

OFFPRINTS FROM NUTRITIONAL ECOLOGY OF
INSECTS, MITES, AND SPIDERS

Edited by Dr. Frank Slansky Jr. and Dr. J. G. Rodriguez
Copyright (c) 1987 by John Wiley & Sons, Inc.

30

Nutritional Ecology of Aquatic Detritivorous Insects

N. H. ANDERSON and

A. S. CARGILL

- 30.1 Introduction
- 30.2 Food Characteristics and Other Relevant Environmental Conditions
 - 30.2.1 Life in Water
 - 30.2.2 Sources of Detritus
 - 30.2.3 Composition and Nutrient Quality of Detritus
- 30.3 Attributes of Feeding Relative to Food Characteristics and the Aquatic Environment
 - 30.3.1 Derivation of the Aquatic Fauna
 - 30.3.2 Detritivory or Omnivory?
 - 30.3.3 Physiological and Nutritional Adaptations
 - 30.3.4 Microbes as Food
 - 30.3.5 Feeding Behavior
 - 30.3.6 Lipid Requirements
- 30.4 Life Cycle Response to Food Quality
 - 30.4.1 Aquatic Insect Xylophages
 - 30.4.2 Shredders
 - 30.4.3 Collectors
- 30.5 Conclusions and Future Research
- References

The authors thank their Stream Team colleagues at Oregon State University for ideas and helpful discussions of this review. The background research of N.H.A. on xylophagous insects was supported by NSF grants DEB 78-10594 and BSR 80-22190. This is Technical Paper No. 7474 of the Oregon Agricultural Experiment Station.

30.1 INTRODUCTION

The detritus pathway is that in which plant or animal material dies and is then attacked by microorganisms. More of the energy fixed by autotrophic organisms is transferred through this route than through the grazing pathway (Mann, 1975). As an operational definition, Boling et al. (1975) defined detritus as all particulate organic matter (particles of reduced carbon compounds $>0.45 \mu\text{m}$ diam) together with associated microbes (fungi, bacteria, protozoa, and other microinvertebrates).

The importance of detritus as a food base for aquatic insects is more similar to that for soil organisms (see Werner and Dindal, Chapter 27) than for other terrestrial systems. Primary production is relatively low in many aquatic systems, and the fauna is largely dependent on allochthonous inputs of litterfall from adjacent terrestrial vegetation. Even where production is high (e.g., aquatic macrophytes in chalk streams or algae in eutrophic lakes) a major portion of the plants is not consumed by insects until after it dies and enters the detritus food chain.

Though the importance of allochthonous organic matter as a food base in aquatic habitats was pointed out in 1912 by Thienemann, it is only during the past two decades that extensive research has been conducted. Kaushik and Hynes's (1971) classic paper on the fate of dead leaves that fall into streams reviewed the earlier work on detritivory and stimulated a host of field and laboratory studies. Since then, the role of detritus in aquatic ecosystems has been discussed in two symposia (Melchionni-Santolini and Hopton, 1972; Anderson and Macfayden, 1976) and the role of insect detritivores has been reviewed by Anderson and Sedell (1979), Cummins and Klug (1979), Wallace and Merritt (1980), and Merritt et al. (1984).

In this chapter we discuss aquatic insects from both lotic (running water) and lentic (standing water) habitats, though the viewpoint is biased toward running water because of our familiarity with stream insects. To some extent, herbivores that utilize living plant material are also discussed, because their methods of feeding may result in the intake of both living and dead material.

The functional feeding group concept of Cummins (1973, 1974) is adopted for comparing detritivore groups. This divides primary consumers (i.e., non-predatory) into four general categories: shredding and gouging, scraping, filter feeding, and deposit collecting. This approach is based on methods of food acquisition and to some extent on the size of food particles selected. It does not distinguish between the kinds of food consumed, but it recognizes that many taxa are omnivorous and that diet switching occurs (Anderson and Cummins, 1979).

The aquatic insect fauna in North America includes about 10,000 species (Merritt and Cummins, 1978). Primary consumer species account for about 60% of these, and probably three quarters of the primary consumers ingest some detritus. The major detritivorous groups are included in the Trichoptera (Hydropsychoidea and Limnephiloidea), Diptera (Chironomidae, Tipu-

lidae, Simuliidae, Culicidae, Psychodidae, Stratiomyidae, and Ephydriidae), Ephemeroptera (Leptophlebiidae, Ephemeridae, Siphonuridae, Tricorythidae, and Caenidae), Plecoptera (Filipalpia), and Coleoptera (Elmidae and Hydrophilidae). In addition to insects, important detritivores in aquatic systems include worms, snails, amphipods, and isopods.

Aquatic detritivores are important in recycling nutrients and transferring energy to higher trophic levels. Fish are frequently the organisms of economic value in aquatic systems, and detritivorous insects are a key element in their diets. On the debit side, the medical importance of blood feeders that are detritivorous as larvae (e.g., Culicidae and Simuliidae; see O'Meara, Chapter 24) and nuisance aspects of mass emergers (e.g., Hydropsychidae, Chironomidae, and Ephemeridae) are the primary concerns.

In the parlance of our industrial society, detritus is a "waste" product that we strive to dispose of; thus its consumption is in no way competing with requirements for food or fiber. In an ecological context, the litter layer on land and debris in aquatic systems may be viewed as a resource awaiting harvest. The effect of detritivores in accelerating decomposition, and thereby returning nutrients to an elemental form, is undoubtedly their key role in aquatic systems. The export of materials and losses of nutrients that are the inevitable consequence of unidirectional flow in streams are partially counteracted by activities of the biota. In streams, the cycles of nutrient and food utilization are drawn out spatially in patterns described as spiraling (Webster and Patten, 1979). Wallace et al. (1977) have shown that the feeding activities of detritivores "tighten" the spirals of particulate organic matter in streams and thereby increase nutrient recycling within the stream reach.

The focus of this chapter is primarily on the feeding ecology and life history strategies that enable aquatic insects to exploit detritus. What behaviors, growth patterns, and digestive mechanisms enable them to utilize this abundant but low-quality, refractory foodstuff? Data on the nutrition and nutritional ecology of aquatic insects are limited. We may be able to infer the nutritional requirements from feeding behavior and life histories, but this is a "broad-brush" approach compared with the stated objectives of nutritional ecology—"identifying responses, their relationships to consumption, utilization and allocation of food, and their consequences for fitness" (Slansky, 1982).

30.2 FOOD CHARACTERISTICS AND OTHER RELEVANT ENVIRONMENTAL CONDITIONS

30.2.1 Life in Water

Living in a liquid medium presents organisms with a different suite of conditions compared with terrestrial habitats. In permanent bodies of water, moisture is obviously not limiting, but oxygen and pH may be. Temperature

range is narrower than on land; water temperature rarely falls below 0°C, and a water body is slow to heat up or cool down, such that diel fluctuations are lessened. The variable nature of dissolved chemicals and oxygen-consuming materials in lakes or streams has physiological implications regarding both osmoregulation and respiration.

Aquatic organisms have to contend with dilution of their food source. Readily assimilable sugars and other soluble organics are leached to the surrounding water. Similarly, contents of cells that are ruptured while being gathered or chewed may be lost, thus placing a premium on sucking types of mouthparts, especially in herbivores and predators. For detritivores, characteristics of the medium have opened new methods of food gathering. For example, silken nets are constructed by many caddisflies and chironomids in streams to trap particles transported by the current, whereas black flies and some mayflies have body parts adapted to filter fine particulate organic matter (FPOM). In standing water, mosquito larvae generate a current with mouth brushes in order to collect bacteria and other suspended particles.

