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Title: THE CONVERSION OF ALLOCHTHONOUS MATERIAL
BY STREAM DETRITIVORES

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The role of detritivores in the conversion of allochthonous leaf material in two small streams in the Cascade Range of Oregon was studied. Their importance in relation to other consumers was estimated from emergence and benthic standing crop data.

Ingestion rates and efficiencies of utilization of bigleaf maple (Acer macrophyllum) and red alder (Alnus rubra) leaves by several species of stream detritivores, one species of stonefly and several species of caddisflies, were measured under field or laboratory conditions. Mean consumption rates varied from 0.04 mg/mg/day for Halesochila taylori larvae (Trichoptera:Limnephilidae) feeding on maple leaves to 0.60 mg/mg/day for Lepidostoma sp. larvae (Trichoptera:Lepidostomatidae) feeding on alder and maple leaves. Ecclisomyia sp. larvae (Trichoptera:Limnephilidae) consumed 0.10 mg/mg/day of maple leaves in the field. All consumption rates were calculated assuming constant feeding rates by the insects and constant rates of leaf decomposition without insects, but a model is discussed that allows non-linear feeding and leaf decomposition rates.

Efficiency of food utilization was measured either as assimilation efficiency, the ratio of assimilated food (ingestion minus egestion) to consumption; or as gross growth efficiency, the slope of the growth:consumption line calculated by linear regression analysis. Assimilation efficiencies ranged from 7.4% for Heteroplectron californicum larvae (Trichoptera:Calamoceratidae) fed on maple leaves to 12% for Lepidostoma sp. larvae fed on alder and maple leaves.

In order to assess the role of microbial communities in leaf utilization by Pteronarcys princeps (Plecoptera:Pteronarcidae), nymphs were fed untreated maple leaves and maple leaves treated to reduce bacterial or fungal populations, for a period of 54 days. Gross growth efficiency when fed on untreated leaves was 4.94% compared with 1.03% for the insects fed antibacterial treated leaves. When fed fungicide treated leaves, the mean consumption rate was less than 10% of the consumption of untreated leaves and mortality was 85% compared with 15% for the insects fed untreated leaves. It was concluded that bacteria play a major role in the utilization of leaves by Pteronarcys princeps and that fungi are important as a stimulus to feeding, although they may also aid in utilization of the leaves.

To aid in classifying the emergence and benthos data into trophic categories, an extensive literature review of the foods of aquatic insects was compiled. The estimated yearly emergence of aquatic insects from Watershed 10 was 81 mg/m^2/yr. of algivores, 253 mg/m^2/yr. of detritivores, and 135 mg/m^2/yr. of carnivores. The mean standing crop of aquatic insects in an old-growth location in Mack Creek was 0.85 g/m^2 of algivores, 3.10 g/m^2 of detritivores, and 2.31 g/m^2 of carnivores; and 0.83 g/m^2 of algivores, 1.57 g/m^2 of detritivores, and 4.04 g/m^2 of carnivores in a clear-cut location.

A model is included describing the cycling of energy within the detrital component of the stream system, reflecting the importance of the fecal material and leaf fragments that return to the detrital pool.

The Conversion of Allochthonous Material by Stream Detritivores

by

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I INTRODUCTION

The food energy for aquatic consumers is derived from two sources: primary production within the system and litter fall from the surrounding watershed. Hynes (1963) suggests that due to typically heavy canopies of riparian vegetation, small streams tend to receive the majority of their energy from terrestrial litter fall rather than from autochthonous primary production.

Aquatic insects are a dominant component in most stream communities and have evolved to maximize the utilization of this allochthonous food source. Stream insects can be broadly categorized as shredders, actively consuming and breaking down the incoming litter material; collectors, feeding on fragments and feces left behind by the shredders; grazers, feeding on aquatic primary producers; or carnivores.

To understand the mechanisms and processes involved in the energy flow within a stream community, it is necessary to have quantitative data on the food sources utilized by the members of the community and to have an understanding of how these food sources are utilized. An investigation of foods of particular organisms is complicated by the numerous microhabitats present in stream systems.

Each habitat has slightly different foods available to its inhabitants and each habitat poses different sampling problems. The available foods also vary with the season, perhaps being higher in allochthonous material in the fall and early winter and higher in autochthonous material in late spring.

The term "detritus" will be broadly defined as any decaying plant or animal material of terrestrial or aquatic origin. Many aquatic insects feed rather indiscriminantly on decomposing material of all kinds and this definition avoids the problem of distinguishing between decomposing allochthonous and autochthonous material. Detritus will also include the bacteria and fungi associated with the organic matter since, as Hynes (1970) suggests, these microorganisms probably provide an important source of nutrition for detrital-feeding invertebrates. Kaushik and Hynes (1971) found an increase in protein content of leaf material with fungal colonization. They also showed, as did Kostalos (1972), that Gammarus (Amphipoda) fed little, if any, on sterilized material, much preferring the non-sterile leaves.

The goals of the stream project of the Western Coniferous Forest Biome I. B. P. study include the formulation of a stream model based on mechanisms and processes of energy transfer and examining the interactions between the stream and the terrestrial system. As a part of the stream project, the general objective of my study was to examine the role and importance of insects as detrital consumers in the stream system, including the following specific objectives:

1. To compile a literature review of the foods of aquatic insects with particular emphasis on stream forms.
2. To estimate consumption rates and food utilization (growth or assimilation efficiency) of several species of insect detritivores.
3. To examine the effects of reducing the detrital microbial populations on consumption rates and food utilization.
4. To estimate the importance of detrital feeding insects in relation to the algal consumers in streams in the H. J. Andrews Experimental Forest.

II SITE DESCRIPTION

The H. J. Andrews Experimental Forest is located in the Willamette National Forest approximately 80 km east of Eugene, Oregon, in the Cascade Mountains. It is a 600 hectare drainage with a mean annual rainfall of 229 to 254 cm and elevations ranging from 457 to 1615 m. The vegetation is old-growth Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), bigleaf maple (*Acer macrophyllum*), and alder (*Alnus rubra*), with young Douglas-fir, young hemlock, and vine maple (*Acer circinatum*) in the clear-cut regions. The watershed is drained by Lookout Creek which is fed by Mack and McRae Creeks.

Watershed 10 is a 10 hectare watershed adjacent to the H. J. Andrews Experimental Forest, ranging in elevation from 435 to 695 m, densely shaded by old-growth Douglas-fir, and with a mean summer flow of approximately 0.2 liters per second.

Mack Creek is a stream of moderate size, with a mean velocity of one to two mps, and a mean width of approximately six to seven m. Study sites were chosen in a section of stream shaded by old-growth Douglas-fir, at an elevation of approximately 775 m, and in a downstream clear-cut section at 745 m.

III LITERATURE REVIEW OF THE FOODS OF AQUATIC INSECTS

Published feeding records of selected aquatic insects, emphasizing stream forms, with some interpretive comments, are given in Table 25. Food types are listed as: 1. algae (a); 2. detritus (d); and 3. animal (c). Percentages of each food, when given, are listed in the same order as the respective food categories. Where one category comprised more than 75% of the diet, only the dominant food type is listed. An attempt was made to find references at the species level, but where these were not available, more general references at the generic or familial level are included. Data reported by Coffman (1967) are also shown in Coffman, Cummins and Wuycheck (1971) and those of Minshall (1965) are repeated in Minshall (1967). The original thesis data are used in both cases since they are more detailed than the published information.

The wide variation in food consumed by species such as Peltoperla brevis (Plecoptera:Peltoperlidae), Baetis spp. (Ephemeroptera:Baetidae), and Hydropsyche betteni (Trichoptera: Hydropsychidae) shown in Table 25 are due to a number of factors. Food availability will vary between locations and some variation in behavior or habitat preference, even within a species, might be expected at different locations. Also, data reported at the generic level or extrapolated to other species are probably less reliable than data reported for the species of interest. For example, the percentage of algae in the diet of Baetis spp. varies from 96% (Minshall, 1965) to 35% (Minckley, 1963) and the percentage of algae in the diet of Ephemerella spp. (Ephemeroptera:Ephemerellidae) varies from 27% (Gilpin and Brusven, 1970) to 75% (Minckley, 1963).

Muttkowski and Smith (1929) and Cummins (1973) state that most aquatic insects are generalistic in feeding habits and are strongly influenced by food availability in a particular location and microhabitat at a particular time. The data reported by Coffman (1967) and Coffman, et al. (1971), for example, are for insects collected from riffle areas in late summer and early fall, and consequently exhibit a much lower detrital portion in the diets than that reported in most other studies. Chapman and Demory (1963) showed that algae in two Oregon streams was most heavily utilized by the insects in late winter and spring and least utilized in the fall. They also found a variation in gut content with time of day for Paraleptophlebia nymphs (Ephemeroptera:Leptophlebiidae) which exhibited a negative response to sunlight and fed most heavily on surface algae during the night and on subsurface detritus during the day.

Variation in food also occurs with age, as indicated by Winterbourne (1971), who showed that Banksiola crotchi larvae (Trichoptera:Phryganeidae) were algal feeders in the early instars and carnivores in the final instar.

Considerable differences between studies arise from the different techniques used to analyze the gut contents. Volume, area, or number of particles are the usual bases for measuring the amounts of food in each of the respective categories. In comparing the importance of each food type in the insects' diet, corrections should preferably be made to a common unit of measurement such as calories, as done by Gilpin and Brusven (1970), rather than making comparisons of number of particles of detritus versus number of animal fragments, for example. Another useful basis for comparison might be assimilable food value. Since animal material is almost entirely assimilable, it should be much more heavily weighted than detritus, for instance, which might be only 10 or 20% assimilable.

A summary of the foods of aquatic insects in some general taxa is shown in Table 1.

Table 1. Foods of Some Groups of Aquatic Insects.

Ephemeroptera	
Baetidae	algae and detritus
Ephemerellidae	algae and detritus
Heptageniidae	algae (some detritus)
Leptophlebiidae	detritus (some algae)
Plecoptera	
Filipalpia	detritus (some algae)
Setipalpia	animal material (a few species are phytophagous)
Trichoptera	
Brachycentridae	algae and detritus (some animal material)
Calamoceratidae	detritus
Glossosomatidae	algae (some detritus)
Hydropsychidae	algae, detritus, and animal material
Hydroptilidae	algae
Lepidostomatidae	detritus
Limnephilidae	algae and detritus
Phryganeidae	algae and detritus
Psychomyiidae	mainly animal material
Rhyacophilidae	animal material (a few species are phytophagous)
Diptera	
Chironomidae (except Tanypodinae)	algae and detritus
Tanypodinae	animal material
Dixidae	algae and detritus
Empididae	detritus (may be carnivorous)
Psychodidae	detritus (probably also algae)
Simuliidae	algae and detritus (also suspended microorganisms)
Tabanidae	animal material (may be phytophagous)
Tipulidae	algae and detritus (some are carnivorous)
Megaloptera	
Corydalidae	animal material
Sialidae	animal material
Coleoptera	
Dryopidae	algae and detritus
Dytiscidae	animal material
Elmidae	algae and detritus
Hydrophilidae	
(larvae)	animal material
(adults)	algae

IV METHODS AND MATERIALS

Consumption and Food Utilization by *Pteronarcys princeps* Nymphs (Plecoptera:Pteronarcidae)

The objective of these experiments was to examine the consumption and growth of *P. princeps* nymphs fed on bigleaf maple leaves and to investigate the effects of reducing the microbial populations present on the leaves. *P. princeps* was selected as a test animal for these experiments since it is a known detrital feeder and actively shreds leaves. It has a three or four year life cycle insuring the presence of nymphs for experimental use at all times of the year and it occurs in abundance in upper Oak Creek and Mack Creek. The large size of the nymphs facilitates handling and increases the precision of consumption and wet weight measurements. In addition, there is information available in the literature on feeding, growth, and respiration for related species.

The experiments were conducted at the Oak Creek Cooperative Fisheries Laboratory in recirculating laboratory streams similar to those used by McIntire *et al.* (1964). Experiment I was designed to examine feeding and growth of *P. princeps* nymphs fed on untreated maple leaves as related to the age of the insects. The objective of Experiment II was to test the effects of reducing the detrital microbial populations on insect consumption, growth and survival.

Temperature was not controlled, but was recorded. Gallon plastic jars were converted to experimental chambers by cutting out the tops and bottoms and replacing them with 333μ Nitex. Insects were collected from upper Oak Creek (see Kerst, 1970, for site description) and allowed to acclimatize for a week or more before beginning the experiments. Specimens were chosen at random from the field collection and a group of five was placed in each of four jars which were randomly positioned in the trough. Four more jars served as controls, with leaves but without insects, to estimate the rate of leaf leaching and decomposition without the insects. For Experiment II, the respective treatments were contained in separate troughs but with the same arrangement of replications in each trough.

Wet weights of each group of five insects were taken by blotting the insects partially dry and weighing them in a covered petri dish with a tissue in the bottom. The dish, lid, and damp tissue were then immediately reweighed for a tare weight. With some practice, these weights were accurate to within 0.5%. A mean of two weighings was taken for each group. Any cast skins were noted and weighed along with the insects.

Wet Weight:Dry Weight Relationship

Following the final experiment, 16 of the nymphs were wet weighed, oven-dried and cooled in a desiccator, and reweighed for a wet weight:dry weight relation as shown in Table 26. This relation was calculated as a linear regression rather than a simple ratio of wet to dry weight since it was felt that the regression line for the sizes of nymphs considered did not necessarily pass through the zero point. The slope of the line was 5.39 g wet weight/g dry weight ± 0.44 S.E. The Y-intercept was significantly different from zero ($P < 0.10$).

Leaf Material

All of the bigleaf maple leaves used in the feeding experiments were collected shortly after leaf fall from a single tree in Corvallis, Oregon. The alder leaves used in the feeding experiments with caddis larvae were collected from several trees in the H. J. Andrews Experimental Forest shortly after leaf fall. The leaves were preleached, oven-dried for a minimum of 48 hours at 60°C. Preleaching was necessary since fresh leaf material may lose considerable amounts of soluble materials in the first few hours in the water, obscuring the amount of feeding by the insects. Before feeding, the major veins and midribs were cut out of the leaves. The leaves were redried and cooled at room humidity before the pre- and post-experiment weighings. Any variation in weight arising from differences in room humidity would be eliminated by the correction for weight loss in the controls as described in the Results.

For Experiments I and II, the leaves were incubated, to allow microbial growth, at 14 °C in water from a laboratory leaf culture for about 48 hours before being placed in the experimental containers. Leaves were replaced approximately every 48 hours and the insects were wet weighed every four or six days.

Antibiotic Treatments Used in Experiment II

Leaves for the various troughs were incubated with the addition of treatments as shown in Table 2.

Table 2. Leaf Treatments During Incubation for Experiment II.

Treatment	Incubation solution
Untreated	--
Antibacterial	Streptomycin (30 mg/l) and penicillin G (30 mg/l)
Antifungal	Actidione (50 mg/l) and Nystatin (50 mg/l) (days 1-14) Actidione (50 mg/l) and sodium propionate (50 mg/l) (days 15-54)
Antibiotic	Antifungal and antibacterial chemicals (days 1-24) Autoclaving (days 25-54)

The treatments and concentrations used initially were described by Hynes and Kaushik (1968). The resistance of aquatic bacteria to various antibiotics was examined by Strzelczyk *et al.* (1971) and their results showed that streptomycin and penicillin G gave 85 to 90% control when used separately. In addition, Kostalos

(1972) showed that treatment of the water with streptomycin and penicillin significantly reduced the numbers of bacteria present on leaves in the water and exerted no harmful effects on *Gammarus minus*. All of the leaf material was given two rinses in distilled water after removal from the incubation solutions to remove some of the residual antibiotics. No chemicals were added to the water in the laboratory troughs.

To minimize contamination, the four troughs were scrubbed and washed with a potassium permanganate solution prior to the experiment and the water supply was filtered through a series of sand and gravel filters. The filters were periodically flushed with potassium permanganate solution. Filtered water was added to each trough at a rate of about two gallons per hour, allowing for a complete change of water every two days.

In order to reduce contamination of the troughs by the insects, the insects were held without food for 24 hours, rinsed with potassium permanganate solution and placed in their respective containers with the treated or untreated leaves. They were allowed to feed for 48 hours to fill their intestinal tracts and become somewhat acclimatized, weighed, given a new food supply and the experiment was begun.

Consumption, Assimilation, and Food Preference of Trichoptera

Feeding, assimilation, and food preference studies were carried out on larvae of *Lepidostoma* sp. (*Lepidostomatidae*), *Heteroplectron californicum* (Calamoceratidae), *Ecclisomyia* sp. (Limnephilidae) and *Halesochila taylori* (Limnephilidae). These species were used since they appeared to be important detrital consumers and were of interest as possible experimental animals for future studies. The brief studies here were designed to gain information on their suitability as experimental animals and to obtain general information on consumption rates and food utilization for a variety of detritivores.

Experiments with *Lepidostoma*, *Heteroplectron californicum* and *Halesochila taylori* were done in a drippery in a controlled temperature room with a slight flow of water through the pans and a water temperature of 14°C. The insects and their food, pre-leached and dry-weighed leaves as before, were enclosed in screen baskets. The screen allowed the fecal material to fall through for easy collecting and also prevented the insects from feeding on the feces. Leaves were also placed in another pan without insects to determine the approximate rate of leaching and decomposition. Assimilation efficiency was calculated as the ratio of assimilated food material (dry weight of consumption minus dry weight of feces) to dry weight of consumption.

Experiments on feeding rates of *Halesochila taylori* and *Ecclisomyia* were carried out in Lookout Creek and Mack Creek, respectively. The insects were collected from the experimental locations immediately prior to the experiment.

Field Sampling

An extensive sampling program for benthic and emerging aquatic insects has been carried out as a part of the stream project. The major emphasis of this thesis is not on field data, but a portion of these data is included as relevant to the role of the detritivore in the stream community.

Emergence sampling was done on Lookout Creek, Mack Creek and Watershed 10. Benthos sampling has been done on Lookout Creek and Mack Creek using a modification of the Coleman-Hynes artificial substrate sampler (Coleman and Hynes, 1970).

V RESULTS

Growth and Consumption Experiments with *Pteronarcys princeps*

Calculation of Consumption

Preliminary experiments showed that some leaching and decomposition of leaves occurred in the absence of insects, so the following equation, in conjunction with "control" leaves, was used to calculate the dry weight of leaves consumed by the insects over the experimental interval:

$$1)\quad X_e = \frac{2(PX_i - X_f)}{1 + P}$$

where;

X_e = the dry weight of leaves eaten by the insects.

X_f = the final dry weight of leaves remaining after the experimental interval, including shredded fragments.

X_i = the initial dry weight of leaves.

P = the mean $X_f{:}X_i$ ratio for the experimental "controls" for the time interval.

This equation assumes a constant rate of feeding by the insects and a constant rate of leaching and decomposition of leaves without the insects. It allows for the fact that the leaf material consumed by the insects is no longer subject to the leaching and decomposition and is derived from the following relationship:

$$2) \qquad P(X_i - X_e/2) - X_e/2 = X_f$$

A more general form of the above relationship, making no assumptions about feeding rate or leaching rate, is included in the Discussion.

