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TROPHIC RELATIONS OF AQUATIC INSECTS[1] 6046

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Annu. Rev. Entomol. 1973.18:183-206. Downloaded from arjournals.annualreviews.org
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INTRODUCTION

One of the most ubiquitous features of freshwater habitats is their present rate of change in response to man-engendered perturbations. Any rehabilitative or management strategy characterized by a high probability for success must rely on fundamental knowledge of the intricacies of freshwater ecosystem structure and function. A basic facet of this structure and function is material cycling and energy flow. In turn, a significant portion of such cycling and flow involves the processing of various forms of organic matter by freshwater invertebrate animals, especially insects. This constitutes a basis for interest in aquatic insect trophic relations—food intake, tissue assimilation, and waste release—with implications ranging from theoretical questions, such as the efficiency of energy transfer, to very specific practical problems: for example, population control of "pest" species represented either by the food or the feeder. As Bates (2) put it, trophic relationships constitute the "cement" holding biological communities together.

Aquatic ecologists have noted (e.g. 31) that the diversity of the ingested food greatly exceeds the diversity of the aquatic insects. Since the majority of species appear to be generalists (polyphagous) rather than specialists (mono- or oligophagous), statements about food habits are subject to considerable variation and require qualification with regard to habitat- and age-specific differences. Therefore, the present focus is on the level at which generalizations are possible and the ecological importance of such generalizations, rather than the food habits of particular species. For those data reviewed, a bias toward North American stream species will be apparent.

Because of the latitude of previous usage, the definition of certain terms is necessary. The compartmentalization of the basic components of food en-

[1] Preparation of this paper and the original research reported was made possible by Contract No. AT(11-1)2002 from the Environmental Sciences Section, Division of Biology and Medicine, US Atomic Energy Commission. Contribution No. 220, Kellogg Biological Station.

[2] The author acknowledges the invaluable assistance of R. C. Petersen, J. C. Wuycheck, F. O. Howard, R. H. King, G. L. Spengler, and G. L. Godshalk, particularly in the area of man's most precious commodity—ideas.

ergy processing by aquatic insects are summarized in Figure 1. Generally, food habit is taken to mean simply what animals ingest—those materials of potential nutritive value that are taken into the digestive tract. Within this framework, herbivory is defined as the ingestion of living plant tissue, algal or vascular; detritivory as the intake of nonliving particulate organic matter and the nonphotosynthetic microorganisms that are always associated with it (detritus); and carnivory as the ingestion of living animal tissue. The material in any category can be taken in either solid form (swallowing, biting, chewing) or liquid form (piercing and sucking). Assimilation follows the digestion of eaten (ingested) food after the movement of the digested substances through the digestive epithelium, after which these substances or their metabolic products are incorporated into the tissues, used as energy sources, or excreted. Egestion is the expulsion of that portion of ingested food not assimilated (feces) and should be distinguished from excretion, which is the elimination of nitrogeneous compounds produced from assimilated material.

Considerable confusion surrounds the designation "selective feeding" which is defined, for the present discussion, as the ingestion of only certain nutritive materials from a range of those that are equally available to the feeding insect. Thus, true selective feeding involves the rejection of some of

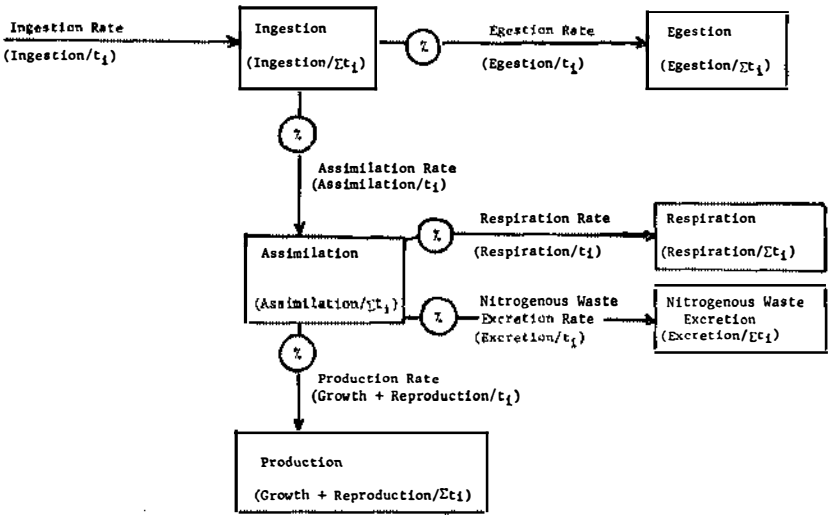

FIGURE 1. Generalized components of an aquatic insect energy budget. Rates are measured over time interval t_i, for example per hour or per day; the boxes represent the summation of rates over some longer period such as a generation or a year. The percentages indicate points for which efficiencies are usually determined. If excretion is primarily as simple nitrogen compounds resulting from catabolic processes, primarily ammonia, the energy cost is included in respiration and the excretion portion deleted.

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the available food substances. The critical point is availability, which is not equivalent to presence. True availability means that no mechanical or other interference is involved that automatically excludes some of the materials without any morphological-behavioral specialization of the insect. In many cases it is difficult, if not impossible, to distinguish between selective feeding and physical (or chemical) restrictions that prevent the intake of all apparently available food materials, or between selective feeding and microhabitat selection. In the latter case, the animal selects a microhabitat on some nonfood basis and automatically is exposed to a narrow range of nutritive substances. Regardless of the morpho-behavioral mechanisms involved, or whether some feature of the habitat or the food itself is the subject of selection, the result is the same—a nutrition based on only a portion of those substances in the environment that could be broadly classified as food. Restricted food intake seems to be preferable terminology since, unlike selective feeding, it does not require that behavioral choice be involved. For many ecological questions, such as general qualitative and quantitative aspects of energy flow through an aquatic ecosystem, the identification of true selection may not be relevant. The ecological and phylogenetic possibilities of polyphagy and monophagy have been contrasted by Dethier (17), who concluded that polyphagy was the primitive condition among phytophagous insects. If species competition is minimized by temporal or microspacial isolation, then polyphagy would be possible on a widespread basis within any given freshwater system. There is some evidence that this is the generalized case (e.g. 27; R. L. Vannote, Stroud Water Resources Center, personal communication; Cummins, Petersen & Howard, unpublished data). Although partitioning of food resources through restriction of diets might increase aquatic insect species diversity, more diversity may be possible if the majority of species are trophic generalists, so that the effect of fluctuations of a specific food source are minimized. Because of caloric and, to a lesser extent, protein similarities of the food materials available in freshwater environments, maximization of nutritive efficiency by selective food intake within plant, detritus, or animal categories is probably rare. To be successful, the energy (or protein) differences between foods must be greater than the energy required by the selective process. Therefore, the general pattern of trophic organization in freshwater ecosystems is most likely based on feeding mechanisms, with food texture and particle size relative to the size of the food gathering device of primary importance.