Temperature and oxygen relationships may affect availability and quality of the detrital resources. Microbial conditioning is usually required before organic matter (OM) becomes palatable or nutritionally available. High temperature stimulates microbial growth, but it also can have a negative effect on the biota, because dissolved oxygen concentration is lower at high temperature and the biochemical oxygen demand of the microbes is greater, often resulting in anoxic conditions. When microbial decomposition occurs under anaerobic conditions, as for example in deep lakes or in large leaf accumulations following autumnal leaf fall in streams, the detrital resource becomes unavailable, at least temporarily, to the insects.

30.2.2 Sources of Detritus

Anderson and Cummins (1979) ranked organic materials potentially available to aquatic insects on an increasing nutritive gradient as (1) wood; (2) terrestrial leaf litter; (3) FPOM; (4) decomposing vascular hydrophytes and algae; (5) living algae, especially diatoms; and (6) animal tissues. Categories 1–4 and their associated microbial flora are the detrital resource.

Riparian vegetation provides most detritus to bodies of water. Headwater streams are maximally influenced by riparian vegetation, because the ratio of shoreline to stream bottom is high. Coarse particulate organic matter (CPOM) is the basic food material for insects in these small streams, because heavy shading limits primary production by algae and vascular plants. In larger streams (orders 4–6), the channels are wide and the canopy of vegetation does not close over them, and direct inputs of CPOM are thus lower. Detrital material in these areas consists of FPOM transported from upstream in addition to decomposing algae and macrophytes growing in the immediate area. The proportion of detritivores in this size of stream will be lower than in small streams because of the increased number of herbivores that feed on algae or macrophytes.

Lakes and ponds receive CPOM from shoreline vegetation and also via transport from streams. In shallow areas there may also be considerable detritus generated from emergent and submerged macrophytes. For example, Mason and Bryant (1975) estimated the annual production in an English reedswamp as $>2500 \text{ g/m}^2$, most of which enters the litter pool. However, most detritus in lakes usually results from the phytoplankton that settles out as fine-particle ooze.

In addition to the breakdown of particulate detritus, another pathway of carbon flow is the formation of organic precipitates (Bowen, 1984) or organic layers on stones (Madsen, 1972, 1974; Calow, 1975). These layers may occur where light levels are too low for primary production, such as on the underside of stones. Rounick and Winterbourn (1983) characterized the material as a polysaccharide slime, with fungal mycelia, bacteria, algae, and FPOM interwoven into a layer up to $80 \mu\text{m}$ thick. They attribute the slime production to bacterial utilization of dissolved organic carbon. Feeding studies indicate that many common stream invertebrates can feed effectively on this thin film with assimilation efficiencies as high as 62–74% (Rounick and Winterbourn, 1983).

The annual allochthonous inputs to forested streams range from 300 to 750 g/m^2 (Anderson and Sedell, 1979). Small streams tend to be very retentive, and some 60–70% of the detritus is retained long enough to be utilized by macro- and microorganisms (Fisher and Likens, 1973; Sedell et al., 1974). In deciduous forests, the litter inputs increase in late summer and peak in the fall. In more northern areas, the snow cover reduces winter inputs but results in a pulse of litter with the spring melt. Coniferous forest and evergreen deciduous forest streams have a more even distribution of inputs throughout the year.

Food quality, rather than quantity, may be the limiting factor for detritivores. For example, wood debris in Pacific Northwest streams may occur at $>50 \text{ kg/m}^2$, but its degradation period is measured in decades or centuries, and the portion immediately available to detritivores is much lower (Anderson et al., 1978). Aquatic macrophytes and algae are low in refractory lignin and cellulose; thus microbial breakdown is rapid, and nutrients are readily available to detritivores. Bowen (1984) found that the capacity for hydrolysis of amorphous detritus derived from organic precipitates is six times greater than that of FPOM derived by fragmentation of plant tissues.

Egglishaw (1964, 1968) found that the abundance of the stream fauna is positively correlated with the rate of decomposition. Petersen and Cummins (1974) confirmed this by showing that shredders exhibit a general preference for species of leaves that decay rapidly. They classified the decay rate as fast (1–1.5% weight loss per day), medium (0.5–1%), or slow ($<0.5\%$). Because there is a continuum of processing rates, there is a stepwise addition of new sources of food when the slower species are conditioned.

Seasonal variation in both palatability and nutrient content of detrital inputs is of significance. Spring and early-summer litterfall is low but con-

sists of high-nutrient flowering parts, tender young leaves, and grass. In western Oregon, monthly inputs to small streams from February through May range from 6 to 10 g/m² (primarily catkins; N. H. Anderson, unpublished data). By this time, leaf litter from the previous autumn has been largely consumed or flushed from the system, so the shredder fauna is quickly attracted to new material.

30.2.3 Composition and Nutrient Quality of Detritus

As discussed earlier, detritus includes associated microbes along with the nonliving portions. Cummins and Klug (1979) indicate that even techniques as rigorous as sonification do not provide for efficient separation of microbes from surface-colonized CPOM or FPOM. Moreover, they conclude that "in stream environments, non-living organic matter probably does not occur without associated microorganisms." Cummins and Klug characterized detritus by particle size, origin, associated microbes, caloric content, percent ash, and carbon:nitrogen ratio (Table 30.1). The CPOM is subdivided into woody and nonwoody components, because the former is highly refractory. Material <0.5 μ m is considered to be dissolved organic matter (DOM).

Detritus is fractionated into a number of pools by biological and abiotic interactions. Leaching removes about 15% of the soluble material in leaves within 1–2 days (Petersen and Cummins, 1974). CPOM is surface- and matrix-colonized by fungi and bacteria, the former being the initial colonizers (Table 30.1). Mycelia penetrate into the leaf matrix owing to their invasive enzymatic characteristics, resulting in both an increase in protein content and a softening of the tissue (Kaushik and Hynes, 1971). The activity of the microbes, along with invertebrate feeding and physical fragmentation by current and mineral particles, results in continuous releases of FPOM, UPOM, and DOM. Bacteria are the dominant colonizers of fine particles because of the large surface area and minimal matrix for mycelial penetration.

Cummins and Klug (1979) indicate that the longer the detritus is recycled within the system, the more refractory it becomes to microbial and animal metabolism. In the lower size range of FPOM and in UPOM, lignin may account for 40%, and humified (complexed) nitrogen for 50% of the total organic content. As a measure of microbial activity, Ward (1977) compared ATP content of different types of detritus of the same particle size that represented three stages of recycling. The activities (nmole ATP/g AFDW) were (1) ground, microbially conditioned hickory leaves, 23.6; (2) feces of *Tipula* fed on hickory leaves, 2.5; and (3) natural stream detritus, 1.7. The ground leaf litter and natural detritus were similar in C:N ratios (14.0 and 17.8, respectively), apparently reflecting the accumulation of unavailable nitrogen in the natural detritus.