Variability in Consumption and Growth Rates

Growth and consumption for various age classes of *P. princeps* nymphs fed on maple leaves are shown in Table 3. The mean consumption rates (Table 4) indicate a distinct difference in consumption rates for final-instar nymphs as compared with consumption rates for nymphs one or two years from maturity.

Significant differences (t-tests) in mean consumption rates occurred between replication 1 and replications 2 and 3 ($P < 0.01$), between replications 2 and 3 and replication 4 ($P < 0.05$), and between replication 1 and replication 4 ($P < 0.10$). This latter difference was perhaps due to interference by the final-instar nymph with feeding by the others, although ample food was present.

The final-instar nymph in replication 4 died in the process of molting during days 8-11, and the uptake of water during molting resulted in a 23% increase in the wet weight of the entire group of five nymphs.

Table 3. Growth and Consumption for *Pteronarcys princeps* Nymphs Fed on Maple Leaves.

Experiment I

Replication	Growth (mg/insect/day)	Consumption (mg/insect/day)
days 1 - 3 (mean temperature 15.2°C)		
1	0.66	0.16
2	0.67	3.69
3	1.41	5.84
4	0.47	1.19
days 4 - 7 (mean temperature 15.7°C)		
1	-5.40	0.13
2	0.02	3.18
3	1.24	3.33
4	-0.90	1.31
days 8 - 11 (mean temperature 13.0°C)		
1	2.40	0.60
2	1.25	7.52
3	-0.21	4.94
4	15.26	1.88
Means 1 (finals)	-0.78 ± 2.45 S.E.	0.30 ± 0.15 S.E.
2 + 3 (sub-finals)	0.75 ± 0.28 S.E.	4.75 ± 0.70 S.E.
4 (one final and four sub-finals)	4.94 ± 5.17 S.E.	1.46 ± 0.21 S.E.

Table 4. Mean Consumption Rates for *P. princeps* Nymphs Fed on Maple Leaves.

Age	Mean consumption ± S.E. mg/insect/day	mg/g/day
Final-instars (rep. 1)	0.30 ± 0.15	1.5 ± 0.7
One final-instar and four sub-finals (rep. 4)	1.46 ± 0.21	29.2 ± 4.2
Sub-finals (reps. 2 and 3)	4.75 ± 0.70	91.5 ± 13.5

Growth:Consumption Relationship

As indicated by Warren (1971), the growth:consumption line does not pass through the zero growth, zero consumption point, since energy is always required for respiration. For this reason, a linear regression analysis of growth versus consumption was used to calculate the gross growth efficiency rather than the conventional growth:consumption ratio. The slope of the growth: consumption line and the corresponding efficiency reported here is therefore somewhat higher than similar values obtained by a growth: consumption ratio. Another reason for using a regression technique is that it allows calculation of growth efficiency even though the mean growth rate is negative.

The following relationship of wet weight growth to dry weight consumption is the result of the linear regression analysis for Experiment I, including only the data for replications 2 and 3 and days 1-7 for replication 4 (Fig. 1):

$$G = -0.57 + 0.24C \qquad R^2 = 0.48$$

Calculation of Gross Growth Efficiency

Calorie per calorie gross growth efficiency was calculated from the regression coefficient for the slope of wet weight growth to dry weight consumption using the following conversion values:

5.39 g wet wt. insect/g dry wt. (Table 26).

4773 cal./g dry wt. *Acer* spp. leaves (Cummins and Wuycheck, 1971).

5300 cal./g dry wt. *Pteronarcys scotti* nymphs (McDiffett, 1970).

Thus,

$$\frac{0.24 \text{ g wet wt. growth/g dry wt. consumption}}{5.39 \text{ g wet wt. insect/g dry wt. insect}} \times \frac{5300 \text{ cal/g dry wt. insect}}{4773 \text{ cal/g dry wt. leaf}} =$$

0.0494 calories of growth per calorie of consumption, a gross growth efficiency of 4.94%.

Growth and Consumption of Untreated Leaves and Leaves Treated to Reduce Microbial Populations

It was apparent from preliminary experiments and from Experiment I that late final-instar nymphs of *P. princeps* should not be used in feeding and growth experiments of this type and that ample food should be provided. Molting might also pose a problem

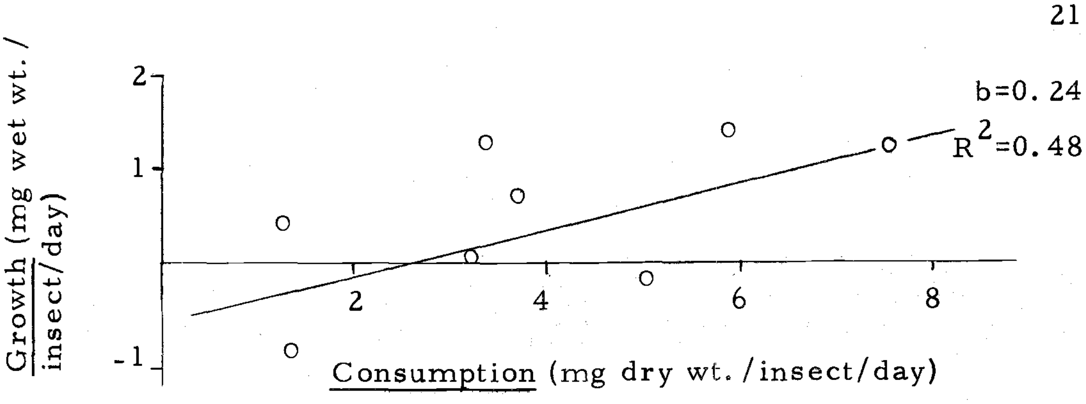


Figure 1. Growth vs. consumption for P. princeps nymphs fed on maple leaves.

in obtaining accurate measurements of insect wet weight growth. In Experiment II, to reduce the variation, final-instar nymphs were excluded and the others were randomly assigned to the respective treatments and replications. Nymphs were not sorted into size classes since an average estimate of growth efficiency over the range of sizes was desired. More accurate growth: consumption relationships would have been obtained if only nymphs of a single size were used, but these relationships might not have been representative of the growth efficiency for other size classes. Early final-instar nymphs may account for a substantial portion of the consumption and growth occurring during the insect's life cycle, but were not available at the time of the experiment.

The growth and consumption by P. princeps nymphs fed on untreated, antibacterial, antifungal, and antibiotic treated bigleaf maple leaves are shown in Table 5. These data are mean values of four replications, excluding replications where mortality occurred, since wet weight could not be reliably measured for these replications.

None of the treatments using Nystatin were included in the final data analysis since it apparently exerts a toxic or inhibitory effect on invertebrates (Kostalos, 1972). This is shown in Figure 4 for the antifungal treatment where inclusion of the Nystatin treatment results in a negative growth efficiency (increased consumption causes reduced growth rate).

Consumption Rates

The mean feeding rates for the respective treatments and 95% confidence limits are shown in Table 6. Using a paired observations comparison of sample means (Steel and Torrie, 1960), with the null hypothesis that the mean of the differences was zero, showed a significant difference ($P < 0.05$) between the consumption of the

Table 6. Mean Consumption Rates for P. princeps Nymphs Fed on Treated and Untreated Leaves.

Treatment	Mean ± S. E. (mg/insect/day)	95% C. L.
Untreated	9.49 ± 1.00	7.23 to 11.75
Antibacterial	10.42 ± 0.93	8.22 to 12.42
Antifungal (excluding Nystatin treatments)	0.46 ± 0.09	0.24 to 0.68
Antibiotic (excluding Nystatin treatments)	3.45 ± 1.17	0.59 to 6,31

Table 5. Growth[1] and Consumption[1] by P. princeps Nymphs Fed on Untreated Leaves and Leaves Treated to Reduce Microbial Populations.

	Untreated		Antibacterial		Antifungal		Antibiotic		
Days	Growth	Consumption	Growth	Consumption	Growth	Consumption	Growth	Consumption	Temperature[2]
1-6	0.45	9.44	0.64	12.43	-1.32	2.41[3]	-1.41	2.54[3]	11.1
7-10	2.37	14.98	0.57	16.82	-1.88	2.05[3]	0.89	2.09[3]	15.0
11-14	0.89	13.69	-0.44	11.70	-0.92	1.54[3]	-1.75	1.01[3]	16.1
15-20	-0.38	11.83	-0.33	12.12	-0.05	0.53[4]	0.07	1.08[4]	16.1
21-24	1.22	9.32	0.09	7.97	-0.84	0.34[4]	-0.66	0.84[4]	11.7
25-30	-0.20	5.55	0.44	8.68	0.18	0.75[4]	-0.69	1.15[5]	13.9
31-34	1.32	8.95	-0.38	8.26	0.97	0.51[4]	2.59	2.43[5]	11.7
35-40	-0.42	6.45	-0.15	7.47	-1.23	0.38[4]	-0.96	2.96[5]	13.9
41-47	0.50	8.52	-1.28	9.81	0.20	0.68[4]	1.82	7.54[5]	17.2
48-54	-1.46	6.12	0.37	7.95	-0.59	0.02[4]	0.40	8.16[5]	15.0
Means	0.43	9.49	-0.05	10.32	-0.55	0.92	0.03	2.98	14.2

[1] mg/insect/day, means of four replications.

[2] Mean temperature in °C.

[3] Leaves treated with Nystatin and Actidione as fungicides.

[4] Sodium propionate and Actidione as fungicides.

[5] Leaves autoclaved.

antibiotic treated leaves and the consumption of the antifungal treated leaves. This difference was probably due to changes in leaf composition caused by autoclaving and the corresponding increase in fungal growth. The method of paired comparisons was useful for this comparison, since there was an obvious increase in consumption rate of the antibiotic treated leaves with time (Table 5). None of the other treatments showed such an increase in consumption rates with time.

Growth Rates

A large portion of the fluctuations recorded in wet weight of the insects is due to the inaccuracy of the method, since error in measurement and growth were of the same order of magnitude. Molting could be another major source of variation, as was shown in Experiment I. Since a linear regression follows the trends of weight increase or decrease rather than emphasizing the fluctuations, analyses of this type were used to calculate growth rates as wet weight (corrected to an initial value of zero) versus time (Fig. 2 and Tables 27 and 28) rather than taking mean values of growth over short time intervals. The calculated growth rates for the insects in the respective treatments are summarized in Table 7.

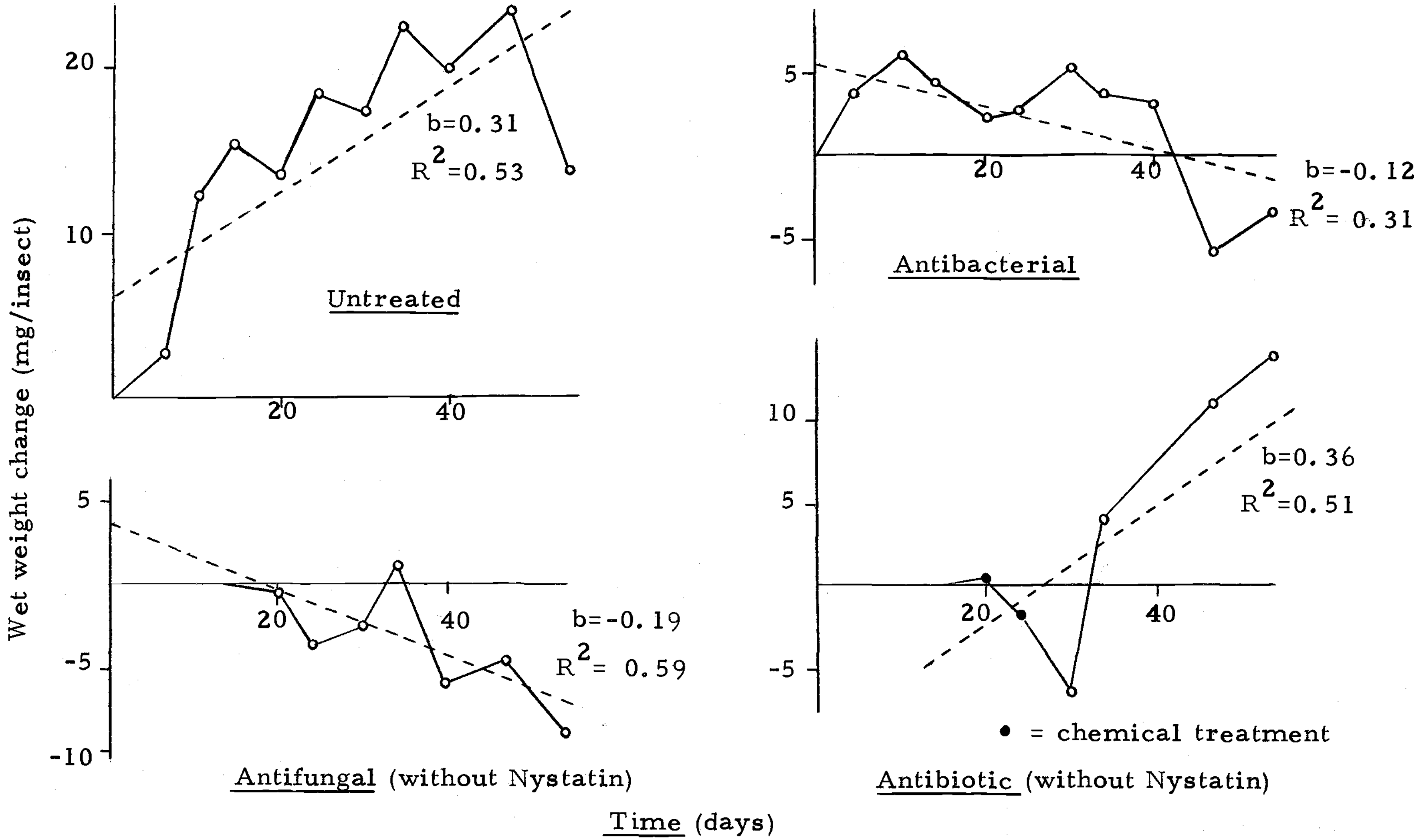


Figure 2. Wet weight increase for *Pteronarcys princeps* nymphs fed on treated and untreated bigleaf maple leaves.

Table 7. Calculated Growth Rates for *P. princeps* Nymphs Fed on Treated and Untreated Leaves.

Treatment	Growth rate ± S.E. (mg wet wt. /insect/ day)	95% C. L.
Untreated	0.31 ± 0.10	0.08 to 0.54
Antibacterial	-0.12 ± 0.06	-0.26 to 0.016
Antifungal (exc. Nystatin treatments)	-0.19 ± 0.07	-0.36 to -0.02
Antibiotic (exc. Nystatin treatments)	0.36 ± 0.14	0.018 to 0.70

The unexpectedly high growth rate for the insects in the antibiotic treatment is undoubtedly due to the effects of the autoclave treatment of the leaves as evidenced in Figure 2. Mean growth rate for the chemical antibiotic treatment (days 1 through 24) was -0.59 mg wet wt. /insect/day compared with 0.63 mg wet wt. /insect/day for the autoclave treatment. As expected from the consumption rates, the insects in the antifungal treatment showed a significant difference in growth rate ($P < 0.05$) compared with the insects fed untreated leaves. The insects in the antibacterial treatment also showed a significant difference in growth ($P < 0.05$) compared with the insects fed untreated leaves, even though the consumption rates in the two treatments were almost identical.

Since the leaves were rinsed prior to placing in the trough, minimal amounts of antibacterial chemicals were used in incubation, and the insects showed no ill effects as a result of the treatment other than decreased growth rate, I believe that the decrease in nutritional value of the food in the antibacterial treatment was the result of a reduction in the bacterial colonization of the leaves rather than a decrease in the numbers of enteric bacteria.

Growth:Consumption Analysis

Linear regression analyses with growth as the dependent variable were used to quantify the relationship between growth, consumption, and temperature for the respective treatments.

The results of days 31 to 34 for the antibiotic treatment were not consistent with a reasonable growth:consumption relationship, since growth exceeded consumption for this time period, and these data were not included in the regression analysis. The unusual weight increase observed probably resulted from the increased food quality of the autoclaved leaves. An increase in gut load or molting on the part of several insects might account for the increased weight.

The regression analyses of growth (wet weight) versus consumption (dry weight) for the respective treatments (Tables 29 through 34) resulted in the relationships shown in Table 8 and Figures 3 and 4.

The differences in slopes of the regression lines were substantial, as shown in Figures 3 and 4, but not statistically significant.

Table 8. Linear Regression Equations of Growth versus Consumption for *P. princeps* Nymphs Fed on Treated and Untreated Leaves.

Treatment	Regression Equation	R^2
Untreated	$G = -1.81 + 0.24C$	0.47
Antibacterial	$G = -0.56 + 0.05C$	0.06
Antifungal (exc. Nystatin treatments)	$G = -0.97 + 1.69C$	0.30
Antibiotic (exc. Nystatin treatments and days 31-34)	$G = -0.83 + 0.23C$	0.56

The regression coefficients for growth versus consumption and the corresponding calorie to calorie growth efficiencies are given in Table 9.

Table 9. Calorie:Calorie Gross Growth Efficiencies for *P. princeps* Nymphs Fed on Treated and Untreated Leaves Calculated from Growth:Consumption Regression Coefficients.

