

Bioenergetics of a stream "collector" organism, *Tricorythodes minutus* (Insecta: Ephemeroptera)^{1,2}

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Abstract

The energy budget of a fine-particle collector organism, *Tricorythodes minutus* Traver (Ephemeroptera: Tricorythidae), was determined under conditions (flow, substratum, temperature) representative of its natural habitat. Digestion time (gut clearance) was rapid (30 min). Ingestion values ranged widely: 33–220 $\mu\text{g dry wt} \cdot \text{mg dry wt}^{-1} \cdot \text{h}^{-1}$ ($= \text{wW} \cdot \text{h}^{-1}$), depending on the type of food provided. Assimilation rates were lowest $\sim 2 \mu\text{g ash-free dry wt} \cdot \text{mg dry wt}^{-1} \cdot \text{h}^{-1}$ ($= \text{aW} \cdot \text{h}^{-1}$), with mixed diatoms, intermediate with the blue-green alga *Anabaena* (~ 23), and high with the blue-green *Lyngbya* (~ 61) and with a pure culture of *Nitzschia* (~ 62). Assimilation efficiencies showed a much narrower spread, being 33, 34, and 57% for mixed diatoms, blue-green algae, and *Nitzschia*. A mean respiration rate of $2.51 \mu\text{l O}_2 \cdot \text{mg dry wt}^{-1} \cdot \text{h}^{-1}$ was derived for *T. minutus* at 20°C. Growth, estimated from length-weight relationships, was $4.5 \text{ wW} \cdot \text{h}^{-1}$. The instantaneous growth rate for *T. minutus* (0.126) is higher than those reported for any other mayfly (0.034–0.060) except *Tricorythodes atratus* (0.153). Cast skins accounted for over 30% of the total production ($G + Ex = 6.5 \text{ wW} \cdot \text{h}^{-1}$). Comparison with *Stenonema pulchellum*, the only other mayfly for which complete energy budget information is available, showed respiration rates to be similar and assimilation and growth of *Tricorythodes* to be 2.9 and 5.3 times higher. However, the major distinction between the two was the high ingestion rate for *Tricorythodes* compared with that for *Stenonema* ($7 \text{ wW} \cdot \text{h}^{-1}$).

Attempts to understand the operation of freshwater ecosystems and the emerging body of data concerning nutritional requirements of their component parts have been facilitated by subdividing insect species into functional groups (Cummins 1973). Studies of energy budgets at the level of the individual or species population are prerequisite to an adequate physiological understanding of the mechanisms regulating insect abundance, distribution, and production in streams. We here attempt to define the significant pa-

rameters in the energy budget of a collector insect (*Tricorythodes minutus*) as an indication of the importance of this animal in the processing of benthic organic matter (through ingestion and assimilation efficiency), the distribution of assimilated energy in the animal, and the proportion allotted to growth.

Many mayflies, including *Tricorythodes*, function in the detritus food chain as collectors of fine particulate organic matter retained by the substratum and by marginal rooted vegetation. *Tricorythodes minutus* is known to feed heavily on detritus (Koslucher and Minshall 1973) and reaches its maximum density in backwater areas and in the silted margins of stream channels (Minshall et al. unpubl.). Given high ingestion rates, *T. minutus* is an important processor of organic detritus in streams in which it is abundant.

Most work on mayflies has been concerned with life histories. Other studies have been concerned with trophic rela-

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tions (Brown 1961; Gilpin and Brusven 1970), growth rate (Harker 1952; Brittain 1976), respiration rate (Fox et al. 1937; Rueger et al. 1969), and production estimates (Waters 1966; Pearson and Kramer 1972; Waters and Crawford 1973; Winterbourn 1974; Hall 1975). Although these studies are necessary in developing a quantitative understanding of how secondary production is controlled throughout the year, complete energy budgets of the nymphal stage of mayfly species are rare. To our knowledge Trama's (1957, 1972) work on *Stenonema pulchellum* is the only previously available study of this type.

Our specific objective was to determine the energy budget for *T. minutus* under physical conditions representative of those found in Deep Creek, Oneida Co., Idaho (IBP station 2: Koslucher and Minshall 1973) which has a temperature of 18°C year-round. In addition, comparisons were made between existing data on growth, respiration, and assimilation rates, and assimilation efficiencies for mayflies and other aquatic insects. Our ultimate goal was to define more clearly the role of "collectors" in stream ecosystems and to provide further insight into the contribution that Ephemeroptera make to benthic production.

We also discuss the utility of various direct and indirect methods of measuring assimilation rate. Lampert (1977) has shown for *Daphnia* that direct methods may underestimate assimilation because of rapid losses of ¹⁴C by respiration during feeding on labeled food. Despite this concern, we show here the consistency among direct estimates and the similarity of direct estimates to the indirect methods requiring measurements of consumption and assimilation efficiency. The similarity of assimilation rates among aquatic insects with similar generation times is also demonstrated.

Methods

The energy budget of the aquatic (nymphal) stage of *T. minutus* was calculated according to equations adapted

from Lawton (1971) and Calow and Fletcher (1972):

$$D = P + R + U = C \times DE,$$

$$A = P + R = C \times AE,$$

$$P = G + Ex + S,$$

where A = assimilation, AE = assimilation efficiency, C = consumption (ingestion), D = absorption, DE = absorption efficiency, Ex = exuvia, G = growth, P = production, R = respiration, S = secretion, and U = excretion. Excretion was not measured but energy losses as exuviae were. Hargrave (1971) has shown excretion to be a nontrivial energy expenditure for *Hyalella azteca*. All measurements were made at or near 18°C because the natural population on which this study is based lives in a spring-fed, warm-water stream. The methods used are presented in detail by McCullough (1975) and only the essential points are summarized here.

Feeding studies—Blue-green algae (*Lyngbya* and *Anabaena*), a natural diatom community, and a pure culture of *Nitzschia* sp. were grown and labeled with ⁵¹Cr and ¹⁴C. ¹⁴C activity densities were within the range (0.01–0.001 μg·cpm⁻¹) preferred for high statistical counting accuracy (Sorokin 1968). Percentage of organic matter was determined as weight loss on ignition (550°C).

