

Growth rates of mayflies in a subtropical river and their implications for secondary production

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Abstract. Mayflies were grown in artificial airlift streams on the bank of the Ogeechee River, Georgia, to estimate their productivity rates. Natural conditions were simulated in the streams by (1) providing flowing water pumped from the river as a natural food source, and (2) immersing the streams in large ambient temperature tanks to sustain diel temperature patterns. Early instars of *Stenonema* spp., *Baetis* spp., and *Tricorythodes* sp. were introduced into streams and their development was followed through late instars or to emergence. The daily instantaneous growth rate (g) was 0.265 mg mg⁻¹ d⁻¹ for *Baetis*, 0.123 for *Stenonema*, and 0.162 for *Tricorythodes* during summer months (mean daily temperature = 27.5°C). These rates allow *Baetis* to complete development in about 19 d in these warmwater rivers, *Stenonema* in about 41 d, and *Tricorythodes* in about 31 d. Each of these taxa is capable of completing several generations over a 6-mo period in which stream temperatures are >20°C. Calculation of instantaneous growth rates (or larval development times) of fast-growing insects is critical to estimation of their production. Approximations of 6-mo production/biomass (P/B) ratios range from 22 for *Stenonema* to 48 for *Baetis*. According to our analyses, mayflies in warmwater systems have considerably shorter development times and higher biomass turnover rates than most previous studies in streams have shown.

Key words: *Ephemeroptera*, *aquatic insects*, *stream ecology*, *cohort production interval*, *development time*, *production/biomass ratio*.

Mayflies (Ephemeroptera) are a major component of stream benthos and can make a substantial contribution to total secondary production (e.g., Fisher and Gray 1983, Krueger and Waters 1983). Good life history data are critical to the application of cohort methods of estimating secondary production (Benke 1984, Waters 1979, Waters and Crawford 1973), and there is an extensive literature on mayfly life histories (e.g., Brittain 1982, Clifford 1982). Unfortunately, many aquatic insects, including several mayfly species, do not possess discernible cohorts because of the asynchronous development and fast growth rates characteristic of polyvoltine life cycles. The problem is especially common in tropical and subtropical systems, but also may exist wherever water temperatures remain above 15°C for a major portion of the year. In such cases, alternative methods must be used to estimate production. The objective of this study was to determine the growth rates of fast-growing mayflies in a warmwater river in the southeastern United

States in order to estimate the production of field populations.

Laboratory growth rates are often used to obtain temperature- and size-specific growth rates for fast-growing aquatic animals. Although high growth rates have been found for some benthic macroinvertebrates (e.g., Mackey 1977), the artificiality of most laboratory studies makes application of these rates to field populations tenuous. Clearly, the best approach for estimating the growth rate of a fast-growing population is to isolate a group of even-aged animals in their natural environment and determine their growth rate over a very short (e.g., 5 d) interval (Gray 1981, Wallace and O'Hop 1985). If isolation of a group of animals in situ is difficult, the best alternative is to grow the animals in an artificial environment that closely simulates the natural environment.

Most studies of mayfly production have shown either univoltine or bivoltine life cycles (Clifford 1982) and that annual production/biomass (P/B) ratios are usually <12 (e.g.,

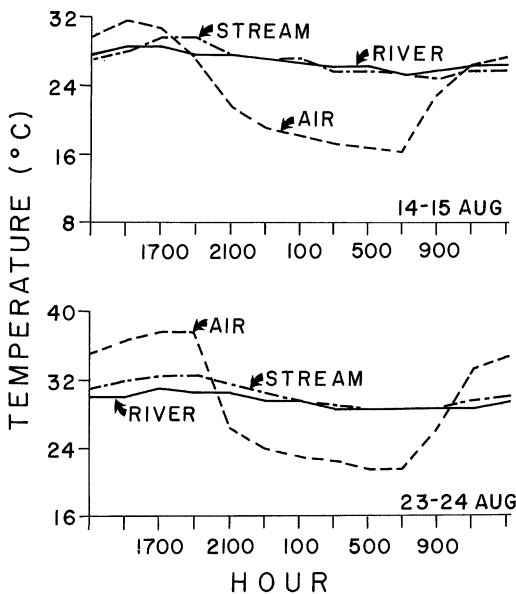


FIG. 1. Diel temperature patterns in the Ogeechee River (River), ambient air (Air), and artificial streams (Stream) on two different dates.

