobble riffle		Pebble riffle		Sand	
	HWC	BHB	HWC	BHB	HWC	BHB	HWC	BHB
January-March 1977 <sup>1</sup>	1.4 ± 0.8	3.8 ± 2.1	0.5 ± 0.3	4.0 ± 1.2	0.1 ± 0.1	1.2 ± 0.5	0.1 ± 0.1	0.9 ± 0.4
April 1977-September 1978 <sup>2</sup>	3.3 ± 0.9	78.4 ± 12.0	2.9 ± 0.6	61.0 ± 7.3	1.5 ± 0.5	30.1 ± 4.3	0.9 ± 0.3	9.8 ± 1.3
Entire period <sup>3</sup>	3.1 ± 0.8	67.5 ± 10.7	2.6 ± 0.6	52.7 ± 6.6	1.4 ± 0.4	25.8 ± 3.9	0.8 ± 0.3	8.5 ± 1.2

<sup>1</sup>HWC n = 7; BHB n = 12 for each substrate

<sup>2</sup>HWC n = 54; BHB n = 70 for cobble riffle and sand, n = 69 for rock face, and n = 67 for pebble riffle substrate

<sup>3</sup>HWC n = 61 for each substrate; BHB n = 82 for cobble riffle and sand, rock face n = 81, and pebble riffle n = 79

of HWC (Table 2). For the entire 21-month study, *Baetis* biomass in BHB was 9.1 X (sandy reach) to 22.2 X (rock face) higher than in similar habitats of HWC. During the initial 3 months of the study (winter 1977), *Baetis* biomass in BHB averaged about 3 X that of HWC. By the summer of 1978, average biomass in BHB was 34 X that of HWC, and the BHB rock face habitat exceeded that of HWC by 105 X. Although densities and standing stock biomass were highest on the rock face substrate of BHB, mean individual biomass was lowest on this substrate (*cf.*, Tables 1 and 2) which indicates that smaller individuals inhabited the rock face substrate of BHB.

Estimated growth rates of *Baetis* in HWC (% AFDM/d, based on mean daily temperatures) ranged from 1.99 (January-February 1977) to 8.05 (August-September 1978), while those of BHB ranged from 2.60 (January-February 1977) to 8.46 (August-September 1978). The average daily growth rate was 4.85% AFDM/day in HWC and 5.21% AFDM/day in BHB. However, we caution that these growth rates may be conservative for BHB since they are based only on mean temperature and do not consider diel temperature changes or enhanced quality of food consumed by *Baetis* in BHB following the clear-cut (*see* Discussion).

*Production.* — Following logging, *Baetis* seasonal production increased in all substrates of BHB. Production in all substrates of BHB followed similar seasonal trends over the 21-month study; total production (g AFDM/m<sup>2</sup>) was highest in rock face (2.567) > cobble riffle (1.811) > pebble riffle (0.851) > sandy reach (0.310) (Fig. 1). Weighted stream production for the period, based on the relative proportion of stream habitat comprised by each substrate type, was 1.112 g AFDM/m<sup>2</sup>. Seasonal *Baetis* production for all substrates in BHB was greatest in spring 1978 (1 year after logging) and began to decline by summer 1978. The largest increases in BHB *Baetis* production occurred between autumn 1977 and spring 1978, or shortly after removal of streamside vegetation (summer to early autumn 1977, Fig. 1).

*Baetis* production in the reference stream, HWC, increased slightly in spring 1977 followed by a stronger peak in spring 1978. Though *Baetis* production in HWC was not as high as that in BHB (Fig. 1), the production on various substrates followed the same trends observed in BHB (rock face > cobble riffle > pebble riffle > sandy reach). Cumulative *Baetis* production (g AFDM/m<sup>2</sup>) for the 21-month period in HWC was as follows: rock face = 0.093; cobble riffle = 0.088; pebble riffle = 0.048; and, sandy reach = 0.025. Weighted stream production for the 21-month period in HWC was 0.063 g AFDM/m<sup>2</sup>, or only 5.7% of that of BHB (1.112 g). The ratio of BHB/HWC *Baetis* production was: rock face = 27.6; cobble riffle = 20.5; pebble riffle = 17.6; and, sandy reach = 12.4.

Production/ $\bar{x}$  Biomass (P/B) ratios for the 21 months ranged from 33.0 (pebble riffle) to 38.0 (rock face) for *Baetis* on various substrates of BHB (*cf.*, Table 2 and above production values for various substrates) over the 604-day period. Assuming a P/B of 5 for a single cohort, this suggests about 6.6 (33.0/5) to 7.6 (38.0/5) cohorts in the 604-day period. P/B ratios ranged from 30.0 (rock face) to 34.3 (pebble riffle) in HWC. As P/B ratios are a measure of growth, those of BHB are probably conservative as we feel growth rates, and hence production, in this stream were underestimated (*see* Discussion).

