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## Energetics, growth, and production of a leaf-shredding stonefly in an Appalachian Mountain stream

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**Abstract.** Laboratory studies were conducted to measure growth, respiration, ingestion, and egestion for a leaf-shredding aquatic insect, *Pteronarcys proteus* (Plecoptera:Pteronarcyidae). These variables were measured for each of three cohorts found in a stream population, and all were a function of nymphal size and temperature. Relative growth rates (RGR) ranged from 0.031 to 0.0037 g g<sup>-1</sup> day<sup>-1</sup>, with small nymphs growing fastest. Ingestion ranged from 5 to 40% of dry body weight per day. Respiration ranged from 330 to 980  $\mu\text{l O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ . Respiration, ingestion, and growth were highest for smallest nymphs and decreased with increasing size of nymphs. Assimilation efficiencies also followed this pattern, except for female nymphs, for which both ingestion and assimilation efficiencies did not decline.

Total assimilation by a population of *Pteronarcys proteus* in a mountain stream was estimated at 119 kcal m<sup>-2</sup> yr<sup>-1</sup>, accounted for primarily by the two oldest cohorts present. Energy flow was greatest at and after autumn leaf abscission and lowest after spring emergence of adults. Annual energetics of the nymphal population were: ingestion = 906, growth = 41, respiration = 78, and egestion = 828 kcal/m<sup>2</sup>.

Annual production of three coexisting cohorts was 0.438 (Cohort 1), 3.158 (Cohort 2), and 4.182 (Cohort 3) g/m<sup>2</sup>. In the stream, instantaneous daily growth rates (IDGR) were highest for smallest nymphs and ranged from 0.018 to no detectable growth. Correlations between temperature and IDGR were not significant except for the youngest cohort, for which growth rates were highest during higher temperatures. Larger nymphs, however, grew fastest after leaf-fall when temperatures were lower. The data show that growth rates of small nymphs were influenced by temperature and growth rates of larger nymphs were affected by food supply. Simulation of growth of nymphs under food-unlimited conditions supported this conclusion. *Pteronarcys proteus* consumed an estimated 41-64% of the litterfall in the study stream.

**Key words:** energetics, stream, shredder, production, growth, respiration, ingestion, insect, *Pteronarcys*.

The trophic structure of stream ecosystems is thought to be chiefly maintained by detritus, from either allochthonous or autochthonous sources (e.g., Cummins 1973, Godshalk and Wetzel 1978, Kaushik and Hynes 1968, Minshall 1967, 1978). In low-order woodland streams, the major source of detritus is autumnal leaf-fall (Fisher and Likens 1973, Hornick et al. 1981), which provides both refugia and food resources for stream micro- and macroconsumers. It has been suggested that the availability of energy in these systems is provided through a microbe-detritus complex (e.g., Kaushik and Hynes 1968, 1971, Petersen and Cummins 1974). General models for detritus processing in streams assign large-particle detritus feeders, or shredders, prominent roles in the comminution of detritus

which in turn becomes a food resource for collectors (Cummins 1974, Cummins and Klug 1979). Thus, by processing large-particle detritus, shredders facilitate energy flow in streams both through the direct conversion of detrital energy into shredder biomass and by the production of fine particulate organic matter (FPOM). In doing so, they provide a link for energy and materials between low- and high-order streams (Cummins 1980, Vannote et al. 1980).

Factors that limit shredder biomass or secondary production include those that regulate their standing crop and influence growth rates (reviewed by Benke 1984). Food, temperature, and their interaction are often-cited factors controlling growth rates of aquatic detritivores (e.g., Anderson and Cummins 1979, Anderson and Sedell 1979, Cummins and Klug 1979, Wallace and Merritt 1980).

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This research was a field and laboratory study of the energetics, growth, and production of a leaf-shredding stonefly, *Pteronarcys proteus*. Specific objectives were to 1) measure rates of ingestion (I), respiration (R), and growth (G) for individuals in each of the age classes or cohorts present in a stream population, 2) determine the effect of temperature and size on these energetic parameters, and 3) use these relationships to estimate annual energy flow and the relationship between food, temperature, and growth in a stream population.

## Methods

### *Study organism*

*Pteronarcys proteus* Newman (Plecoptera: Pteronarcyidae) is distributed from Quebec south to Virginia, and the genus *Pteronarcys* is widespread throughout North America (Claassen 1931, Hitchcock 1974). Nymphs of *P. proteus* are categorized as shredders (Merritt and Cummins 1984) ingesting primarily leaf detritus and occasionally small quantities of moss and animal matter (Perry 1985). In southern Appalachian Mountain streams, *Pteronarcys* nymphs are generally most abundant in leaf and organic debris accumulations during autumn, winter, and spring. In summer, when leaf packs are scarce, they are found in organic debris under medium to large stones in fast water. Adults generally emerge in late spring (May), and mating, egg deposition, and death occur within one to two weeks (Perry 1985). Eggs undergo a non-obligatory diapause until the following spring when temperature increases and they hatch (Miller 1939). Nymphal life lasts 3–4 years through 12 male instars and 13 female instars (Holdsworth 1941a, 1941b). Such lengthy life cycles are described as merovoltine (Butler 1984).