Treatment	Regression coefficient	Growth efficiency
Untreated	0.24 ± 0.09 S.E.	4.94%
Antibacterial	0.05 ± 0.06 S.E.	1.03%
Antifungal (exc. Nystatin treatments)	1.69 ± 1.14 S.E.	34.82%
Antibiotic (exc. Nystatin treatments and days 31-34)	0.23 ± 0.10 S.E.	4.74%

The multiple regression analyses of growth (wet weight) versus consumption (dry weight) and temperature (°C) for the respective treatments are shown in Tables 29 through 34 and result in the

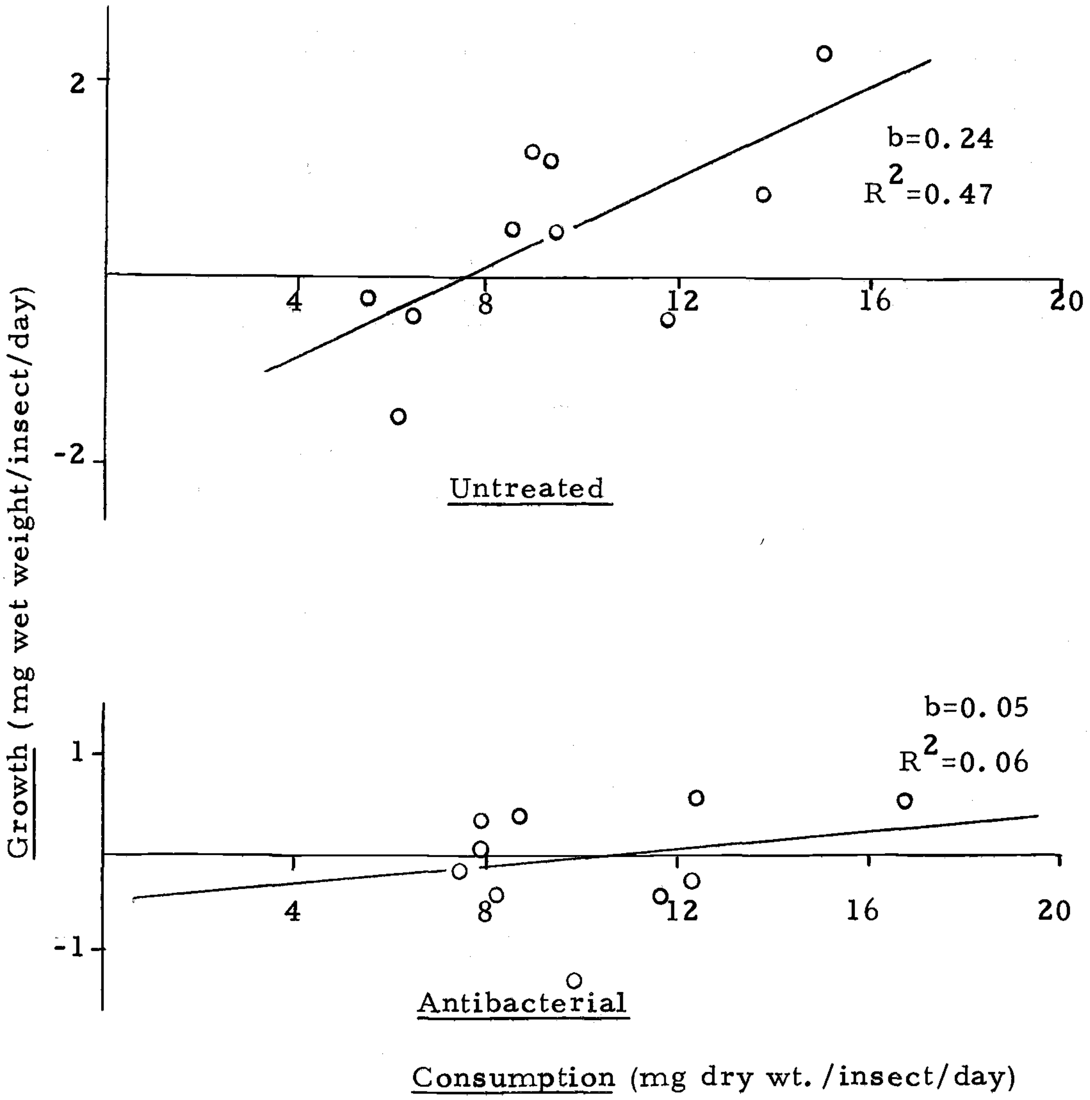


Figure 3. Growth vs. consumption for P. princeps nymphs fed on treated and untreated leaves.

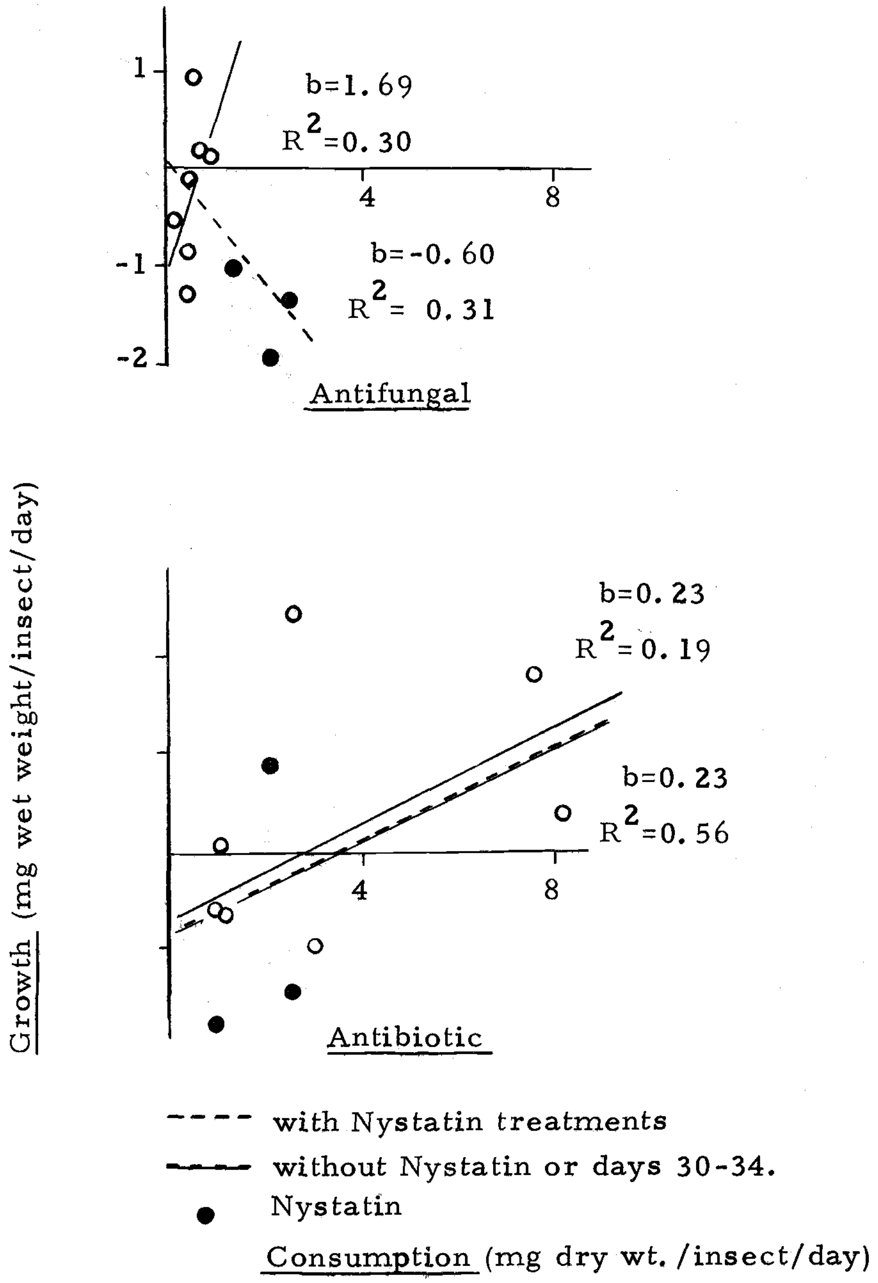


Figure 3. Growth vs. consumption for P. princeps nymphs fed on treated leaves.

regression equations shown in Table 10.

Table 10. Regression Equation of Growth:Consumption: Temperature for P. princeps Nymphs Fed on Treated and Untreated Leaves.

Treatment	Regression equation	R^2
Untreated	$G = 0.82 + 0.27C - 0.21T$	0.63
Antibacterial	$G = 1.60 + 0.08C - 0.17T$	0.43
Antifungal (exc. Nystatin treatments)	$G = -0.49 + 1.74C - 0.04T$	0.31
Antibiotic (exc. Nystatin treatments and days 31-34)	$G = -4.92 + 0.13C + 0.30T$	0.78

Calculating calorie to calorie growth efficiencies from the growth: consumption: temperature regression coefficients gives the efficiencies shown in Table 11.

Table 11. Calorie: Calorie Gross Growth Efficiencies for P. princeps Nymphs Fed on Treated and Untreated Leaves Calculated from Growth: Consumption: Temperature Regression Coefficients.

Treatment	Regression coefficient	Growth efficiency
Untreated	0.27 ± 0.08 S.E.	5.56%
Antibacterial	0.08 ± 0.06 S.E.	1.65%
Antifungal (exc. Nystatin treatments)	1.74 ± 1.29 S.E.	35.85%
Antibiotic (exc. Nystatin treatments and days 31-34)	0.13 ± 0.10 S.E.	2.67%

As can be noted, the addition of temperature to the regression analyses caused little change in the growth:consumption regression coefficient and as with the linear regression of growth versus consumption, the differences in growth:consumption regression coefficients were substantial but not statistically significant. The very high efficiency of the insects fed on antifungal treated leaves was the result of the very low consumption rate since the insects were almost certainly feeding on their own feces in preference to the unpalatable leaves, although the screens on the experimental chambers allowed escape of most of the fecal material. Also, it is probable that the growth:consumption relationship is a curvilinear one, with a very high slope at low consumption rates, tapering to a lower slope at higher consumption rates (Warren, 1971). A curvilinear relationship such as this would show very high growth efficiency at low consumption rates such as occurred in the antifungal treatment.

The very low correlation of growth to consumption in the antibacterial treatment is undoubtedly due in part to the low slope of the growth:consumption line, since the actual fit of the points to the line appeared to be as good as the fit for the untreated regression line (Fig. 3) ($R^2 = 0.47$). This reduction of correlation with slopes approaching zero is an artifact of the analysis, since a line with zero slope would obviously show no correlation between growth and consumption.

Lending credibility to the measurements of gross growth efficiency for insects fed on untreated leaves is the fact that the linear regression analysis of growth versus consumption gave a regression coefficient of 0.24 for both Experiments I and II.

Consumption: Temperature Analysis

There was no significant linear correlation between consumption and temperature over the range of 11.1 to 17.2°C. R^2 values for temperature versus consumption were 0.03 for the antifungal treatment (excluding Nystatin treatments), 0.31 for the antibiotic treatment (excluding Nystatin treatments) and 0.06 for the untreated and antibacterial treatments.

Respiration

Respiration rates can be calculated from the growth: consumption: temperature regression equation for a given temperature and at zero consumption, assuming that the relationship is linear when extrapolated to zero consumption. For the multiple regression of growth: consumption: temperature, using the equation derived from feeding on untreated leaves and at 15°C, the calculated respiration is 2.33 mg wet wt. loss/insect/day, equivalent to 6.1 mg/g/day for an insect weighing 380 mg wet weight, or approximately 2.3 calories/insect/day. If the growth:consumption: temperature relationship is non-linear, the respiration rate could be substantially higher. Using the respiration equation derived by McDiffett (1970) for *Pteronarcys scotti* nymphs, respiration for *P. princeps* nymphs can be calculated as approximately seven calories/ insect/day, or 1.8 mg/g/day for an insect weighing 380 mg.

Mortality

The only major mortality occurred in the antifungal treatment, where the mortality was 85% for days 15 to 54 (excluding the Nystatin treatments). The mortality among the insects in other treatments appears to be within the range of expected mortality (Fig. 5). The observed mortality was directly related to consumption rates in the various treatments. No signs of cannibalism were observed.

Effectiveness of Treatments in Reduction of Microbial Populations

To assess the effectiveness of the treatments, an attempt was made to measure the rates of growth of bacteria and fungi on nutrient agar, without success. However, Botan, *et al.* (1960) indicate a peak in heterotrophic bacterial numbers in cultures in marsh water and sterilized dried plankton in 25 hours to three or

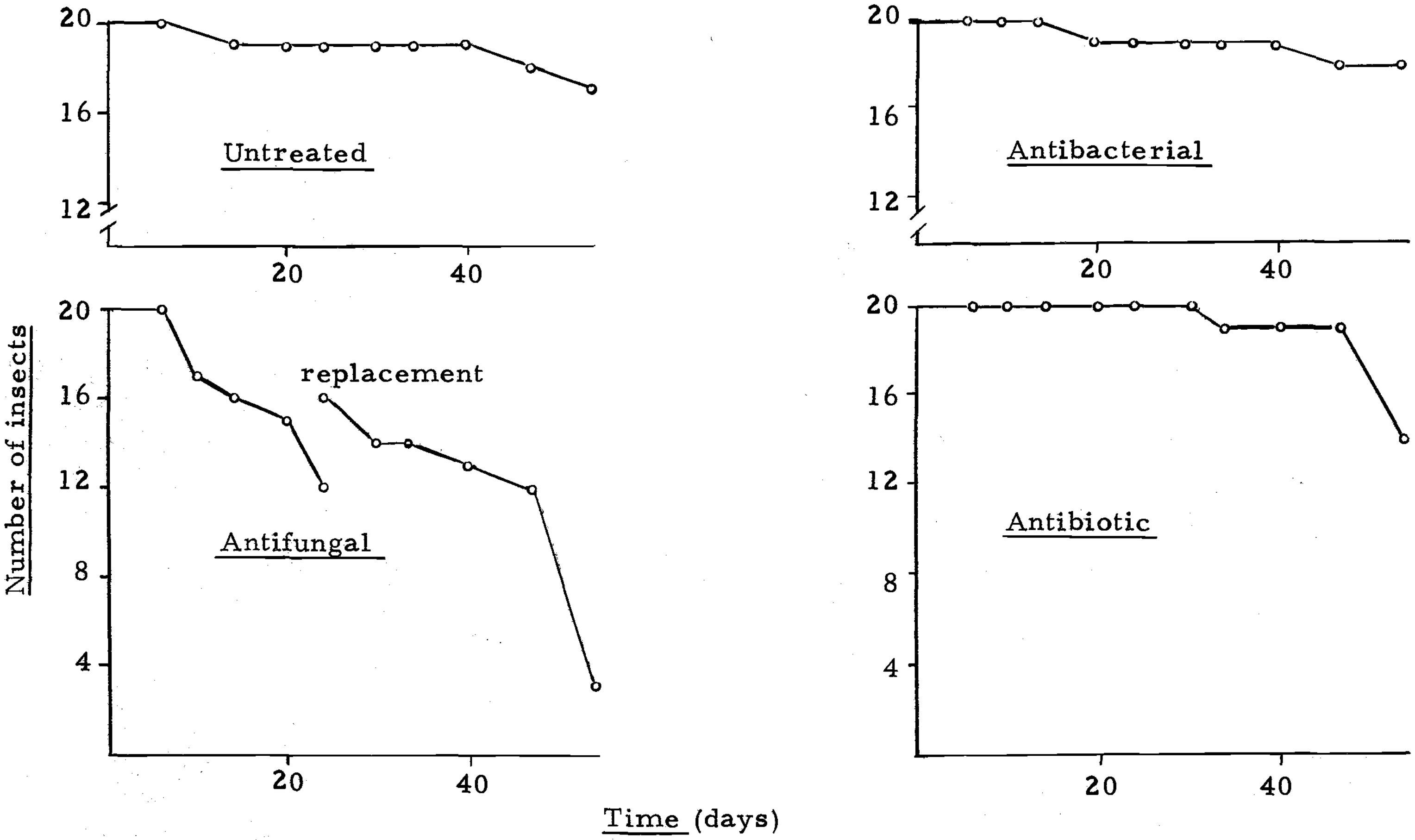


Figure 5. Survivorship of Pteronarcys princeps nymphs fed on treated and untreated bigleaf maple leaves.

four days, and Nilsson (1964) showed hyphomycete fungal growth and sporulation on alder leaves in two to three days, with maximum growth at 20°C. These data indicate that the incubation time of approximately 48 hours and the time in the troughs of 48 hours were probably long enough to allow maximum microbial growth if desired, and short enough to minimize undesirable microbial colonization, with the exception of the autoclave treatment. In this treatment, the process of autoclaving broke down many of the larger organic molecules in the leaves causing a marked increase in leaching and decomposition of the "control" leaves in the autoclaved treatment compared with the other treatments as shown in Table 12.

Table 12. Mean Percent Weight Loss for Treated and Untreated Leaves Without Insect Feeding.

Treatment	Mean weight loss by "control" leaves (%/day) ± S.E.
Untreated	0.90 ± 0.07
Antibacterial	0.85 ± 0.08
Antifungal	0.89 ± 0.07
Antibiotic (chemical)	0.78 ± 0.08
(autoclaved)	2.82 ± 0.15

The increase in available nutrients in the autoclaved trough would encourage microbial growth on the leaves increasing the protein content of the leaves (Kaushik and Hynes, 1971) and the digestibility of the leaves by the insects.

Toward the end of the experiment, it appeared that microbial levels in the troughs had risen to a level where the pre-digested autoclaved leaves were almost immediately colonized upon initiation into the trough and were as palatable as the untreated leaves. Earlier in the experiment, the consumption rate in the autoclaved treatment was much lower than in the untreated treatment. Another indication of bacterial and fungal contamination is that in the growth: consumption: temperature multiple regression, the insects in the antibiotic treatment showed increased growth with increased temperatures. Also, in the consumption: temperature regression, the antibiotic treatment showed a high temperature: consumption slope of 0.45 ($R^2 = 0.31$). All of the other treatments showed decreased growth with increased temperatures and temperature: consumption slopes of 0.01 to 0.21 (R^2 values from 0.03 to 0.06). These factors suggest increased microbial growth rates in the autoclaved treatment with higher temperatures, affecting the palatability and nutritional value of the leaves. Contamination of the troughs was also evident in the build-up of algae during the last few days of the experiment.

It has been suggested by Kaushik and Hynes (1971) that considerable competition occurs between bacterial and fungal communities on a leaf and that the initial elimination of the fungi, for example, would result in an increase in bacterial growth inhibiting the regrowth of fungi. The regrowth of fungi would therefore be more rapid in an antibiotic treatment than on leaves initially treated only with fungicide. This could partially explain the higher consumption rates in the antibiotic treatment compared with the antifungal treatment, particularly if some inoculum was present in the troughs.

Improvements in Experimental Design

The most important change that could be made in future experiments of this nature is the alteration of the antibiotic treatment. The increased palatability and apparent microbial growth on the autoclaved leaves compared with the chemical treatments obscured any meaningful differences that might have occurred. If the chemical treatments had been continued throughout the experiment, differences would have been more obvious, but no information would have been obtained on the direct effects of the chemicals on the insects (e. g., reduced palatability of the treated leaves due to the presence of chemical residues). The most promising solution is the use of gas sterilization (Kostalos, 1972) or ultraviolet irradiation as the antibiotic treatment. These would presumably have much less effect on the leaf structure and would leave little or no residue behind to affect the insects. If either of these techniques proved successful, the treatment could be extended to the antibacterial and antifungal treatments by incubating sterile leaves in inoculant from an appropriate bacterial or fungal culture.

The growth measurements could be substantially improved by using a more sensitive balance that would allow standardization of the time the insects are allowed to air dry before the measurement is taken. If time allowed, it would also be profitable to individually weigh and measure the insects to reduce the variation caused by molting. Insects of the same physiological age should also be used, preferably measuring efficiency for several different ages.

For species of insects that do not require running water, small confined experimental chambers would have several advantages. Microbial contamination of the chambers could be minimized, insects could be held at several discrete temperatures, and fecal material could be collected for assimilation calculations. In Experiment II, an attempt was made to collect the fecal material, but since the experiment was not designed with this in mind, no meaningful results were obtained.

Summary of the Effects on *Pteronarcys princeps* of Reducing Microbial Populations on the Food Source.

Compared with nymphs fed untreated leaves, *P. princeps* nymphs exhibited the following responses when fed on bigleaf maple leaves treated as indicated (Table 13). All the differences except the

Table 13. Effects on P. princeps Nymphs of Reducing Microbial Populations on the Food Source

Treatment	Effect
Antifungal or antibiotic	Reduced consumption rates
Antibacterial	No reduction in consumption rates
Antifungal or antibacterial	Reduced growth rate
Antibiotic	No reduction in growth rate
Antibacterial	Reduced growth efficiency
Antifungal	Increased mortality

reduced growth efficiency were significant at the $P < 0.05$ probability level.