Before feeding experiments with the natural diatom community and blue-green algae, *Tricorythodes* nymphs were kept on nonlabeled fine particulate stream detritus for at least 24 h. Nymphs fed on *Nitzschia* were acclimated at least 24 h on nonlabeled *Nitzschia*. Acclimation and feeding on mixed diatoms was done at 18°C; those utilizing blue-green algae and *Nitzschia* were done at 20°C. *Tricorythodes* used in feeding experiments was never kept in the laboratory for more than 1 week.

Nymphs were acclimated and fed in plastic petri dishes with a hypodermic needle inserted through the side to supply aeration. Fine gravel (~20% cover) was provided as a substratum and food generally covered the remainder of the

dish. After acclimation, nymphs were transferred by pipette through filtered water into dishes with labeled food to eliminate extraneous nonlabeled food. Nymphs with black wingpads were not used because the gut begins to atrophy at this stage.

Measurement of radioactivity in food, feces, and animals—Samples of labeled food were placed on preweighed membrane filters (Gelman AN-450) which were dried (50°C) and weighed to the nearest 0.1 μg on an electrobalance. After feeding, animals were either killed immediately or allowed to clear their guts by feeding on nonlabeled food and were then analyzed for radioactivity remaining in the tissues. Nonlabeled food in petri dishes plus the labeled feces produced were filtered on membrane filters and dried. ^{51}Cr activity was counted on a Packard autogamma scintillation counter. Samples were then oxidized (Packard sample oxidizer), and the ^{14}C counted on a liquid scintillation counter.

Estimation of digestion time, gut fraction, and preliminary consumption rate—Digestion time is equal to gut-filling time if feeding is continuous as it is in *T. minutus*. Digestion time (gut-filling time) was measured at 17.8° and 21°C by transferring nymphs, preconditioned 24 h on partially decomposed *Cladophora* and detritus at experimental temperatures, to petri dishes containing the same food source mixed with powdered charcoal. Animals were killed after 5, 6–7, and 10 min of feeding on the marked food. Entire guts were dissected from the body and the fraction of the gut filled by the marked food was used to estimate digestion time.

The gut fraction (percentage of total dry weight comprised by gut + contents) was measured by separating entire guts from nymphs and placing guts + contents and the remaining tissues on preweighed foil squares. Sample dry weight (50°C) and ash weight (550°C, 24 h) were obtained on an electrobalance. Ingestion rates were estimated by dividing gut fraction in $\mu\text{g dry wt} \cdot \text{mg dry wt}^{-1}$ (=wW) by digestion time.

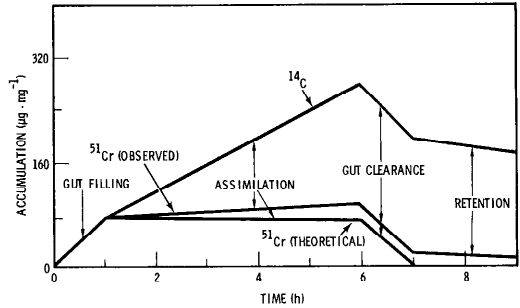


Fig. 1. Accumulation and retention of labeled food measured by ^{51}Cr and ^{14}C . Feeding takes place for 6 h, after which animal is transferred to nonlabeled food. Ingestion rate = $80 \text{ wW} \cdot \text{h}^{-1}$; AE = 50%; gut-loading time = 1 h.

Consumption rate—Mean activity densities of food samples ($\mu\text{g dry wt} \cdot \text{cpm}^{-1}$ or $\mu\text{g ash-free dry wt} \cdot \text{cpm}^{-1}$) multiplied by ^{51}Cr or ^{14}C activity of animal samples yielded absolute consumption by the method of Sorokin (1968): $C = \mu\text{g} \cdot \text{cpm}^{-1} \times \text{cpm} = \mu\text{g}$. Consumption rate was calculated by dividing absolute consumption (μg) by animal dry weight (mg) and feeding time (h). Consumption rate, determined with both ^{51}Cr and ^{14}C , was used in conjunction with gut fraction to estimate digestion time. Digestion time also was estimated from the ratio of $^{14}\text{C}:^{51}\text{Cr}$ accumulations after various feeding periods; this ratio equals 1.0 at gut filling and increases afterward at a rate dependent on AE. Accumulation is used in the context of gut + tissue when digestion time is exceeded during feeding on labeled food, and consumption is used when referring to feeding times less than the digestion time or when gut filling was not achieved even though normal digestion time was exceeded.

Assimilation rate and efficiency—Assimilation rates were obtained in four different ways, two (dual label and conventional ^{14}C) by direct measurement.

In the dual-label method ^{14}C is assimilated with the organic fraction of food at a rate governed by the ingestion rate and assimilation efficiency and the accumulation of ^{14}C -labeled food after gut filling assumes a lower slope than for the ingestion rate. At the same time, food accu-

mulation, monitored by ^{51}Cr uptake, approaches a plateau at gut filling which is slightly inclined due to a low rate of ^{51}Cr assimilation by tissues (Fig. 1). If we assume respiratory loss of ^{14}C after gut filling to be low, the initial rate of accumulation (gut + tissue) after gut filling gives the assimilation rate. In addition, ^{14}C estimates of accumulation after gut filling minus ^{51}Cr estimates of the gut fraction (corrected for ^{51}Cr assimilation) indicate ^{14}C assimilation after gut filling.

In the conventional ^{14}C method (Sorokin 1968) of calculating assimilation rate, the animals were allowed to feed on ^{14}C -labeled food and then to clear their guts on the nonlabeled food for a period exceeding digestion time. ^{14}C remaining in tissues indicates assimilation during the time allowed for feeding on labeled food, assuming that consumption rate was constant and that respiratory losses were minimal.