*Food analysis.* — The most striking differences in *Baetis* gut contents were the diatom concentrations during logging and site preparation vs. those of autumn 1977 through summer 1978 in BHB (Fig. 2 and Table 3). Diatoms averaged 20.2% of the projected area of gut contents in BHB during logging vs. 52.1% following logging. Using arcsine-transformed data, there were no significant differences in diatom contents between *Baetis* guts from BHB and HWC across all 7 seasons of the study (winter 1977 through summer 1978, paired t-test,  $P > .20$  [Zar, 1974]). However, during the last 4 seasons (autumn 1977-summer 1978) seasonal diatom contents were significantly higher ( $P < .10$ ) in *Baetis* guts in BHB than in HWC (paired t-test). Diatom concentrations in all *Baetis* guts in BHB from autumn 1977 through summer 1978 were significantly higher ( $P < .10$ ) than those during logging and site preparation in BHB (t-test).



Conversely, there were no significant differences in diatom concentrations in *Baetis* guts in HWC between these periods (t-test,  $P > .50$ ). During the last 4 seasons, *Baetis* in BHB had a 10-30 X greater standing stock biomass and maintained a 1.2-2 X higher

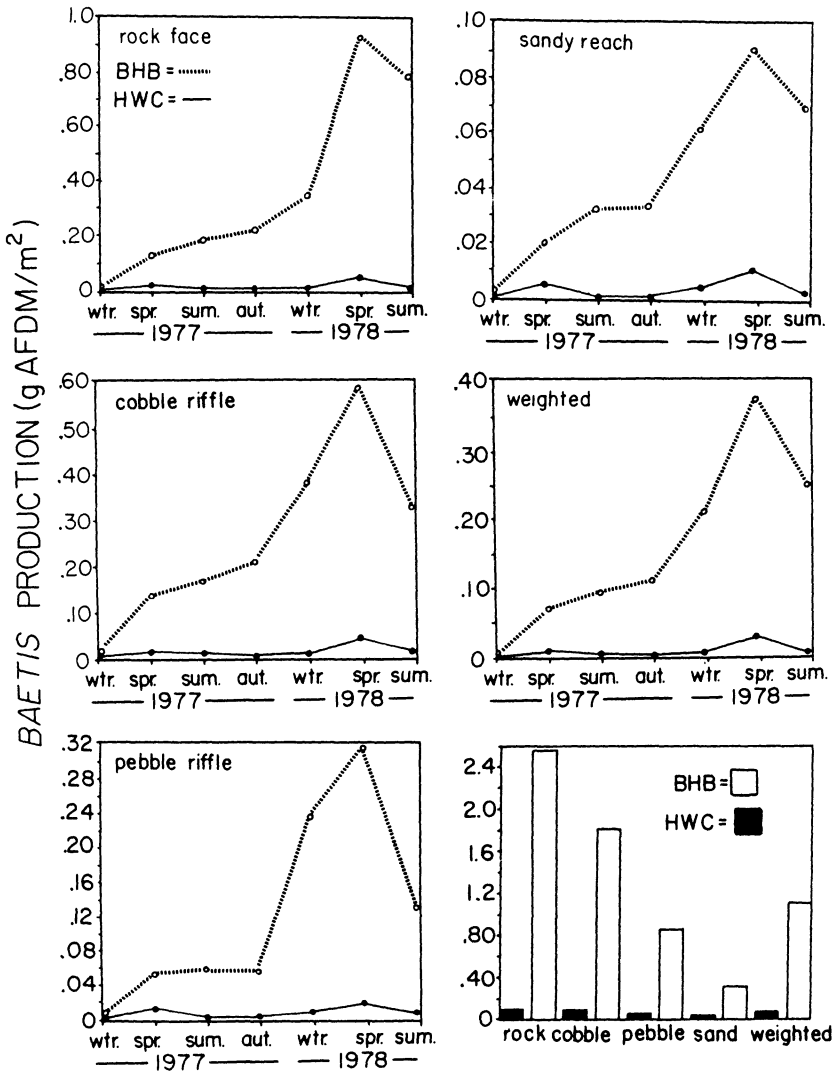


Fig. 1.—*Baetis* production (g AFDM per m<sup>2</sup>) for each season (winter = January-March; spring = April-June; summer = July-September; and, autumn = October-December) on various substrates (rock face, cobble riffle, pebble riffle and sandy reach) of Big Hurricane Branch (BHB) and Hugh White Creek (HWC). Weighted production is based on the proportion of each stream occupied by each substrate type. Logging was initiated on the BHB catchment in January 1977 and site preparation (removal of streamside vegetation and logging slash from stream) was completed by early autumn 1977. Note different scales on figures and that the pattern of response is basically similar for all substrates in BHB, only the magnitude was different. Bar graph, lower right, represents the cumulative *Baetis* production (g AFDM per m<sup>2</sup>) for the 21-month period by substrate in each stream

diatom content in their guts as compared to *Baetis* in HWC (Table 3 and Fig. 2); this certainly suggests a much higher diatom consumption rate/m<sup>2</sup> in BHB. Filamentous algae and vascular plant detritus comprised less than 0.1% of the gut contents in both streams and no evidence of animal consumption was observed in the 156 guts examined.

