Reprint

#3

Freshwater Biology (1986) **16,** 287–300

Effects of overhead canopy on macroinvertebrate production in a Utah stream

DAVID J. BEHMER and CHARLES P. HAWKINS* Department of Biology and
Chemistry, Lake Superior State College, Sault Ste. Marie, Michigan 49783,
and *Department of Fisheries and Wildlife and Ecology Centre, UMC 52,
Utah State University, Logan, Utah 84322, U.S.A.

SUMMARY. 1. Macroinvertebrate abundance and production were compared between an open and shaded site of a stream in the Wasatch Mountains, Utah. Mean biomass was significantly higher at the open site for midges (Chironomidae), 4.6×; *Baetis bicaudatus,* 5.7×; *Baetis tricaudatus,* 2.3×; *Drunella coloradensis,* 12× and *Cinygmula* sp., 1.6×. Abundance of most other macroinvertebrates (except black flies: Simuliidae) was also greater at the open site, but differences were not significant. Black fly biomass was 1.7× greater at the shaded site.

2. Seasonal production, estimated by the size–frequency and instantaneous growth rate methods, was greater at the open site than the shaded site for most taxa (except black flies) and reflected differences in standing crops between the sites rather than differences in rate of growth. Excluding black flies, production at the open site was twice as high as at the shaded site.

3. The greater abundance and production of most invertebrate taxa at the open site is probably associated with either higher quality food (algae and algal detritus), or a phototactic attraction to sunlit areas.

4. Sampling of large cobbles was an efficient method of sampling all taxa except *Cinygmula* sp. which was more abundant on smaller substrate particles.

Introduction

Human activities influence the amount of riparian vegetation along stream banks. Fish managers often recommend removal of riparian trees and shrubs along trout streams to increase sun-light penetration and allow increased growth of algae and aquatic macrophytes within the stream (White & Brynildson, 1967; Hunt, 1979). The enhanced plant growth is assumed to increase stream productivity by increasing the base of the food chain and preventing fine sediments from shifting over gravel and rubble. The coarse substrates provide trout spawning sites and habitat for many invertebrates consumed by trout.

Correspondence: Dr David J. Behmer, Department of Biology and Chemistry, Lake Superior State College, Sault Ste. Marie, Michigan 49783, U.S.A.

In western states of the U.S.A., clear-cut logging operations, grazing, and other activities have removed much of the riparian canopy along many streams. The invertebrate community response to removal or modification of the riparian vegetation has been the topic of a number of recent studies (e.g. Newbold, Erman & Roby, 1980; Murphy, Hawkins & Anderson, 1981; Hawkins *et al.*, 1983). Although erosion and sedimentation confound effects, the evidence from these studies suggests that streams with open canopies are more productive than similar shaded streams. However, studies of stream invertebrates usually measure only invertebrate density and biomass. Recent authors have suggested or shown that production is a better measure of the relationship between invertebrates and their environment (Benke, Van Arsdall & Gillespie, 1984; O'Hop, Wallace & Haefner, 1984). To date, however, few workers have measured production for all the invertebrates in a stream (Hopkins, 1976; Neves, 1979; Krueger & Waters, 1983; Benke *et al.*, 1984), and only Hopkins (1976) related production of the entire fauna to riparian vegetation.

The primary objective of this study was to compare production of the invertebrate fauna between two sites that contrasted in canopy cover within the same nonperturbed stream.

Methods

Study sites

The left fork of the Blacksmith Fork River is a third order stream located in the Wasatch Mountains, Cache County, Utah, U.S.A. The drainage basin is arid, mountainous and sparsely forested, mostly with Utah juniper (*Juniperus osteosperma* Little). Vegetation along the stream is much denser. Riparian tree species usually consist of willow (*Salix* spp.), narrowleaf cottonwood (*Populus angustifolia* James) and box elder (*Acer negundo* Jaeg. & Beissn). The geology of the surrounding area consists of limestone rock formations. The stream bottom in the research area is mostly cobbles and gravel, with some sand and very little silt. The stream is supplied with a constant supply of cool groundwater in all seasons.

Open and shaded research stations were chosen at the site of the Friendship Campground, U.S. Forest Service, approximately 4.8 km upstream from the junction of the Left Fork with the mainstem of the Blacksmith Fork River. The campground was closed because of flood damage in 1982 and 1983 and the site is now relatively undisturbed by human activity. Two 30 m research sites were chosen to represent stream segments with contrasting degrees of overhead canopy. Streambed shading was measured with an angular densiometer (Brown, 1969) as percentage of overhead canopy. The sites were located in close proximity to minimize physical differences other than shading. The open site (4% canopy) was 80 m upstream from the shaded site (61% canopy). Average overhead canopy of seven random sites within ±4 km of the research area was 35%; the research sites represent approximate extremes in canopy for the general area.

The research sites were similar in physical characteristics (Table 1). Water chemistry measurements taken by Osborn (1981) indicate that the Left Fork is a hardwater stream with relatively high levels of phosphorus and nitrogen. Water levels and discharge did not vary greatly during the study. Maximum daily temperature was near constant during the study (10–11°C) except for the last sampling date when it reached a low of 8°C. The percentage of streambed consisting of cobbles >10 cm longest dimension (Table 1) was approximated visually from ten random transects taken across each site.

Field and laboratory methods

Sampling of stream invertebrates poses many problems. All samplers have limitations (Hynes, 1970) and habitat and substrate diversity contribute to the high variability associated with benthic samples. Most stream production researchers have sampled only riffle areas of streams (e.g. Waters, 1966; Pearson & Kramer, 1972; Waters & Crawford, 1973; Neves, 1979; Kreuger & Waters, 1983). Conventional samplers such as the Surber or Hess are difficult to use if the streambed contains many large cobbles. Researchers have used individual cobbles as sampling units for various purposes (e.g. Thorup, 1966; Corkum & Pointing, 1979; Cuffney & Minshall, 1981), but only Neves (1979) based production estimates on sampled cobbles. In this study we sampled two

TABLE 1. Physical characteristics (July–October 1984) of open and shaded study sites, and general chemical characteristics (1979–80) of the Left Fork of the Blacksmith Fork River

	Physical characteristics	
	Open site	Shaded site
Overhead canopy (%)	4	61
Average water temperature (°C)	10	10
Average velocity ($m\ s^{-1}$)	0.9	0.8
Average width (m)	8.5	6.9
Average depth (cm)	23	33
Average discharge ($m^3\ s^{-1}$)	1.8	1.8
Cobbles >10 cm longest dimension (%)	49	44

Chemical characteristics—from Osborn (1981)	
Total alkalinity ($mg\ l^{-1}$ as $CaCO_3$)	194
Total dissolved phosphorus ($\mu g\ l^{-1}$)	12.2
Nitrate nitrogen ($\mu g\ l^{-1}$)	170
pH	7.7

similar riffle habitats and used individual cobbles as sampling units.