In summary, detritus includes fungi, bacteria, microinvertebrates, exudates, epiphytic and senescent algal cells, and the substrate itself. The re-

Table 30.1. General Characteristics of Detritus in Streams (particles $<0.5 \mu\text{m}$ are considered dissolved organic material)

Category	Size	Description	Associated microbes	Caloric content (kcal/g AFDW)	% Ash	Carbon : nitrogen ratio
CPOM (coarse particulate organic matter)						
Nonwoody	$>1 \text{ mm}$	Leaves, needles, other nonwoody plant parts	Fungi, bacteria; surface and matrix colonized. Lesser importance: protozoans, rotifers, nematodes, microarthropods)	4.8	10–30	20–80 : 1
Woody	$>1 \text{ mm}$	All wood and woody parts	As above but lower densities. Primarily surface-colonized until late in decomposition	4.5	40–50	220–1340 : 1
FPOM (fine particulate organic matter)	$<1 \text{ mm}, >50 \mu\text{m}$	Fragments of CPOM; feces; flocculated material from DOM; microbial cells; sloughed algae; organic films on mineral particles	Primarily bacteria colonizing surfaces; protozoans on particles $>250 \mu\text{m}$	4.5	—	7.4–37.8 : 1
UPOM (ultrafine particulate organic matter)	$<50 \mu\text{m}, >0.5 \mu\text{m}$	Fragments of CPOM and FPOM; flocculated material from DOM: organic films on clay particles	Bacteria sparsely colonizing surfaces or associated with flocculated organics	—	—	—

Source: Cummins and Klug (1979). Reproduced, with permission, from the *Annual Review of Ecology and Systematics*, Volume 10, © 1979 by Annual Reviews Inc.

fractory nature and low nutrient quality of detritus dictate feeding strategies that require some combination of high consumption rate, selective ingestion, microbial symbionts, omnivory, and low metabolic rate associated with slow growth and long life cycles.

30.3 ATTRIBUTES OF FEEDING RELATIVE TO FOOD CHARACTERISTICS AND THE AQUATIC ENVIRONMENT

30.3.1 Derivation of the Aquatic Fauna

Aquatic insects are probably derived from terrestrial ancestors, with the change of habitat having occurred independently at least 100 times (Miall, 1895; Usinger, 1956). As all of the major orders had appeared by the Triassic (>200 million years BP) and extant aquatic forms are generally of a primitive type, the ancient lineage of aquatic insects is apparent. The association with shaded streams for such an extended period has allowed for the evolution of many species that are active during the winter, when leaf detritus is most abundant (Hynes, 1970). Ross (1963) postulates that the ancestral habitat of Trichoptera is woodland streams, because the majority of primitive genera in each family occur in cool, moderately rapid, small streams that run through shaded woodlands.

The terrestrial origin of detritivorous insects has implications pertaining to physiological adaptations; Cummins and Klug (1979) point out that amphipods, such as *Gammarus*, and some mollusks have digestive cellulases, reflecting their marine phylogenetic origin, whereas in aquatic insect detritivores, cellulases are uncommon except when associated with gut symbionts. Possession of cellulases may result in a wider food-niche breadth for the marine derivatives, because these species are able to utilize a greater array of detritus and algae.

30.3.2 Detritivory or Omnivory?

Aquatic insect detritivores can best be described as omnivores because of the heterogeneous nature of their main food and the tendency of some species to switch diets, especially in the last instar. A "mouthful" of detritus will contain some algae (herbivory), microinvertebrates (predation), and fungi (mycophagy), as well as dead plant material (detritivory), making trophic analysis difficult. Also, the exact source of the insect's nutrition from within the detrital milieu is in question. Diet switching as larvae grow appears to be a common phenomenon, especially in Trichoptera. This indicates that detritus is at best nutritionally incomplete or at worst something that is incidentally ingested in large quantities while the young insect is searching for suitably small prey.

The foregoing difficulties have given rise to the functional feeding concept

that emphasizes mode of food acquisition over what food is actually eaten. The functional categories that consume the most detritus are shredders and filtering and gathering collectors.

30.3.3 Physiological and Nutritional Adaptations

Little is known about the nutritional needs of aquatic insect detritivores or how these needs change during the life cycle. It thus becomes somewhat tenuous to describe behavioral, physiological, or life history patterns as being adapted for nutritional acquisition. Protein is frequently a limiting nutrient and the one to which most adaptations are supposedly directed. Acquisition of essential lipids, carbohydrates, vitamins, sterols, minerals, and so on also gives rise to adaptive mechanisms, but there is little information on the relative importance of the different nutrients as limiting factors.

Gut pH and digestive enzymes have been studied in a few aquatic insects (Table 30.2). The crane fly *Tipula abdominalis* has a very alkaline midgut, possibly an advantage in digesting "bound" protein, whereas caddisflies and stoneflies have neutral midguts. The pH range in different parts of the digestive tract may optimize different endogenous or acquired enzyme activity (Martin et al., 1980, 1981a,b). Symbionts may assist the insect in degradation of cellulose and related components.

Bärlocher (1982, 1983) proposed two distinct strategies for shredder exploitation of leaf detritus by comparing digestive adaptations of *T. abdominalis* from Martin et al. (1980) with his work with *Gammarus fossarum*. In *T. abdominalis*, the strongly alkaline fore- and midguts have high proteolytic activity but no activity toward major plant polysaccharides, al-

Table 30.2. Midgut pH of Aquatic Detritivores

Order and species	pH
<i>Plecoptera</i>	
<i>Pteronarcys californica</i> ^a	6.5–7.3
<i>P. picteti</i> ^a	7.0–7.7
<i>Trichoptera</i>	
<i>Agrypnia vestita</i> ^b	6.8–7.3
<i>Phryganea</i> sp. ^b	7.1–7.3
<i>Pycnopsyche guttifer</i> ^b	7.1–7.8
<i>Diptera</i>	
<i>Xylotopus par</i> ^c	8.3–9.8
(posterior midgut with attached microbes)	7.2
<i>Tipula abdominalis</i> ^d	9.6–11.2

^a Martin et al. (1981a).

^b Martin et al. (1981b).

^c Kaufman (1983).

^d Martin et al. (1980).

though some fungal-derived glucans are digested. In *G. fossarum*, its own enzymes and fungal exoenzymes digest carbohydrates (cellulose, hemicellulose, and pectin) in the slightly acid anterior gut, and the alkaline posterior gut digests microbial and leaf proteins.

The digestive strategy of *G. fossarum* is effective when food is abundant and also for a highly mobile animal that can seek out the few good leaves or exploit alternative food sources. By contrast, the high pH level of *T. abdominalis* is metabolically expensive to maintain but effective when exhaustive extraction of refractive nitrogen is required. *Tipula abdominalis* is a slow-moving, obligate shredder that through much of its life cycle only has available postconditioned detritus. Bärlocher (1983) found that in detritus samples collected in April, between 60 and 90% more extractable protein was available at pH 11 (*T. abdominalis* gut) than at pH 8 (*G. fossarum* gut).

The role of symbionts in aquatic detritivore nutrition has been primarily descriptive (see Cummins and Klug, 1979). Some insects, notably *T. abdominalis*, have specialized hindgut caeca with dense microbial populations that are assumed to play an important role in the insect's nutrition. Bacteria are attached to the foregut wall in the caddisfly *Zealandopsyche ingens* (Winterbourn, 1982b) and in the midgut of the midge *Xylotopus par* (Kaufman, 1983).

30.3.4 Microbes as Food

A central question in the nutritional ecology of detritivores is the relative importance of microbes themselves as a food source compared with the OM on which they are situated. The rapid gut turnover time (often <1 hr for many collectors) may indicate that the digestive mechanism is largely a matter of stripping microbial nutrients rather than digestion of the more refractory detritus. The quantitative importance of fungi for *Gammarus pseudolimnaeus* was demonstrated by Bärlocher and Kendrick (1975) and of bacteria for the snail *Planorbis contortus* by Calow (1974). Fredeen (1964) reared black fly larvae on pure cultures of bacteria, but Baker and Bradnam (1976) calculated that in a British chalk stream, "although *Simulium* digests at least 50% of the bacteria it ingests, non-living detrital materials still account for the major proportion of its energy intake."

