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Source: *BioScience*, Vol. 24, No. 11 (Nov., 1974), pp. 631-641
Published by: Oxford University Press on behalf of the American Institute of Biological Sciences
Stable URL: https://www.jstor.org/stable/1296676
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Structure and Function of Stream Ecosystems

Kenneth W. Cummins

It has been stated often that the selection of appropriate methodological strategies for ecological investigations are highly dependent upon the question being addressed. Unfortunately this awareness has not become fully operational—questions often being formulated only after data collection. Frequently, traditional ecological studies have been taxonomic inventories of biological communities—information of limited use in answering certain function- and process-oriented questions. Such inventories seem an inappropriate fabric from which to weave important ecological generalizations. As long as the species is assumed to be the basic ecological unit, ignoring for the moment problems in defining such units, the perpetually incomplete state of our taxonomic knowledge will constitute a major constraint for the development of ecological theory.

This assumption, that species recognition is the fundamental prerequisite for ecological insight, has proven particularly troublesome to the study of flowing water (or lotic) ecological systems. For example, immature stages (nymphs, larvae) of stream insects usually dominate the macroinvertebrate role in energy transformations, but the adults (usually males) constitute the coin of species identification. In addition, diatoms, the dominant lotic algae, present particularly difficult taxonomic problems. However, perhaps only the lack of attention paid the microbial components—bacteria and fungi—of natural communities has allowed the taxonomic focus to endure this long. Discrepancies between morphological, physiological, and genetic species definitions of microorganisms make it apparent how untenable a taxonomic foundation for all ecological questions can be. Thus, there is a need to identify functional groups of organisms, at least partially independent of traditional taxonomic determinations, in order to address important process-oriented ecological questions. It is certainly true that we would not now be in a position to search for other units from which to construct our generalizations without the extensive taxonomic (phylogenetic) information presently available. Nor would it be disputed that continued effort in taxonomic discovery and revision will benefit ecology.

Although it was recognized long ago that functional roles were filled by different taxa in similar habitats separated geographically, the concept of a taxonomic foundation for all of ecology has persisted. For example, Shelford (1914, 1937) discussed such analogous species groups in aquatic systems and Lindeman (1942) and others later assumed biotic categorizations on bases other than taxonomic—particularly nutritional habits (trophic levels).

Unfortunately, investigations are often initiated with an uneven and incomplete taxonomic inventory, followed by assignment of organisms to trophic levels on the basis of scant literature generalizations and concluded with poor approximations of exchange rates. Rarely is this descriptive exercise accompanied by the synthetic insight that the trophic level conceptual framework was intended to facilitate. In many instances trophic categorization has proven as restrictive as taxonomic identification in answering process-oriented questions. This is particularly true since most schemes of trophic partitioning cannot deal adequately with the functional roles concerning community metabolism of particulate (detritus) and dissolved organic matter.

The goal of the discussion that follows is to identify some of the process-oriented questions confronting modern stream ecologists—both theoretical and practical, to examine possible methods of qualifying and quantifying functional groups involved in these processes, to speculate on the impact of process-function investigations on the continual evolution of stream ecosystem theory and, finally, to examine the implications of such an approach to stream management strategies. Some interrelationships between these elements in the development of theory and management programs are conceptualized in Figure 1.