### *Study area*

The study was conducted in a reach of Little Stony Creek, a third-order tributary of the New River in the Ridge and Valley Province of Virginia. The stream originates from springs in Clinch sandstones of Silurian age and flows for approximately 19.4 km through a mixed deciduous forest. A sampling site (elevation 612 m) was established in a 500-m reach 8.2 km from the confluence with the New River near the

town of Pembroke (Giles County), Virginia. Riparian trees along the reach included maple (*Acer rubrum* L., *Acer saccharum* Marsh.), white oak (*Quercus alba* L.), dogwood (*Cornus florida* L.), birch (*Betula lenta* L.), American sycamore (*Platanus occidentalis* L.), and poplar (*Populus deltoides* Marsh.). Stream width in the study reach varied from 2 to 6 m and depth varied from 5 to 26 cm. Substrate consisted primarily of boulders (256–768 mm) and cobbles (64–256 mm) with some pebbles (16–64 mm). The study site was a typical riffle/run in the lower reaches of the stream.

### *Laboratory studies*

*Collection and maintenance of nymphs.*—Nymphs were collected from Little Stony Creek by a kick net with 350- $\mu$ m mesh or 150- $\mu$ m mesh when it was necessary to collect small instars. Collections were made during August, November, and January so that experimental temperatures of 5°, 10°, and 20°C would coincide approximately with water temperatures in Little Stony Creek. The insects were placed in stream water in insulated containers and returned to the laboratory.

Three size-classes, which represented three cohorts, were selected for energetics measurements. They consisted of nymphs with approximately 1 year of growth, Cohort 1 (5–25 mg dry weight); 2 years of growth, Cohort 2 (40–70 mg); and mature nymphs with just less than 3 years of growth, Cohort 3, which was further divided into males (90–130 mg) and females (180–250 mg).

Red maple leaves (*Acer rubrum*) were used for food during the experiments. Sufficient leaves for the entire experiment were collected in autumn and placed in Little Stony Creek in mesh bags for four weeks. After removal from the stream, the leaves were rinsed and frozen. Before use as food, leaves were soaked in aerated stream water for one week at 10°C, then pieces (2–10 cm<sup>2</sup>) were cut from the blades, avoiding the larger veins.

*Growth and ingestion.*—Laboratory growth was measured by comparing nymphal weights taken at the beginning and end of experimental periods (28–85 days) at three temperatures (5°, 10°, and 20°C). Initial weights were taken on carefully blotted individuals. Final weights were taken on nymphs killed by freezing and

weighed wet. Nymphs were then dried at 50°C for 24–48 hours to obtain dry weights and water correction factors for calculating dry weight equivalents. Relative growth rates (RGR) were calculated as increases in dry weight per unit insect dry weight (final) per day.

Ingestion rates were determined using short-term (2–3 days) feeding experiments using gravimetric methods. Leaf material used as food was blotted between filter paper, subsampled for ash-free dry weight determination (AFDW), weighed wet, and put into the experimental cages. Subsamples were weighed, dried, reweighed, and ashed at 550°C for one hour to determine wet weight to AFDW ratios. At the end of an experiment, uneaten food was removed, blotted, weighed, dried, and ashed for AFDW determinations. Ingestion (I) was estimated as the difference between initial and final AFDW of leaf material after correction for weight of orts (see below). Losses to leaching and microbial decomposition were estimated in cages without nymphs. The entire procedure was repeated four to seven times at 5°, 10°, and 20°C. Ingestion rates of small nymphs were means computed from experiments using five or more individuals. Only actively feeding nymphs were used in experiments. At the conclusion of an experiment, insects were dried and weighed as described above.

Small particles generated by feeding were distinguished from feces for large nymphs as follows. Starved nymphs were fed measured amounts of food for 2–4 hours, then the food was removed before fecal release began. Particles were filtered out and weighed, and a ratio of orts:food was calculated. Smaller nymphs (<30 mg) fed by skeletonizing, and their fecal pellets were clearly separable from orts.

*Respiration rates.*—Respiration rates were measured using a Gilson differential respirometer. Nymphs were collected from the stream when mean daily water temperatures were near desired experimental temperatures and were acclimated to test conditions for at least 48 hours before measurements. Nymphs were tested either in groups (smaller instars) or individually in flasks containing stream water and Nitex screen substrate. Measurements lasted from 2 to 12 hours, depending on temperature and nymphal size, and were conducted under reduced lighting. Flasks were shaken at a mod-

erate rate (50 cycles per minute) to create water movement. After several trials at the experimental temperatures, insects were killed, dried at 50°C, and weighed.

#### Field studies

*Secondary production.*—Nymphs were collected approximately monthly from May 1983 to July 1984 using a 0.25-m<sup>2</sup> metal frame fitted with a 350- $\mu$ m mesh net. A 150- $\mu$ m mesh net was used during summer to ensure capture of the smallest instars. At least four samples were taken, but often more (maximum of 16) were needed to collect an adequate number of nymphs in all cohorts. Nymphs were stored frozen until measurements of head capsule width, wet weight, and dry weight (24 hr, 50°C) were made. Sex was also determined for individuals of sufficient size. Production was calculated by:

$$P = G\bar{B}$$

where P = production (g/m<sup>2</sup>) for a sample interval, G = instantaneous growth rate, and  $\bar{B}$  = mean standing stock (biomass, g/m<sup>2</sup>) during the interval (Chapman 1968, Waters and Crawford 1973). Calculations were made separately for each interval between sampling dates for one year and summed for annual production. Instantaneous growth rates over the interval were calculated as:

$$G = \ln(W_2/W_1)$$

where  $W_2$  = dry weight at the end of an interval, and  $W_1$  = dry weight at the beginning of an interval. Because there were obvious differences in size, growth rates for male and female nymphs in Cohorts 2 and 3 were followed separately.

*Benthic organic matter.*—Standing stock of benthic particulate organic matter was surveyed by randomly sampling riffle areas using a 150- $\mu$ m mesh net and 0.25-m<sup>2</sup> frame. Three samples were taken approximately monthly, and material collected was separated into four categories: Fine (<150–600  $\mu$ m), Medium (0.6 mm–1 cm), Coarse (>1 cm), and Wood (sticks, nuts, and bark). After sorting and removal of animals, samples were oven dried at 50°C, weighed, and subsampled for determination of AFDW.