Ten samples were collected from each study site on 6 July, 25 July, 19 August, 14 September and 8 October 1984. A pair of random numbers was used as coordinates to randomly locate each sample. Cobbles >10 cm (longest dimension) were used exclusively as samples on the first two sampling dates. At each site on 19 August and subsequent sampling dates we collected five cobbles (>10 cm) and five samples from a 655 cm^2 area of the streambed containing no cobbles >10 cm. The latter samples (termed intercobble samples) were paired with the cobble samples; each was collected within 0.5 m of the randomly located cobble sample.

Cobble samples were collected by placing a back-up net (mesh size 0.67×0.84 mm) immediately downstream from each cobble while lifting the cobble from the stream bottom. Organisms dislodged in the sampling process and trapped in the net were included with the sample. Organisms were brushed from the cobble into a pan of water and the contents of the pan were poured through a Tyler sieve with 0.5 mm mesh for collection and transfer to Kahle's solution. The greatest length, width and height of each cobble were measured for later calculation of cobble surface area.

Intercobble samples were collected with the same net used for cobble samples. A wire loop attached to the straight leading edge of the net was laid on the stream bottom upstream of the net. The loop defined an area of 655 cm^2 and the substrate inside the loop was thoroughly disturbed to a depth of about 2 cm. All small cobbles (<10 cm) were brushed clean of organisms or placed inside the net, and the net contents were collected as previously described.

Organisms were identified to the species level where possible, although no attempt was made to identify species of taxa that occurred uncommonly. Organisms were sorted, counted and grouped into 1.0 mm length classes with the aid of a binocular microscope. Length measurements of mayfly and stonefly nymphs were from the tip of the head to the end of the abdomen. Dry weights in mg (mgDW) were calculated with length–weight equations from various sources. General equations used for Simuliidae and Chironomidae were taken from Smock (1980). Smock's general equation for larval caddisflies was used for the several species of Rhyacophilidae. Unpublished equations of K. W. Cummins were used for weight calculation of *Baetis bicaudatis* Dodds, *Baetis tricaudatis* Dodds, *Cinygmula* sp., *Serratella tibialis* McDunnough, and miscellaneous slender Plecoptera. We developed equations for *Epeorus longimanus* (Eaton), *Arctopsyche grandis* (Banks), *Glossosoma* sp., *Hesperoperla pacifica* Illies and *Drunella coloradensis*

Dodds based on specimens oven-dried to constant weight. The equations for *H. pacifica,* and *D. coloradensis* were calculated from preserved specimens. Total weight (biomass) for each important taxon was calculated for each sample as the sum of products of geometric mean weight and number of individuals for 1.0 mm size classes.

Total surface area of each of ten cobbles randomly picked from the study sites was determined by wrapping the cobble in aluminium foil and estimating the area with graph paper. Planar area of each of these cobbles was estimated by tracing the perimeter of the cobble onto graph paper. These area estimates, and the three linear measurements made on each cobble, were used to develop equations for estimating surface area of cobbles.

One algal species, *Hydrurus foetidus* (Vill.) Kirchn., was common on cobbles at the open site in the early part of the study. The dry mass of *H. foetidus* was measured for nineteen cobbles from the open site for correlation with invertebrate abundance.

Analysis of densities and biomass

Numbers and biomass of organisms for sampled cobbles generally increased with size of the cobble. To express these per unit area we divided number and biomass of each taxon by the area of the cobble. Total surface area and planar area of each sampled cobble was estimated by the following equations developed from ten cobbles:

$$\text{Planar area (cm}^2) = -12.48 + 0.810LW - 0.356D \qquad (1)$$

$$\text{Total surface area (cm}^2) = -23.50 + 0.723L^2 + 1.886W^2 + 1.744D^2 \qquad (2)$$

where L (cm) is the longest horizontal dimension of the cobble, W (cm) is the longest horizontal dimension perpendicular to L, and D (cm) is the greatest vertical dimension. Coefficients of determination (r^2) for these equations were: equation (1), 0.962; equation (2), 0.994.

Average densities (m^{-2}) and biomass (m^{-2}) of important taxa, and the variances of these estimates, were calculated for nontransformed data by formulae of Cochran (1977):

$$R = \sum^{n} Y / \sum^{n} X = \bar{Y}/\bar{X} \qquad (3)$$

$$s_R^2 = \frac{1}{nX^2}\left(\frac{\sum^{n} Y^2 - 2R\sum^{n} XY + R^2 \sum^{n} X^2}{n-1}\right) \qquad (4)$$

where R is an average ratio, Y is density or biomass, X is area of the cobble and n is the number of samples.

For intercobble samples, where the streambed area sampled (X) was the same for each sample (655 cm^2), conventional methods of estimating the mean and variance were used. Cochran's (1977) methods also reduce to conventional estimates when X is constant.

Variances of densities and biomass increased with the mean for all taxa indicating the need for data transformation before statistical analyses could be performed. The method proposed by Taylor (1961) was used to choose a variance-stabilizing transformation. The linear regression of log variance on log mean was calculated for densities of all important taxa. Random distribution of organisms (Poisson model) is indicated when slope (b) and exponentiated intercept (a) of this regression are both 1. Although some values of b were near 1, values of a were never close to 1. Downing (1979) also found the Poisson distribution a poor model for benthos populations. Most b values were near 2 suggesting a logarithmic transformation (Elliott, 1977). After trying several forms data were transformed with $\log_e \{(Y+1)/X\}$, where Y is density or biomass and X is area sampled. This transformation was applied to all taxa although some taxa had b values close to 1 indicating that the square root transformation would be more appropriate. Use of the logarithmic transformation for all taxa allowed consistency in calculation of confidence limits for mean densities and biomass; these were calculated for transformed means but applied to the arithmetic means as described by Elliott (1977).

Two-way analysis of variance (ANOVA) of transformed data was used to test significance of differences in densities and biomass between open and shaded sites. Although canopy as such was not replicated in this study, we argue that significant differences between sites most probably are due to canopy effects (see Discussion).

Relative abundance of invertebrates on cobbles compared to intercobble substrate was estimated by dividing the biomass (m^{-2}) of each cobble sample by the biomass (m^{-2}) of its paired intercobble sample. Means and variances of these ratios were calculated by equations (3) and (4) and *t* tests of differences between mean ratios for open and shaded sites were applied to log-transformed data.

