

THE UTILIZATION OF LEAF LITTER BY STREAM DETRITIVORES¹

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Abstract. Investigations of large and fine particle feeding detritivores (shredders and collectors) fed on conditioned hickory leaves (*Carya glabra*) revealed density-dependent intra- and interspecific interactions. Shredder (*Tipula* and *Pycnopsyche*) growth rates ranged from 0.47 to 1.53% increase in body wt/day depending upon density, species combinations, and culture temperature. Collector (*Stenonema*) growth rate ranged from 0.13 to 1.80% body wt/day, being greatest at high densities, particularly in combination with shredders. Food consumption ranged from 15.7 to 33.2% body wt/day for shredders and 4.0 to 23.2% body wt/day for collectors. After non-shredder feeding losses are accounted for, estimated shredder standing crop required to account for processing of reported leaf litter inputs compare generally to measured shredder standing crop.

INTRODUCTION

A considerable body of data accumulated on streams (e.g. Cummins 1966 and Hynes 1970a, 1970b) indicates that most, if not all, running waters which have not been significantly altered by man are predominantly heterotrophic. That is, the maintenance of stream community structure and function is dependent upon the import of organic matter from autotrophically dominated terrestrial communities (Nelson and Scott 1962, Hynes 1963, Eglishaw 1964, Minshall 1967, Triska 1970, Fisher 1971, Hall 1971, Fisher and Likens 1972). Thus rivers and streams, like soil communities and the benthic compartments of lakes, oceans, and estuaries, are detritus based and dependent upon excess production available by export from other systems. Therefore, it is not surprising that the distribution of certain stream insects is closely correlated with components of forest biomes (Ross 1963).

Some of the mechanisms involved in the degradation of vascular plant tissue in lotic environments have been the subject of recent studies (Kaushik and Hynes 1968, 1971, Hynes and Kaushik 1969, Vanote 1970, Triska 1970, Fisher 1971, Fisher and Likens 1972), but the functional relationships among vascular plant tissue, dissolved organic matter, microbial organisms (fungi and bacteria), and animals have yet to be clearly defined. These general rela-

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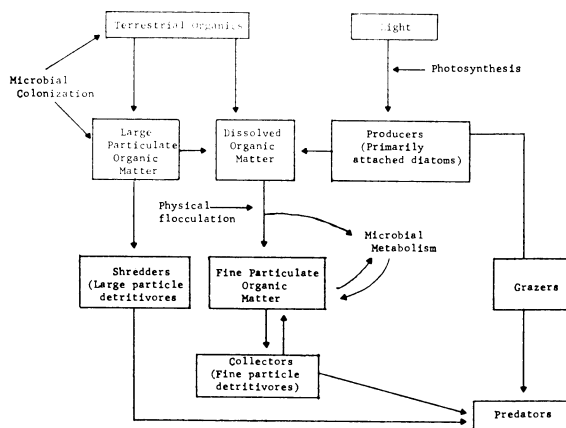


FIG. 1. A simplified compartmentalization of woodland stream ecosystem structure.

tionships are summarized in highly simplified form in Fig. 1. The present study was concerned with detritivore feeding, growth, and survivorship as influenced by amount of food and density-dependent intra- and interspecific interactions.

Although vascular hydrophytes are often important in nutrient cycling and alteration of the physical nature of streams, these plants seldom significantly enter the trophic structure while they are living. Therefore, the vascular hydrophytes also constitute an autotrophic compartment exporting production to the heterotrophic remainder of the system.

Increase in nitrogen content of leaves in stream water has been documented and the dominance of fungi over bacteria inferred from the presumed selective action of bactericides and fungicides (Kaushik and Hynes 1968, 1971, Hynes and Kaushik 1969, Triska 1970). Triska (1970) correlated leaf disappearance with aquatic hyphomycete abundance and measured changes over time in respiration of discs cut from leaf tissue, and in caloric content. Fisher (1971) and Fisher and Likens (1972) showed

that for Bear Brook, a small tributary of Hubbard Brook, particulate organic matter is largely processed in a given stream, while a large portion of the dissolved organic is apparently exported. Considerable work has been completed on the large particle detritivores, or "shredders" (Fig. 1), which feed predominantly on leaf litter that falls or is blown or washed into streams. The species studied, *Tipula abdominalis* (Vannote 1970), *Peltoperla maria* (Wallace et al. 1970), *Pteronarcys scotti* (McDiffett 1970), *Pycnopsyche scabripennis* (Triska 1970), and *P. scabripennis*, *P. gentilis* and *P. luculenta* (Mackay 1972), all show preferences for certain leaf types. These preferences are undoubtedly directly or indirectly mediated through the microbial flora of the leaves. That is, the shredders, through mechanical and/or chemical stimuli, select leaves that are maximally colonized by fungi and bacteria. Observations in our laboratory and by others (e.g. Triska 1970)

indicate that generally the same microorganisms attack all species of vascular plant tissue entering the stream. The differences in rates of leaf processing are due to differing lengths of time required to initiate and complete the microbial-animal successional pattern on various leaf species.

The fate of the fine particles produced in profusion as a result of shredder feeding—feces and leaf fragments broken loose in the feeding process—has yet to be studied in detail. Undoubtedly these particles are rich substrates for microbial populations and constitute a high quality food source for a large number of fine particle feeding detritivores or "collectors" (Fig. 1).

