DETRITUS PROCESSING BY MACROINVERTEBRATES IN STREAM ECOSYSTEMS

◆6175

N. H. Anderson

Department of Entomology, Oregon State University, Corvallis, Oregon 97331

James R. Sedell[1]

Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331

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 probably transferred through this route than through the grazing pathway (98). Detritus cannot be precisely defined in terms of its chemical composition or associated microorganisms. As an operational definition, Boling et al (16) defined it as all particulate (>0.45-μm particle diameter) organic matter (reduced carbon compounds) together with associated microbiota—fungi, bacteria, protozoa, and other microinvertebrates. Microbes are included as part of the detritus because the relationship between them and the organic substrate is so intimate that independence is never observed in nature; also, efficient separation techniques applicable to field-collected detritus are nonexistent.

The role of detritus in aquatic ecosystems was discussed in two recent symposia (1, 109). Studies of biological decomposition are interdisciplinary in nature and were a theme of the International Biological Programs in freshwater, marine, and terrestrial projects (1). Thus, with the upsurge of interest in this topic, it is timely to review contributions, especially on the

[1]Current address: Forest Resources Center, Weyerhaeuser Co., Centralia, Washington 98531.

role of macroinvertebrates that feed on detritus, and in so doing affect particle size reduction and eventual mineralization of the material.

A central feature of stream ecosystems is the unidirectional flow of the water. In addition to shaping the physical habitat, the current influences the kind and distribution of the fauna, and the transport and deposition of food material (126). Although autochthonous primary production by diatoms, other algae, and macrophytes is significant in some situations (99, 107, 119, 162), the preponderance of allochthonous inputs to streams is emphasized in recent literature (24, 31, 36, 39, 70, 97, 99, 111, 112, 116, 162). Hynes (73) suggested that the watershed, rather than the stream, should be the basic unit of study because of the dependence of the stream on inputs of organic and inorganic material, and Ross (132) showed that the distribution of some stream taxa was associated with the distribution of the riparian vegetation. In viewing a stream as a continuum from headwaters to mouth, the influence of riparian vegetation and its litter contribution will vary with stream order and position along the continuum (33, 34; R. L. Vannote, personal communication).

The degradation of detritus in streams is extremely complex. Such aspects as preconditioning in the terrestrial habitat, physical abrasion, leaching, and microbial colonization are discussed only briefly, as our focus is primarily on the role of macroinvertebrates. The functional feeding group concept of Cummins (31, 32) is adopted for comparing detritivore groups. Historically, leaf litter has been considered the major allochthonous input to streams. However, we place considerable emphasis on wood debris in this review because its importance to streams has received little attention previously.

ALLOCHTHONOUS AND AUTOCHTHONOUS INPUTS TO STREAMS

The River Continuum

A river system is a large network of smaller tributaries coalescing into larger rivers. The small first- to third-order streams comprise about 85% of the total length of running waters (86). The basic features that characterize the river as a continuum from headwaters to mouth are the decreasing direct influence of the adjacent vegetation of the watershed, the increasing importance of inputs from upstream tributary systems, and increasing algal production.

Headwater streams are maximally influenced by riparian vegetation through shading and as the source of organic matter inputs, because the ratio of shoreline to stream bottom area is high. Even in grasslands, the distribution of trees and shrubs follows perennial and intermittent water-

courses except where land-use practices have resulted in removal or suppression of riparian vegetation. These low-light, relatively constant-temperature headwaters receive significant amounts of coarse particulate organic matter (CPOM; >1-mm diameter) from the watershed. Their most striking biological features are the paucity of primary producers (algae and vascular plants) and the abundance of invertebrates that feed on CPOM (32, 33).

The shift from heterotrophy to autotrophy usually occurs in the range of third- or fourth-order (intermediate-sized) streams, though the transition is gradual and varies with geographic region (108). Fourth- to sixth-order rivers are generally wide and the canopy of vegetation does not close over them. Direct inputs of CPOM from the riparian zone are lower because of the reduced ratio of length of bank to area of river bottom. Detrital material transported from upstream is largely as fine particulate organic material (FPOM; <1-mm diameter).

Leaf and Wood Inputs

Of the organic material that falls or slides into first-order streams every year, less than 50% may be flushed downstream to higher-order streams. In general, small streams are very retentive, not mere conduits exporting materials quickly to the sea. Some 60–70% of the annual particulate inputs are retained long enough to be biologically utilized by stream macro- and microorganisms (48, 134). Debris dams serve as effective retention devices for smaller organic material, allowing time for microbial colonization and utilization, and for invertebrate consumption of this material. Functionally, the invertebrates of streams flowing through forests have evolved to gouge, scrape, and shred wood and leaves and to gather the fine organic matter derived from breakdown of coarser material (6, 32).

The timing of litter inputs is given in Table 1 for both coniferous and deciduous forests. The deciduous forest 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 snow melt (48). The coniferous forest and evergreen deciduous forest streams show a more even distribution of inputs throughout the year (134, 151, 165).

The seasonal quality of the inputs varies and is of significance in terms of nutrient content. Spring and early summer inputs, although quantitatively smaller, consist primarily of high-nutrient pollen, flower parts, and insect frass (49, 134, 165). Inputs of wood and lichens in Oregon came predominantly in the winter and spring (134). In general, the inputs of organic material to streams are greater than that received on the forest floor. Since streams are at the bottom of slopes, and are wet, they serve as effective traps for blowing leaves and for materials that roll or slide down hills (73).

Table 1 Comparison of allochthonous inputs to streams with various types of riparian vegetation

Stream	Forest type	Seasonal inputs				Total inputs (g/m²/yr)	Ref.
		W	S	S	F		
Middle Bush, NZ	Southern beech (Nothofagus)	34	284	136	113	567	165
Smith Creek, MI	Mixed hardwood	32	95	101	424	669	—[a]
Coweeta, NC	White pine	22	48	52	197	319[b]	160
	Old field	46	18	60	162	286[b]	160
	Mixed hardwood	14	34	35	271	352[b]	160
Doe Run, KY	Mixed hardwood	31	12	67	245	355[c]	82, 90
Bear Brook, NH	Mixed hardwood	10	80	195	375	660	48
Stampen, Sweden	Alder-pasture	48	70	199	403	708	121
H. J. Andrews, OR	Douglas-fir, Hemlock	270	150	90	220	730	151
Camp Creek, ID	Spruce, fir	ND[d]	ND	239	239	ND	—[e]

[a] D. Mahan and K. W. Cummins, personal communication.
[b] Just litter fall, no lateral movement.
[c] Leaf litter only.
[d] ND, No data available.
[e] G. W. Minshall and R. C. Petersen, personal communication.

Although leaf litter has received the greatest attention by stream ecologists, woody debris represents over 70% of the inputs to a coniferous forest stream (151) and also a large fraction in deciduous forest streams (48). Christensen's (25, 26) review of litter fall in woodlands of the temperate and tropic zones indicates that wood comprises 15–49% of total litter fall in deciduous forests (excluding estimates of bole wood).

Froehlich (56) estimated natural wood accumulations in several Oregon streams to be 20–70 metric tons per 40 m of stream. Recent surveys have demonstrated that heavy loading of wood debris is not merely a local phenomenon of the headwater streams of the Northwest. Our preliminary estimates of total debris loading for first- or second-order streams in old-growth stands are as follows (kg/m²): Oregon (Douglas-fir-hemlock), 25–40; Idaho (spruce-lodgepole pine), 7; New Hampshire (spruce-fir), 4; Tennessee (spruce-fir), 10 and (mixed hardwood), 13. The amount of small debris (<10-cm diameter) in all areas ranged from 1–4 kg/m² (G. Lienkaemper, F. Swanson, and J. Sedell, unpublished data).

Macrophyte Inputs

The contribution of macrophytes to streams has been reviewed by Westlake (161) and Fisher & Carpenter (47). Maximum biomass occurs in summer

or early fall and ranges from 0.4–0.7 kg (dry weight)/m² for fertile temperate waters down to 0.01–0.02 kg (dry weight)/m² in infertile, deep, or turbid waters. Mosses are the only significant macrophytes in small, densely shaded streams. The contribution of macrophytes to the productivity of stream ecosystems ranges from 1% in the River Thames, to 9–13% in intermediate-sized rivers, and up to 30% in springs, and it may be almost 100% of the primary production in polluted unshaded sections of some rivers (47). These plants are not usually grazed upon and thus represent a source of autochthonous detritus. The decomposition of macrophytes is quite rapid (ca 50% weight loss in a week) compared with terrestrial leaf material (ca 5–25% weight loss in a week).

In addition to their role as an energy source, macrophytes act as a structural modifier of the stream system during the summer growth and corresponding low-flow period. Macrophyte stands increase the stream bed area and reduce flow velocities, thereby enhancing sedimentation and retention of seston and drifting leaf material. By retaining drifting organic material and by providing a large surface area for epifaunal and microbial processing, macrophyte stands may expedite summertime detrital processing in streams where they occur.

INVERTEBRATES INVOLVED IN DETRITUS PROCESSING

To address process-oriented ecological questions, Cummins (32) has stressed the need to identify functional groups of organisms that are at least partially independent of taxonomic determinations, because accepting the species as the basic ecological unit would mean that the "perpetually incomplete state of our taxonomic knowledge will constitute a major constraint for the development of ecological theory." He further argues that the trophic categorization, built upon Lindeman's (89) classic contribution, has also proven as restrictive as taxonomic identification in answering process-oriented questions, because most schemes of trophic partitioning cannot deal adequately with the community metabolism of detritus. Wiggins & Mackay (163) have integrated systematics and the functional feeding concept. For the Nearctic Trichoptera, the generic level provides a reasonable indication of the kinds of organic material available as a food source in aquatic habitats (163).

