THE ECOLOGICAL ENERGETICS OF THE NET-SPINNING CADDISFLY, *Hydropsyche venularis* BANKS (TRICHOPTERA:HYDROPSYCHIDAE)

by

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INTRODUCTION

The functional feeding group classification proposed by Cummins (1973) defines collectors as organisms that derive their nutrition by ingesting fine and ultrafine particulate organic matter (FPOM, 50 um - 1000 um; UPOM, 0.5 um - 50 um) and the microbial biomass associated with these particles. Collector-filterers, or filter feeders, are animals adapted to collect the organic matter which is suspended in the water column (seston). Filter-feeder consumption, and subsequent assimilation, of seston may increase the retention time of energy and nutrients within a river system while feces produced may serve as food for other stream organisms (Wallace et al. 1977).

The Hydropsychoidea (Insecta:Trichoptera) are filter feeders which consume FPOM captured on silken nets produced by salivary secretions. Wallace et al. (1977) and Wallace and Merritt (1980) pointed out the importance of filter feeders in streams and the need for determining bioenergetic relationships in this group.

Energetic studies are important in understanding the function of ecosystems. Energetic studies of aquatic ecosystems are of two types: ecosystem and organism. Ecosystem energetics deal with energy processing by consumer populations usually on the basis of unit area per unit time (i.e. $cal/m^2/yr$). These studies are useful in assessing

impacts of perturbations on energy processing in a stream and are also necessary for modelling purposes. Studies of organism level energetics are far more common than ecosystem level studies (see literature review). In these studies, rates of energy processing are usually determined on an individual or weight specific basis (i.e. cal/ind/hr or cal/mg/hr). Organism energetics contribute significantly to aquatic ecology since in order to understand the productive processes within the river system, we must also understand the underlying physiological pattern of response of the animal components to varying conditions within that river system (Grodzinski et al. 1975). Organism level studies combined with ecosystem level studies are necessary to fully understand the structure and function of stream ecosystems (Cummins 1974). Although net-spinning Trichoptera are very important in the structure and function of streams and rivers, very few studies have dealt with quantifying their energetic relations.

The purpose of my research was to determine the energy relations of a filter-feeding caddisfly in a southern Appalachian stream. My specific objectives were: (1) to develop a set of bioenergetic equations for the net-spinning caddisfly, *Hydropsyche venularis* and (2) to develop new methods, or modify existing methods, for determining consumption and growth of filter-feeding caddisflies in the field.

LITERATURE REVIEW

There have only been a few studies dealing with filter-feeding Trichoptera biology and ecology which have energetic implications. Edington and Hildrew (1973) used assimilation, growth, and respiration as a means to explain longitudinal distribution of two hydropsychids, *Diplectrona felix* and *Hydropsyche fulvipes* (=*instabilis*). They found that when *D. felix*, a headwater species, was placed in a temperature regime similar to that experienced by *H. fulvipes*, a downstream species, respiration increased. When *H. fulvipes* was placed in a temperature regime similar to that normally experienced by *D. felix* the same result occurred. Because of this, Edington and Hildrew concluded that the efficiency of each species was impaired if kept at temperatures which they normally do not experience.

Hildrew and Edington (1979) extended their findings in a later study. Three species were examined which occurred progressively further downstream. These were: *D. felix*, *H. instabilis*, and *H. pellucidula*. The temperature at which respiration rate reached 1 mg O_2/g dry-wt/hr was determined for each species. For the three species these temperatures were: *D. felis*, 14.5^{o}C; *H. instabilis*, 16°C; and *H. pellucidula*, 21°C. This increase closely matched the thermal regime experienced by each species. They concluded that this pattern of metabolic response increases the

efficiency with which assimilated energy is incorporated into tissue and growth and secondly, this pattern of metabolic response allows the adoption of activity levels appropriate to resource availability rather than diel fluctuations in temperature.

Philipson and Moorhouse (1976) examined the effects of oxygen tension and temperature on the respiration and ventilation rates of four species of Polycentropodidae. They found that conditions which produce respiratory stress (low oxygen tension, high temperature, or both) increase the cost of ventilation to 60-70% of the active oxygen uptake. They concluded that activity, other than ventialtion, is probably minimal during times of respiratory stress.

Recently, Benke and Wallace (1980) calculated annual consumption from production estimates and food habits of six species of filter-feeding caddisflies. They estimated an annual consumption of 5331 mg ash-free dry weight/m^2 would account for 1000 mg ash-free dry wt/m^2 of caddisfly production in a southern Appalachian headwater stream.

Complete energy budgets are available for two members of the Hydropsychidae, Cheumatopsyche analis (McCullough 1975) and Hydropsyche occidentalis (McCullough et al. 1979). Both of these studies were conducted primarily in the laboratory using radiolabeled diatoms, algae, or watercress as food.

C.analis consumption rates varied from 4.24 to 35.15 ug dry-wt/mg/hr feeding on diatoms. Absorption of diatoms, determined by measuring residual radioactivity in larvae after 24 hrs, was 9.45% indicating the majority of food ingested was egested as feces. Assimilation efficiency was determined to be 47.2% using a dual label isotope technique (McCullough 1975).

H. occidentalis, feeding on diatoms, consumed 29.2 - 31.3 ug dry weight (DW)/mg/hr in laboratory experiments. Field consumption rates were approximatley twice laboratory values. The assimilation rate was 7.5 ug ash-free dry weight (AFDW)/mg DW/hr. Field growth rates ranged from 3.6 to 4.4 ug DW/mg/hr and metabolic rate was about 2.3 ul O_2/ mg/hr (McCullough et al. 1979).

Hydropsyche venularis is a common species in the southeastern U. S., found primarily in medium to large rivers (Flint et al. 1979). Gordon and Wallace (1975), Wallace (1975), and Schuster and Etnier (1978) have discussed the biology, habitat requirements, and distribution of H. venularis. H. venularis is generally found on top of rocks in fast-flowing waters. The largest populations are usually found associated with the macrophyte Podostemum ceratophyllum (Michaux)(Wallace 1975, Parker, 1980). Podostemum ceratophyllum (common name, river weed) occurs as a dense mat of tangled filaments that are firmly

attached to the larger rocks in riffles. When associated with this plant, larvae generally build a vertical tunnel-like retreat which extends from the base of the food capture net down into the sand and gravel that accumulates at the base of the *Podostemum*. Food capture nets generally project well into the current because they are supported by the outer stems of *Podostemum* (Wallace 1975). Parker (1980) compared the food habits, life history, and secondary production of *H. venularis* between an impounded and a free-flowing river in Virginia. *H. venularis* was omnivorous in both rivers feeding primarily on detritus and animal matter. Parker reported 3 generations per year for *H. venularis*. Food and habitat influenced secondary production of *H. venularis* with highest production levels occurring either where there were large quantities of zooplankton (lake outlet) or dense mats of *Podostemum* (free-flowing river).

MATERIALS AND METHODS

STUDY SITE

Field experiments were conducted at a riffle in Little River, a fifth order stream, in Montgomery County, Virginia. The site was located on County Route 787, approximately 1.0 miles south of the intersection of County Routes 693 and 787. The headwaters of Little River are in Floyd County, Virginia. The river flows north through wooded and agricultural land before joining the New River. At the study site the riparian vegetation is primarily hardwood, but there is very little shading of the riverbed. The bottom of the river was covered with thick mats of *Podostemum*. This provided an excellent habitat for *H. venularis* and a number of other aquatic insects. Some physical parameters at this site were reported by Kondratieff et al. (1981). Water temperatures ranged from $-0.5^{\circ}C$ in winter to greater than $25^{\circ}C$ in summer. Larvae used in laboratory experiments were also collected at this site.

GENERAL METHODS

Fifth instar *H. venularis* larvae were used in all experiments since Parker (1980) showed that *H. venularis* gained 83% of its final weight during the 5th instar.

Weights

Dry weights were determined by placing samples (whole larvae, gut contents, feces, seston, etc.) into tared aluminum pans and drying at 60°C for 36 hrs. After drying, pans and samples were placed in a desiccator for 12 hrs and then rapidly weighed to the nearest 0.01 mg on a Mettler B9 balance. Ash-free dry weights (AFDW) were then determined by heating the material to 500°C in a muffle furnace for 1 jr. After ashing, the sample was wetted with distilled water to replace water of hydration in the inorganic clays and dried at 105°C for 24 hrs (Weber 1973). At the end of the final drying the sample was cooled in a desiccator and reweighed.

Length-Dry Weight Regression Line

Fifth instar *H. venularis* larvae were collected monthly from March to October 1980 in order to determine an equation to predict dry weight from length. Larvae were picked from rocks and killed in CO_2 saturated water (club soda) to prevent regurgitation of gut contents and extraction of lipids from body tissues which can occur if preservatives such as formalin or alcohol are used. The distance between the anterior edge of the fronto-clypeus and the point of attachment of the anal prolegs was measured with a microscope equipped with an optical micrometer. Measured larvae were then dried as described above. Since it was essential

to have a body length-dry weight regression line that gave a high degree of predictability (r^2), several linear and non-linear models were tested on the data. The equation which best predicted dry weight from length was:

$$Y = 2.619 - 6.859 (X) + 4.736 (X^2) \quad (1)$$

where Y = $\log_{10}$ dry weight (mg), X = $\log_{10}$ length (mm), r^2= 0.88, and N = 177.

Temperature

Water temperature was measured with a hand-held thermometer in all field experiments. In order to determine the effects of temperature on the various processing rates, Q_{10} values were calculated using the equation:

$$Q_{10} = (V_2/V_1)^{(10/(t_2-t_1))} \quad (2)$$

where Q_{10} = increase in rate with a 10°C change in temperature, V_1=rate at temperature t_1, and V_2=rate at temperature t_2 (Grodzinski et al. 1975).

Statistical Analysis

All statistics, with the exception of t-tests, were determined on the VPI & SU IBM SYSTEM/370 computer using the Statistical Analysis System (SAS) (Helwig and Council 1979). All regression lines, analysis of covariance (ANCOVA) tests, and Duncans Multiple Range tests were calculated using the GLM procedure. T-tests were calculated from the procedure outline in Sokal and Rolhf (1969). A $\log_{10}$ transformation was used when it was necessary to transform data for

regression analysis.

ENERGY BUDGET PARAMETERS

Energy Budget

The energy budget equation used in this study was:

$$C = G + R + E \quad (3)$$

where C = amount of energy consumed as food (consumption rate), G = amount of energy converted to body tissue (growth rate), R = amount of energy lost as a result of metabolic processes (metabolic rate), and E = amount of energy passed from the body as feces (egestion rate). I attempted to calculate each component of equation 3 independently of the others in order to determine residual energy, i.e., the percent of consumed energy not accounted for by G, R, and E.

Consumption Rate

In order to determine consumption rate it was necessary to develop a method using a material which would serve as a gut marker and a device for entraining the gut marker when it was released in the field. A gut marker was prepared by mixing Wayne[R] dog food and Day-Glo[R] fluorescent pigment in a ratio of 12.5:1 (w:w). The dog food was soaked in tap water for 0.5 hr, placed in a blender, saturated with water, and homogenized until thoroughly mixed. Day-Glo was added to the homogenate, thoroughly mixed, poured into

an enamel pan lined with aluminum foil, and dried at 105°C. After drying, the hardened mixture was ground in an Intermediate Wiley Mill (#20 mesh). This produced a mean particle size of 170.9 um X 106.6 um.

The filter-feeding entrainment device (FFED) (Fig. 1) was constructed from acrylic tubing that measured 30.48 cm (12 in) outside diameter and 29.85 cm (11.75 in) inside diameter. The tubing was cut into 45.72 cm long sections, which were then cut longitudinally into two equal halves. Strips of 6.35 mm (0.25 in) thick acrylic sheets that were 2.54 cm wide were attached at each longitudinal edge with acrylic cement. Foam rubber that was 5.08 cm (2 in) thick was attached to each acrylic strip with waterproof contact cement so that the FFED would seal tightly against an irregular bottom.