Lawson et al. (1984) used ^{15}N enrichment of leaf detritus to estimate microbial biomass in their study of growth of *T. abdominalis* fed on pignut hickory leaves. They demonstrated that the amount of microbial biomass (either fungi or bacteria) does not influence larval growth, although the microbial community structure has a significant influence on consumption rate, assimilation efficiency, and growth rate. *Tipula abdominalis* requires fungi and bacteria in its diet but not as direct sources of C and N; 73–89% of their growth is derived from the leaf matrix itself.

In partitioning the indirect contribution of fungi and bacteria, Lawson et al. (1984) found that pure cultures of fungi or leaves colonized by fungi alone

are poor food for *T. abdominalis*. However, the metabolic activities of fungi are important for subsequent bacterial colonization. Thus a low growth rate is to be expected in the initial stages of leaf decomposition, but the combined activities of fungi and bacteria result in biochemical modifications of the leaf and increase the availability of microbial metabolites, markedly improving the digestibility of leaves over time.

30.3.5 Feeding Behavior

Behavioral adaptations for feeding vary both within and between functional feeding groups. A major question is the degree of selectivity practiced by detritivores. Food choice is easier to observe with large-particle shredders, or when the food can be manipulated for scrapers (Hart, 1981) or filtering collectors (Fuller and Mackay, 1981), than it is for gathering collectors. The latter live within or on the food milieu, which is a mixture of fine inorganic and organic particles, and it is difficult to distinguish food acquisition behavior from other activities. The separation between gathering and filtering is blurred, because species in burrows such as the mayfly *Hexagenia limbata* or tube-building midges use body undulations to cause a current that draws both particles in transport and sediments into their burrows (Cummins and Klug, 1979).

Cammen (1980) reviewed ingestion rates for deposit feeders and developed an empirical model: $C = 0.381 \cdot W^{-0.742}$ (where C = organic matter ingested and W = body size). This relation is consistent for 19 species in three phyla and indicates that total ingestion (inorganic and organic) can almost entirely be explained by the OM ingested and body mass of the feeders. This model suggests that deposit feeders can maintain a rate of intake of OM independent of the organic content of the food by actively adjusting their feeding rate according to some perception of food quality.

Data from Davies (1975) for chironomids and from Zimmerman et al. (1975) for *H. limbata* suggest that gathering collectors are selective for organic particles among the mineral particles, but to date there are no definitive studies that demonstrate selection of the highest-quality components of the detrital material. Mattingly et al. (1981) compared growth rates of the midge *Stictochironomus annulicrus* fed on *Tipula* feces mixed in three proportions with ashed sand of the same size range. Larvae grew fastest on the mixture with the largest amount of feces and slowest on that with the lowest amount; thus this collector apparently does not select for food quality. Detritivores feeding on the organic layer on stones are also considered to be nonselective browsers within the constraints set by body size and mouthpart morphology (Winterbourn, 1982a). Differential digestion, as shown for tubificid worms feeding on bacteria (Brinkhurst and Chua, 1969), indicates that selective assimilation could compensate for nonselective ingestion.

The size of particles selected by filtering collectors increases as the individual grows because of the increase in size of the food-gathering body parts

and/or the catch nets that are constructed. This can result in selection for high-quality material; for example, filtering caddisflies switch diets in the last instar, consuming more animal material trapped in their nets (Fuller and Mackay, 1980; Wallace and Merritt, 1980). Six species of filter-feeding caddisflies in a southern Appalachian stream produce more detritus than they consume by egesting lower-quality feces that include undigested algae and animal components. Thus these animal populations may influence their own densities by affecting food quality and quantity through their feeding activities (Wallace and Merritt, 1980).

The preference of shredders for well-conditioned detritus over newly fallen leaves or sterilized leaves is well documented (see references in Anderson and Sedell, 1979). They will also preferentially choose leaf species that are high in nitrogen or relatively low in defensive compounds (e.g., phenolics, glycosides, and waxy cuticles). Fungi may play a role in detoxifying these compounds as well as in softening the leaf and increasing nutrients. Arsuffi and Suberkropp (1984) found that preferences exhibited by caddisfly larvae are not accounted for by either the fungal species or conditioning time alone but rather by their interaction. The most palatable leaves are those colonized by fungi subsequent to the appearance of detectable pectin lyase activity.

In laboratory studies shredders prefer pure fungal mycelia over leaf detritus and also specific species of fungi (Bärlocher and Kendrick, 1973, 1975; Rossi and Fano, 1979; Suberkropp et al., 1983). Cargill (1984) obtained greater growth of the caddisfly *Clistoronia magnifica* on pure mycelia than on leaf detritus, but the full life cycle was not completed on a diet of fungi alone.

30.3.6 Lipid Requirements

Hanson et al. (1983) and Cargill (1984) have shown that lipids can be a limiting nutritional factor for detritivores. Cargill reared *C. magnifica* on a series of diets from the third instar to adult and through hatching of the next generation. Larvae fed detritus alone did not complete development, those fed fungi plus high-nitrogen leaf detritus matured but did not reproduce, and animals fed detritus plus wheat grains completed development and reproduced. Larvae on all diets had nearly the same growth until the final instar, when their metabolism shifted to synthesis and storage of triglycerides derived from wheat starch. Sufficient nonstructural carbohydrates and assimilable lipids are not present in the detritus or fungi to allow for energy storage. Protein content of the food is not important for growth in the final instar, but acquisition of energy reserves as triglycerides is critical for successful reproduction.

Cargill et al. (1985) found that shredders can respond behaviorally to the changing metabolic needs associated with reproductive maturation. Fifth-instar larvae of nine species of caddisflies show definite preferences for

essential polyunsaturated fatty acids and triglycerides. Third- and fourth-instar larvae of the same species have no preference for the lipids. Thus predation and/or herbivory by many final-instar shredders may be aimed at lipid rather than protein acquisition.

30.4 LIFE CYCLE RESPONSE TO FOOD QUALITY

30.4.1 Aquatic Insect Xylophages

A small number of species in each major aquatic insect order exploit wood debris as facultative or obligate xylophages (Dudley and Anderson, 1982). Methods of feeding include surface scraping, gouging, and tunneling. The obligate xylophages are specialized to exploit a patchy but abundant and long-lasting food resource that is extremely low in nitrogen (C : N ratio 220–1340 : 1). Xylophagy in aquatic systems is further restricted because microbial degradation under water occurs on wood surfaces rather than within the wood matrix (Anderson et al., 1984). Wood that has decayed in a terrestrial habitat before entering the water has enhanced texture and nutritional qualities and an increased volume of food and habitat. Anderson et al. (1978) indicated that the nutritional consequences of xylophagy are perhaps the most important adaptive hurdle for wood feeders, because growth rate is regulated by the rate of conversion of refractory C and N to a digestible resource by the enzymatic activity of microbes. Consequences of wood exploitation by aquatic xylophages are an extremely low metabolic rate and a long life cycle, similar to many terrestrial xylophages (Haack and Slansky, Chapter 15).