It must be recognized that a functional feeding group classification provides only a generalized picture of the community. Most aquatic insects are opportunistic feeders and thus cannot be rigidly placed in a single functional group. A noncritical acceptance of the placement of genera, families, or

other taxa in the functional categories given by Merritt & Cummins (110) could impede a better understanding of trophic relations and the development of new approaches to stream ecology.

The early qualitative studies of gut contents (18, 78, 79, 85, 91, 113–115, 123, 137, 145, 168) revealed that a number of insects consume detritus. More recent community studies substantiate the fact that a majority of benthic species ingest a component of detritus (27, 69, 112, 133). The guts of 74 of 75 species of a riffle community contained some detritus, although only five species were classified as detritivores (>50% of the diet); for many species the pattern was for young individuals to consume detritus, but to shift to algal or animal ingestion concomitant with maturation (27).

Hynes (69) demonstrated the seasonal significance of detritus in that the growth of winter-active forms was based almost entirely on allochthonous material, and these taxa accounted for about two thirds of the productivity of the stream. Egglishaw (40) showed that almost 70% of the riffle inhabitants of a Scottish stream were associated with plant detritus, and he provided experimental evidence that they were not merely using detritus for shelter but also for food. Rabini & Minshall (126) explained preference of benthic insects for substrate in the 1.0- to 3.5-cm particle size range because it served as a better detritus food-collecting device than did substrates greater than 4.5 cm.

Functional Group Classification of Detritivores

Merritt & Cummins (110) have tabulated the taxa of insects in various functional groups. The shredder group in most areas is dominated by Trichoptera (Limnephilidae, Lepidostomatidae, Sericostomatidae, Oeconesidae) (30, 60, 61, 74, 94, 95, 120, 135, 147, 163, 166); by craneflies (35, 124, 153); and by Plecoptera (Pteronarcidae, Peltoperlidae, Nemouridae) (44, 45, 104, 157). Though these are the dominant taxa, partitioning of the shredding activities between community members at a particular site has not been assessed.

A number of noninsect invertebrates are detritivores that feed on CPOM, including amphipods, isopods, crayfish, and snails (71, 80, 88, 102, 111, 112, 118, 125, 133). Their sometimes high biomass, mixed age distribution, and continuous presence in the water more than compensates for their low species richness in their impact on the food resource. They tend to be more abundant in hard waters or eutrophic situations (71). Many are extreme trophic generalists (102, 105, 112, 133, 159). Though some of these taxa, such as crayfish, engulf or tear leaf material, many of the others do not have the chewing behavior of typical shredders. Amphipods and snails scrape or rasp the softer tissues, leaving the veins intact. Even though they may be considered fine-particle feeders (124), their feeding causes particle-size re-

duction and is important in the initial degradation of CPOM. Similarly, the feeding by some stoneflies (157) and mayflies (124) is by scraping fine particles of soft tissue from the leaf substrate.

Fine-particle feeders are partitioned into filter feeders that obtain suspended materials from the water column, and collector-gatherers that occur where FPOM has been deposited. Filtering may be accomplished by morphological structures (head fans of black flies, coxal-femoral hairs of *Isonychia*) or by behavioral activities (net building by caddisflies and midges, pumping by bivalve mollusks, or body undulations of *Chironomus*) (71). The collector-gatherer guild includes many of the mayflies, some stoneflies, many Diptera (ptychopterids, some tipulids, psychodids, many chironomids), oligochaete worms, and small gammarids and isopods. These taxa occur where FPOM has settled out in pools or backwaters, or where it is trapped by vegetation or entrained into the streambed.

Indirect evidence of the quantities of FPOM available, especially in rivers, is afforded by the vast populations of filter feeders and collectors that occur as nuisance swarms in the adult stage—black flies (51, 130), mayflies (53), and caddisflies (28, 54).

Two pathways recently suggested in the production and utilization of FPOM are the roles of gougers and compactors. Feeding by the elmid beetle, *Lara avara,* and the caddisfly, *Heteroplectron californicum,* on wood results in superficial channels or gouges that are intermediate between tunnels, typical of terrestrial wood borers, and the shredding of leaves (6). Fecal production and mechanical abrasion by these taxa contributes to the pool of FPOM. At the other end of the particle size scale, compactors produce fecal pellets that are considerably larger than the size of the ingested particles. The nets of philopotamid caddisflies can retain particles of less than 0.5×0.5 μm and the larvae egest compact fecal pellets (155). The feces of *Ptychoptera townesi* larvae from a pool habitat are several times the diameter of the ingested particles (E. Grafius, personal communication). Fecal pellets of black flies sediment from suspension much more readily than do the food particles (83). Particle size can be increased and thus make detritus available again for species requiring larger particles or for those in other habitats. This allows for recycling of FPOM, but the magnitude of this pathway is unknown. Rates of physical or biological breakdown of fecal pellets may be habitat specific.

FACTORS INFLUENCING AVAILABILITY AND UTILIZATION OF DETRITUS BY SHREDDERS

The quantity, quality, timing, and retention of allochthonous inputs to streams are a function of the watershed (73, 108). Most studies have been

in temperate deciduous forests so the emphasis has been on the autumnal pulse of leaf fall. The autumnal inputs may also be characteristic of other biomes, because deciduous trees and shrubs follow water courses, especially in desert and grassland areas.

Leaves accumulate in areas of reduced current and tend to form leaf packs or dams on the upstream side of rocks, sticks, or other obstructions. These accumulations, then, provide the sites of shredder activity. Major leaf accumulations may resist breakdown because of inaccessibility or low dissolved oxygen levels. The feeding activities of large shredders, such as *Tipula,* are important in loosening up the material that aids in penetration by other species (K. W. Cummins, personal communication). Lepidostomatid caddisflies, nemourid stoneflies, and snails are more abundant on small accumulations or on individual leaves than within closely appressed leaf packs (N. H. Anderson, unpublished data). Leaves that become buried are characteristically black in color, indicating anoxic conditions. Degradation is delayed depending on how long the leaves are buried. The relative food quality may be decreased, but presumably these leaves will eventually re-enter the food nexus.

Much of the more easily digestible material in leaves is never available to shredders, because soluble organic material is rapidly leached and enters the dissolved organic matter (DOM) pool. Leaf litter loses 5–27% of its dry weight within the first day, depending on the species of leaf and the degree of leaching that occurred in the terrestrial environment prior to introduction into the stream (124).

Leaf decomposition in the absence of macroinvertebrates is discussed by several authors (11, 13, 80, 139, 140, 148, 164). Decomposition as related to attractiveness and utilization of detritus by shredders has been termed conditioning (32). This is an interaction of biochemical and physical processes largely mediated by microorganism colonization. Conversion of plant tissue into microbial materials (microbial production) and partial decomposition of plant tissue into subunits that are digestible by detritus feeders (microbial catalysis) are important mechanisms of conditioning (13). Fungi, which penetrate the leaf matrix, are especially important (10, 13, 59, 80, 81, 95, 148), but bacteria, diatoms, protozoans, rotifers, and nematodes may also be prevalent on the leaf surface (32, 37, 74, 139, 140). Conditioning rate is largely temperature dependent (32, 141), but it is also affected by water chemistry and pH (41–43, 80, 169), and especially by qualitative species characteristics of leaf texture. Though higher temperature increases conditioning rate, many of the aquatic hyphomycete fungi are active colonizers below 10°C (148).

Kaushik & Hynes (80) concluded that feeding preference was associated with rate of decay, which in turn was related to fungal colonization and

protein content of the food. Amphipods and isopods exhibited feeding choices in the same order as decay rate: elm > maple > alder > oak > beech. Nitrogen levels increased due to fungal colonization, especially if the water was enriched with nitrogen and phosphate. Thus conditioned leaves are a higher-quality foodstuff because of the protein content. The supply of protein-rich detritus is maintained through the fall, winter, and spring, because leaf species decay at different rates and those that decay first tend to be eaten first (80). Leaf quality for shredders may decline from "over-conditioning." Assimilation efficiency of *Lepidostoma quercina* fed on alder leaves decreased slightly with increase in conditioning time (60).

Ingestion rates by *Lepidostoma* spp. increased with conditioning time of the leaves (5). *L. quercina* fed on alder leaves had constant consumption rates for the first 3 weeks of conditioning, but after that time the regression line indicated an increase of 5% per day for each additional day of incubation. *L. unicolor* also showed an increased consumption of Douglas-fir needles with increased conditioning, but conditioning required several weeks or months compared with 3 weeks for alder. Alder is exceptionally palatable even without conditioning, as *L. quercina* consumed about 60% of body weight per day of leached but unconditioned leaves (5).

Shredders are not important in leaf degradation in all studies. Mathews & Kowalczewski (103) discounted invertebrate feeding as important in leaf disappearance in the River Thames. Kaushik & Hynes (80) indicated that decay rates were not enhanced by mechanical shredding after the first few weeks. Reice (129) found no direct relation between numbers of individuals or of species and the rate of decomposition of leaf packs. He concluded that the direct role of macrodecomposers was minor. His data indicated an absence of shredder taxa in this third-order North Carolina stream in June. A similar lack of shredders was suggested (135) for the results in the River Thames. The relative abundance, or activity, of the fungi and bacterial components may affect shredder feeding. Thus low fungal populations, but high levels of bacteria, on *Nothofagus* leaves was suggested (37) as a reason for low shredder activity and slow degradation of beech leaves.

Kaushik & Hynes (80) indicate similarities between decay mechanisms in aquatic and soil systems. Temperature and initial composition of leaves govern the rate of decomposition in both systems. The level of nitrogen uptake (nitrogen factor of agronomists) depends on the leaf species. A change in the supply of phosphorous alters the quantity of immobilized nitrogen. Soil fungi are also important on leaves in water.