METHODS

The methods, summarized in Fig. 2, involved measurements of changes in organic content (particulate and dissolved) and animal growth and mortality in

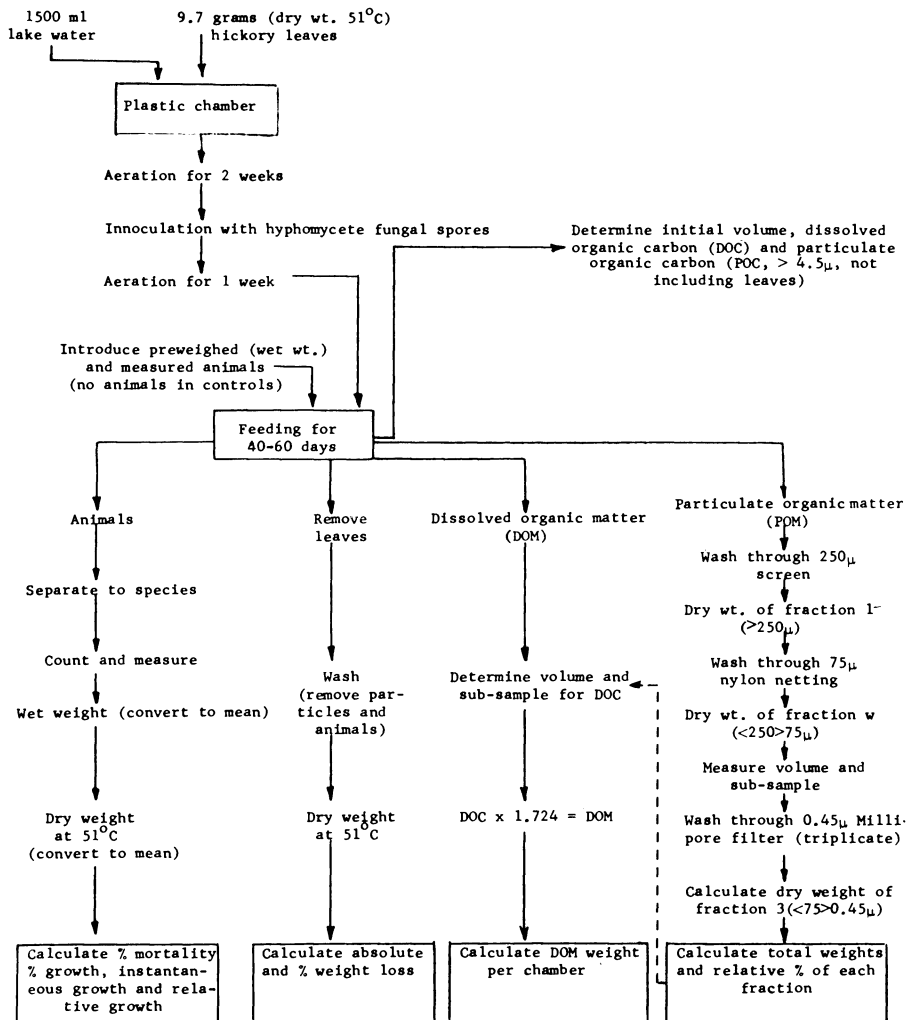


FIG. 2. Design of large (shredder) and small (collector) particle feeding detritivore growth and consumption experiments.

TABLE 1. Replication, densities, and combinations of animals used in the growth experiments

Number of chambers	Total number of individuals per chamber	Duration of experiment (days)	Number of individuals per chamber					
			<i>Stenonema</i>	<i>Tipula</i>	<i>Pycnopsyche lepida</i>	<i>P. scabripennis</i>	<i>P. guttifer</i>	<i>Pteronarcys</i>
3	Control	110	0	0	0	0	0	0
3	10	57	10	0	0	0	0	0
3	30	86	30	0	0	0	0	0
3	10	105	0	10	0	0	0	0
3	30	51	0	30	0	0	0	0
2	10	110	0	0	10	0	0	0
3	30	64	0	0	30	0	0	0
2	10	102	0	0	0	0	10	0
1	10	98	0	0	0	10	0	0
3	10	73	0	0	0	0	0	10
3	20	110	10	10	0	0	0	0
3	60	60	30	30	0	0	0	0
3	20	95	0	10	10	0	0	0
2	40	75	10	0	0	0	30	0
3	30	86	10	10	10	0	0	0
3 ¹	30	61	10	10	10	0	0	0

¹Elevated temperature, 17°C.

2-liter chambers (plastic blow-mold bottles with a portion of one side removed). The data were collected to allow the calculation of "biomass budgets," with respiratory loss obtained by difference, and the evaluation of the effect of various species combinations and densities on growth and survivorship.

Pignut hickory leaves (*Carya glabra*), picked from a single tree just prior to autumnal abscission, constituted the food source in all experimental chambers except one set in which mats of the aquatic hyphomycete (Fungi Imperfecti) *Lunulospora curvula*, grown in sterile, malt extract liquid culture (Thornton 1963), were used. We placed these mats between layers of 1 mm mesh plastic screen to simulate the physical environment of leaf litter. Each growth chamber was filled with 1.5 liters of water from a large experimental stream (Cummins 1972; the stream had been originally filled, 3 months earlier, with Gull Lake water, a deep hardwater trout lake). After an initial period of leaf leaching and conditioning, each chamber was inoculated with organic foam from Augusta Creek, a small woodland, hardwater brown trout stream (Kalamazoo and Barry Counties, Michigan). Such organic foam, which collects in front of obstructions and in backwaters below riffles, is an excellent source of aquatic hyphomycete spores. Large amounts of foam, collected in plastic bags, condense to small amounts of fluid, rich in spores. We inoculated each chamber (except the *L. curvula* set) with 25 ml of such fluid. Percent leaf weight loss due to leaching during the initial period was determined independently. All but one set of aerated chambers were maintained in a large water bath at a mean temperature of 5°C under natural light cycles. Temperature fluctuations in the chambers during the experiments (periods of 57 to 110

days, January through May) were similar to those occurring in Augusta Creek over the same time interval (chambers = 0.1–20°C, August Cr. = 0.1–12°C). One set of three chambers was held in a controlled temperature box at 17°C under a 12 hr on–12 hr off light regime.