The elmid beetle *Lara avara* is a dominant xylophage in Pacific northwest coniferous forest streams (Anderson et al., 1978; Steedman and Anderson, 1985). It exemplifies some of the adaptive syndromes proposed by Mattson (1980) that allow herbivores feeding on poor-quality food to obtain sufficient N to complete their life cycle. With fewer than five North American species in the subfamily Larinae, *L. avara* occupies an isolated phylogenetic position and is unusual in its feeding habits and large size for an elmid (larvae are 10 mm long and weigh 10–15 mg dry weight). Steedman and Anderson (1985) estimated that its life cycle requires 4–7 years, a consequence of its low growth rate (0.1–0.7% body weight per day); its large body size apparently provides a mechanical advantage for processing woody material. The respiratory rate (0.12–0.32 $\mu\text{l O}_2/\text{mg} \cdot \text{hr}$ at 10–15°C) of *L. avara* is only 10–25% that of comparable-size caddisflies or stoneflies. Although its feeding rate is low (<10% body weight per day), feeding is not interrupted by either seasonal or diel changes in quantity or quality of available food, and ingestion rate does not differ greatly over a temperature range of 5–15°C (Steedman, 1983).

The assimilation efficiency of *L. avara* larvae ranges from 5–12%; they

lack cellulases and a symbiotic gut flora. Thus their nutrition results from a "passive" strategy based on absorption of soluble nutrients liberated from wood by microbial enzymes. In addition, they use their own enzymes to digest fungal, bacterial, and microfaunal cells mechanically disrupted by feeding. By gouging the microbial-infected surface layers, *L. avara* is able to ingest more high-quality nitrogen and presumably more vitamins and sterols than are available in unconditioned wood.

Population studies by Kaufman (1983) in Michigan of *X. par* have demonstrated that this midge utilizes wood more efficiently than does *L. avara* or any other known aquatic xylophage. *Xylotopus par* is one of the largest midges in temperate lotic systems (mature larvae are 1.5–2.0 cm long with a dry weight >5 mg). The larvae colonize decayed deciduous wood, with densities in optimal substrates exceeding 5000/m². Kaufman suggests that the high densities reflect this organism's specialization and lack of interspecific competition as well as its insulation from predation. *Xylotopus par* is predominantly univoltine, with the potential to be bivoltine. Under conditions of high temperature and exceptional substrate quality, the interval from egg to adult may be only 2 months. Early-instar larvae tunnel into the surface layer, and their activity softens the deeper wood by opening gas exchange avenues that enhance penetration by microbial decay organisms. Final-instar larvae may penetrate as deep as 2 cm, where competition with surface inhabitants and predation pressure are reduced, but at the cost of low growth rate associated with diminished food quality.

The importance of terrestrial decay for preconditioning was demonstrated by comparing "bait" blocks of basswood, ash, and poplar that had decayed on land. *Xylotopus par* had the fastest growth rate (6.2%/day) on basswood, perhaps related to greater softness, degree of decay, and nitrogen content. Kaufman pointed out that wood softness could be important by allowing for more wood to be ingested per unit effort.

Aspects of digestive physiology in *X. par* that may aid in assimilation of the woody detritus include a long gut retention time (7 hr at 25°C); an abundant and localized group of anaerobic bacteria in the posterior midgut; and an alkaline anterior midgut that may free bound proteins in the wood (Kaufman, 1983).

30.4.2 Shredders

Lepidostoma caddisflies are shredders that exhibit resource partitioning and distinctive growth patterns associated with differential utilization of deciduous leaves and conifer needles. *Lepidostoma unicolor* is a generalized feeder widely distributed in western North America. At Marion Lake, British Columbia, Winterbourn (1971) reported that the flight period is May to August and that larvae are shredders of deciduous leaves, selecting the most decayed leaves but showing no preference between maple, alder, or poplar. *Lepidostoma quercina* is restricted to the Coast Range from Oregon to Brit-

ish Columbia and has an early spring flight period. *Lepidostoma unicolor* and *L. quercina* co-occur in western Oregon streams (along with 2 or 4 other *Lepidostoma* spp.). *Lepidostoma quercina* larvae have rapid growth in late autumn, when water temperature is declining but when deciduous leaf input is high, whereas *L. unicolor* has limited growth over the winter and then a rapid spurt from late May to early July, when final instars increase from 1.6 to 4.7 mg dw (Grafius and Anderson, 1979, 1980). The latter species exploits refractory conifer needles when water temperature is increasing, in contrast to *L. quercina*, which has a higher-quality food source (deciduous leaves) but at a time when temperature is decreasing. In laboratory feeding trials at 15°C, *L. unicolor* has a growth rate of 4% per day on alder and 2.6% per day on conifer needles, whereas *L. quercina* grows at 1.9% per day on alder and loses weight on a conifer needle diet (Anderson and Grafius, 1975).

Using a simulation model incorporating temperature and diet effects on growth rate, Grafius and Anderson (1979) attempted to mimic the development of a field population of *L. quercina* (Fig. 30.1). The initial model predicted an appropriate maximal size for larvae, but the timing of maximal weight was 2–3 months earlier than what actually occurred in the field. They postulated a shortage of high-quality food (alder leaves) in late summer due to competition with other detritivores (especially snails) and a switch to the more abundant but lower quality maple leaves. When they simulated an 80-day delay in developmental time, a close fit between simulated growth rate and the field data occurred (Fig. 30.1).

Otto (1974) also found that food quality differences between leaf species affects the growth pattern of a shredder caddisfly *Potamophylax cingulatus*. In autumn, when alder leaves are plentiful, there is a steady increase in fat content of larvae, but from January to May, when beech leaves are the main food, fat content drops. From May onward, the additional inputs of fresh leaves and macrophytes allow an increase in growth rate and fat content up to pupation. Otto (1974) demonstrated by feeding trials that the slow growth during winter and spring is food-related, as opposed to being only a function of temperature; larvae fed beech leaves were 27% below and those fed alder were 25% above the weights of the field population. The addition of alder leaves caused exceptionally high consumption and a resultant increase in growth.

30.4.3 Collectors

Based on the contention that the ultimate measure of food quality is the growth response, Ward and Cummins (1979) compared growth rates at 10, 15, and 20°C of the midge *Paratendipes albimanus* using detritus of known origin and particle size (75–250 µm). Substrates with higher microbial populations produced greater growth rates in the following order: pignut hickory leaves > white oak leaves > insect feces > natural stream detritus. Depending on temperature, between 68 and 94% of the variance in growth rates