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Food Substances and Feeding Mechanisms

Classification systems.—General categorizations of trophic relationships are based on the nature of the food, for example, trophic levels indicating the number of transformations above plants (41), or on feeding mechanisms (e.g. 31, 32, 34, 72). Yonge (72) distinguished between fine particle feeders, large particle ingestors, and cell or tissue fluid extractors. General studies of freshwater ecosystems have often grouped the aquatic insects as primary and

secondary consumer trophic levels, that is herbivores and carnivores (e.g. 51), or the herbivore category may be further subdivided into algal and detrital feeders and the overlap between herbivores and carnivores combined as omnivores (e.g. 11, 12, 14, 47, 48).

A combination of food categories and feeding mechanisms has been used to devise what is only one of a great many possible classification systems (Table 1). The most useful organization of any set of data will, of course, depend upon the questions being asked. Organizing on the basis of the general types of feeding mechanisms shown in Table 1 associates each type with a broad food category: shredders—vascular plant tissue; collectors—detrital particles; scrapers—attached algae; predators—live prey.

The compartmentalization of feeding and food types, particularly when such partitioning reflects the source of food income, is often useful; an example is shown in Figure 2 for a generalized woodland stream ecosystem. The emphasis is on the detritus processing portion of the trophic structure since primary production in woodland streams is normally quite low. For all freshwater systems, the majority of the carbon-to-carbon-bond energy built up by vascular plant photosynthesis, terrestrial or aquatic, is extracted through processes within detritus food chains rather than by phytophagous animals. This generalization may also apply to algae, although aquatic insect grazing has been implicated in the reduction of attached algal standing crops (20; see related study on tadpoles, 19) or, as shown for snails (37), algal production may increase while standing crop remains constant. Certainly, the classification of all nonpredaceous aquatic insects as herbivores obscures the dominant role of detrital food chains in most freshwater ecosystems.

Nutritional relationships.—The nutritional requirements of aquatic insects may be broadly classed as two somewhat distinct problems: the intake of adequate calories to meet immediate energy costs and to lay aside energy stores; and the procurement of sufficient protein (essential amino acids) to sustain adequate growth. Because large energy savings can be achieved behaviorally, for example, through reduced locomotion, and since all food materials are calorically rather similar, maximization of calorie intake by dietary selection seems unlikely; algae, vascular hydrophytes, microbes, and invertebrates represent a total range of about 3.5 to 5.5 calories/mg (4.0 to 6.5 cal/ash-free mg, 15). However, total protein may be less evenly distributed (5, 6), although the kinds of amino acids available from any proteinaceous food source are probably fairly constant (6, 61).

A close correspondence between food ingested and food assimilated would be expected from evolutionary processes, but the presence of a material in the digestive tract does not prove nutritional importance. For example, significant amounts of mineral sediment can be found in the guts of many periphyton grazers and fine particle detritivores (11, 12, 44). The mineral substance is not nutritionally significant, but coatings of adsorbed organic material and associated bacteria may be extremely important. Such mineral

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TABLE 1. A general classification system for aquatic insect trophic categories

General category based on feeding mechanism	General particle size range of food (microns)	Subdivision based on feeding mechanisms	Subdivision based on dominant food	North American aquatic insect taxa containing predominant examples
Shredders	>10³	Chewers and miners	Herbivores: living vascular plant tissue	Trichoptera (Phryganeidae, Leptoceridae) Lepidoptera Coleoptera (Chrysomelidae) Diptera (Chironomidae, Ephydridae)
		Chewers and miners	Detritivores (large particle detritivores): decomposing vascular plant tissue	Plecoptera (Filipalpia) Trichoptera (Limnephilidae, Lepidostomatidae) Diptera (Tipulidae, Chironomidae)
Collectors	<10³	Filter or suspension feeders	Herbivore-detritivores: living algal cells, decomposing organic matter	Ephemeroptera (Siphlonuridae) Trichoptera (Philopotamidae, Psychomyiidae, Hydropsychidae, Brachycentridae) Lepidoptera Diptera (Simuliidae, Chironomidae, Culicidae)
		Sediment or deposit (surface) feeders	Detritivores (fine particle detritivores): decomposing organic matter	Ephemeroptera (Caenidae, Ephemeridae, Leptophlebiidae, Baetidae, Ephemerellidae Heptageniidae) Hemiptera (Gerridae) Coleoptera (Hydrophilidae) Diptera (Chironomidae Ceratopogonidae)
Scrapers	<10³	Mineral scrapers	Herbivores: algae and associated material (periphyton)	Ephemeroptera (Heptageniidae Baetidae, Ephemerellidae) Trichoptera (Glossosomatidae, Helicopsychidae, Molannidae, Odontoceridae, Goreridae) Lepidoptera Coleoptera (Elmidae, Psephenidae) Diptera (Chironomidae, Tabanidae)
		Organic scrapers	Herbivores: algae and associated material (periphyton)	Ephemeroptera (Caenidae, Leptophlebiidae, Heptageniidae, Baetidae) Hemiptera (Corixidae) Trichoptera (Leptoceridae) Diptera (Chironomidae)
Predators	>10³	Swallowers	Carnivores: whole animals (or parts)	Odonata Plecoptera (Setipalpia) Megaloptera Trichoptera (Rhyacophilidae, Polycentropidae, Hydropsychidae) Coleoptera (Dytiscidae, Gyrinidae) Diptera (Chironomidae)
		Piercers	Carnivores: cell and tissue fluids	Hemiptera (Belastomatidae, Nepidae, Notonectidae, Naucoridae) Diptera (Rhagionidae)