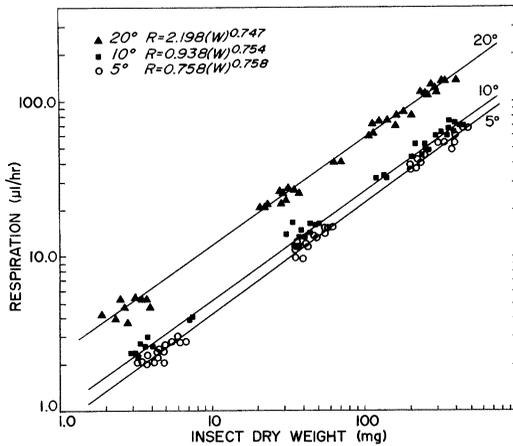


FIG. 1. Individual respiration rates by nymphs at three temperatures.  $R$  is respiration,  $W$  is dry weight of individual nymphs.

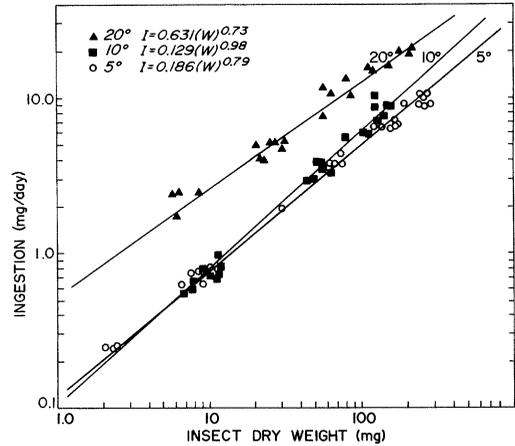


FIG. 2. Individual ingestion rates of stream-conditioned red maple leaf by nymphs at three temperatures.  $I$  is ingestion,  $W$  is dry weight of individual nymphs.

## Results and Discussion

### Laboratory bioenergetics

Growth measured in the short-term laboratory trials fit a linear model, and because of the usefulness in developing energy budgets, laboratory growth is expressed as relative growth rate (RGR) (Table 1). Growth rates for laboratory-reared 2nd- and 3rd-instar nymphs are included in Table 1 to provide growth rates for newly hatched nymphs, which were only rarely collected in field samples. In general, RGR's were low compared with a mean RGR of  $0.040 \text{ g g}^{-1} \text{ d}^{-1}$  reported for a survey of 36 species of aquatic detritivores (Slansky and Scriber 1982). However, a low RGR seems reasonable for a mero-voltine detritivore like *P. proteus*.

Respiration varied with temperature and size of individuals (Fig. 1). There was a positive relationship between the log of individual weight and log of oxygen consumption at each experimental temperature. Analysis of covariance showed no differences among the slopes at different temperatures; the mean slope was 0.753. This coefficient has been commonly observed to be between 0.7 and 0.8 for other stoneflies (McDiffett 1970, Poole 1981) and other insects (e.g., Edwards 1958, Reichle 1967, Smalley 1960).

The  $Q_{10}$  (Schmidt-Nielsen 1979) values respiration rates between  $5^\circ$  and  $10^\circ$  and  $10^\circ$  and  $20^\circ\text{C}$  were 1.44 and 2.34, respectively. Similar values were observed for *Pteronarcys californica*

TABLE 1. Mean relative growth rates (RGR) as grams dry weight gain per gram dry insect weight per day calculated for cohorts grown at three temperatures. Values in parentheses are one standard deviation and number of measurements.

Temp (°C)	2nd-3rd Instars	Cohort 1	Cohort 2	(Male) Cohort 3	(Female) Cohort 3
5°	—	0.0076 (0.0084; 18)	0.0047 (0.0045; 28)	0.0027 (0.0020; 14)	0.0037 (0.0026; 16)
10°	—	0.0076 (0.0084; 18)	0.0047 (0.0045; 28)	0.0040 (0.0029; 11)	0.0049 (0.0038; 12)
20°	0.031 (0.013; 54)	0.0173 (0.0078; 17)	0.0115 (0.0049; 17)	0.0056 (0.0048; 14)	0.0068 (0.0063; 19)

TABLE 2. Summary energy budgets for *P. proteus* at three temperatures calculated for three cohorts. Coefficient of variation is given in parentheses.