From these data and from data presented by Kaushik and Hynes (1971) and Kostalos (1972), it is clear that at least some stream detritivores require fungal colonization as a stimulus to feeding. For P. princeps nymphs, bacterial colonization is apparently not necessary to stimulate feeding, but is important in utilization of the leaves.

Ingestion and Utilization of Leaves by Caddis Larvae

Feeding experiments were carried out in the gallon jar experimental chambers in the field using Halesochila taylori and Ecclisomyia larvae. The mortality in the 21 day experiment using

Halesochila taylori was 54%, cannibalism apparently having occurred, and these data were discarded. Ecclisomyia was found to consume 0.05 mg of bigleaf maple leaves/insect/day (Table 14), equivalent to 0.10 mg/mg/day. Mortality in this case was 2% for the eight day experiment. In the laboratory, Halesochila taylori larvae consumed 0.63 mg of maple leaves/insect/day or approximately 0.04 mg/mg/day. Neither Ecclisomyia nor Halesochila taylori were suitable for assimilation studies, since some destruction of their needle and bark cases occurred almost constantly, making accurate measurements of consumption and fecal production impossible.

Ingestion and egestion rates and assimilation efficiencies for Lepidostoma larvae are shown in Tables 15 and 16. The mean consumption rate for fourth-instar larvae was 0.17 mg of maple leaves/insect/day, or 0.55 mg/mg/day. Fourth- and fifth-instar larvae fed on a mixture of alder and maple leaves showed a consumption rate of 0.44 mg/insect/day, or 0.61 mg/mg/day. They showed a preference for alder leaves, consuming approximately 70 mg of alder for every 30 mg of maple. However, when the maple leaves were incubated for 48 hours prior to the experiment, the consumption of maple and alder were almost equal. The assimilation efficiency for the experiment using only maple leaves was 9.8% while the insects fed on both alder and maple leaves assimilated

Table 14. Consumption of Bigleaf Maple Leaves by Ecclisomyia Larvae.

Rep. No.	No. of insects	Leaf weight loss mg	%	Calculated consumption (mg) /insect	/insect/day
1	0	4.90	4.52	--	--
2	10	9.62	7.87	0.53	0.07
3	0	3.50	3.11	--	--
4	15	3.65	3.13	-0.04	-0.005
5	0	2.44	2.24	--	--
6	15	8.10	7.43	0.28	0.03
7	0	5.10	4.52	--	--
8	15	11.91	10.28	0.48	0.06
9	10	9.29	8.64	0.55	0.07
10	15	11.32	10.06	0.40	0.06
Mean (without insects)			3.60		
Means (with insects)			7.90	0.38 0.09 S.E.	0.05

Mean dry weight (mg) per insect (14 specimens) = 0.50 ± 0.06 S.E.
Total mortality = 2 (one in rep. 4 and one in rep. 10).

Table 15. Ingestion, Egestion, and Assimilation by 40 Fourth-Instar Lepidostoma Larvae Fed on Maple Leaves.

Days	Consumption	Feces	Assimilation efficiency (%)
1	6.96 mg	6.51 mg	6.9
2-7	27.77 mg	24.92 mg	10.3
8-11	26.49 mg	(not measured)	--
Means			
mg/insect/day	0.17	0.11	
mg/mg/day	0.55	0.36	

Assimilation efficiency = 9.8%

Table 16. Ingestion, Egestion, and Assimilation by 30 Fourth-Instar and 10 Fifth-Instar Lepidostoma Larvae Fed on Alder and Maple Leaves

Days	Consumption (mg)	Feces (mg)	% of Total consumption		Remarks
			Alder	Maple	
1-7	109.02	97.15	68	32	All alder was consumed
8-10	56.44	45.48	74	26	--
11-14	73.28	73.59	100	--	Only alder used
15-17	60.21	46.79	54	46	Maple leaves pre-incubated

Means
mg/insect/day 0.44 9.39
mg/mg/day 0.61 0.54
Assimilation efficiency = 12%.

approximately 12% of what was consumed.

Table 17 shows the results of the feeding and assimilation studies with Heteroplectron californicum. The mean consumption of maple and alder leaves was 1.35 mg/insect/day or 0.07 mg/mg/day, and the assimilation efficiency was measured as 7.4%. Heteroplectron californicum showed a marked preference for alder leaves and almost 87% (by weight) of the leaves consumed were alder.

Summary of Consumption Rates, Growth Efficiencies and Assimilation Efficiencies

Table 18 summarizes the experimental data obtained on ingestion and egestion of leaves and the growth or assimilation efficiencies obtained for the respective species.

Table 17. Ingestion, Egestion, and Assimilation by Heteroplectron californicum Larvae Fed on Alder and Bigleaf Maple Leaves.

Days	Consumption (mg)	Feces (mg)	% of Total consumption Alder	Maple	No. of insects
1-6	31.1	--	88	12	8
7-9	60.36	--	79	21	9
10-13	65.70	60.82	93	7	9

Mean consumption	
mg/insect/day	1.38
mg/mg/day	0.07

Assimilation efficiency = 7.4%.

Table 18. Summary of Consumption Rates, Growth Efficiencies and Assimilation Efficiencies.

Taxa	Consumption (mg/mg/day)	Efficiency (%)	Food source
P. princeps	0.14	5.56 growth	Untreated maple
Lepidostoma sp.	0.60	10.13 assimilation	Alder and maple
Heteroplectron californicum	0.07	7.43 assimilation	Alder and maple
Halesochila taylori	0.04	--	Maple
Ecclisomyia sp.	0.10	--	Maple

Field Sampling

Data for the biomass of insect emergence from Watershed 10, from June, 1972 through May, 1973, for the respective taxa are shown in Table 19. Substantial quantities of Empididae (Diptera, mainly Hilara sp.) and Mycetophilidae (Diptera) were also collected in the emergence but were not included since these groups were of of questionable origin and trophic status. Monthly data for the emergence, grouped into trophic categories, are shown in Figure 6, indicating 17% algal feeders, 54% detrital feeders, and 29% carnivores by weight. This grouping assumes that all insects classified as algal-detrital feeders consume equal quantities of both food sources. Gilpin and Brusven (1970) showed that for the mayflies studied, the overall ratio of detritus consumed to algae consumed was very nearly 1:1, however, for Watershed 10, the proportion of algal feeders collected in the emergence is almost certainly overestimated since less than 1% of the energy input to the stream is provided by autochthonous primary production (Lyford, 1973).

The benthos data from Mack Creek, July, 1972 through May, 1973 (Table 20 and Fig. 7), indicate that the benthic standing crop of insects in the old-growth section of the stream is 14% algal feeders, 49% detrital feeders, and 37% carnivores. The standing crop in the clear-cut region is approximately 13% algal feeders, 24% detrital feeders, and 63% carnivores.

Table 19. Aquatic Insect Emergence from Watershed 10 (mg/m^2/mo.).

Month	Chironomidae	Leuctridae	Capniidae	Chloroperlidae	Perlodidae	Trichoptera	Ephemeroptera
June	1.35	2.49	0	2.08	0	2.44	9.09
July	15.05	2.05	0	1.25	0	8.00	30.98
August	19.04	0.85	0	0	0	0.50	9.05
September	18.71	44.00	0	0	0	4.95	6.65
October	11.34	25.28	0	0	0	60.69	0
November	0.30	0	0	0	0	0	0
December	0	0	1.37	0	0	0	0
January	0.49	0	0.40	0	0	0	0
February	0.79	0.19	4.11	0	0	0	0
March	1.94	2.23	0.23	0	0	0	0
April	3.85	25.69	0.45	27.65	0	0	0
May	11.76	1.83	0	43.97	60.06	3.19	4.10
Total (mg/m^2/yr.)	84.60	104.61	6.56	74.95	60.06	79.77	59.86

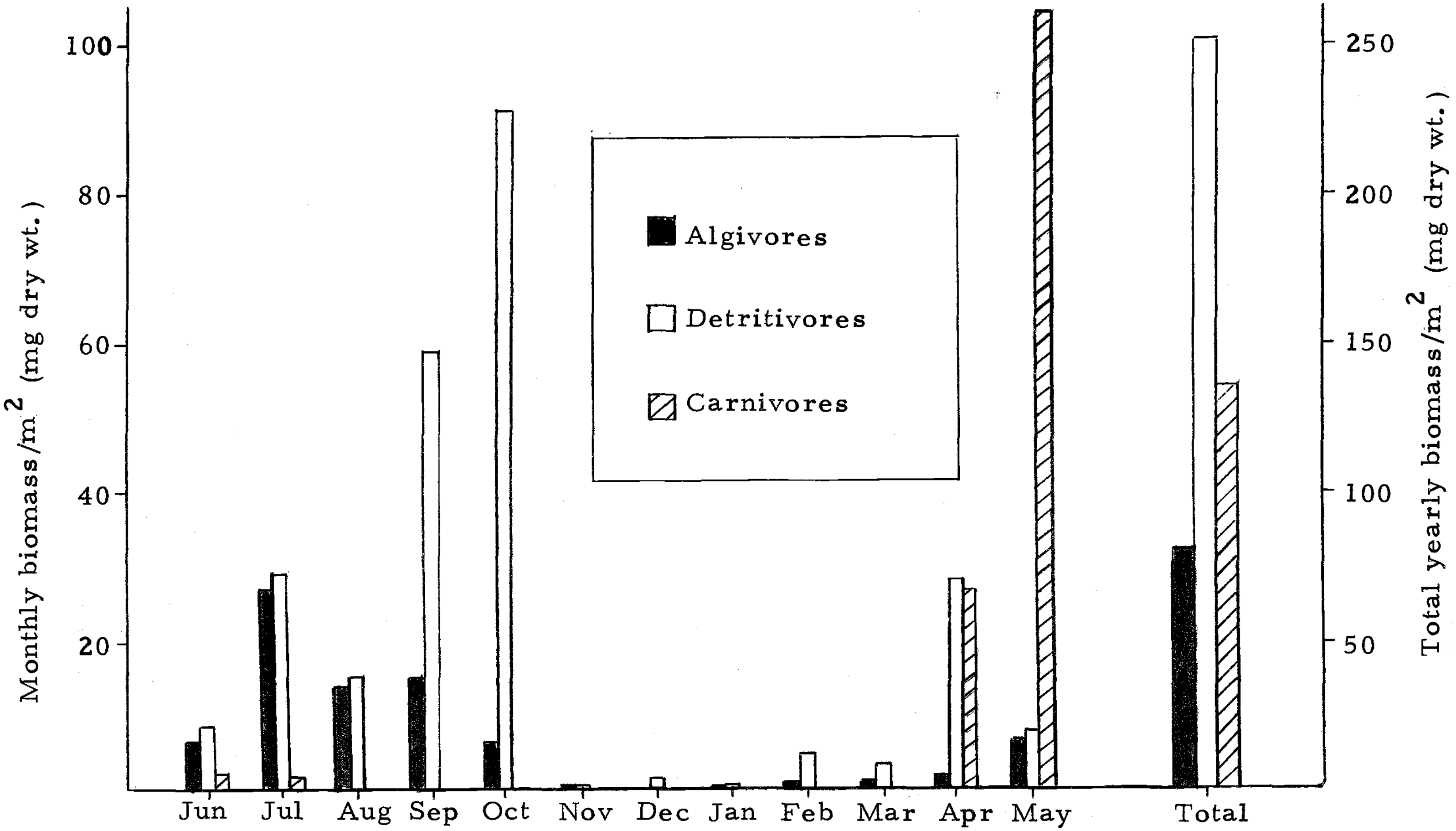


Figure 6. Aquatic insect emergence (mg/m^2) for Watershed 10 grouped in trophic categories.

Table 20. Mean Biomass/m^2 of Benthic Insects in Two Locations in Mack Creek.

Taxa	Mean of six bi-monthly samples (July, 1972 to May, 1973)	
	Old-growth (mg/m^2)	Clear-cut (mg/m^2)
Diptera		
Chironomidae (except Tanypodinae)	151.55	242.41
Tanypodinae	81.81	67.54
Other Diptera	23.91	20.14
Plecoptera		
Leuctridae	133.37	53.82
Nemouridae	195.94	94.33
Pteronarcidae	1333.98	340.34
Perlidae	1119.85	3810.28
Perlodidae	154.91	13.08
Chloroperlidae	304.34	115.99
Other Plecoptera	57.68	59.49
Trichoptera		
Lepidostomatidae	316.22	248.35
Rhyacophilidae	119.65	31.00
Glossosomatidae	12.59	149.62
Hydropsychidae	417.83	1.69
Limnephilidae	144.41	3.60
Other Trichoptera	33.86	129.91
Ephemeroptera		
Baetis	109.50	338.59
Cinygmula	158.17	161.44
Ephemerella	145.14	73.35
Other Ephemeroptera	217.23	271.19
Other insects		
Elmidae	65.62	0
Megaloptera	526.05	0
Total biomass (g/m^2)	6.26	6.41

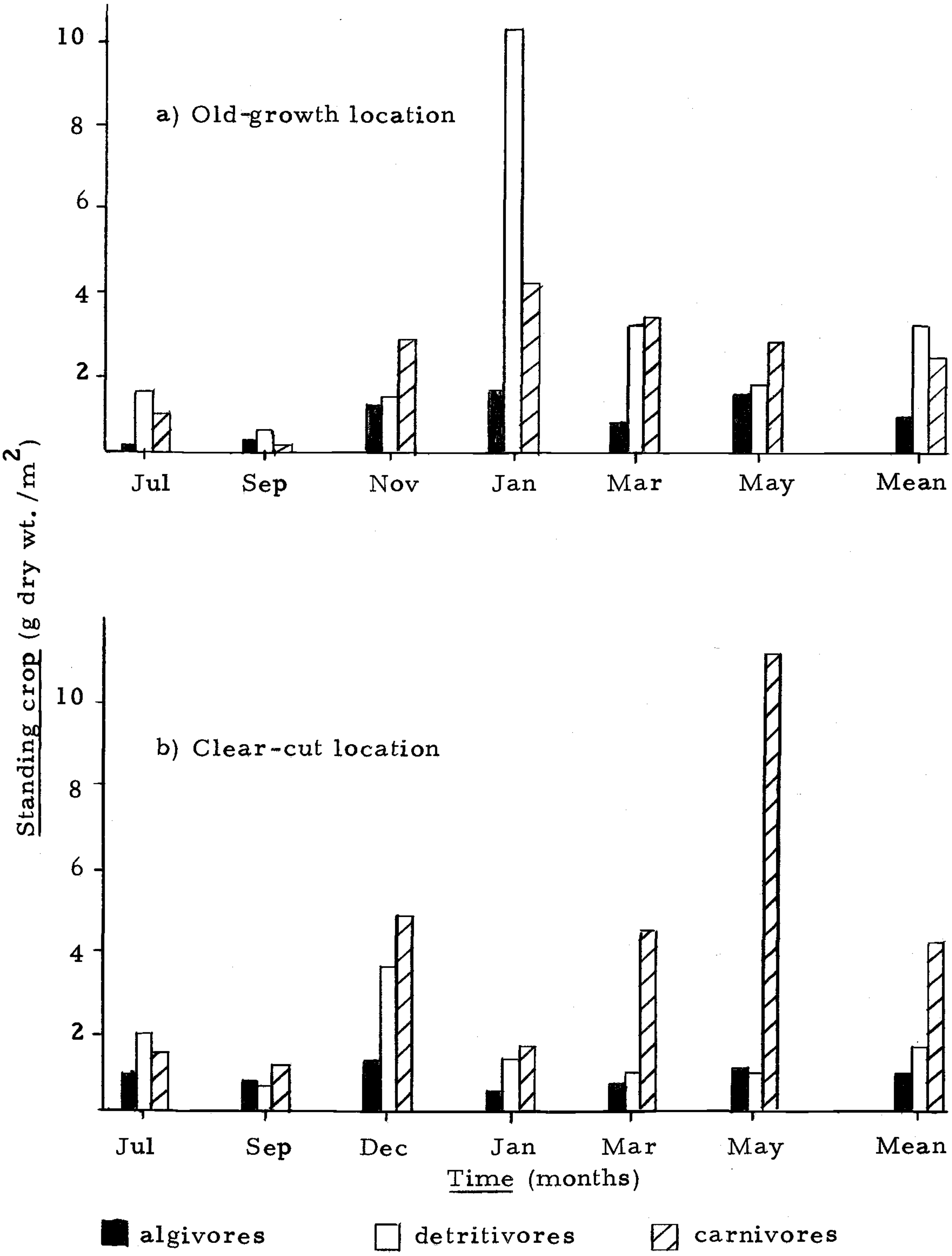


Figure 7. Standing crop of benthic insects grouped into trophic categories for two locations in Mack Creek.

As was shown in the emergence data from Watershed 10 and the benthos data from Mack Creek, detritivores form the dominant portion of the primary consumers in both streams. The standing crop of insect detritivores in the old-growth section of Mack Creek was substantially higher than in the clear-cut section, reflecting the food availability. The standing crop of algal feeders was nearly the same in both locations as was the algal production (Lyford, 1973). The standing crop of insect carnivores was considerably higher in the clear-cut location compared with the old-growth location, perhaps due to a higher turnover rate for the primary consumers in the clear-cut section. Chironomidae and Ephemeroptera were more plentiful in the clear-cut section and species of both groups are known to be multivoltine, while a large proportion of the standing crop in the old-growth section (21%) was comprised of Pteronarcys princeps, a species that has a three or four year life cycle. As a result of higher turnover rates for the insects in the clear-cut section, the production of insects is probably higher in the clear-cut section than in the old-growth section, even though the total standing crops of insects in the two locations were almost identical.

VI DISCUSSION

Non-Linear Consumption Model

All of the consumption rates were calculated using equation 1, page 16, assuming a constant rate of leaf weight loss without insects and a constant feeding rate by the insects. These assumptions are reasonably valid for moderately long-term studies using pre-leached leaves, but for very short-term or long-term studies or unleached leaf material, the assumptions may be misleading. The rate of leaf weight loss due to leaching and microbial decomposition probably often approximates an exponential decay curve, as shown in Figure 8a, approaching a constant rate only after the highly soluble compounds, such as simple sugars and starches, have been leached from the leaf.