After inoculation, 7 days were allowed for spore germination, hyphal development, and bacterial growth (based on observations of colonization times from the field and laboratory), before animals collected from Augusta Creek were introduced into the chambers. Table 1 lists the replications, densities, and combinations employed. The following species were used: shredders—crane fly larvae [Diptera, Tipulidae, *Tipula abdominalis* (Say) and *T. caloptera* (Loew)], caddisfly larvae [Trichoptera, Limnephilidae, *Pycnopsyche lepida* (Hagen), *P. guttifer* (Walker), and *P. scabripennis* (Rambur)], and stonefly nymphs [Plecoptera, Pteronarcidae, *Pteronarcys pictetii* (Hagen)]; collectors—mayfly nymphs [Ephemeroptera, Heptageniidae, *Stenonema fuscum* (Clemens), *S. tripunctatum* (Banks), *S. interpunctatum* (Say), and *S. canadense* (Walker)].

All crane fly larvae were in the third and fourth instars and were grouped roughly according to total length. The animals to be placed in any one set of replicate chambers were sized by selecting an individual to which all the others were matched. This produced fairly uniform groups with the initial wet weight C.V. (coefficient of variation) ranging from 3 to 36%. Stonefly nymphs, in the terminal and penultimate instars, were sized according to head width. The caddisfly larvae *Pycnopsyche lepida* and *P. scabripennis* were in the terminal instar and *P. guttifer* in the terminal and penultimate instars as sized by head width. The mayfly nymphs were placcd

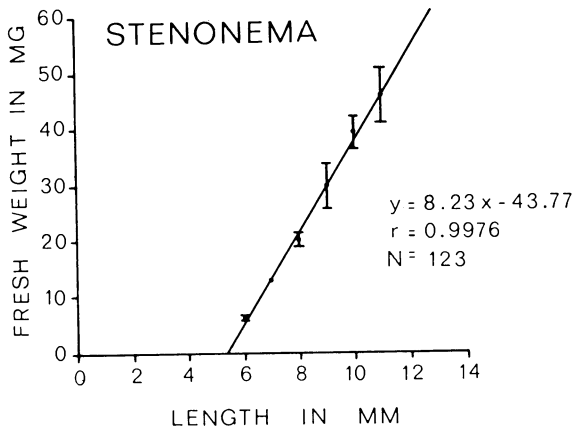


FIG. 3. Size (total length less cerci) wet weight relationship for *Stenonema* nymphs. Vertical bars are standard deviations; formulae for the regression and correlation coefficient are also shown.

TABLE 2. Determinations of % water from wet (blotted dry) and dry (51°C) weights for benthic stream invertebrates used in the growth chamber experiments

Animals Species	Number	\bar{x} % H ₂ O	S.D.	S.E.	C.V. (S.D. as % \bar{x})
<i>Stenonema</i>	155	79.87	3.51	0.28	4.4
<i>Tipula</i>	186	94.51	0.89	0.07	0.9
<i>Pycnopsyche lepida</i>	150	79.19	3.54	0.29	4.5
<i>P. guttifer</i>	18	86.60	1.30	0.31	1.5
<i>P. scabripennis</i>	12	81.22	2.37	0.68	2.9

in groups according to total length to the nearest mm (without caudal cerci); length-wet weight relationship is shown in Fig. 3. Initial and final animal wet weights were determined to the nearest mg after blotting; final dry weights (51°C) were measured to the nearest 0.1 mg and % water calculated (Table 2). Instantaneous growth rate was calculated as

$$G_i = \frac{\ln \bar{x} \text{ final individual dry wt} - \ln \bar{x} \text{ initial individual dry wt}}{\text{time interval.}}$$

Since growth rates obtained in this fashion were never significantly different ($P < .01$) from the calculation of relative growth rates (Waldbauer 1968) as

$$GR = \frac{\left(\frac{\bar{x} \text{ final individual dry wt} - \bar{x} \text{ initial individual dry wt}}{\text{time interval}} \right)}{\text{median individual dry weight over time interval}}$$

the latter has been reported throughout.

Initial and final dry weights (51°C) of leaves were determined to the nearest mg, and dissolved organic matter (as carbon) was measured by Dr. R. G. Wetzel (Kellogg Biological Station) according to procedures described by Menzel and Vaccaro (1964).

Ingestion was estimated from leaf weight loss and consumption indices (CI), and efficiencies of con-

version of food to growth (ECI) were calculated after Waldbauer (1968) as follows:

$$CI = \frac{\text{mg dry wt food ingested over period}}{\text{median dry wt of animals over period} \times \text{days}} = \text{mg ingested/mg animal/day;}$$

$$ECI = \frac{GR}{CI} .$$

RESULTS AND DISCUSSION

Growth rates and survivorship for the shredders (*Tipula* and *Pycnopsyche*) and collectors (*Stenonema*) are summarized in Tables 3-5 according to density and species combinations. As shown in Table 3, *Tipula* growth rate was fairly constant over the range of densities and species combinations investigated and at the elevated temperature (17°C). An increase of approximately 1% of body weight per day (0.7%-1.5%) or relative growth rates averaging 0.007 mg/mg/day (.006-.009) were observed (Table 3). Density-dependent growth is indicated, being greater at lower densities, including cases of low density because of reduced survivorship during the experiment. *Tipula* survivorship was higher when larvae were raised in combination with other shredders and lower when grown alone or together with *Stenonema*.