In the field, the FFED was placed over an area of rock on which large numbers of food capture nets were visible One 1 of stream water was collected in a Nalgene® jar. Approximately 30 g of gut marker was added to the water. This mixture was shaken vigorously for 1-2 min and then immediately dumped into the upstream end of the FFED. Timing was started at the moment of release. At the end of the experimental time, which varied from 2-10 min, larvae in the area covered by the FFED were collected with a dip net and killed in club soda. The larvae were returned

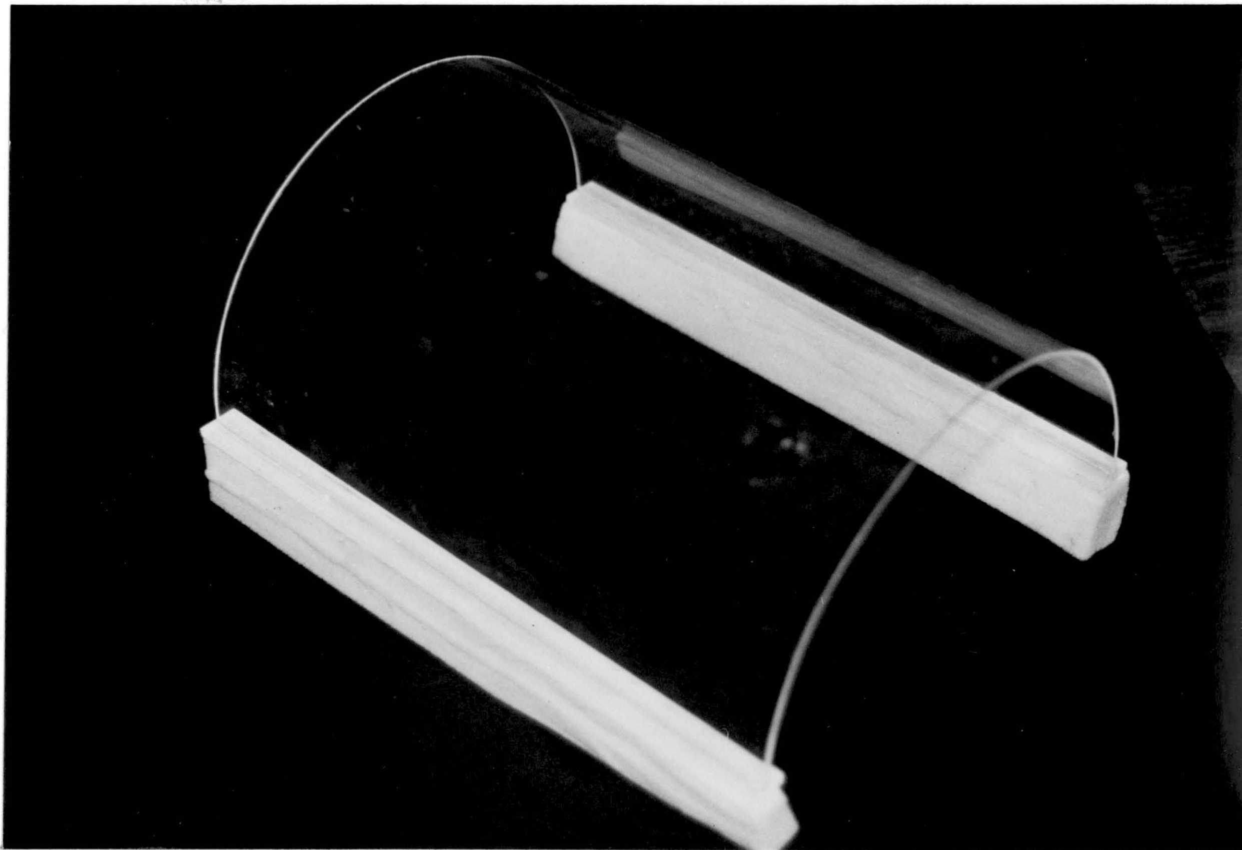

Figure 1. The filter-feeding entrainment device (FFED).

to the laboratory and the entire foregut removed intact. This was done by gently pulling the head capsule away from the thorax. The foregut usually remained attached to the head.

The distance between the anterior ventral apotome and posterior end of the proventriculus and the distance between the anterior ventral apotome and the gut marker were measured using a microscope equipped with an optical micrometer. Division of the latter by the former distance gave the ratio (percent) of the foregut the marker had traversed. Foregut passage time (FGPT) was calculated by dividing the experimental time (hrs) by the percent of the foregut the marker had travelled during a particular time interval.

Additional 5th instar _H_. _venularis_ larvae were collected, killed, and returned to the lab to analyze the weight of foregut contents. The length of each larva was measured with an optical micrometer and then the foregut contents dissected from the body. The foregut contents of individual larvae were filtered onto preweighed 13 mm Gelman^{R} glass fiber filters and dried. The sample filters were then weighed on a Cahn^{R} electrobalance to the nearest 0.01 mg. A regression of body weight (determined from the length-dry weight regression line) and foregut content weight showed no significant relationship. Therefore, a mean value was determined by summing the total weight of

foregut contents and dividing by the total number of larvae (N=18). The mean weight of the foregut contents of 5th instar H. venularis was 223.57 ug/individual. Weight specific consumption rate was calculated using the equation:

Consumption rate (ug/mg/hr) = 223.57/dry wt/FGPT

where 223.57 is the mean dry weight (ug) of the foregut contents of 5th instar H. venularis, dry weight = dry weight (mg) of each larva determined from the length-dry weight regression line, and FGPT is as described above.

Growth Rate

Growth rates were also determined in the field. Fifth instar larvae were removed from rocks by hand and anesthetized with CO_2 saturated water for approximately 30 sec. Initial weights of larvae were determined by measuring the length of each larva and converting this to dry weight with the length-dry weight regression line. Measured larvae were marked by placing a small drop of enamel paint on a single thoracic segment. Four colors of enamel paint (red,orange, white and chartreuse) were used. Twelve individual larvae could be recognized by the combination of color and particular thoracic segment. Experimental larvae were placed securely on rocks covered with Podostemum from which all other hydropsychids had been removed. These rocks were placed in 35.5 cm diameter plastic pans and covered with a fiberglass windowscreen

bag to prevent larvae from being immediately washed from the rocks. The covered pans were placed in the stream and left overnight to allow larvae to settle and build retreats. The following morning the bag was removed and the rock-filled pans were left in the stream for 4-10 days. Larvae were able to feed under natural temperature and flow conditions. Experimental temperature was determined by averaging the water temperature the morning the experiment began and the morning the experiment ended. At the end of the experimental time, all of the pans were removed and the rocks examined carefully for marked larvae. Marked larvae were removed from the rocks and killed in CO_2 saturated water.

Final weights were determined by drying larvae to a constant weight. Growth rate was determined by the equation:

$$\text{Growth rate (ug/mg/hr)} = (WF - WU)/WM/\text{time}$$

where WF = final weight (ug), WU = initial weight (ug), WM = initial weight (mg), and time = experimental time interval (hrs).

<u>Metabolic Rate</u>

Oxygen consumption was determined using a Gilson differential respirometer at 5, 10, 15, 20, and 25°C. Reaction flasks contained 5 ml of tap water which had been dechlorinated by allowing it to stand overnight. A small circle of nylon windowscreen served as substrate, and 5 N KOH-saturated filter paper was used to absorb CO_2. Individual

larvae were placed in flasks and allowed to acclimate for 6-12 hrs. Flasks were slowly shaken to prevent oxygen stratification. All experiments were conducted with the laboratory fluorescent lights operating. Experimental times were 12 hrs at 5^oC, 4 hrs at 10^oC, and 2 hrs at 15, 20, and 25^oC. Two readings were taken for each experimental and control flask (water, screen, and KOH) and averaged. Average control readings were subtracted from experimental readings. After completion of an experiment, larvae were killed and dried to a constant weight. Metabolic rate was determined by the equations:

$$\text{Metabolic rate (ul } O_2\text{/mg/hr)} = \text{(ul } O_2\text{/DW)/time}$$

where time = experimental time (hrs), and DW = dry weight (mg), and ul O_2 = average (N=2) amount of O_2 consumed during the experimental time.

Egestion Rate

Ideally it would be best to collect feces as it is produced from undisturbed caddisflies. However, at the present this is not possible in flowing water, so a system was developed to collect the feces in the field but not *in situ*. An aluminum pan (42 X 32 X 8 cm) served as a water bath and ice cube trays (26.5 X 10.5 X 4 cm) served as holding cells for the insects and the feces they produced. The aluminum pan was filled with stream water and placed in a shallow area. Ice cube trays were filled

with filtered water and floated on the water in the aluminum pans. The temperature in the ice cube trays remained at ambient stream temperature for at least 2 hrs, provided the aluminum pan was out of direct sunlight.

Larvae were collected with a dip net and placed singly in compartments of the ice cube trays. At the end of the experimental period (1 hr for all experiments), all larvae were removed from the ice cube trays and killed in CO_2 saturate water. Feces was collected from the compartments with a micropipette, placed in a clean vial, and frozen.

In the laboratory, larvae from a single ice cube tray were dried and an average weight determined. Feces from a single tray was filtered onto a tared 13 mm Gelman^R glass fiber filter, dried at 60°C, and weighed. Egestion rate was determined by the equation:

$$\text{Egestion rate (ug/mg/hr)} = (WF - WT)/DW/\text{time}$$

where WF = weight of the glass fiber filter plus feces (ug), WT = tare weight of filter (ug), DW = mean dry weight of larvae from a single ice cube tray, and time = experimental time (1 hr).

CALCULATION OF CALORIC CONTENTS

Food and Feces

To determine the caloric content of food it was

necessary to evaluate the food habits of H. venularis and the organic content of the gut material. On 9 July 1980, H. venularis larvae were collected from Little River and the foregut contents dissected out and mounted in sucrose on a microscope slide (Parker 1980). The contents of 2 to 4 guts were placed on each slide to assure sufficient density of items to count. The percent of the field occupied by animal, diatoms, other algae, vascular plant detritus, and unidentified detritus was determined for 5 randomly selected fields per slide with a compound microscope (40X). There were 2 replicate slides. Results are presented in Table 1.

The organic content of food and feces was determined by separately dissecting the foregut and hindgut contents from 10 individual larvae and filtering each onto preweighed glass fiber filters. Dry weights and ash-free dry weights (AFDW) were determined as described above.

Caloric content was determined by the method in Table 1. I assumed the specific gravity (g/ml) of all food categories was the same, and therefore, the percent volume of a food category in the diet was equivalent to the percent weight of that food category in the diet. The percent volume of each food category was multipled by the appropriate caloric value reported in Cummins and Klug (1979), and resulting caloric values were summed to give an estimate

Table 1. Food habits of 5th instar *H. venularis* and method for approximation of caloric content of food.

SLIDE	FOOD CATEGORY[1]	PERCENT VOLUME		CALORIC VALUE[2]		CALORIES	$\bar{X}$ cal/mg AFDW
	AN	0.46	X	5.8	=	2.7	
	DI	0.00	X	5.6	=	0.0	
1	OA	0.36	X	4.6	=	1.7	
	VPD	0.18	X	4.5	=	0.8	
	DET	0.00	X	4.5	=	0.0	
	TOTAL					5.2	
							5.0
	AN	0.12	X	5.8	=	0.7	
	DI	0.00	X	5.6	=	0.0	
2	OA	0.67	X	4.6	=	3.1	
	VPD	0.21	X	4.5	=	0.9	
	DET	0.00	X	4.5	=	0.0	
	TOTAL					4.7	

[1]AN = animal, DI = diatoms, OA = other algae, VPD = vascular plant detritus, DET = unidentifiable detritus.

[2]From Cummins and Klug (1979).

of the calories per mg AFDW of food. The values for each slide were then averaged to give a mean caloric content of 5.0 cal/mg AFDW of food.

Because my food habit data were limited, I attempted to verify my caloric values by calculating caloric values with the same methods from the data of Parker (1980). Parker's food habit data for _H_. _venularis_ was for 3rd and 4th instar larvae and was determined monthly for 1 year. The caloric values of food calculated from Parker's data using my method was 4.5 cal/mg AFDW, or only 10% less than my value of 5.0 cal/mg AFDW.

Analysis of the organic content (mg AFDW/mg dry weight) of the food and feces revealed that the food was 38% organic while the feces was 25% organic. I assumed the caloric content per mg AFDW is the same in food and feces. The caloric content per mg dry weight may be determined by multiplying the caloric content of food and feces (4.9 cal/mg AFDW) by the organic content of the food (0.38) and feces (0.25). This yielded values of 1.8 cal/mg dry weight of food and 1.2 cal/mg dry weight of feces.