The insect feeding rate can vary widely over short or long periods of time, depending on factors such as food quality and availability, and the behavior of the insect. For example, Sedell (1971) found distinct diurnal feeding patterns for Neophylax concinnus larvae (Trichoptera: Limnephilidae) and Anderson (1967) and Waters (1969) found diel periodicity in drift of several species of Trichoptera indicating corresponding fluctuations in feeding activity. The insect feeding rate therefore almost certainly fluctuates over short time periods due to behavior patterns, as well as over long

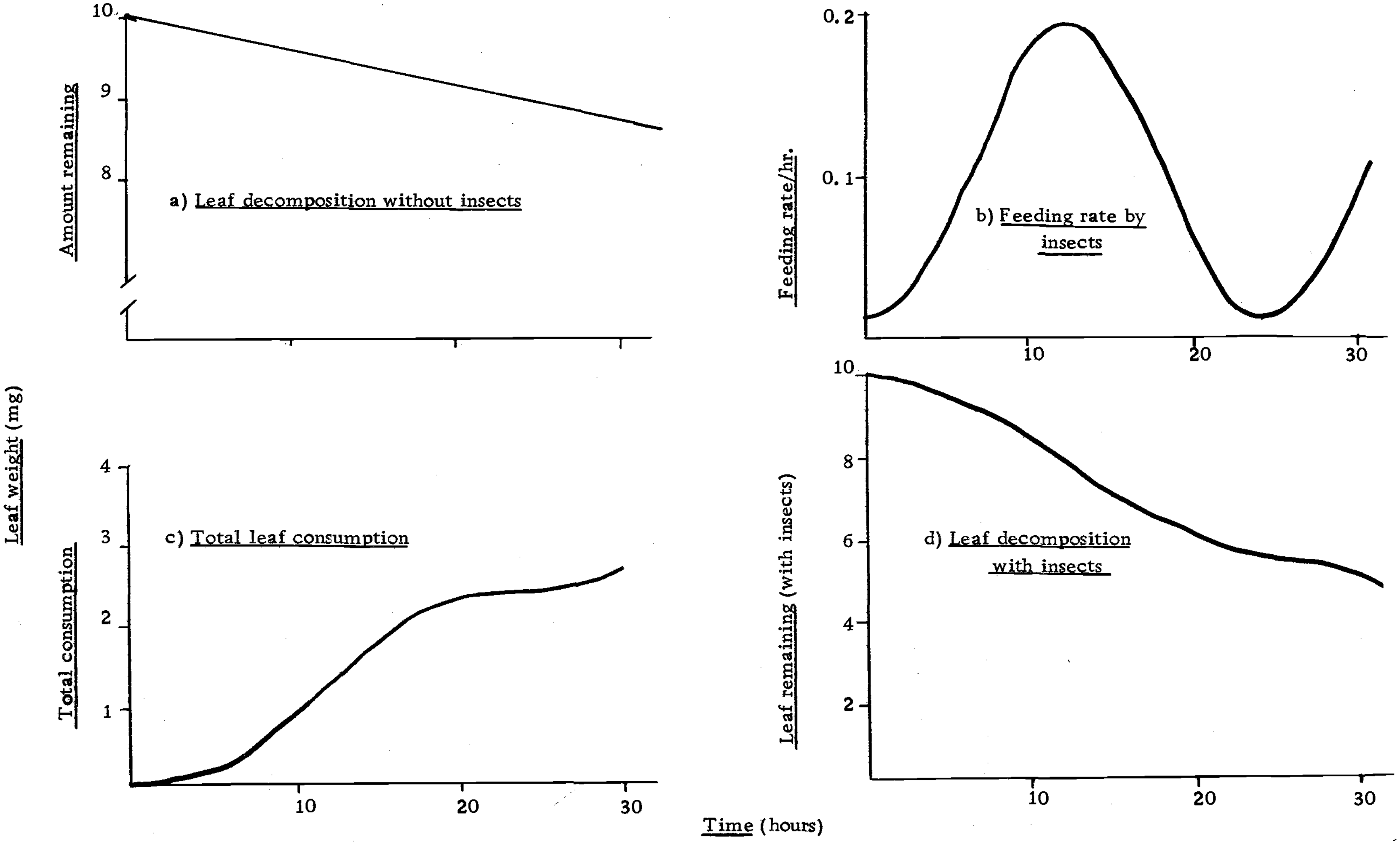


Figure 8. Hypothetical leaf decomposition and insect feeding.

time intervals due to food quality and availability. The feeding rate of the insect versus time might appear as in Figure 8b, with time in units of hours, days or weeks, and the total consumption would then appear as in Figure 8c, being the integral of the feeding rate function.

Subtracting the insect's consumption at any given time from the leaf weight at the same time gives Figure 8d, where

$$\text{Total consumption} = \int_0^t Y_i \, dt = Y_t - Y_{1_t}$$

Y = $f(t)$ describing the quantity of leaf remaining at time t without insect feeding,

Y_1 = $g(t)$ describing the quantity of leaf remaining at time t with insect feeding,

Y_i = $h(t)$ describing the feeding rate of the insects.

Differentiating both sides of the above equation gives

$$\begin{aligned}\text{Consumption rate} = Y_i &= d(Y - Y_1)/dt \\ &= dY/dt - dY_1/dt\end{aligned}$$

presumably $f(t)$ and $g(t)$ could be derived experimentally perhaps using a computer curve-fitting program to aid in the data analysis.

As an example of this type of analysis for changes in feeding rate over a long time interval, data were used from Edwards and

Heath (1963) showing area loss in terrestrial leaf litter contained in fine mesh bags compared with leaf litter in coarse mesh bags (Fig. 9a). These data show a change in feeding rate of the invertebrates (mainly earthworms) as the leaf material became initially conditioned and then as most of the palatable portions were eaten. One can subtract the amount present in the coarse mesh bags from the amount present in the fine mesh bags at any given time and arrive at a graph of total consumption versus time (Fig. 9b). The slope of the consumption graph can then be taken for small increments of time and an approximate graph of feeding rate versus time is obtained (Fig. 9c). In the analysis of these particular data, the use of curve-fitting and differentiating techniques is probably not valid or useful since no exact curve could be defined on the basis of the six data points. Similar analysis, with or without curve-fitting, could be performed on data obtained on a short-term basis.

Leaf Preference

Bigleaf maple leaves were chosen as a food source in most of the experiments since maple is a predominant stream-side deciduous species in the H. J. Andrews Forest and leaves are present in the streams throughout most of the fall and winter, providing a long-term food source for detritivores. Maple leaves were known to be a palatable food for stream detritivores from laboratory tests

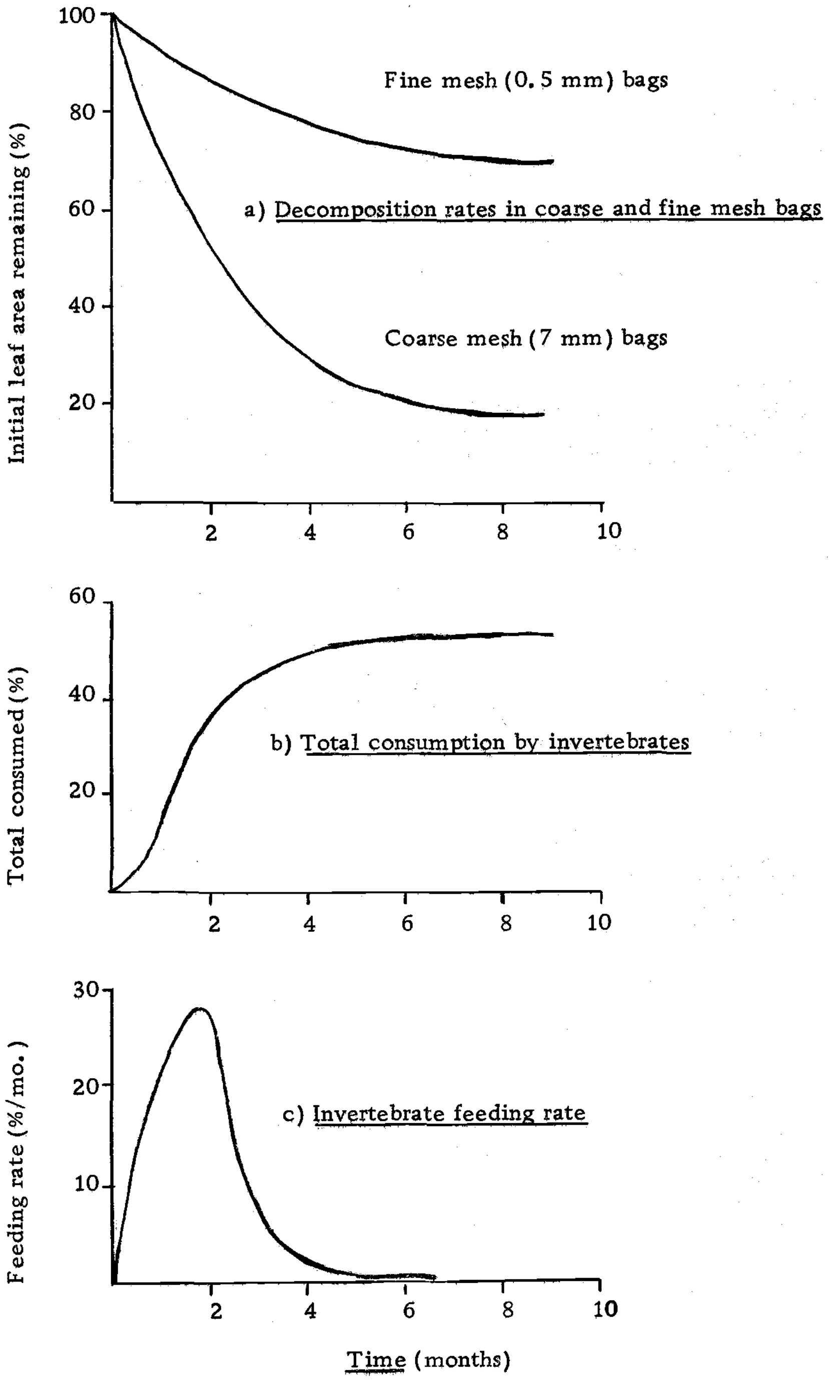


Figure 9. Terrestrial leaf decomposition and invertebrate feeding derived from data of Edwards and Heath (1963).

and data presented in Kaushik and Hynes (1971).

In the present study, insects fed readily on maple leaves, much preferring them to oak leaves. However, Lepidostoma and Heteroplectron californicum preferred alder leaves, consuming as much as 87 mg of alder to 13 mg of maple leaves in the case of Heteroplectron californicum. It has been suggested that this preference for alder leaves is due to the high nitrogen and protein content of alder leaves compared with other species. Goldman (1961) reports alder leaves as 2.31% nitrogen versus 0.52% for other species. Kaushik and Hynes (1971) give the following percentages of nitrogen and protein respectively for leaves of deciduous species: alder, 2.12, 11.5; maple, 0.78, 4.4; elm, 1.13, 6.3; and oak, 1.33, 7.8. However, leaf preference is not directly correlated with either nitrogen or protein content. Kaushik and Hynes (1971) found elm and maple leaves to be most preferred by Gammarus, Asellus, and Hyalella and Wallace et al. (1970) found oak leaves to be least palatable to Peltoperla maria. In the present study, alder leaves were preferred in most cases and maple leaves were acceptable, but oak leaves were not fed upon, even in the absence of other food, until they had been in the water for at least several weeks.

Rather than total nitrogen or protein, the choice of food may be related to the actual nutritional value of the leaves. Richter (1943) showed that rats actively selected a nutritionally complete food source.

In contrast, Trager (1947) states that food preference in insects is independent of nutritional value and is based on previous experience.

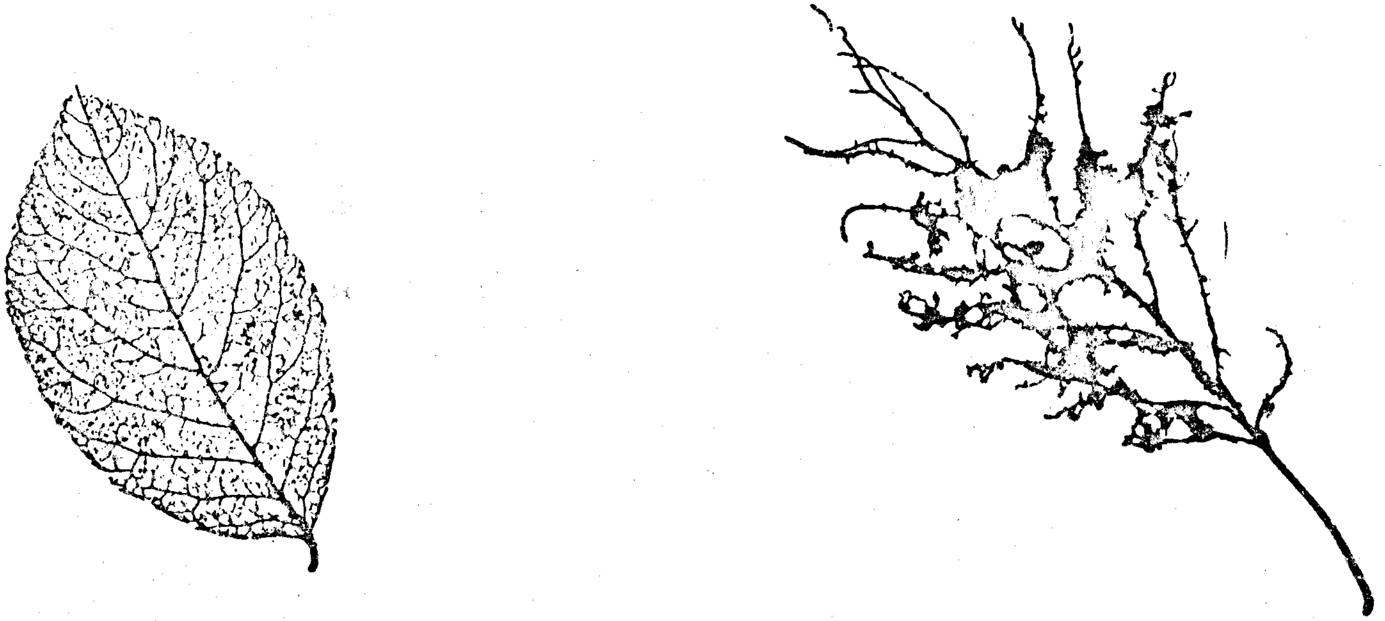
A major factor affecting the palatability of leaves is the degree of decomposition and the associated growth of microorganisms. As shown by Kaushik and Hynes (1971), Kostalos (1972) and the present study, the presence of fungal growth on the leaf appears to be a prerequisite for feeding. Lepidostoma in the preliminary studies of Trichoptera showed no apparent preference for either alder or maple leaves when the latter were incubated for 48 hours prior to placing in the water with the unincubated alder leaves compared with a 3:1 preference for alder when both species were unincubated. In support of the insects' preference for alder leaves, Nilsson (1964) found aquatic hyphomycetes to be most common and most rapidly growing on alder leaves compared with other deciduous species.

The presence of high quantities of certain chemicals in the leaf, such as tannin in oak and walnut leaves, almost certainly has a deterent effect on insect feeding.

The texture of the leaf also seems to have a bearing on its palatability (Hargrave, 1972). Leaves for the growth:consumption experiments with P. princeps were all collected from the same tree at the same time, but there was considerable variability in leaf thickness and texture. One type of leaf, apparently from the edge of the canopy was very thick, tough, and leathery, and was quite unpalatable. The other type of leaf was much thinner and more fragile when dry and was much more palatable. Most oak leaves would presumably fall in the former category of leathery leaves and this could explain their general unpalatability.

The texture of the leaf and the feeding mechanism of the detritivore are directly related, since only efficient shredders will be able to utilize the more leathery leaves. In the Xeroxed picture of leaves after insect feeding (Fig. 10), the variability in feeding technique is not related to the size of the insect. The specimens of Halesochila taylori and Heteroplectron californicum weighed approximately 16 and 20 mg each, respectively. This variation in feeding technique must be a result of variation in mouthpart structure and action. Ecclisomyia, an efficient algal grazer, was by far the poorest shredder of the insects tested, scraping off only the outer layers of the leaf and leaving behind a transparent mesophyll layer. It seems reasonable to assume that for an insect such as Ecclisomyia, the texture of the food source would be a major factor in selection of food, while for very efficient shredders such as P. princeps or Halesochila taylori, the choice would tend to be based on other factors.

Food preference also varies with the organism being studied. In the present study Lepidostoma preferred alder 3:1 over maple and



Heteroplectron californicum *Halesochila taylori*

Figure 10. Alder leaves after feeding by two species of caddis larvae for five to seven days.

Heteroplectron preferred alder by a ratio of 8:1. Oak leaves were found to be unpalatable as was shown by Wallace et al. (1970). Kaushik and Hynes (1971), however, found oak and alder to be equally palatable to Asellus, Gammarus and Hyalella, but they preferred elm or maple leaves.

In reality, preference for a given leaf species probably involves all of the above factors, including individual or species preference, protein or nitrogen content, degree of decomposition and microbial colonization, overall nutritional value, chemical factors such as the presence of tannin, varying feeding mechanisms, and previous experience or conditioning of the individual insect or species. It is not known whether the feeding stimulus is an olfactory or a gustatory one, but this might prove pertinent to investigate. It would be particularly interesting to determine the mechanism by which the insects detect the presence or absence of fungi on the leaf.

Assimilation Efficiency

The assimilation efficiencies (dry weight of ingestion minus egestion/dry weight of consumption) were 7.4%, Heteroplectron californicum fed on maple and alder leaves; 9.8%, fourth-instar Lepidostoma fed on maple leaves; and 12%, fourth and fifth-star Lepidostoma fed on alder and maple leaves. Lawton (1970) has shown differences in assimilation efficiencies of Pyrrhosoma nymphula (Odonata: Zygoptera) nymphs depending on food source and instar, but found no differences with changes in temperature (4 and 10°C), changes in feeding rate, or during diapause or metamorphosis for final-instar nymphs. Assimilation efficiencies reported from some other studies are found in Table 21.

From Table 21, it is clear that leaf detritus is among the most poorly assimilated food sources, with an average assimilation efficiency of 10 to 12%, compared with 30 to 75% for diatoms or green algae, and 70 to 95% for animal matter.

The major factor responsible for the low assimilation efficiencies of detritivores is the presence of higher quantities of cellulose and lignin and lower quantities of more digestible carbohydrates in the leaf material, compared to live plant tissue. Cellulase is apparently present in the alimentary tracts of only a few insects (Ctenolepisma [Thysanura], and Schistocera gregaria) although in S. gregaria enzyme activity is not great enough to be of nutritional value except possibly under starvation conditions (Evans and Payne, 1964). Cellulase is also known to occur in some wood-boring beetles (Anobiidae and Cerambycidae) and hemicellulase is present in the Scolytidae (Chapman, 1969). Nielson (1961) found no evidence of cellulase or ligninase in any of the soil insects studied. Many wood-eating insects such as termites rely on enteric

Table 21. Assimilation Efficiencies of Terrestrial and Aquatic Invertebrates on Various Food Sources.