Production estimates

For all important taxa, production was estimated by the size–frequency method first proposed by Hynes (1961) and modified by Hamilton (1969). Annual estimates of production including Benke's (1979) modification were calculated as:

$$P=\{\Sigma(\bar{n}_j-\bar{n}_{j+1})\,(W_jW_{j+1})^{1/2}\}i(365/\mathrm{CPI}) \quad (5)$$

where n_j is the mean number of individuals in size class *j*, W_j is the weight at median length of size class *j*, *i* is the number of length classes through which a species or a group of species grows and CPI is the cohort production interval. To change this calculation for seasonal rather than annual estimates of production, the last two terms were modified. An assumption of the size–fequency method is that growth in length is linear with time. The length classes in this study were 1 mm in length. The number of these classes for a taxon (*i*) was considered an estimate of the maximum length attained. The CPI was measured in days. The value *i*/CPI then estimates the daily growth rate in length of the taxon. The estimated average daily growth in length of each taxon was used in place of *i*/CPI in our modified equation and multiplied by the actual number of days for which production was estimated (rather than 365). When separation of individual cohorts was possible, we also used the instantaneous growth rate (IGR) method to estimate production.

Growth estimates for *S. tibialis* were easily made because a single cohort was present and recruitment of new individuals by growth into the cohort did not occur. Recruitment of individuals by growth into the populations of *E. longimanus*, *Cinygmula* sp., *A. grandis* and *Glossosoma* sp. occurred throughout the study. To eliminate the bias to growth estimates caused by recruitment we assumed linear growth in length (an assumption of the size–frequency method) and adjusted the length–frequency distributions of these organisms for each sample except the first by iteratively solving the following equation:

$$M_{j+1}-M_j=L_{j+1}-L_j \quad (6)$$

where M_j is the minimum length of the taxon at sampling date *j*, M_{j+1} is a trial value of a new minimum length for sample $j+1$, L_j is the mean length on date *j* and L_{j+1} is the mean length on sampling date $j+1$ excluding organisms less than length M_{j+1}. A computer was used to solve the equation for M_{j+1} which was then used as the lower boundary of the length–frequency distribution of sample $j+1$. Organisms $<M_{j+1}$ in length were considered 'recruits' and dropped from the length–frequency distribution.

We used the adjusted frequency distributions to calculate adjusted mean weights for calculation of instantaneous growth rates used in IGR production estimates, and the same distributions were used to generate adjusted mean lengths. Average daily growth rates in length were estimated by slopes of least squares regressions of adjusted mean lengths versus time in days; regression formulae were also used to estimate the standard errors of these estimates. Data from only cobble samples were used to estimate mayfly growth rates because intercobble samples were not taken throughout the study. However, growth rates of *Glossosoma* sp. and *A. grandis* were pooled estimates based on both types of samples (separate calculations of growth rates for each sample type did not differ significantly).

Where growth rates were difficult or impossible to estimate it was necessary to choose a value for the CPI to estimate production. Choosing a CPI for midges and black flies is particularly difficult because literature estimates of field growth rates are generally lacking. Benke *et al.* (1984) have thoroughly reviewed the available literature on these groups and we relied heavily on their review in choosing our CPI values. Midges in this study grew to a maximum length of about 8 mm. Benke *et al.* (1984) used 20 or 23 days as the CPI for midges with similar maximum size. The average temperature in their study was 19.0°C. The mean water temperature in this study was 10.0°C. We therefore doubled

Benke's CPI values resulting in a CPI value of 40 days for midges. Benke *et al.* (1984) used an 18 day CPI for black flies that had a maximum size of about 5 mm. McCullough, Minshall & Cushing (1979) reported a larval stage of <28 days for Simuliids at a mean temperature of 15.5°C. Because black flies in this study reached lengths of 7 mm a CPI of 40 days also seemed appropriate.

B. bicaudatus and *B. tricaudatus* are very similar species. Because each reached a maximum length of 6 mm we have assumed equal growth rates for the two species. Data of Waters (1966) indicate an approximate CPI of 50 days for *B. tricaudatus* at temperatures ranging from 14 to 20°C. However, Corkum & Pointing (1979) indicate a much longer CPI for *B. tricadudatus*; from their data we estimate a CPI of 105 days at an average temperature of 14°C.

Both *Baetis* species apparently had two summer generations in this study. Nymphs developed black wing pads at lengths of approximately 5 mm. Peak densities of nymphs >5 mm occurred on 25 July and on 8 October; the latter date is not a true peak but was the last sampling date. The true peak probably occurred in late October indicating approximately 90 days for a generation including the egg stage.

Although it was not generally possible to estimate growth rates of *Baetis* spp., because of biases due to recruitment and emergence, the period from 9 September to 8 October was used to generate recruitment-adjusted growth rates as described above. Bias from emergence was minimal during this period. Estimates of growth in length for this period ranged from 0.0708 to 0.0808 mm day^{-1} and provide estimates of 74–85 days for *Baetis* spp. to grow 6 mm. We chose a CPI of 80 days for both *Baetis* spp.

Although methods for calculating confidence intervals have recently been reported for size–frequency production estimates (Krueger & Martin, 1980), we have followed Benke *et al.* (1984) in not calculating them. The method assumes that growth is estimated without error. Furthermore, the assumption of normality of data necessary for hypothesis tests and confidence intervals is violated by production estimates, because invertebrate densities and biomass typically do not follow the theoretical normal distribution, and data transformations cannot be incorporated into the methods of Krueger & Martin (1980).

Results

Total surface area estimates of ten cobbles estimated by equation (2) were all within 9% of the actual areas. Planar area estimates of the same ten cobbles by equation (1) were within 16% of the actual planar area measurements. Although equation (2) ($r^2=0.994$) gave better results than equation (1) ($r^2=0.962$), correlation analysis indicated little difference between the two measures of area as predictors of numbers or biomass of organisms sampled. Examination of sixty correlations of number and biomass of various taxa with total cobble surface and sixty correlations of the same numbers and biomass with planar area showed thirty-four of the correlations to be higher with planar rock area. This result indicated that planar area was just as good a predictor of numbers and biomass as total cobble surface. Estimates based on planar areas are also more comparable to studies based on conventional samples; therefore all calculations below are reported in terms of planar area.

Average density, average biomass, and epilithic production of important taxa were estimated for the time period when sufficient numbers of these organisms were present in samples (Table 2). Mean biomass and density were generally greater at the open site and were significantly greater for *Baetis bicaudatus* ($P<0.0005$), *B. tricaudatus* ($P<0.0005$), midges ($P<0.0005$), and *Cinygmula* sp. (biomass, $0.001<P<0.002$; density, $0.01<P<0.02$). Black fly abundance and production appear to be considerably higher for the shaded site, but black flies were very contagious in distribution. Because high variances were associated with black fly estimates, differences did not approach significance (density, $P>0.5$; biomass, $0.2<P<0.5$). Density and biomass differences were tested by two-way ANOVA (site versus date) and results were consistent for all taxa except *Glossosoma* in that site×date interactions did not occur. *Glossosoma* sp. was more abundant in samples taken from the shaded site on 19 August but was

TABLE 2. Mean density ($\bar{N}$) and biomass ($\bar{B}$) and epilithic production of nine taxa for open and shaded study sites. Production estimates are by size–frequency and instantaneous growth rate (IGR) methods. Estimates of daily growth rates in length are given with ±2 standard errors. Confidence limits (95%) for mean densities and biomass are based on transformed data, but means are of original data.