Waters 1977, Zelinka 1980). A few studies have provided evidence that annual P/B ratios for some mayflies are substantially higher when development times are much less than a year (Fisher and Gray 1983, Hall et al. 1980). In general, if populations have short development times (e.g., 15–30 d), annual P/B ratios can be as high as 60–120 (Benke 1984, Benke et al. 1984). The results presented in this paper will demonstrate that growth rates of three mayfly genera in a warmwater river are sufficiently high that P/B ratios over the warmest 6 mo of the year are considerably higher than most published estimates for annual P/B.

Study site and organisms

Our study site was the Ogeechee River, a 6th-order blackwater river in the Coastal Plain of Georgia. Mean annual discharge from 1937 to 1981 was 66.8 m³/s with a characteristically wide range from 3.7 to 816 m³/s. Mean annual water temperature for 1983 was 18.0°C with a minimum of 2.9°C, a maximum of 32.0°C, and a total of almost 6600 degree-days for the year. During the research period from 13 June to 28 August 1983, the mean river temperature was 26.7°C with a range of 21.9 to 32.0°C. See Wallace and Benke (1984) for other site characteristics.

Woody substrates (snags) are the major stable habitat in Coastal Plain rivers and are colonized by a high diversity of macroinvertebrates. Although Benke et al. (1984) found relatively low densities of mayflies on snags in the Satilla River, mayfly densities are much higher in the Ogeechee (Wallace and Benke 1984). *Stenonema* (including *S. modestum*, *S. integrum*, and *S. exiguum*), and *Baetis* (*B. intercalaris* and *B. ephippiatus*) are particularly abundant throughout the year. Species in these two genera, as well as *Tricorythodes* sp., which occurred primarily during summer months, were the principal organisms of study.

Stenonema modestum was by far the most abundant *Stenonema* species collected (approximately 2/3 of all *Stenonema*) during the summer of 1983. Because we could not differentiate species as early instars, we had to treat *Stenonema* at the genus level. We encountered the same problem for *Baetis*, and both species were combined for our analyses. *Tricorythodes* appeared to be a single species, but could not be identified at the species level without adult verification.

Methods

All mayfly larvae were collected directly from snags and reared in airlift artificial streams based on the design of Lawson (1982). To maintain natural stream temperatures, all streams were partially submerged (to below their own water lines) in a large circular water tank (ca. 3200 L), located about 20 m from the river bank. Water was pumped directly from the Ogeechee River by submersed pumps and circulated through the large tanks. Temperatures of air, river, and artificial stream water were monitored daily. In spite of wide diel variation in air temperature, stream and river temperatures were similar (Fig. 1).

Natural and continuous supplies of seston (mostly fine amorphous detritus) and nutrients were supplied by pumping river water directly to each stream. Fine amorphous detritus is the principal food resource for all mayflies found in the Ogeechee River, regardless of whether they are gathering or filtering collectors (Wallace et al. 1986). Water replacement times in the streams varied between 12 and 20 min. Before reaching the streams, the river water was filtered through a sieve (mesh opening = 90 μm)

to remove drifting mayflies and large organic debris that could clog inflow lines. All streams were cleaned before the beginning of a growth experiment. Streams were not "preconditioned" before stocking with larvae since fine detritus accumulated in streams within a day.

Two procedures were used to estimate growth rates. The first procedure, used only for *Stenonema* and *Tricorythodes*, confined individual mayflies (the smallest found on snags) to small plastic mesh barrels (inside height = 56 mm, diameter = 43 mm, mesh openings = 200 μm), manufactured for use as tea baskets (Toby Tea-Boy, Ltd., Aldridge, England) (Fig. 2). Barrels allow individual animals to be monitored, rather than a population. Three or four early-instar individuals of different sizes were placed in each barrel after measurement of head width and body length using a dissecting microscope with an ocular micrometer. Barrels were placed, partially submerged, on the sand-gravel bottom of an artificial stream. Maximum current velocity in a stream was about 30 cm/s, but velocities inside barrels were reduced. At 5-d intervals, barrels were temporarily removed from streams to remeasure mayflies. The top of each barrel twisted apart from the bottom, so that mayflies could be measured within the barrel. Fine detritus from the seston settled out into each barrel providing food for mayflies. No other food or substrate appeared to be necessary for mayfly growth. In fact, barrels were gently agitated in the stream water to remove excess detritus every time mayflies were re-measured.

