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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	19	1	113-121	1972
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F. B. TRAMA

TRANSFORMATION OF ENERGY BY AN AQUATIC HERBIVORE
(*STENONEMA PULCHELLUM*) EPHEMEROPTERA¹

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ABSTRACT

A laboratory study of the energy budget for mayfly nymphs, *Stenonema pulchellum*, was made using a cultured diatom, *Navicula minima*, as the sole source of nutrition. Calorific equivalents were determined with an oxygen semi-microbomb, and food intake was estimated by a radiophosphorus tagging technique. The 33-day energy budget representing a 1 mm increase in body length was computed for individuals ranging from 4 to 7 mm in length. In this study, the calories expended via respiration were approximately three times those stored as growth.

1. INTRODUCTION

Detailed analyses of energy budgets for individual organisms or populations have limited value in assessing energy flow in an ecosystem. This is especially true when measurements are made under laboratory conditions. While the ultimate and most useful goal is the analysis and understanding of ecosystem energetics, detailed information on individuals and populations can be instrumental in discovering principles and mechanisms or simply used to indicate correct orders of magnitude.

Present knowledge of energy flow for herbivorous freshwater invertebrates is based upon data from few studies (Phillipson 1966). Prior to the studies by Richman (1958) on a cladoceran and Trama (1957) on a mayfly, the work of Ivlev (1939) on the bioenergetics of *Tubifex tubifex* represented all that was known for this trophic level in fresh water. Furthermore, because *Tubifex* is a detritus feeder its characterization as an herbivore is questionable.

Odum (1957) and Teal (1957) reported on energy flow studies in freshwater ecosystems, and their findings have been widely cited. Their work, along with that of others, has been summarized in several ecology textbooks (Odum 1959, Phillipson 1966, Kormondy 1969, Whittaker 1970). These broad studies at the ecosystem level, while valuable, do indicate a need for more detailed studies on the individual and population level in order to define the fundamental laws governing ecological energetics.

2. METHODS

Culturing Techniques

Nymphs of the mayfly, *Stenonema pulchellum*, are a common inhabitant of freshwater streams in eastern North America (Birks 1953) and were abundant

¹ This paper originated from a portion of a thesis submitted in partial fulfillment of a Ph. D. at the University of Michigan. Assistance and guidance rendered by Dr. David C. Chandler is gratefully acknowledged.

in riffle areas of the Huron River, Washtenaw County, Michigan. Specimens were hand picked from rocks and transported to the laboratory where they were kept in aerated river water at 20°C. Physical and chemical data were not taken routinely at times of collection, but river water temperatures ranged from near zero in winter to about 25°C in late summer. The diatom, *Navicula minima*² was isolated from its natural habitat, and a clone was cultured in a modified Chu No. 10 medium (Chu 1942).

A special procedure was devised to permit quantitative manipulation of the source of food-energy, *Navicula*. A series of sterile, preweighed ($\pm 10 \mu\text{g}$) circular coverslips were arranged in a circle inside a 15 cm petri dish containing sterile culture medium. They remained immobile once they were firmly pressed onto the bottom plate. A coverslip, bearing a heavy growth of diatoms was then placed in the center of the circle. Diatoms grew outward from this "inoculum" covering the bottom of the petri dish and the coverslips in a fairly uniform layer. In this fashion coverslips were covered on one side only and were easily manipulated with clean, fine-tip forceps. Growth on the petri dish bottom was harvested and used to determine the calorific content.

Biomass and Calorific Values

Nymphs were placed in size classes and held without food for 96 hours. The live weight, dry weight and organic content (loss-on-ignition) of size groupings were determined as outlined by Welch (1948).

Navicula biomass was estimated by oven drying at 60°C for 24 hours and reweighing ten preweighed coverslips covered with a heavy growth of the diatoms. Coverslips were then ignited in a muffle furnace at 600°C for 30 min and reweighed to determine the organic fraction.