Taxon	Time period (days)	Canopy cover	Mean daily growth rate (mm day^{-1}) or CPI	Density $\bar{N}$ (no. m^{-2})	Biomass $\bar{B}$ (mgDW m^{-2})	Epilithic production Size-freq.	Epilithic production IGR
Epeorus longimanus	7/6–8/19 (44)	Open	0.0434±0.0161	$502\overset{\times}{\div}1.31$	$435\overset{\times}{\div}1.43$	361	357
		Shade	0.0360±0.0284	$386\overset{\times}{\div}1.31$	$290\overset{\times}{\div}1.43$	212	226
Cinygmula sp.*	7/6–8/19 (44)	Open	0.0454±0.0360	$419\overset{\times}{\div}1.28$	$320\overset{\times}{\div}1.31$	369	316
		Shade	0.0646±0.0342	$257\overset{\times}{\div}1.28$	$199\overset{\times}{\div}1.31$	322	245
Serratella tibialis	7/6–8/19 (44)	Open	0.0610±0.0136	$236\overset{\times}{\div}1.44$	$55\overset{\times}{\div}1.31$	117	133
		Shade	0.0635±0.0064	$133\overset{\times}{\div}1.44$	$48\overset{\times}{\div}1.31$	93	108
Glossosoma sp.	8/19–10/8 (50)	Open	0.0227±0.0037	$1846\overset{\times}{\div}1.39$	$697\overset{\times}{\div}1.23$	689	558
		Shade	0.0196±0.00045	$1431\overset{\times}{\div}1.39$	$452\overset{\times}{\div}1.23$	408	323
Arctopsyche grandis	8/19–10/8 (50)	Open	0.126±0.0745	$512\overset{\times}{\div}1.44$	$730\overset{\times}{\div}1.43$	1596	1790
		Shade	0.132±0.0620	$546\overset{\times}{\div}1.44$	$815\overset{\times}{\div}1.43$	1886	1979
*Baetis bicaudatus**	7/6–10/8 (94)	Open	CPI=80 days	$2214\overset{\times}{\div}1.33$	$284\overset{\times}{\div}1.22$	1676	—
		Shade	CPI=80 days	$630\overset{\times}{\div}1.33$	$50\overset{\times}{\div}1.22$	335	—
*Baetis tricaudatus**	7/6–10/8 (94)	Open	CPI=80 days	$3565\overset{\times}{\div}1.25$	$377\overset{\times}{\div}1.20$	2333	—
		Shade	CPI=80 days	$1731\overset{\times}{\div}1.25$	$166\overset{\times}{\div}1.20$	1053	—
Chironomidae*	7/6–10/8 (94)	Open	CPI=40 days	$2431\overset{\times}{\div}1.40$	$144\overset{\times}{\div}1.23$	2035	—
		Shade	CPI=40 days	$471\overset{\times}{\div}1.40$	$31\overset{\times}{\div}1.23$	423	—
Simuliidae	7/6–10/8 (94)	Open	CPI=40 days	$3104\overset{\times}{\div}1.82$	$473\overset{\times}{\div}1.78$	4581	—
		Shade	CPI=40 days	$4983\overset{\times}{\div}1.82$	$820\overset{\times}{\div}1.78$	7873	—

*Mean density and biomass significantly greater for open site at $P<0.01$.

more abundant in the open samples thereafter. Differences in production between open and shaded sites were not tested statistically (see explanation in previous section), but these differences show the same trend as differences in mean biomass.

It was not possible to estimate growth rates of all taxa, but when estimated, growth rates (mm day^{-1}) did not differ significantly between sites and generally did not contribute greatly to differences in production estimates between canopy types (Table 2). However, all growth rates were calculated from only three estimates of mean length. Confidence limits for these estimates are too wide to be useful with only one degree of freedom, but standard errors of the estimates are given in Table 2.

Daily $P/\bar{B}$ ratios of important taxa were significantly correlated with average weights ($r=-0.726$, $P<0.001$; both variables transformed to natural logarithms). The geometric mean regression describing this relationship (Fig. 1) is

$$\log_e\{(\text{daily } P/\bar{B})\times 10^2\} = 3.75 - 0.655 \log_e(\bar{W}\times 10^2) \quad (7)$$

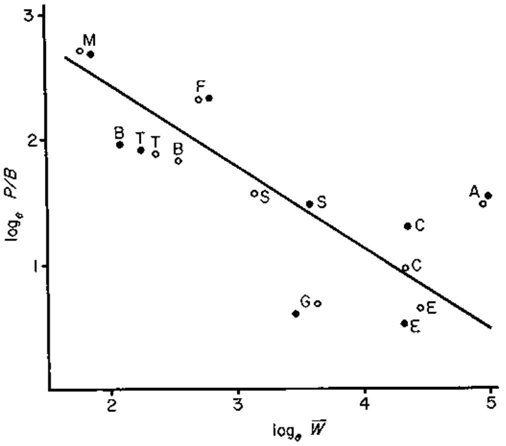

FIG. 1. Relationship between daily production/biomass ratios and mean body weight ($\bar{W}$) for nine taxa collected from open and shaded sites of the Left Fork of the Blacksmith Fork River, Utah. Data from the open site are indicated by open circles, and data from the shaded site by filled circles. Taxa are indicated as follows: M=midges; B=*Baetis bicaudatus*; F=black flies; T=*Baetis tricaudatus*; E=*Epeorus longimanus*; C=*Cinygmula* sp.; S=*Serratella tibialis*; G=*Glossosoma* sp.; A=*Arctopsyche grandis*.

where daily $P/\bar{B}$ (mgDW mgDW^{-1} day^{-1}) and $\bar{W}$ (mgDW) are calculated from Table 2. Daily $P/\bar{B}$ is the size–frequency production estimate divided by $\bar{B}$ and by time period in days; $\bar{W}=\bar{B}/\bar{N}$, and the factor 10^2 was applied to avoid negative logarithms. Because production can be estimated as $P=G\bar{B}$ (IGR method), $P/\bar{B}$ can be considered an average specific growth rate, G, expressed here as a daily rate. Mayfly, midge, and black fly $P/\bar{B}$ ratios lie relatively close to the regression line, but *Arctopsyche grandis* grew rapidly for its body weight and *Glossosoma* sp. grew slowly (Fig. 1).