In the second procedure, early instars of either *Stenonema* or *Baetis* were introduced as a population to an artificial stream. This unconfined environment was probably more natural than inside the barrels, but it was not possible to follow individual growth. The streams used in the population procedure were modified by adding a plexiglas false bottom that replaced the sand-gravel mixture and created current velocities comparable to the faster velocities found in the river (50 cm/s). These velocities seem important to survival of *Baetis*, which could not be reared successfully in barrels. Six or seven small sticks were lodged within the artificial stream channel to provide a natural substrate to which mayflies could cling. Mayfly densities were roughly equivalent to field densities. Initial measurements were made of head

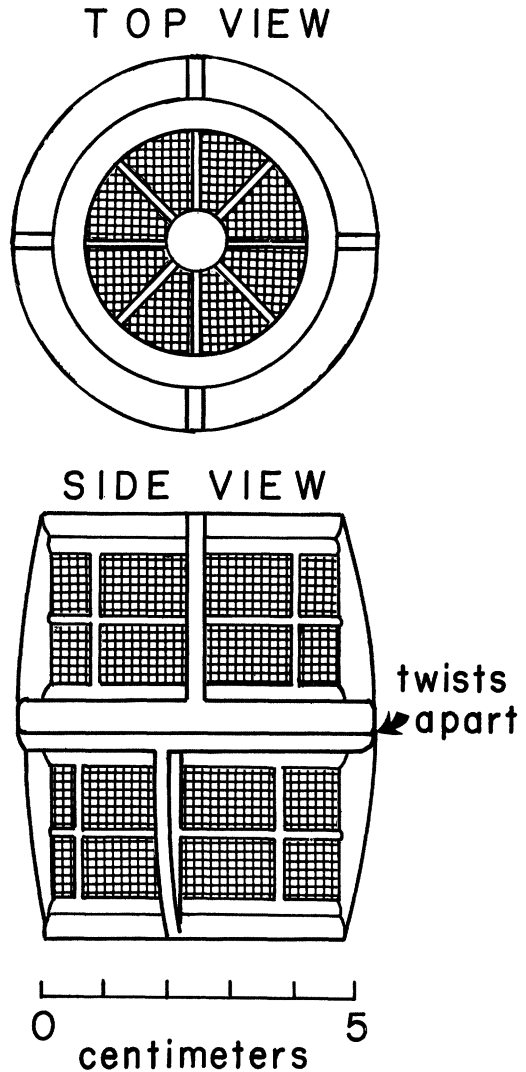


FIG. 2. Plastic mesh barrel (Toby Tea-Boy) used for growth experiments of *Stenonema* spp. and *Tricorythodes* sp. Note that barrel twists apart at the center for introducing, removing, or measuring larvae.

width and body length. Experiments were terminated either before emergence or when most of the insects had emerged. Emergent mayflies were retained by 1-mm mesh covering the streams.

We collected several sizes of *Baetis*, *Stenonema*, and *Tricorythodes* larvae to determine length-dry mass relationships. Head width and body length were measured for individuals before drying in an oven at 60°C for 24 hr. Insects were kept in a desiccator for <1 hr before weighing on a Mettler 5-place balance.

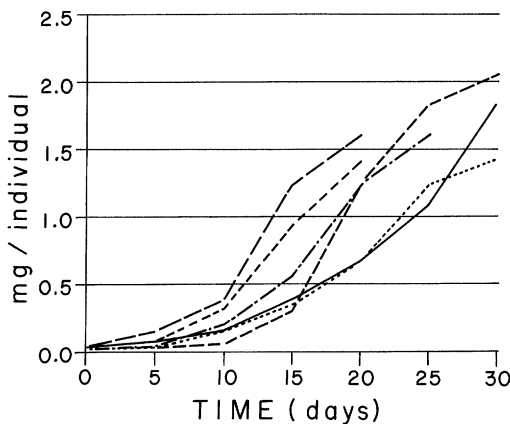


FIG. 3. Biomass growth patterns for six individual *Stenonema* beginning at 0.05 mg dry mass. End of each growth line indicates the last size measured before emergence which occurred less than 5 d later. Final larval sizes at emergence were probably greater than last measured size since they continued growing at almost 12% per day until emergence.