Shredder Feeding Experiments

Comparisons of the several studies of shredder feeding are difficult because of differences in experimental procedure and in objectives. The impact of

a species on leaf degradation can be demonstrated by different methods from those used to elucidate the food value of detritus. For example, Wallace, Woodall & Sherberger (157) demonstrated preferences by *Peltoperla maria* for various leaf species and showed that the characteristic mode of feeding was by scraping the cuticle and mesophyll. They used oven-dried leaves and a 2-week feeding period; this would not allow for normal colonization and conditioning by fungi. Thus the low consumption may be due to experimental procedure. Their data suggest that leaf tissue was used as food since bacteria were too sparce to contribute significantly as food. This study indicates that *P. maria* contributes to leaf degradation, and that tannins and ligninlike compounds are more rapidly leached from the feces than from intact leaves. However, growth of the larvae was not examined, so no inference can be drawn concerning assimilation of detritus. A similar comment holds for several other studies; that is, without some measurement of growth or development, the food value of detritus to the organism cannot be determined.

Iversen (75) demonstrated a relationship between gross growth efficiency (growth/ingestion) and the nitrogen content of leaves. Feeding preference of *Sericostoma personatum* was also associated with nitrogen, with the order of preference and the nitrogen content being alder (4.2% N) > oak (1.9% N) > beech (1.2% N) = spruce (1.4% N). Larvae fed on beech or spruce doubled their weight in 10 weeks, whereas a fourfold increase occurred in those fed oak or alder. The food quality of alder is apparent as growth was highest, but ingestion rate was less than half of that for larvae fed on the other three leaf species. Alder is a fast conditioning leaf whereas the others are all in the slow group (see below). The leaves were incubated in a stream for a month prior to feeding. This would allow for microbial colonization, but only alder would be fully conditioned in that time. In terms of leaf degradation, the larvae shredded 4–6 times body weight per week of the resistant types of leaves, compared with only 2.2 times body weight per week of alder leaves. Accounting for differences in size, because of superior growth on alder, the consumption per larva [mg (dry weight)/ week] was alder, 17.5; oak, 31.7; spruce, 22.2; and beech, 25.4.

Food quality was a limiting factor for larval growth of *Potamophylax cingulatus* (118, 120, 121). Compared with stream-dwelling larvae, those fed alder were heavier and those fed beech leaves were smaller. Preference for alder was coupled with assimilation efficiencies of up to 35%. Green leaves of either species picked from the tree were preferred to withered leaves (alder picked from the ground and beech from the stream). Thus, *P. cingulatus* was responding as a herbivore-detritivore rather than as a strict detritivore. In the field, the larvae grew rapidly until alder leaves were depleted in January. Beech leaves were the chief food available for the next

4 months, and the fat content of the larvae decreased from 13% to less than 8%. From May onward, macrophytes and fresh leaves from riparian vegetation afforded a higher-quality food source, increasing the fat and energy content before pupation.

Cummins et al (35) used a mass-balance approach with various shredders and collectors to quantify the factors involved in both utilization and degradation of leaves. They used hickory leaves with a standard leaching time, innoculation with hyphomycete spores, and a conditioning period prior to feeding. Degradation products (leaf fragments, feces, DOM) were not removed until the end of an experiment (7–15 weeks). This aspect of the experimental design probably explains the low survivorship and makes interpretation of growth rates suspect. However, the data on leaf degradation are important. Leaf weight loss in chambers containing *Tipula* was always greater than 50%; *Pycnopsyche* feeding resulted in leaf losses of 41–50%, even though the larvae all lost weight; *Pteronarcys* larvae all died within a week, but in this short time they caused 40% leaf weight loss compared with 26% in the control in 110 days.

The microcosm data for *Tipula* and *Pycnopsyche* were used to partition leaf breakdown into mechanical breakage (5%), leaching (9.6%), microbial utilization (17.7%), shredder feeding (19.1%), collector feeding (9%), and residual detritus (40.6%) (35). On this basis, the standing crop of *Tipula* and *Pycnopsyche* in their Michigan stream could process at least half of the estimated large particulate organic matter inputs for an eastern woodland stream. This estimate of processing is conservative, even for these two major shredders, because as indicated above the growth rates are too low, which probably means that ingestion was underestimated. In addition, earlier instars than were used in the feeding experiments would have higher densities and faster feeding rates (35). If this is accounted for, and the entire shredder guild is included, it is possible that detritus food is limiting rather than in excess.

McDiffett's (104) energy budget for *Pteronarcys scotti* is often cited for the amount of leaf material shredded, and for the low assimilation efficiency of detritivores (10.6%). He used a mixture of leaf species collected from a stream and thus of unknown food quality. Neither ingestion nor egestion was measured directly because of difficulty in separating feeding fragments from feces. The assimilation efficiency may be too low, because egestion was calculated from fecal collections without concomitant feeding by the larvae, and gut emptying rate may be reduced when animals are not feeding (20). Estimation of the impact of *P. scotti* on leaf breakdown was possible with gravimetric techniques, as both fragmentation and egestion result in particle size reduction. Leaf weight loss by feeding averaged 29.1% of dry body weight per day, whereas egestion (by nonfeeding larvae) was 17.9%. As-

similation efficiency calculated on the basis of leaf weight loss is 38.5%, which McDiffett believes is too high because some leaf material is fragmented but not ingested. Though the estimates of assimilation efficiency may be equivocal, the calculated impact of the larvae in litter degradation is not affected; this amounts to 4.5 g of leaf tissue per larva per year.

For a detritivore about half the size of *P. scotti,* Winterbourn & Davis (166) estimated that a larva of the caddisfly *Zealandopsyche ingens* shredded 1.2 g of *Nothofagus* leaves per year. This included estimates for both ingestion and case material. Extrapolating to field population densities, 11% of the leaf and twig inputs, or 16% of the leaf inputs, of the New Zealand stream could be processed by *Z. ingens.*

Bärlocher & Kendrick (10, 12, 13) have provided the most definitive data to date on the interrelations of fungi and invertebrates in leaf degradation in aquatic systems. *Gammarus* were fed conditioned leaves or cultured fungi. The controlled diets and daily cleaning of rearing containers enabled them to measure growth in a system with low mortality. The weight increase of *Gammarus* in 9 weeks on the four most suitable fungi averaged 62%, compared with 26% on elm leaves and 12% on maple. Some fungi were unsuitable as the sole food source and the animals died just as fast as did starved ones. Growth rate on the elm leaves was only half of that with mycelia of the best fungus, but consumption of elm leaves was about 10 times greater than that of mycelia. Growth of *Gammarus* fed on fresh leaf disks was attributed to digestion of leaf substrate, and not to the microorganisms, because they estimated that bacteria and fungi contributed less than 0.01% of the biomass.

Assimilation efficiency of *Gammarus* fed on unconditioned elm or maple leaves was about 10% of the dry weight and 14–18% of the protein, compared with 43–76% for dry weight and 73–96% for protein on cultures of fungal mycelia (12). These results and the presumed preference of detritivores for leaves with high mycelia concentrations indicate that fungi will be considerably more significant in the diet than is suggested by estimates of microbial biomass per unit weight of decomposed leaves. Changes in the leaf brought about by microbial excretions or secretions, or experimentally by a hydrolytic agent (HCl), can also increase palatability of leaves for *Gammarus* (13).

Despite the evidence given above for the nutritional quality of some types of detritus and for demonstrated growth with a detritus diet, there are few, if any, convincing studies of shredder species that can complete their life cycle feeding exclusively on decaying leaves. Most studies of gut contents indicate variable diets (27, 133). *Gammarus* feed on dead animal material when it is available (133), and many detritivores switch to algal material as

they grow older (27, 32, 57). The caddisfly, *Clistoronia magnifica*, could not be reared to a normal pupal weight on conditioned alder leaves; it required a supplement such as wheat grains or enchytraeid worms (2–4).

Field Studies of Leaf Processing

Field studies have been conducted using litter bags (37, 66, 76, 80, 103, 122, 146) or leaf packs (14, 124, 127–129, 135, 141, 149, 150). Bags have the advantage of preventing losses due to abrasion or breakage, but they deny access of large shredders and may inhibit normal microbial processing because of reduced water exchange rates and possible anaerobic conditions (124). Leaf packs are considered analogues of natural autumnal leaf accumulations (124). Leaves are fastened together with plastic buttoneers or by stringing on monofilament and attaching the pack to the upstream face of a brick in the stream.

The reported rates of leaf weight loss and the role of invertebrates in various studies are highly variable. In part, this is due to differences in methodology, timing, and duration of experiments, and to sample processing techniques, but there are also apparent differences between geographic regions and litter species, and in both the microbial and invertebrate complexes. Weight loss is directly proportional to temperature, and interspecific differences in degradation rates can be overridden by temperature (141). However, Reice (128) reported faster processing of white ash at a lower temperature, as did Triska & Sedell (149) for four leaf species. In both instances there was a marked absence of shredders associated with the slower decomposition. Degradation of sycamore leaf packs in a pastureland stream was slow and resulted mainly from microbial processing (14). The absence of shredders in this system was attributed to the predominance of an unpalatable, or slowly processed, type of leaf, and the lack of the range of leaf types typical of woodland streams (14).

The most extensive field study was by Petersen & Cummins (124), who compared mean weight loss of seven deciduous leaf species in Augusta Creek, Michigan. Values of k, in an exponential decay model, were used to compare 23 species from their studies and from literature values. Exponential loss rates of 0.5% per day are characteristic of "slow" leaves such as oak, beech, or poplar, compared with 1.5% for "fast" leaves such as elm and ash. From the results of their field studies in both fall and winter, and laboratory and artificial stream experiments, they constructed a processing budget using hickory, a species with a medium processing coefficient. The components of the budget were (a) leaching (24 hr), 15%; (b) conditioning (30 days), 7%; and (c) animal-microbial conversion (90 days), 43% (animal = 24%, microbial = 19%). The remaining amount would continue to be

processed by microbes and invertebrates, but after 120 days (September to December) leaf packs are rare, so this residue has been fragmented and is in another category subject to different processing rates (124).