Taxa	Food	Assim. eff. (%)	Source
Acroneuria californica and *A. pacifica* (Plecoptera)	Invertebrates	82.8	Brocksen, *et al.*, 1968
Asellus aquaticus	Sediment	70	Levanidov, 1949
B. crotchi	Algae	30	Winterbourne, 1971
B. crotchi (final instar)	Invertebrates	70	Winterbourne, 1971
Conocephalus (Orthoptera)	Grass	38	Van Hook, 1971
Hyalella azteca	Subsurface sediment	6.5	Hargrave, 1970
H. azteca	Surface sediment	15	Hargrave, 1970
H. azteca	^{14}C-bacteria	60-80	Hargrave, 1970
H. azteca	^{14}C-diatoms	75	Hargrave, 1970
H. azteca	^{14}C-green algae	45-55	Hargrave, 1970
H. azteca	^{14}C-blue green algae	5-15	Hargrave, 1970
Lepidoptera spp.	Plant material	30	Evans, 1939
Pteronarcys scotti	Leaf detritus	10.6	McDiffett, 1970
Pteronemobrius (Orthoptera)	Grass	44	Van Hook, 1971
Pteronemobrius	Leaf litter	36	Van Hook, 1971
P. nymphula (second instar)	*Daphnia*	95	Lawton, 1970
P. nymphula (final instar)	Invertebrates	83-91	Lawton, 1970
Schistocera gregaria (Orthoptera)	Plant tissue	28-43	Dadd, 1960

bacteria or flagellates for the breakdown of cellulose.

The alternative to digestion of cellulose is the consumption of bacteria or fungi that have already made the transformation from cellulose to usable carbohydrates and it has been suggested that a large portion of the aquatic detritivores receive nutrients in this manner. Hargrave (1970) states that *H. azteca* is incapable of digesting cellulose or lignin, indicating a dependence on extra-gastrointestinal digestion, and Wallace, *et al.* (1970) found no evidence of enteric bacteria present in the alimentary canal of *P. maria* in sufficient numbers to significantly aid in digestion. The present study also suggests that aquatic bacteria, at least are required by *P. princeps* for efficient utilization of leaf detritus. Kaushik and Hynes (1971) showed that aquatic fungi would actually increase the calorific value of leaf detritus if sufficient nutrients were present in the water.

Growth Efficiency

The gross growth efficiencies for *P. princeps* nymphs in this study were 4.94% from Experiment I, growth:consumption linear regression; 4.94% from Experiment II, growth:consumption regression; and 5.56% from Experiment II, growth:consumption:temperature regression. These values are well within the range reported by McDiffett (1970) for *P. scotti*, where gross growth efficiencies were from 2.8% to 6.5% with a mean of 3.6% over 17 months. Other values reported in the literature are listed in Table 22.

A more common method of expressing growth efficiency is as net growth efficiency, calculated as the ratio of growth to assimilation (Warren, 1971). No measurements of assimilation were made for P. princeps, but assuming a 10% assimilation efficiency, the net growth efficiency for P. princeps would be approximately 50%. Other net growth efficiencies reported in the literature are shown in Table 23.

From the comparisons of assimilation and growth (Tables 21 and 22), one can see that leaf detritus is a generally poor food source when compared with live plant tissue or animal material, as shown in the low assimilation efficiencies and gross growth efficiencies of the detritivores. The comparison of net growth efficiencies, however, shows that the assimilated leaf detritus is probably as good a source of nutrition as assimilated plant material or animal material.

Consumption

The consumption rates found in this study varied from 0.04 mg/mg/day for Halesochila taylori larvae fed on maple leaves to 0.60 mg/mg/day for Lepidostoma larvae fed on maple and alder leaves. Some consumption rates for other species are listed in Table 24.

Table 22. Gross Growth Efficiencies for Terrestrial and Aquatic Organisms on Various Food Sources.

Taxa	Food	Gross growth eff. (%)	Source
B. crotchi	Algae	7	Winterbourne, 1971
B. crotchi (final instar)	Invertebrates	40	Winterbourne, 1971
Beef cattle	Grass	4.1	Phillipson, 1966
Young beef cattle and chickens	--	35	Phillipson, 1966
Daphnia pulex	Plankton	4-13	Armstrong, 1960

Table 23. Net Growth Efficiencies for Terrestrial and Aquatic Invertebrates on Various Food Sources.

Taxa	Food	Net growth eff. (%)	Source
Carnivores	Invertebrates	59 (net production)	Teal, 1957
Herbivores	--	25 (net production)	Teal, 1957
Daphnia pulex	Plankton	55-59	Armstrong, 1960
Lepidoptera spp.	Plant material	60	Evans, 1939
Orthoptera spp.	Plant material	15.6	Odum, *et al.*, 1962
P. scotti	Leaf detritus	34.2	McDiffett, 1970

Table 24. Consumption Rates for Terrestrial and Aquatic Invertebrates on Various Food Sources.

Taxa	Food	Rate (mg/mg/day)	Source
H. azteca	^{14}C-bacteria and algae	0.7-1.2	Hargrave, 1970
Lepidoptera spp.	Plant material	0.26	Evans, 1939
Neophylax concinnus	Aufwuchs	0.8-1.6	Sedell, 1971
P. scotti	Leaf detritus	0.06	McDiffett, 1970
Pycnopsyche gentilis and *P. luculenta* (Trichoptera)	Leaves (several spp.)	0.02-1.13	Mackay and Kalff, 1973
Schistocera gregaria	Plant tissue	0.5-1.0	Davey, 1954
Stenonema pulchellum (Ephemeroptera)	Algae	0.13-0.22	Trama, 1957

VII CONCLUSION

As a summary of the experimental results obtained in this study, Figure 11 is a model of the detritus-processing pathway, including feeding rate, assimilation, fecal production, metabolism and respiration, and growth or production rate. Feeding rate of 0.10 mg/mg of insect/day to 0.50 mg/mg/day was taken from the experiments using P. princeps and the several species of Trichoptera. Assimilation efficiency (10%) was estimated from the experiments with the caddis larvae. No estimations of leaf fragmentation by the detritivores were made, but from general observations, it is apparent that at least 10% of the amount of food ingested will be fragmented but not ingested. Gross growth efficiency was estimated as 5% from the P. princeps experiments and the food assimilated but not used for growth was assumed to be used in respiration and metabolism.

Perhaps the most important part of the energy transfer shown in Figure 11 is the flow of fragments and feces back into the detrital pool. The fragments and fecal material are in the form of fine particles that are readily available for bacterial and fungal colonization and the substantially increased surface area, compared with the original leaf, allows for much higher microbial densities than could occur on the intact leaf. This increase in microbial growth and the

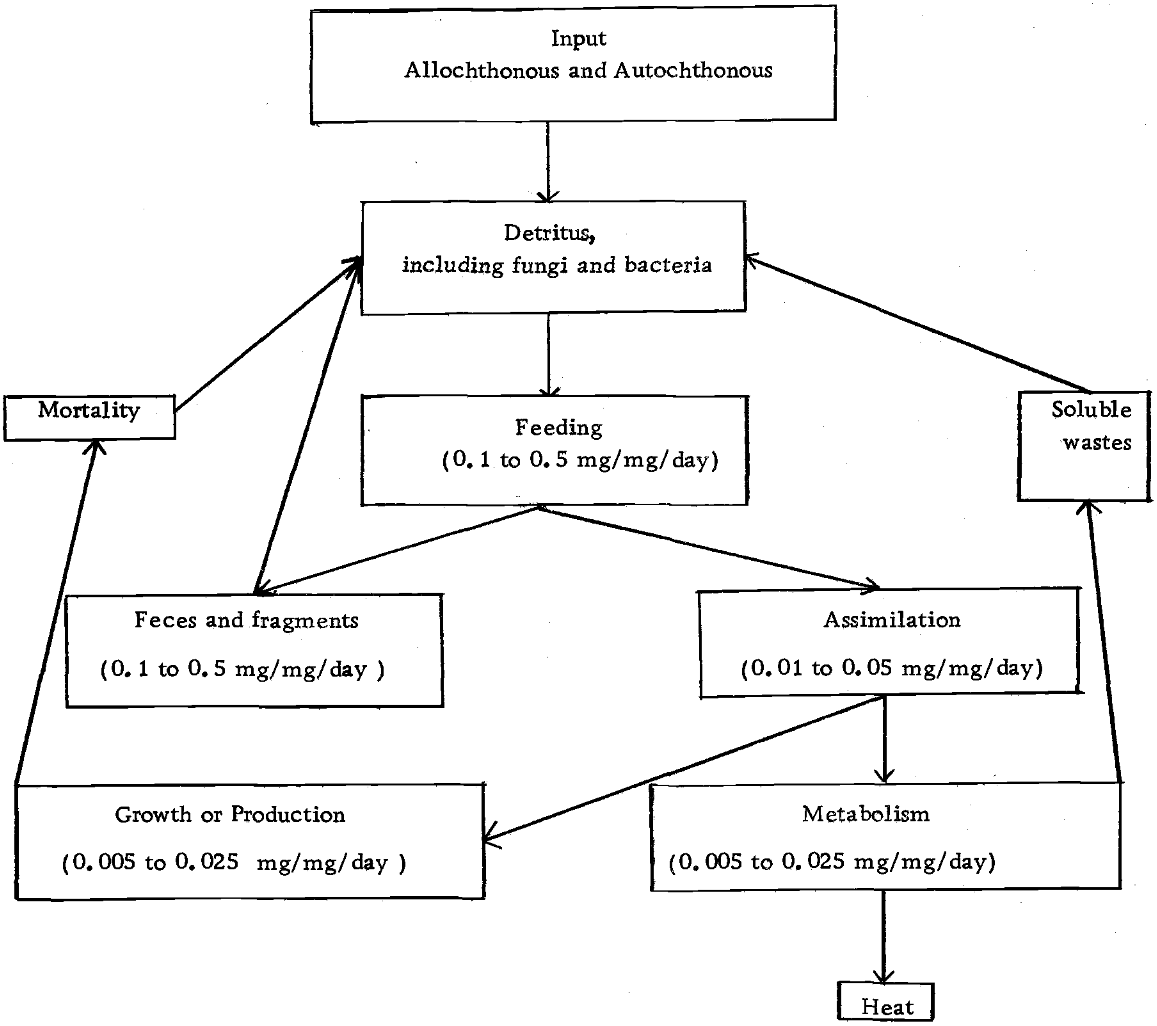


Figure 11. Model of the dynamics of a detrital food pathway.

small particle size makes the fecal material and fragments a much better food source for collector organisms than the original leaf. Assimilation efficiencies for these insects might be as high as 70% as indicated by Hargrave (1970) who found H. azteca to assimilate 60-80% of the ^{14}C-labeled bacteria present in bottom sediment.

Applying this model to the benthos data for Mack Creek indicates that the total amount of detritus processed by the detritivores in the old-growth section is of the order of 0.31 to 1.55 $g/m^2/day$ or approximately 113 to 565 $g/m^2/yr$.

The basic assumption of the above detrital processing model is that all of the detritus is utilized and processed in the same manner as the leaves used in the experiments with P. princeps and the caddis larvae. No information has at present been obtained on the actual amounts and kinds of detritus available in Mack Creek or on the effect of changes in food density on consumption or food utilization. Further research is necessary on the rates of processing and utilization of naturally occurring detritus by stream invertebrates.

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APPENDICES

APPENDIX I

Table 25. Foods of Aquatic Insects.

Taxa	Food Categories and % Composition	Reference	Remarks
Ephemeroptera			
Baetidae			
Baetis bicaudatus	ad(41, 57)[3]	Gilpin & Brusven, 1970	38 specimens, 26 empty
B. herodes	d(96)[2]	Minshall, 1965	measured monthly
B. parvus	ad(41, 53)[3]	Gilpin & Grusven, 1970	10 specimens, 1 empty
B. phoebus	d(78)[2]	Minshall, 1965	measured monthly
B. rhodani	ad	Jones, 1950	fed on red algae
B. tricaudatus	ad(45, 52)[3]	Gilpin & Brusven, 1970	74 specimens, 31 empty
B. vagans	ad(35, 65)[2]	Minckley, 1963	data reported graphically
Baetis sp.	ad(50, 50)[2]	Muttkowski & Smith, 1929	2 specimens
Baetis sp.	a	Ivanova, 1958	in lab preference study
Baetis sp.	ad(70, 30)[3]	Chapman & Demory, 1963	Deer Cr. 290 specimens
Baetis sp.	ad(55, 45)[3]	Chapman & Demory, 1963	Needle Br. 220 specimens
Callibaetis fluctuans	d	Morgan, 1911	fed on artificial diets of ground plant material

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Ephemeroptera			
Baetidae			
Callibaetis sp.	a	Morgan, 1911	---
Centroptilum album	a(88)[1]	Coffman, 1967	riffle areas in Aug & Oct
C. luteolum	a	Ivanova, 1958	lab preference study
C. rufostrigatum	d(95)[2]	Minshall, 1965	measured monthly
Centroptilum sp.	ad(40, 58)[3]	Gilpin & Brusven, 1970	13 specimens, 8 empty
Cloeon dipterum	a	Wissmeyer, 1926	---
C. dipterum	a	Ivanova, 1958	in lab preference study
C. dipterum	a	Brown, 1960	---
Pseudocloeon sp.	a(99)[1]	Coffman, 1967	riffle areas in Aug & Oct
Baetiscidae			
Baetisca bajkovi	a	Lehmkuhl, 1972	---
Caenidae			
Caenis anceps	a(92)[1]	Coffman, 1967	riffle areas in Aug & Oct

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a = algal feeding   d = detrital feeding   c = carnivorous

[1] based on food calories   [2] based on number of food items   [3] based on food volume or area

Taxa	Food Categories and % Composition	References	Remarks
Ephemeroptera (cont.)			
Caenidae			
Caenis horaria	d	Moon, 1938	---
Ephemerellidae			
Drunella sp.	ad(37, 45)^3	Muttkowski & Smith, 1929	25 specimens
Ephemerella aestiva	ad(69, 31)^1	Coffman, 1967	from riffles in Aug & Oct
E. coloradensis	ad(40, 51)^3	Gilpin & Brusven, 1970	7 specimens
E. doddsi	ad(52, 45)^3	Gilpin & Brusven, 1970	55 specimens, 25 empty
E. doddsi	c	Snow, 1973 unpublished	can be carnivorous on other mayflies
E. dorothea	ad(49, 51)^1	Coffman, 1967	from riffles in Aug & Oct
E. edmundsi	ad(27, 70)^3	Gilpin & Brusven, 1970	5 specimens, 2 empty
E. flavilinea	ad(41, 56)^3	"	85 specimens, 11 empty
E. grandis	ad(43, 50)^3	"	97 specimens, 16 empty

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a = algal feeding d = detrital feeding c = carnivorous

^{1}based on food calories ^{2}based on number of food items ^{3}based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Ephemeroptera (cont.)			
Ephemerellidae (cont.)			
E. hecuba	ad(55, 44)[3]	Gilpin & Brusven, 1970	41 specimens, 8 empty
E. hystrix	ad(48, 47)[3]	"	4 specimens
E. inermes & *infrequens*	ad(37,60)[3]	"	147 specimens, 43 empty
E. ignita	d	Ivanova, 1958	lab preference study
E. margarita	ad(46, 55)[3]	Gilpin & Brusven, 1970	20 specimens, 10 empty
E. notata	ad	Jones, 1950	---
E. spinifera	c(80)[3]	Gilpin & Brusven, 1970	6 specimens, 5 empty
E. subvaria	a(75)[2]	Minckley, 1963	data reported graphically
E. teresa	ad(30, 70)[3]	Gilpin & Brusven, 1970	2 specimens
E. tibialis	ad(43, 55)[3]	"	96 specimens, 8 empty
Emphemerella sp.	ad(36, 60)[2]	Muttkowski & Smith, 1929	28 specimens
Ephemerella sp.	ad(60, 40)[3]	Chapmån & Demory, 1963	Deer Cr., 7 specimens

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	References	Remarks
Ephemeroptera (cont.)			
Ephemeridae			
Ephemera simulans	c(87)[1]	Coffman, 1967	from riffles in Aug and Oct
E. varia	a(82)[1]	"	"
Hexagenia bilineata	d	Fremling, 1960	---
H. limbata	ad	Hunt, 1953	---
Hexagenia sp.	ad	Morgan, 1911	---
Heptageniidae			
Anepeorus sp.	c	Burks, 1953	on basis of mouthparts
Anepeorus sp.	c	Edmunds, 1957	on basis of mouthparts
Chirotenetes sp.	a	Clemens, 1917	---
Chirotenetes sp.	c	Morgan, 1911	---
Cinygmula sp.	ad(40, 60)[3]	Chapman & Demory, 1963	Deer Cr., 229 specimens
Cinygmula sp.	ad(35, 65)[3]	Chapman & Demory, 1963	Needle Br., 98 specimens

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Ephemeroptera (cont.)			
Heptageniidae (cont.)			
Cinygmula sp.	ad(40, 53)^{3}	Gilpin & Brusven, 1970	128 specimens, 39 empty
Epeorus albertae	ad(46, 54)^{3}	"	30 specimens, 12 empty
E. grandis	ad(28, 73)^{3}	"	5 specimens, 3 empty
E. longimanus	ad(38, 61)^{3}	"	41 specimens, 12 empty
E. pleuralis	d(85)^{2}	Minshall, J., 1964	25 specimens
Epeorus sp.	ad(60, 40)^{3}	Chapman & Demory, 1963	Deer Cr., 30 specimens
Epeorus sp.	ad(25, 75)^{3}	"	Needle Br., 8 specimens
Heptagenia criddlei	ad(55, 45)^{3}	Gilpin & Brusven 1970	56 specimens, 14 empty
H. lateralis	d	Jones, 1950	---
H. sulphurea	d	Ivanova, 1958	lab preference study
H. sp.	d(76)^{2}	Muttkowski & Smith, 1929	34 specimens
Heptagenia sp.	ad	Morgan, 1911	---
Pseudiron sp.	c	Edmunds, 1957	on basis of mouthparts
Rhithrogena hageni	ad(45, 55)^{3}	Gilpin & Brusven, 1970	38 specimens, 11 empty

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a = algal feeding　　d = detrital feeding　　c = carnivorous

[1] based on food calories　　[2] based on number of food items　　[3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Ephemeroptera (cont.)			
Heptageniidae (cont.)			
R. robusta	ad(41, 55)[3]	Gilpin & Brusven, 1970	4 specimens, 3 empty
R. semicolorata	d	Jones, 1950	---
Stenonema canadense	a(87)[1]	Coffman, 1967	from riffles in Aug and Oct
S. fuscum	a(80)[1]	"	"
S. tripunctatum	a(79)[1]	"	"
Stenonema sp.	d(80)[2]	Minckley, 1963	data presented graphically
Stenonema undet.	ad(70, 30)[1]	Coffman, 1967	from riffles in Aug & Oct
Isonychiidae			
Isonychia albomanicata	c(57)[1]	Coffman, 1967	from riffles in Aug & Oct
Isonychia sp.	c	Burks, 1953	partly predaceous
Leptophlebiidae			
Blasturus sp.	a	Morgan, 1911	---