Assimilation rate also was calculated as mean $C \times AE$ and as $G + R + Ex$. Assimilation rate derived by summing field and laboratory measures of growth, respiration, and exuvia production was taken as a standard to which assimilation as $C \times AE$ was compared assuming digestion times of 7, 30, and 60 min. Ingestion rate (calculated as gut fraction/digestion time) was then divided into the standard assimilation rate to determine what AE was necessary to produce the required assimilation. This AE was then compared to those derived by the ^{14}C and dual-label methods.

Assimilation efficiency was calculated according to the dual-label method (Calow and Fletcher 1972). The dual-label method is superior to the ^{14}C method because respiratory losses of ^{14}C during feeding do not affect the results, as only activity in food and feces is measured.

Production rate—Data from Newell (1976) on field growth rates and frequency of molting during nymphal growth were used in production calculations. Growth rate was followed from 2.5- to 6.0-mm size for 12 individual nymphs (7 ♀, 5 ♂) enclosed in screened containers at Deep Creek and supplied with natural

food. Percentage of dry body weight for mean size individuals at each molting stage was calculated by weighing dry cast skins and relating length of cast skin to dry weight of a nymph by a length-dry wt regression calculated for 200 individuals. The caloric equivalent for *Tricorythodes* from Deep Creek is 4.676 cal·mg dry wt $^{-1}$ (=cW) (Brass 1971); a caloric equivalent for cast skins for *Hedriodiscus* (Diptera) was taken from Stockner (1971).

Respiration—Respiration rate was measured in a circulating flow-through system at 20°C and 6.8 cm·s $^{-1}$ current velocity with a galvanic cell O $_2$ electrode. A piece of monofilament screen (Nitex) provided a substrate. Two respiration rate measurements of *Tricorythodes* ranging in size from 2.4 to 4.5 mm were made on animals with a mean dry weight of 383 ($n = 124$) and 273 μg ($n = 314$). Percent saturation levels, determined according to Montgomery et al. (1964) declined from 84.2 to 40.0% O $_2$ saturation in experiment 1 (495 min); in experiment 2 saturation declined from 82.7 to 49.6% in 305 min. Although galvanic cells consume oxygen, only about 0.4% of the total O $_2$ consumption was due to the probe.

Results and discussion

Digestion time, gut fraction, and preliminary consumption rates—*Tricorythodes* feeding on *Cladophora* marked with carbon dust could fill its gut in 7 min at 18° and 21°C. The gut fraction averaged 8.70% (SD 2.49, $n = 8$) of the total body weight (including gut contents), which is equivalent to a full gut load of 87 wW. If digestion time were 7 min (8.57 gut loads per hour) with a gut fraction of 87 wW, consumption rate would equal 745.6 wW·h $^{-1}$. Further experimentation suggested that these high rates may have been due to rapid initial gut-filling rates even though nymphs were preconditioned 24 h before transfer to marked food. *Tricorythodes*, preconditioned 24 h on *Nitzschia*, was fed on ^{14}C -labeled *Nitzschia* (exp 1) and sampled after feeding periods of between 8 and 56 min. Within 8 min, animals had accumulated 28.7 wW ($n = 3$) of diatoms

and after 24 min the food accumulated reached a maximum (61.9 wW) not exceeded during the remainder of feeding (Fig. 2). Thus, the gut appeared to be full at $t = 24$ min and the plateau for accumulated activity may indicate a temporary cessation of feeding due to diminishing hunger on a rich (highly organic) food source. However, since test animals were prefed 24 h on the experimental food, hunger would not explain the initial uptake rate. Assuming that food accumulation between 8- and 24-min samples continues at sustained levels and that digestion time is ~ 30 min, we calculate the mean consumption rate from these samples to be $193.9 \text{ wW} \cdot \text{h}^{-1}$ (SD 48.2, $n = 6$, 46 total animals). If digestion time is ~ 1 h, then the mean consumption rate based on accumulation of food after 32 to 56 min of feeding is $79.1 \text{ wW} \cdot \text{h}^{-1}$ (SD 16.9, $n = 4$, 29 total animals).

Consumption and assimilation rates and assimilation efficiency—The rate of assimilation of ^{14}C -labeled blue-green algae was monitored by hourly collections of nymphs from $t = 1$ to 6 h and again at $t = 22.5$ h. A quadratic equation fit to the uptake curve was used to calculate the accumulation at $t = 1.0$ - and 6.0 -h periods. The increase in accumulation during this 5-h interval yielded the mean assimilation rate, because digestion time was known to be < 1 h. The gut fraction, ingestion rate, and AE were then calculated (formula 1).

Formula 1:

$$\begin{aligned} &^{14}\text{C-derived mean assim rate (A)} \\ &= \frac{(\text{gut + tissue accum at } t = x \text{ h}) - (\text{gut + tissue accum at } t = 1.0 \text{ h})}{(x - 1) \text{ h}} \end{aligned}$$

$$\begin{aligned} &^{14}\text{C-derived gut fraction} \\ &= \frac{(\text{gut + tissue accum}) - (\text{mean A})}{(\text{No. h beyond gut filling});} \end{aligned}$$

$$\text{ingestion rate (C)} = \frac{\text{gut fraction}}{\text{digestion time (h);}}$$

$$\text{AE} = \text{A} : \text{C}.$$

Assimilation rate also was calculated from ^{51}Cr - and ^{14}C -derived accumulation

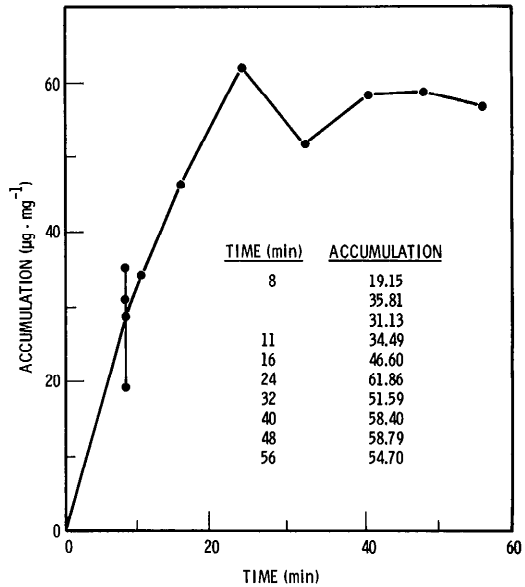


Fig. 2. Accumulation of diatoms (wW) vs. time at 20°C by *Tricorythodes minutus*.

values after a specified feeding period (formula 2). The ^{51}Cr -derived accumulation value was corrected for ^{51}Cr assimilation by a mean ^{51}Cr assimilation rate applied to the time beyond the gut-filled point. The corrected gut fraction was subtracted from the ^{14}C -derived gut + tissue accumulation value, yielding the absolute assimilation in the interval between gut filling and termination of the feeding period. The corrected gut fraction divided by the digestion time equals ingestion rate.