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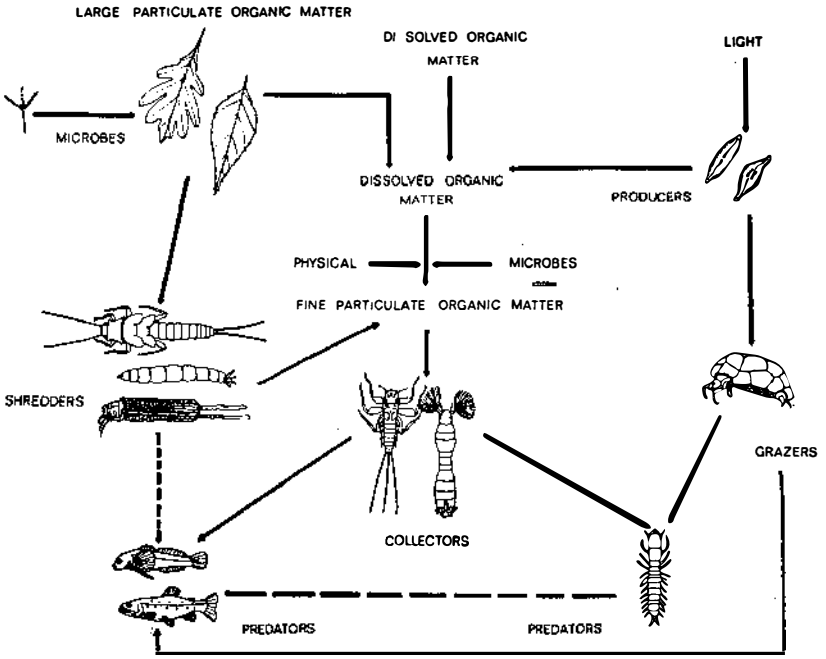

FIGURE 2. A simplified view of trophic relationships in a woodland stream community using the categories of Table 1. Deciduous leaves and photosynthesis by diatoms are utilized, together with soil runoff, as representative of energy inputs to the system. *Pteronarcys, Tipula,* and *Pycnopsyche* are shown as typical shredders, *Stenonema* and *Simulium* as collectors, *Glossosoma* as a grazer, and *Nigronia* and the fish *Cottus* and *Salmo* as predators. Litter microbes are characterized by fungi (such as aquatic hyphomycetes) and fine particle microbes by bacteria. Dashed arrows indicate less frequent exchange.

particles may also enhance digestion through mechanical damage to cellular food since the presence of a grinding crop is rare among periphyton and detrital feeders (7). Differential rates of digestion of food items also renders the nutritional interpretation of visual gut analyses difficult. Presumably, the items digested most rapidly, and therefore least likely to be observed and enumerated, might be of maximum nutritional significance. For example, in predator gut analyses careful inspection for oligochaete chaetae is necessary since the worms are digested very rapidly.

Investigations, such as the work of Brown (7) on the mayfly, *Chloeon dipterum,* have shown that algal cells, for example small diatoms, Chlorococcales and fine filaments, are still viable when taken from the hind gut and placed on culture medium. For other algal forms, viability was reduced as a function of gut residence time. However, the conclusion that viable algal cells

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in the hind gut have served no nutrient function for the ingestor must await the evaluation of the possible role of algal excretions. A gut residence time of 4 to 12 hr could allow for significant inputs from algal cells without digestion, particularly if such excretion or leakage were enhanced by particular osmotic or electrochemical conditions.

Very little is known about the digestive capabilities or efficiencies of aquatic insects. For example, a review by Welch (70) of aquatic consumer assimilation and net growth efficiencies (assimilation÷ingestion and growth ÷assimilation respectively) includes only one aquatic insect, the predaceous damselfly *Lestes sponsa* (21). Although we might infer similarities with terrestrial forms for aquatic representatives of orders that are predominantly terrestrial (Hemiptera, Lepidoptera, Coleoptera, Diptera), extension of such generalizations to the truly aquatic orders (Plecoptera, Ephemeroptera, Odonata, Trichoptera, Megaloptera) is not warranted. All aquatic insects undoubtedly have the enzymatic capability to digest significant components of protein, lipid, and carbohydrate. As Kidder (38) pointed out, the majority of invertebrate animals require the same ten to twelve amino acids. Cellulose and lignin (for herbivores and detritivores) and chitin (for carnivores) represent substances that undoubtedly can be digested only through the activity of a specific enteric flora or fauna. Although definitive work remains to be done, the high percentage of cellulose in leaf material, particularly litter from which a great many labile organics are rapidly leached, suggests that digestion by enteric symbionts would be a likely mechanism at least in some species of shredders. However, since evidence for dependence of litter feeding detritivores on the microbial flora has been presented (e.g. 45, 67), conversion of leaf cellulose accomplished by fungi and bacteria external to the feeding insect may be the critical event. The nitrogen (36) and caloric content (67) of leached leaf litter increases by virtue of the growth and metabolism of microbial populations. In addition to feeding preference experiments (45, 67), in which it is extremely difficult to control microbial levels, tracer studies have indicated a dependence of detritivores on the microbial flora rather than the leaf substrates. When glucose-^{14}C is used to label leaves previously incubated in a natural stream, *Lepidostoma* larvae become tagged (both ingestive and assimilative phases, see below). After a correction was made for adsorption, the radioactive lable in the larval tissue was incorporated by the digestion and assimilation of microbial biomass (Cummins, Petersen, Howard & Wuycheck, unpublished data).

Critical studies of the regulation of food intake in aquatic insects have not been made. In terrestrial species, the most common regulating device is fullness of the digestive tract mediated through stretch receptors associated with the gut (18, 22, 25, 53, 69). The work of House (30) with sphingid larvae and that of Gordon (24) with cockroaches suggest that feeding rate can be regulated on the basis of nutrient content of the food. The protein content of the artificial diet used by House (30) was manipulated by chang-

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ing the cellulose content; feeding rate increased as protein content decreased. These results have important implications for possible regulation of feeding and growth rates in aquatic insects. Vascular hydrophytes differ in protein content (6), as does leaf litter in relation to leaching period and microbial activity (36, 39). However, evidence for nonselective feeding both by vascular hydrophyte shredders (e.g. 3) and litter shredders such as *Tipula* species from small woodland streams, providing the leaves are appropriately conditioned (Cummins, unpublished data), suggests that nutritionally mediated regulation of feeding habits or rates is not likely. In fact, with regard to stream *Tipula,* the apparently more nutritionally suitable food is ingested more rapidly than the less suitable food. However, the differences observed (43) may be entirely dependent on the degree of mechanical interference with the feeding process attributable to different leaf types or degree of conditioning.

The regulation of insect predator feeding by prey density has been most thoroughly investigated by Holling (29) in experiments with mantids. The data show that lack of food increases the area of the field of response of the predator to prey and therefore feeding rate, but not capture success or the rate at which captured prey are devoured. These findings are probably quite applicable to nymphal Odonata, and, as Lawton (40) has suggested, maximum feeding rates observed in the laboratory may be significantly higher than natural rates in the field where prey density is more variable and generally lower.