The seasonal timing of leaf pack or litter bag experiments will have a major effect on results, because the life cycles of shredders are keyed to the predictable timing of seasonal inputs. Leaves presented in the summer are unlikely to be attacked by the same species complex, or life history stages, as those exposed in the fall or spring.

Our Oregon studies illustrate the importance of life history considerations. Conifer needles in a third-order stream had a decay coefficient of 0.006 from November to April, but this increased to 0.018 in May–June, largely because of feeding by final-instar larvae of *Lepidostoma unicolor* (135). In a first-order stream with an impoverished shredder fauna, the *k*-value was 0.003.

The life cycle of *Lepidostoma quercina* is timed to exploit deciduous leaf inputs in the autumn, in contrast to *L. unicolor*, which does most of its growing in the spring and early summer (3, 60). A simulation model that mimicked the field growth pattern of *L. quercina* was based on differential growth rates that depended on food quality. Rapid growth occurred when high-quality leaves (alder) were available from August to November, and slow growth on low-quality leaves (maple) for the remainder of the feeding period until February (60, 61).

In the absence of shredders, alder leaves lost 50% of their weight in 70–90 days at 6°C (149). With a typical shredder fauna at a similar temperature in November–December, 50% weight loss occurred in about 40 days (135). In midsummer, at about 15°C, alder leaves in mesh bags were completely skeletonized in less than a month (N. H. Anderson, unpublished data). Shredders were largely excluded by the bags and microbial activity was responsible for disintegrating the leaf tissue. Tissue loss, though, was primarily due to fine-particle collectors or scrapers, such as snails, leptophlebeid mayflies, and nemourid stoneflies. Thus, temperature had a pronounced effect on degradation rate, but invertebrate feeding activity was also important. In the summer the invertebrate contribution to processing was not via shredding behavior but by surface scraping.

WOOD DEGRADATION BY INVERTEBRATES

As was indicated previously, wood debris may account for the major component of organic material in forested streams. Neither the rates of degradation nor the mechanisms of breakdown in water have received much attention, but it is apparent that wood decays more slowly in water than on land. Regulation of terrestrial wood decomposition rate by arthropods

and annelids has been reported by Ausmus (8) and Swift (143). They view the major role of invertebrates as regulating the decomposition in wood via four mechanisms: (*a*) translocation of nutrients from distant feeding sites and subsequent defecation in wood; (*b*) passive translocation of microbial cells and spores into wood channels; (*c*) regulation of microbial succession, catabolism rate, and nitrogen fixation rate at microsites within wood channels; and (*d*) increased cation and anion exchange capacity of wood, which results in increased probability of nutrient interruption and decreased probability of nutrient loss. Many of these same mechanisms probably occur in the processing of wood in lotic habitats. Unlike the terrestrial system where moisture is a controller of decomposition, waterlogging restricts the processing in streams to the surface layers. Most of the feeding by invertebrates will be associated with the microbially conditioned surface layer.

Anderson et al (6) proposed a general scheme of wood processing by invertebrates in small stream ecosystems. Invertebrate impact may be similar to that of shredders that process leaf litter in terrestrial and aquatic habitats when the full decomposition cycle of wood debris is considered. That is, a 1% consumption per year would result in the same impact in a 20-year period required for wood disappearance as the 10–20% of the annual degradation attributed to invertebrates for leaf litter on the ground or in streams (29, 58, 124, 134).

Wood feeding by aquatic insects has been reported for species of caddisflies, stoneflies, craneflies, midges, and beetles (19, 68, 71, 87, 95, 131, 144, 166). About 40 taxa were recorded in our study of invertebrates associated with wood in western Oregon streams (6). Wood quality or texture is important for colonization by invertebrates (6, 19, 131). This is influenced by the species of wood, degree of waterlogging, and the soundness or decay class. Although softness can be due to the period of submergence, it is more commonly related to the condition of the wood when it fell into the water. Thus the amount of mycological invasion and attacks by wood borers in the terrestrial habitat may have considerable influence on its attractiveness in the stream and on its rate of degradation. Aquatic xylophages associated with various types, or textures, of wood include the following: the midge, *Brillia* sp., an early colonizer of phloem on newly fallen branches; the elmid, *Lara avara* and the caddisfly, *Heteroplectron californicum,* as gougers on firm, waterlogged wood; and the craneflies, *Lipsothrix* spp., in wood that is in the latest stages of decomposition (6).

Assimilation efficiencies of aquatic xylophages are presumed to be low, as there is little evidence of direct utilization of woody tissue for nutrition. A symbiotic gut flora has not been demonstrated for *L. avara* or *H. californicum* (6). Further work in this line is needed because gut symbionts are important in nitrogen fixation and cellulose digestion by wood borers in

both marine and terrestrial habitats (17, 22, 55, 100). Based on studies of *L. avara* it was suggested that strategies for exploitation of the low-quality, nitrogen-poor wood substrates will likely include slow growth rates and long life cycles (6).

The indirect role of invertebrates in feeding on senescent microflora, exposing more surface area, and spreading fungal spores are additional roles that invertebrates play in the processing of wood (6, 8, 143). Particles abraded by feeding and other activites, as well as the feces egested, all become part of the FPOM pool and potential food for collectors.

Wood as Habitat and Habitat Modifier

The refractory properties of wood, especially the large bole wood, result in this material providing a major element of stability in small stream systems. The physical buffering capacity, habitat formation, and invertebrate response to large wood inputs, based on Oregon Cascade Range streams, are illustrated in Figure 1. About 25% of the area of the stream bed in very small streams is composed of wood, and another 25% is organic debris and sediments stacked up behind the wood residues. As a result, half of the stream habitat is either wood or wood-created habitat. In third- to fourth-order streams, only about 12% of the area is occupied by wood, and a similar amount is wood-created habitat (Figure 1). In this size of stream, about 75% of the stream bed is mineral substrates. The role of wood in larger streams (>fourth order), both as habitat and as habitat generator, is greatly diminished because the stream power is sufficient to deposit wood near shore or on the bank (142).

First- and second-order streams have the greatest amount of wood-associated habitat area but a low standing crop of invertebrates. Shredders and gougers are the major functional groups whereas grazers are uncommon (Figure 1). These streams also have a large proportion of collectors associated with the FPOM in debris-created habitats. Despite the high gradient of first-order streams (30–50%), harpacticoid copepods are the most numerous invertebrates (J. R. Sedell, unpublished data), but their impact in turnover from FPOM has not been determined.

There is a greater diversity of both functional roles and species of invertebrates in third- to fourth-order streams. Biomass is also increased, as is indicated by the size of circles (Figure 1). The grazers, and rasping invertebrates such as snails, may make a significant contribution to the FPOM pool by their consumption of periphyton and the surface of wood debris.

A potential approach that could provide significant insight into the processing capabilities of the stream's biota would be to compare the quality and particle size of FPOM on the stream bottom with the quantity and quality of FPOM inputs and exports from a stream reach. Of the two major

types of organic inputs, leaf litter is characterized by a turnover measured in months, whereas the turnover time of wood debris is at least years and may be decades. The product of both substrates is FPOM, which is further processed by microbes and invertebrates. Both wood and FPOM in small streams are considered refractory, but they function differently. Wood effectively buffers the system physically (through habitat formation) and, to a lesser extent, metabolically (as a source of reduced carbon), although its contribution of FPOM may be substantial. On the other hand, FPOM buffers the system metabolically, but not physically, because it is readily exported. In fact, FPOM is the major particulate export to downstream reaches.
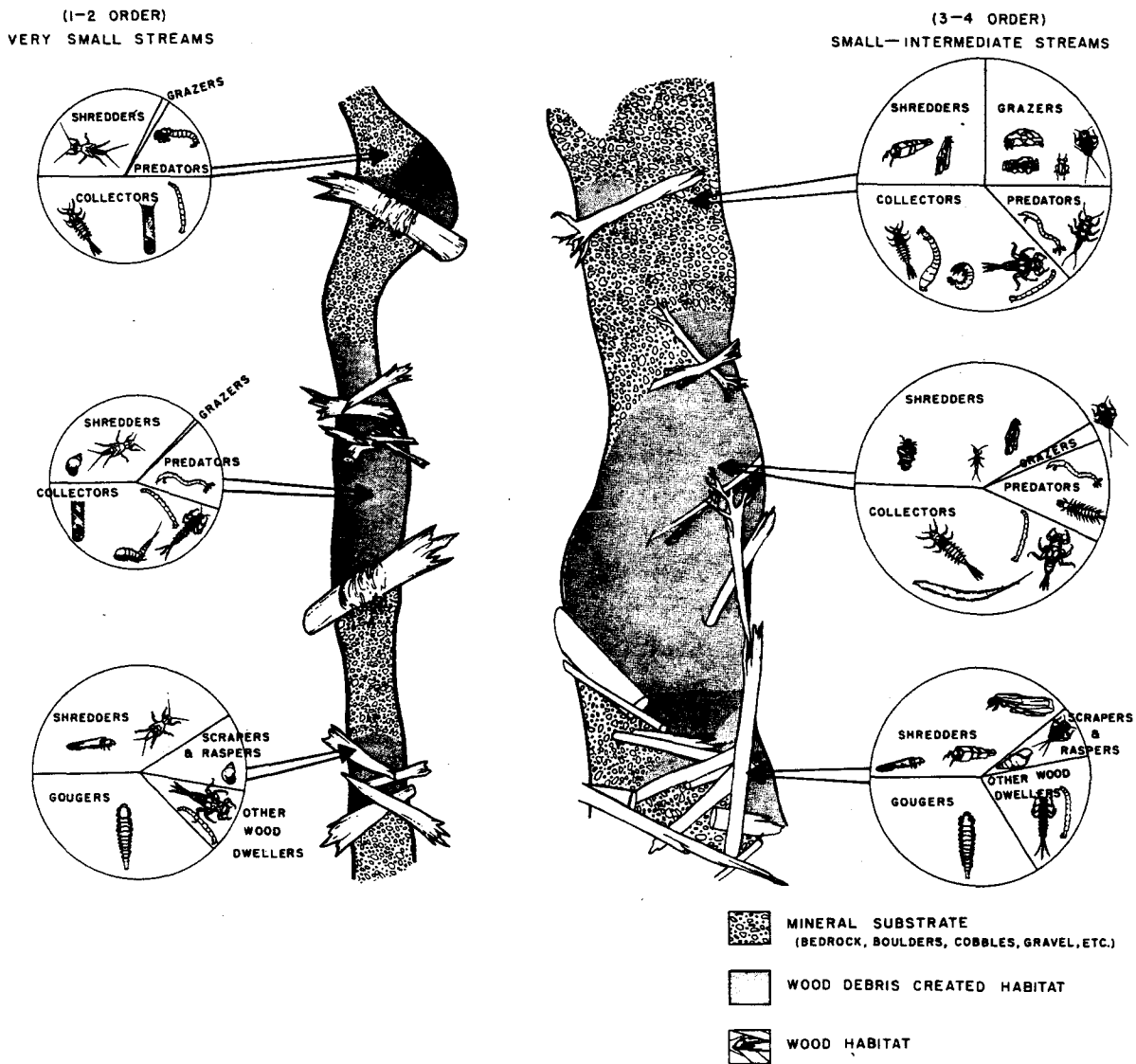