Leaf weight loss in chambers with *Tipula*, always greater than 50%, was maximum at the elevated temperature in chambers with *Pycnopsyche* and *Stenonema* (Table 6). In this elevated temperature experiment, *Tipula* at low density (10/chamber) showed good survivorship (70%) and maximum relative growth (.009 mg/mg/day).

Although *Pycnopsyche lepida* and *P. scabripennis* fed when held separately, resulting in leaf weight losses from 41% to 50% (Table 6), they all lost weight (Table 4). Either the food quality was not sufficient (*P. lepida* has been shown to switch from detrital to algal feeding in the last larval instar, Cummins 1964), or these individuals of that instar completed their feeding cycle and would normally have been burrowing into the sediments initiating the spring-summer period of inactivity characteristic of these species (e.g., *P. lepida*, Cummins 1964). Thus, leaves were passed through the guts, but the larvae lost weight (-.0025 to -.0047 mg/mg/day) at an extremely consistent rate at all densities and species combinations tested. The rate was highest and the survivorship lowest (37%) at the elevated temperature (Table 4). *P. guttifer* larvae in penultimate and early terminal instar fed and grew. Although the differences were not significant ($P > .05$) because of variations between chambers, *P. guttifer* grew more at higher densities and in the presence of *Stenonema*.

In order to obtain enough mayfly nymphs (*Stenonema*) for the growth experiments we had to use

TABLE 3. Comparison of *Tipula* growth rates (mg dry wt) and survivorship at various densities and in combination with other species; all chambers started with 9.7 gms (dry weight) of hickory leaves. The means are for sets of 3 chambers. Mean temperature = 5°C

<i>Tipula</i> density	Other species	Other species density	<i>Tipula</i>			
			Total % growth increase ± S.D.	Growth %/day ± S.D.	Survivorship % ± S.D.	Relative growth (mg/mg/day) ± S.D.
10	—	—	116.8 ± 67.6	1.102 ± 0.638	66.7 ± 25.2	0.0066 ± 0.0024
30	—	—	38.8 ± 5.0	0.750 ± 0.109	56.6 ± 28.9	0.0064 ± 0.0006
10	<i>Stenonema</i>	10	168.6 ± 95.5	1.533 ± 0.868	43.3 ± 28.9	0.0079 ± 0.0024
30	<i>Stenonema</i>	30	39.0 ± 5.6	0.661 ± 0.094	56.7 ± 29.7	0.0055 ± 0.0006
10 ¹	<i>Stenonema</i> + <i>Pycnopsyche lepida</i>	10	75.7 ± 40.0	1.304 ± 0.690	70.0 ± 17.3	0.0091 ± 0.0039
10 ²	<i>Stenonema</i> + <i>Pycnopsyche lepida</i>	10	85.5 ± 51.0	1.018 ± 0.607	— ³	0.0068 ± 0.0028
10	<i>Pycnopsyche lepida</i> <i>Pycnopsyche lepida</i>	10	81.9 ± 20.2	0.862 ± 0.213	73.3 ± 15.28	0.0061 ± 0.0011

¹Elevated temperature of 17°C.

²Two chambers.

³Several animals lost

TABLE 4. Comparison of *Pycnopsyche* growth rates (mg dry wt) and survivorship at various densities and in combination with other species; all chambers started with 9.7 gms (dry weight) of hickory leaves. The means are for sets of 3 chambers. Mean temperature = 5°C

<i>Pycnopsyche</i>		Other species	Other species density	<i>Pycnopsyche</i>			
Species	Density			Total % growth change ± S.D.	%/day ± S.D.	Survivorship % ± S.D.	Relative growth (mg/mg/day) ± S.D.
<i>P. lepida</i> ¹	10	—	—	-24.2 ± 0.4	-0.22 ± <0.01	65.0 ± 7.1	-0.0025 ± <0.0001
<i>P. lepida</i>	30	—	—	-22.3 ± 3.9	-0.35 ± 0.06	64.5 ± 13.5	-0.0040 ± 0.0007
<i>P. lepida</i>	10	<i>Stenonema</i>	10	-19.9 ± 3.5	-0.33 ± 0.06	66.7 ± 11.5	-0.0037 ± 0.0007
<i>P. lepida</i>	10	<i>Tipula</i>	10	-25.0 ± 5.2	-0.26 ± 0.06	76.7 ± 20.8	-0.0031 ± 0.0008
<i>P. lepida</i> ²	10	<i>Stenonema</i> + <i>Tipula</i>	10	-25.1 ± 5.8	-0.40 ± 0.09	36.7 ± 20.8	-0.0047 ± 0.0012
<i>P. lepida</i>	10	<i>Stenonema</i> + <i>Tipula</i>	10	-27.8 ± 5.7	-0.33 ± 0.07	63.3 ± 20.8	-0.0039 ± 0.0010
<i>P. guttifer</i> ¹	10	—	—	47.6 ± 1.1	0.47 ± 0.01	30.0 ± 0.0	0.0076 ± 0.0010
<i>P. guttifer</i> ¹	30	<i>Stenonema</i>	10	61.1 ± 30.1	0.84 ± 0.41	28.3 ± 7.07	0.0063 ± 0.0024
<i>P. scabripennis</i> ³	10	—	—	-34.4 ± —	-0.351 ± —	60.0 ± —	-0.0043 —

¹Two chambers.

²Elevated temperature of 17°C.

³One chamber.

sizes ranging from 6 to 11 mm, although only a single mm size class was used in any given chamber. Smaller nymphs would be expected to have faster relative growth rates, but weight increase was more decisively affected by food supply and density than by initial size (Table 5). The only set of chambers in which *Stenonema* lost weight contained hyphomycete fungal hyphae and no leaves. Survivorship was high, and cast skins and feces were recovered from the chambers at the end of the experiment. Although the hyphomycetes may have constituted a nutritionally inadequate food supply, mechanical problems associated with nymphal feeding on hyphal mats between layers of plastic screen may well have been responsible for the lack of growth.