Cohort/Weight	Temp.	Ingestion	=	Growth	+	Regression	+	Egestion
<u>1</u> 10 mg	5°C	1.15 mg		0.076 mg		106 $\mu$ l		0.887 mg
		5.68 cal		0.40 cal		0.52 cal		4.76 cal
		(110)		(110)		(12)		
	10°C	1.23 mg		0.076 mg		127.5 $\mu$ l		0.930 ml
		6.08 cal		0.40 cal		0.62 cal		5.06 cal
			(25)		(110)			
20°C	3.39 mg		0.173 mg		2.987 $\mu$ l		2.691 mg	
	16.7 cal		0.92 cal		1.46 cal		14.37 cal	
	(40)		(45)		(10)			
<u>2</u> 50 mg	5°C	4.09 mg		0.235 mg		356.1 $\mu$ l		3.228 mg
		20.2 cal		1.24 cal		1.74 cal		17.22 cal
		(15)		(95)		(15)		
	10°C	5.95 mg		0.235 mg		428.3 $\mu$ l		4.961 mg
		29.4 cal		1.24 cal		2.10 cal		26.60 cal
			(25)		(98)		(26)	
20°C	10.97 mg		0.575 mg		1004 $\mu$ l		8.628 mg	
	54.1 cal		3.04 cal		4.92 cal		46.14 cal	
	(60)		(43)		(26)			
<u>3 male</u> 100 mg	5°C	7.08 mg		0.27 mg		600 $\mu$ l		5.754 mg
		35.0 cal		1.43 cal		2.94 cal		30.64 cal
		(55)		(74)		(20)		
	10°C	11.75 mg		0.40 mg		721 $\mu$ l		10.081 mg
		58.0 cal		2.12 cal		3.5 cal		52.38 cal
			(82)		(73)		(29)	
20°C	18.2 mg		0.56 mg		1691 $\mu$ l		14.664 mg	
	90.0 cal		2.96 cal		8.28 cal		78.65 cal	
	(61)		(86)		(12)			
<u>3 female</u> 200 mg	5°C	12.2 mg		0.74 mg		1011 $\mu$ l		9.681 mg
		60.4 cal		3.92 cal		4.95 cal		51.40 cal
		(55)		(70)		(22)		
	10°C	23.2 mg		0.98 mg		1216 $\mu$ l		20.080 mg
		114.6 cal		5.2 cal		5.96 cal		103.46 cal
			(110)		(76)		(10)	
20°C	30.1 mg		1.36 mg		2850 $\mu$ l		23.72 mg	
	148.7 cal		7.2 cal		14.0 cal		127.52 cal	
	(72)		(91)		(13)			

by Knight and Gaufin (1966), but higher values (2 to 3 $\times$ ) were reported for the same species by Poole (1981). Using reported respiration rates for *P. scotti* (McDiffett 1970),  $Q_{10}$  was computed to be 1.45 and 1.5 for temperatures between 5° and 10°C and 10° and 15°C, respectively.

$Q_{10}$  reflects metabolic responses to temperature changes and may also reflect the degree to which organisms tolerate or compensate for temperature effects (Hochachka and Somero 1973, Schmidt-Nielsen 1979). Our results sug-

gest that *P. proteus* compensates poorly for higher temperatures and that the change from 10° to 20°C caused the greatest metabolic displacement, and temperatures approaching 20°C may be suboptimal. A temperature of 20°C was reported as suboptimal for *Pteronarcys dorsata* reared in the laboratory, resulting in reduced emergence success, fecundity, and life span (Nebeker 1971).

Ingestion rates varied with size and temperature (Fig. 2). Relative ingestion rates, expressed

as percent dry body weight/day ranged between 3.4 and 21.4% at 5°C, 6.1 and 28.2% at 10°C, and 9.1 and 33.4% at 20°C. Similar values were calculated for *P. scotti* from egestion rates reported by McDiffett (1970), but our rates were lower than ingestion rates (27–61%) reported for *P. californica* (Poole 1981).

Laboratory measurements of ingestion rates may be misleading because feeding preference may alter consumption rates (e.g., Arsuffi and Suberkropp 1984, Kaushik and Hynes 1971, Wallace et al. 1970). When stream-conditioned dogwood leaves (*Cornus florida*) were used as food, consumption by *P. proteus* increased up to 3× over ingestion of red maple reported here. Conditioning time, as well as leaf species, may affect ingestion rates by *P. proteus* (Golladay et al. 1983).

Based on the equation  $I = G + R + E$ , where  $I$  is ingestion,  $G$  is growth,  $R$  is respiration, and  $E$  is egestion, energy budgets were constructed for insects representing Cohorts 1, 2, 3-male, and 3-female (Table 2). Ingestion, growth, and respiration were calculated from relationships in Figures 1 and 2 using the following conversions:

Ingestion—4.94 cal/mg AFDW (McDiffett 1970)

Biomass—5.30 cal/mg dry weight (McDiffett 1970)

Respiration—0.0049 cal/ $\mu$ l O<sub>2</sub> (Brody 1945)

Egestion was calculated by difference and includes all unmeasured energy losses such as exuviae, excretion, and dissolved organic secretions. Energy lost through excretion was considered small and not measured. For example, excretion as ammonia, reported for *P. californica* by Poole (1981), was 0.08 mg per g insect per day. In a study of *P. scotti*, exuviae accounted for 6–12% of production (McDiffett 1970).

Data from Table 2 were used to calculate energetic efficiencies (modified from Waldbauer 1968):

AE, assimilation efficiency =  $(I - E)/I$

NGE, net growth efficiency =  $G/(I - E)$

GGE, gross growth efficiency =  $G/I$

In general, growth rates (Table 1) and energetic efficiencies (Table 3) were inversely related to size or age among Cohorts 1, 2, and 3-male. Changes in growth patterns observed for *P. proteus* were similar to those summarized for insects by Waldbauer (1968) and Scriber and Slan-

TABLE 3. Summary of efficiencies (percent) for *P. proteus*.

Cohort Weight	Temperature (°C)	Assimilation Efficiency	Net Growth Efficiency	Gross Growth Efficiency
1 10 mg	5°	16.2	43.7	7.1
	10°	16.9	39.2	6.6
	20°	14.2	38.5	5.4
2 50 mg	5°	14.8	41.6	6.2
	10°	11.4	37.2	4.2
	20°	12.5	32.7	5.6
3 male 100 mg	5°	12.5	32.7	4.1
	10°	9.7	37.5	3.6
	20°	12.5	26.4	3.3
3 female 200 mg	5°	14.7	44.2	6.5
	10°	9.7	46.6	4.5
	20°	14.2	34.0	4.8
Mean		13.5	38.3	5.2

sky (1981). The general pattern is one in which RGR, RCR (relative consumption rate), and AE tend to decline from early to late instars and NGE tends to increase. GGE may increase, decrease, or remain the same. Cohort 3 was an exception in which rates and efficiencies for female nymphs were similar to those of Cohort 2 and higher than those of Cohort 3-males.