Figure 1 Schematic representation of the relative abundance of habitat types and associated invertebrates in first- and second-order and third- and fourth-order forested streams.

FACTORS INFLUENCING AVAILABILITY
AND UTILIZATION OF FPOM BY COLLECTORS

FPOM is reutilized many times within the benthic food chain. The process of energy conservation or strategy that increases the efficiency of nutrient recycling within the system has been termed spiraling (160). Activities of the biota tend to counteract the export and losses of nutrients that are an inevitable consequence of the unidirectional flow; systems that process materials efficiently are said to have "tighter" spirals than those that export much of it to downstream reaches.

Fine particles are produced in several ways: by physical abrasion (with microbial activity increasing the rate); by the direct enzymatic activity of microbes; by the feeding activites of invertebrates, both through egestion and fragmentation; and by flocculation of DOM (92). Direct input of FPOM due to runoff and resuspension will also increase its availability to the fauna. The range of food quality available to collectors is possibly even greater than that for shredders. At this stage of degradation the source or identity of particles may be difficult to discern, as FPOM is a combination of shredded riparian material, feces, autochthonous macrophytes, algae, and a component of live and dead microbes. Benthic deposits generally contain less organic matter than does the suspended material. In the River Thames, the organic matter was seston (20–80%), epiphytic detritus (40%), and bottom sediments (15%) (15). In the River Lambourn, the seston was 30–90% organic matter compared with only 11–12% in the easily suspended fraction of the bottom deposits (133).

Net-spinning caddisflies partition the FPOM resource through variations in mesh dimensions, differences in microdistributional patterns of the nets, and temporal variation in net construction (156). The mean particle size of detritus in the gut is correlated with the mesh openings of the capture net (96, 154, 155). Headwater stream caddisflies exploit a wider spectrum of particle sizes, but in both large and small streams the nets of fine-particle feeders have similar-sized apertures. The guts of *Arctopsyche irrorata* from headwaters contained a considerable component of animal material as well as recognizable leaf fragments, whereas guts of the large river species, *Hydropsyche incommata*, contained amorphous detritus, which Wallace, Webster & Woodall (156) believed to be fecal material that had been ingested and egested several times during downstream transport, as well as aggregates derived from DOM.

The filter feeding of black fly larvae has been extensively investigated (23, 50, 138, 152). Generally they are considered nonselective feeders, except for an appropriate size of particles. Particles ingested are commonly in the range of 10–100 μm (23, 138). Recent work with moorland black flies has

indicated that over half of the material ingested by some species is less than 1 μm in length (167). The dense populations of black fly larvae at lake outfalls has been attributed to the rich food supply of plankton (93, 152), but in most streams and rivers the dominant material ingested is detritus (23, 84, 138), or suspended clay and mineral particles along with the associated microbes (50, 52).

Carlsson et al (21) have shown that the species complex of black fly larvae at lake outfalls in Lapland occur in denser aggregations and have faster growth than the same species or other species further downstream. Phytoplankton and coarse detritus (>2 μm) occurred in similar amounts in all reaches, so they concluded that small particles, from 2 μm down to colloidal size, were the resource that maintained the huge larval aggregations at the lake outlet. This material is produced by decomposition on the lake bottom in winter and is washed into the river during ice melt.

Studies of *Simulium* spp. in an English chalk stream indicate the magnitude of processing by filter feeders in a system where decayed macrophytes provide a major component of the suspended detritus (83, 84). Gut filling times were determined to be 20–30 min. As food is passed so rapidly that there is little time for digestion, several authors have suggested that the nutritional value is derived primarily from "stripping" bacteria from refractory particles, but Baker & Bradnam (9) calculated that some of the energy intake is directly from the detritus. Ladle, Bass & Jenkins (84) used an assimilation efficiency of 5% for calculating the energy transformation in the chalk stream. At peak densities in the summer (80 X 10^6 for a 200-m stream reach), they calculated that 1246 kg of solids were ingested to produce 7 kg of black fly tissue. On a daily basis (per m^2) this was 12.8 g ingested, 0.64 g assimilated, and 0.066 g of production. Assuming no input of material other than that carried by the inflowing water, and excluding reingestion of feces, they calculated a theoretical distance for complete removal of the suspended solids by black fly filtering to be in the order of 0.6 km.

Benthic organisms that feed by pumping suspended particulates (e.g. bivalves, *Chironomus*), or deposit feeders such as oligochaetes or *Hyallela*, occur in lentic habitats or areas of streams and rivers with reduced current. Data on detrital feeding by these taxa is mostly from marine or lake studies, but it should also be applicable to lotic habitats (38, 46, 62–64, 101, 117). Benthic deposits are ingested and stripped of microbes and reutilized several times. For example, the tubificid fauna of Toronto Harbor was calculated to ingest the top 20-mm layer 4–12 times per year (7). The snail *Potamopyrgus jenkinsi*, which occurs in chalk streams at densities of 50,000 per m^2, feeds on organic materials in the mud. Assimilation efficiency is only about 4%, and a field population was estimated to produce 140 g of feces/m^2/day

(67). These investigations indicate the tremendous impact invertebrate populations can have in altering and processing FPOM.

Hargrave (65) attributes invertebrate feces with a central role in sediment decomposition. Bacteria are relatively sparse on detritus until it is passed through invertebrate guts; it is then rapidly colonized by successions of microorganisms, with maximum activity within 2–3 days. Reworking of sediment and detritus by invertebrates thus provides space for further microbial activity. Hargrave stressed the need for quantifying the role of feces in detritus-based communities and supports the suggestion (77) that fecal pellets be treated as organisms.

Radiophosphorous-labeled alder leaves were used to demonstrate the role of the shredder *Pteronarcys californica* on nutrient availability to the collectors *Hydropsyche* and *Simulium* (136). Compared with controls without shredders, there was a 35–100% increase in ^{32}P in the experimental trials for *Hydropsyche* and a 600–700% increase for *Simulium*.

The low food quality of FPOM detritus prevents multiple generations of the midge *Paratendipes albimanus* in Michigan streams (158). The field growth pattern is characterized by discontinuous increases in biomass, separated by intervals when no growth occurs. Growth periods correlated well with microbial densities, measured by ATP activity and respiration. Lack of growth in mid-spring and summer appeared to be related to low food quality. Conditioned leaf fragments of hickory and oak produced laboratory growth rates 1.3–3 times greater than did *Tipula* feces or native detritus collected from the stream. The feces produced higher growth rates than did the detritus. The conditioned leaf particulates were considered to be a fresh detritus of high quality with a short potential stream residence time, whereas native detritus would have a long residence time. In the natural environment then, the native detritus would provide collectors with an abundant but low-quality food source during most of the year, but inputs of fresh leaves are required to achieve spurts of rapid growth (158).

CONCLUDING REMARKS

In 1970, Hynes (72) concluded his review of stream insect ecology with the statement that the role of allochthonous organic matter in the nutrition of aquatic insects was almost uninvestigated. The literature citations given here for the last decade indicate that stream biologists have heeded Hynes' suggestion to explore this area. The significance of detritus in streams is now well documented, and a conceptual framework for organic matter processing has evolved. This framework has lead to process-oriented mathematical models of stream community metabolism (105), detritus processing (16),

and a stream ecosystem model that includes the processes of shredding, grazing, collecting, and predation (106). These models are a significant step towards an understanding of stream processes, especially in pointing to areas of research that need attention. Quantification of most of the processes involved in detritus degradation is either lacking or still very crude, and field measurements are currently inadequate to provide satisfactory validation of the stream model processes.

The role of macroinvertebrates in detritus degradation in streams is still not well defined. The amount that shredding enhances litter losses seems to be quite variable, depending both on environmental and leaf characteristics. The regulatory role of decomposition rates of woody debris by invertebrates is virtually unknown. Thus, further work in a range of geographic situations and use of standardized techniques for field studies is warranted.

Specific areas that we believe need further attention include the factors affecting food quality of detritus, and the effects of food quality in the dynamics of invertebrate populations. It is obvious, but needs to be emphasized, that population sampling techniques are not yet satisfactory for benthic invertebrates. Wood debris represents a large fraction of the organic material in most streams. The strategies of exploitation of this refractory, low-quality food source need further investigation. Mechanisms of nitrogen enrichment of this material would seem to be important. Finally, the dynamics of microbial populations is central to both degradation and to exploitation of detritus. This subject needs to be investigated by ecologists trained in microbiological and biochemical techniques.