Variance in estimates of *Stenonema* survivorship was high, but the trend was toward reduced mortality at low densities and in the absence of shredders; the least interaction was with *Tipula* (Table

5). Although growth was enhanced by increased *Stenonema* density alone (0.1%/day at 10/chamber and 0.5%/day at 30/chamber), the best growth was at low *Stenonema* and high shredder density. Leaf weight loss in chambers containing only *Stenonema* was less than 25% and not significantly different from the controls (Table 6). This suggests that *Stenonema* feeding was on the leaf surfaces, on fine particles, physically and microbially produced from DOM, and on the nymphs' own feces, rather than on the leaf tissue and microbes growing in the leaf matrix. This negligible effect of the mayflies on the leaf substrate indicates that the leaf weight loss (less controls) which occurred in chambers with both collectors and shredders can be attributed primarily to the feeding of shredders.

As shown in Table 6, in all but the control and low-density *Stenonema* chambers the percent DOM was significantly reduced. DOM was greater in the

TABLE 5. Comparison of *Stenonema* growth rates (mg dry wt) and survivorship at various densities and in combination with shredder species; all chambers started with 9.7 gms (dry weight) of hickory leaves. The means are for sets of 3 chambers. Mean temperature = 5°C

<i>Stenonema</i> density	Shredder species	Shredder density	<i>Stenonema</i>					
			size class(es) in mm		Total % growth increase ± S.D.	Growth %/day ± S.D.	Survivorship % ± S.D.	Relative growth ± S.D. mg/mg/day
			initial	final				
10 ¹	---	---	6.0	---	-11.0 ± 9.4	-0.225 ± 0.194	76.6 ± 15.3	-0.0025 ± 0.0022
10	---	---	8.0-9.0	---	7.1 ± 1.9	0.125 ± 0.033	70.0 ± 26.5	0.0012 ± 0.0003
30	---	---	9.0-11.0	9.5-14.0	43.3 ± 13.0	0.503 ± 0.151	35.5 ± 15.7	0.0041 ± 0.0010
10	<i>Tipula</i>	10	9.0-11.0	10.0-14.0	22.7 ± 21.0	0.208 ± 0.193	50.0 ± 26.5	0.0018 ± 0.0015
30 ²	<i>Tipula</i>	30	8.0	8.0-10.0	24.2 ± 9.5	0.403 ± 0.158	58.3 ± 21.2	0.0036 ± 0.0012
10	<i>Pycnopsyche lepida</i>	10	7.0	8.0-9.0	22.3 ± 6.6	0.366 ± 0.108	40.0 ± 20.0	0.0033 ± 0.0009
10 ²	<i>Pycnopsyche guttifer</i>	30	6.0-8.0	7.5-11.5	74.1 ± 4.8	0.938 ± 0.061	40.0 ± 14.1	0.0068 ± 0.0003
10	<i>Tipula</i> + <i>Pycnopsyche lepida</i>	10	6.0	6.5-9.5	120.7 ± 7.1	1.802 ± 0.474	36.7 ± 11.5	0.0083 ± 0.0004

¹Raised on pure hyphomycetes (*Lunulospora curvula*) without leaves (fungi layered on fiberglass screening).

²Based on two chambers only.

TABLE 6. Comparison of amounts of particulate (in three size categories) and dissolved organic matter produced in control and animal growth chambers. All chambers in triplicate at a mean temperature of 5°C unless otherwise indicated

Species	Total number of individuals per chamber	% dry weight loss ± S.D. of leaves	% dry weight ± S.D. of the total organic matter (except leaves) in each of the three particulate (POM) and the dissolved (DOM) organic matter categories			
			POM > 250µ	POM < 250µ > 75µ	POM < 75µ > .45µ	DOM (< .45µ)
Controls	0	26.1 ± 3.2	23.1 ± 6.3	14.6 ± 2.1	41.0 ± 2.8	21.3 ± 4.9
<i>Stenonema</i>	10	18.9 ± 0.6	31.1 ± 4.1	23.1	20.4	25.5
<i>Stenonema</i>	30	24.1 ± 6.7	30.0 ± 7.4	16.1 ± 10.1	28.9 ± 16.3	12.2 ± 4.3
<i>Tipula</i>	10	63.9 ± 14.4	74.1 ± 5.4	13.2 ± 2.8	8.8 ± 2.2	3.9 ± 0.4
<i>Tipula</i>	30	68.6 ± 7.9	(combined) 87.0 ± 4.9		7.5 ± 4.1	5.5 ± 1.1
<i>Pycnopsyche lepida</i> ¹	10	40.9 ± 2.6	51.2 ± 15.3	26.3 ± 2.7	19.4 ± 18.6	5.8 ± 3.4
<i>P. lepida</i>	30	58.1 ± 12.1	69.7 ± 13.4	16.9 ± 10.5	10.6 ± 9.3	2.9 ± 0.9
<i>P. guttifer</i> ¹	10	43.0 ± 2.3	63.0 ± 11.1	28.0 ± 8.5	4.5 ± 0.9	4.4 ± 1.8
<i>P. scabripennis</i> ²	10	53.6	75.5	21.4	<0.1	3.2
<i>Pteronarcys</i> ³	10	39.9 ± 3.2	23.6 ± 12.4	10.9 ± 7.9	58.4 ± 7.8	7.1 ± 1.2
<i>Tipula</i> and <i>Stenonema</i>	20	49.8 ± 12.1	71.0 ± 3.3	11.5 ± 5.7	14.4 ± 5.7	3.2 ± 2.2
<i>Tipula</i> and <i>Stenonema</i>	60	67.3 ± 9.2	70.6 ± 8.9	8.3 ± 4.9	18.7 ± 8.1	2.4 ± 0.3
<i>Tipula</i> and <i>P. Lepida</i> ¹	20	69.4 ± 3.9	75.0 ± 4.7	11.7 ± 0.6	11.0 ± 4.0	2.4 ± 0.2
<i>P. guttifer</i> and <i>Stenonema</i> ¹	40	51.7 ± 12.9	67.8 ± 3.5	20.3 ± 2.6	8.7 ± 1.3	3.1 ± 1.3
<i>Tipula, P. lepida</i> and <i>Stenonema</i>	30	56.7 ± 7.4	69.3 ± 5.1	23.4 ± 3.2	3.8 ± 3.5	3.4 ± 0.6
<i>Tipula, P. lepida</i> and <i>Stenonema</i> ⁴	30	85.6 ± 2.1	57.8 ± 13.9	10.6 ± 5.8	29.9 ± 20.1	1.8 ± 0.6