Oxygen microbombs were not commercially available as they are today, and a semi-microbomb (70 ml) was utilized. Samples varying from 11 to 80 mg were mixed with sufficient benzoic acid (206–258 mg) to produce a temperature change of 1.5°C. This method was suggested by Dr. Shelby D. Gerking (personal communication) and has been detailed by Richman (1958).

Oxygen Consumption

Oxygen consumed by non-fasting mayflies was determined by the unmodified Winkler technique using 250 ml glass, stoppered bottles. Tests were conducted over a 24 hr period, at 15, 20 and 25°C and in the dark; a sufficient number of organisms (never more than ten) was used to produce a decrease of one to two milligrams oxygen per liter. Temperature was controlled to within $\pm 1^\circ\text{C}$ in all experiments. All bottles were gently agitated at 12 and 24 hours.

A single control bottle was run with each series, and the oxygen consumed was calculated by subtracting oxygen content of the blank from that of the experimental bottle at the end of 24 hours.

Ingestion Rate and Growth

Preweighed coverslips covered by a rich growth of *Navicula* were transferred to culture medium spiked with radioactive phosphorus ($< 10 \mu\text{Ci P-32}$). The diatoms were effectively tagged after 30 minutes' exposure under a light source. Clean coverslips were used as controls but rarely showed radioactivities above background.

A coverslip bearing labeled diatoms was presented to isolated nymphs that had been held for 24 hours in the dark with a surplus of *Navicula*. Feeding rates were measured over a 12 hr period, at 20°C, and in the dark; the time period was empirically determined to allow adequate ingestion of radioactive food and to leave about 50% uneaten. Mayflies with surgically removed mouthparts served as controls and their radioactivity was subtracted from the experimentals.

Oven-dried samples were assayed using a thin end-window GM detector and decade scaler. To covert corrected radioactivity of the consumer into terms of

² More precisely identified as *N. minima* var. *atomoides* (Grun.) Cl by Dr. Ruth Patrick, Curator of Limnology, Academy of Natural Sciences of Philadelphia.

diatom biomass ingested, it was necessary to weigh the diatom residue remaining on the coverslip upon which the nymph had been feeding.

Conditions for determining rate of growth were identical to those employed in measuring ingestion rates but the diatoms were not made radioactive. Every seven days body length was measured, number of molts noted, and the water renewed. Surplus food was always present.

3. RESULTS

Food Intake

Based on six determinations, the mean calorific value of *Navicula* was 3218 cal/g dry weight (S.E. \pm 82). This was equivalent to 4963 cal/g organic matter since the ash-free weight was 63.5% of total dry weight.

The estimated quantity of food ingested by the nymphs in a 12 hr period is presented in Table I; calorific equivalents are also given. Values

Table I. Food ingested by various size classes of *S. pulchellum* in 12 hours at 20°C

Length (mm)	No. of measurements	Food (mean \pm S.E.)	
		μ g dry wt.	cal.
4	15	54.5 \pm 2.4	0.176 \pm 0.008
5	17	73.2 \pm 3.3	0.233 \pm 0.011
6	10	125.6 \pm 4.5	0.403 \pm 0.014
7	10	135.2 \pm 5.2	0.432 \pm 0.017

ranged from 54.5 to 135.2 μ g ingested per 12 hours depending upon size of the animal. The relation between length and quantity of food ingested is non-linear and possibly sigmoidal. Due to the rather large variance associated with each mean value (Table I) a definite relationship between size and calories ingested was not evident. Nevertheless, mean calorific equivalents were used in formulating the energy budget.