Future work may well concentrate on management implications of detritus in stream systems. Currently, the effects of addition, or removal, of detritus from stream ecosystems are largely speculative. However, it is apparent that logging and stream cleanup both influence channel morphology and the stream biota. Debris removal may reduce the diversity of available habitats and may also lead to channelization (142). Channelization, coupled with shorter forest rotation, may keep the stream perpetually cleaned and unstable, both physically and biologically. Under these conditions the role of the stream biota in utilizing and recycling nutrients within the watershed would seem to be minimized.

Literature Cited

1. Anderson, J. M., Macfayden, A., eds. 1976. *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes.* Oxford: Blackwell. 474 pp.
2. Anderson, N. H. 1976. Carnivory by an aquatic detritivore, *Clistoronia magnifica. Ecology* 57:1081–85
3. Anderson, N. H. 1976. The distribution and biology of the Oregon Trichoptera. *Oregon Agric. Exp. Stn. Tech. Bull. No. 134,* 152 pp.
4. Anderson, N. H. 1978. Continous rearing of the limnephilid caddisfly, *Clistoronia magnifica* (Banks). In *Proc. 2nd Int. Symp. Trichoptera,* ed. M. I. Crichton, pp. 317–29. The Hague: W. Junk
5. Anderson, N. H., Grafius, E. 1975. Utilization and processing of allochthonous material by stream Trichoptera. *Verh. Int. Ver. Limnol.* 19:3022–28
6. Anderson, N. H., Sedell, J. R., Roberts, L. M., Triska, F. J. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. *Am. Midl. Nat.* In press
7. Appleby, A. G., Brinkhurst, R. O. 1970. Defecation rate of three tubificid oligochaetes found in the sediment of Toronto Harbour Ontario. *J. Fish. Res. Board Can.* 27:1971–82
8. Ausmus, B. S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. *Ecol. Bull. Stockholm* 25:180–92
9. Baker, J. H., Bradnam, L. A. 1976. The role of bacteria in the nutrition of aquatic detritivores. *Oecologia Berlin* 24:95–104
10. Bärlocher, F., Kendrick, B. 1973. Fungi in the diet of *Gammarus pseudolimnaeus. Oikos* 24:295–300
11. Bärlocher, F., Kendrick, B. 1974. Dynamics of the fungal population on leaves in a stream. *J. Ecol.* 62:761–91
12. Bärlocher, F., Kendrick, B. 1975. Assimilation efficiency of *Gammarus pseudolimnaeus* feeding on fungal mycelium or autumn-shed leaves. *Oikos* 26:55–59
13. Bärlocher, F., Kendrick, B. 1975. Leaf-conditioning by microorganisms. *Oecologia Berlin* 20:359–62
14. Benfield, E. F., Jones, D. S., Patterson, M. F. 1977. Leaf pack processing in a pastureland stream. *Oikos* 29:99–103
15. Berrie, A. D. 1976. Detritus, microorganisms and animals in fresh water. See Ref. 1, pp. 323–38
16. Boling, R. H., Goodman, E. D., Van Sickle, J. A., Zimmer, J. O., Cummins, K. W., Petersen, R. C., Reice, S. R.

17. 1975. Toward a model of detritus processing in a woodland stream. *Ecology* 56:141–51
17. Breznak, J. A., Brill, W. J., Mertins, J. W., Coppel, H. C. 1973. Nitrogen fixation in termites. *Nature* 244:577–79
18. Brown, D. S. 1961. The food of the larvae of *Chloeon dipterum* L. and *Baetis rhodani* (Pictet). *J. Anim. Ecol.* 30:55–75
19. Brown, H. P. 1973. Survival records for elmid beetles, with notes on laboratory rearing of various dryopoids. *Entomol. News* 84:278–84
20. Calow, P. 1975. Defecation strategies of two freshwater gastropods, *Ancylus fluviatilus* Mull. and *Planorbis contortus* Linn. with a comparison of field and laboratory estimates of food absorption rate. *Oecologia Berlin* 20:51–63
21. Carlsson, M., Nilsson, L. M., Svensson, B., Ulfstrand, S., Wotton, R. S. 1977. Lacustrine seston and other factors influencing the blackflies inhabiting lake outlets in Swedish Lapland. *Oikos* 29:229–38
22. Carpenter, E. J., Culliney, J. L. 1975. Nitrogen fixation in marine shipworms. *Science* 187:551–52
23. Chance, M. M. 1970. The functional morphology of the mouthparts of blackfly larvae. *Quaest. Entomol.* 6:245–84
24. Chapman, D. W. 1966. The relative contributions of aquatic and terrestrial primary producers to the trophic relations of stream organisms. *Spec. Publ. Pymatuning Lab. Field Biol.* 4:116–30
25. Christensen, O. 1975. Wood litter fall in relation to abscission, environmental factors and the decomposition cycle in a Danish oak forest. *Oikos* 26:187–95
26. Christensen, O. 1977. Estimation of standing crop and turnover of dead wood in a Danish oak forest. *Oikos* 28:177–86
27. Coffman, W. P., Cummins, K. W., Wuycheck, J. C. 1971. Energy flow in a woodland stream ecosystem. I. Tissue support trophic structure of the autumnal community. *Arch. Hydrobiol.* 68:232–76
28. Corbet, P. S., Schmid, F., Augustin, C. L. 1966. The Trichoptera of St. Helen's Island, Montreal. I. The species present and their relative abundance at light. *Can. Entomol.* 98:1284–98
29. Crossley, D. A., Witkamp, M. 1964. Effects of pesticides on biota and breakdown of forest litter. *Proc. VIII Int. Congr. Soil Sci. Bucharest* 3:87–91

30. Cummins, K. W. 1964. Factors limiting the microdistribution of the caddisflies *Pycnopsyche lepida* (Hagen) and *Pycnopsyche guttifer* (Walker) in a Michigan stream. *Ecol. Monogr.* 34:271–95

31. Cummins, K. W. 1973. Trophic relations of aquatic insects. *Ann. Rev. Entomol.* 18:183–206

32. Cummins, K. W. 1974. Structure and function of stream ecosystems. *BioScience* 24:631–41

33. Cummins, K. W. 1975. The ecology of running waters: theory and practice. *Proc. Sandusky River Basin Symp. Int. Jt. Comm. Great Lakes, Heidelberg Coll., Tiffin, Ohio,* p. 277–93

34. Cummins, K. W. 1977. From headwater streams to rivers. *Am. Biol. Teach.* 39:305–12

35. Cummins, K. W., Petersen, R. C., Howard, F. O., Wuycheck, J. C., Holt, V. I. 1973. The utilization of leaf litter by stream detritivores. *Ecology* 54:336–45

36. Darnell, R. M. 1964. Organic detritus in relation to secondary production in aquatic communities. *Verh. Int. Ver. Limnol.* 15:462–70

37. Davis, S. F., Winterbourn, M. J. 1977. Breakdown and colonization of *Nothofagus* leaves in a New Zealand stream. *Oikos* 28:250–55

38. Edwards, R. W. 1964. Some effects of plants and animals on the conditions in freshwater streams with particular reference to their oxygen balance. In *Advances in Water Pollution Research,* ed. B. A. Southgate, 1:319–37. Oxford: Permagon

39. Efford, I. E. 1969. Energy transfer in Marion Lake, British Columbia; with particular reference to fish feeding. *Verh. Int. Ver. Limnol.* 17:104–8

40. Egglishaw, H. J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. *J. Anim. Ecol.* 33:463–76

41. Egglishaw, H. J. 1968. The quantitative relationship between bottom fauna and plant detritus in streams of different calcium concentrations. *J. Appl. Ecol.* 5:731–40

42. Egglishaw, H. J. 1972. An experimental study of the breakdown of cellulose in fast-flowing streams. *Mem. Ist. Ital. Idrobiol.* 29: Suppl., pp. 405–28

43. Egglishaw, H. J., Morgan, N. C. 1965. A survey of the bottom fauna of streams in the Scottish Highlands. Part II. The relationship of the fauna to the chemical and geological conditions. *Hydrobiologia* 26:173–83

44. Elton, C. S. 1956. Stoneflies, a component of the aquatic leaf-litter fauna in Wytham Woods, Berkshire. *Entomol. Mon. Mag.* 92:231–36

45. Elwood, J. W., Cushman, R. M. 1975. The life history and ecology of *Peltoperla maria* in a small spring fed stream. *Verh. Int. Ver. Limnol.* 19:3050–56

46. Fenchel, T. 1970. Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum. Limnol. Oceanogr.* 15:14–20

47. Fisher, S. G., Carpenter, S. R. 1976. Ecosystem and macrophyte primary production of the Fort River, Massachusetts. *Hydrobiologia* 47:175–87

48. Fisher, S. G., Likens, G. W. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. *Ecol. Mongr.* 43:421–39

49. Fittkau, E. J. 1964. Remarks on limnology of central-Amazon rainforest streams. *Verh. Int. Ver. Limnol.* 15:1092–96

50. Fredeen, F. J. H. 1964. Bacteria as food for blackfly larvae in laboratory cultures and in natural streams. *Can. J. Zool.* 42:527–38

51. Fredeen, F. J. H. 1977. A review of the economic importance of blackflies in Canada. *Quaest. Entomol.* 13:219–29

52. Fredeen, F. J. H., Arnason, A. P., Berck, B. 1953. Adsorption of DDT on suspended solids in river water and its role in black-fly control. *Nature* 171:700

53. Fremling, C. R. 1960. Biology of a large mayfly, *Hexagenia bilineata* (Say), of the upper Mississippi River. *Iowa State Univ. Agric. Home Econ. Exp. Stn. Res. Bull.* 482:842–52

54. Fremling, C. R. 1960. Biology and possible control of nuisance caddisflies of the upper Mississippi River. *Iowa State Univ. Agric. Home Econ. Exp. Stn. Res. Bull.* 483:856–79

55. French, J. R. 1975. The role of termite hindgut bacteria in wood decomposition. *Mater. Org.* 10:1–13

56. Froehlich, H. A. 1973. Natural and man-caused slash in headwater streams. *Logger's Handb. Proc. Pac. Log. Congr.* 33:15–17; 66–70; 82–86

57. Fuller, R. L., Stewart, K. W. 1977. The food habits of stoneflies in the upper Gunnison River, Colorado. *Environ. Entomol.* 6:293–302

58. Gist, C. S., Crossley, D. A. 1975. A model of mineral-element cycling for an invertebrate food web in a southeastern

hardwood forest litter. In *Mineral Cycling in Southeastern Ecosystems,* ed. F. G. Howell, J. B. Gentry, M. H. Smith, pp. 84–86. Springfield, Va.: Natl. Tech. Inf. Serv.