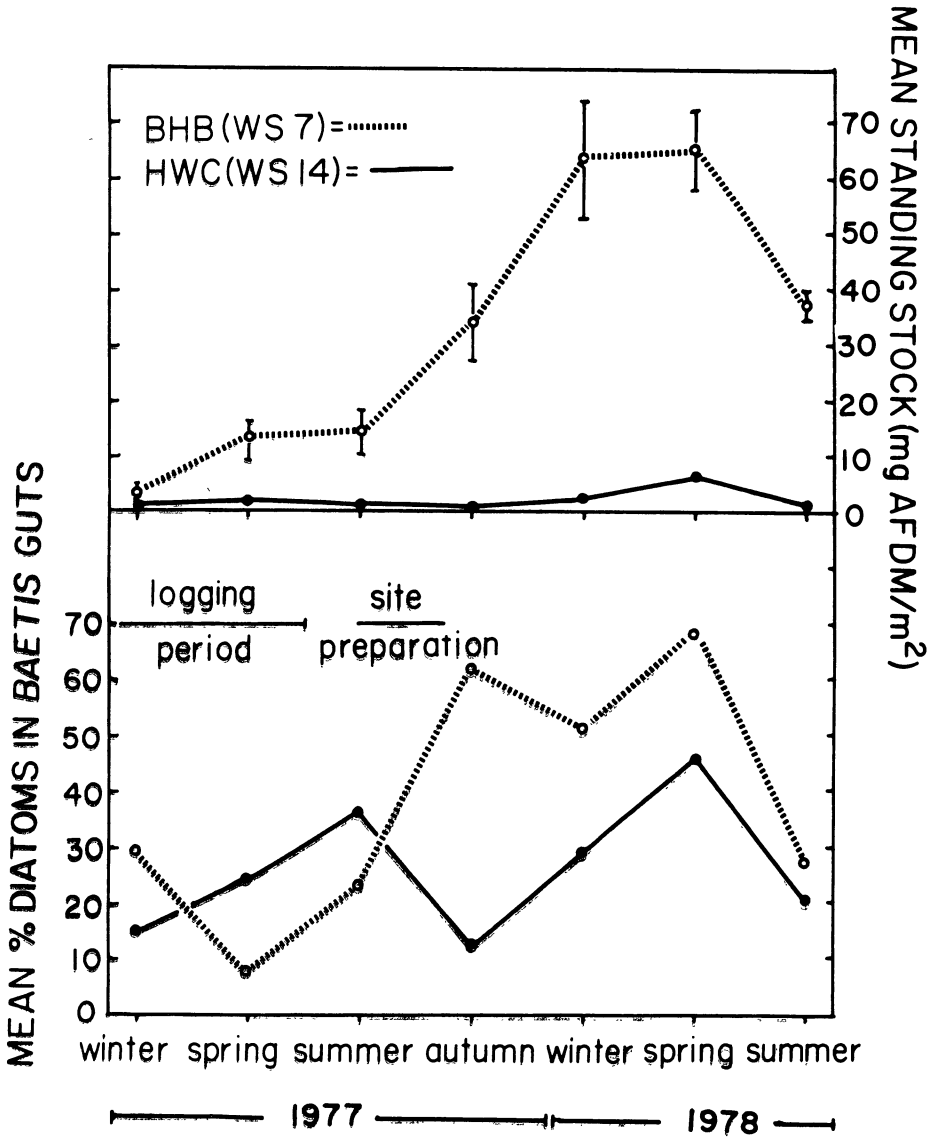


Fig. 2. — Mean (weighted) standing stock biomass of *Baetis* spp. in HWC and BHB (bars on BHB = sp of weighted monthly means, n = 12/season). Lower figure, mean percent (by projected area — see text) of diatoms in *Baetis* guts (all habitats) by season. Note that following the clear-cut and streamside vegetation removal (site preparation), *Baetis* guts from BHB had 1.2-2 X the diatom content of those from HWC while BHB had 10-30 X more standing stock biomass. This indicates a much greater diatom consumption per m<sup>2</sup> of substrate in BHB

Diatoms composed up to 80% of the gut contents of some *Baetis* specimens from the rock face substrate in BHB ( $\bar{x}$  = 53.1% diatoms) compared to those collected in the cobble riffle and pebble riffle substrates ( $\bar{x}$  = 37.2% diatoms). Seasonal mean percentages of diatoms in guts were significantly higher ( $P < 0.05$ , paired t-test, arcsine transformation) for specimens from rock face substrates than from cobble riffle and pebble riffle substrates (summer 1977 through late summer 1978). Although insufficient data were available to allow comparable testing between the cobble and pebble riffle habitats, the mean percentage of diatoms was higher in the cobble riffle ( $\bar{x}$  = 38.3%) than in those from the pebble riffle ( $\bar{x}$  = 34.4%) following clear-cutting.