Prey digestive tract contents may be important sources of predator nutrition. In particular, predators feeding on the early instars of other species may take in food that has little fat reserves and minimal structural protein elaboration, and is surrounded by an indigestible chitinous shell. The most nutritional portion of such prey may be the digestive tract, packed with food material which has been partially altered physically and chemically. Therefore, at least to some extent, predators might be considered to feed on prey digestive tracts.

Radiotracers provide a most useful tool for studying ingestion and assimilation rates (13, 58, 63), although correlated laboratory and field data are required for reliable interpretation. Tracers can be used to partition the aquatic macroconsumers generally into herbivore, detritivore, and carnivore categories. A portion of the system is enclosed in two separate containers in which natural conditions are simulated (for example, for stream studies the author uses 5-liter circulating chambers operated in situ). One chamber is inoculated with bicarbonate-^{14}C which is incorporated by the photosynthetic food, the other with an organic substrate such as glucose-^{14}C which is taken up by the bacteria and fungi. After about 2 hr (or at intervals up to 12 hr) samples of plants, detritus, and all the aquatic insects are collected. The animals are sorted into general taxonomic and morphological categories and then subgroups on the basis of size (if necessary, the chambers can be

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stocked with additional animals, but replicate chambers are preferable so that natural densities are maintained). The specific radioactivities of the plant, detrital, and animal food are determined, and corrected animal adsorption determinations are made using prepupae, pupae, or molting (nonfeeding) larvae; all results are compared on a per-unit-weight basis. The general result is that herbivores are maximally tagged in the bicarbonate-^{14}C chambers, detritivores in the organic-^{14}C chambers, and predators variously labeled in both chambers. The results shown in Figure 3 are for the trichopteran *Hydropsyche betteni* which is a herbivore-detritivore-carnivore in the system

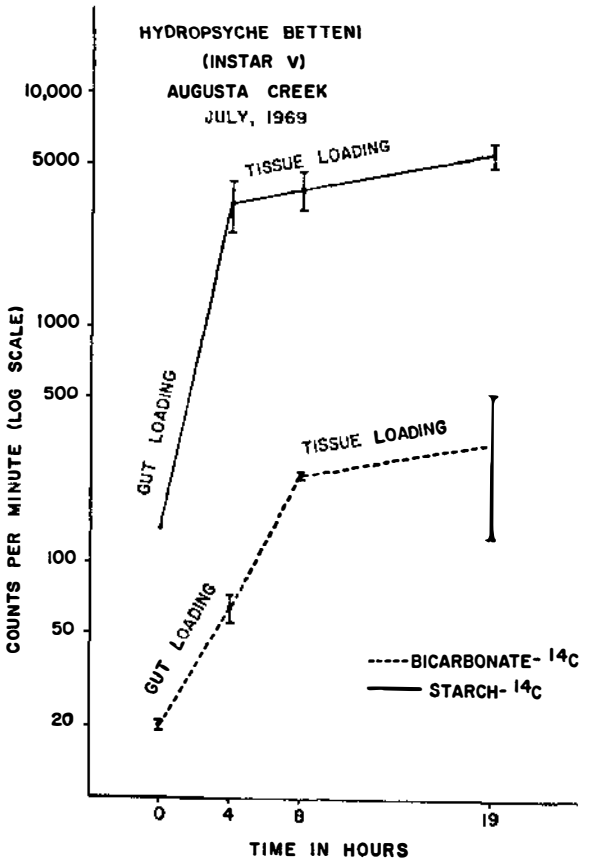

FIGURE 3. Tracer uptake per individual by terminal instar *Hydropsyche betteni* larvae over a 19-hr period at 15°C in chambers containing natural stream sediments and normal animal densities. Separate chambers were used for bicarbonate and starch. Each determination is based on three to eight larvae; vertical bars indicate one standard deviation.

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studied (Augusta Creek, Mich.). *H. betteni* has also been reported to be predominantly a carnivore (12), a herbivore (47), and a herbivore-detritivore (51). Since the specific activity of the food was approximately the same in both chambers, greater intake of detritus is indicated. The amount of animal feeding was judged to be small during the experiment by comparison to the activity levels in a known predator (*Acroneuria*). It can be seen that the data provide an estimate of 4 to 8 hr for gut loading time (steep slope), and assimilation, uncorrected for respiratory loss, also is indicated.

Since gut loading times or ingestion rates have been determined only rarely (e.g. 7, 26, 58), approximations from tracer studies are useful as are visual observations such as those made by Petersen (Kellogg Biological Station, unpublished data). Animals are shifted from one food source to another or an inert material is added to the food so that the progress of a bolus through the digestive tract can be followed. In a study using the trichopteran *Neophylax oligius,* Petersen quick-froze the larvae in liquid nitrogen at each sampling time (Figure 4). A gut loading time between 8 and 24 hr is indicated, although, similar to the data for *H. betteni,* appreciable filling was achieved in 4 to 8 hr. Actually, the three sections of the curve, 0 to 2, 2 to 4 or 8, and 4 or 8 to 23 hr, correspond roughly to fore-, mid-, and hind-gut filling. The ingestion rates for a number of aquatic insects are compared in

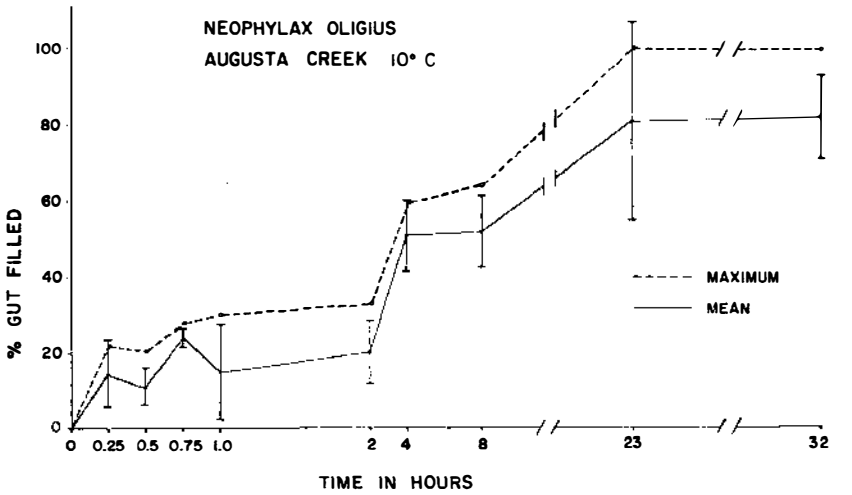

FIGURE 4. Determination of gut loading time with *N. oligius* from Augusta Creek. The percentage of gut filled ± S.E. was based on ocular micrometer measurements on individual guts from 10 animals for each time interval, quick-frozen in liquid nitrogen. Larvae were allowed to graze on filter pads onto which *Ankistrodesmus* from culture had been drawn. (From R. C. Petersen, Kellogg Biological Station, unpublished data.)