¹Two chambers only.

²One chamber only.

³All animals dead after 7 days.

⁴Elevated temperature, 17°C.

high-density *Stenonema* and the *Pteronarcys* chambers than in the remaining growth experiments involving shredders and collectors. All *Pteronarcys* had died within 7 days after initiation of the experiment so the results resemble in many respects those obtained for the controls and *Stenonema* chambers. For example, only in these chambers was the conversion to, and accumulation of, particles > 250 µ 30% or less; in all other chambers the percentage, which ranged from 51% to 76%, consisted primarily of shredder feces. The striking impact of *Pteronarcys* in just 7 days is indicated by extensive leaf weight loss and the heavy accumulation of feces (large particles, > 250 µ). The intermediate particle size (75 µ-

250 µ) represents a combination of broken shredder feces, collector feces, leaf fragments, particles physically aggregated from DOM and fine particles, and microbes. The origin of these intermediate-sized particles from DOM is indicated by the lack of significant differences in % dry weight between the control and animal chambers (Table 6). The only fecal material included in the fine particle category (.45 µ-75 µ) would be highly fragmented, with this size fraction undoubtedly being dominated by bacteria. The accumulation of fine particles in the *Pteronarcys*' chambers (58.4% dry wt, Table 6) probably represented microbial growth associated with nymph mortality. The high percentage of fine particles in the

elevated temperature experiment (29.9% dry wt, Table 6) also probably reflects increased microbial growth. An average of 20% of the initial biomass (leaf plus animal plus microbes) was respired during the experiments, approximately half due to microbial

(controls) and half to insect metabolism (average shredder chambers minus controls; Table 7).

As shown above, the overall activity in the chambers was the conversion of leaf substrate to DOM (leaching), animal biomass, smaller particles (in-

TABLE 7. Mass balance sheets for chamber growth experiments, based on the relationship: Initial leaf weight (after leaching) + Initial DOM + Initial animal weight = Final animal weight + Final leaf weight + Final POM + Final DOM + R where R, obtained by difference, is animal plus microbial respiration. Leachate is not included in the initial DOM which was 0.002 g. Initial and final animal, leaf and POM are dry weights at 51°C. DOM was calculated from DOC as shown in Fig. 1. All values are means of three chambers, followed by coefficients of variation, at 5°C unless otherwise indicated

Species	Densities	Initial wts (g)			Final wts (g)					Respiration as a % of total initial wt. (animal+leaf +DOM)				
		DOM +leaf	Animal	Animal	Leaf	POM	DOM	Respiration						
Control	0		—	—	7.167	4.3	0.398	9.9	0.109	20.5	1.240	23.9	13.9	
<i>Stenonema</i>	10		0.058	0.042	7.867		0.278		0.095	33.2 ¹	0.734		8.2	
<i>Stenonema</i>	30		0.216	26.8	0.113	53.8	7.367	8.8	0.728	35.0	0.095	33.2 ¹	0.829	46.0
<i>Tipula</i>	10		0.196	27.3	0.258	33.3	3.500	40.0	3.338	27.8	0.135	21.2	1.882	23.5
<i>Tipula</i>	30		0.742	15.5	0.584	55.0	3.043	25.2	3.343	26.8	0.190	6.8	2.498	16.3
<i>Pycnopsyche lepida</i> ²	10		0.360	6.0	0.116	88.0	5.733	4.4	1.351	34.5	0.074	23.0	2.000	16.9
<i>P. lepida</i>	30		1.115	9.2	0.643	7.8	4.067	28.8	3.273	26.7	0.095	33.2 ¹	1.954	8.5
<i>P. guttifer</i> ²	10		0.077	17.0	0.024	90.8	5.500	4.8	1.764	25.5	0.078	12.5	1.627	17.3
<i>P. scabripennis</i> ³	10		0.535	—	0.181	—	4.500	—	2.601	—	0.088	—	2.081	—
<i>Tipula</i> + <i>Stenonema</i>	10		0.202	10.8	0.156	39.6	4.867	24.1	2.666	27.7	0.083	51.0	1.347	35.9
<i>Tipula</i> + <i>Stenonema</i>	30		1.028	36.0	0.675	37.3	3.177	28.0	3.874	13.4	0.095	33.2 ¹	2.124	30.8
<i>Tipula</i> + <i>P. lepida</i> ¹	10		0.567	5.6	0.517	32.2	3.050	16.2	3.821	6.4	0.095	33.2 ¹	2.000	5.8
<i>P. guttifer</i> + <i>Stenonema</i>	30		0.292	25.3	0.084	72.6	4.683	26.7	3.239	38.3	0.095	33.2 ¹	1.106	24.4
<i>Tipula</i> + <i>P. lepida</i> + <i>Stenonema</i>	10		0.565	2.8	0.236	12.7	4.200	17.2	2.686	16.2	0.095	33.2 ¹	2.265	14.1
<i>Tipula</i> + <i>P. lepida</i> + <i>Stenonema</i>	10		0.724	11.5	0.357	48.2	1.400	14.3	5.555	30.7	0.095	33.2 ¹	2.233	84.5

¹Mean of all chambers in which final DOM was measured.
²Two chambers only.