*Trophic basis of production.*—Production estimates and *Baetis* foregut contents were used to estimate the trophic basis of production and food consumption necessary to support production (Benke and Wallace, 1980). We used the following literature values from several mayfly bioenergetic studies. For assimilation efficiency (assimilation/ingestion = AE), we used 33% for diatoms, 10% for detritus and 33% for fungal material. McCullough *et al.* (1979) found 33% AE for *Tricorythodes minutus* Traver nymphs feeding on mixed diatoms. We have not found literature values for AE of fungal material by mayflies; therefore, we assumed that it is assimilated with the same efficiency as diatoms (33%). Detritus assimilation efficiencies generally range from ca. 2-30% for aquatic insects, and it is traditionally presumed that the accompanying microbial biomass is the main food item associated with the latter (Ward and Cummins, 1979). However, Baker and Bradnam (1976) found little evidence of direct bacterial assimilation by *Baetis*, and Brown (1961) found gut passage time was only 30 min for *Baetis*; both of these findings suggest low assimilation efficiencies. Fisher and Gray (1983) found an average AE of about 10% for *B. quilleri* McDunnough nymphs feeding on detritus in a desert stream. Since the detritus in this desert stream contained a considerable amount of dead algae, the 10% AE we used for detritus may be an overestimate. We used 42% for a net production efficiency (production/assimilation = NPE). This NPE value is intermediate between 39% found by Fisher and Gray (1983) and 44.2% for *Isonychia bicolor* (Walker), reported by Sweeney (1978). The contribution of each food type (diatoms, amorphous detritus and fungi) to seasonal production was calculated us-

TABLE 3.—Seasonal means of gut contents (percent by projected area) of *Baetis* nymphs from Hugh White Creek (HWC) and Big Hurricane Branch (BHB) for winter 1977 through summer 1978

Season	HWC			BHB		
	Diatoms (%)	Amorphous detritus (%)	Fungi (%)	Diatoms (%)	Amorphous detritus (%)	Fungi (%)
Winter 1977	15.0	80.5	4.5	30.0	68.0	2.0
Spring 1977	24.0	76.0	0.0	7.5	92.5	0.0
Summer 1977	36.3	63.4	0.3	23.3	73.4	3.3
Autumn 1977	12.2	78.4	9.4	62.1	37.1	0.8
Winter 1978	29.1	67.0	3.9	50.9	48.5	0.6
Spring 1978	45.7	53.1	1.2	68.5	25.4	6.1
Summer 1978	20.7	75.6	3.7	26.7	72.2	1.1
mean for 1st 3 seasons <sup>a</sup>	25.1	73.3	1.6	20.2	78.0	1.8
mean for last 4 seasons <sup>b</sup>	26.9	68.5	4.6	52.1	45.8	2.1
mean for entire period	26.1	70.5	3.4	38.4	59.6	2.0

<sup>a</sup>corresponds to logging and site preparation

<sup>b</sup>postlogging period on Big Hurricane Branch

ing the above values for AE for various food types and 42% NPE following the procedure outlined by Benke and Wallace (1980).

Estimates of seasonal food consumption necessary to account for *Baetis* production are shown in Figure 3. The most striking difference between HWC and BHB is the large diatom consumption of BHB. Diatom consumption increased several-fold following logging and site preparation of the BHB catchment and was ca. 2.3 g AFDM per m<sup>2</sup> in spring 1978. By late summer 1978, diatom contents of foreguts, total diatom consumption and *Baetis* production were decreasing in BHB. Estimates of total food consumed by *Baetis* and their contribution to production indicate that, overall, diatoms comprise the most important food resource for *Baetis* in both HWC and BHB (Table 4). Amorphous detritus was the most important food resource contributing to production only during the initial logging operations on the BHB catchment, whereas diatoms represented about 70% of the assimilable calories for *Baetis* in BHB during the 1st year following deforestation of the catchment. The latter period corresponds with that of maximum *Baetis* production in BHB.