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TABLE 2. Comparison of ingestion data for selected aquatic insects[a]

Taxon	Food	CI	CI as % body wt/day	Reference
Plecoptera				
Pteronarcys scotti	Conditioned leaves, mixed species	0.062	6.2	43
Ephemeroptera				
Stenonema pulchellum	Culture of *Navicula minima*	0.130–0.220	13–22	66
Stenonema spp.	Culture of *Ankistrodesmus* spp.	0.082	8.2	Petersen, unpublished
	Culture of *Lunulospora curvula*	0.020	2.0	
Stenonema spp. (Low density)	Conditioned hickory leaves	0.232	23.2	Cummins, Petersen,
(High density)	Conditioned hickory leaves	0.040	4.0	Howard, Wuycheck, unpublished
Trichoptera				
Neophylax concinus	Natural stream substrate	0.80–1.60	80–160	58
Diptera				
Tipula abdominalis	Conditioned leaves, mixed species	0.030–0.051	3.0–5.1	68
Tipula sp.	Well conditioned hickory leaves	0.173	17.3	
	Hickory leaves—short conditioning time	0.088	8.8	Cummins et al, unpublished
	Oak leaves—short conditioning time	0.030	3.0	

[a] Consumption index = CI = dry weight of food ingested per dry weight of animal per day (69).

Table 2. If species of aquatic insects are compared according to consumption index [CI = dry wt food ingested per dry weight of animal per day; (69), (Table 2)], the values are quite comparable except for the very high value for the grazer *Neophylax concinnus* (58). Since feeding rate has been shown

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to be temperature dependent (e.g. 26), the differences would presumably be reduced if all were corrected to the same temperature. Excluding the *Neophylax* data, from 2 to 23% of the body weight is ingested per day by the species given, which include collectors, grazers, and shredders.

Food Habits

Over 50 years have elapsed since Muttkowski & Smith (49) made their observations on the food habits of aquatic insects. After a literature survey it is difficult to avoid the conclusion that, in general, we know little more than they did. Their contention with regard to food habits that "local conditions beget local results" must certainly still stand as the basic generalization for trophic relations of aquatic insects. Ecological generalizations requiring taxonomic competence are often reached in the absence of the latter, but rarely have combined talents such as those of Muttkowski & Smith been applied to the question of what aquatic insects eat; and the data were presented at a level of detail never tolerated by contemporary editors.

Methods.—Brown (8) reviewed the frequently used observational methods of gut analysis; these involve determining the relative abundance of various food items either by a qualitative ranking, such as the percentage of individuals examined containing a given type of food or the proportion of various foods in the gut, or by quantitative procedures similar to those used in plankton counting (7–9, 28). An extension of this latter method as used by Cummins et al (14; also 11, 12) is shown in Figure 5. A further refinement of algal intake estimates is possible if the cells are enumerated in size and shape categories which enable volume calculations to be made. The estimate of total volume can be converted to biomass, for example from the data of Nalewajko (50). A series of determinations of biomass per unit area are required for various types of detritus (for example using preweighed membrane filters that are cut into equal sections for microscopical measurements, weighing, and ashing). Certainly, automated particle size and image (size and shape) analyzers will be employed in gut analyses of aquatic insects as will biochemical and immunochemical (e.g. 16) methods.

The detailed work of Brown (7–9) on two baetid mayflies stands as a model for visual study of aquatic insect food habits. Nymphs of various sizes from several habitats were studied seasonally in the laboratory and the field. Experiments were conducted on food particle size selection and digestion, and an excellent study was made of the morphology and functioning of the mouth parts in relation to feeding and habitat adaptations. (Data on larval mouth and digestive tract structure are also available for a number of trichopteran species: see refs. 23, 35, 54–56.) With the addition of temperature- and age-dependent ingestion, assimilation, growth, and respiration rates, the important work of Brown (7–9) exemplifies the type of data required for representative freshwater species.

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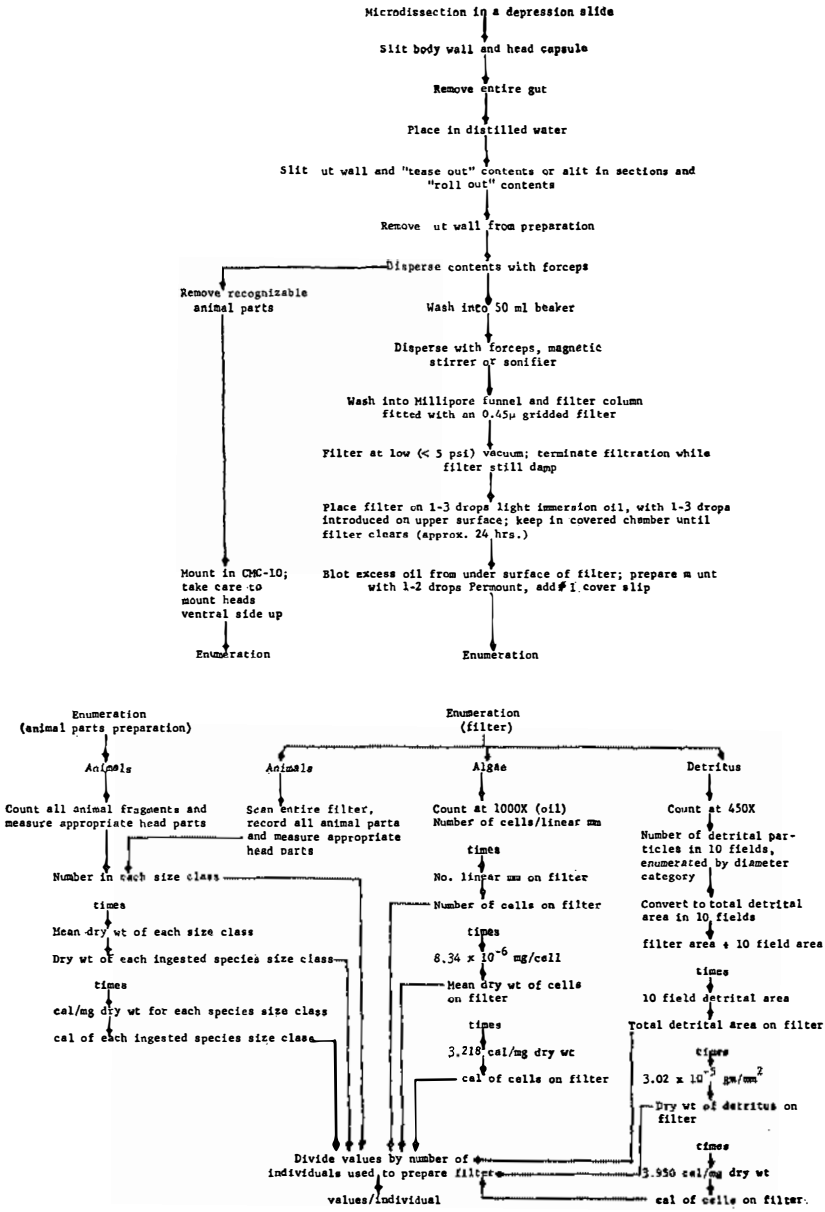