Formula 2:

$$\begin{aligned} &^{51}\text{Cr-derived gut accum} \\ &= \frac{[(^{51}\text{Cr-derived gut + tissue accum}) - (^{51}\text{Cr-derived assim rate})] \cdot [(\text{No. h to end of feeding period}) - (\text{No. h to end of gut filling})]}{\text{assim rate (A)}} \end{aligned}$$

$$\begin{aligned} &^{14}\text{C-derived gut fraction} \\ &= \frac{[(^{14}\text{C-derived gut + tissue accum}) - (^{51}\text{Cr-derived gut accum})]}{\text{No. h elapsed from gut filling to end of feeding period}} \end{aligned}$$

$$\text{ingestion rate (C)} = \frac{\text{gut fraction}}{\text{digestion time (h);}}$$

$$\text{AE} = \text{A} : \text{C}.$$

Table 1. Gut fraction (wW), assimilation rate (A) and efficiency (AE), and ingestion rate (C) of *Tricorythodes* feeding on *Lyngbya*. Values calculated according to formula 1 (see text) and are corrected for digestion (gut filling) times of 7, 30, and 60 min. Values for nymphs of size class I based on a 1.0-h gut + tissue accumulation; for size class II, time period is 2.0 h. Assimilation rate determined according to conventional ^{14}C method.

Digestion time (min)	Gut + tissue	Tissue	A	Gut fraction	C	AE
	(wW)					
Size class I (2.6–3.5 mm)						
7	142.3 (1 h)	77.4 (3-h defecation)	77.4 (66.7)*	73.9	634.1	12.2
30				103.6	207.2	37.3
60				142.3	142.3	54.4
Size class II (3.6–4.5 mm)						
7	205.9 (2 h)	127.8† (6-h defecation)	63.9 (55.1)*	85.6	734.0	8.7
30				110.1	220.2	29.0
60		120.8 (9-h defecation)		142.0	142.0	45.0

* Ash-free dry wt·mg⁻¹.

† Used in calculation.

In experiment 2 we measured the accumulation of food during 1.0 and 2.0 h of feeding on ^{14}C -labeled *Lyngbya* by size classes I and II. Since subsequent experiments revealed that digestion time was equal to from 7 min to 1.0 h depending on conditions, assimilation rate and AE could not be calculated according to the conventional ^{14}C method. Accumulation of food after 1.0 and 2.0 h of feeding by the two size classes was corrected for assimilation of ^{14}C after possible digestion times of 7, 30, and 60 min. Consequent ingestion rates, gut fraction, and AE values were calculated (Table 1). Values of food (gut + tissue) accumulation in size class II after 2.0-h feeding, followed by 6.0- and 9.0-h defecation, were nearly equal, indicating that ^{14}C loss due to respiration during a 3.0-h period was low. Although ^{14}C respiratory losses may be greater during and immediately after ingestion of ^{14}C -labeled food (Conover and Francis 1973), we assumed that the total loss was small. Assimilation rates based on ^{14}C remaining in tissues after defecation were applied to the period between gut filling and termination of feeding period to correct the gut + tissue accumulation and derive the gut fraction (formula 1). Gut fractions based on a digestion time of 30 min were similar to

gravimetric estimates. Gut fraction, consumption rate, and AE at each digestion time for the two size classes were similar (Table 1).

Accumulation of food by *Tricorythodes* feeding on ^{14}C -labeled *Anabaena* (exp 3) was similar for the two size classes (383 and 332 wW) after 22.5 h. Uptake of food (Y in wW) in relation to accumulation of ^{14}C over time (X in h) was not significantly different ($P < 0.05$; *t*-test) for the two size classes and therefore is best described by the single curvilinear regression: $Y = -0.75X^2 + 32.31X + 13.28$ ($r^2 = 0.96$). Accumulation during the initial 6-h feeding period was approximately linear, but the 22.5-h value for each size class was less than expected by extrapolation of the initial linear portion, indicating some respiratory ^{14}C loss. Based on the regression of accumulation vs. time and 13.8% ash, the accumulation rates between $t = 1.0$ and 6.0 h (due to assimilation because digestion time is < 1 h) were 27.3 and 26.6 wW·h⁻¹ for size classes I and II. Mean assimilation rate for the two size classes was 23.3 μg ash-free dry wt·mg dry wt⁻¹·h⁻¹ (aW·h⁻¹). Gut + tissue accumulations were derived from the regression equations for the two size classes at 1.0 and 2.0 h. Absolute assimilation from time of gut filling (7, 30,

Table 2. The ¹⁴C-derived gut fraction, consumption rate, and assimilation efficiency of *Tricorythodes* feeding on *Anabaena*. Calculations made according to formula 1 for ¹⁴C gut + tissue accumulations at feeding times of *t* = 1.0 and 2.0 h with corrections for assumed digestion times of 7, 30, and 60 min. Mean assimilation rate of 26.96 wW·h⁻¹ used for AE correction.

Feeding (h)	Digestion (min)	Size class	Gut fraction (wW)	C	AE
1.0	7	I	41.5	356.0	7.6
		II	25.1	215.1	12.5
	30	I	51.8	103.7	26.0
		II	35.4	70.8	38.1
	60	I	65.3	65.3	41.3
		II	48.9	48.9	55.1
2.0	7	I	25.3	216.9	12.4
		II	25.7	220.2	12.2
	30	I	35.5	71.1	37.9
		II	35.9	71.8	37.5
	60	I	49.0	49.0	55.0
		II	49.4	49.4	54.6

or 60 min) to end of the feeding period (1.0 and 2.0 h) was calculated from the mean assimilation rate and subtracted from the gut + tissue accumulation to yield the gut fraction. Ingestion rates and AE were then derived for the three digestion times (Table 2). AE values for a digestion time of 30 min ranged from 26 to 38%, which corresponds to those found for *Lynghya*.