The values for production and consumption in Figure 1 and Table 4 are based on areal weighted values for each stream. *Baetis* biomass and production on the moss-covered rock face substrates were >2X higher than weighted stream biomass and production. Diatoms were also significantly higher in guts of *Baetis* nymphs from the rock face substrate. To account for the >2g AFDM per m<sup>2</sup> *Baetis* production in the rock face substrate, estimated diatom consumption was ca. 12 g AFDM/m<sup>2</sup> during the year following clear-cutting, or about 2X the weighted stream diatom consumption of 5.9 g.

#### DISCUSSION

*Baetis* production increased in all substrates of BHB following logging. This implies that the mechanisms responsible for the increase were ecosystem-level phenomena and

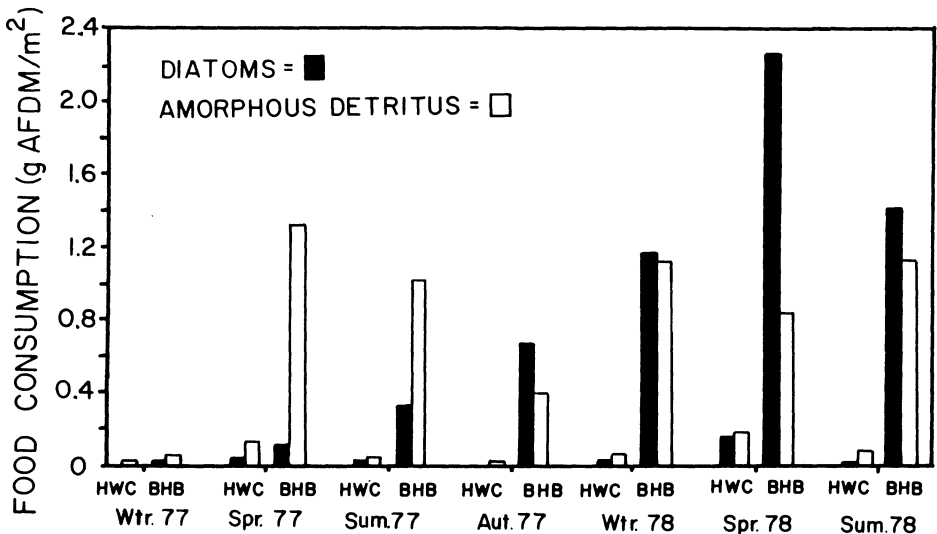


Fig. 3. — Estimated seasonal food consumption by *Baetis* in Hugh White Creek (HWC) and Big Hurricane Branch (BHB) based on areal percentage of food types in guts and literature-derived bioenergetic efficiencies and *Baetis* production in each stream (see text). Fungal material, which represented a minor portion of food consumed (Table 3), was omitted for clarity. Note that diatom consumption in BHB closely follows trends in production whereas amorphous detritus consumption in BHB does not (cf. with Fig. 1). The values are based on weighted stream production and guts analyzed from all substrate types. Rock face substrate *Baetis* consumed 2 X the diatoms shown here

were substrate-mediated to the extent that the magnitude of the response was greatest in the more physically stable substrates (Gurtz and Wallace, 1984). In all cases, *Baetis* production was more strongly skewed toward larger substrates in BHB than HWC (Fig. 4). For example, the ratios of *Baetis* production in the rock face/cobble riffle, cobble riffle/pebble riffle, and pebble riffle/sandy reach substrates of BHB were 1.47, 2.13 and 2.75, while those of HWC were 1.05, 1.83 and 1.94, respectively. BHB had more extensive sediment input during road-building, higher transport rates of organic and inorganic seston, and more extensive sand-dominated areas that began to erode with the removal of logging slash from BHB during the late summer of 1977 (Gurtz *et al.*, 1980). Larger substrates, associated with higher current velocities, were less susceptible to deposition of fine organic and inorganic particles (Gurtz and Wallace, 1984). The physically stable larger substrates, in conjunction with colonization by mosses, serve as sites for accumulation of algae. Hains (1981) observed that diatom cell counts were ca. 17 X higher in moss-covered substrates of BHB than in those of HWC.

— Diatoms generally comprised a smaller proportion of the *Baetis* food in HWC ( $\bar{X} = 26.1\%$ , Table 3) than BHB. This percentage is surprisingly high since autochthonous production in HWC was very low, 2.9 g DM·m<sup>-2</sup>·year<sup>-1</sup> (Hains, 1981; Webster *et al.*, 1983). Diatoms composed up to 60% of the gut contents in some *Baetis* from rock face and cobble riffle substrates in HWC during the spring of 1978. In fact, the latter *Baetis* contained more diatoms in their guts than organisms found in open sun-lit reaches of larger Coweeta streams (*cf.*, Georgian and Wallace, 1983). *Baetis tricaudatus* has been observed to spend more time foraging in patches with high periphyton densities than in areas with low periphyton densities (Wiley and Kohler, 1981). *Baetis* is placed in both the collector-gatherer and scraper functional groups by Merritt and Cummins (1978). In HWC and BHB, our species of *Baetis* seemed to function more as scrapers. They appeared to be too selective to be categorized as “collector-gatherers.” Only three pieces of vascular plant detritus, out of >8700 particles examined, were found in the contents of 156 guts examined from the two streams.