Body Tissue

Literature values of caloric contents for species of _Hydropsyche_ range from 5.6 - 5.9 cal/mg dry weight (Cummins and Wuycheck 1971; Brass 1971, as cited by McCullough et al. 1979). I assumed a value of 5.6 cal/mg dry weight for

H. venularis.

Metabolic Energy

The respiratory quotient (R.Q.) was not measured for *H. venularis* in this study. I assumed *H. venularis* was feeding on a diet of protein and carbohydrate and thus an R. Q. of 0.88 was used (McDiffett 1970). This results in an estimated caloric value of 4.9 cal/ml O_2 consumed.

RESULTS

CONSUMPTION RATE

Effect of Temperature

The relationship between consumption rate and temperature is shown for all larvae combined in Table 2. These results show *H. venularis* consumed from 20 to greater than 100% of its own body weight per hour with a mean rate of 764.5 ug/mg/hr. This value is extremely high when compared to other reported values (Table 3).

These high consumption rates may be due to differential rates of food passage in the foregut. McCullough (1975) showed that food moved progressively slower through the gut of *Simulium* as feeding time increased. Because I used only the foregut for determining gut passage time, a rapid, initial movement of gut marker through the foregut probably occurred in association with swallowing the food. If this occurred, then a large percentage of the foregut would be rapidly filled with marker leading to an underestimate of gut passage time and, therefore, an overestimate of consumption rate.

To determine if differential gut passage rates occurred, I did a regression of percent of gut travelled vs. feeding time. If gut passage was constant, then the intercept of the regression line should be approximately zero (zero percent of gut travelled at zero time). The resulting

Table 2. Means and standard errors for consumption rates of *H. venularis* at 3 experimental temperatures.

TEMPERATURE (°C)	N	CONSUMPTION RATE (ug/mg/hr)
15.5	18	289.26 (32.75)
23.5	50	1082.74 (79.77)
28.0	25	468.10 (44.12)

Table 3. Direct and indirect measurements of consumption rate of several species of Hydropsychidae.

SPECIES	CONSUMPTION RATE ug/mg/hr	METHOD[1]	SOURCE
Arctopsyche irrorata	6.4	TBP	Benke and Wallace (1980)
Parapsyche cardis	7.6	TBP	Haefner and Wallace (1981)
Cheumatopsyche parentum	15.5	TBP	Parker (1980)
Hydropsyche occidentalis	30.5	ISO	McCullough et al. (1979)
H. occidentalis	59.3	LAD	McCullough et al. (1979)
H. venularis	764.5	MLAD	This study

[1] TBP = trophic basis of production; ISO = determined with radioisotopes; LAD = method of Ladle et al. (1972); MLAD = modified method of Ladle et al. (1972) used in this study.

equation was:

$$Y = 0.01 (X) + 0.67 \qquad (N=5, r^2=0.66)$$

where Y = percent of gut travelled and X = the feeding time in hrs. The intercept was significantly different from zero (t-test, P 0.05) and indicated that 67% of the foregut was passed at feeding time equal to zero. Therefore, the food passed through approximately 2/3 of the foregut initially, probably due to swallowing. Since 67% of the foregut filled immediately, the measured percent of the gut containing marker was corrected by subtracting 0.67. This correction was applied to all data. If the measured percent was less than 0.67 it was discarded. Table 4 shows the corrected results. The corrected values, although still high, are much more comparable to previously reported values. The overall mean was 161.85 ug/mg/hr.

Fig. 2 shows the relationship between consumption rate and temperature. Consumption increased between 15.5° and 23.5°C, then decreased. Significant differences (P 0.05) in consumption existed between 15.5° and 23.5° and 23.5° and 28.0° with Q_{10} values of 7.10 and 0.04, respectively. Consumption rates at 15.5° and 28.0°C were not significantly different (P 0.05).

Regression of consumption rate on temperature gave:

$$Y = -6.752 + 0.848 (X) - 0.020 (X^2)$$
$$(N=55, r^2=0.46)$$

Table 4. Means and standard errors for consumption rate of *H. venularis* at 3 experimental temperatures, corrected for swallowing of food.

TEMPERATURE (°C)	N	CONSUMPTION RATE* (ug/mg/hr)
15.5	18	58.49 (9.08) a
23.5	25	280.71 (20.66) b
28.0	12	69.27 (19.06) a

*Means not followed by the same letter are significantly different at the 0.05 level (Least Significant Range (LSR) Test).

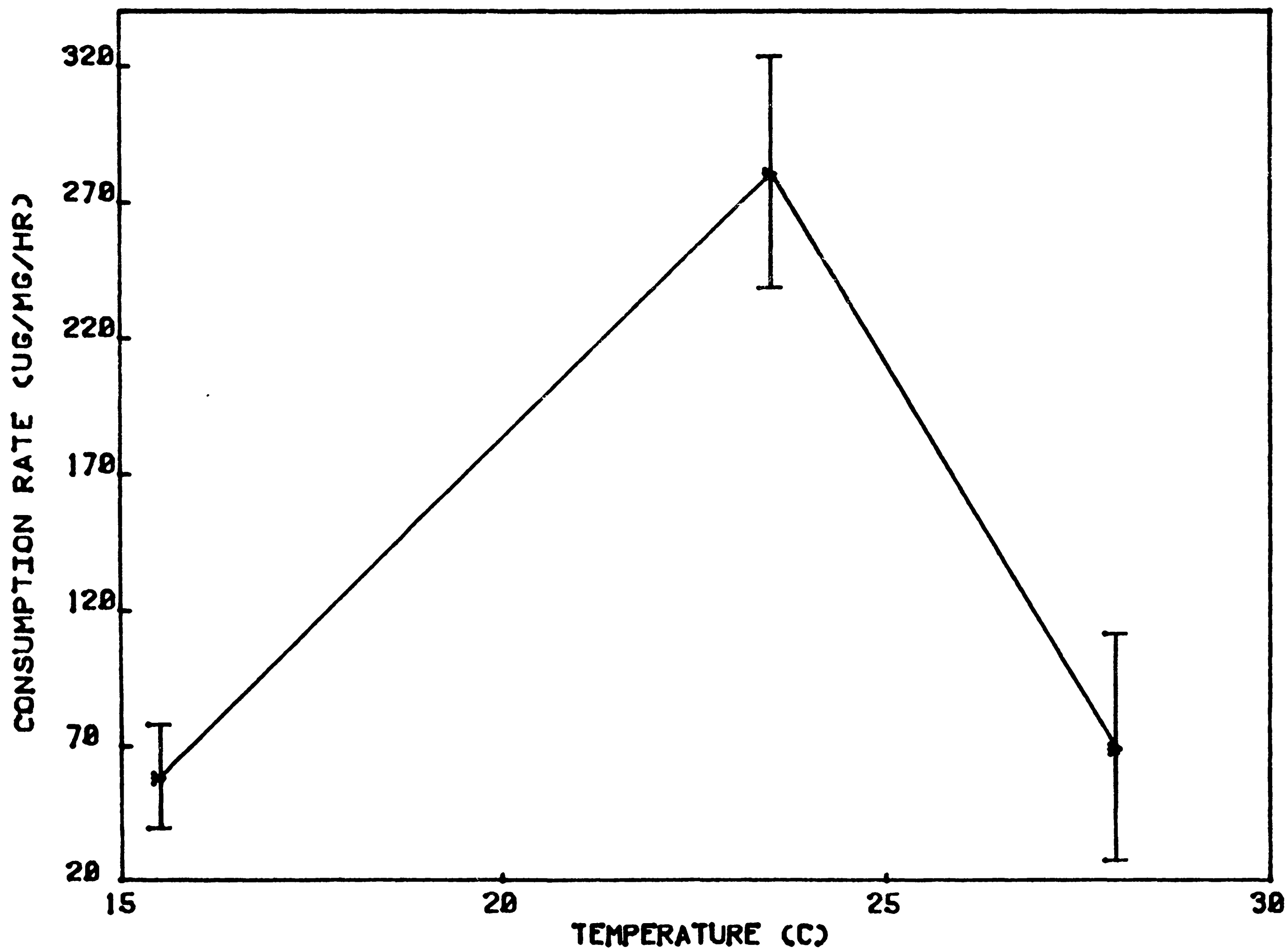

Figure 2. Means and 95% confidence intervals for consumption rate of *H. venularis* at 3 experimental temperatures.

where Y = log consumption rate (ug/mg/hr) and X = temperature (^{o}C).

Effect of Body Weight

All larvae used in consumption experiments were placed in arbitrary weight classes. The weight classes (WC) were: 1.00 - 3.99 mg (WC 1), 4.00 - 4.99 mg (WC 2), 5.00 - 5.99 mg (WC 3), 6.00 - 6.99 mg (WC 4), 7.00 - 7.99 mg (WC 5), 8.00 - 8.99 mg (WC 6), 9.00 - 9.99 mg (WC 7), 10.00 - 15.00 mg (WC 8). A least significant range test (LSR) indicated that consumption rate did not differ significantly (P 0.05) among the weight classes (Table 5) and, therefore, a regression of consumption on body weight was not significant.

Interaction of Body Weight and Temperature

Table 6 presents regressions relating consumption rate to body weight at each experimental temperature. Significant regressions (P 0.05) were found at 15.5 and 23.5^{o}C. A series of regressions relating consumption rate to temperature for each weight class revealed a significant regression (P 0.05) only for WC 1.

A multiple regression to predict consumption rate from temperature and body weight gave:

$$Y = -6.972 - 0.682\,(X_w) + 0.914\,(X_t) - 0.021(X_t^2)$$
$$(N=55,\ r^2=0.54)$$

where Y = log consumption rate (ug/mg/hr), X_w = log dry weight (mg), and X_t = temperature (^{o}C).

Table 5. Means and standard errors of consumption rate for different weight classes of *H. venularis*

WEIGHT CLASS	WEIGHT RANGE	$\bar{X}$ WEIGHT (mg)	N	CONSUMPTION RATE* (ug/mg/hr)
1	1.00-3.99	3.05	23	210.09 (50.70) a
2	4.00-4.99	4.40	6	200.68 (76.39) a
3	5.00-5.99	5.39	6	81.64 (40.86) a
4	6.00-6.99	6.22	5	171.50 (49.84) a
5	7.00-7.99	7.53	4	66.39 (20.39) a
6	8.00-8.99	8.42	5	96.96 (32.04) a
7	9.00-9.99	9.56	2	220.60 (1.15) a
8	10.00-15.00	12.06	4	81,70 (27.54) a

*Means not followed by the same letter are singificantly different at the 0.05 level (LSR).

Table 6. Regression equations relating the effect of body weight to consumption rate for *H. venularis* at 3 experimental temperatures.

TEMPERATURE (°C)	N	REGRESSION[1]		
		a	b	r^2
15.5	18	2.183	-0.792	0.34*
23.5	25	2.892	-0.773	0.24*
28.0	12	1.800	-0.315	0.01^{ns}

[1] log consumption rate = log a + b (log dry weight)

*Regression is significant at the 0.05 level.

^{ns}Regression is not significant.

GROWTH RATE

Effect of Temperature

Fig. 3 shows the means and 95% confidence intervals for growth rate at each experimental temperature. There was an apparent increase in growth rate between 3.0 and 3.5°C although the mean growth rates at these temperatures were not significantly different (P 0.05) (Duncans New Multiple Range test)(Table 7). Between 3.5 and 19.5°C there was a plateau. Above 19.5°C growth rate increased rapidly. Significant differences (P 0.05) in growth were found between 3.0 - 21.0°, 3.0 - 23.8°, and 21.0 - 23.8°C (Table 7). Q_{10} values calculated for each pair of means were: 4.42 (3.0 - 21.0°C), 4.35 (3.0 - 23.8°C), and 4.40 (21.0 - 23.8°C).

Regression of growth rate on temperature gave:

$$Y = 0.192 + 0.106\ (X)$$
$$(N=47,\ r^2=0.25)$$

where Y = growth rate (ug/mg/hr) and X = temperature (°C).