FIGURE 5. Methods for preparation (upper portion) and enumeration (lower portion) of aquatic insect gut contents. The density of material on the filter is adjusted by selection of filter size (diameter) and number of individuals gutted. Enumeration leads to the estimation of number of items, weight, and calories of algae, detritus, and animals per individual. The number of animals ingested is based on the identification and reconstruction (largely with head parts) of animal fragments to estimate the numbers and size of prey eaten (12).

Generalizations.—Generalizations of aquatic insect food habits at the generic, familial, or ordinal level are usually based on incomplete studies of very few species. Often, similarity in morphology or habitat is used as the basis for extrapolation. For example, the presence of a modified labium in all nymphal Odonata is considered sufficient evidence to conclude that all species are predaceous, even though the food habits of only an insignificant number of species have actually been studied. A good example is the trichopteran family Rhyacophilidae. Most general treatments report that the free living larvae of this family are predaceous. The generalization is based on the data of Lloyd (42) on *Rhyacophila fuscula,* of Muttkowski & Smith (49) on three undetermined *Rhyacophila* species in North America, and on two European species from Slack (60), Badcock (1), and Jones (33). However, recent studies on species from the rich *Rhyacophila* fauna of Western North America (over 80 species) have revealed a herbivore (*R. verrula*) which feeds on green algae and vascular plants, especially aquatic mosses (62, 64), and an omnivore (*R. vaefes*) which splits its intake between algae, detritus, and animals (64). Examination of the data of Muttkowski & Smith (49) reveals that at least one species should be classified as an omnivore. Thus, this family in the holarctic region might be characterized only as predominantly predaceous, but many species have yet to be examined.

Differences within a single species have also been reported. The discrepancies in observed food habits of the net-spinning caddis larva *Hydropsyche betteni* have already been described. A similar case is represented by the trichopteran *Glossosoma nigrior*. As shown in Figure 6, the food habits of this species are strikingly dissimilar in two different streams. Much greater algal ingestion characterized the population of Linesville Creek (Pennsylvania), known to have more periphyton growth than the other stream, Augusta Creek (Michigan), where detritus and detrital feeding predominate. It is interesting to note that terminal instar larvae of the detrital feeding population attain a final dry weight only about one third of that characteristic of the algal feeding population. Possibly the difference is due to less adequate nutritional characteristics of detritus relative to the requirements of *G. nigrior,* although a temperature effect, for example on feeding rate (26), has not been ruled out.

In addition to trophic differences between two populations of the same species from different locations, age-specific variations within the same population are also shown in Figure 6. Greater detrital feeding in the earlier instars of *Glossosoma* and *Stenonema* is indicated. This pattern is consistent for many herbivore-detritivore species (12). Thus locations where detritus accumulates tend to serve as the "nurseries" of freshwater habitats. With regard to *G. nigrior* in Augusta Creek (Figure 6), the shift to more algal feeding in the later instars corresponds with periods of reduced stream flow, allowing for greater mobility of the larvae which are at the same time in larger, heavier mineral cases, and maximum periphyton development. Animal ingestion

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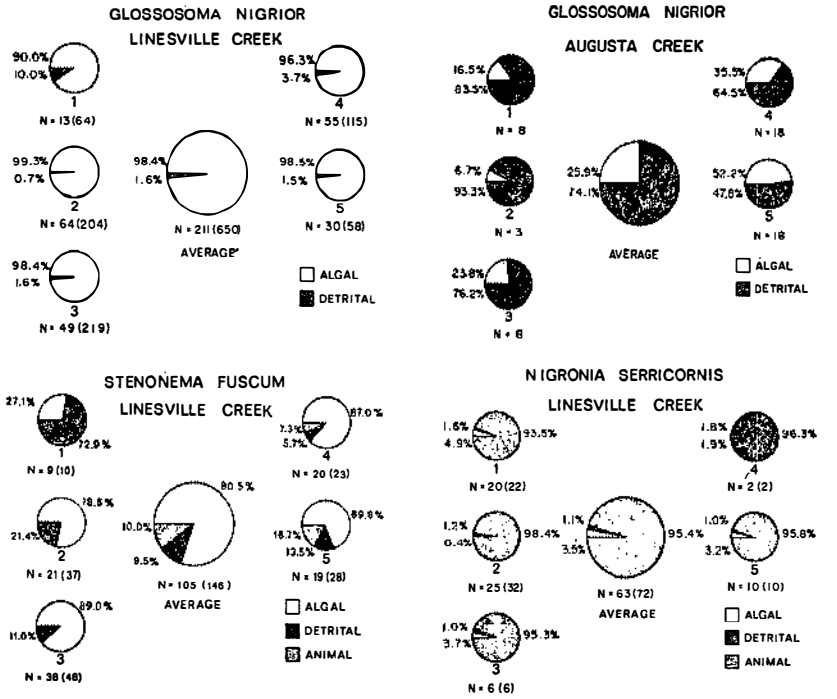

FIGURE 6. Trophic relations of *Glossoma nigrior* (Trichoptera), *Stenonema fuscum* (Ephemeroptera) and *Nigronia serricornis* (Megaloptera). *N* is the number gutted; the total number collected in Linesville Creek quantitative samples analyzed is given in parentheses. Percentage of food composition is shown by instar (1–5) for *Glossosoma* and *Nigronia;* several *Stenonema* instars are combined in each category. The average dietary composition over the larval or nymphal period is also included. The amounts of the three types of food are given according to caloric content (see Figure 5).

by large *Stenonema fuscum* nymphs (Figure 6) is a function of size. The brushing and scraping activities of the nymphs are quite nonselective, so that algal cells, detrital particles, or animals (predominately first instar midge larvae) in the right particle size range are taken in. This type of positive relationship between food size and size of feeder has also been shown for species that are predominantly predators (e.g. the plecopteran *Acroneuria,* 59). As discussed previously, the detritus and algae in the guts of the predator *Nigronia serricornis* (Figure 2) probably represents the contents of prey digestive tracts.