Differences between sexes in Cohorts 1 and 2 were not measured but may not be as great as those in Cohort 3 because size did not differ significantly between the sexes until well into the second year of growth. Females of *P. proteus* grow to almost twice the size of males, probably because of both higher ingestion rates and greater efficiencies. Sexual dimorphism in size is a feature of many other insects (e.g., Butler 1982, Clifford et al. 1979, McDiffett 1970, Patterson and Vannote 1979, Poole 1981, Svensson 1977). Calow (1981) suggested that males optimize and females maximize their use of available food, which may be the case for *P. proteus*, since mature female nymphs fed more continuously and were not as selective among different food types as mature male nymphs under laboratory conditions.

Mean efficiencies for *P. proteus* fell within the ranges reported for other species of *Pteronarcys* (McDiffett 1970, Poole 1981). In general, efficiencies for *P. proteus* were lower than means reported for detritivores by Slansky and Scriber

TABLE 4. Instantaneous daily growth rates (IDGR) of nymphs collected from Little Stony Creek. Temperature is the mean daily water temperature (°C) during the sample interval. The annual value represents IDGR calculated from one year's growth.

	Annual	Minimum (Interval/Temp.)	Maximum (Interval/Temp.)
Cohort 1	0.0106	0.0039 (Mar.-Apr./4.4°)	0.0180 (May-Jun./16.0°)
Cohort 2			
Male	0.0049	0.0060 (Aug.-Sep./19.7°)	0.0076 (Nov.-Dec./6.5°)
Female	0.0057	0.0022 (Aug.-Sep./19.7°)	0.0074 (Dec.-Feb./2.4°)
Cohort 3			
Male	0.0019	0.0013 (Aug.-Sep./19.7°)	0.0089 (Nov.-Dec./6.5°)
Female	0.0032	-0.0018 (Aug.-Sep./19.7°)	0.0143 (Nov.-Dec./6.5°)

(1982). Lower AE and GGE may be a result of ecological factors, such as low quality food and allelochemicals. Lower NGE in *P. proteus* appears to be related to the intrinsic ability of this species to convert assimilated food into biomass.

#### Growth rates of the field population

Dry weight data for each cohort/sex in Little Stony Creek were used to calculate instantaneous daily growth rate (IDGR):

$$\text{IDGR} = G/\text{days in interval.}$$

IDGR varied from 0.018 (Cohort 1) to no detectable growth, or even to a negative IDGR in Cohort 3 during late summer (Table 4). Another reduction of mean nymphal size was observed during fasting and metamorphosis of pre-emergent nymphs in late spring; IDGR during this interval was not used in our analyses. In general, growth rates were low or similar to those from studies from other aquatic insects (Slansky and Scriber 1982).

Mean daily temperature and IDGR were not significantly correlated ( $p < 0.05$ ) nor were IDGR and summed (accumulated) degree-days for the population as a whole. Also, IDGR and temperature were not significantly correlated within individual cohorts/sexes, except for Cohort 1, for which there was a significant relationship ( $p < 0.05$ ). The laboratory studies with *P. proteus* demonstrated that, when nymphs were given

ample food, growth rates increased in a predictable manner with temperature. The growth/temperature relationship was observed only for Cohort 1 in the stream population, indicating that some other factor influenced growth rates of Cohorts 2 and 3. Temperature in Little Stony Creek began to increase in March (Fig. 3) at a time when benthic particulate organic matter (POM) was near its annual minimum (Fig. 4). The lack of growth response to temperature by larger nymphs may be due to food limitation.

A computer model was used to simulate growth of *P. proteus* in Little Stony Creek to further examine the influence of food supply on growth rates. We used the relationship between growth and water temperature (as influenced by nymphal weight and cohort) obtained from the laboratory energetics measurements. Initial weights for each cohort were mean dry weights of nymphs measured in June. Since laboratory growth was measured with unlimited food available, these simulations provide a "potential" growth response by *P. proteus* in Little Stony Creek. Results of the simulations support the conclusion that growth of Cohorts 2 and 3 was food limited (Fig. 5). Simulated nymphal sizes for Cohort 1 (Year 1, Fig. 5) were not much different from measured sizes for most of the study period. However, simulated sizes exceeded measured sizes early in the study period for both sexes of Cohorts 2 and 3. Although mean temperatures were highest in August and September (Fig. 3), field-measured IDGR for Co-

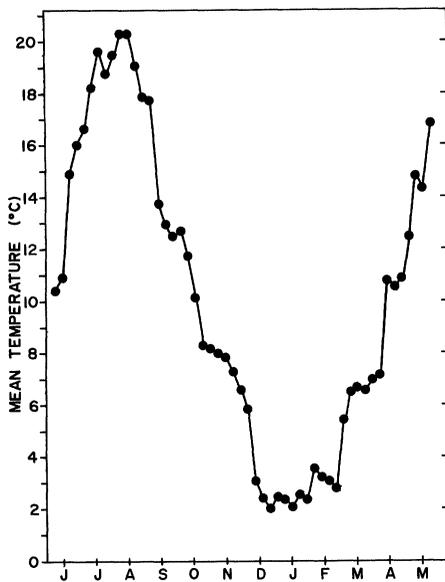


FIG. 3. Mean weekly water temperature in Little Stony Creek.

horts 2 and 3 were lowest for that period (Table 4). The highest IDGR for Cohorts 2 and 3 occurred after leaf-fall when temperatures were low and large-particle benthic POM was more abundant. The highest rates of growth for smaller nymphs (Cohorts 1 and 2-male), however, were measured in May and June, when stream temperatures were rising and coarse particulate organic matter (CPOM) was not abundant (Fig. 4). Growth of large nymphs appeared to be related to the seasonal availability of CPOM. It is reasonable to conclude that smaller nymphs use the more constant supply of FPOM and thus their growth is more influenced by thermal regime.