Results

Regressions were developed to predict dry mass from head width for *Baetis* and *Stenonema*:

$$\log DM = 3.325 \log HW + 0.102 \text{ (Baetis)} \\ (r^2=0.96; n=49)$$

$$\log DM = 3.035 \log HW - 0.736 \text{ (Stenonema)} \\ (r^2=0.83; n=67)$$

where DM = mg dry mass and HW = mm head width.

For *Tricorythodes*, we used the regression developed by McCullough et al. (1979) for *Tricorythodes minutus*:

$$\ln DM = 3.222 \ln BL - 4.688$$

where BL = mm body length. We weighed a few *Tricorythodes* from the Ogeechee River, and the data points fell closely on the regression, so we assumed that this was an acceptable regression for our species. For all the analyses to follow, head width (*Baetis* and *Stenonema*) or body length (*Tricorythodes*) was converted to dry mass from these field-derived regressions in order to estimate individual growth rate.

Approximately 60 small *Stenonema* were grown in combinations of 3 or 4 individuals per barrel. Twenty individuals died within the first 5 d; however, the 40 remaining larvae grew well, with 35 reaching emergence. The growth patterns of the six individuals that began at

TABLE 1. Estimates of daily instantaneous growth rates (g) from barrel determinations at a mean temperature of 27.5°C.

Taxon	No. of Individuals	No. of 5-d Growth Intervals	$g \pm 1 \text{ SE}$ (mg mg ⁻¹ d ⁻¹)
<i>Stenonema</i> spp.	40	153	0.116 ± 0.006
<i>Tricorythodes</i> sp.	10	29	0.162 ± 0.014

<0.05 mg dry mass (the smallest individuals collected) and emerged illustrate some of the variability in growth observed among individuals (Fig. 3). Although a sigmoid growth pattern is followed by at least 4 of these 6 individuals, this was not always the case. Approximately 1/3 of the 35 larvae had higher growth rates in the 5 d before emergence than the preceding 5 d.

Separate daily instantaneous growth rates for individual *Stenonema* in barrels were calculated as:

$$g = \ln(W_{t+5}/W_t) \times 1/5$$

where W_t and W_{t+5} are individual biomass values determined at 5-d intervals from length-mass regressions.

Forty individual *Stenonema* provided 153 estimates of instantaneous growth with mean $g=0.116$ (Table 1). A significant inverse relationship was seen between g and the geometric mean body mass between intervals ($g=-0.051DM+0.153$), but the slope was slight, and the regression accounted for little of the variance ($r^2=0.16$).

Ten small *Tricorythodes* were successfully grown in the barrels. A total of 29 5-d growth intervals resulted in a mean instantaneous growth rate of 0.162 (Table 1). No significant relationship was found between body mass and g .

Daily growth rates were also estimated from "population" growth procedures. The same growth equation as above was used, except that the time interval was determined by the length of the growth period. In the first *Stenonema* trial, 21 small larvae were introduced into a stream, and 17 were recovered after 14 d of growth. In the second trial, 43 were introduced and the experiment ended when 18 had emerged. A mean emergence time was determined and we

TABLE 2. Daily instantaneous growth rates (g) based on population procedures at a mean temperature of 27.5°C. $n(0)$ = number of animals introduced to stream, $n(t)$ = number of animals recovered, $W(0)$ = mean dry mass of animals introduced to stream, $W(t)$ = mean mass of animals recovered, and t = estimated period of growth to termination or emergence.