³One chamber only.
⁴Elevated temp, 17°C.

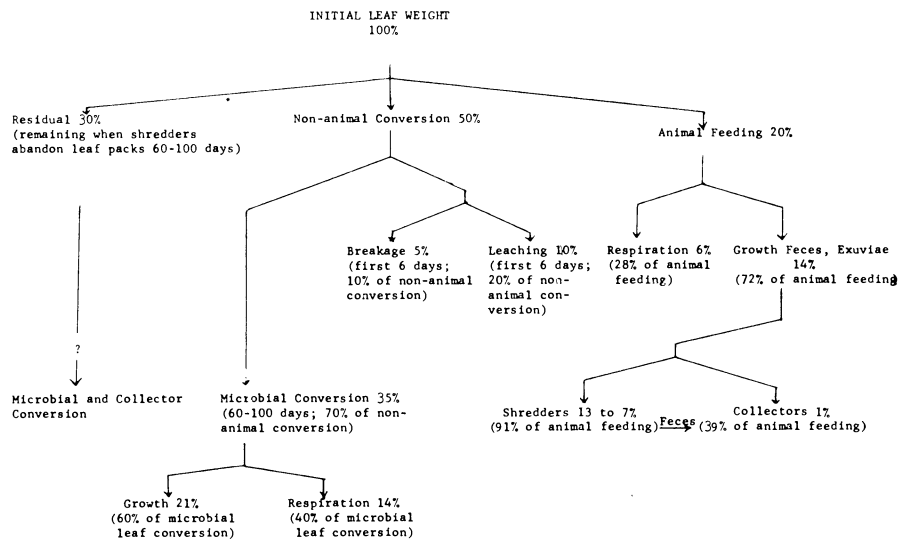


FIG. 4. Summary of relationships in leaf conversion to microbial (bacteria and fungi) and animal (shredder and collector) respiration and growth (see Table 9). Shredders = large particle feeding detritivores; collectors = fine particle feeding detritivores.

TABLE 8. Comparison of food consumption and efficiency of food conversion by *Tipula*, *Pycnopsyche* and *Stenonema* in the present study to selected literature values. (CI = consumption index = mg dry wt food ingested/mg dry wt of animal/day; ECI = efficiency of conversion of ingested food = Relative growth rate/CI; DF = density factor = median mg animals/median mg food in growth chambers over the period as a percent. CI and ECI after Waldbauer 1968)

Taxa	Food	Temp (°C)	CF	DI	ECI	Author
<i>Tipula</i>						
<i>T. spp.</i>	Conditioned hickory leaves	5	3.66 ¹	0.157	0.042	Present study
"	"	"	10.75 ¹	0.187	0.034	
"	"	11	2.45	0.088	0.565	Cummins, Petersen, Howard, Wuycheck, King, Holt, Unpubl. Vannote, 1970
"	Conditioned oak leaves	9	11.09	0.030	0.393	
"	Conditioned hickory leaves	10	3.98	0.187	0.028	
<i>T. abdominalis</i>	Conditioned leaves, mixed spp.	— ²	— ²	0.041	— ²	
<i>Pycnopsyche</i>						
<i>P. guttifer</i>	Conditioned hickory leaves	5	0.71 ¹	0.332	0.023	Present study
<i>P. gentilis</i>	Conditioned leaves, several spp.	— ²	— ²	0.585	—	
<i>P. luculenta</i>	"	"	"	0.536	"	Mackay, 1972
<i>P. gentilis</i>	Conditioned beech leaves	"	"	0.033	"	
<i>P. luculenta</i>	"	"	"	0.023	"	
<i>P. gentilis</i>	"Fungal culture" on maple leaves	"	"	1.300	"	
<i>P. luculenta</i>	"	"	"	0.728	"	
<i>P. gentilis</i>	"Bacterial culture" on maple leaves	"	"	0.739	"	
<i>P. luculenta</i>	"	"	"	0.136	"	
<i>P. gentilis</i>	"Sterile" maple leaves	"	"	0.030	"	
<i>P. luculenta</i>	"	"	"	0.006	"	
<i>Pteronarcys scotti</i>	Conditioned leaves, mixed spp.	10, 15	— ²	0.062	— ²	
<i>Stenonema</i>						
<i>S. spp.</i>	Conditioned hickory leaves	5	0.60 ¹	0.232	0.005	Present study
"	"	"	4.04 ¹	0.040	0.103	
"	Algae (culture of <i>Ankistrodesmus</i> spp.)	12	— ²	0.082	— ²	Petersen, unpubl.
"	Fungi (culture of <i>Lunulospora curvula</i>)	12	— ²	0.020	— ²	
<i>S. pulchellum</i>	Algae (culture of <i>Navicula minima</i>)	20	— ²	0.188 ³	0.118 ³	Trama, 1957
<i>Neophylax concinnus</i>	Algae and detritus (natural stream substrates)	4-5	— ²	1.200	— ²	Sedell, 1971
Mixed species						
<i>Tipula</i> spp. + <i>Stenonema</i> spp.	Conditioned hickory leaves	5	2.60 ¹	0.114	0.043 ³	Present study
<i>T. spp.</i> + <i>S. spp.</i>	"	"	14.09 ¹	0.106	0.043 ³	
<i>P. guttifer</i> + <i>Stenonema</i> spp.	"	"	2.77 ¹	0.235	0.028 ³	
"	"	"	"	"	"	

¹Initial weight of leaves after 24 hrs leaching

²necessary data not given

³median or mean value

cluding bacteria), and CO₂, with DOM being further converted to POM in the animal chambers. The shredders were quite efficient at converting leaf tissue to smaller particles, their own biomass, and respiration; greater than 50% conversion was a feature of all chambers containing *Tipula* and/or *Pycnopsyche*. The partitioning of the leaf conversion has been summarized in Fig. 4.