#### Secondary production

Mean annual standing stock, or biomass, for the population was  $2.8 \text{ g/m}^2$ , most of which was represented by Cohort 3 (Table 5). Annual production was estimated to be  $7.8 \text{ g/m}^2$ , of which 53.7% was contributed by Cohort 3 and 40.6% by Cohort 2. Production and biomass were much higher than those in other studies of aquatic detritivores (Table 5) except for the higher values for *P. californica* in the Provo River, Utah (Poole 1981). Although the estimated production for *P. proteus* appears high compared to

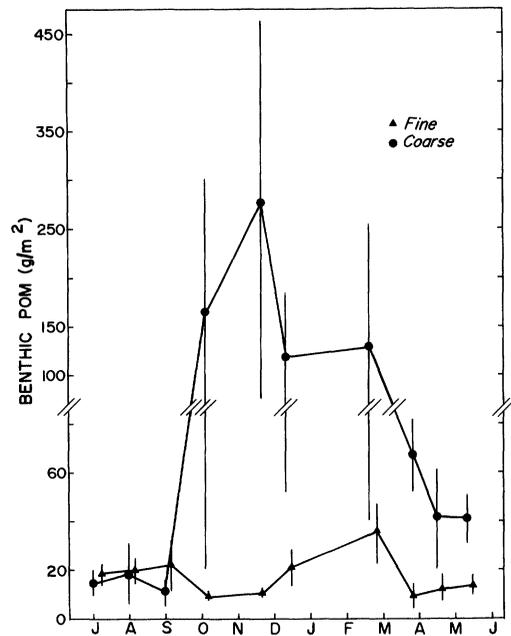


FIG. 4. Standing stock (AFDW) of benthic particulate organic matter (POM) in the study area in Little Stony Creek. Coarse particulates represent the mean  $\text{g/m}^2$  of POM  $> 1 \text{ cm}$ , excluding wood,  $\pm 1 \text{ SD}$ . Fine particulates represent the mean  $\text{g/m}^2$  of POM  $< 1 \text{ cm}$ ,  $\pm 1 \text{ SD}$ .

other stream shredders (Table 5), it is not particularly high compared with production reported for non-shredding detritivores in other habitats. These exceed  $25 \text{ g/m}^2$  for Trichoptera (Benke et al. 1984, Cudney and Wallace 1980) and Diptera (Benke et al. 1984, Mackey 1977).

High annual production suggests that *P. proteus* is well-adapted for using vascular plant detritus within the food and temperature regimes found in Little Stony Creek. *Pteronarcys proteus* does not appear to differ significantly from other shredders in terms of energetic efficiencies or growth rates, and it relies primarily on leaf detritus for nutrition (Perry 1985). The large size it attains is exceptional, and size may confer advantage in the ability to exploit allochthonous inputs to the stream. Larger size may permit greater mobility, thus better foraging success in a lotic habitat characterized by a spatially and temporally patchy food supply. Once food is located, large size may facilitate shredding of leaf detritus, permitting *P. proteus* to both consume at higher rates than smaller co-existing

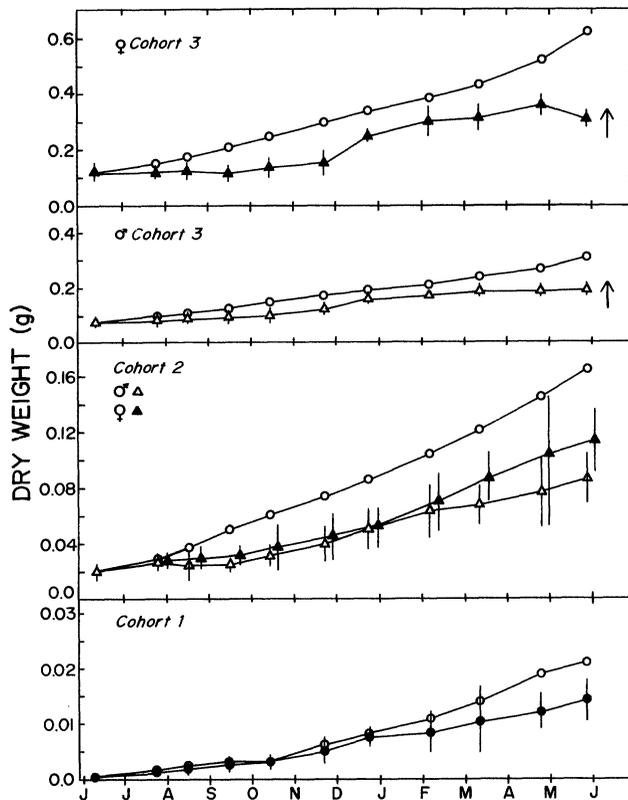


FIG. 5. Measured growth vs. calculated growth for each cohort/sex in Little Stony Creek. Open circles represent results of simulation of growth of *P. proteus* from laboratory data. Error bars represent  $\pm 1$  SD, and arrows indicate emergence of *P. proteus* adults.

shredders and to use harder (or less conditioned) leaf species as food. In Little Stony Creek, *P. proteus* dominates the shredder guild, followed by *Peltoperla maria*. Other shredder species that are relatively common include *Tipula* sp. and *Pycnopsyche* sp.