Therefore, because of habitat and age specific differences in food habits within the same species, generalizations seem unwarranted in most instances,

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even at the broad level of algal, vascular plant, detrital, and animal food categorization. Since within, and often between, these categories most species studied seem to be nonselective generalists in their food habits, the kinds of food available and their relative proportions will essentially define the trophic relations. It is also apparent that the study of the food habits of aquatic immatures, like their taxonomy, has been characterized by preoccupation with mature representatives. For many ecological questions it will be more critical to gather data on early stages when population density, and probably feeding and growth rates, are maximized. However, under the assumption that identifying the dominant food habits of species according to one or more of the categories above is useful as an initial step to more detailed work or for purposes of comparison between habitats, a short list of selected data from the literature has been prepared (Table 3). Food habits of the fluid feeding Hemiptera (except Corixidae) have not been included in the table since only qualitative data are available and the midges have not been treated to the extent that their dominance in freshwater habitats warrants. In general, the Tanypodinae are considered to be predaceous, the Orthocladinae to be detrital-algal feeders, the Diamesinae to be algal feeders, and the Chironominae to be algal-detrital feeders with some leaf mining (34) and predaceous species (52). Truly parasitic Orthocladinae and Chironominae have been described (52). Good quantitative data are scarce for the Lepidoptera, Coleoptera, and non-midge Diptera, despite their importance in freshwaters.

Conclusions

Freshwater ecosystems of the temperate zone might be generalized as having a reasonably constant biomass of macrobenthic animals, dominated by aquatic insects (plus mollusks, annelids, and crustaceans), which is turning over at a rate controlled primarily by temperature, seasonal temperature adjustments being much less pronounced in running waters in which a very significant amount of feeding and growth occurs in the fall and winter. The temperature control of biomass turnover is mediated primarily through the positive correlation between temperature and feeding rate and temperature and respiration; thus, the ratio of feeding, or respiration, to growth is fairly constant. The aquatic insects are supplied with consistent and abundant food supplies of similar caloric and protein content. Their assimilative efficiency is independent of temperature over wide ranges and fairly constant over the broad range of food quality normally ingested (predators may have a higher efficiency than herbivore-detritivores, 70). Food resources are partitioned on the basis of particle size and whether active (prey), stationary (periphyton, vascular plants, deposited detritus), or in suspension (plankton and fine particle detritus in standing waters, particulate drift in streams and rivers). Within any general food compartment, specific utilization is determined by temporal and microspatial isolation of potential competitors—size (age) groups of a

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large number of species that are all trophic generalists within the particle size ranges that they are capable of ingesting. Although the data on aquatic insects are not extensive enough to determine the validity of all aspects of these generalizations, the information at hand supports the contention that most aquatic insects are best termed polyphagous or generalists and that availability, most frequently delineated by food particle size and texture, is the key to trophic relationships among aquatic insects.

TABLE 3. Food habits of selected aquatic insects

Taxon	Habitat	Type of analysis[a]	Food habits (%)				Reference
			Algae	Live vascular plant tissue	Detritus	Animals	
Odonata							
Zygoptera							
Lestidae							
Lestes sponsa	Ponds (Poland)	A				100	21
Agrionidae (=Coenagrionidae)							
Pyrrhosoma nymphula	Ponds (England)	A				100	40
Plecoptera							
Filipalpia							
Pteronarcidae							
Pteronarcys californica	Subalpine rivers (Wyoming)	A	53.9		42.3	3.8	49
Nemouridae							
Taeniopteryx maura	Woodland stream (Pennsylvania)	A	0.2		1.0	98.6	11
Setipalpia							
Perlidae							
Acroneuria pacifica	Subalpine rivers (Wyoming)	A	6.3		16.3	77.4	49
Phasganophora capitata	Woodland stream (Pennsylvania)	A	1.6		0.3	98.1	11
Perlodidae							
Arcynopteryx curvata	Experimental (seminatural) stream (Washington)	A	70.2	2.4	6.9	20.5	65
A. subtruncata		A	38.5	0.6	7.7	53.2	65
Isogenus nonus		A	29.3	0.9	6.9	62.9	65
Rickera sorpta		A	12.5	0.1	7.9	79.5	65
Ephemeroptera							
Siphlonuridae							
Isonychia albomanicata	Woodland stream (Pennsylvania)	A	25.8		17.5	56.7	11
	Woodland stream (New York)	B	84.6		10.0	5.4	10

[a] Type of Analysis: A = based on % of each category in the gut, B = based on % of individuals examined having item in gut. Zeros are recorded, blanks mean the category was not reported (e.g. gut contents of prey in predators).

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TABLE 3 (Continued)

Taxon	Habitat	Type of analysis[a]	Food habits (%)				Reference
			Algae	Live vascular plant tissue	Detritus	Animals	
Baetidae							
Centroptilum album	Woodland stream (Pennsylvania)	A	87.7		12.3	0	11
Baetis vagans	Woodland river (Kentucky)	A	~41		~59		47
Heptageneildae							
Stenonema fuscum	Woodland stream (Pennsylvania)	A	80.5		9.5	10.0	Figure 6
S. tripunctatum	Woodland stream (Pennsylvania)	A	78.6		13.1	8.3	11
Ephemerellidae							
Ephemerella aestiva	Woodland stream (Pennsylvania)	A	69.4		30.6	0	11
Caenidae							
Caenis anceps	Woodland stream (Pennsylvania)	A	92.1		7.9	0	11
Leptophlebiidae							
Habrophlebioides americana	Woodland stream (Pennsylvania)	A	49.1		50.9	0	11
Megaloptera							
Corydalidae							
Nigronia serricornis	Woodland stream (Pennsylvania)	A	3.5		1.1	95.4	Figure 6
N. fasciata	Woodland stream (Kentucky)	A			~12	~88	48
Trichoptera							
Rhyacophilidae							
Rhyacophila arnaudi		A	0.6	0.5	5.3	93.5	64
R. vagrita		A	6.5	0.4	6.0	87.1	64
R. vepulsa	Experimental	A	1.8	1.0	6.4	90.8	64
R. vaccua	(seminatural)	A	2.6	1.2	3.5	92.7	64
R. vaefes	stream	A	39.4	3.7	20.7	36.2	64
R. verrula	(Washington)	A	30.7	63.7	3.7	1.9	64
R. grandis		A	0	5.0	5.0	90.0	64
R. dorsalis	Chalk stream (England)	B	14.0	14.0	0	72.0	60
R. dorsalis	Subalpine stream (Scotland)	B	22.4	0.1		76.5	57
Glossosomatidae							
Glossosoma nigrior	Woodland stream (Pennsylvania)	A	98.4		1.6	0	Figure 6
	Woodland stream (Michigan)	A	25.9		74.1	0	
G. boltoni	Subalpine stream (Scotland)	B	99.0	1.0		0	57