The high ingestion rates on blue-green algae are noteworthy in light of conflicting reports concerning the nutritional value of blue-greens for invertebrates. *Anabaena* has been found to provide very high AE for some invertebrates (Arnold 1971; Monakov 1972) but to be digested very little by others (D. Schindler 1968; Hargrave 1970). J. Schindler (1971) felt that blue-green algae caused mechanical interference with feeding. Since the blue-green algae in this research were chopped into short fragments, consumption most likely was facilitated. High ingestion rates or high AE by themselves do not necessarily indicate the nutritional value of blue-green algae because they may not provide sustained long term growth due to toxic factors, mucilaginous sheaths, or vitamin defi-

Table 3. Mean gut fraction, ingestion rate (C), assimilation rate (A), and assimilation efficiency (AE) for *Tricorythodes* fed on diatoms for periods of 0.75, 1.0, and 5.0 h (experiments 5 and 6). ⁵¹Cr-derived gut + tissue accumulations corrected for ⁵¹Cr assimilation at rate equivalent to 2.0 wW·h⁻¹. Values calculated according to formula 2 based on digestion times of 7, 30, and 60 min. Mean assimilation rate derived according to formula 1.

Exp.	Digestion (min)	Mean gut fraction (wW)	Mean C	Mean A	Mean AE
			(wW·h ⁻¹)		
5	7	23.6	202.4	12.3	6.1
	30	24.4	48.7	17.3	35.4
	60	25.6	25.6	12.2	47.7
6	7	15.5	133.1	9.6	7.2
	30	16.3	32.6	15.3	47.0
	60	17.1	17.1	13.6	79.1

ciency when used exclusively (Arnold 1971). Obviously, growth is the only real measure of food quality.

In experiment 4, the mean ⁵¹Cr- and ¹⁴C-derived accumulation values on diatoms for seven multiple-animal samples for three size classes were 39.8 and 39.0 wW in 0.5 h. For a digestion time of 30 min the ingestion rate equaled about 80 wW·h⁻¹, which corresponds to the rate on *Anabaena*.

Accumulation of ⁵¹Cr- and ¹⁴C-labeled diatoms after feedings of 0.75, 1.0, and 5.0 h was determined in experiments 5 and 6. Because feeding times may have exceeded digestion times, assimilation rates were not calculated by conventional methods. Instead ⁵¹Cr-derived values for food accumulation at 0.75, 1.0, and 5.0 h were corrected for ⁵¹Cr assimilation during the time following gut filling according to formula 2 (Table 3). The difference between mean 1.0- and 5.0-h ⁵¹Cr-derived accumulations in the two experiments yielded ⁵¹Cr assimilation rates equivalent to 3.0 and 2.4 wW·h⁻¹ during the 4.0-h interval. In experiment 6, 14 nymphs fed for 1.0 h on diatoms retained an equivalent of 2.0 wW of ⁵¹Cr. This assimilation rate was used to correct ⁵¹Cr accumulations. The corrected ⁵¹Cr-derived value (gut fraction) was then subtracted from the ¹⁴C-derived (gut + tis-

Table 4. Mean assimilation rate (A) and AE of *Tricorythodes* feeding experiments 1-3 and 5-6 based on 30-min digestion time.

Exp.	Method	A ($\text{wW}\cdot\text{h}^{-1}$)	A ($\text{aW}\cdot\text{h}^{-1}$)	A $\text{cW}\cdot\text{h}^{-1}$	AE (%)	Food
1	^{14}C $AE \times C$ (uptake)	111.2	62.4	0.341	57.4	<i>Nitzschia</i>
2	Formula 1	70.6	60.9	0.297	33.2	<i>Lyngbya</i>
3	Formula 2	27.0	23.3	0.113	35.0	<i>Anabaena</i>
5	Formula 2	17.3	3.2	0.014	35.4	diatoms
	Formula 1	10.5	2.0	0.009		
6	Formula 2	15.3	2.8	0.013		
	Formula 1	13.3	2.5	0.011	47.0	diatoms
	^{14}C	10.2	1.9	0.009		

sue) value, yielding tissue accumulation during the time from the end of gut filling (7, 30, or 60 min) to the end of the feeding period (0.75, 1.0, and 5.0 h). The mean assimilation rate for *Tricorythodes* feeding on diatoms with a digestion time of 30 min was $3.2 \text{ aW}\cdot\text{h}^{-1}$ in experiment 5 and $2.8 \text{ aW}\cdot\text{h}^{-1}$ in experiment 6 (Table 4).

Assimilation rates on diatoms in experiments 5 and 6 were also determined by subtracting ^{14}C -derived accumulations at $t = 1.0 \text{ h}$ from those at 5.0 h according to formula 1. The assimilation rates for the two experiments were 2.0 and $2.5 \text{ aW}\cdot\text{h}^{-1}$ (Table 4). The assimilation rate of animals fed 1.0 h on ^{14}C -labeled food (experiment 6) followed by 1.5-h defecation showed an assimilation rate of $1.9 \text{ aW}\cdot\text{h}^{-1}$. On the basis of Rattlesnake Creek diatoms (18.47% organic matter, $4.520 \text{ cal}\cdot\text{mg}$ ash-free dry wt^{-1}), assimilation rates between 1.9 and $3.2 \text{ aW}\cdot\text{h}^{-1}$ correspond to rates of 0.009 to $0.014 \text{ cW}\cdot\text{h}^{-1}$.