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Ephemeroptera (cont.)			
Leptophlebiidae			
Choroterpes sp.	a(79)[1]	Coffman, 1967	from riffles in Aug & Oct
Habrophleboides			
americana	ad(49, 51)[1]	Coffman, 1967	from riffles in Aug & Oct
Leptophlebia marginata	d	Moon, 1938	---
L. vespertina	d	Moon, 1938	---
Paraleptophlebia			
bicornuta	ad(33, 66)[3]	Gilpin & Brusven, 1970	30 specimens, 7 empty
P. debilis	ad(36, 61)[3]	"	7 specimens, 1 empty
P. heteronea &			
memorialis	ad(31, 65)[3]	"	33 specimens, 7 empty
P. columbiae	ad(27, 72)[3]	"	6 specimens
P. mollis	d	Hynes & Kaushik, 1968	fed on leaves in lab

a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	References	Remarks
Ephemeroptera (cont.)			
Leptophlebiidae (cont.)			
Paraleptophlebia sp.	d(95)³	Chapman & Demory, 1963	Deer Cr., 444 specimens
Paraleptophlebia sp.	d(95)³	Chapman & Demory, 1963	Needle Br., 371 specimens
Oligoneuriidae			
Oligoneuriella rhenana	a	Pinet, 1962	---
Siphlonuridae			
Ameletus sp.	d(77)²	Muttkowski & Smith, 1929	25 specimens
Ameletus sp.	ad(40, 60)³	Gilpin & Brusven, 1970	57 specimens, 6 empty
Metreturus pecatonia	c	Burks, 1953	on basis of mouthparts
Metreturus sp.	c	Edmunds, 1957	"
Siphlonurus lacustris	d	Jones, 1950	---
S. occidentalis	adc	Edmunds, 1960	fed on live mosquito larvae in lab

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Ephemeroptera (cont.)			
Siphlonuridae			
S. occidentalis	d(79)[3]	Gilpin & Brusven, 1970	5 specimens, 1 empty
Siphlonurus sp.	ad	Morgan, 1911	also some mayfly fragments
Tricorythidae			
Tricorythodes minutus	d(83)[1]	Gilpin & Brusven, 1970	5 specimens
Plecoptera			
Filipalpia			
Capniidae			
Allocapnia granulata	ad	Frison, 1929	---
A. vivipara	ad	"	---
A. recta	ad	"	---
A. mystica	ad	"	---
Leuctridae			
Leuctra claasseni	d	"	---

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a = algal feeding   d = detrital feeding   c = carnivorous

[1] based on food calories   [2] based on number of food items   [3] based on food volume or area

Taxa	Food Categories and % Composition	References	Remarks
Plecoptera (cont.)			
Filipalpia (cont.)			
Leuctridae			
L. hippopus	d	Jones, 1950	---
Nemouridae			
Nemoura delosa	d(97)[2]	Minshall, 1965	measured monthly
N. vallicularia	d(100)[2]	"	"
N. vallicularia	d	Wu, 1923	---
Nemoura sp.	ad	Needham & Claassen, 1925	---
Nemoura sp.	d(100)[3]	Chapman & Demory, 1963	23 specimens
Peltoperlidae			
Peltoperla brevis	a(90)[2]	Chapman & Demory, 1963	Deer Cr., 4 specimens
P. brevis	d(100)[2]	"	Needle Br., 2 specimens
P. maria	d	Wallace, et al, 1970	---

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Plecoptera (cont.)			
Filipalpia (cont.)			
Pteronarcidae			
Pteronarcys californica	d^2	Muttkowski & Smith, 1929	virtually 100% detritus
P. princeps	d	Grafius, 1974	lab study
P. scotti	d	McDiffett, 1970	lab study
Pteronarcys spp.	ad	Needham & Claassen, 1925	---
Taeniopterygidae			
Brachyptera sp.	a	Hynes, 1941	---
Taeniopteryx fasciata (=*Strophoteryx*)	ad	Frison, 1929	---
T. maura	$c(99)^1$	Coffman, 1967	riffle areas in Aug and Oct
T. nivalis	ad	Frison, 1929	---

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Plecoptera (cont.)			
Setipalpia (cont.)			
Chloroperlidae			
Alloperla sp.	c	Chapman & Demory, 1963	Deer Cr. & Needle Br., 52 specimens
Alloperla sp.	dc	Ellis, 1970	scavengers on dead alevins and salmon eggs
Chloroperla sp.	ad	Frison, 1935	---
Chloroperla sp.	c(99)[1]	Coffman, 1967	riffle areas in Aug & Oct
Kathroperla perdita	ad(50, 50)[3]	Chapman & Demory, 1963	Deer Cr., 6 specimens
K. perdita	d(95)[3]	Chapman & Demory, 1963	Needle Br., 20 specimens
Perlidae	c	Frison, 1935	---
Acroneuria californica	c	Chapman & Demory, 1963	Deer Cr. and Needle Br., 35 specimens

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	References	Remarks
Plecoptera (cont.)			
Setipalpia (cont.)			
Perlidae (cont.)			
A. lycorias	c(99)[1]	Coffman, 1967	riffle areas in Aug & Oct
A. pacifica	c(77)[2]	Muttkowski & Smith, 1929	49 specimens
A. pacifica	c	Chapman & Demory, 1963	Deer Dr.; 5 specimens
Phasganophora capitata	c(98)[1]	Coffman, 1967	riffle areas in Aug & Oct
Perlodidae			
Arcynopteryx curvata	ac(70, 21)[3]	Thut, 1969a	87.9% chironomids
A. subtruncata	ac(39, 53)[3]	Thut, 1969a	animals were 85.6% chironomids
Isogenus decisus	c(100)[2]	Minshall, 1965	measured monthly
I. nonus	ac(29, 63)[3]	Thut, 1969a	animals were 85.6% chironomids
I. subvarius	c	Minckley, 1963	---

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Plecoptera (cont.)			
Setipalpia (cont.)			
Perlodidae (cont.)			
Isoperla bilineata	ad	Frison, 1935	---
I. clio	dc (18, 82)[2]	Minshall, 1965	measured monthly
I. confusa	c	Frison, 1935	---
I. decepta	c	"	---
I. duplicata	c	"	---
I. grammatica	c	Jones, 1950	---
I. minuta	ad	Frison, 1935	---
I. mchri	c	"	---
I. richardsoni	c	"	---
Perla verticalis	c[2]	Muttkowski & Smith, 1929	virtually 100% carnivores, 5 specimens, 1 empty

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Plecoptera (cont.)			
Setipalpia (cont.)			
Perlodidae (cont.)			
Perlodes mortoni	c	Jones, 1950	---
Rickera sorpta	c(80)[3]	Thut, 1969a	animals were 95.4 chironomids
Trichoptera			
Brachycentridae			
Brachycentrus americanus	a(97)[1]	Mecom & Cummins, 1964	sometimes feeds on "drift"
B. nigrosoma	ac	Murphy, 1919	older larvae become carnivorous
B. subnubilis	d	Hanna, 1957	also fed on diatoms, etc.
Brachycentrus sp.	ac(73, 18)[2]	Muttkowski & Smith, 1929	---
Micrasema sp.	a(90)[3]	Chapman & Demory, 1963	Deer Cr., 36 specimens

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Trichoptera (cont.)			
Brachycentridae (cont.)			
Micrasema sp.	a(75)[3]	Chapman & Demory, 1963	Needle Br., 10 specimens
Calamatoceratidae			
Ganonema americanum	d	Lloyd, 1921	---
Heteroplectron californicum	d	Grafius, 1974	lab studies
Glossosomatidae			
Agapetus fuscipes	a	Douglas, 1958	---
A. fuscipes	a	Anderson, 1972 (unpublished)	---
Glossosoma boltoni	a	Badcock, 1949	mainly diatoms
G. boltoni	a	Jones, 1950	blue-green algae, 10 specimens
G. boltoni	a	Scott, 1958	---

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	References	Remarks
Trichoptera (cont.)			
Glossosomatidae (cont.)			
G. intermedium	d(88)[2]	Minshall, 1965	---
G. nigrior	a(98)[1]	Coffman, 1967	riffle areas in Aug & Oct
G. nigrior	a	Cummins, *et al* 1966	---
Glossosoma sp.	a(95)[3]	Chapman & Demory, 1963	26 specimens
Goeridae			
Goera calcarata	a(99)[1]	Coffman, 1967	riffle areas in Aug & Oct
Silo nigricornis	a	Slack, 1936	10 specimens
Helicopsychidae			
Helicopsyche borealis	ac(67, 31)[1]	Coffman, 1967	riffle areas in Aug & Oct
Hydropsychidae			
Cheumatopsyche sp.	ac(50, 42)[1]	Coffman, 1967	"
Diplectrona modesta	d(86)[2]	Minshall, 1965	---

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a = algal feeding

d = detrital feeding

c = carnivorous

[1] based on food calories

[2] based on number of food items

[3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Trichoptera (cont.)			
Hydropsychidae (cont.)			
Hydropsyche betteni	c(98)[1]	Coffman, 1967	riffle areas in Aug & Oct
H. betteni	a	Minckley, 1963	---
H. borealis	ad	Coffman, Cummins & Wuycheck, 1971	no animal fragments
H. bronta	ac(39, 55)[1]	Coffman, 1967	riffle areas in Aug & Oct
H. instabilis	a	Jones, 1950	some detritus
H. slossonae	c(80)[1]	Coffman, 1967	riffle areas in Aug & Oct
Hydropsyche sp.	ac(54, 42)[2]	Muttkowski & Smith, 1929	27 specimens
Hydropsyche sp.	adc	Slack, 1936	10 specimens
Hydropsyche sp.	a	Badcock, 1949	some detritus and animals
Hydroptilidae			
Agraylea multiplicata	a(100)[2]	Minckley, 1963	---

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[1] based on food calories　　[2] based on number of food items　　[3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Trichoptera (cont.)			
Hydroptilidae (cont.)			
A. sexmaculata	a	Barnard, 1971	filamentous algae
Orthotrichia tetensii	a	Lepneva, 1964	---
Lepidostomatidae			
Lepidostoma sp.	d(95)[3]	Chapman & Demory, 1963	Deer Cr. & Needle Br. 93 specimens
Lepidostoma sp.	d	Brusven and Scoggan, 1969	fed on dead squawfish
Lepidostoma sp.	d	Grafius, 1974	lab study
Leptoceridae			
Arthripsodes transversus	-	Resh, 1972	bacterial grazers
Anthripsodes sp.	c	Lehmkuhl, 1970	freshwater sponges
Anthripsodes spp.	c	Resh, 1972	freshwater sponges
Leptocerus sp.	ac	Slack, 1936	5 specimens

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[1] based on food calories   [2] based on number of food items   [3] based on food volume or area

Taxa	Food Categories and % Composition	References	Remarks
Trichoptera (cont.)			
Leptoceridae (cont.)			
Oecetis spp.	c	Ross, 1944	---
Setodes sp.	ac	Merrill & Wiggins, 1971	---
Limnephilidae			
Anabolia nervosa	adc	Slack, 1936	18 specimens
A. nervosa	d	Jones, 1950	some algae
Apatania muliebris	a	Elliott, 1971	---
Acroecia consicia	d	Lloyd, 1921	---
Astenophylax argus	d	"	---
Chilostigma difficilis	d	"	---
Drusus annulatus	a	Gower, 1966	---
Dicosmoecus sp.	d	Brusven and Scoggan, 1969	fed on dead squawfish
Ecclisomyia sp.	ad	Grafius, 1974	---

a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	References	Remarks
Trichoptera (cont.)			
Limnephilidae (cont.)			
Ecclisopteryx guttulata	a	Scott, 1958	---
Frenesia difficilus	d	Flint, 1956	---
F. missa	d	Flint, 1956	---
Glyphotaelius sp.	ad	Slack, 1936	10 specimens
Halesochila taylori	d	Winterbourne, 1971	---
H. taylori	d	Grafius, 1974	lab study
Halesus guttifer	d	Lloyd, 1921	---
H. radiatus	d	Jones, 1950	---
Halesus sp.	ad	Slack, 1936	20 specimens
Limnephilus combinatus	ad	Lloyd, 1921	aquatic macrophytes
L. flavicornis	d	Hanna, 1957	also fed on diatoms, etc.
L. indivisus	ad	Lloyd, 1921	---

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[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	References	Remarks
Trichoptera (cont.)			
Limnephilidae (cont.)			
L. lunatus	d	Hanna, 1957	also fed on diatoms, etc.
L. rhombicus	d	Slack, 1936	10 specimens
L. submonilifer	ad	Lloyd, 1921	---
Neophylax autumnus	ad(33, 67)[2]	Minshall, 1965	varies with season
Neophylax nacatus	a(100)[1]	Coffman, 1967	riffle areas in Aug & Oct
N. concinnus & *oligius*	ad(28-37, 62-73)[1]	Sedell, 1971	40 specimens
Platyphylax designata (= *Hesperophylax*)	a	Lloyd, 1921	---
Potamophylax stellatus	d	Hanna, 1957	also fed on diatoms, etc.
Psychoglypha sp.	d	Brusven, 1969a	fed on dead squawfish
Pycnopsyche antica	d(91)[1]	Coffman, 1967	riffle areas in Aug & Oct
P. guttifer	d	Cummins, 1964	also some algae

a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Trichoptera (cont.)			
Limnephilidae (cont.)			
P. guttifer	d	Feldmeth, 1970	lab feeding studies
P. lepida	d	Cummins, 1964	also some algae
P. lepida	d	Feldmeth, 1970	lab feeding studies
P. scabripennis	d	Lloyd, 921	---
Pycnopsyche sp.	d(90)^2	Minckley, 1963	data presented graphically
Stenophylax latipennis	d	Scott, 1958	---
S. stellatus	a	Badcock, 1949	also some detritus and invertebrates
Stenophylax sp.	a	Slack, 1936	10 specimens
Thremma sp.	ad(64, 36)^2	Muttkowski & Smith, 1929	23 specimens
Molannidae			
Molanna augusta	ac	Slack, 1936	12 specimens

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a = algal feeding d = detrital feeding c - carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	References	Remarks
Trichoptera (cont.)			
Odontoceridae			
Odontocerum albicorne	ac	Slack, 1936	12 specimens
O. albicorne	ac	Jones, 1949	---
O. albicorne	adc	Scott, 1958	---
Psilotreta indecisa	a(97)[1]	Coffman, 1967	riffle areas in Aug & Oct
Philopotamidae			
Chimarra aterrima	ad(65, 31)[1]	Coffman, 1967	riffle areas in Aug & Oct
Chimarra marginata	a	Badcock, 1949	---
Phryganeidae			
Agrypnia pagetana	a	Haage, 1970	filamentous algae and *Fucus*
Banksiola crotchi	ac	Winterbourne, 1971	carnivorous in final instar
Neuronia clathrata	a	Gatjen, 1926	---
N. pardalis	d	Lloyd, 1921	---

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Trichoptera (cont.)			
Phryganeidae (cont.)			
N. phalaenoides	a	Gatjen, 1926	---
N. postica	d	Lloyd, 1921	---
N. reticulata	a	Gatjen, 1926	---
N. rufierus	ad	Kolenkina, 1951	---
N. stygipes	d	Lloyd, 1921	---
Oligostomis reticulata	ad	Kolenkina, 1951	---
Phryganea grandis	--	Smirnov, 1962	aquatic macrophytes
P. grandis	c	Haage, 1970	---
P. interrupta	ad	Lloyd, 1921	---
P. minor	a	Gatjen, 1926	---
P. obsoleta	a	"	---
P. striata	a	"	---

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^{1}based on food calories ^{2}based on number of food items ^{3}based on food voluem or area

Taxa	Food Categories and % Composition	Reference	Remarks
Trichoptera (cont.)			
Phryganeidae (cont.)			
P. striata	ad	Kolenkina, 1951	preferred leaf detritus & *Cladophora*
P. varia	a	Gatjen, 1926	---
P. vestita	ad	Lloyd, 1921	aquatic macrophytes
Psychomyiidae			
Polycentropus flavomaculatus	c	Badcock, 1949	---
P. flavomaculatus	c	Jones, 1950	---
Psychomyia flavida	a(94)[1]	Coffman, 1967	riffle areas in Aug & Oct
Rhyacophilidae			
Rhyacophila arnaudi	c(94)[2]	Thut, 1969b	---
R. dorsalis	c	Slack, 1936	---

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Trichoptera (cont.)			
Rhyacophilidae (cont.)			
R. dorsalis	c	Badcock, 1949	---
R. dorsalis	c	Scott, 1958	---
R. fuscula	c	Lloyd, 1921	also some filamentous algae
R. grandis	c(90)[2]	Thut, 1969b	2 specimens
R. parantra	d(96)[2]	Minshall, 1965	---
R. vaccua	c(93)[2]	Thut, 1969b	---
R. vaefes	adc(39, 21, 36)[2]	Thut, 1969b	---
R. vagrita	c(87)[2]	"	---
R. verrula	-	"	31% algae, 64% vascular plant (i.e. moss)
R. verrula	a	Smith, 1968	*Prasiola* and watercress

a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Trichoptera (cont.)			
Rhyacophilidae (cont.)			
R. vepulsa (*narvae*)	c(91)[2]	Thut, 1969b	---
Rhyacophila sp.	dc(28, 49)[2]	Muttkowski & Smith, 1929	32 specimens
Rhyacophila spp.	c	Ross, 1944	---
Rhyacophila sp.	c	Chapman & Demory, 1963	Deer Cr. & Needle Br., 16 specimens
Sericostomatidae			
Sericosoma personatum	d	Slack, 1936	10 specimens
S. personatum	d	Jones, 1950	---
Diptera			
Blepharoceridae	a	Wirth & Stone, 1968	---
Chaoboridae			
Chaoborus nyblasi	c	Dodson, 1970	---

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[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (Cont.)			
Chaoboridae (Cont.)			
C. flavicans	c	Dodson, 1970	---
Ceratopogonidae	c	Kajak & Pieczynski, 1966	---
Palpomyia spp.	d(95)[1]	Coffman, 1967	riffle areas in Aug & Oct
Chironomidae	ad(71, 29)[2]	Muttkowski & Smith, 1929	6 specimens
Chironomidae (except Tanypodinae)	ad	Badcock, 1949	---
Orthocladiinae (=Hydrobaeninae)	d(90)[3]	Chapman & Demory, 1963	Deer Cr., 316 specimens
Orthocladiinae	d(85)[3]	Chapman & Demory, 1963	Needle Br., 255 specimens
Pelopiinae	c	Kajak & Pieczynski, 1966	---
Tanypodinae (=Pelopiinae)	c	Badcock, 1949	---

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[1] based on food calories   [2] based on number of food items   [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (cont.)			
Chironomidae (cont.)			
Brillia flavifrons	ad(42, 58)[1]	Coffman, 1967	riffle areas in Aug & Oct
Corynoneura sp.	ad(66, 34)[1]	"	"
Genus nr. *Corynoneura* sp.	ad(68, 32)[1]	"	"
C. taris	a(77)[1]	"	"
Crictopus exilis	a(94)[1]	"	"
C. sp. nr. *junus*	a(93)[1]	"	"
undet. *Crictopus*	a(100)[1]	"	"
Cryptochironomus sp. A	d(94)[1]	"	"
Cryptochoronomus sp. B	a(100)[1]	"	"
Cryptochoronomus sp. C	c(100)[1]	"	"
Cryptochoronomus sp. 3	c(100)[1]	"	"
C. vulneratus	ad(57, 43)[1]	"	"