Oxygen Consumption

Mean oxygen consumption by non-fasting nymphs (4-7 mm) was

Table II. Oxygen consumed by various size naiads of *S. pulchellum* at various temperatures (number of measurements given in parentheses)

Length (mm)	Oxygen Consumption (mean \pm S.E.) (μ l/mg/hr)		
	15°C	20°C	25°C
4	1.20 \pm 0.06 (4)	1.78 \pm 0.05 (6)	2.56 \pm 0.11 (5)
5	1.33 \pm 0.09 (6)	1.69 \pm 0.05 (6)	2.68 \pm 0.09 (8)
6	1.22 \pm 0.05 (4)	1.70 \pm 0.06 (6)	2.67 \pm 0.08 (4)
7	1.28 \pm 0.04 (4)	1.78 \pm 0.11 (5)	2.60 \pm 0.06 (5)
Mean	1.26 \pm 0.04 (18)	1.74 \pm 0.03 (23)	2.63 \pm 0.04 (22)

Table III. Growth and number of molts for *S. pulchellum* at 20°C over an eight-week period

No. of nymphs	Mean length of nymphs in successive weeks								Total growth in 8 weeks	Mean growth per week	Total No. of molts	Molts/nymphs in 8 weeks	Mean growth per molt	
	0	1	2	3	4	5	6	7						8
5	3.0	—	3.5	3.5	3.8	4.0	4.2	4.4	5.1	2.1	0.26	39	7.8	0.27
6	3.2	—	3.6	3.8	4.0	4.3	4.5	4.7	5.0	1.8	0.23	37	6.1	0.30
10	3.5	—	3.9	4.0	4.3	4.6	4.8	5.0	5.3	1.8	0.23	65	6.5	0.28
6	3.6	3.8	3.8	3.9	4.1	4.4	4.5	4.6	4.9	1.3	0.16	26	4.3	0.30
10	3.8	4.0	4.3	4.6	4.8	5.0	5.2	5.5	5.6	1.8	0.23	68	6.8	0.26
20	4.0	4.2	4.5	4.7	4.7	4.9	5.1	5.2	5.3	1.3	0.16	98	4.9	0.27
20	4.5	4.8	5.0	5.2	5.2	5.5	5.7	5.8	6.1	1.6	0.20	115	5.8	0.28
20	5.0	5.3	5.5	5.7	6.0	6.2	6.4	6.6	6.8	1.8	0.23	127	6.4	0.28
										1.7	0.21		6.1	0.28
										Mean				

Dash (—) indicates no data available.

1.26, 1.74, and 2.63 microliters per milligram dry weight per hour at 15°C, 20°C and 25°C, respectively. These mayflies apparently consumed oxygen in direct proportion to their mass (Table II) and have an oxygen Q_{10} value of about 2.1. An oxy-calorific equivalent of 5 cal/ml oxygen (Ivlev 1934, Swift, French 1954) was used to convert oxygen consumed into calories expended.

Growth

Nymphs ranging in size from 3 to 5 mm grew linearly at approximately 0.21 mm per week over an 8 week period (Table III). Interestingly, the average increase in length per molt was fairly constant (Table III), and could theoretically have been used to measure growth indirectly. To increase their body length 1.0 mm these nymphs required an estimated 33 days.

The calorific value per unit weight increased as the *S. pulchellum* nymphs increased in length and dry weight (Table IV, Fig. 1). This

Table IV. Mean weights and calorific values \pm S.E. of various size nymphs of *S. pulchellum*

Length (mm)	Weight (mg)		Calorific equivalent	
	Live	Dry	cal/dry gram	cal/nymph
4	2.45	0.51	5295 \pm 116	2.70
5	4.62	0.96	5396 \pm 44	5.18
6	7.24	1.29	5552 \pm 53	7.16
7	10.06	2.01	5710 \pm 37	11.48
8	—	—	5975 \pm 29	—

Dash (—) indicates no data available.

increase in calorific value could be associated with an increased lipid synthesis since gonad development was evident in nymphs greater than 6 mm in length. No measurements of lipid content were made, however. The difference in calories per nymph between any two size classes was assumed to be growth or net production.

Energy Budget

A 33 day energy budget was constructed from data collected at 20°C and is summarized in Table V. This budget represents a 1.0 mm increase in length. Because ingestion rate and oxygen consumption were measured on specific size classes, it was expedient to assume a linear relationship between successive size classes. For example, the average daily ingestion rate over 33 days was simply the mean of the measured ingestion rates for nymphs of successive size classes.