Estimated net primary production was 78 g AFDM·m<sup>-2</sup>·year<sup>-1</sup> in BHB and 2.6 g AFDM·m<sup>-2</sup>·year<sup>-1</sup> in HWC during 1977-1978 (Hains, 1981; Webster *et al.*, 1983). Estimated *Baetis* diatom consumption from autumn 1977 through summer 1978 was 5.788

TABLE 4.—*Baetis* production (mg AFDM/m<sup>2</sup>) attributable to various food materials in Hugh White Creek (HWC) and Big Hurricane Branch (BHB). Data are based on areal percentages of food in *Baetis* guts and assume an assimilation efficiency of 33% for diatoms and fungi, and 10% for detritus, and a net production efficiency of 42%. See Benke and Wallace (1980) for details of procedure

Season	Stream and food type					
	HWC			BHB		
	Diatoms	Amorphous detritus	Fungal material	Diatoms	Amorphous detritus	Fungal material
Winter 1977	0.6	1.0	0.2	3.2	2.2	0.2
Spring 1977	5.5	5.2	0.0	15.0	55.5	0.0
Summer 1977	3.6	1.9	0.0	44.6	42.6	6.3
Autumn 1977	0.4	0.7	0.3	92.3	16.7	1.2
Winter 1978	3.7	2.6	0.5	161.9	46.8	1.9
Spring 1978	21.6	7.6	0.6	312.5	35.1	27.8
Summer 1978	3.1	3.4	0.6	190.9	47.4	7.9
Total	38.5	22.5	2.2	820.5	246.3	45.3
Percent of total	61.0	35.6	3.4	73.9	22.1	4.0

g AFDM and  $0.234 \text{ g AFDM} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  in BHB and HWC, respectively (Table 3). Thus, the proportion of net primary productivity consumed by *Baetis* was 7.4% ( $[5.788/78] \times 100$ ) for BHB and 9.0% ( $[0.234/2.6] \times 100$ ) for HWC. BHB *Baetis* spp. probably consumed more than 7.4% as *Baetis* production was probably underestimated in BHB (see below). Notwithstanding the 28.9 X higher autochthonous production in BHB, these results suggest that a similar proportion of periphyton production was harvested by *Baetis* in each stream. Hains (1981) observed that algal cell counts/cm<sup>2</sup> remained relatively constant (about 17 X higher in rock face habitats from BHB than HWC) throughout his study, and primary production was much higher in BHB. He suggested several possibilities for constant cell counts, among them increased herbivory in BHB. Our results support this and reinforce Minshall's (1978) assertion that periphyton standing crop is not always indicative of productivity when heavily grazed by invertebrates (see Lamberti and Resh, 1983).

The actual production of *Baetis* in BHB is probably considerably higher than we have estimated since there are several potential sources of error associated with our production calculations. Losses of shed exuviae during molts represent ca. 45.6% of the total biomass production in the mayfly, *Isonychia bicolor* (Sweeney, 1978). *Baetis* spp. may molt about 25 times during their juvenile development (Berner, 1959). Since growth rates used in this study are based on field growth rates (Humpesch, 1979), exuviae losses are not taken into account in the present study.

Since temperature-based growth rates did not differ greatly between streams, the dramatic increase in production in BHB relative to HWC was primarily due to the