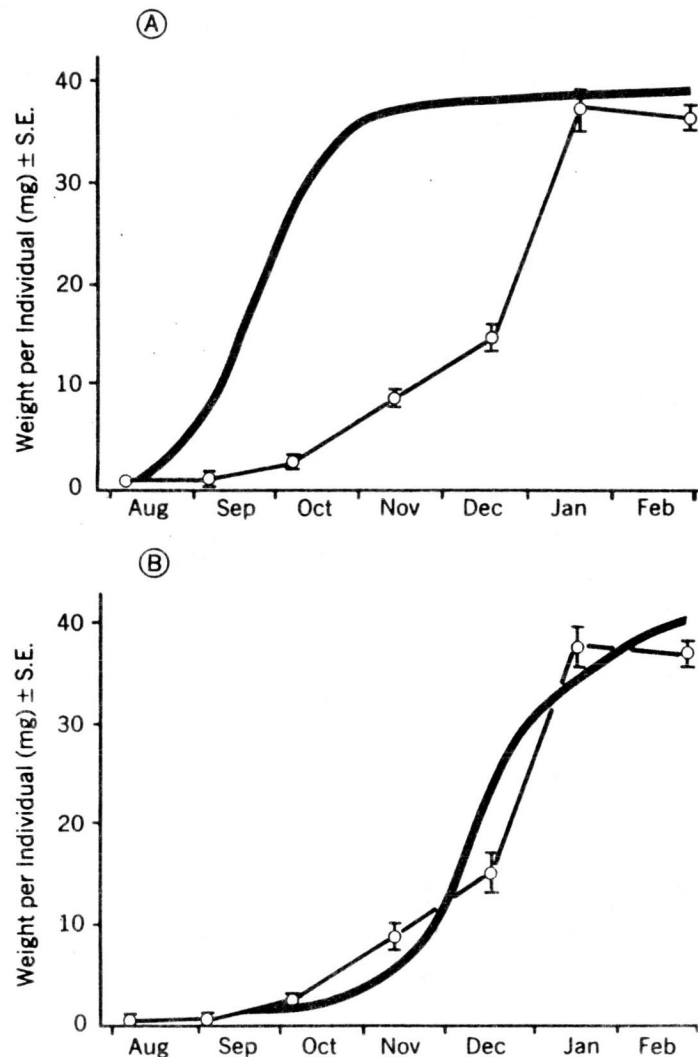


Fig. 30.1. Comparisons of field mean weights (open circles) with results of simulation modeling of *Lepidostoma quercina* growth (a) when food was unlimited and (b) when alder leaves were limited for the first 80 days of simulation. (From "Population dynamics, bioenergetics, and role of *Lepidostoma quercina* Ross (Trichoptera: Lepidostomatidae) in an Oregon woodland stream" by E. Grafius and N. H. Anderson, *Ecology*, 1979, **60**, 433-441. Copyright © 1979 by the Ecological Society of America. Reprinted by permission.)

could be explained by microbial activity, measured as either ATP or respiration. In view of the data from Baker and Bradnam (1976) and Lawson et al. (1984) that microbial biomass is insufficient as a direct source of C and N, the enhanced growth of *P. albimanus* at higher microbial levels should probably be attributed to their biochemical modifications of the detritus.

Ward and Cummins (1979) found that a combination of temperature and food quality provides the best explanation of the field growth pattern of *P. albimanus*. In the field, larvae emerge in July and grow to about 1 μg and then cease growing for the rest of the summer. By contrast, when fed ground hickory leaves at comparable temperatures, they complete a generation in 2

Table 30.3. Growth Rate (G)^a of *Ephemerella infrequens* Reared on Various Diets at Ambient Stream Temperature for 7–8 Weeks

Initial larval size	Diet				
	Fish food flakes ^b	Algae on stones	Alder leaves	Ground alder leaves	Ground alder wood
4.0–4.5 mm	4.51	5.25	2.52	4.44	0.79
6.0–7.0 mm	2.52	2.26	2.15	2.43	0.67

Field populations (8 streams): G (range) = 1.18–2.89.

^a G = instantaneous rate of growth ($\times 100$).

^b Tetramin; >46% crude protein.

Source: Hawkins (1982).

months. There is a second spurt of growth in October–November, shortly after the autumnal diatom bloom and leaf inputs, which continues until stream temperature drops to 4°C. A third period of rapid growth occurs in the spring and continues until emergence in June–July; this coincides with increased water temperature and high microbial respiratory activity. *Paratendipes albimanus* is univoltine in streams but bivoltine in lakes, where algal-derived detritus provides a higher-quality food source.

Hawkins (1982) compared effects of diet on growth rates of two size classes of the mayfly *Ephemerella infrequens* in the laboratory for 7–8 weeks (Table 30.3). This species is primarily a gathering collector, but it is also a scraper and shredder. As expected, small larvae have faster growth rates than large larvae. Gross effects of food quality are evident in that growth on ground wood is only 15–30% that on other foods. Algae, high-protein artificial diet, and ground alder leaves all produce growth rates much higher than those calculated for several field populations (Table 30.3). Hawkins suggested that the response to food under field conditions will be an adjustment of population density rather than of individual growth rate. There probably is food limitation of *E. infrequens*, because densities are lowest in detritus-based streams and greatest in those with more algae. Thus, although field densities attain levels sufficient to reduce individual growth compared with that in the laboratory, severe depression of growth rate is not observed, probably because excess individuals are lost by downstream drift.

30.5 CONCLUSIONS AND FUTURE RESEARCH

In this chapter we have emphasized the heterogeneous nature of the food resources exploited by aquatic detritivores. There is now good evidence that the detritus substrate, rather than just the microbiota, is the basic food source for some species (e.g., *T. abdominalis* and *Z. ingens*). However, in most detritivores there is a definite requirement for a supplement of higher

quality food in the form of microbes, algae, or animal tissue in order to complete development. Isolation of the role of nutrition in life histories is difficult to achieve without controlled laboratory or field experiments because of the heterogeneity of the food and because of diet switching during development.

Our focus in detailing life histories has been on differences in growth rate, because this directly affects duration of life cycles (i.e., voltinism), size at maturity (and therefore fecundity, which is positively correlated with female size), and survival. Temperature and food quality and quantity are control parameters with significant interactions on rate of growth.

Butler (1984) pointed out that voltinism should be viewed as a life-history variable at the population level and not as a characteristic of a species. Cohort splitting under conditions of food limitation may result in some individuals spending an additional year or more as larvae because they did not achieve appropriate size for metamorphosis in their first season (Pritchard, 1978). The life-cycle examples for xylophages and collectors indicate that larval duration is not fixed and is closely related to food quality. The benefits of a long larval duration for increased feeding and concomitant weight gain represent a trade-off in that prolongation of the larval stage lengthens the period of vulnerability to both biotic and abiotic mortality factors.

Life-cycle patterns are assumed to reflect an optimal solution to problems associated with maximizing individual fitness. Timing of feeding or growth periods is thus expected to be keyed to the availability of preferred or appropriate foods. Most shredders exhibit growth during winter (Hynes, 1970), but there is a range of growth patterns. For example, *L. quercina* grows rapidly in autumn and early winter, exploiting the fast-decaying leaves during the major period of litterfall. Larvae reach maximal weight by December and then have a period of arrested development until pupation in early spring. *Lepidostoma unicolor* and *P. cingulatus* have slower growth over winter and continue feeding the following spring and summer. This pattern of delaying development until temperatures are higher seems to involve a greater risk in exposure to mortality and to a food mix composed of refractory resident detritus interspersed with occasional high-quality items.

The quality of detritus has usually been considered in terms of protein (N), level of microbial activity (ATP or respiration), or proportion of refractory structural materials (lignin : cellulose ratio). Feeding deterrents or allelochemicals have received little or no attention. Compared with terrestrial herbivores, the importance of allelochemicals to aquatic detritivores is probably low because of both leaching and microbial conditioning. However, bioassays used in food quality studies to demonstrate reduction in larval growth do not distinguish between effects due to reduced feeding and those due to postingestive physiological phenomena.

Preference for lipid-coated detritus by caddisfly shredders indicates a nutritionally based response to changing metabolic requirements (Cargill et al., 1985). Lipids are the first specific chemicals to be identified as cues for

detritivores feeding on fungal-colonized detritus. The preference for lipids occurs in the final instar apparently as a dietary requirement for accumulation of an energy store.

Continued research is warranted both for a basic understanding of nutritional ecology of aquatic detritivores and because of management implications for aquatic resources. For example, canopy removal by logging may shift the faunal composition from a detritus-based to an algal-based community. Nutrient enrichment from agriculture, forestry, or domestic effluents leads to increased algal production and high-quality detritus exploited by nuisance organisms such as black flies and hydropsychid caddisflies. The relatively unselective feeding and high rates of ingestion of fine particles by gatherers and filterers leads to bioaccumulation of adsorbed synthetic chemicals and a resultant transfer of these materials up the food chain to fish, birds, and other predators.