Effect of Body Weight

Fig. 4 shows the mean growth rate and 95% confidence intervals for each weight class. Growth rate varied widely within each weight class with negative values (weight loss) being common. Despite the wide variation in rates, means for each weight class were generally close (Table 8). A DNMRT indicated that WC 1 and WC 8 had significantly

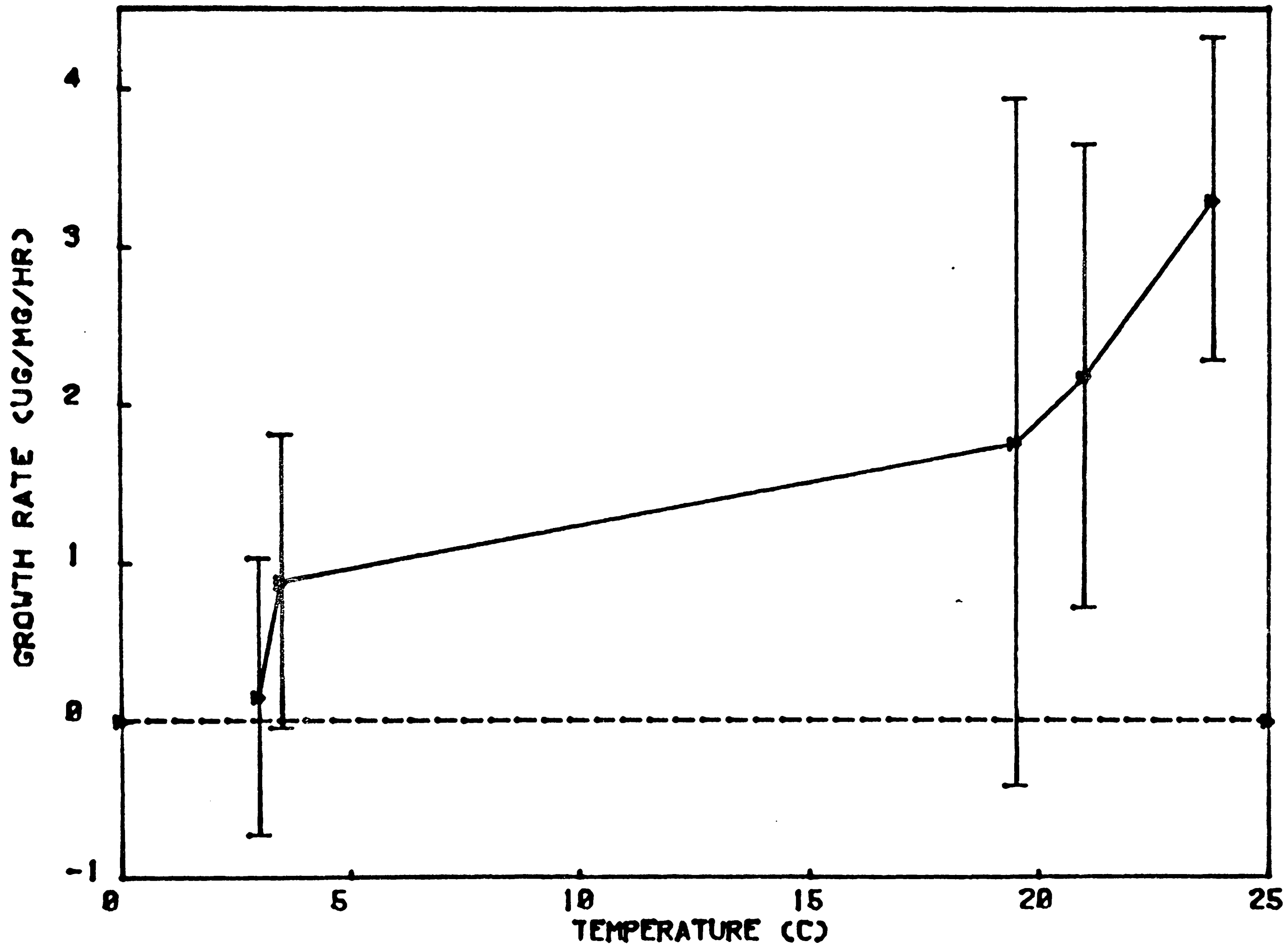

Figure 3. Means and 95% confidence intervals for growth rate of *H. venularis* at 5 experimental temperatures. Dashed line indicates zero growth.

Table 7. Means and standard errors for growth rate of *H. venularis* at 5 experimental temperatures.

TEMPERATURE (°C)	N	GROWTH RATE* (ug/mg/hr)
3.0	9	0.15 (0.38) a
3.5	14	0.88 (0.43) ab
19.5	8	1.76 (0.92) ab
21.0	8	2.18 (0.62) b
23.8	8	3.30 (0.43) c

*Means not followed by the same letter are significantly different at the 0.05 level (DNMRT).

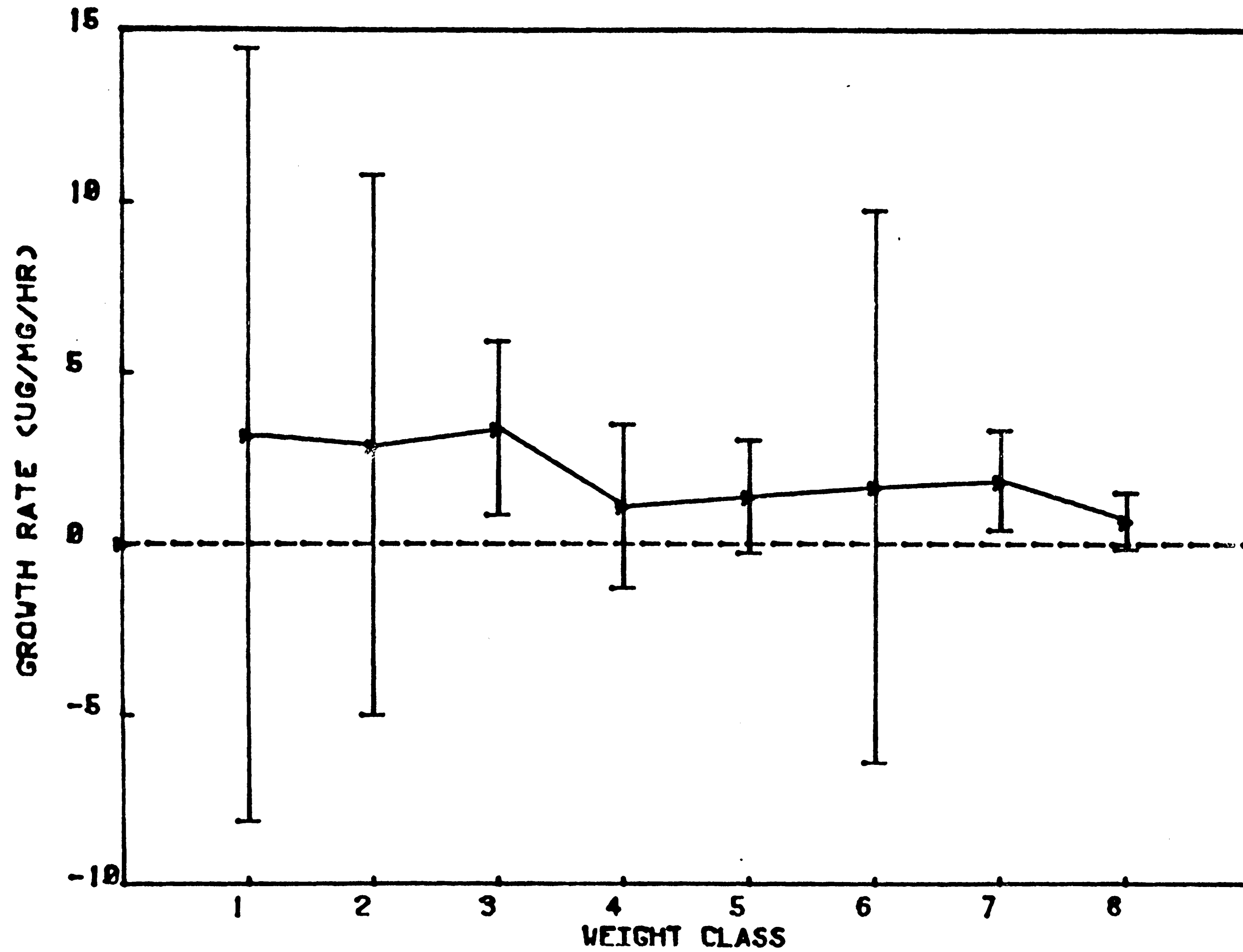

Figure 4. Means and 95% confidence intervals for growth rate of each weight class of *H. venularis*. Dashed line indicates zero growth.

Table 8. Means and standard errors of growth rate for different weight classes of *H. venularis*.

WEIGHT CLASS	$\bar{X}$ WEIGHT (mg)	N	GROWTH RATE* (ug/mg/hr)
1	3.21	2	3.15 (0.89) a
2	4.53	3	2.86 (1.84) ab
3	5.25	4	3.36 (0.80) ab
4	6.80	3	1.09 (0.56) ab
5	7.45	8	1.38 (0.70) ab
6	8.44	3	1.66 (1.88) ab
7	9.75	5	1.85 (0.53) ab
8	13.35	19	0.68 (0.40) b

*Means not followed by the same letter are significantly different at the 0.05 level (DNMRT).

different growth rates (P 0.05).

Regression of growth rate on body weight gave:

$$Y = 4.050 - 0.265\ (X)$$
$$(N=47,\ r^2=0.27)$$

where Y = growth rate (ug/mg/hr) and X = larval dry weight mg).

Interaction of Body Weight and Temperature

Regression equations relating growth rate to body weight at each temperature showed a significant relationship only at 19.5°C. Regressions relating growth rate to temperature for each weight class showed no significant relationships.

A multiple regression relating growth rate to temperature and body weight gave:

$$Y = 2.546 - 0.219\ (X_w) + 0.085\ (X_t)$$
$$(N=47,\ r^2=0.43)$$

where Y = growth rate (ug/mg/hr), X_w = larval dry weight (mg), and X_t = temperature (°C).

METABOLIC RATE

The results of the metabolic rate experiments have recently been reported elsewhere (Howell and Voshell 1982). However, for the sake of completeness these results are also reported here.

Effect of Temperature

The relationship between metabolic rate and temperature is shown in Fig. 5. From 5 to 15°C metabolic rates were low. A plateau exists between 10 and 15°C. Between 15 and 20°C there was a sharp increase in metabolic rate which continued up to 25°C. There were no significant differences (P 0.05) in metabolic rates between 5 and 15°C (Table 9). Significant differences were found between metabolic rates (P 0.05) at 5 - 20°C, 5 - 25°C, 10 - 20°C, 10 - 25°C, 15 - 20°C, 15 - 25°C, and 20 - 25°C with corresponding Q_{10} values of 3.99, 3.20, 3.98, 2.97, 12.90, 4.62, and 1.65, respectively. The low Q_{10} values between 20 - 25°C may indicate an area of metabolic compensation for temperature (Q_{10} 2.00).

Regression of metabolic rate on temperature gave:

$$Y = -0.847 + 0.54\ (X)$$
$$(N=219,\ r^2=0.66)$$

where Y = log metabolic rate (ul O_2/mg/hr) and X = temperature (°C).

Effect of Body Weight

The mean metabolic rate and 95% confidence intervals for each weight class are shown in Fig. 6. Metabolic rate decreased with increasing body weight. A DNMRT indicated that the metabolic rate of WC 1 was significantly higher (P 0.05) than any other weight class (Table 10).