Much of the variation in assimilation rates (Table 4) could be a function of differences in percentage organic matter of the various foods. Rattlesnake Creek diatoms were very low in organic matter compared with values reported in the literature (Nalewajko 1966) and also provided low assimilation rates. Assimilation rates on Rattlesnake Creek diatoms calculated by two variations of ^{14}C accumulation (formulae 1 and 2) and the conventional ^{14}C method yielded similar results in experiments 5 and 6 (Table 4).

Assimilation rates on blue-green algae were 10-30 times greater than on Rattlesnake Creek diatoms; percentage organic matter of blue-green algae was 4.7 times greater. Assimilation rates on blue-green algae were 3.1 to 8.0 times greater than necessary to supply the energy of $G + R + Ex$. It is uncertain whether growth rates would be significantly higher on blue-green algae over an extended period or whether ingestion rate would diminish gradually and reduce the assimilation rate.

AE values derived from assimilation and ingestion rates on diatoms, based on 30-min digestion, were 35.4 and 47.0% in experiments 5 and 6 (Table 4). Mean AE derived by the dual-label method for nymphs feeding on mixed diatoms was 37.6% (SD 8.83, $n = 6$). The fact that AE estimates correspond to the dual-label estimate, supports the contention that a 30-min digestion time and the ingestion rates derived using this time are reasonable. The similarity of the AE estimate (27.6%), calculated as $(G + R + Ex):C$ (Table 5), to the dual-label AE for *Tricorythodes* feeding on mixed diatoms further supports the 30-min digestion time estimate and the resulting ingestion rate.

Short digestion times such as those found for *T. minutus* are not uncommon. *Baetis rhodani* and *Chloeon dipterum* have gut passage times of 30 min (Brown 1961) and *Simulium* has times of 20-30 min (Ladle et al. 1972) and 20-75 min depending on species, temperature, and

Table 5. Comparison of bioenergetics of *Tricorythodes minutus* and *Stenonema pulchellum* (Trama 1957).

<i>Tricorythodes minutus</i> 3.0-4.0-mm nymphs; growth at 18°C; respiration at 20°C; calc for mean wt of 0.6375 mg (cW·h ⁻¹)		<i>Stenonema pulchellum</i> 4.0-5.0-mm nymphs; growth at 20°C; respiration at 20°C; calc for mean wt of 0.735 mg (cW·h ⁻¹)	
G	0.021	0.004 based on 5.295 cW	
R	0.012	0.009 based on 1.78 μl O ₂ ·mg dry wt ⁻¹ ·h ⁻¹ and 5.0 cal·ml ⁻¹ O ₂	
Ex	0.003	not determined	
A	0.037	0.013 (calc from G + R)	
C*	0.135 based on 30-min digestion time, 8% gut fraction	0.029	
AE	27.4	44.8	

* For *Stenonema* caloric value of diatoms = 3.128 cW; for *Tricorythodes* caloric value of diatoms = 4.520 cal·mg ash free dry wt⁻¹ and diatoms contain 18.47% organic matter.

instar (Mulla and Lacey 1976). Ingestion rates from experiments 5 and 6 were based on gut fractions of 15.5 to 25.6 wW, which are considerably less than the gravimetrically determined gut fraction of 87 wW. The quantity of food in the gut at any instant may vary on a diel cycle (Mecom 1970) or among individuals (Winterbourn 1974) and it is possible that defecation may occur before a maximum gut-load is achieved. For this reason the dual-label AE estimate is more reliable than the conventional ¹⁴C estimate.

Although a high AE is usually associated with low ingestion rates and consequently long gut retention times, the ingestion rate for *Tricorythodes* was quite high. High AE and ingestion rates produced high assimilation rates. When assimilation rates from other bioenergetics studies are converted to similar units, we find that several other invertebrates assimilate <0.01–0.05 cW·h⁻¹ throughout larval growth, during at least a portion of the larval stage, or at warm water temperatures (Cummins 1975; McCullough 1975; Nilsson 1974; Otto 1974). High assimilation rates found during early instars often decline with age (see Lawton 1971; Otto 1974) and may increase dramatically with temperature (Nilsson 1974). Species with more than one generation per year, such as *Glossosoma nigrior*, *Gammarus pulex*, and *Si-*

mulium, appear to be more inclined to exhibit assimilation rates >0.01 cW·h⁻¹ during a significant portion of their life than species which require a year or more to complete the larval stage such as *Pyrrhosoma nymphula* (Lawton 1971) and *Pteronarcys scotti* (McDiffett 1970) which have assimilation rates ranging primarily from about 0.001 to 0.01 cW·h⁻¹.

Growth—A regression equation was derived relating body length (tip of head to base of cerci) to dry weight for 200 *T. minutus* nymphs: $\text{Log}_e Y = -4.688 + 3.222 \text{ log}_e X$ where $X = \text{length (mm)}$ and $Y = \text{dry weight (mg)}$. A mean of 7.59 d was required for 12 nymphs isolated in growth chambers in Deep Creek to grow 1 mm on natural foods at a temperature of 18°C (Newell 1976). Increase in body length was followed for these specimens from about 2.5 to 6 mm; growth was linear over this size interval. From the regression equation, the mean dry weights of 3.0- and 4.0-mm animals were determined to be 354 and 921 μg.

Respiration—Mean respiration rate in experiment 1 was 3.88 μl O₂·mg dry wt⁻¹·h⁻¹. In experiment 2 the plot of cumulative O₂ consumption (Y in mg) vs. time (X in min) for O₂ determinations at 10–30-min intervals over 310 min showed a curvilinear relationship: $Y = -273.8 + 18.15X - 0.02X^2$ ($r^2 = 1.00$).

Rate of oxygen consumption changed at $t = 190$ min when saturation declined to 59.8%. The mean respiration rates for the two time intervals (0 to 190 and 190 to 305 min) were 2.51 and 1.38 $\mu\text{l O}_2 \cdot \text{mg dry wt}^{-1} \cdot \text{h}^{-1}$.