Taxon	$n(0)$	$W(0)$	$n(t)$	$W(t)$	t	g
<i>Stenonema</i> spp.						
Trial 1	21	0.141	17	0.788	14	0.123
Trial 2	43	0.079	18	2.46	26.4	0.130
<i>Baetis</i> spp.						
Trial 1	36	0.128	19	0.766	7.43	0.241
Trial 2	48	0.059	9	0.766	8.89	0.288

assumed that all individuals reached an emergence weight of 2.46 mg (based on numerous field measurements; D. I. Jacobi, unpublished data). Both trials resulted in similar growth rate estimates (0.12–0.13, Table 2). These values were very close to the average growth rate obtained from the barrel procedure ($g=0.116$).

Two similar trials runs were made for *Baetis* in which 36 and 48 individuals were introduced and growth proceeded through emergence. Survival to emergence varied from 20% to >50%. Since we observed no evidence of food limitation in the population procedures, and growth rates were high, the mortality does not appear to be food-related. Some larvae were probably injured during the initial handling period or if they drifted through the turbulent airlift of the stream. A mean emergence time was determined for each trial run, and we assumed that individuals had reached an emergence weight of 0.766 mg (also based on field measurements; D. I. Jacobi, unpublished data).

Growth rates of both runs were reasonably close ($g=0.241$ and 0.288 , Table 2).

Our growth rate calculations were applied to field data from a single summer date (6 August 1982) to illustrate the calculation of daily production (Table 3). Mayflies other than the three major genera formed only about 10% of total mayfly biomass on this date. A modest daily growth rate of 0.12 was assumed for the other mayflies (about the same as *Stenonema*), in order to estimate total mayfly daily production. Even a substantial error in this assumption probably would not result in a large change in total mayfly production. The three mayfly genera were quite similar in their daily production, but *Baetis* had the highest value as a result of its high growth rate.

Discussion

In order to use the instantaneous growth rate method to estimate secondary production, it is important to obtain growth rates that accurately reflect what occurs in the natural environment. We believe that our growth systems closely simulated conditions in the Ogeechee River, because: (1) system temperatures closely tracked those from the river; (2) a natural supply of sestonic food and water was supplied continuously; (3) current velocities in the population growth experiments were similar to those in the river, although conditions in the barrels may have been more similar to those found in leaf packs and root mats attached to snags; and (4) growth rates of individual *Stenonema* grown in barrels and those grown as a population were very close, suggesting that either procedure can support realistic growth for this genus.

The significance of our growth rate deter-

TABLE 3. Daily production for selected snag mayflies in the Ogeechee River, 6 August 1982 (mean of 20 snag samples). All density and biomass units are per m^2 of snag surface. See Benke et al. (1984) for details of sampling procedure.

Taxon	Density (no./ $m^2 \pm 1$ SE)	Biomass (mg/ $m^2 \pm 1$ SE)		Daily Growth Rate (g)		Daily Production (mg $m^{-2} d^{-1}$)
<i>Baetis</i> spp.	781 \pm 191	69 \pm 14	×	0.265	=	18.3
<i>Stenonema</i> spp.	728 \pm 192	119 \pm 32	×	0.123	=	14.6
<i>Tricorythodes</i> sp.	1084 \pm 156	62 \pm 11	×	0.162	=	10.0
Other mayflies	652	31	×	0.120	=	3.7
Total mayflies	3246 \pm 661	282 \pm 51				46.6

TABLE 4. Estimates of CPI, and a 6-mo P/B ratio based on a constant mean daily growth rate (mean values from all growth experiments of each species).

Taxon	g	CPI (d)	6-Mo P/B
<i>Stenonema</i>	0.123	40.7	22
<i>Baetis</i>	0.265	18.9	48
<i>Tricorythodes</i>	0.162	30.9	30

minations can be placed in a better perspective by making approximations of larval development time, or cohort production interval (CPI, Benke 1979), and the P/B ratio over an extended time interval. Given a constant daily growth rate, CPI can be approximated from

$$\text{cohort P} = g \times \text{cohort B} \times \text{CPI}$$

where cohort P = production of a hypothetical cohort, g = daily growth rate, cohort B = mean standing stock biomass over the time interval of the cohort. Rearrangement yields

$$\text{CPI} = (\text{cohort P/cohort B}) \times 1/g$$

If we assume cohort P/B = 5 (see Waters 1977, 1979) CPI is approximately equal to 5/g. Applying this to our mayfly growth rates results in CPIs ranging from 19 to 41 (Table 4).