[a] Type of Analysis: A = based on % of each category in the gut, B = based on % of individuals examined having item in gut. Zeros are recorded, blanks mean the category was not reported (e.g. gut contents of prey in predators).

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TABLE 3 (Continued)

Taxon	Habitat	Type of analysis[a]	Food habits (%)				Reference
			Algae	Live vascular plant tissue	Detritus	Animals	
Philopotamidae							
Chimarra aterrima	Woodland stream (Pennsylvania)	A	65.0		31.0	4.0	11
Psychomyiidae							
Psychomyia flavida	Woodland stream (Pennsylvania)	A	94.0		4.0	2.0	11
Polycentropidae							
Nyctiophylax sp. A	Woodland stream (Pennsylvania)	A	1.0		1.0	98.0	11
Polycentropus cinereus	Subalpine lake (British Columbia)	B	0		0	100	71
Hydropsychidae							
Hydropsyche betteni	Woodland stream (Pennsylvania)	A	2.0		1.0	97.0	11
H. bronta		A	39.0		6.0	55.0	11
H. slossonae		A	18.0		3.0	79.0	11
H. fulvipes	Subalpine stream (Scotland)	B	28.2	19.4		52.4	57
Hydroptilidae							
Agraylea multiplicata	Woodland river (Kentucky)	A	100				47
Phryganeidae							
Ptilostomis ocellifera	Subalpine lake (British Columbia)	B	16.7		0	83.3	71
Brachycentridae							
Brachycentrus americanus	Woodland streams (Wisconsin)	A	80	15		5	46
Lepidostomatidae							
Lepidostoma unicolor	Subalpine stream (British Columbia)	B	0		92.7	7.3	71
Neophylacidae							
Neophylax oligius and *N. concinnus*	Woodland stream (Pennsylvania)	A	63–72	0	28–37	0–0.5	58
Calamoceratidae							
Heteroplectron californicum	Subalpine stream (British Columbia)	B	0		100	0	71
Sericostomatidae							
Sericostoma personatum	Chalk stream (England)	B	0	0	70	30	60

[a] Type of Analysis: A = based on % of each category in the gut, B = based on % of individuals examined having item in gut. Zeros are recorded, blanks mean the category was not reported (e.g. gut contents of prey in predators).

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TABLE 3 (Continued)

Taxon	Habitat	Type of analysis[a]	Food habits (%)				Reference
			Algae	Live vascular plant tissue	Detritus	Animals	
Odontoceridae							
Odontocerum albicorne	Subalpine stream (Scotland)	B	28.9	28.1		43.0	57
	Chalk stream (England)	B	52.9			47.1	60
Psilotreta indecisa	Woodland stream (Pennsylvania)	A	97.0		2.0	1.0	11
Leptoceridae							
Oecetis inconspicua	Subalpine lake (British Columbia)	B			7.7	92.3	71
Helicopsychidae							
Helicopsyche borealis	Woodland stream (Pennsylvania)	A	66.6		2.7	30.7	11
Goeridae							
Goera calcarata	Woodland stream (Pennsylvania)	A	99.0		1.0	0	11
Limnephilidae							
Clistoronia magnificata	Subalpine lake (British Columbia)	B	0		92.1	7.9	71
Halesochila taylori		B	0		87.0	13.0	71
Psychoglypha alascensis		B	0		80.0	20.0	71
Pycnopsyche scabripennis	Woodland stream (Pennsylvania)	A	9.0		91.0	0	11
Stenophylax latipennis	Subalpine stream (Scotland)	B	18.7	79.7		1.6	57
Coleoptera							
Elmidae							
Stenelmis beameri							
larvae	Woodland stream	A	71.3		7.2	21.5	11
adult	(Pennsylvania)	A	59.4		40.6	0	11
Psephenidae							
Psephenus herricki	Woodland stream (Pennsylvania)	A	97.7		2.3	0	11
Diptera							
Tipulidae							
Tipula nobilis	Woodland river (Kentucky)	A	90.9		9.1	0	47

[a] Type of Analysis: A = based on % of each category in the gut, B = based on % of individuals examined having item in gut. Zeros are recorded, blanks mean the category was not reported (e.g. gut contents of prey in predators).

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TABLE 3 (Continued)

Taxon	Habitat	Type of analysis[a]	Food habits (%)				Reference
			Algae	Live vascular plant tissue	Detritus	Animals	
Simuliidae							
Prosimulium hirtipes	Woodland stream (Pennsylvania)	A	89.9		10.1	0	11
Chironomidae							
Tanypodinae							
Thienemannimyia series sp. 2		A	0.1		0.2	99.7	11
Orthocladinae							
Eukiefferiella brevinervis		A	99.4		0.6	0	11
E. sordens		A	81.1		18.9	0	11
Corynoneura taris		A	77.4		22.6	0	11
Brillia cf. *flavifrons*		A	42.2		57.8	0	11
Chironominae							
Microtendipes cf. *pedellus*		A	87.0		13.0	0	11
Dicrotendipes neomodestus		A	87.1		12.9	0	11
Polypedilum cf. *scalaenum*		A	84.6		15.4	0	11
Micropsectra cf. *polita*		A	79.8		19.1	1.2	11
Rheotanytarsus exigua		A	66.2		26.9	6.9	11

[a] Type of Analysis: A =based on % of each category in the gut, B =based on % of individuals examined having item in gut. Zeros are recorded, blanks mean the category was not reported (e.g. gut contents of prey in predators).

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