Energy budget of Tricorythodes—The energy budget parameters derived for *T. minutus* are given in Table 5. Assimilation rates were calculated by summing $G + R + Ex$ for nymphs between 3.0 and 4.0 mm in terms of $\text{cW} \cdot \text{h}^{-1}$. The increase in dry weight during this interval was 567 μg . Subtracting the 8% gut fraction from this yields 522 μg of tissue growth during the 7.59 d at 18°C required for the 1-mm increase in length. This is equivalent to 2.9 $\mu\text{g dry wt} \cdot \text{indiv}^{-1} \cdot \text{h}^{-1}$ or 4.5 $\text{wW} \cdot \text{h}^{-1}$. Relative growth rate was based on a mean dry weight of 638 μg during the interval, assuming linear weight increase; this growth rate is equivalent to 0.021 $\text{cW} \cdot \text{h}^{-1}$, using a caloric equivalent of 4.767 cW (Brass 1971). A mean respiration rate of 2.51 $\mu\text{l O}_2 \cdot \text{mg dry wt}^{-1} \cdot \text{h}^{-1}$ at 20°C was used for *Tricorythodes*. This is similar to the range of 1.86–2.66 for *C. dipterum* (Kamler 1969) and the mean of 1.74 at 20°C for *Stenonema pulchellum* (Trama 1972). With an assumed RQ of 0.88, typical of combined carbohydrate and protein metabolism, energy utilization is 4.90 $\text{cal} \cdot \text{ml O}_2^{-1}$ consumed and the mean respiration rate for the growth interval becomes 0.012 $\text{cW} \cdot \text{h}^{-1}$.

Molting occurs 18–22 times during growth between 0.5 and 6.0 mm in the nymphal stage, depending on sex (Newell and Minshall in press). If this length is divided into 20 equal increments, based on the simplifying assumption of linear growth, nymphs increase 0.275 mm in length per molt. The dry weight of nymphs from each size interval, computed from the length-dry weight regression, was multiplied by the percent of total dry weight made up by the cast skin (8.31%, SD 1.87, $n = 16$). The weight of skins shed during the four molts which occur during the 3.0–4.0-mm interval is 234 μg or 1.3 $\mu\text{g} \cdot \text{indiv}^{-1} \cdot \text{h}^{-1}$ averaged for the 7.59-d period. Using the caloric equivalent of 3.185 cW (ash-free) for exu-

viae and a mean percentage ash of 50.33% (SD 13.05, $n = 15$), we calculate the energy lost as exuviae to be 0.0032 $\text{cW} \cdot \text{h}^{-1}$. The combined weight of skins shed in the last 15 of 20 molts is equivalent to 45.9% of the maximum weight of a nymph and is 31.4% of total production ($G + Ex$). Energy lost as exuviae accounted for only 2.8% of assimilated energy during the life cycle of a damselfly nymph *P. nymphula* (Lawton 1971) and 1.9% for the caddisfly *Potamophylax cingulatus* (Otto 1974). Lasker (1966), however, found that 15.3% of assimilated carbon is lost as exoskeleton in the marine crustacean *Euphausia pacifica*. The mean assimilation rate during the 3.0–4.0-mm interval was 0.037 $\text{cW} \cdot \text{h}^{-1}$, the net growth efficiency ($G:A$) was 58.1%, and net production efficiency ($P:A$) was 66.7%. Energy lost as excretion was not measured, although it has been shown to be of importance in bioenergetics studies (Hargrave 1971).

Comparison with the energy budget of Stenonema—The energy budget for *S. pulchellum* (Trama 1972) is the only other one published for a mayfly. The major distinction between *Tricorythodes* and *Stenonema* is the high ingestion rate for *Tricorythodes*. The mean consumption rate calculated from Trama (1972) for 4–7-mm *Stenonema* feeding on diatoms was 7.3 $\text{wW} \cdot \text{h}^{-1}$; the range for 2.6–5.5-mm *Tricorythodes* was 32.6–220.2 $\text{wW} \cdot \text{h}^{-1}$. If we assume a mean gut fraction of 80 wW and a 30-min digestion time, the ingestion rate for *Tricorythodes* was 160 $\text{wW} \cdot \text{h}^{-1}$. Although digestion time studies were not discussed by Trama (1957, 1972), they are necessary for correct estimation of consumption rate. Cummins et al. (1973) found a maximum consumption rate of 23.2% $\text{dry wt} \cdot \text{d}^{-1}$ for *Stenonema* spp. feeding on conditioned hickory leaves. Assuming a gut fraction of 80 wW for *Stenonema*, we calculate that the gut contents would be replaced every 8.27 h and ingestion rate would equal 9.7 $\text{wW} \cdot \text{h}^{-1}$, which is equivalent to Trama's finding.

Although the respiration rates of *Tricorythodes* and *Stenonema* are similar,

Table 6. Growth rate and production characteristics of selected mayfly species.

	Instantaneous G^* $g \cdot g^{-1} \cdot d^{-1}$	Cohort TR	Annual TR	Nymphal stage (d)	Generations yr^{-1}	Reference
<i>Tricorythodes minutus</i>	0.126 (5.74)	6.0		34 d field (18°C) 48.4 d lab	2-4	Newell 1976
<i>Tricorythodes atratus</i>	0.153 (7.49)	5.8 7.5	25	49	2	Hall 1975
<i>Baetis vagans</i>	0.046 max	—	9.7	60 (summer gen) 240 (winter gen)	3	Waters 1966
<i>Ephemerella subvaria</i>	0.024 0.060 max (6.2)	4.2	5.8	254	1	Waters and Crawford 1973
<i>Leptophlebia vespertina</i>	0.034			342	1	Brittain 1976
<i>Deleatidium</i> sp.	3.89 (summer gen) 0.85 (winter gen)				2	Winterbourn 1974

* Life cycle G in parentheses.