It was not possible to estimate production of other invertebrates by the size–frequency method or other conventional methods, because of difficulty in separating species or cohorts and/or small sample sizes. *Hesperoperla pacifica* was not collected in sufficient numbers to separate cohorts and no growth rate estimates were possible. Other Plecoptera species were much smaller in size (maximum length <8 mm) and lumped into a single group containing representatives of the families Chloroperlidae, Nemouridae, Perlodidae and Perlidae. The caddisfly family Rhyacophilidae was represented by at least three species, but none was abundant. *Drunella coloradensis* contributed measurably to the standing crop because of its large size (up to 12 mm), but it was not abundant in samples and had completed emergence midway through the study period. Average weights of these taxa ($\bar{B}/\bar{N}$) were estimated and daily $P/\bar{B}$ ratios calculated from equation (7). Approximate production estimates based on these $P/\bar{B}$ ratios and $\bar{B}$ values were obtained for the 94-day sampling period (Table 3). Estimates of mean density and biomass were higher at the open site for all taxa, but differences were significant only for *D. coloradensis* ($P<0.001$ for density and biomass) and Rhyacophilidae ($P<0.005$ for density).

The average ratio of cobble biomass (m^{-2}) to intercobble biomass (m^{-2}) of taxa was calculated (equations (3) and (4)) for paired samples (Table 4). These ratios permit extrapolation of epilithic biomass estimates to estimates for the entire stream bottom, and allow comparison with other studies based on conventional sampling techniques. Average ratios were significantly greater for the open site for *Baetis bicaudatus* ($0.0005<P<0.001$) and *B. tricaudatus* ($0.02<P<0.05$), but did not differ significantly between sites for other taxa (*t* tests, log-transformed data).

Ratios for midges and *Seratella tibialis* differed considerably (but not significantly) between open and shaded sites. The low ratio for midges at the shaded site was weighted heavily by an intercobble sample taken in a rare silty area of the stream. This sample contained an unusually high number of midges; excluding this sample (and its paired value) gives a ratio of 1.35 for midges at the shaded site. Ratios for *S. tibialis*, Rhyacophilids, and some other taxa had high standard errors partly because of small sample sizes. We combined ratio estimates for open and shaded areas where they

TABLE 3. Mean density ($\bar{N}$), mean biomass ($\bar{B}$), and epilithic production of less abundant taxa. Daily $P/\bar{B}$ ratios are estimated by equation (7) (see text) from mean weights. Epilithic production estimates are for the entire 94-day study period and are calculated from the values of $\bar{B}$ and $P/\bar{B}$ below.

Taxon	Canopy cover	$\bar{N}$ (no. m^{-2})	$\bar{B}$ (mgDW m^{-2})	$\bar{W}$ (mg)	Daily $P/\bar{B}$	Epilithic production (mgDW)
Hesperoperla pacifica	Open	$103\overset{\times}{\div}1.28$	$637\overset{\times}{\div}1.60$	6.18	0.00632	378
	Shade	$79\overset{\times}{\div}1.28$	$417\overset{\times}{\div}1.60$	5.25	0.00703	276
Rhyacophilidae*	Open	$67\overset{\times}{\div}1.20$	$114\overset{\times}{\div}1.31$	1.70	0.0147	158
	Shade	$30\overset{\times}{\div}1.20$	$21\overset{\times}{\div}1.31$	0.70	0.0263	52
Chloroperlidae, Nemouridae, Perlodidae and Perlidae	Open	$251\overset{\times}{\div}1.32$	$40\overset{\times}{\div}1.18$	0.158	0.0697	262
	Shade	$232\overset{\times}{\div}1.32$	$32\overset{\times}{\div}1.18$	0.136	0.0769	231
Drunella coloradensis†	Open	$34\overset{\times}{\div}1.22$	$87\overset{\times}{\div}1.33$	2.58	0.0112	92
	Shade	$5\overset{\times}{\div}1.25$	$7\overset{\times}{\div}1.37$	1.35	0.0171	11

*Mean density significantly greater for open site at *P*0140.01.

†Mean density and biomass significantly greater for open site at $P<0.01$.

TABLE 4. Average ratio of cobble to intercobble biomass (R) for paired samples. Values in parentheses are standard errors of the average ratios. The factor multiplied by the average epilithic biomass of these taxa (see Tables 2 and 3) equals the average biomass for the entire substrate ($\bar{B}$) for the time periods indicated in Tables 2 and 3.

Taxon	Canopy cover	Sample size	R (cobble/intercobble biomass)	Factor*	Substrate $\bar{B}$ (mgDW m^{-2})
Epeorus longimanus	Open	5	1.59 (1.00)	0.757	330
	Shade	5	2.47 (1.23)	0.737	214
	Combined	10	1.90 (0.79)		
Cinygmula sp.	Open	5	0.66 (0.13)	1.386	444
	Shade	5	0.49 (0.17)	1.419	282
	Combined	10	0.57 (0.11)		
Serratella tibialis	Open	5	0.84 (0.30)	0.796	44
	Shade	5	2.42 (1.69)	0.779	37
	Combined	10	1.66 (0.86)		
Glossosoma sp.	Open	15	3.57 (0.97)	0.624	435
	Shade	15	4.00 (1.24)	0.592	268
	Combined	30	3.75 (0.74)		
Arctopsyche grandis	Open	15	6.63 (2.14)	0.570	419
	Shade	15	5.42 (2.14)	0.538	438
	Combined	30	5.93 (1.51)		
Baetis bicaudatus	Open	15	3.03 (0.60)	0.657	187
	Shade	15	5.72 (1.44)	0.541	27
Baetis tricaudatus	Open	15	2.29 (0.26)	0.678	256
	Shade	15	3.62 (0.93)	0.650	108
Chironomidae	Open	15	2.78 (0.55)	0.781	112
	Shade	15	0.74 (0.35)	0.762	24
	Combined	30	1.75 (0.41)		
Simuliidae	Open	15	96.00 (64.5)	0.495	234
	Shade	15	53.00 (30.5)	0.452	371
	Combined	30	70.50 (35.7)		
Hesperoperla pacifica	Open	15	1.67 (0.83)	0.776	494
	Shade	15	1.94 (1.10)	0.756	315
	Combined	30	1.78 (0.69)		
Chloroperlidae, Nemouridae, Perlodidae and Perlidae	Open	15	2.11 (0.84)	0.781	31
	Shade	15	1.52 (0.61)	0.762	24
	Combined	30	1.75 (0.52)		
Rhyacophilidae	Open	15	3.52 (2.49)	0.713	81
	Shade	15	0.35 (0.33)	0.688	14
	Combined	30	2.28 (1.27)		

*Factor=$0.488+0.512/R$ for open site, or $0.444+0.556/R$ for shaded site, where R=combined R except for *Baetis* spp. where R differed significantly between open and shaded sites.

did not differ significantly. Confidence limits based on log-transformed data appeared too narrow when applied to the original data (ratios of log-transformed data were often much lower than ratios of nontransformed data). We give standard errors of ratio estimates in Table 4 rather than confidence limits.