It is possible to approximate P/B ratios for our mayflies over a 6-mo period because mean daily water temperatures in the Ogeechee River are typically >20°C (mostly >22°C) from May through October. Although mayfly growth rate has been shown to increase with temperature below 20°C (e.g., Allan 1985, Humpesch 1979, Welton et al. 1982), growth rates of mayflies in the Ogeechee River are not well correlated with temperature between 22 and 30°C (A. C. Benke, unpublished data). If growth rates (Table 3) are assumed to be constant from May through October, the 6-mo P/B ratio can be approximated by multiplying daily g by 182 (Table 4).

The growth rate and CPI for *Stenonema*, although not particularly high in comparison with some mayflies, represent a higher rate of growth and development than previously reported for any heptageniid mayfly. Most *Stenonema* species are univoltine (Clifford 1982), which means that their annual P/B values are probably about 5. Kondratieff and Voshell (1980) have provided evidence of two generations per year for *S. modestum*, but our data show

that development is faster in the Ogeechee River (CPI = 41 d). A larval development time of 41 d is consistent with the growth curves presented in Figure 3 which show that >96% of an individual's biomass is accumulated in the final 25–35 d of larval life, allowing 5–15 d between hatching and reaching the 0.05 mg size.

Baetis species have been recognized as being multivoltine in many locations (Clifford 1982), but their annual P/B ratios are rarely reported to be greater than 12 (e.g., Allan 1985, Zelinka 1980) in contrast to our 6-mo estimate of 48. Although development may be fairly rapid at cool temperatures (<20°C; e.g., Brittain 1975, Humpesch 1979, Wallace and Gurtz 1986), the highest growth rate has been found by Gray (1981) for *Baetis quilleri*, which could complete development in 13 d or less in a warm (20–25°C) desert stream subject to catastrophic flooding. Fisher and Gray (1983) applied Gray's growth data to quantitative field sampling to obtain daily P/B (i.e., g) values of about 0.30, somewhat higher than we found for members of this genus (0.24–0.29). Sweeney and Vannote (1984) found that *Cloeon triangulifer* (Baetidae) could complete larval development in the field in 37 d at a mean temperature of 19.9°C, and, in the laboratory, in 27 d at 25°C. Additional, but less detailed, evidence shows that other baetid mayflies in tropical or subtropical environments can complete larval development in less than 30 d (Hynes 1975, Marchant 1982).

Fisher and Gray (1983) also estimated daily P/B values of about 0.37 for *Tricorythodes dimorphus*. This extremely high growth rate is more than twice as high as we found for *Tricorythodes* (0.162) in the Ogeechee River. Hall et al. (1980) estimated daily P/B values of 0.14 for *Tricorythodes atratus* in a Minnesota stream during warm months (16–26°C), much closer to our estimates.

In summary, growth rates of mayflies in warmwater environments can be very high. In our study, they varied from 12% to almost 30% per day, but they can be even higher (Fisher and Gray 1983). These rapid growth rates are considerably higher than our general perception of mayfly growth and mean that CPIs can be <3 weeks for some species for at least part of the year. Furthermore, it is clear from our approximations of CPI that all mayflies from

our study are capable of completing several generations during a 6-mo period, unless long delays occur in adult or egg stages. Our approximations of 6-mo P/B ratios ranging from 22 to 48 are substantially higher than previous reports of annual P/B ratios, with the exception of Fisher and Gray (1983). Unless other factors (e.g., food quality or quantity, or a high minimum emergence temperature) can be shown to play a strong role, annual P/B ratios of 30 to 60 should be expected for many mayfly species in warmwater environments.