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[1] based on food calories　[2] based on number of food items　[3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (cont.)			
Chironomidae (cont.)			
Einfeldia synchrona	ad	Danks, 1971	no filter-feeding mechanism observed
Endochironomus dispar	a	Walshe, 1951	filter-feeders
E. tendens	a	"	"
E. albipennis	a	"	"
Eukiefferiella sp. 2	ad(57, 43)[1]	Coffman, 1967	riffle areas in Aug & Oct
Eukiefferiella sp. nr. *brevinervis*	a(99)[1]	"	"
E. sp. nr. *longicalcar*	a(100)1	"	"
E. sp. nr. *sordens*	a(81)[1]	"	"
genus nr. *Eukiefferiella*	a(77)[1]	"	"
Glyptotendipes barbipes	ad	Kimerle, 1969	in waste stabilization lagoon

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[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (cont.)			
Chironomidae (cont.)			
G. foliicola	d	Walshe, 1951	possibly live plant tissue
G. gripekoveni	d	"	"
G. pallens	d	"	"
G. viridis	d	"	"
Hydrobaenus sp. nr. *paradorenus*	a(88)[1]	Coffman, 1967	riffle areas in Aug & Oct
Lauterborniella marmorata (=*Zavreliella*)	ad	Walshe, 1951	---
Limnochironomus modestus	a(87)[1]	Coffman, 1967	riffle areas in Aug & Oct
Genus nr. *Metriocnemus* sp.	a(80)[1]	"	"
Micropsectra sp.	d	Walshe, 1951	---

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[1] based on food calories   [2] based on number of food items   [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (cont.)			
Chironomidae (cont.)			
Microtendipes pedellus	d	Walshe, 1951	---
M. pedellus	a(87)[1]	Coffman, 1967	riffle areas in Aug & Oct
Paraclunio alaskensis	a	Morley & Ring, 1972	intertidal
Pelopia punctipennis	c	Kajak & Stanczykowska, 1968	---
Pentaneura auriensis	c(100)[1]	Coffman, 1967	riffle areas in Aug & Oct
P. carnea group sp.	c(100)[1]	"	"
P. melanops group sp.	c(100)[1]	"	"
P. psilosella	c(100)[1]	"	"
P. sp. A	c(100)[1]	"	"
Pentapedilum sordens	a	Walshe, 1951	filter-feeder
Phaenopsectra jucundus	a(87)[1]	Coffman, 1967	riffle areas in Aug & Oct
P. obediens	ad(43, 57)[1]	"	"

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[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (cont.)			
Chironomidae (cont.)			
Polypedilum fallax group sp.	c(93)^1	Coffman, 1967	riffle areas in Aug & Oct
P. scalaenum	a(85)^1	"	"
P. sp. nr. *sordens*	a(83)^1	"	"
Polypedilum sp.	d	Walshe, 1951	---
Procladius sp. nr. *abumbratus*	c(100)^1	Coffman, 1967	riffle areas in Aug & Oct
P. choreus	c	Kajak & Stanczykowska, 1968	---
Psectrocladius sp. nr. 4	a(80)^1	Coffman, 1967	riffle areas in Aug & Oct
Saunderia clavicornis	a	Morley & Ring, 1972	intertidal
S. marinus	a	"	"
S. pacificus	a	"	"

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[1] based on food calories   [2] based on number of food items   [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (cont.)			
Chironomidae (cont.)			
Sergentia coracina	d	Walshe, 1951	---
Stempellina bausei	d	"	---
S. sp. nr. *johannseni*	a(86)[1]	Coffman, 1967	riffle areas in Aug & Oct
Tanytarsus conversus	a (84)[1]	"	"
T. dissimilis	ad	Cavanaugh & Tilden, 1930	"
T. sp. nr. *exigua*	a(74)[1]	Coffman, 1967	riffle areas in Aug & Oct
T. exigua	ad(66, 27)[1]	"	"
T. sp. nr. *polita*	a(80)[1]	"	"
T. sp. 3	a(87)[1]	"	"
T. sp. 4	ad(47, 53)[1]	"	"
T. sp. 5	a(100)[1]	"	"
T. rivulorum (=*Rheotanytarsus*)	a	Walshe, 1951	filter-feeders

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[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (cont.)			
Chironomidae (cont.)			
Tanytarsus sp.	ad	Walshe, 1951	---
Tendipes anthracinus (=*Chironomus*)	d	"	---
Tendipes dissidens (=*Einfeldia*)	d	"	---
T. dorsalis dorsalis	d	"	---
T. riparius	d	"	---
T. plumosus flaveolus	a	"	filter-feeders
T. plumosus plumosus	a	"	"
Trichocladius sp. nr. 3	c(77)[1]	Coffman, 1967	riffle areas in Aug & Oct
Zavrelia sp. nr. *pentatoma*	ad(61, 27)[1]	"	"

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Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (cont.)			
Dixidae			
Dixa sp.	d(95)[3]	Chapman & Demory, 1963	Deer Cr., 4 specimens
Empididae			
Hemerodromia sp.	ad(34, 66)[1]	Coffman, 1967	riffle areas in Aug & Oct
Psychodidae			
Psychoda alternata	ad(39, 61)[1]	"	"
Simuliidae			
Prosimulium caudatum	d(87)[3]	Speir, 1973 (unpublished)	30 specimens, Feb & Mar
P. dicum	d(84)[3]	"	26 specimens, Feb & Mar
Simulium arcticum	-	Fredeen, 1963	reared on bacterial suspension
S. articum	ad(39, 58)[3]	Speir, 1973 (unpublished)	34 specimens, May

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[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (cont.)			
Simuliidae (cont.)			
S. canadense	ad(33, 62)[3]	Speir, 1973 (unpublished)	18 specimens, May
S. venustum	-	Fredeen, 1963	reared on bacterial suspension
S. verecundum	-	"	"
S. vittatum	d(88)[3]	Speir, 1973 (unpublished)	14 specimens, Oct
S. vittatum	d	Fredeen, 1963	reared on bacterial suspension
Simulium spp.	a (79)[2]	Muttkowski & Smith, 1929	---
Simulium sp.	d(95)[3]	Chapman & Demory, 1963	33 specimens
Simulium sp.	a(90)[3]	Coffman, 1967	riffle areas in Aug & Oct
Twinnia nova	a(81)[3]	Speir, 1973 (unpublished)	9 specimens, Mar, this species has no head fans

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[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Diptera (cont.)			
Tabanidae			
Chrysops spp.	c	Philip, 1931	lab studies
Tabanus sp.	ad(74, 26)[1]	Coffman, 1967	riffle areas in Aug & Oct
Tabanus sp.	c	Philip, 1931	lab studies
Tipulidae			
Antocha sp.	a(93)[1]	Coffman, 1967	riffle areas in Aug & Oct
Dicranota sp.	d(78)[1]	"	"
Eriocera fultonensis	c(96)[1]	"	"
Tipula nobilis	a(90)[2]	Minckley, 1963	data presented graphically
Tipula sp.	c(76)[1]	Coffman, 1967	riffle areas in Aug & Oct
Megaloptera			
Corydalidae			
Chauliodes sp.	c	Chandler, 1968	---

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[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Megaloptera (cont.)			
Corydalidae (cont.)			
Nigronia serricornis	dc(85, 15)[3]	Minshall, 1965	---
Sialidae			
Sialis californica	c	Azam, 1968	---
S. joppa	c(100)[3]	Minshall, 1965	---
S. rotunda	c	Azam, 1968	---
Sialis spp.	c	Ross, 1937	---
Coleoptera			
Dryopidae	-	Leech & Chandler, 1968	larvae are probably root feeders
Helicus sp. (adults)	ad(26, 74)[1]	Coffman, 1967	riffle areas in Aug & Oct
Dytiscidae			
Acilius sp.	c	Balduf, 1935	adults & larvae all carnivorous

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[1] based on food calories　　[2] based on number of food items　　[3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Coleoptera			
Dytiscidae			
Colymbetes sp.	c	Balduf, 1935	adults & larvae all carnivorous
Coptotomus sp.	c	"	"
Cybister spp.	c	"	"
Dytiscus spp.	c	"	"
Limnaea sp.	c	"	"
Hydroporus sp.	c	"	"
Elmidae	ad	Badcock, 1949	---
Dubiraphia sp. (adults)	ad(26, 74)[1]	Coffman, 1967	riffle areas in Aug & Oct
Optioservus quadrimaculatus (adults)	ad(65, 35)[3]	Chapman & Demory, 1963	Deer Cr., 6 specimens

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[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Coleoptera (cont.)			
Elmidae (cont.)			
O. quadrimaculatus			
(adults)	d(100)[3]	Chapman & Demory, 1963	Needle Br., 1 specimen
Optioservus sp. (larvae)	a(90)[1]	Coffman, 1967	riffle areas in Aug & Oct
Optioservus sp. (adults)	a(76)[1]	"	"
Stenelmis beameri			
(larvae)	ac(71, 22)[1]	"	"
S. beameri (adults)	ad(59, 41)[1]	"	"
Hydrophilidae			
all larvae except			
Berosus spp.	c	Balduf, 1935	----
Berosus spp.	a	"	adults and larvae
Enochrus sp.	a	"	adults

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

Taxa	Food Categories and % Composition	Reference	Remarks
Coleoptera (cont.)			
Hydrophilidae (cont.)			
Laccobius sp.	a	Balduf, 1935	adults
Hydrophilus obtusatus	a	"	"
Tropisternis sp.	a	"	"
Hydrous triangularis (=*Hydrophilus*)	-	Wilson, 1923	adults may be predaceous
Hydrophilus piceus	c	Miller, 1963	adults & larvae
Tropisternis sp.	ad	Spangler, 1960	adults
Psephenidae			
Ectoporia sp.	a(98)[1]	Coffman, 1967	riffle areas in Aug & Oct
Psephenus herricki	a(98)[1]	Coffman, 1967	"
P. herricki	a	Murvosh, 1971	---

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a = algal feeding d = detrital feeding c = carnivorous

[1] based on food calories [2] based on number of food items [3] based on food volume or area

APPENDIX II

Table 26. Wet vs. Dry Weight for Pteronarcys princeps Nymphs.

Specimen	Wet weight (mg)	Dry weight (mg)	% Dry/wet weight
1.	326.80	49.87	15.26
2.	321.10	45.46	14.18
3.	317.58	54.60	17.19
4.	337.76	53.60	15.87
5.	200.62	41.97	20.92
6.	335.64	47.71	14.21
7.	314.93	40.52	12.87
8.	202.00	32.40	16.04
9.	566.35	99.11	17.50
10.	204.32	33.01	16.16
11.	578.00	90.00	15.57
12.	261.73	44.42	16.97
13	241.83	34.00	14.06
14.	204.86	28.00	13.67
15.	200.26	20.87	10.42
16.	311.66	56.46	18.12
Means	307.84	48.25	15.56
			$s_{\bar{x}} = 0.60$

Linear regression of wet weight vs. dry weight.

$b = 5.39$ gm wet wt./gm dry wt. $s_b = 0.438$

$R^2 = 0.9148$ $F = 150.44$ sign. at 0.01.

Table 27. Linear Regression Analysis of Insect Weight[1] versus Time[2] for *P. princeps* Nymphs Fed on Untreated and Antibacterial Treated Bigleaf Maple Leaves.

Untreated

Growth = a + b (Time)

a = 6.47783 std. error of a = 2.97609

b = 0.31123 std. error of b = 0.09827

Analysis of Variance

Source	Deg of freedom	Sum of squares	Mean square
Total	10	553.63817	55.36382
Regression	1	291.81265	291.81265
Residual	9	261.82551	29.09172

F = 10**

$R^2 = 0.52308$

Antibacterial Treatment

Growth = a + b (Time)

a = 5.05434 std. error of a = 1.80771

b = -0.11960 std. error of b = 0.05969

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	10	139.69049	13.96905
Regression	1	43.090306	43.09031
Residual	9	96.600185	10.73335

F = 4.03*

$R^2 = 0.30847$

[1] mg wet weight corrected to a starting value of zero

[2] Days

*Significant at P = 0.10.

** Significant at P = 0.05.

Table 28. Linear Regression Analysis of Insect Weight[1] versus Time[2] for P. princeps Nymphs Fed on Antifungal and Antibiotic Treated Leaves.

Antifungal treatment (without Nystatin treatments)

Growth = a + b (Time)
a = 3.19544 std. error of a = 2.30313
b = -0.19153 std. error of b = 0.06530

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	7	81.37489	11.62498
Regression	1	47.94316	47.94316
Residual	6	33.43172	5.57195

F = 8.6**

$R^2 = 0.58916$

Antibiotic treatment (without Nystatin treatments)

Growth = a + b (Time)
a = -9.48654 std. error of a = 5.09693
b = 0.36020 std. error of b = 0.14337

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	7	330.73260	47.24751
Regression	1	169.55825	169.55825
Residual	6	161.17435	26.86239

F = 6.3**

$R^2 = 0.51267$

[1] mg wet weight corrected to a starting value of zero.

[2] Days

** Significant at P=0.5.

Table 29. Linear Regression Analysis of Growth[1], Consumption[2], Temperature[3], for *P. princeps* Nymphs Fed on Untreated Bigleaf Maple Leaves for 54 Days.

Growth = a + b (Consumption)

$a = -1.814$ std. error of $a = 0.880$

$b = 0.237$ std. error of $b = 0.088$

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	9	10.744290	1.19381
Regression	1	5.070796	5.07080
Residual	8	5.673494	0.70919

F = 7.15**

$R^2 = 0.471953$

Growth = a + b_1 (Consumption) = b_2 (Temperature

$a = 0.825$ std. error of $a = 1.740$

$b_1 = 0.272$ std. error of $b_1 = 0.082$

$b_2 = -0.210$ std. error of $b_2 = 0.123$

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	9	10.7442900	1.19381
Regression	2	6.7336798	3.36684
Residual	7	4.0106102	0.57294

F = 5.88**

$R^2 = 0.62672$

[1] mg wet weight

[2] mg dry weight

[3] degrees C

** Significant at P=.05.

Table 30. Linear Regression Analysis of Growth[1], Consumption[2], and Temperature[3], for P. princeps Nymphs Fed on Antibacterial Treated Bigleaf Maple Leaves for 54 Days.

Growth = a + b (Consumption)

a = -0.562 std. error of a = 0.736

b = 0.050 std. error of b = 0.064

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	9	3.158810	0.35098
Regression	1	0.195023	0.19502
Residual	8	2.963787	0.37047

F = 0.53 n.s.

$R^2 = 0.0617395$

Growth = a + b_1 (Consumption) + b_2 (Temperature)

a = 1.602 std. error of a = 1.189

$b_1 = 0.081$ std. error of $b_1 = 0.059$

$b_2 = -0.175$ std. error of $b_2 = 0.083$

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	9	3.158810	0.3509789
Regression	2	1.3572861	0.6786430
Residual	7	1.8015239	0.2573606

F = 2.637 n.s.

$R^2 = 0.4296827$

[1] mg wet weight

[2] mg dry weight

[3] Degrees C

Table 31. Linear Regression Analysis of Growth[1], Consumption[2], and Temperature, for Nymphs of P. princeps Fed on Antifungal Treated Bigleaf Maple Leaves for 54 Days.

Growth = A + b (Consumption)

$a = 0.004$ std. error of $a = 0.380$

$b = -0.599$ std. error of $b = 0.319$

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	9	6.702560	0.74473
Regression	1	2.055236	2.055236
Residual	8	4.647324	0.58092

F = 3.54*

$R^2 = 0.3066345$

Growth = $a + b_1$ (Consumption) + b_2 (Temperature)

$a = 0.193$ std. error of $a = 1.919$

$b_1 = -0.604$ std. error of $b_1 = 0.343$

$b_2 = -0.013$ std. error of $b_2 = 0.129$

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	9	6.7025600	0.7447289
Regression	2	2.0619751	1.0309876
Residual	7	4.6405849	0.6629407

F = 1.56 n. s.

$R^2 = 0.3076399$

[1] mg. wet weight

[2] mg dry weight

[3] Degrees C

* Significant at P=.10.

Table 32. Linear Regression Analysis of Growth[1], Consumption[2], and Temperature[3], for P. princeps Nymphs Fed on Antifungal Treated (without Nystatin Treatments) Bigleaf Maple Leaves for 54 days.

Growth = a + b (Consumption)

$a = -0.968$	std. error of $a = 0.583$
$b = 1.688$	std. error of $b = 1.142$

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	6	3.3181714	0.5530286
Regression	1	1.0095590	1.0095590
Residual	5	2.3086124	4.6172248

$F = 2.18$ n. s.

$R^2 = 0.3042516$

Growth = a + b_1 (Consumption) + b_2 (Temperature)

$a = -0.493$	std. error of $a = 2.115$
$b_1 = 1.744$	std. error of $b_1 = 1.289$
$b_2 = -0.035$	std. error of $b_2 = 0.149$

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	6	3.3181714	0.5530286
Regression	2	1.0412542	0.5206271
Residual	4	2.2769172	0.5622931

$F = 0.91$ n. s.

$R^2 = 0.3138036$

[1] mg wet weight

[2] mg dry weight

[3] Degrees C

Table 33. Linear Regression Analysis of Growth[1], Consumption[2], and Temperature[3], for P. princeps Nymphs Fed on Antibiotic Treated Bigleaf Maple Leaves for 54 days.

Growth = a + b (Consumption)

a = -0.655 std. error of a = 0.656
b = 0.230 std. error of b = 0.168

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	9	17.852400	1.98360
Regression	1	3.397282	3.39728
Residual	8	14.455118	1.080689

F = 1.88 n.s.

$R^2 = 0.1902983$

Growth = a + b_1 (Consumption) + b_2 (Temperature)

a = -0.293 std. error of a = 3.310
$b_1 = 0.238$ std. error of $b_1 = 0.192$
$b_2 = -0.027$ std. error of $b_2 = 0.243$

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	9	17.852400	1.9836000
Regression	2	3.4234254	1.7117127
Residual	7	14.428975	2.0612821

F = 0.84 n.s.

$R^2 = 0.1917628$

[1] mg. wet weight

[2] mg. dry weight

[3] Degrees C

Table 34. Linear Regression Analysis of Growth[1], Consumption[2], and Temperature[3], for P. princeps Nymphs Fed on Antibiotic Treated (without Nystatin treatments on Days 31-34) Bigleaf Maple Leaves for 54 days.

Growth = a + b (Consumption)

$a = -0.830$ std. error of $a = 0.484$

$b = 0.228$ std. error of $b = 0.102$

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	5	5.3105333	1.0621067
Regression	1	2.9558723	2.9558723
Residual	4	2.3546610	0.5886652

F = 5.03*

$R^2 = 0.5566056$

Growth = $a + b_1$ (Consumption) + b_2 (Temperature)

$a = -4.921$ std. error of $a = 2.382$

$b_1 = 0.128$ std. error of $b_1 = 0.101$

$b_2 = 0.304$ std. error of $b_2 = 0.175$

Analysis of Variance

Source	Deg. of freedom	Sum of squares	Mean square
Total	5	5.3105333	1.0621067
Regression	2	4.1393587	2.0696794
Residual	3	1.1711746	0.3903915

F = 5.30 n.s.

$R^2 = 0.7794620$

[1] mg. wet weight

[2] mg dry weight

[3] Degrees C

* Significant at $P = .10$.