Epilithic mean biomass estimates (Tables 2 and 3) were extrapolated to means for the entire streambed by multiplying the epilithic estimates by the factor

$$A+R/(1-A) \tag{8}$$

where A is the proportion of the stream bed consisting of >10 cm cobbles ($A=0.488$ for the open site and 0.444 for the shaded site, and R is the mean cobble/intercobble biomass ratio (Table 4)).

Taxa listed in Tables 2 and 3 accounted for over 95% of the estimated epilithic standing crop of all invertebrates at the study sites. The remaining biomass was made up of taxa that were rare or in an early stage of development and contributed little to the total biomass because of their low density or small size.

The mean epilithic biomass of the taxa listed in Tables 2 and 3 for the study period was approximately 3.4 gDW m^{-2} planar rock area at the open site and 2.6 gDW m^{-2} at the shaded site. Corresponding estimates for the entire stream bottom are 2.8 gDW m^{-2} at the open site and 2.0 gDW m^{-2} at the shaded site. Minimum estimates of epilithic production for these taxa are 14.6 gDW m^{-2} planar rock area at the open site and 13.2 gDW m^{-2} at the shaded site. These estimates are very close but black flies accounted for more than 50% of the epilithic production at the shaded site. Epilithic production of taxa excluding black flies was 10.1 gDW m^{-2} at the open site and 5.3 gDW m^{-2} at the shaded site.

We grouped taxa into four feeding guilds for more specific comparisons of production between sites. *Glossosoma* sp. was considered an obligate scraper/grazer. All black fly production and half the production of *A. grandis* (Cuffney & Minshall, 1981) was assigned to the filter-feeding guild. Predator production included that of Rhyacophilidae, all stonefiles except Nemouridae, half the production of *D. coloradensis* (Hawkins, 1985), and half that of *A. grandis* (Cuffney & Minshall, 1981). All other taxa were lumped into the collector-gatherer/facultative grazer guild. Production of these guilds for the open site was (gDW m^{-2}): obligate scrapers/grazers, 0.7; filter-feeders, 5.4; predators, 1.6; and collector-gatherers/facultative grazers, 7.0. The ratio of production at the open site to that at the shaded site for these feeding guilds was 1.7, 0.6, 1.1 and 2.8 respectively. Predators accounted for 28.8% and 26.5% of the total epilithic biomass and 10.9% and 11.1% of the total epilithic production at the open and shaded sites respectively.

The correlation between the dry weight of the algae *Hydrurus foetidus* and density of each important taxon was calculated (all data log-transformed); only the correlation for midges was significant (r=0.916; P<0.001).

Discussion

Cobble sampling

The method of sampling large cobbles was an efficient way of collecting most invertebrates in this study. Only *Cinygmula* sp. was consistently more abundant in intercobble samples. Preference for cobbles of some of the genera studied here has also been noted by other authors: *Baetis*, Hughes (1966a) and Corkum & Pointing (1979); *Arctopsyche*, Cuffney & Minshall (1981); *Epeorus* and *Glossosoma*, Neves (1979).

Sampling a specific substrate helps to reduce the variability associated with stream invertebrate samples and should lead to more accurate comparisons among different sites within and between streams. Some problems are associated with cobble samples, however. Estimation of the surface area of each cobble is time consuming. Calow (1972) covered rocks with latex to estimate surface area. Neves (1979) placed cobbles of fairly uniform size in the stream; he estimated the average surface area of a subsample of his cobbles by covering them with aluminium foil and used his subsample mean to estimate the total area of all cobbles sampled. The equations developed in this study provided a rapid method of approximating total or planar cobble area.

Estimation of the total cobble surface in most instances will not represent the 'effective' use area for organisms. The entire cobble surface is often not available to organisms because cobbles are frequently partially embedded in the stream bottom. Neves (1979) estimated that 5–10% of the area of his artificially-placed cobbles was inaccessible to invertebrates. In this study some cobbles may have been as much as 50% embedded. Also various taxa utilize different portions of cobbles. Some species may only reside on the lee side of the cobble, protected from the current, while others (e.g. black flies) may be attached to the upstream side; or, species may make varying use of the top of the cobble versus the bottom. Microdistributions of various species were not investigated in this study, but are assumed to exist, and would help to explain why total rock surface did not appear to be any better a predictor of numbers or biomass than planar rock area.

Production estimates

All production estimates in this study are minimal estimates. Production estimates do not include very small organisms nor the production of exuviae. In calculating growth rates (and production) for some taxa small individuals considered 'recruits' were excluded from the calculations. If these individuals are from late-hatching eggs of the same cohort, their production should be included with the cohort. Sample calculations with and without these small individuals indicated that they contributed less than 3% of the cohort production, and, since it could not be determined if they were late hatchers of the cohort or early hatchers of the next generation, their production was not included in our calculations. Growth rate estimates may also be too low since no adjustment was made for emergence or pupation and low growth rates in turn are reflected in underestimation of production. *Baetis* spp. are known to drift (Waters, 1966; Pearson & Kramer, 1972). We did not attempt to measure drift and must assume that its effects on our production estimates would occur equally for open and shaded sites.

Kroger (1972) found that Surber samples can greatly underestimate invertebrate densities because small species pass through the mesh and other organisms are lost around the net due to backwash. The same biases may well apply to our samples, but the backwash effect is probably minimized by sampling cobbles. Underestimation of production may be greatest at the open site because small species (e.g. midges and *Baetis* spp.) were more abundant there. Although production in general may be underestimated, biases generally apply to estimates for both sites. Thus the estimates should provide a reasonably accurate picture of the relative amount of production at the two sites.

We used a modification of the $P/\bar{B}$ method to estimate production of uncommon taxa. Banse & Mosher (1980) first suggested that body mass was a good predictor of $P/\bar{B}$, but Benke *et al.* (1984) urged caution in applying this relationship. Average body mass was a reasonably good predictor of $P/\bar{B}$ in this study, but this could be due, at least in part, to the relatively constant water temperature that occurred throughout the study period. Further studies are indicated to determine the general accuracy of the $P/\bar{B}$ method.

Comparisons of our estimates of mean biomass and production with other studies are difficult because we did not estimate annual or cohort production, and our estimates are of epilithic production. Neves (1979) reported an average epilithic biomass of 0.61 gDW m^{-2} for a softwater stream in northeastern U.S.A. His figure applies to the entire cobble surface. Planar cobble area in this study averaged about 30% of total cobble area. Applying this conversion factor, Neves' (1979) figure becomes 2.0 gDW m^{-2} planar cobble area and compares to our figures of 3.4 gDW m^{-2} (open site) and 2.6 gDW m^{-2} (shaded site). The higher figures for our study are consistent with other studies that show higher invertebrate abundance in hardwater streams (e.g. Osborn, 1981; Krueger & Waters, 1983). Osborn reported a mean annual biomass of 6.4 g m^{-2} ash free dry weight for the Left Fork of the Blacksmith Fork River based on samples taken within 5 km of our study sites. Our mean biomass figures, July–October (for the entire substrate but not ash free mass), are 2.8 gDW m^{-2} and 2.0 gDW m^{-2} at open and shaded sites respectively. Two consecutive years (1983 and 1984) of unusually high runoff and flooding with consequent streambed scouring may explain our lower figures.