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Literature Cited

- ALLAN, J. D. 1985. The production ecology of Ephemeroptera in a Rocky Mountain stream. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22:3233-3237.
- 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. 1984. Secondary production of aquatic insects. Pages 289-322 in V. H. Resh and D. M. Rosenberg (editors). The ecology of aquatic insects. Praeger Publishers, New York.
- BENKE, A. C., T. C. VAN ARSDALL, JR., D. M. GILLESPIE, AND F. K. PARRISH. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecological Monographs 54:25-63.
- BRITAIN, J. E. 1975. The life cycle of *Baetis macani* Kimmins (Ephemeroptera) in a Norwegian mountain biotope. Entomologica Scandinavica 6: 47-51.
- BRITAIN, J. E. 1982. Biology of mayflies. Annual Review of Entomology 27:119-147.
- CLIFFORD, H. F. 1982. Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. Quaestiones Entomologicae 18:15-90.
- FISHER, S. G., AND L. J. GRAY. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. Ecology 64:1217-1224.
- GRAY, L. J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. American Midland Naturalist 106: 229-242.
- HALL, R. J., T. F. WATERS, AND E. F. COOK. 1980. The role of drift dispersal in production ecology of a stream mayfly. Ecology 61:37-43.
- HUMPESCH, U. H. 1979. Life cycles and growth rates of *Baetis* spp. (Ephemeroptera: Baetidae) in the laboratory and in two stony streams in Austria. Freshwater Biology 9:467-479.
- HYNES, J. D. 1975. Annual cycles of macroinvertebrates of a river in southern Ghana. Freshwater Biology 5:71-83.
- KONDRATIEFF, B. C., AND J. R. VOSHELL, JR. 1980. Life history and ecology of *Stenonema modestum* (Banks) (Ephemeroptera: Heptageniidae) in Virginia, USA. Aquatic Insects 2:177-189.
- KRUEGER, C. C., AND T. F. WATERS. 1983. Annual production of macroinvertebrates in three streams of different water quality. Ecology 64: 840-850.
- LAWSON, P. W. 1982. A simple air powered pump for laboratory streams. Freshwater Invertebrate Biology 1:48-52.
- MACKAY, A. P. 1977. The growth and development of larval Chironomidae (Diptera). Oikos 28:270-275.
- MARCHANT, R. 1982. Life spans of two species of tropical mayfly nymph (Ephemeroptera) from Magela Creek, Northern Territory. Australian Journal of Marine and Freshwater Research 33: 173-179.
- MCCULLOUGH, D. A., G. W. MINSHALL, AND C. E. CUSHING. 1979. Bioenergetics of a stream "collector" organism, *Tricorythodes minutus* (Insecta: Ephemeroptera). Limnology and Oceanography 24:45-58.
- SWEENEY, B. W., AND R. L. VANNOTE. 1984. Influence of food quality and temperature on life history characteristics of the parthenogenetic mayfly, *Cloeon triangulifer*. Freshwater Biology 14:621-630.
- WALLACE, J. B., AND A. C. BENKE. 1984. Quantification of wood habitat in subtropical Coastal Plain streams. Canadian Journal of Fisheries and Aquatic Sciences 41:1643-1652.
- WALLACE, J. B., A. C. BENKE, A. H. LINGLE, AND K. PARSONS. 1986. Trophic pathways of macroinvertebrate primary consumers in subtropical

- blackwater streams. *Archiv für Hydrobiologie Monographische Beiträge*. In press.
- WALLACE, J. B., AND M. E. GURTZ. 1986. Responses of *Baetis* mayflies (Ephemeroptera) to catchment logging. *American Midland Naturalist* 115:25-41.
- WALLACE, J. B., AND J. O'HOP. 1985. Life on a fast pad: waterlily leaf beetle impact on water lilies. *Ecology* 66:1534-1544.
- WATERS, T. F. 1977. Secondary production in inland waters. *Advances in Ecological Research* 10:91-164.
- WATERS, T. F. 1979. Influence of benthos life history upon the estimation of secondary production. *Journal of the Fisheries Research Board of Canada* 36:1425-1430.
- WATERS, T. F., AND G. W. CRAWFORD. 1973. Annual production of a stream mayfly population: a comparison of methods. *Limnology and Oceanography* 18:286-296.
- WELTON, J. S., M. LADLE, AND J. A. B. BASS. 1982. Growth and production of five species of Ephemeroptera larvae from an experimental recirculating stream. *Freshwater Biology* 12:103-122.
- ZELINKA, M. 1980. Differences in the production of mayfly larvae in partial habitats of a barbel stream. *Archiv für Hydrobiologie* 90:284-297.

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