59. Grafius, E. J. 1974. *The conversion of allochthonous material by stream detritivores.* MS Thesis. Oregon State Univ., Corvallis. 133 pp.

60. Grafius, E. J. 1977. *Bioenergetics and strategies of some Trichoptera in processing and utilizing allochthonous materials.* PhD thesis. Oregon State Univ., Corvallis. 186 pp.

61. Grafius, E., Anderson, N. H. 1979. Population dynamics, bioenergetics, and role of *Lepidostoma quercina* Ross in an Oregon woodland stream. *Ecology.* In press

62. Hargrave, B. T. 1970. The effect of a deposit feeding amphipod on the metabolism of benthic microflora. *Limnol. Oceanogr.* 15:21–30

63. Hargrave, B. T. 1970. The utilization of benthic microflora by *Hyalella azteca. J. Anim. Ecol.* 39:427–37

64. Hargrave, B. T. 1972. Prediction of egestion by the deposit-feeding amphipod *Hyalella azteca. Oikos* 23:116–24

65. Hargrave, B. T. 1976. The central role of invertebrate faeces in sediment decomposition. See Ref. 1, pp. 301–21

66. Hart, S. D., Howmiller, R. P. 1975. Studies on the decomposition of allochthonous detritus in two southern California streams. *Verh. Int. Ver. Limnol.* 19:1665–74

67. Heywood, J., Edwards, R. W. 1962. Some aspects of the ecology of *Potamopyrgus jenkinsi* Smith. *J. Anim. Ecol.* 31:239–50

68. Hynes, C. D. 1965. The immature stages of the genus *Lipsothrix* in the western United States. *Pan Pac. Entomol.* 41:165–72

69. Hynes, H. B. N. 1961. The invertebrate fauna of a Welch mountain stream. *Arch. Hydrobiol.* 57:344–88

70. Hynes, H. B. N. 1963. Imported organic matter and secondary productivity of streams. *Int. Congr. Zool.* 4:324–29

71. Hynes, H. B. N. 1970. *The Ecology of Running Waters.* Toronto: Univ. Toronto Press, 555 pp.

72. Hynes, H. B. N. 1970. The ecology of stream insects. *Ann. Rev. Entomol.* 15:25–42

73. Hynes, H. B. N. 1975. The stream and its valley. *Verh. Int. Ver. Limnol.* 19:1–15

74. Iversen, T. M. 1973. Decomposition of autumn-shed beech leaves in a spring brook and its significance for the fauna. *Arch. Hydrobiol.* 72:305–12

75. Iversen, T. M. 1974. Ingestion and growth in *Sericostoma personatum* in relation to the nitrogen content of ingested leaves. *Oikos* 25:278–82

76. Iversen, T. M. 1975. Disappearance of autumn shed leaves placed in bags in small streams. *Verh. Int. Ver. Limnol.* 19:1687–92

77. Johannes, R. E., Satomi, M. 1966. Composition and nutritive value of faecal pellets of a marine crustacean. *Limnol. Oceanogr.* 11:191–97

78. Jones, J. R. E. 1949. A further ecological study of calcareous streams in the "Black Mountain" district of South Wales. *J. Anim. Ecol.* 18:142–58

79. Jones, J. R. E. 1950. A further ecological study of the River Rheidol: the food of the common insects of the mainstream. *J. Anim. Ecol.* 19:159–74

80. Kaushik, N. K., Hynes, H. B. N. 1971. The fate of dead leaves that fall into streams. *Arch. Hydrobiol.* 68:465–515

81. Kostalos, M., Seymour, L. R. 1976. Role of microbial enriched detritus in the nutrition of *Gammarus minus. Oikos* 27:512–16

82. Krumholz, L. A. 1972. Degradation of riparian leaves and the recycling of nutrients in a stream ecosystem. *Univ. Kentucky Water Resour. Inst. Res. Rep. No. 57,* 36 pp.

83. Ladle, M. 1972. Larval Simuliidae as detritus feeders in chalk streams. *Mem. Ist. Ital. Idrobiol.* 29: Suppl., pp. 429–39

84. Ladle, M., Bass, J. A. B., Jenkins, W. R. 1972. Studies on production and food consumption by the larval Simuliidae of a chalk stream. *Hydrobiologia* 39: 429–48

85. Leathers, A. L. 1922. Ecological study of aquatic midges and some related insects, with special reference to feeding habits. *Bull. US Bur. Fish.* 38:1–61

86. Leopold, L., Wolman, M. G., Miller, J. P. 1964. *Fluvial Processes in Geomorphology.* San Francisco: W. H. Freeman. 522 pp.

87. LeSage, L., Harper, P. P. 1976. Notes on the life history of the toed-winged beetle, *Anchytarsus bicolor* (Melsheimer). *Coleopt. Bull.* 30:233–38

88. Levanidov, U. Y. 1949. Significance of allochthonous material as a food resource in a water body as exemplified by the nutrition of the water louse, *(Asellus*

aquaticus) *Tr. Vses. Gidrobiol. Ova.* 1:100–17 (In Russian)

89. Lindeman, R. L. 1942. The trophic-dynamic aspects of ecology. *Ecology* 23:399–418

90. Liston, C. R. 1972. *Contributions of allochthonous detritus to the energy regime of Doe Run, Meade County, Kentucky.* PhD Thesis. Univ. Louisville, Ky. 104 pp.

91. Lloyd, J. T. 1921. The biology of North American caddis fly larvae. *Bull. Lloyd Libr. Entomol. Ser.* 21:1–124

92. Lush, D. L., Hynes, H. B. N. 1973. The formation of particles in freshwater leachates of dead leaves. *Limnol. Oceanogr.* 18:968–77

93. Maciolek, J. A., Tunzi, M. G. 1968. Microseston dynamics in a simple Sierra Nevada lake-stream system. *Ecology* 49:60–75

94. Mackay, R. J., Kalff, J. 1969. Seasonal variation in standing crop and species diversity in a small Quebec stream. *Ecology* 50:101–9

95. Mackay, R. J., Kalff, J. 1973. Ecology of two related species of caddisfly larvae in the organic substrates of a woodland stream. *Ecology* 54:499–511

96. Malas, D., Wallace, J. B. 1977. Strategies for coexistence in three species of net-spinning caddisflies in second-order southern Appalachian streams. *Can. J. Zool.* 55:1829–40

97. Mann, K. H. 1964. The pattern of energy flow in the fish and invertebrate fauna of the River Thames. *Verh. Int. Ver. Limnol.* 15:485–95

98. Mann, K. H. 1972. Introductory remarks. *Mem. Ist. Ital. Idrobiol.* 29:Suppl., pp. 13–16

99. Mann, K. H. 1975. Patterns of energy flow. In *River Ecology*, ed. B. A. Whitton, pp. 248–63. Oxford: Blackwell. 725 pp.

100. Mannesmann, R. 1972. Comparison of twenty-one commercial wood species from North America in relation to feeding rates of the Formosan termite, *Coptotermes formosanus* Shiraki. *Mater. Org.* 8:107–20

101. Marzolf, G. R. 1966. The trophic position of bacteria and their relation to the distribution of invertebrates. *Spec. Publ. Pymatuning Lab. Field Biol.* 4:131–35

102. Mason, J. C. 1963. *Life history and production of the crayfish, Pacifastacus leniusculus trowbridgii (Stimpson), in a small woodland stream.* MS Thesis. Oregon State Univ., Corvallis. 204 pp.

103. Mathews, C. P., Kowalczewski, A. 1969. The disappearance of leaf litter and its contribution to production in the River Thames. *J. Ecol.* 57:543–52

104. McDiffett, W. F. 1970. The transformation of energy by a stream detritivore, *Pteronarcys scotti. Ecology* 51:975–88

105. McIntire, C. D. 1973. Periphyton dynamics in laboratory streams: a simulation model and its implications. *Ecol. Monogr.* 43:399–420

106. McIntire, C. D., Colby, J. A. 1979. A hierarchical model of lotic ecosystems. *Ecol. Monogr.* In press

107. McIntire, C. D., Phinney, H. K. 1965. Laboratory studies of periphyton production and community metabolism in lotic environments. *Ecol. Monogr.* 35:237–57

108. Meehan, W. R., Swanson, F. J., Sedell, J. R. 1977. Influences of riparian vegetation on aquatic ecosystems with particular reference to salmonid fishes and their food supply. In *Importance, Preservation and Management of Riparian Habitat*, pp. 137–45. Washington DC: USDA For. Serv. Gen. Tech. Rep. R-M 43. 217 pp.

109. Melchionni-Santolini, U., Hopton, J. W., eds. 1972. Detritus and its role in aquatic ecosystems. *Mem. Ist. Ital. Idrobiol.* 29:Suppl., pp. 1–540

110. Merritt, R. W., Cummins, K. W., eds. 1978. *An Introduction to the Aquatic Insects of North America.* Dubuque, Iowa: Kendall-Hunt. 512 pp.