Our estimates of predator production as a percentage of total production (10.9%, open site; 11.1%, shaded site) compare well with Neves (1979) estimates of 11.1–13.6% and are somewhat lower than those of Benke *et al.* (1984) (16.6–17.7%).

Effects of canopy on invertebrate abundance and production

In this study four mayfly species (*B. bicaudatus, B. tricaudatus, Cinygmula* sp. and *D. coloradensis*), midges (Chironomidae), and Rhyacophilid caddisflies were significantly more abundant in an open stream reach compared to an adjacent shaded site. Although significant differences between sites could be the result of a confounding of overhead canopy with other factors, the sites were closely adjacent and very similar in physical characteristics. We therefore interpret differences between sites as due to canopy effects, but the possibility of other factors influencing the results cannot be totally discounted.

Baetis spp. in general seem to show a marked preference for sunlit areas. Thorup (1966) reported *B. rhodani* much more abundant in open sections of a Denmark stream, and Hughes (1966b) noted the same distribution of *B. harrisoni* in Natal streams. Towns (1981) artificially shaded segments of a New Zealand stream and found chironomids (three species) more abundant in unshaded segments—a result consistent with this study. Towns (1981) and Hughes (1966b) reported some species that were more common in open areas and others that preferred shade, but most species seem to predominate in open areas. Hopkins (1976) found much higher biomass and production of the entire invertebrate fauna in open portions of two New Zealand streams; he noted only three species confined to shaded areas. Hawkins, Murphy & Anderson (1982) studied six Oregon streams affected by logging and found greater abundance of most invertebrates in clear-cut areas. They concluded that canopy type was more important than substrate in influencing invertebrate abundance and guild structure. Hawkins *et al.* (1983) also found salmonid fish populations and sculpins (*Cottus* spp.) to be more abundant in unshaded streams of Oregon and California although salamanders were not.

Several hypotheses have been advanced to explain differences in invertebrate abundance associated with shading. Hughes (1966b) discussed possible indirect effects of shading on algal abundance, abundance of organic detritus (from trees), temperature and oviposition behaviour of adults. In a laboratory study (Hughes, 1966a) found that *B. harrisoni* nymphs were more active in sunlight than shade, but hypothesized that their movement is suppressed when they find a desired microhabitat—nymphs collect on cobbles and current velocity may be the key factor in their choice of microhabitat. If *B. bicaudatus* and *B. tricaudatus* show similar behavioural responses, it would explain their greatest abundance on cobbles and at the open site in this study. Midge densities in this study were highly correlated with density of the algae *H. foetidus*. Hynes (1970) states that such an association has often been noted for chironomids and the inference is that the larvae are attracted to the algae for food.

Hawkins *et al.* (1982) emphasized the importance of food quality (as measured by microbial respiration rate and relative chlorophyll content—see Anderson & Cummins (1979)) rather than food quantity in influencing invertebrate abundance. Algae and algal detritus evidently provide higher quality food than organic debris from trees. Hawkins *et al.* (1982) found more aufwuchs and higher quality detritus in clear-cut areas, and invertebrate guilds known to consume these food sources (and their predators) were generally most abundant in open areas. However, they found lower densities of scrapers (but greater biomass) in open compared to shaded areas. In this study most taxa were more abundant at the open site (including *Glossosoma* sp., a scraper), with *Baetis* spp., *Cinygmula* sp., *D. coloradensis,* midges and Rhyacophilids being significantly more abundant. The greater production of the collector-gatherer/facultative grazers at the open site (2.8-fold greater than the shaded site) strongly suggests that higher quality food was available to these taxa at the open site.

Growth of aufwuchs may inhibit some species. Towns (1981) found more black flies in shaded stream sections. Black flies in this study also appeared to be more abundant at the shaded site, but were not significantly more abundant. Aufwuchs growth on cobbles may prevent black flies from attaching (Towns, 1981). Sommerman, Sailer & Esselbaugh (1955) reported that diatoms can actually grow over and smother the larval black flies.

Although several studies have examined the relationship between shading and invertebrate densities and biomass, few have measured production in relation to shading. Allen (1951) reported greater production in unshaded sections of the Horokiwi stream, New Zealand. Hopkins (1976) found production in open areas of two New Zealand streams to be at least 2–4 times greater than shaded areas of the same streams. His production figures reflect similar differences in average biomass between open and shaded sites.

O'Hop *et al.* (1984) reported faster growth and shorter life cycles of the stonefly *Peltoperla maria* Needham and Needham in a stream draining a clear-cut basin compared to a nearby undisturbed stream. Production of *P. maria* was similar in both streams even though its density was twice as high in the undisturbed stream. The clear-cut stream was slightly warmer and had more nutrients than the undisturbed stream, and had greater microbial biomass associated with its detritus.

Growth rates did not differ significantly between sites for any of our taxa. This might be expected since the sites were closely adjacent and did not differ in water temperature. However, Hawkins (1985) reported no difference in growth rates of five of six species of Ephemerellid mayflies between open and shaded sites of several western U.S.A. streams although densities and biomass differed. Carrying capacity for these mayflies may have been food-related at each site resulting in the same amount of food available per individual regardless of population densities.

In this study of a nonperturbed stream, biomass and production were greater for most taxa at the open site with the notable exception of black flies. Greater algal growth and higher quality food provided by the algae may explain this result. Only the biomass of *H. foetidus* was measured in this study, and midge abundance was correlated with this algae. Presumably other members of the aufwuchs community are also more abundant (many microscopic in size or occurring at other seasons) in open stream reaches and enhance invertebrate production in these reaches. Greater production of a taxon at the open site in this study was always a reflection of greater standing crop compared to the shaded site rather than faster growth.

Acknowledgments

The senior author thanks Dr Ross Bulkley, Cooperative Fishery Research Unit, Utah State University, for providing laboratory space and facilities. Dr Ray Lynn, Utah State University, identified the algae *H. foetidus*. Bryce Smith, Gale Gleason, Gerald Johnson and Ray Reilly, Lake Superior State College, reviewed the manuscript.

References

Allen K.R. (1951) The Horokiwi Stream: a study of a trout population. *New Zealand Marine Department Fisheries Bulletin,* **10,** 238 pp.