#### Population energy flow

Population energy flow was estimated by calculating respiration and ingestion for an "average" nymph in each cohort for the 12 sample intervals during the study. Field measurements of population density, nymphal size, stream temperature, and growth for each cohort obtained from the field study were then used to calculate population ingestion and respiration for each interval. Respiration was calculated using the relationships between temperature and nymphal size measured in the laboratory (Fig.

1). Ingestion was calculated in a similar manner based on temperature and nymphal size. Since the relationships between ingestion rate, nymphal size, and stream temperature were measured under unlimited food conditions in the lab, ingestion calculated in this manner was considered "potential" ingestion. An estimate of "actual" ingestion by stream insects was back-calculated by using our estimates of assimilation efficiency (Table 3) based on laboratory data, growth calculated from field data, and respiration based on laboratory respiration equations (Fig. 1). Egestion (E) was then calculated as the difference between ingestion (I) and assimilation.

Daily estimates of I, R, G, and E were summed for a sample interval and converted to population values using mean nymphal densities (Fig. 6). The interval values were then summed for annual estimates (Table 6). On a population ba-

TABLE 5. Comparison of secondary production rates of *P. proteus* and other leaf-shredding aquatic insects.

	Cohort	Annual Production (g/m <sup>2</sup> )	Biomass (g/m <sup>2</sup> )	Annual P/B	Stream
<b>Plecoptera</b>					
<i>Pteronarcys proteus</i>	1	0.438	0.160	2.73	Little Stony Creek Virginia, USA (This study)
	2	3.158	0.944	3.35	
	3	<u>4.182</u>	<u>1.697</u>	2.46	
		7.776	2.801	2.78	
<i>Pteronarcys californica</i>	1	—	0.130	—	Warm River Idaho, USA (Poole 1981)
	2	—	1.457	—	
	3	—	<u>2.720</u>	—	
		11.97 <sup>a</sup>	4.307		
	1	—	0.011	—	Provo River Utah, USA (Poole 1981)
	2	—	2.95	—	
	3	—	<u>5.33</u>	—	
	23.05 <sup>a</sup>	8.29			
<i>Peltoperla maria</i> <sup>b</sup>		0.528 <sup>c</sup>	0.138	3.83	Sawmill Branch Grady Branch North Carolina, USA (O'Hop et al. 1984)
		0.471 <sup>c</sup>	0.113	4.17	
<b>Trichoptera</b>					
<i>Sericostoma personatum</i>	1	0.036	0.006	5.64	Rold Kilde, Denmark (Iversen 1980)
	2	0.342	0.080	4.28	
	3	<u>0.549</u>	<u>0.294</u>	1.87	
		0.927	0.380	2.44	
	1	0.009	0.0012	—	Fonstrup Baek, Denmark (Iversen 1980)
	2	0.480	0.095	5.05	
	3	<u>0.449</u>	<u>0.148</u>	3.03	
	0.938	0.244	3.84		
<i>Lepidostoma cascaden</i> <sup>b</sup>		0.310	0.084	3.70	Mack Creek Oregon, USA
<i>L. unicolor</i>		0.230	0.024	9.60	(Grafius and Anderson 1980)

<sup>a</sup> Calculated using P/B ratio of *P. proteus*.

<sup>b</sup> All cohorts or instars.

<sup>c</sup> Mean of four estimates.

sis, ingestion was estimated to be 906 kcal m<sup>-2</sup> yr<sup>-1</sup> for *P. proteus* in Little Stony Creek, of which 41 kcal m<sup>-2</sup> yr<sup>-1</sup> (4.5%) was used for growth and 78 kcal m<sup>-2</sup> yr<sup>-1</sup> (8.7%) for respiration (Table 6). Most of the energy transformation (G + R, or assimilation), 119 kcal m<sup>-1</sup> yr<sup>-1</sup>, was through the 2nd and 3rd cohorts (41 and 55%, respectively).

Population energetics in Table 6 are sensitive to field data (i.e., accuracy of population density and weight data) and estimates of assimilation efficiency, since I (and E) were calculated from AE. The difficulty with adequately sampling

small nymphs resulted in underestimating population density of Cohort 1 and biased the values in Figure 6, although this cohort accounts for only a small percentage of the total energy flow. Also, only one species of leaf (red maple) in one state of conditioning was used to determine the relationship between AE and temperature, while a variety of leaf species is present in Little Stony Creek. Assuming that softer leaf species would be consumed first because of preference behavior, ingestion at and shortly after leaf-fall is probably underestimated. Red maple leaves are not common in leaf packs after

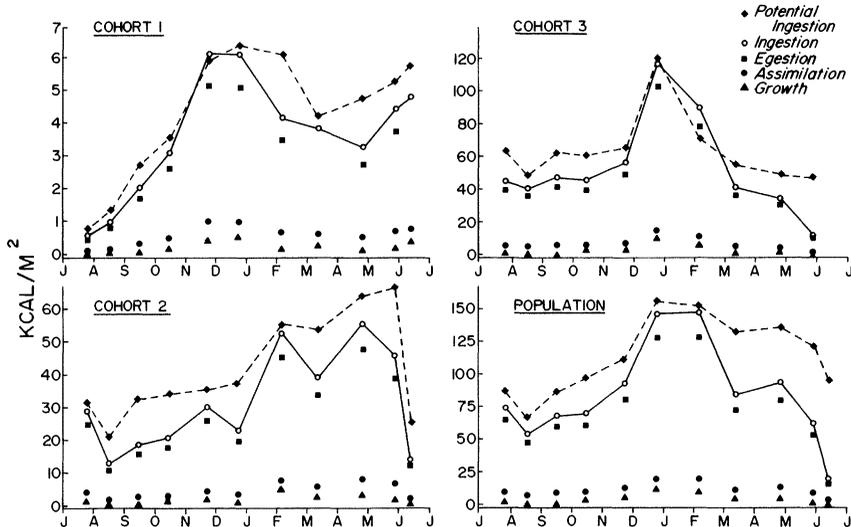


FIG. 6. Population energetics of *P. proteus* in Little Stony Creek during the study period. Assimilation is the sum of growth and respiration, while the difference between growth and assimilation in the figure represents respiration.