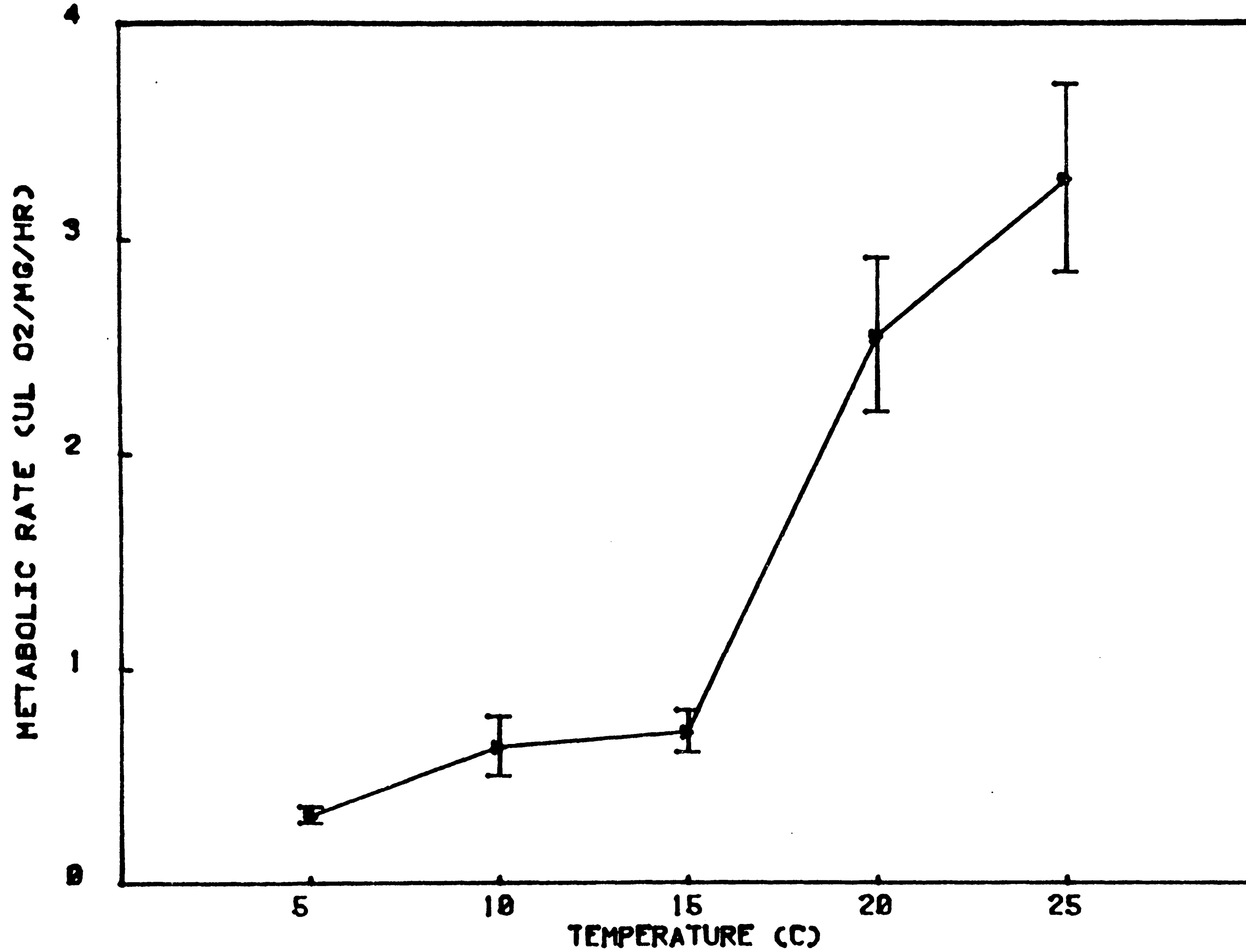

Figure 5. Means and 95% confidence intervals for metabolic rate of *H. venularis* at 5 experimental temperatures.

Table 9. Means and standard errors of metabolic rate of *H. venularis* at 5 experimental temperatures.

TEMPERATURE (°C)	N	METABOLIC RATE* (ul O_2/mg/hr)
5	49	0.32 (0.02) a
10	48	0.64 (0.07) a
15	43	0.71 (0.05) a
20	37	2.55 (0.18) b
25	42	3.28 (0.22) c

*Means not followed by the same letter are significantly different at the 0.05 level (DNMRT)-

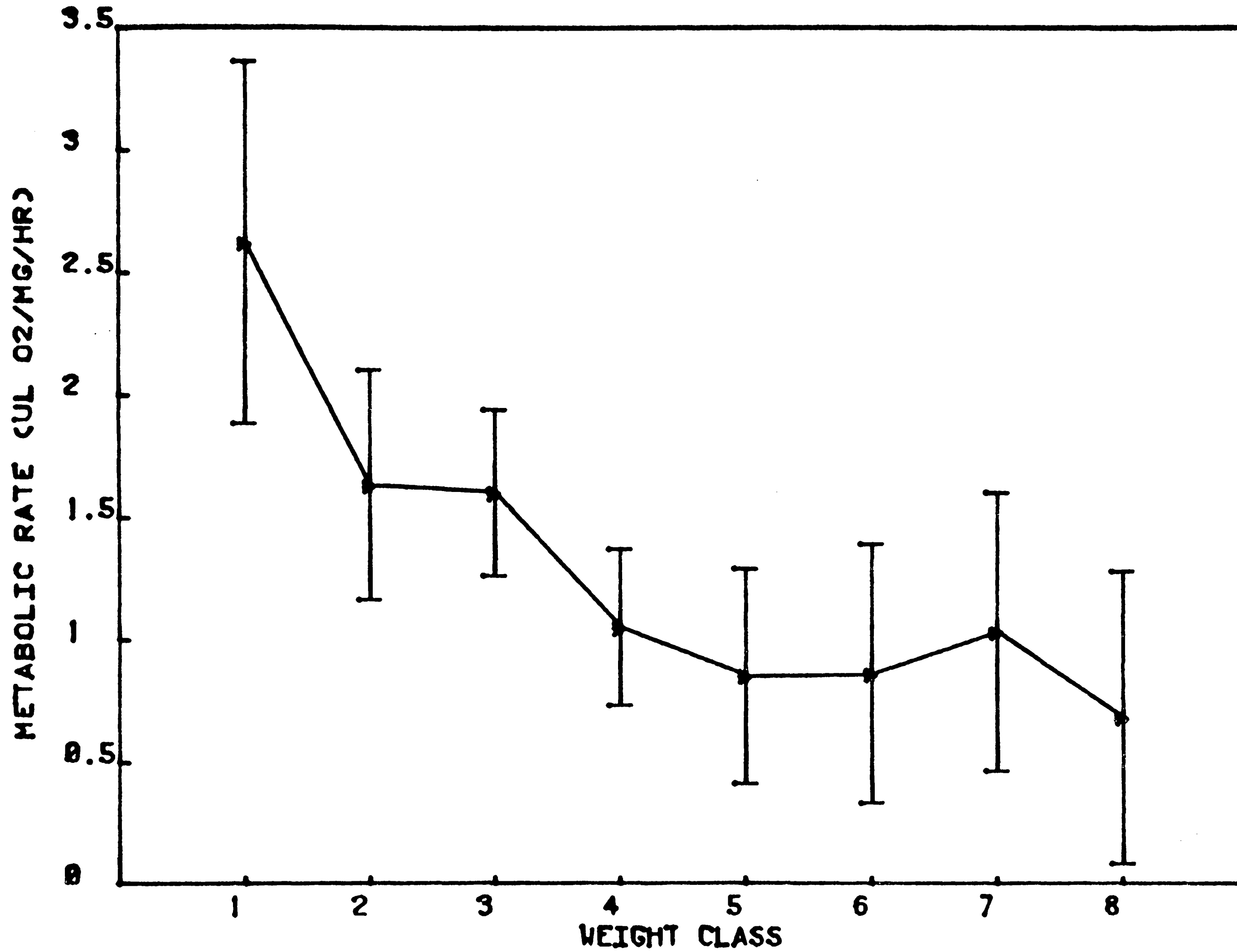

Figure 6. Means and 95% confidence intervals for metabolic rate of each weight class of *H. venularis.*

Table 10. Means and standard errors of metabolic rate for different weight classes of *H. venularis*.

WEIGHT CLASS	$\bar{X}$ WEIGHT (mg)	N	METABOLIC RATE* (ul O_2/mg/hr)
1	3.01	34	2.62 (0.36) a
2	4.61	28	1.63 (0.23) b
3	5.53	43	1.60 (0.17) b
4	6.42	38	1.05 (0.16) bc
5	7.50	23	0.85 (0.21) bc
6	8.46	17	0.86 (0.25) bc
7	9.40	20	1.03 (0.27) bc
8	11.42	16	0.68 (0.28) c

*Means not followed by the same letter are significantly different at the 0.05 level (DNMRT).

Regression of metabolic rate on dry weight gave:

$$Y = 0.543 - 0.800 (X)$$
$$(N=219, r^2=0.09)$$

where Y = log metabolic rate (ul O_2/mg/hr) and X = log larval dry weight (mg).

Interaction of Body Weight and Temperature

Table 11 presents regressions relating metabolic rate to body weight at each experimental temperature. Regressions were significant (P 0.05) at 5, 15, 20, and 25°C, with the greatest effect of body weight occurring at 15°C.

The effects of temperature on metabolic rate for each weight class are shown in Table 12. Metabolic rate was positively correlated with temperature for all weight classes. Analysis of covariance indicated that slopes of regressions for all weight classes were not significantly different (P 0.05).

Regression of metabolic rate on body weight and temperature gave:

$$Y = -0.611 - 0.273 (X_w) + 0.052 (X_t)$$
$$(N=219, r^2=0.67)$$

where Y = log metabolic rate (ul O_2/mg/hr), X_w = log larval dry weight (mg), and X_t = temperature (°C).

EGESTION RATE

Effect of Temperature

Table 13 presents the means and standard errors for

Table 11. Regression equations relating the effect of body weight to metabolic rate for H. venularis at 5 experimental temperatures.

TEMPERATURE (^{o}C)	N	REGRESSION[1]		
		a	b	r^2
5	49	-0.181	-0.387	0.14*
10	48	-0.450	0.159	0.01^{ns}
15	43	0.723	-1.149	0.41*
20	37	0.923	-0.743	0.46*
25	42	0.775	-0.416	0.16*

[1] log metabolic rate = log a + b (log body weight)

*Regression is significant at the 0.05 level.

^{ns}Regression is not significant.

Table 12. Regression equations relating the effect of temperature to metabolic rate for different weight classes of *H. venularis*.

WEIGHT CLASS	N	REGRESSION[1]		
		a	b	r^2
1	34	-1.079	0.072	0.53*
2	28	-0.720	0.050	0.55*
3	43	-0.827	0.050	0.72*
4	38	-0.785	0.050	0.85*
5	23	-0.796	0.047	0.67*
6	17	-0.831	0.047	0.62*
7	20	-0.837	0.050	0.81*
8	16	-0.803	0.043	0.69*

[1]log metabolic rate = log a + b log(temperature)

*Regression is significant at the 0.05 level.

Table 13. Means and standard errors of egestion rate for *H. venularis* at 3 experimental temperatures. Each observation (N) was a mean of 12 individual larvae.

TEMPERATURE (°C)	N	EGESTION RATE* (ug/mg/hr)
5	4	9.18 (2.29) a
10	2	10.70 (0.61) a
15	4	12.60 (3.22) a

*Means followed by the same letter are not significantly different at the 0.05 level (DNMRT).

egestion rate at 3 experimental temperatures. Mean values for each temperature were not significantly different (P 0.05) (Table 13) so no regression of egestion rate vs. temperature was calculated. The overall mean for egestion rate was 10.85 ug/mg/hr.

Effect of Body Weight

Because only 1 observation was available for most of the weight classes, a plot of egestion rate vs. weight class was not included. Table 14 presents the means for each weight class. The smaller weight classes (2,3,4) had higher egestion rates than larger weight classes (6,7,8), but the sample size was very small (e.g. N=1 for WC 2, 3, 6, and 7). Regression of egestion on body weight was not significant (P 0.05).

Interaction of Body Weight and Temperature

Regression of egestion rate on body weight at each temperature and egestion rate on temperature for each weight class were not significant (P 0.05). A multiple regression of egestion rate on temperature and body weight also failed to show a significant relationship (P 0.05).

ENERGY BUDGET

An energy budget was calculated for 5th instar larvae weighing 1, 8, and 15 mg between 15 and 25°C. Equations relating weight specific rates of C, G, and R to body weight

Table 14. Means and standard errors* of egestion rate for different weight classes of *H. venularis*.

WEIGHT CLASS	N	EGESTION RATE (ug/mg/hr)
1	-	-
2	1	4.74 (-)
3	1	5.41 (-)
4	3	6.78 (0.13)
5	-	-
6	1	8.89 (-)
7	1	9.39 (-)
8	3	10.46 (0.27)

*Where N=1 there is no standard error.

and temperature were used to generate values of C, G, and R for appropriate sized larvae and temperatures. Since egestion (E) showed no relationship to temperature and body weight, the overall mean egestion rate of 10.85 ug/mg/hr was used. The values of C, G, R, and E were converted to calories using the caloric equivalents described in Materials and Methods. I assumed that assimilation rate (A) was approximately equal to the sum of growth and metabolic rate. Assimilation efficiency (AE) was calculated as (A/C) X 100, gross growth efficiency (GGE) was calculated as (G/C) X 100, and net growth efficiency (NGE) was calculated as (G/A) X 100 (Grodzinski et al. 1975).