Anderson N.H. & Cummins K.W. (1979) The influence of diet on the life histories of aquatic insects. *Journal of the Fisheries Research Board of Canada,* **36,** 335–342.

Banse K. & Mosher S. (1980) Adult body mass and annual production/biomass relationships of field populations. *Ecological Monographs,* **50,** 355–379.

Benke A.C. (1979) A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnology and Oceanography,* **24,** 168–171.

Benke A.C., Van Arsdall T.C., Jr & Gillespie D.M. (1984) Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecological Monographs,* **54,** 25–63.

Brown G.W. (1969) Predicting temperatures of small streams. *Water Resources Research,* **5,** 68–75.

Calow P. (1972) A method for determining the surface areas of stones to enable quantitative density estimates of littoral stonedwelling organisms to be made. *Hydrobiologia,* **40,** 37–50.

Cochran W.G. (1977) *Sampling Techniques,* 3rd edn. John Wiley and Sons, New York.

Corkum L.D. & Pointing P.J. (1979) Nymphal development of *Baetis vagans* McDunnough (Ephemeroptera: Baetidae) and drift habits of large nymphs. *Canadian Journal of Zoology,* **57,** 2348–2354.

Cuffney T.F. & Minshall G.W. (1981) Life history and bionomics of *Arctopsyche grandis* in a central Idaho stream. *Holarctic Ecology,* **4,** 252–262.

Downing J.A. (1979) Aggregation, transformation, and the design of benthos sampling programs. *Journal of the Fisheries Research Board of Canada,* **36,** 1454–1463.

Elliott J.M. (1977) *Some methods for the statistical analysis of samples of benthic invertebrates,* 2nd edn. Freshwater Biology Association Scientific Publication 25, 156 pp.

Hamilton A.L. (1969) On estimating annual production. *Limnology and Oceanography,* **14,** 771–782.

Hawkins C.P. (1985) Food habits of ephemerellid mayflies (Ephemeroptera: Insecta) in streams of Oregon. *American Midland Naturalist,* **113,** 343–352.

Hawkins C.P. (1986) Variation in individual growth rates and population densities of ephmerellid mayflies. *Ecology* (in press).

Hawkins C.P., Murphy M.L. & Anderson N.H. (1982) Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology,* **63,** 1840–1856.

Hawkins C.P., Murphy M.L., Anderson N.H. & Wilzbach M.A. (1983) Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Canadian Journal of Fisheries and Aquatic Sciences,* **40,** 1173–1185.

Hopkins C.L. (1976) Estimate of biological production in some stream invertebrates. *New Zealand Journal of Marine and Freshwater Research,* **10,** 629–640.

Hughes D.A. (1966a) The role of responses to light in the selection and maintenance of microhabitat by the nymphs of two species of mayfly. *Animal Behavior,* **14,** 14–33.

Hughes D.A. (1966b) Mountain streams of the Barberton area, eastern Transvaal. Part II. The effect of vegetational shading and direct illumination on the distribution of stream fauna. *Hydrobiologia,* **27,** 401–438.

Hunt R.L. (1979) *Removal of woody streambank vegetation to improve trout habitat.* Technical Bulletin 115, Wisconsin Department of Natural Resources, Madison, Wisconsin, 36 pp.

Hynes H.B.N. (1961) The invertebrate fauna of a Welsh mountain stream. *Archiv für Hydrobiologie,* **57,** 344–388.

Hynes H.B.N. (1970) *The Ecology of Running Waters.* University of Toronto Press, Toronto, Ontario.

Kroger R.L. (1972) Underestimation of standing crop by the Surber sampler. *Limnology and Oceanography,* **17,** 475–478.

Krueger C.C. & Martin F.B. (1980) Computation of confidence intervals for the size–frequency (Hynes) method of estimating secondary production. *Limnology and Oceanography,* **25,** 773–777.

Krueger C.C. & Waters T.F. (1983) Annual production of macroinvertebrates in three streams of different water quality. *Ecology,* **64,** 840–850.

McCullough D.A., Minshall G.W. & Cushing C.E. (1979) Bioenergetics of lotic filter-feeding insects *Simulium* spp. (Diptera) and *Hydropsyche occidentalis* (Trichoptera) and their function in controlling organic transport in streams. *Ecology,* **60,** 585–596.

Murphy M.L., Hawkins C.P. & Anderson N.H. (1981) Effects of canopy modification and accumulated sediment on stream communities. *Transactions of the American Fisheries Society,* **110,** 469-478.

Neves R.J. (1979) Secondary production of epilithic fauna in a woodland stream. *American Midland Naturalist,* **102,** 209–224.

Newbold J.D., Erman D.C. & Roby K.B. (1980) Effects of logging on macroinvertebrates in streams with and without buffer strips. *Canadian Journal of Fisheries and Aquatic Science,* **37,** 1076–1085.

O'Hop J., Wallace J.B. & Haefner J.D. (1984) Production of a stream shredder, *Peltoperla maria* (Plecoptera: Peltoperlidae) in disturbed hardwood catchments. *Freshwater Biology,* **14,** 13–21.

Osborn T.G. (1981) Stream insect production as a function of alkalinity and detritus processing, Ph.D. dissertation, Utah State University.

Pearson W.D. & Kramer R.H. (1972) Drift and production of two aquatic insects in a mountain stream. *Ecological Monographs,* **42,** 364–385.

Smock L.A. (1980) Relationships between body size and biomass of aquatic insects. *Freshwater Biology,* **10,** 375–383.

Sommerman K.M., Sailer R.I. & Esselbaugh C.O. (1955) Biology of Alaskan black flies (Simuliidae, Diptera). *Ecological Monographs,* **25,** 345–385.

Taylor L.R. (1961) Aggregation, variance, and the mean. *Nature,* **189,** 732–735.

Thorup J. (1966) Substrate type and its value as a basis for the delimitation of bottom fauna communities in running waters. In: *Organism–substrate relationships in streams.* Special Publication No. 4, Pymatuning Lab of Ecology, University of Pittsburgh. (Eds K. W. Cummins, C. A. Tryron, Jr and R. T. Hartman). Edwards Bros., Ann Arbor, Michigan.

Towns D.R. (1981) Effects of artificial shading on periphyton and invertebrates in a New Zealand stream. *New Zealand Journal of Marine and Freshwater Research,* **15,** 185–192.

Waters T. (1966) Production rate, population density and drift of a stream invertebrate. *Ecology,* **57,** 595–604.

Waters T.F. & Crawford G.W. (1973) Annual production of a stream mayfly population: a comparison of methods. *Limnology and Oceanography,* **18,** 286–296.

White R.J. & Brynildson O.M. (1967) *Guidelines for management of trout stream habitat in Wisconsin.* Technical Bulletin 39, Wisconsin Department of Natural Resources, Madison, Wisconsin, 64 pp.

(Manuscript accepted 14 June 1985)