Ingestion and conversion of food by *Tipula*, *Pycnopsyche* and *Stenonema* determined in the present study are compared to selected data from the literature in Table 8. Since we estimated ingestion from leaf weight loss, the data are approximations subject to error caused by changes in leaf weight, other than animal ingestion, that occurred in the experimental but not the control chambers.

An overestimate of feeding would result from non-ingestion leaf weight loss due to leaf fragmentation and leaching (greater than controls) resulting from animal feeding and movements. Although McDiffett (1970) observed considerable leaf frag-

mentation by feeding *Pteronarcys*, this was not a significant factor in our experiments with *Tipula*, *Pycnopsyche*, and *Stenonema*. Also, Mackay (1972) found no such losses in her *Pycnopsyche* feeding studies. Similarities in final DOM concentrations (Table 7) and a large initial leaching weight loss (8%) suggest that additional leaching in the experimental chambers was not significant.

An underestimate of feeding would result from increases in leaf weight resulting from greater microbial growth in and on the leaves in the experimental chambers as compared to the controls or the ingestion of feces (coprophagy) by the animals. Although greater microbial development on leaves in the experimental chambers was not detected by microscopic examination, it is possible that grazing masked increased turnover of fungi and bacteria. *Pycnopsyche* and *Tipula* probably ingest fecal materials, but observations and gut analyses suggest that such feeding by shredders is minimal. *Stenonema* undoubtedly ingest feces, as indicated by increased

TABLE 9. Comparison of reported large particle detritus input, corrected for non-animal feeding losses, and calculated shredder feeding required to process it (using $CI = .21 = \text{mean of } Pycnopsyche \text{ guttifer} \text{ and } Tipula$) to a measure of shredder standing crop. Estimates of leaching, microbial utilization and residual after animal feeding from present study; mechanical breakage and fine particle (collectors) feeding from Cummins (1972) and unpublished field and experimental studies

Source of input (first 3 entries) and standing crop (last entry) data	Total input of large particle detritus (g/m ² /day)	Large particle detritus weight loss not due to animal feeding (g/m ² /day)			Residual detritus remaining after 84 days (g/m ² /day) -40.6%	Total animal processing -9% due to fine particle feeders (collectors) = processing by shredders (g/m ² /day)	Standing crop of shredders required (first 3 entries) or available (last entry) for processing input	
		Mechanical breakage -5%	Leaching -9.6%	Microbial utilization -17.7%			Numerical No/m ²	Biomass g/m ²
Murless (Univ. Georgia, pers. comm.)	4.20	3.99	3.59	2.84	1.13	1.03	175	4.90
Vannote 1970	3.00	2.85	2.56	2.03	0.81	0.74	126	3.52
Fisher 1971	1.70	1.61	1.45	1.15	0.46	0.42	71	2.00
Howard (Kellogg Biol. Sta., unpubl. data)	—	—	—	—	—	—	51	1.43

growth at high densities or in combination with other species, and the CI values in Table 8 must be considered minimal although they are in the range of other data reported for *Stenonema*. A considerable range of CI estimates are represented in Table 8, from .006 on inadequate food to 1.300 on apparently high quality food. An examination of the values indicates that food quality, for example leaf species and degree of conditioning, is critical in determining CI and related efficiencies.

Only *Tipula* and *P. guttifer* showed increased growth per individual as a function of overall leaf utilization. In the case of *Tipula*, elevated temperature maximized growth and leaf conversion (Tables 3, 4, and 6). Although *P. lepida* and *P. scabripennis* converted leaf tissue to particles, animal weight loss was quite consistent over a considerable range of leaf utilization, the amount being related primarily to animal mortality (Tables 4 and 6). *Stenonema* growth was not related directly to leaf weight loss but rather to animal density, the presence of shredders and, as discussed above, coprophagy (Tables 5 and 6).

Using the data for *Tipula*, the mean mg dry wt leaf conversion per individual per day was 3.5 and 4.1 for the sets of chambers containing initial larval densities of 10 and 30 respectively. This is equivalent to CI values of 0.157 and 0.187 mg dry wt leaf/mg dry wt *Tipula*/day (Table 8) and compares to 12.4 mg leaf/*Pteronarcys* individual/day or a CI of 0.062 from the data of McDiffett (1971). Table 9 shows calculated standing crops of shredders necessary to process levels of large particle detritus reported for several woodland streams, after non-shredder feeding losses have been accounted for. These are compared to an estimate of shredder standing crop from field samples taken in Augusta Creek. Close agreement is indicated between the calculated processing of the input reported by Fisher (1971) for Bear Brook and standing crop estimates (*Tipula* and *Pycnopsyche*) measured by Howard (un-

publ.) in Augusta Creek. If a shredder standing crop of 41/m², or 1.4 g/m² is expressed as a percent of the total numerical (17,354/m²) or biomass (34.6 g/m²) standing crop reported for a woodland stream by Coffman et al. (1971), the values are 0.3% and 4.0% respectively.

Despite smaller size, earlier life stages than those used in the present experiments may well have an even greater impact on large particle detritus conversion through higher densities and faster feeding rates. Clearly, the role of shredders (large particle detritivores) is an important influence on microbial and collector (fine particle detritivore) metabolism and growth.

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