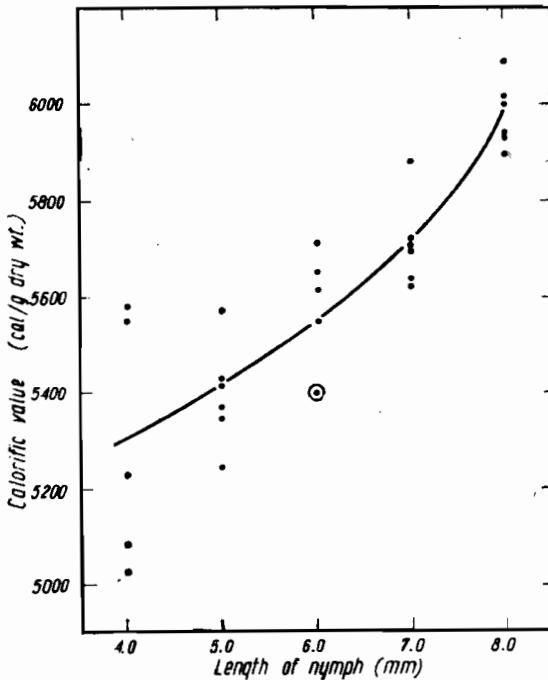


Fig. 1. Calorific values of various size classes of *S. pulchellum* nymphs. Each point represents a single measurement made on a composite sample. The circled point indicates two observations of equal value. Curve is drawn through the arithmetic mean of observations

Mean efficiency of growth was 14.5% and metabolic expenditure amounted to 38.6%. By difference, the energy lost through egestion was estimated to be 46.9% (Table V).

Table V. Energy budget for *S. pulchellum* at 20°C. Budget based on the mean growth rate of 1 mm per 33 days

Initial length of nymphs (mm)	Caloric Intake (cal)	Metabolic Loss		Growth		Egestion	
		Cal.	%	Cal.	%	Cal.	%
4.0	13.53	5.08	37.6	2.48	18.3	5.97	44.1
5.0	21.02	7.76	37.0	1.98	9.4	11.28	53.6
6.0	27.56	11.37	41.2	4.32	15.7	11.87	43.1
Mean	20.70	8.07	38.6	2.93	14.5	9.71	46.9

4. DISCUSSION

Ivlev (1945) and others have utilized the following equation to describe transfer paths of energy in an organism:

$$Q = Q' + Q_r + Q_t + Q_v + Q_w \quad (1)$$

where, Q — the gross energy of consumed food, Q' — the energy accu-

mulated as growth, Q_r — unassimilated energy of food, Q_t — the energy of primary heat, Q_v — the energy of external work, and Q_w — the energy of internal work. Ricker (1946) indicated that $Q_t + Q_v + Q_w$ could be combined and treated as a single factor, respiration, thereby simplifying computations:

$$Q = Q' + Q_r + Q_m \quad (2)$$

where, $Q_m = Q_t + Q_v + Q_w$ = total metabolic expenditure of energy estimated by respiration. Calories assimilated from the energy intake (Q) can be determined from the relationship:

$$\text{assimilation} = \text{growth} + \text{respiration} \quad (3)$$

used by Lindeman (1942) and Slobodkin (1962).

Using equation (3) the mean assimilation was 53.1% for the mayfly nymphs used in this study. This agreed with a mean of 50.35% for *Tubifex tubifex* (Ivlev 1939) but was more than twice the maximum assimilation percentage reported by Richman (1958) for pre-adult *Daphnia*. According to Richman, percentage of calorific intake assimilated by daphnia was inversely related to the concentration of food available per day. Herbivorous mammals assimilate in the order of 50% of their calorific intake (Kleiber 1961) which is low in comparison with carnivores.