February when leaf species with slower rates of decomposition and processing (e.g., oak) predominate. Thus ingestion may be overestimated for the three sample periods after February, possibly mitigating prior underestimates of ingestion.

In contrast, our estimates for growth are conservative since they do not include exuviae. Respiration estimates are also probably conservative, since rates were measured with resting nymphs rather than with actively foraging nymphs. Thus assimilation, the sum of G and R, may be considered a conservative estimate.

TABLE 6. Annual population energetics (kcal/m<sup>2</sup>) for *P. proteus* in Little Stony Creek. Totals calculated for sexes include one-half Cohort 1 values.

Cohort	Ingestion	Growth	Respiration	Egestion
1	39.3	2.4	3.9	33.0
2-Female	183.1	9.5	16.1	157.4
3-Female	285.7	14.2	22.8	248.7
Total	488.4	25.0	40.9	422.5
2-Male	156.9	6.9	15.1	134.9
3-Male	240.9	7.6	20.3	212.9
Total	417.5	15.8	37.4	364.4
Total (both sexes)	906.0	40.7	78.3	827.6

Energy flow in populations depends on the complex interaction of several factors, important among which are temperature, population dynamics, and food availability. Energy flow in *P. proteus* in Little Stony Creek appears to be closely related to autumnal leaf-fall when peak ingestion and assimilation occur (Fig. 6). During that same time, the greatest proportion of assimilated energy is put into growth. Insect density and timing of life cycle events also influence population assimilation rates. Loss of Cohort 3 to emergence in May and June resulted in the lowest population assimilation rates for the study period (Fig. 6, Population). Limited availability of CPOM during spring (Fig. 4) may also reduce energy flow.

Energy assimilation (119 kcal m<sup>-2</sup> yr<sup>-1</sup>) by *P. proteus* in Little Stony Creek appears to be considerably higher than that measured in other shredder populations. For example, Otto (1975) estimated the assimilation of a caddisfly population as about 10 kcal m<sup>-2</sup> yr<sup>-1</sup>, and assimilation for a salt marsh grasshopper was 29.4 kcal m<sup>-2</sup> yr<sup>-1</sup> (Smalley 1960).

#### Leaf processing by *P. proteus*

In woodland streams where channel morphology promotes the physical retention of allochthonous inputs, shredders facilitate en-

TABLE 7. Comparison of insect leaf consumption in small streams. Percent ingested is the estimated percent of leaf input to the stream ingested by the shredder species.

Species	Annual Ingestion (g/m <sup>2</sup> )	Annual Leaf Input (g/m <sup>2</sup> )	Percent Ingested	Study Stream
<i>Pteronarcys proteus</i>	182	248–391	47–73	Little Stony Creek Virginia, USA (This study)
<i>Peltoperla maria</i>	14 <sup>a</sup>	286 <sup>b</sup>	5	Sawmill Branch
	12 <sup>a</sup>	353 <sup>b</sup>	3	Grady Branch North Carolina, USA (O'Hop et al. 1984)
<i>Zelandopsycha ingens</i>	54–109	330	15–31	Middle Bush Stream New Zealand (Winterbourn and Davis 1976)
<i>Sericostoma personatum</i>	49	300–690	7–16	Fonstrup Baek, Denmark
	50	500–700	7–10	Rold Kilde, Denmark (Iversen 1980)

<sup>a</sup> Calculated from egestion estimate, using assimilation efficiency = 20%.

<sup>b</sup> From Webster and Patten (1979).

tainment and export of particles through comminution of CPOM to FPOM (e.g., Wallace et al. 1982). The portion of annual leaf input processed by *P. proteus* in Little Stony Creek was approximated using estimates of litter input and shredder ingestion rates. Leaf input was estimated by the litterfall model of Gasith and Hasler (1976) as modified for use with streams in forested watersheds by Webster et al. (1979). Values for litterfall in eastern deciduous forests of the U.S. range from 320 to 504 g m<sup>-2</sup> yr<sup>-1</sup> (Cromack and Monk 1975, Fisher and Likens 1973, Gosz et al. 1973, Hall 1972, Sharpe et al. 1980, Webster and Patten 1979). Using these ranges in the litterfall model, annual input to the study reach in Little Stony Creek may range from 248 to 391 g m<sup>-2</sup> yr<sup>-1</sup>, based on a stream width of 4.5 m. Ingestion of leaf detritus by *P. proteus* in the study reach was estimated as 182 g m<sup>-2</sup> yr<sup>-1</sup>, which accounts for 47 to 73% of annual leaf input. Compared with certain insect shredders in other streams, *P. proteus* processed a substantial portion of the annual litter input (Table 7). It may be expected that a species with a relatively low AE and high production must process large amounts of food. Although no data are available, it is reasonable to assume that very young nymphs, which rely more on FPOM, are secondary consumers in the processing of leaf detritus initiated by larger, mature nymphs.

Thus, *P. proteus*, as a population of several size classes coexisting throughout the year, is able to exploit a wider range of particulate sizes that constitute the detrital energy base.

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