111. Minckley, W. L. 1963. The ecology of a spring stream Doe Run, Meade County, Kentucky. *Wildl. Monogr.* 11:1–124

112. Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology* 48:139–49

113. Moon, H. P. 1939. Aspects of the ecology of aquatic insects. *Trans. Soc. Br. Entomol.* 6:39–49

114. Morgan, A. H. 1913. A contribution to the biology of mayflies. *Ann. Entomol. Soc. Am.* 6:371–413

115. Muttkowski, R. A., Smith, G. M. 1929. The food of trout stream insects in Yellowstone National Park. *Roosevelt Wildl. Ann.* 2:241–63

116. Nelson, D. J., Scott, D. C. 1962. Role of detritus in the productivity of a rock outcrop community in a Piedmont stream. *Limnol. Oceanogr.* 7:396–413

117. Newell, R. 1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica. Proc. Zool. Soc. London* 144:25–45

118. Nilsson, L. M., Otto, C. 1977. Effects of population density and of presence of

Gammarus pulex L. on the growth in larvae of *Potamophylax cingulatus* Steph. *Hydrobiologia* 54:109–12

119. Odum, H. T. 1956. Primary production in flowing waters. *Limnol. Oceanogr.* 1:102–17

120. Otto, C. 1974. Growth and energetics in a larval population of *Potamophylax cingulatus* (Steph.) in a south Swedish stream. *J. Anim. Ecol.* 43:339–61

121. Otto, C. 1975. Energetic relationships of the larval population of *Potamophylax cingulatus* in a south Swedish stream. *Oikos* 26:159–69

122. Park, D. 1974. On the use of the litter bag method for studying degradation in aquatic habitats. *Int. Biodeterior. Bull.* 10:45–48

123. Percival, E., Whitehead, H. 1929. A quantitative study of the fauna of some types of stream-bed. *J. Ecol.* 17:282–314

124. Petersen, R. C., Cummins, K. W. 1974. Leaf processing in a woodland stream. *Freshwater Biol.* 4:343–68

125. Prus, T. 1971. The assimilation efficiency of *Asellus aquaticus* L. *Freshwater Biol.* 1:287–305

126. Rabeni, C. F., Minshall, G. W. 1977. Factors affecting microdistribution of stream benthic insects. *Oikos* 29:33–43

127. Reice, S. R. 1974. Environmental patchiness and the breakdown of leaf litter in a woodland stream. *Ecology* 55:1271–82

128. Reice, S. R. 1977. The role of animal associations and current velocity in sediment-specific leaf litter decomposition. *Oikos* 29:357–65

129. Reice, S. R. 1978. The role of detritivore selectivity in species-specific litter decomposition in a woodland stream. *Verh. Int. Ver. Limnol.* 20:In press

130. Rempel, J. G., Arnason, A. P. 1947. An account of three successive outbreaks of the black fly, *Simulium arcticum*, a serious livestock pest in Saskatchewan. *Sci. Agric.* 27:428–45

131. Rogers, J. S., Byers, G. W. 1956. The ecological distribution, life history, and immature stages of *Lipsothrix sylvia*. *Occ. Papers Mus. Zool. Univ. Mich. No. 572*, 14 pp.

132. Ross, H. H. 1963. Stream communities and terrestrial biomes. *Arch. Hydrobiol.* 59:235–42

133. Scorgie, H. R. A. 1974. *Studies on the food of invertebrates in the River Lambourn, with particular reference to the role of detritus in the trophic economy of the community.* PhD thesis. Univ. Reading, England. 139 pp.

134. Sedell, J. R., Triska, F. J., Hall, J. D., Anderson, N. H., Lyford, J. H. 1974. Sources and fates of organic inputs in coniferous forest streams. In *Integrated Research in the Coniferous Forest Biome, Conif. For. Biome, Ecosyst. Anal. Stud., US/IBP, Bull. No. 5*, ed. R. H. Waring, R. L. Edmonds. pp. 57–69. Seattle: Univ. Washington

135. Sedell, J. R., Triska, F. J., Triska, N. S. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. I. Weight loss and associated invertebrates. *Verh. Int. Ver. Limnol.* 19:1617–27

136. Short, R. A., Maslin, P. E. 1977. Processing of leaf litter by a stream detritivore: Effect on nutrient availability to collectors. *Ecology* 58:935–38

137. Slack, H. D. 1936. The food of caddisfly larvae. *J. Anim. Ecol.* 5:105–15

138. Speir, J. A. 1976. *The ecology and production dynamics of four species of black flies in western Oregon streams.* PhD thesis. Oregon State Univ., Corvallis. 297 pp.

139. Suberkropp, K., Klug, M. J. 1974. Decomposition of deciduous leaf litter in a woodland stream. I. A scanning electron microscopic study. *Microb. Ecol.* 1:96–103

140. Suberkropp, K., Klug, M. J. 1976. Fungi and bacteria associated with leaves during processing in a woodland stream. *Ecology* 57:707–19

141. Suberkropp, K., Klug, M. J., Cummins, K. W. 1975. Community processing of leaf litter in woodland streams. *Verh. Int. Ver. Limnol.* 19:1653–58

142. Swanson, F. J., Lienkaemper, G. W., Sedell, J. R. 1976. History, physical effects and management implications of large organic debris in western Oregon streams. *USDA For. Serv. Gen. Tech. Rep. PNW-56*, 15 pp.

143. Swift, M. J. 1977. The roles of fungi and animals in the immobilization and release of nutrient elements from decomposing branch-wood. *Ecol. Bull. Stockholm* 25:193–202

144. Teskey, H. J. 1976. Diptera larvae associated with trees in North America. *Mem. Entomol. Soc. Can.* 100:1–53

145. Thienemann, A. 1912. Der Bergbach des Sauerland. *Int. Rev. Ges. Hydrobiol. Hydrogr.* 4: Suppl., pp. 1–125

146. Thomas, W. A. 1970. Weight and calcium losses from decomposing tree leaves on land and water. *J. Appl. Ecol.* 7:237–41

147. Thorup, J., Iversen, T. M. 1974. In-

gestion by *Serocostoma personatum* Spence. *Arch. Hydrobiol.* 74:39–47

148. Triska, F. J. 1970. *Seasonal distribution of aquatic hyphomycetes in relation to the disappearance of leaf litter from a woodland stream.* PhD thesis. Univ. Pittsburgh, Pa. 189 pp.

149. Triska, F. J., Sedell, J. R. 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. *Ecology* 57:783–92

150. Triska, F. J., Sedell, J. R., Buckley, B. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. II. Biochemical and nutrient changes. *Verh. Int. Ver. Limnol.* 19:1628–39

151. Triska, F. J., Sedell, J. R., Cromack, K., McCorson, F. M. 1979. Nitrogen budget of a small coniferous forest stream: Influence of allochthonous inputs and associated biological processes. *Ecol. Mongr.* In press

152. Ulfstrand, S. 1968. Benthic animal communities in Lapland streams. *Oikos* 10: Suppl., pp. 1–120

153. Vannote, R. L. 1970. Detrital consumers in natural systems. In *The Stream Ecosystem, Tech. Rep. No. 7*, ed. K. W. Cummins, pp. 20–23. E. Lansing: Michigan State Univ. Inst. Water Resour. 42 pp.

154. Wallace, J. B., Malas, D. 1976. The significance of the elongate rectangular mesh found in capture nets of fine particle filter feeding Trichoptera larvae. *Arch. Hydrobiol.* 77:205–12

155. Wallace, J. B., Malas, D. 1976. The fine structure of capture nets of larval Philopotamidae: with special emphasis on *Dolophilodes distinctus. Can. J. Zool.* 54:1788–802

156. Wallace, J. B., Webster, J. R., Woodall, W. R. 1977. The role of filter feeders in flowing waters. *Arch. Hydrobiol.* 79: 506–32

157. Wallace, J. B., Woodall, W. R., Sherberger, F. F. 1970. Breakdown of leaves by feeding of *Peltoperla maria* nymphs. *Ann. Entomol. Soc. Am.* 63:562–67

158. Ward, G. M., Cummins, K. W. 1978. Effects of food quality on growth rate and life history of a stream collector [*Paratendipes albimanus* (Meigen)]. *Ecology.* In press

159. Warren, C. E., Wales, J. H., Davis, G. E., Doudoroff, P. 1964. Trout production in an experimental stream enriched with sucrose. *J. Wildl. Manage.* 28: 617–60

160. Webster, J. R. 1975. *Analysis of potassium and calcium dynamics in stream ecosystems on three southern Appalachian watersheds of contrasting vegetation.* PhD thesis. Univ. Georgia, Athens. 232 pp.

161. Westlake, D. F. 1975. Macrophytes. See Ref. 99, pp. 106–28

162. Wetzel, R. G. 1975. Primary production. See Ref. 99, pp. 230–47

163. Wiggins, G. B., Mackay, R. J. 1979. Some relationships between systematics and trophic ecology in nearctic aquatic insects, with special reference to Trichoptera. *Ecology.* In press

164. Willoughby, L. G. 1974. Decomposition of litter in freshwater. In *Biology of Plant Litter Decomposition*, ed. C. H. Dickinson, G. J. F. Pugh, 2:659–81. London: Academic

165. Winterbourn, M. J. 1976. Fluxes of litter falling into a small beech forest stream. *NZ J. Mar. Freshwater Res.* 10:399–416

166. Winterbourn, M. J., Davis, S. L. 1976. Ecological role of *Zelandopsyche ingens* in a beech forest stream ecosystem. *Aust. J. Mar. Freshwater Res.* 27:197–215

167. Wotton, R. S. 1977. The size of particles ingested by moorland stream blackfly larvae. *Oikos* 29:332–35

168. Wu, C. F. 1923. Morphology, anatomy and ethology of *Nemoura. Bull. Lloyd Libr. Entomol. Ser.* 23:1–81

169. Zdanowski, M. K. 1977. Microbial degradation of cellulose under natural conditions. A review. *Pol. Arch. Hydrobiol.* 24:215–25