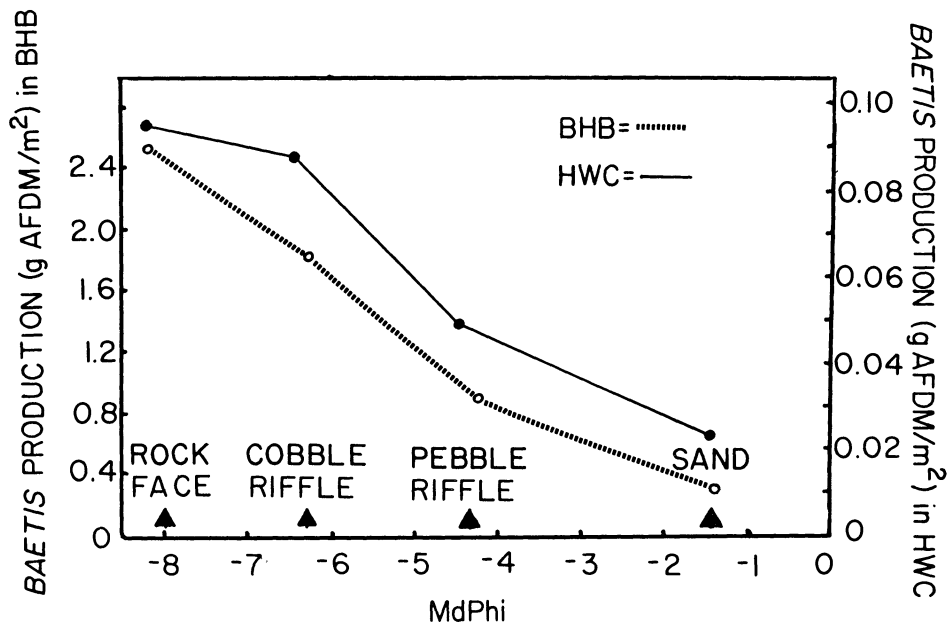


Fig. 4. — *Baetis* spp. production for different substrates in Big Hurricane Branch (BHB) and Hugh White Creek (HWC) based on the median Phi in each stream for various substrates ( $\Phi = -\log_2$  of substrate particle size in mm). Note that even with the much higher production in BHB, the same trends exist in each stream in that production on rock face substrate > cobble riffle > pebble riffle > sand. However, the distribution of production is more strongly skewed toward the larger, and more stable substrates in the disturbed catchment stream (BHB; slope =  $-0.35$ ) than in that of the reference stream (HWC; slope =  $-0.01$ ) (note very different scales for BHB and HWC)

large increase in standing stock biomass in BHB. Factors that might have influenced *Baetis* biomass in BHB include: (1) enhanced survivorship in BHB as compared to HWC; (2) lower drift losses in BHB; (3) higher values for G in BHB than those used here, which are based only on daily mean temperatures, and (4) possible enhanced recruitment of females to the sun-lit stream.

We have no evidence that enhanced survivorship resulting from lower predation is primarily responsible for the increase in biomass of *Baetis* in BHB. Mean densities of predators, based on weighted stream densities, did not change significantly during the study in BHB compared to HWC (Gurtz and Wallace, 1984). Predator densities actually increased in the rock face habitats in BHB, where *Baetis* production was highest, relative to HWC. Much of the increase in predators in rock face substrates of BHB was attributable to perlotid stoneflies (Gurtz and Wallace, 1984), which are known predators of *Baetis* (e.g., Peckarsky, 1980; Allan, 1982). The rapidly increasing populations of *Baetis* may have been subjected to a lower overall rate of predation if their initial increase exceeded the reproductive capacity of larger univoltine and semivoltine predators. We have insufficient data to investigate any potential lag time between *Baetis* and populations of predators. Faster growth rates may also enhance survivorship (see below).

Since production studies assume that immigration and emigration are in equilibrium (Waters, 1966), drift losses represent potential sources of errors in our estimates. Comparative drift losses from the two catchments are available for 15-16 July 1977. During this 24-hr period the *Baetis* drift density (#/100 m<sup>3</sup> of discharge) = 6.4 for HWC and 200.6 from BHB. Stream discharge during this 24-hr period was 640.8 m<sup>3</sup> for HWC vs. 1087.2 m<sup>3</sup> for BHB. Drift losses from each catchment on the above date may be estimated as a percentage of the entire upstream source area on either catchment: (total number drifting/[stream area X weighted standing stock density]) X 100. The percentage of *Baetis* exported per day from HWC was 0.060% vs. 0.315% for BHB. Thus, the daily drift loss for BHB on this date, as a proportion of the total standing stock was 5.22 X higher than that of HWC. Subsequent data from 1977-1978 suggest that these high drift losses from BHB vs. HWC were maintained or exceeded (J. O'Hop, pers. comm.).

The growth rates used for *Baetis* spp. in BHB may be higher than those used here. McCullough *et al.* (1979) reported daily growth rates for *Tricorythodes minutus* ranging from 12.6-15%. Hall *et al.* (1980) indicated daily growth rates of ca. 15% for *Tricorythodes atratus* McDunnough. Brittain (1975) found that *Baetis macani* Kimmins completed larval development in 1 month in a Norwegian lake at temperatures < 8 C. Gray (1981) and Fisher and Gray (1983) found *B. quilleri* required only 10-13 days for juvenile development in a desert stream with summer temperatures of 20-28 C. Although most *Baetis* spp. are multivoltine (Clifford, 1982), our study is confounded by the presence of several species which can only be identified in later instars with existing keys (i.e., Morihara and McCafferty, 1979). It is questionable that all species have the same temperature-dependent growth rates at temperatures that range from 0.5-20.5 C as found in this study. Growth rates used here for BHB may be underestimates because of higher maximum temperatures in BHB and increased diel temperature fluctuation of 2 C following the clear-cut (Swift, 1983). Maximum diel fluctuation occurred in April and September in BHB, 5.9 and 4.5 C, respectively, while in HWC maximum diel change was greatest in April (2.4 C) and November (1.5 C). Sweeney (1978) showed that development rates for *Isonychia bicolor* (Walker) were positively correlated with increased magnitude of diel temperature pulse.