Table 15 summarizes the calculated energy budgets. Fig. 7 shows the change in AE between 15 and 25°C for 1, 8, and 15 mg larvae estimated using the regressions described above. AE decreased with increasing temperature for all sizes of larvae. The highest AE was 33% for 8 mg larvae at 15°C, and the lowest AE was 2% for 1 mg larvae at 19 - 23°C. AE was higher for 8 mg larvae than for 1 and 15 mg larvae between 15 - 19°C. Above 19°C, AE was approximately the same for 8 and 15 mg larvae. AE of 1 mg larvae was always low.

Fig. 8 shows NGE for 1, 8, and 15 mg larvae between 15 - 25°C. NGE was highest for 1 mg larvae at all

Table 15. Energy budgets for 1, 8, and 15 mg *H. venularis* larvae at 15, 20, and 25 °C, calculated from regression equations.

TEMPERATURE (°C)	WEIGHT (mg)	ENERGY UTILIZATION (cal/mg/hr)				AE (%)	GGE (%)	NGE (%)	RESIDUAL (%)
		C	G	R	E				
	1	0.196	0.020	0.007	0.013	14	10	74	79
15	8	0.047	0.012	0.004	0.013	33	24	74	39
	15	0.031	0.003	0.003	0.013	21	10	47	37
	1	1.537	0.023	0.013	0.013	2	1	63	97
20	8	0.372	0.014	0.007	0.013	6	4	65	90
	15	0.242	0.005	0.006	0.013	5	2	46	90
	1	1.076	0.025	0.024	0.013	5	2	51	94
25	8	0.261	0.016	0.014	0.013	11	6	55	84
	15	0.170	0.008	0.011	0.013	11	5	40	81

C = Consumption Rate, G = Growth Rate, R = Metabolic Rate, E = Egestion Rate, AE = Assimilation Efficiency ((G+R)/C), GGE = Gross Growth Efficiency (G/C), NGE = Net Growth Efficiency (G/G+R)), Residual = Residual Energy (C-(G+R+E)/C).

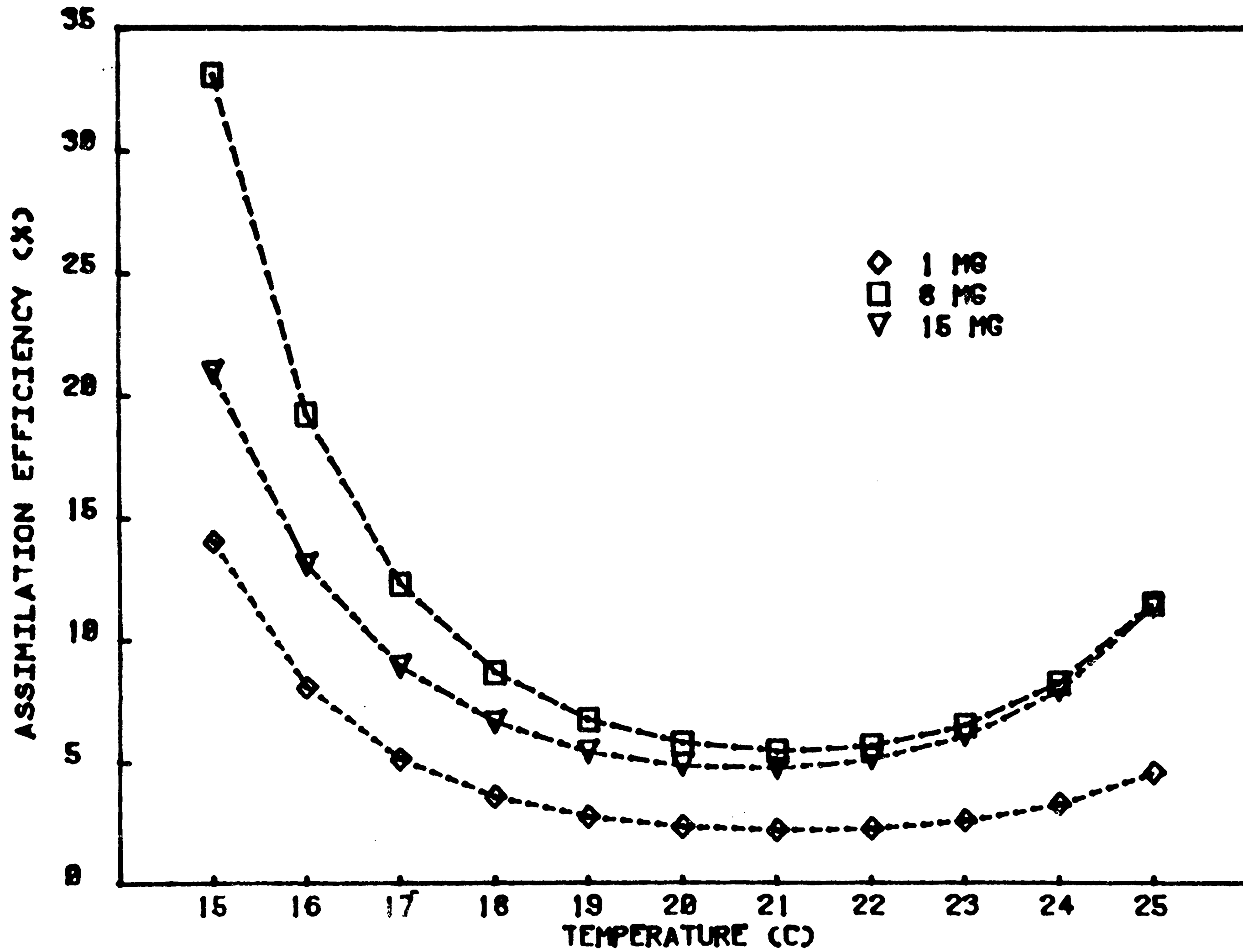

Figure 7. Assimilation efficiency of 1, 8, and 15 mg H. venularis at 15 to 25°C. Values determined as ((G+R)/C) X 100.

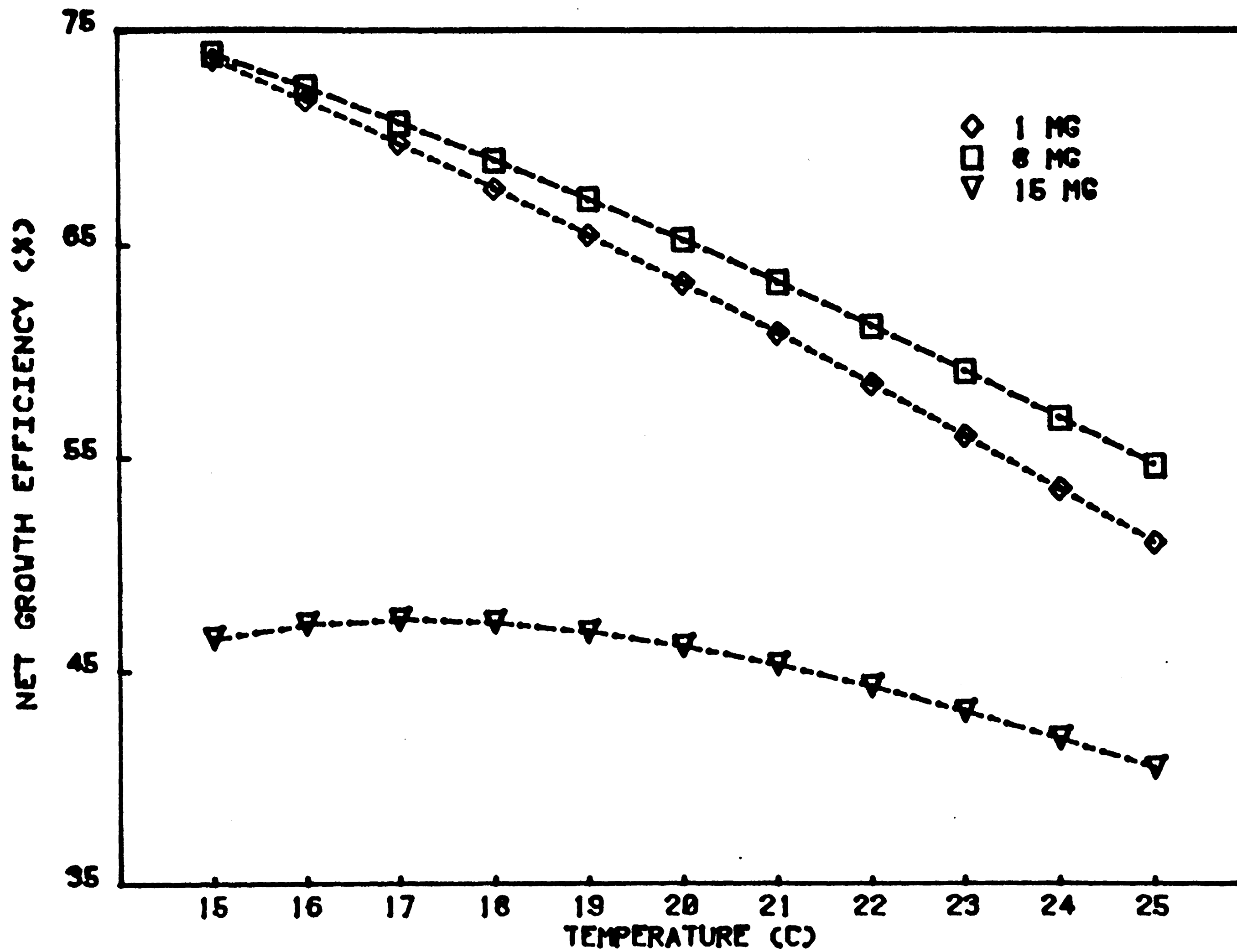

Figure 8. Net growth efficiency of 1, 8, and 15 mg *H. venularis* at 15 to 25°C. Values determined as (G/(G + R)) X 100.

temperatures with the greatest NGE being 74% at 16 - 17°C. NGE of 8 mg larvae was similar to 1 mg larvae and was highest (73%) at 15°C while NGE of 15 mg larvae was always less than 50%. NGE decreased with increasing temperature for all sizes of larvae although the decrease for 15 mg larvae was small.

GGE followed a pattern similar to AE (Fig. 9). GGE of 1 mg and 15 mg larvae was similar over the entire temperature range. The highest GGE of these larvae was 11% at 15°C. GGE of 8 mg larvae ranged from 24% at 15°C to 4% at 20 - 23°C.

Residual percent was high for all sized larvae and temperatures. The smallest residuals were at 15°C for 8 and 15 mg larvae. At higher temperatures residual was always greater than 60% with a maximum of 97% residual energy at 20°C for 1 mg larvae (Fig. 10).