The gross efficiency of growth may be defined as:

$$\frac{\text{calories accumulated}}{\text{calories consumed}} \quad (4)$$

where calories accumulated includes all products of storage — protoplasm, cellulose, keratin, reproductive bodies, etc. As Brody (1945) and Ivlev (1945) pointed out, in accordance with Rubner's law the gross efficiency in initial stages of biological growth is fairly constant and approximates 35%. With increasing age, however, this efficiency declines and regularly reaches zero in organisms with determinant growth patterns. Brody (1945) estimated an efficiency of 35% for early post-natal growth in cattle with a rapid decline to only 5% at the end of two years.

Nymphs from 4 to 7 mm in length exhibited a mean gross efficiency of 14.5% (Table V) which can be taken as representative for a major portion of their life span since nymphs normally attain a maximum length of 9 mm. It must be noted that stages younger than those studied may have average efficiencies between 14.5 and 35% while later stages (8–9 mm) could be less than 14.5%. Richman (1958) found that gross

efficiencies of growth in pre-adult *Daphnia* decreased from 13.22 to 3.87% as the food supply was increased. For adults he found that essentially all growth was transformed into production of young and gross efficiency for producing young was from 16.52 to 10.02%, depending upon food supply.

The energy expenditure required for normal animal activities (= respiration) is of considerable interest in analysing energy budgets for individuals, populations or trophic levels. Those individuals or species populations that have a rapid metabolism and turnover will utilize a greater share of the energy flow. Since a significant portion of the energy lost at each trophic transfer can be attributed to respiration, the relationship between calories stored as growth and calories lost via respiration will have a direct bearing on the rate at which food is being produced for the next trophic level. If assimilation is assumed to be fixed, it follows from equation (3) that any increase in respiration must be accompanied by a decrease in growth or, in other words, net productivity.

From this study it appears that *S. pulchellum* nymphs have a high metabolic demand. The mean metabolic loss amounted to 8.07 cal while only 2.93 cal were stored as growth (Table V). The mean ratio of respiration to growth (8.07/2.93) was 2.76. This same ratio computed for *Tubifex* (Ivlev 1939) was 0.62; for *Daphnia* 0.79 to 0.37, depending upon food supply (Richman 1958); and for *Microtus* 0.68 (Golley 1960), which could be typical for small, herbivorous mammals. Production of mayfly biomass, if one were to generalize from this study, is consequently an expensive process in terms of calories expended to calories stored.

The relationship between gross efficiency of growth and gross ecological efficiency (Slobodkin 1962, Phillipson 1966) though somewhat similar is far from analogous. Slobodkin (1962) has given an excellent summarization of the relevance of energy studies in ecology and the significance of ecosystem efficiencies. He concluded that ecological efficiencies are of the order 5 to 20% (10% most probable) and assimilation percentages for most organisms generally of the order of 20 to 40%. Consequently, percentage of consumed energy transmitted from prey to predator cannot exceed the maximum assimilated.

5. SUMMARY

Few detailed energy budgets for herbivorous freshwater invertebrates have been reported. More such data are needed in order to generalize and hypothesize further on energy flow in populations and communities under more or less natural conditions.

Nymphal forms of *S. pulchellum* ranging in size from 4 to 7 mm ingested the equivalent of 0.176 to 0.432 cal in a 12 hr period at 20°C. Oxygen consumption did not vary significantly over the entire range of sizes tested, and nymphs had a mean consumption of 1.74 μ l/mg per hour at 20°C. Growth measurements revealed

that each molt resulted in a body length increase of about 0.28 mm regardless of the size of the nymph. Growth rate was approximately constant during the eight week period of observation and amounted to 0.21 mm per week or 1.0 mm per 33 days.

A mean gross efficiency of growth of 14.5% can be accepted as representative for a major portion of the life cycle in this case. It was in good agreement with the findings of others working with *Tubifex* and *Daphnia*. However, *Stenonema* lost through respiration roughly three times as many calories relative to those stored as growth. The ratio of 2.76 implied high metabolic demand in these aquatic insects as opposed to a ratio of about 0.7 for *Tubifex* and *Daphnia*.

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