Food quality in combination with temperature may also influence growth rates (e.g., Anderson and Cummins, 1979). Solar radiation to BHB increased following logging, as did concentrations of several nutrients (W. Swank, pers. comm.). During the period of October 1977 to September 1978, total net autochthonous production in BHB was ca. 29.8 X more than that of HWC (Hains, 1981; Webster *et al.*, 1983). Aquatic inverte-

brate assimilation efficiencies and relative growth rates are considerably higher (3-4 X) for algae than detritus (*e.g.*, Fuller and Mackay, 1981). Thus, potentially enhanced growth may result from increased food quality and abundance via several pathways: (1) higher assimilability per unit mass of food; (2) less energy expenditure in feeding per assimilable calorie, and (3) less searching time for food and hence lower energy expenditure. Therefore, increased food quality and abundance in BHB may result in higher *Baetis* growth rates compared to HWC.

Higher growth rates of *Baetis* in BHB could result in shorter life cycles, thereby increasing voltinism and recruitment. Whereas higher temperatures and faster growth rates may result in smaller terminal body size and fewer eggs per female (Sweeney, 1978), increased food quality may have a positive influence on body size and fecundity (Anderson and Cummins, 1979; Colbo and Porter, 1981). Lower fecundity/individual may also be partially offset by increasing voltinism. Assuming that the rate of mortality of *Baetis* for an exponential survivorship curve would be relatively constant for a species regardless of length of life cycle, then shorter life cycles would result in a higher proportion of offspring reaching the reproductive stage at an earlier age. This could effectively increase survivorship. Diel temperature fluctuation, in combination with potentially higher food quality and abundance, would result in higher values for growth in BHB than those based on slightly elevated temperature regimes. These in turn may influence survivorship and fecundity if more individuals reach the reproductive stage at an earlier age.

The response of *Baetis* to the clear-cut was not long-lasting. Subsequent seasonal samples during 1982 and 1983-1984 indicate large declines in *Baetis* populations as streamside vegetation formed a rather dense canopy over BHB. Likewise, periphyton primary production in BHB had decreased from 78 g AFDM m<sup>-2</sup> year<sup>-1</sup> in 1977-1978 to 7.9 g in 1980-1981 (Webster *et al.*, 1983). The decline in *Baetis* populations in BHB coincides with the 10-fold decrease in primary production. Conversely, the initial increase in *Baetis* production closely parallels that of elevated levels of primary production in BHB following logging. These observations provide strong inference that *Baetis* populations were responding directly to changes in autochthonous production. These processes can be traced to abiotic changes associated with light, nutrients and temperature following logging.

Taxa other than *Baetis* which may exploit these short-term increases in primary production include the Chironomidae, other baetids such as *Pseudocloeon* spp., and Ephemerellidae (Ephemeroptera). *Baetis* spp. abundances were >10X that of *Pseudocloeon* spp. in BHB. *Pseudocloeon*, with multivoltine life cycles (Clifford, 1982), was largely confined to the lower elevations of BHB and was negatively correlated with elevation in BHB (Gurtz, 1981). Several genera, *sensu stricto*, and species of Ephemerellidae, which are primarily univoltine (Clifford, 1982), also increased in BHB, primarily in the lower reaches of the stream (Gurtz and Wallace, 1984). However, following the clear cut, overall abundances of ephemerellids in BHB were only 4 X that of HWC vs. 20 X for *Baetis*.

In summary, species with short, multivoltine life cycles and high fecundity possess the ability to assume a dominant role in processing stream energy inputs. In desert streams subject to severe and unpredictable flooding, the majority of macroinvertebrates, including *Baetis*, possess these characteristics (Gray, 1981; Fisher and Gray, 1983). In physically stable, heavily shaded Coweeta headwater streams (*i.e.*, HWC), *Baetis* comprise a minor component of the standing stock biomass. However, the potential importance of these species in such streams should not be underestimated. When "typical" heterotrophic energy pathways of these streams are altered by disturbances, species such as *Baetis* may assume major roles in processing energy inputs. Larger univoltine or semivoltine species probably could not respond as quickly in order to exploit the relatively short-lived 2-year abundance of periphyton to the extent that *Baetis* did in



this study. In this respect, the response of *Baetis* to disturbance is somewhat similar, albeit slower and of lower magnitude, than those of invertebrates in desert streams.

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