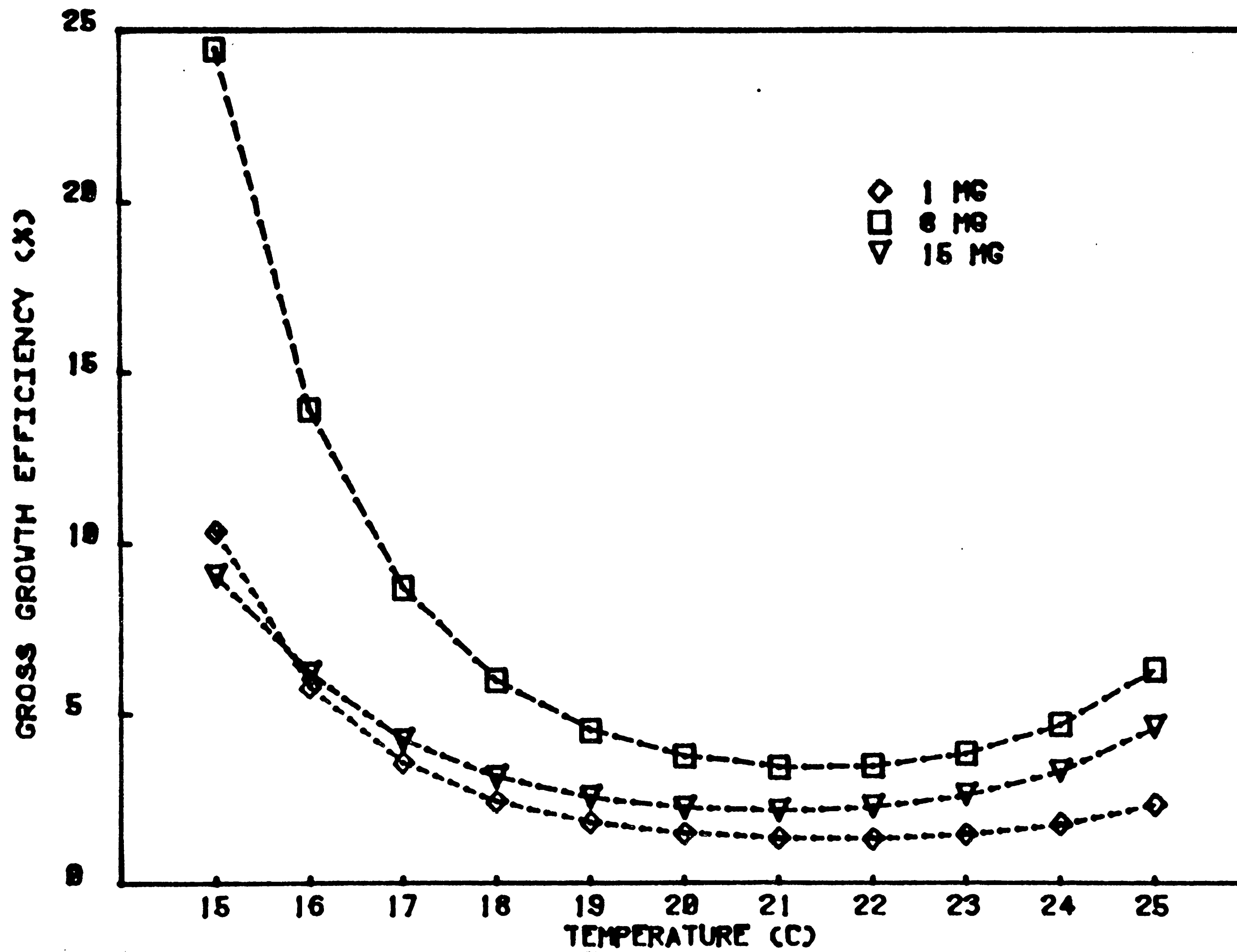

Figure 9. Gross growth efficiency of 1, 8, and 15 mg *H. venularis* at 15 to 25 ^{0}C. Values determined as (G/C) X 100.

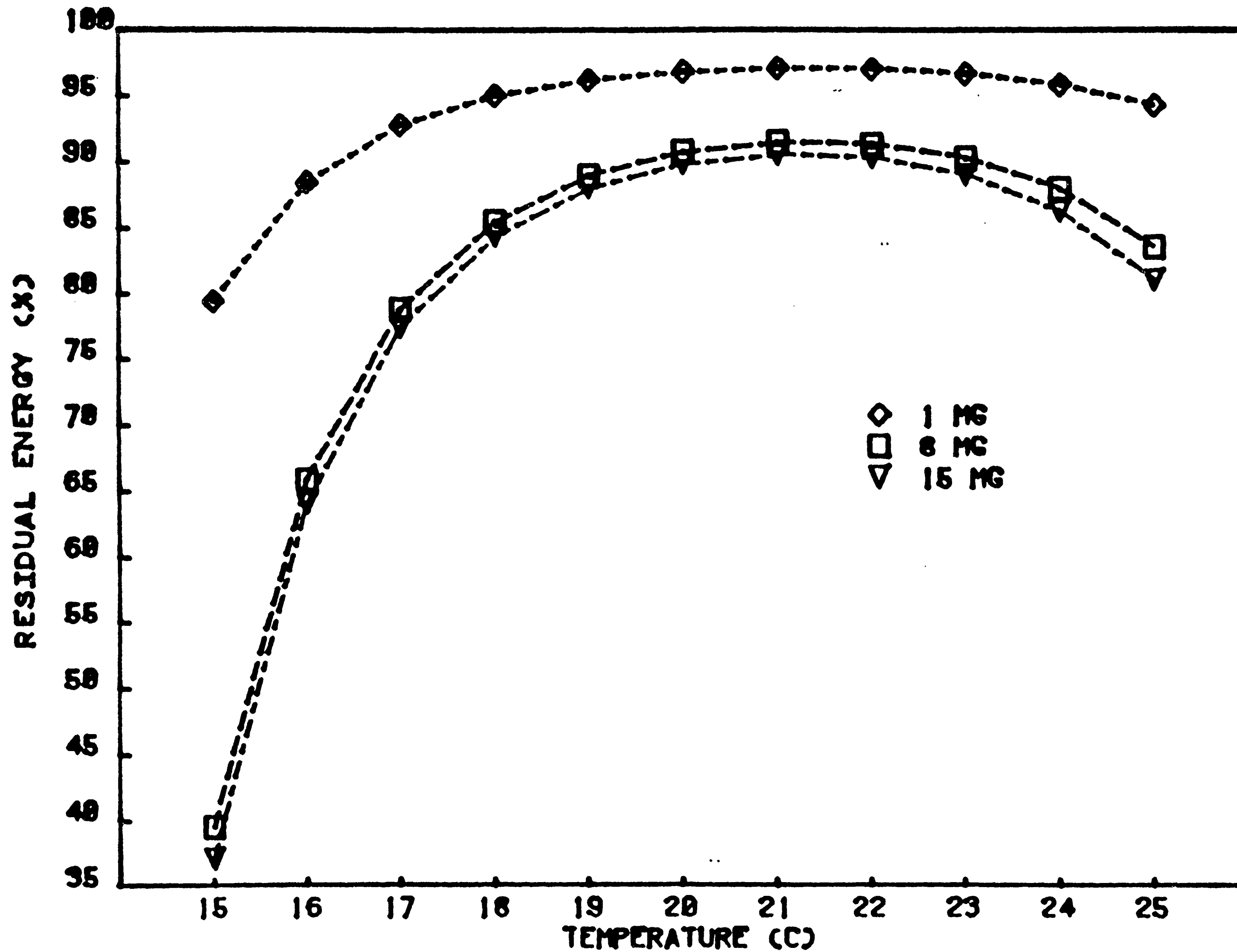

Figure 10. Residual energy from energy budgets of 1, 8, and 15 mg H. venularis at 15 to 25 °C. Values determined as ((C - (G + R + E))/C) X 100.

DISCUSSION

CONSUMPTION RATE

The shape of the temperature-consumption rate curve, although having only 3 points, is typical of the response of many invertebrates to high temperatures (Fig. 2). In this case increasing temperatures between 15.5 - 23.5^{o}C stimulated H. venularis to feed. Above 23.5^{o}C consumption rate dropped. Therefore, at some point between 23.5 and 28.0^{o}C a critical point may exist where increasing temperature causes feeding to be inhibited.

Temperature can have a very pronounced effect on processing rates. Variable temperature regimes frequently stimulate processing rates relative to constant temperatures (Scriber and Slansky 1981). All H. venularis larvae used in this study were exposed to natural temperature regimes in the Little River. As Vannote and Sweeney (1980) have shown, 4th and 5th order rivers (such as Little River) tend to have large diel temperature fluctuations. In contrast, Deep Creek station 2, where McCullough et al. (1979) collected H. occidentalis, is a spring-fed creek with a relatively constant temperature (18°C). The differences in temperature regimes at these two sites may account for the 2-3X greater consumption of H. venularis compared to H. occidentalis.

Although I have no data on food quality other than organic content of seston, a comparison of my results to those collected by McCullough et al. (1979) reveals that field consumption rates of H. occidentalis averaged 59.5 ug/mg/hr when feeding on 18% organic matter. In the laboratory, McCullough et al. found that H. occidentalis consumed an average of 30.5 ug/mg/hr feeding on radiolabeled Nitzshia with an organic content of 56%, In my study, H. venularis consumed an average of 161.87 ug/mg/hr feeding on 38% organic matter in the Little River. If organic content is taken as an index of food quality, then increased consumption rates may compensate for low amounts of organic matter by passing more particles through the gut faster (Cummins and Klug 1979, McCullough et al. 1979). Cammen (1980) demonstrated this inverse relationship between consumption rate and organic content of food with several species representing three phyla. Considering the differences in consumption rate between H. occidentalis and H. venularis (2-3X higher for H. venularis) it appears that organic content may be adequate for predicting changes in consumption rate, but inadequate for explaining the magnitude of consumption.

Decreasing consumption rate with increasing body weight may be related to the increasing amounts of metabolically inactive tissue (e.g. lipids) in the total body

weight. Becuase of this, all weight specific rates tend to decrease with increasing body weight (Scriber and Slansky 1981). H. occidentalis larvae studied by McCullough et al. (1979) were probably 4th instar (Dale McCullough pers. comm.). I used only 5th instar H. venularis larvae in my experiments. The higher consumption rate of H. venularis may be due to a need for certain essential lipids (e.g. cholesterol) which cannot be synthesized. Approximately 84% of the final dry weight of hydropsychids is gained during the 5th instar (Parker 1980), with the majority of the weight probably being lipids (Scriber and Slansky 1981). These lipids are stored as energy reserves prior to pupation. Fourth instar larvae, such as those studied by McCullough et al. (1979), would have no need to store large quantities of lipids.

Deep Creek station 2, Idaho, where McCullough et al. (1979) did their research, is a scraper-periphyton community (see Cummins and Kulg 1979, Fig. 3). McCullough (1975) pointed out that the most abundant species at this site was the elmid beetle, Optioservus divergens, a scraper. The food of H. occidentalis consisted mostly of diatoms, other algae, and probably scraper feces. Periphytic materials generally have low C:N ratios (high food quality) (Cummins and Klug 1979). In contrast,

Little River, Virginia, has a collector-FPOM community (Cummins and Klug 1979, Fig. 2) with the dominant species being *H. venularis* and other hydropsychids, *Isonychia* mayflies, and polycentropodid caddisflies. The food of these insects comes primarily from seston which generally has very high C:N ratios (low food quality, Cummins and Klug 1979). The differences in food quality as indicated by C:N ratios may account for differences in the consumption of hydropsychids in Idaho and Virginia.

GROWTH RATE

The growth rate I determined for *H. venularis* was lower than the growth rate determined for *H. occidentalis* by McCullough et al. (1979) (1.65 ug/mg/hr vs. 4.00 ug/mg/hr, respectively). The differences can probably be explained by differences in the size of larvae used in the two experiments.

The shape of the growth rate - temperature curve is typical of the response of poikilothermic animals to a large temperature range (Fig. 3). Wieser (1973), in his book dealing with effects of temperature on poikilotherms stated that the curve rises steeply in the lower temperature range and then flattens out. However, the Q_{10} values found in this study show that *H. venularis* does not follow the general pattern proposed by Wieser.

of high Q_{10} at low temperatures and low Q_{10} at higher temperatures. Instead, H. venularis maintains a rather high Q_{10} of 4.4 over the entire temperature range studied. High Q_{10} would be expected in areas where energy utilization (in this instance growth) can rapidly respond to temperature change. This would allow organisms living in fluctuating temperatures to start growing as fast as possible when temperatures are warm. Three advantages to growing as fast as possible have been pointed out by Scriber and Slansky (1981): (a) rapid passage through stages prone to high mortality, (b) completion of growth during a short growing season or ephemeral food supply, and (c) an increase in the number of generations per year.

The relationship between growth rate and body weight again follows the general pattern of most processing rates with growth rate decreasing with increasing body weight. Because of the small sample size for most wieght classes, it is difficult to evaluate these results in great detail. If only the mean values for growth rate of each weight class is considered it appears H. venularis has a rather constant growth rate during the 5th instar.

METABOLIC RATE

Some general features of the method used to determine metabolic rate must be considered. Using the Gilson

respirometer to determine metabolic rates of lotic insects obviously has disadvantages. The main disadvantage is the absence of flowing water in the respiratory flask. Hydropsychid larvae indicate respiratory stress by undulating their abdomen. During the course of the experiments I only noticed abdominal undulations at the highest temperature. Therefore, I assumed the absence of flowing water to have little effect on metabolic rates at lower temperatures. Another problem which has an effect on the results is the phenomenon of specific dynamic action (SDA). SDA is the increase in metabolism by as much as 92% over starvation levels (Heiman and Knight 1975, Scriber and Slansky 1981). Since I made no attempt to determine how much food was eaten prior to my experiments, I have no way to determine the effect of SDA.