Nutritional requirements of a broader range of detritivores need to be assessed using defined diets in controlled laboratory settings. The entire range of nutritionally important compounds (proteins, lipids, carbohydrates, vitamins, minerals, sterols, etc.) should be considered, with emphasis on potential changes in nutritional needs at various times in the life cycle. There are undoubtedly a number of diverse physiological and behavioral strategies used by larvae for extracting sufficient nutrients from the generally poor quality food. In further experiments to elucidate these strategies, the reproductive and feeding characteristics of adults need to be taken into consideration.

An understanding of physiological adaptations and nutritional requirements is basic to elucidating mechanisms of food utilization and allocation. However, further field studies are also necessary to put this information in the context of nutritional ecology. Is food quality or quantity a limiting factor for populations of aquatic detritivores? Sweeney (1984) noted that species composition varies in different parts of a lake or stream because of human activities: "thus many field experiments on nutrition are presently underway, but unfortunately only a few of these have been recognized, and even fewer are being monitored."

REFERENCES

- Anderson, J. M. and A. Macfayden (eds.). 1976. *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*. Blackwell, Oxford.
- Anderson, N. H. and K. W. Cummins. 1979. The influences of diet on the life histories of aquatic insects. *J. Fish. Res. Bd. Can.* **36**, 335-342.
- Anderson, N. H. and E. Grafius. 1975. Utilization and processing of allochthonous material by stream Trichoptera. *Verh. Int. Verein. Limnol.* **19**, 3083-3088.
- Anderson, N. H. and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annu. Rev. Entomol.* **24**, 351-377.

- Anderson, N. H., J. R. Sedell, L. M. Roberts, and F. J. Triska. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. *Am. Midl. Nat.* **100**, 64–82.
- Anderson, N. H., R. J. Steedman, and T. Dudley. 1984. Patterns of exploitation by stream invertebrates of wood debris (xylophagy). *Verh. Int. Verein. Limnol.* **22**, 1847–1852.
- Arsuffi, T. L. and K. Suberkropp. 1984. Leaf processing capabilities of aquatic hyphomycetes: Interspecific differences and influence on shredder feeding preferences. *Oikos* **42**, 144–154.
- Baker, J. H. and L. A. Bradnam. 1976. The role of bacteria in the nutrition of aquatic detritivores. *Oecologia (Berl.)* **24**, 95–104.
- Bärlocher, F. 1982. The contribution of fungal enzymes to the digestion of leaves by *Gammarus fossarum* Koch (Amphipoda). *Oecologia (Berl.)* **52**, 1–4.
- Bärlocher, F. 1983. Seasonal variation of standing crop and digestibility of CPOM in a Swiss Jura stream. *Ecology* **64**, 1266–1272.
- Bärlocher, F. and B. Kendrick. 1973. Fungi in the diet of *Gammarus pseudolimnaeus*. *Oikos* **24**, 295–300.
- Bärlocher, F. and B. Kendrick. 1975. Assimilation efficiency of *Gammarus pseudolimnaeus* (Amphipoda) feeding on fungal mycelia or autumn-shed leaves. *Oikos* **26**, 55–59.
- Boling, R. H., E. D. Goodman, J. A. Van Sickle, J. O. Zimmer, K. W. Cummins, R. C. Petersen, and S. R. Reice. 1975. Towards a model of detritus processing in a woodland stream. *Ecology* **56**, 141–151.
- Bowen, S. H. 1984. Organic precipitates in aquatic food chains. *Bull. Marine Sci.* **35**, 440–448.
- Brinkhurst, R. O. and K. E. Chua. 1969. Preliminary investigations of the exploitation of some potential nutritional resources by three sympatric tubificid oligochaetes. *J. Fish. Res. Bd. Can.* **26**, 2659–2668.
- Butler, M. G. 1984. Life histories of aquatic insects. In V. H. Resh and D. M. Rosenberg, eds. *The Ecology of Aquatic Insects*. Praeger, New York, pp. 24–55.
- Calow, P. 1974. Evidence for bacterial feeding in *Planorbis contortus* Linn. (Gastropoda: Pulmonata). *Proc. Malac. Soc. Lond.* **41**, 145–156.
- Calow, P. 1975. On the nature and possible utility of epilithic detritus. *Hydrobiologia* **16**, 81–96.
- Cammen, L. M. 1980. Ingestion rate: An empirical model for aquatic deposit feeders and detritivores. *Oecologia (Berl.)* **44**, 303–310.
- Cargill, A. S. 1984. The role of lipids in the nutrition of shredding aquatic insects. Ph.D. dissertation, Oregon State University, Corvallis.
- Cargill, A. S., K. W. Cummins, B. J. Hanson, and R. R. Lowry. 1985. The role of lipids as feeding stimulants for shredding aquatic insects. *Freshwat. Biol.* **15**, 455–464.
- Cummins, K. W. 1973. Trophic relations of aquatic insects. *Annu. Rev. Entomol.* **18**, 183–206.
- Cummins, K. W. 1974. Structure and function of stream ecosystems. *Bioscience* **24**, 631–641.

- Cummins, K. W. and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annu. Rev. Ecol. Syst.* **10**, 147-172.
- Davies, I. J. 1975. Selective feeding in some arctic Chironomidae. *Verh. Int. Verein. Limnol.* **19**, 3149-3154.
- Dudley, T. and N. H. Anderson. 1982. A survey of invertebrates associated with wood debris in aquatic habitats. *Melandria* **39**, 1-21.
- Egglishaw, H. J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. *J. Anim. Ecol.* **33**, 463-476.
- Egglishaw, H. J. 1968. The quantitative relationship between bottom fauna and plant detritus in streams of different calcium concentrations. *J. Appl. Ecol.* **5**, 731-740.
- Fisher, S. G. and G. W. Likens. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. *Ecol. Monogr.* **43**, 421-439.
- Fredeen, F. J. H. 1964. Bacteria as food for black fly larvae in laboratory cultures and in natural streams. *Can. J. Zool.* **42**, 527-548.
- Fuller, R. L. and R. J. Mackay. 1980. Feeding ecology of three species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. *Can. J. Zool.* **58**, 2239-2251.
- Fuller, R. L. and R. J. Mackay. 1981. Effects of food quality on the growth of three *Hydropsyche* species (Trichoptera: Hydropsychidae). *Can. J. Zool.* **59**, 1133-1140.
- Grafius, E. and N. H. Anderson. 1979. Population dynamics, bioenergetics, and role of *Lepidostoma quercina* Ross (Trichoptera: Lepidostomatidae) in an Oregon woodland stream. *Ecology* **60**, 433-441.
- Grafius, E. and N. H. Anderson. 1980. Population dynamics and role of two species of *Lepidostoma* (Trichoptera: Lepidostomatidae) in an Oregon coniferous stream. *Ecology* **61**, 808-816.
- Hanson, B. J., K. W. Cummins, A. S. Cargill, and R. R. Lowry. 1983. Dietary effects on lipid and fatty acid composition of *Clistoronia magnifica* (Trichoptera: Limnephilidae). *Freshwat. Invert. Biol.* **2**, 2-15.
- Hart, D. D. 1981. Foraging and resource patchiness: Field experiments with a grazing stream insect. *Oikos* **37**, 46-52.
- Hawkins, C. P. 1982. Ecological relationships among western Ephemerellidae: Growth, life cycles, food habits, and habitat relationships. Ph.D. dissertation, Oregon State University, Corvallis.
- Hynes, H. B. N. 1970. *The Ecology of Running Waters*. University of Toronto Press, Toronto.
- Kaufman, M. G. 1983. Life history and feeding ecology of *Xylotopus par* (Coquillett) (Diptera: Chironomidae). M.S. thesis, Central Michigan University, Mount Pleasant.
- Kaushik, N. K. and H. B. N. Hynes. 1971. The fate of dead leaves that fall into streams. *Arch. Hydrobiol.* **68**, 465-515.
- Lawson, D. L., M. J. Klug, and R. W. Merritt. 1984. The influence of the physical, chemical, and microbiological characteristics of decomposing leaves on the growth of the detritivore *Tipula abdominalis* (Diptera: Tipulidae). *Can. J. Zool.* **62**, 2339-2343.