the growth rate of *Tricorythodes* is nearly 5.3 times greater (Table 5). Whereas only 7.59 d are required for *Tricorythodes* to grow 1 mm at 18°C, *Stenonema* requires 33 d at 20°C. Energy loss as exuviae was not measured for *Stenonema*. This may cause a substantial underestimate in total production; Ide (1935) estimated that *Stenonema canadense* undergoes 30 to 45 molts. *Tricorythodes*, with a $G:A = 58\%$, is able to direct nearly twice as much assimilated energy into growth as is *Stenonema*. These differences could be attributed to *Stenonema* being reared in the laboratory, even though food was unlimited, or could be a result of an intrinsic difference in growth potential. Low laboratory-derived growth rates also may be caused by improper food, as *Stenonema* has been considered a detritivore (Cummins et al. 1973). The low growth efficiency ($G:R = 46\%$) for *Stenonema* (vs. 174% for *Tricorythodes*) may be typical of slow-growing animals. Evidently considerable variation occurs between insects (at least at the family level) in assimilation rate and in the distribution of assimilated energy. Because assimilation is the key to measuring energy flow to secondary produc-

ers (Edmondson 1974), generalizations regarding the relationship of assimilation rate vs. a complex of factors such as temperature, food supply and quality, and generation time would be useful. To increase the reliability of energy budget analysis, however, combinations of methods (direct and indirect) are preferable to strict reliance on a single method.

Comparison with growth rates for other Ephemeroptera—The similarity of growth rate estimates for *T. minutus* and *Tricorythodes atratus* (Table 6) is striking. The growth rate for *T. minutus* was determined to be $4.5 \text{ wW} \cdot \text{h}^{-1}$ at 18°C at station 2 Deep Creek; adding production of exuviae yields a total production rate of $6.5 \text{ wW} \cdot \text{h}^{-1}$. Growth rates calculated from Hall's (1975) data on mean mg dry wt $\cdot \text{m}^{-2}$ and production $\cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ranged from 5.8 to 6.3 $\text{wW} \cdot \text{h}^{-1}$ in riffles and from 5.5 to 6.3 in pools during nymphal growth. Except for *T. minutus* and *T. atratus*, instantaneous growth rates of all other mayfly species presented are considerably lower. Daily instantaneous values, such as for *Ephemerella subvaria*, are lower than the maximum values which for most mayflies are found in the young and pre-emergent instars.

The magnitude of the growth rate of a species seems to be determined primarily by temperature, food type, maximum size attained, and species. Mayfly species presented in Table 6 have nymphal development times ranging from 34 to 342 d. The number of generations per year seems to vary with locality and environmental variables (Macan 1957). Newell (1976) found a correlation between number of generations per year and the number of degree-hours above 5°C experienced by *T. minutus* nymphs. Relatively short nymphal periods have been reported for mayflies other than *Tricorythodes*. For example, *Caenis* sp. has a minimum development time of 42–49 d at 23°C (Hall et al. 1970) and *Baetis vagans* completes its summer generations in about 60 d (Waters 1969). Fremling (1967) was able to rear *Hexagenia bilineata* at 24–27°C to its maximum length (20 mm) in 79 d; about 120 and 180 d were required for *Leptophlebia cupida* (Clifford 1969) and *Ephemerella doddsi* (Radford and Hartland-Rowe 1971) to complete nymphal growth even though mature nymphs were 14 and 16 mm long. The mean maximum size of mature male and female *T. minutus* was only 5.5 mm, which may explain the difference in development time.

The cohort turnover ratio (TR) for *T. minutus* is estimated to be about 6. Waters (1969) observed that cohort turnover ratios are relatively constant for freshwater invertebrates, ranging from 2.5 to 5 with a mode of 3.5. Because production (P) = $G\bar{B}$ and $TR = P:\bar{B}$ (where \bar{B} = mean biomass), the life cycle G should approximate cohort TR , although it was found to be generally 1 unit greater for several invertebrate species (Waters 1969). The life cycle G , which is $\ln(\text{final dry wt}) - \ln(\text{initial dry wt})$, must be divided by the number of days spent in the nymphal stage to calculate daily instantaneous G (Waters 1966). Therefore, even though there is a high degree of similarity in cohort TR and life cycle G , the instantaneous G is governed by the nymphal development time.

Several factors involved in estimating

population production, and subsequently cohort TR and G , by direct sampling methods, cause underestimations of production. These include underrepresentation of small nymphs due to sampling errors (Waters 1966), emigration of large nymphs from the population by drift (Winterbourn 1974), continuous recruitment of young nymphs to the population thereby lowering the mean biomass of the cohort (Macan 1957; Winterbourn 1974), indistinct cohorts, sampling intervals too short to detect changes in mean size (Clifford 1969), and sampling intervals too far apart relative to the life span of the species (Edmondson 1974). Indirect estimation of production rates of benthic invertebrates by calculating consumption by predators (Benke 1976) indicates that an annual TR of 30 would not be unusual. The disagreement between direct and indirect methods (where cohort TR = annual TR) indicates that the direct estimates may yield TR values which are too small. Also, due to the correspondence of TR and G , life cycle growth rates such as those found for *Tricorythodes*, though dependent possibly on warm temperatures and abundant food in a desert stream with abundant insolation, may be more typical of aquatic collectors than previously assumed on the basis of such direct methods of calculation. The use of "in stream" growth chambers for individual specimens, as for *T. minutus*, and of radioactive tagging procedures to identify cohorts in the field (McCullough et al. in press) are improved methods of measuring species growth rates. Methods such as these may resolve the discrepancies between direct and indirect calculations of production and TR .

Addendum

Sweeney (1978) has recently published a new energy budget for a lotic mayfly, *Isonychia bicolor*. The energy budget parameters (mean of male and female) for nymphs in 25-d growth periods under ambient temperatures (White Clay Creek, Pennsylvania: mean = 18.5°C) are intermediate (G —0.0115; R —0.0092; Ex —

0.0003; $A=0.0209 \text{ cW}\cdot\text{h}^{-1}$) between those of *Tricorythodes* and *Stenonema*. *Isonychia* requires only 40–45 d to complete summer nymphal growth in White Clay Creek. The assimilation rate for *Isonychia* is slightly less than that of *Tricorythodes* and is typical of fast-growing animals, which have assimilation rates of 0.01 to 0.05 $\text{cW}\cdot\text{h}^{-1}$. The G:A and G:R ratios for *Isonychia* (55% and 126%) are similar to the 58% and 174% calculated for *Tricorythodes*.

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