Precht et al. (1973) stated that zones of plateau in temperature metabolism curves coincide with temperatures biologically important to the animal and represent zones of adaptation. _H. venularis_ appears to be adapted to 10 - 15°C. Q_{10} values are general indices of response to temperature (Grafius and Anderson 1979). Poikilotherms normally exhibit Q_{10} values of 2.0 - 3.0, therefore, values less than 2.0 may be considered areas where metabolic compensation for temperature is occurring. _H. venularis_

had a Q_{10} of 3.2 between 5 - 25°C which is slightly above the normal for poikilotherms.

Ross (1956) hypothesized that caddisflies evolved in cold headwater streams with temperatures that did not exceed 20°C. The exploitation of downstream areas was accomplished as caddisflies evolved physiological mechanisms that allowed them to survive in the lower oxygen concentrations of warm water. _H. venularis_ is considered to be a downstream species (e.g., in the Little River, the temperature reaches greater than 25°C in the summer and averages greater than 20°C from late June to early September). Therefore, downstream species such as _H. venularis_ should be adapted to both low and high temperatures with some mechanism (enzyme system, behavioral, etc.) becoming active at 20°C to allow for metabolic compensation at higher temperatures. The ancestral headwater species would have no such mechanism to compensate for high temperatures. The plateau at 10 - 15°C and the low Q_{10} value at 20 - 25°C lend some support to this hypothesis. Edington and Hildrew (1973) reported that the metabolic rate of _Diplectrona felix_, a headwater species, increased between 20 - 25°C, but a downstream species, _Hydropsyche fulvipes_ (=_instabilis_) was able to decrease metabolic rate between 20 - 25°C. _H. fulvipes_ had a temperature-metabolic rate curve similar to _H. venularis_, with

plateaus at 10 - 15° and 20 - 25°C.

Although the regression of metabolic rate vs. body weight was significant (P 0.05), there was a very low r^2 (r^2 = 0.09). This indicates that, although a relationship exists between body weight and metabolic rate, body weight is not a good predictor of metabolic rate. It would seem reasonable that metabolic rates of aquatic insects with apneustic respiratory systems would also be related to surface area, as Betalanffy (1957) has discussed for other animals that respire by means of gil (e.g. fish).

The similarity of regression equations in Table 12 indicates _H. venularis_ respiration responds to temperature in a uniform manner during the 5th instar. Vannote and Sweeney (1980) hypothesized that aquatic insects have evolved mechanisms of compensation for respiration and growth which are adjusted to particular thermal patterns. The similarity of the regressions in Table 12 indicates such a mechanism. When temperature increases, the effect on metabolic rate is approximately the same over the entire size range of the instar.

The body weight-metabolic rate regressions were highly variable for each temperature and showed no ordered pattern of body weight influence on metabolic rate (Table 11). It appears that _H. venularis_ has a weight independent metabolic rate at 10°C. This also supports the hypothesis

that 5th instar H. venularis larvae are best adapted to 10 - 15°C. Weight independent metabolic rate would be expected in the range of maximal thermal adaptation because respiratory enzymes would be expected to operate most efficiently between these temperatures. Between 15 - 20°C metabolic rate is highly weight dependent. Keister and Buck (1974) have stated that 15°C appears also for many other activities. As temperature increases and cool adapted compensation mechanisms begin to fail, metabolic rate would be directly related to the weight of the organism.

Becuase metabolic rate of smaller larvae was significantly higher than that of larger larvae, I used the equations for weight class 1 and 8 from Table 12 to predict changes in metabolic rate between 10 - 20°C. At 10°C, WC 1 and WC 8 had similar metabolic rates of 0.43 and 0.42 ul O_2/mg/hr, respectively. However, at 20°C metabolic rate of WC 1 was 50% greater than WC 8. Q_{10} values for WC 1 and WC 8 were 5.1 and 2.7, respectively, between 10 - 20°C. As stated above, high Q_{10} values represent areas where great sensitivity to temperature change occur. I observed that during the winter 3rd, 4th, and 5th instar larvae are located up in the outer stems of the Podostemum that covers the rocks, where they actively maintain capture nets. Large larvae are restricted to accumulations of sediment at the base of Podostemum.

They do not maintain capture nets and appear to be inactive. This would be a competitive advantage to smaller larvae who could increase their weight during the winter months. Hildrew and Edington (1979) have shown that larger larvae will attack smaller larvae when suitable habitat is limited in the springtime. Therefore, there may be temporal separation of larger and smaller larvae during the winter.

EGESTION RATE

The egestion rate of H. venularis was very low relative to consumption rates. This is probably due to the method employed to determine egestion. Since larvae were deprived of food at the time egesta was collected, gut retention may have increased drastically. Hargrave (1972), in a study of egestion by an amphipod, included a survey of literature values for egestion rate. He found that animals which were starved egested less than 50% of their body weight daily, but animals that fed during feces collection egested a wieght of material equal to or much greater than (up to 7500%) their body weight. From this he concluded that many deposit feeding invertebrates depend on ingestion to force material through the gut. My data would tend to support this hypothesis. Becuase of the method used for this aspect of the research,

I consider the egestion rates to be grossly underestimated.

A final point should be made concerning egestion rate. Although I did not measure dissolved organic wastes, these products may form a large percentage of the egesta. Heiman and Knight (1975) found that dissolved organic wastes were equal to or greater than solid organic wastes for the stonefly, Acroneuria (=Callineuria) california. The significance of this to my study is minimal, but when interpreting energy bugets where AE is calculated as (C-F)/C, dissolved wastes should be considered. AE can be overestimated by 50% or more if dissolved wastes are not considered.

ENERGY BUDGET

The rates of energy processing (C, G, R) in Table 15 have the same responses to temperature and size as the rates of material processing (i.e. increasing rates with increasing temperature and decreasing rates with increasing body size) (Scriber and Slansky 1981). AE ranged from 2 - 33% and generally decreased with increasing temperature and increased with increasing body weight. The low values at 20 - 21°C reflect the point where consumption is maximum or approaches maximum. The higher AE at temperatures above 21°C is due to decreasing consumption. Lawton (1971) pointed out three relationships which may

exist between AE and feeding rate: Type A where AE remains constant over a wide range of feeding rates, Type B where AE decreases with increased feeding rate, and Type C where AE increases with increasing feeding rate. *H. venularis* appears to have a Type B relationship. AE decreases as feeding rate increases to a maximum. As feeding begins to slow, AE again increases. Assimilation efficiencies determined for *H. venularis* in this study fall into the range of most detritivores (Welch 1968; Ladle et al. 1972; Heiman and Knight 1975; Wallace et al. 1977; Wallace and Merritt 1980).

NGE decreases with increasing temperature for small larvae much more rapidly than for larger larvae because there is little metabolically inactive tissue in smaller larvae. *H. venularis* is obtaining an ample supply of energy from the food consumed as indicated in Table 15. Therefore, if calories are a potential limiting factor in *H. venularis* bioenergetics, consumption rates would be expected to be much lower. Apparently, some nutrient in the food (i. e. nitrogen, lipids) is limited in availability, and *H. venularis* must consume a large amount of seston to obtain required quantities of that nutrient. Seston in general has a very high C:N ratios (Naiman and Secall 1979) which would lend support

to a hypothesis that nitrogen is limiting. Wotton (1978) found that Simulium consumed large quantities of carbon and had a very low AE feeding on natural seston. Scriber and Slansky (1981) pointed out that nutrients appear to be important regulators of energy flow at all levels.

Growth rates in this study fell within the range of terrestrial insects fed on leaves containing approximately 1% total organic nitrogen per unit dry weight.

To date the only detailed bioenergetic study of a net-spinning caddisfly has been the work of McCullough et al. (1979). A comparison of their results to mine indicate that H. venularis and H. occidentalis utilize approximately the same amount of energy for growth and metabolism. These similarities are not surprising considering the equivalent position the two species hold in their respective streams.

Differences do occur in calories ingested. At 18°C H. occidentalis consumed an average of 0.09 cal/mg/hr compared to 0.22 cal/mg/hr for H. venularis (calculated for 8 mg larvae at 18°C from regression equation). Considering the similarity in growth and metabolic requirements, it appears that energy is not a limiting factor for either species.

The overall energy budget for _H. venularis_ in cal/mg/hr is: C = 0.53, G = 0.01, R = 0.01, AE = 8%, NGE = 56%, GGE = 5%. Residual energy averaged 85%. This large amount of unaccounted for energy is probably due to the underestimation of egesta. If egesta could have been measured adequately I believe the residual energy would have been much smaller.

CONCLUSIONS

It appears that members of the genus Hydropsyche have similar requirements in terms of calories for growth and respiration. These requirements are a small portion of the total energy consumed and are reflected by low assimilation efficiencies. Energy does not appear to be limiting to these caddisflies. Therefore, essential nutrients (nutrients are defined here as any material essential to life) must account for the high consumption rates and low efficiencies found for most detritivores. Consumption of large quantities of material is necessary to acquire adequate amounts of a nutrient. Low assimilation efficiencies (in terms of calories) results in a large number of calories being passes through the gut and egested as feces.

Egestion of a large quantity of feces may be significant. Wallace et al. (1977) pointed out that the role of filter-feeders in flowing waters is to capture the organic matter in the water column and prevent its export downstream. By doing so nutrients and material are retained and utilized within the system. This process has been termed spiralling by Webster (1975) and is analogous to nutrient cycling in terrestrial ecosystems. The greater the percentage of organic matter entering the water column that is converted to inorganic CO_2, the

tighter the spiralling and more efficient is the ecosystem.

High consumption rates would not make a contribution to nutrient retention unless: (1) a large number of calories or nutrients are converted to body tissue (high AE and GGE) for use by consumers at higher trophic levels, (2) ingested materials are converted to CO_2 through respiration or (3) the ingested, but unassimilated, material is modified in some way that makes it more available to consumers. Results of this study do not support the first 2 hypotheses. *H. venularis* does, however, appear to modify seston in a way which makes this material available to other consumers. I observed that the fecal pellet produced by *H. venularis* is considerably larger than the food ingested. Changing small particles of suspended FPOM into larger particles provides a food resource for collector-gatherers in depositional areas and for other collector-filterers.

Cammen (1980) recently hypothesized that sediment mixing and nutrient recycling would be greater in areas with low sediment organic content than in areas with richer sediment since consumption is generally inversely related to organic content of food. If collector-filterers respond to a low quality food source by increasing consumption above physiological requirements, then, the

egested material becomes a resource which otherwise would not be available for other consumers. This would increase the efficiency of the ecosystem.

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THE ECOLOGICAL ENERGETICS OF THE NET-SPINNING CADDISFLY, *Hydropsyche venularis* Banks (TRICHOPTERA: HYDROPSYCHIDAE)

Douglas Alan Howell

The study of organism level energetics in conjunction with ecosystem level energetics can lead to a better understanding of the structure and function of stream ecosystems. The purpose of this study was to calculate energy budget equations for a net-spinning caddisfly, *Hydropsyche venularis* Banks, and to develop, or modify, methods used to determine consumption and growth in the field. The method used to determine consumption rate was a modification of the procedure used by Ladle et al.(1972). Growth rate was determined by mark-recapture and metabolic rate was determined in a Gilson respirometer. Egestion rate was determined by a new method.

Consumption rate was found to be higher than other values reported for hydropsychids. Growth and metabolic rate were similar to that reported by McCullough et al. (1979) for *H. occidentalis*. Egestion was much lower than would be predicted from consumption and cast doubt as to the usefulness of the new method. Energy budgets were calculated from regression equations relating the various processing rates to body weight and temperature for

1, 8, and 15 mg larvae at 15 to 25°C. The overall energy budget was: C - 0.53 cal/mg/hr, G - 0.01 cal/mg/hr, R - 0.01 cal/mg/hr, AE - 8%, NGE - 56%, GGE - 5%. Egestion was constant at 0.01 cal/mg/hr.

The high consumption rate of *H. venularis,* above that necessary for growth and maintainence may be significant in the processing of energy in Little River. Feces produced by *H. venularis* are larger than the particles ingested. The fecal pellets are then available to other filter-feeders and deposit feeders. Higher consumption rates may therefore increase the efficiency of the ecosystem.