- Madsen, B. L. 1972. Detritus on stones in small streams. *Mem. Inst. Ital. Idrobiol.* **29** (Suppl.), 385-403.
- Madsen, B. L. 1974. A note on the food of *Amphinemura sulcicollis* (Plecoptera). *Hydrobiologia* **45**, 169-175.
- Mann, K. H. 1975. Patterns of energy flow. In B. A. Whitton, ed. *River Ecology*. Blackwell, Oxford, U.K., pp. 248-263.
- Martin, M. M., J. S. Martin, J. J. Kukor, and R. W. Merritt. 1980. The digestion of protein and carbohydrate by the stream detritivore, *Tipula abdominalis* (Diptera: Tipulidae). *Oecologia (Berl.)* **46**, 360-364.
- Martin, M. M., J. S. Martin, J. J. Kukor, and R. W. Merritt. 1981a. The digestive enzymes of detritus-feeding stonefly nymphs (Plecoptera: Pteronarcyidae). *Can. J. Zool.* **59**, 1947-1951.
- Martin, M. M., J. J. Kukor, J. S. Martin, D. L. Lawson, and R. W. Merritt. 1981b. Digestive enzymes of larvae of three species of caddisflies (Trichoptera). *Insect Biochem.* **11**, 501-506.
- Mason, C. F. and R. J. Bryant. 1975. Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L. *J. Ecol.* **63**, 71-95.
- Mattingly, R. L., K. W. Cummins, and R. H. King. 1981. The influence of substrate organic content on the growth of a stream chironomid. *Hydrobiologia* **77**, 161-165.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annu. Rev. Ecol. Syst.* **11**, 119-161.
- Melchionni-Santolini, U. and J. W. Hopton (eds.). 1972. Detritus and its role in aquatic systems. *Mem. Inst. Ital. Idrobiol.* **29** (Suppl.), 1-540.
- Merritt, R. W. and K. W. Cummins (eds.). 1978. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque, IA.
- Merritt, R. W., K. W. Cummins, and T. M. Burton. 1984. The role of aquatic insects in the processing and cycling of nutrients. In V. H. Resh and D. M. Rosenberg, eds. *The Ecology of Aquatic Insects*. Praeger, New York, pp. 134-163.
- Miall, L. C. 1895. *The Natural History of Aquatic Insects*. Macmillan, London.
- Otto, C. 1974. Growth and energetics in a larval population of *Potamophylax cingulatus* (Steph.) (Trichoptera) in a south Swedish stream. *J. Anim. Ecol.* **43**, 339-361.
- Petersen, R. C. and K. W. Cummins. 1974. Leaf processing in a woodland stream. *Freshwat. Biol.* **4**, 343-368.
- Pritchard, G. 1978. The study of dynamics of populations of aquatic insects: The problem of variability in life history exemplified by *Tipula sacra* Alexander (Diptera: Tipulidae). *Verh. Int. Verein. Limnol.* **20**, 2634-2640.
- Ross, H. H. 1963. Stream communities and terrestrial biomes. *Arch. Hydrobiol.* **59**, 235-242.
- Rossi, L. and A. E. Fano. 1979. Role of fungi in the trophic niche of the congeneric detritivorous *Asellus aquaticus* and *A. coxalis* (Isopoda). *Oikos* **32**, 380-385.
- Rounick, J. S. and M. J. Winterbourn. 1983. The formation, structure and utilization of stone surface organic layers in two New Zealand streams. *Freshwat. Biol.* **13**, 57-72.

- Sedell, J. R., F. J. Triska, J. D. Hall, N. H. Anderson, and J. H. Lyford. 1974. Sources and fates of organic inputs in coniferous forest streams. In R. H. Waring and R. L. Edmonds, eds. *Integrated Research in the Coniferous Forest Biome*. Coniferous Forest Biome Ecosystems Analysis Studies. U.S. IBP Bull. No. 5.
- Slansky, F., Jr. 1982. Insect nutrition: An adaptationist's perspective. *Flor. Entomol.* **65**, 45-71.
- Steedman, R. J. 1983. Life history and feeding role of the xylophagous aquatic beetle, *Lara avara* LeConte (Dryopoidea: Elmidae). M.S. thesis, Oregon State University, Corvallis.
- Steedman, R. J. and N. H. Anderson. 1985. Life history and ecological role of the xylophagous aquatic beetle, *Lara avara* LeConte (Dryopoidea: Elmidae). *Freshwat. Biol.* **15**, 535-546.
- Suberkropp, K., T. L. Arsuffi, and J. P. Anderson. 1983. Comparison of degradative ability, enzymatic activity, and palatability of aquatic hyphomycetes grown on leaf litter. *Appl. Environ. Microbiol.* **46**, 237-244.
- Sweeney, B. W. 1984. Factors influencing life-history patterns of aquatic insects. In V. H. Resh and D. M. Rosenberg, eds. *The Ecology of Aquatic Insects*. Praeger, New York, pp. 56-100.
- Thienemann, A. 1912. Der Bergbach des Sauerland. *Int. Rev. Ges. Hydrobiol.* **4** (Suppl.), 1-125.
- Usinger, R. L. (ed.). 1956. *Aquatic Insects of California*. University of California Press, Berkeley.
- Wallace, J. B. and R. W. Merritt. 1980. Filter-feeding ecology of aquatic insects. *Annu. Rev. Entomol.* **25**, 103-132.
- Wallace, J. B., J. R. Webster, and W. R. Woodall. 1977. The role of filter feeders in flowing waters. *Arch. Hydrobiol.* **79**, 506-532.
- Ward, G. M. 1977. The influence of detrital food quality and temperature on the life history and growth of *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae) in a Michigan headwater stream. Ph.D. dissertation, Michigan State University, East Lansing.
- Ward, G. M. and K. W. Cummins. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). *Ecology* **60**, 57-64.
- Webster, J. R. and B. C. Patten. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. *Ecol. Monogr.* **49**, 51-72.
- Winterbourn, M. J. 1971. The life histories and trophic relationships of the Trichoptera of Marion Lake, British Columbia. *Can. J. Zool.* **49**, 623-635.
- Winterbourn, M. J. 1982a. The invertebrate fauna of a forest stream and its association with fine particulate matter. *N.Z. J. Mar. Freshwat. Res.* **16**, 271-281.
- Winterbourn, M. J. 1982b. Food utilization by a stream detritivore, *Zealandopsyche ingens* (Trichoptera: Oeconesidae). *Int. Rev. Ges. Hydrobiol.* **67**, 209-222.
- Zimmerman, M. C., T. E. Wissing, and R. P. Rutter. 1975. Bioenergetics of the burrowing mayfly, *Hexagenia limbata*, in a pond ecosystem. *Verh. Int. Verein. Limnol.* **19**, 3039-3049.