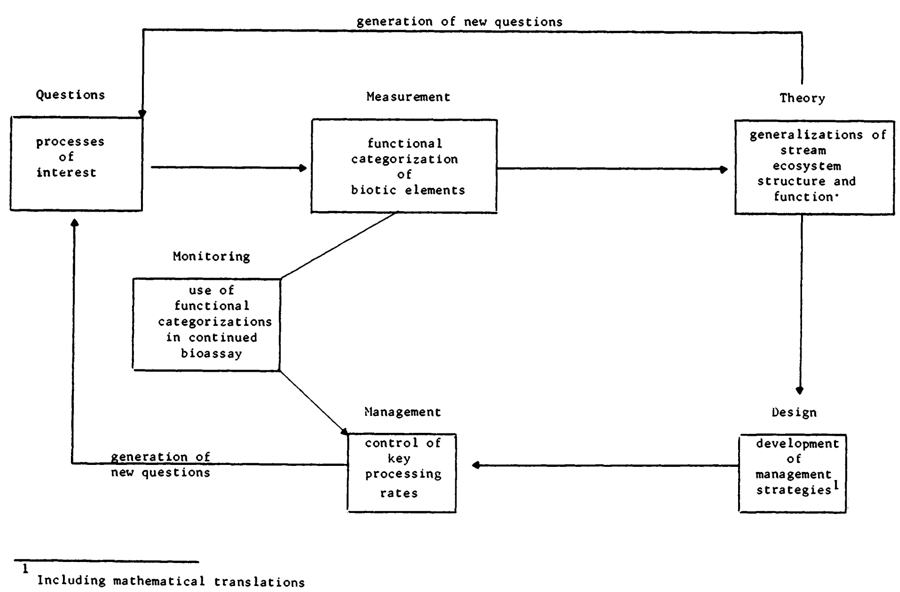

Fig. 1. A schematic representation of the interrelationships between process oriented questions, functional group evaluation, theory generation, and management strategies.

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STREAM ECOSYSTEM STRUCTURE AND FUNCTION

The present status of our knowledge of stream ecosystem structure and function is based on a number of generalizations that have been tested to some degree—primarily in woodland streams of the temperate zone (Teal 1957, Hynes 1961, Nelson and Scott 1962, Egglishaw 1964, 1968, Minshall 1967, Tilly 1968, Hynes 1970, Hall 1971, Cummins et al. 1972, Fisher and Likens 1973, Cummins[1], Petersen and Cummins[2], Boling et al.[3]).

Two intriguing features of such streams are: first, a dependence for the majority of their energy supply on the import of organic matter elaborated in the terrestrial system through which the stream flows (the watershed), and second, the utilization of a great deal of this organic input during the fall-winter period of lowest annual temperatures. That is to say, stream communities are heterotrophic (dependent upon food produced outside the stream) and temperature compensated (having organisms that can process organic matter at reasonable rates below "normal" temperature optima).

A portion of the reduced carbon compounds entering the stream as particles (particulate organic matter or POM) and in solution (dissolved organic matter or DOM), and similar materials produced in the stream itself, are processed to carbon dioxide and nutrients. Certain amounts are bound up for varying periods in resident biological components (standing crops) and the remainder is exported (Fig. 2). As Fisher and Likens (1973) showed for the tiny first order stream, Bear Brook (New Hampshire), 99% of the energy input is imported from the terrestrial surroundings (i.e., it is allochthonous) with only 1% derived from stream photosynthesis by mosses. The inputs were divided between dissolved (47% DOM) and particulate (53% POM) organic matter; 66% of the organic input was estimated to be exported downstream and 34% processed to CO_2.

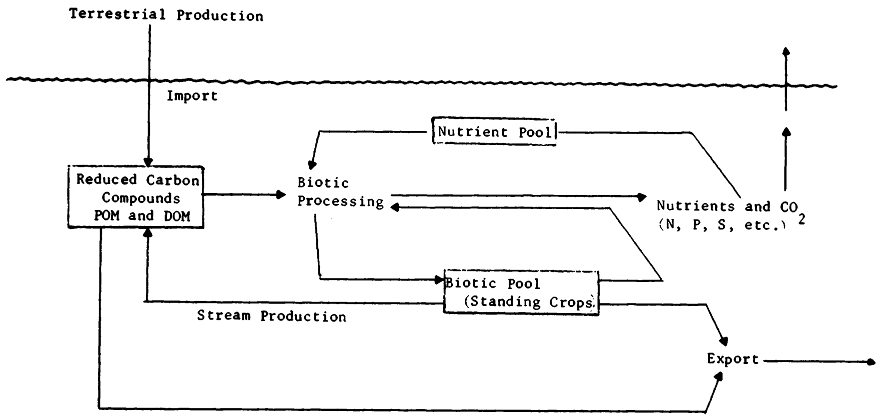

Fig. 2. Diagrammatic representation of the fate of reduced carbon compounds of terrestrial and stream origin: processing to nutrients and CO_2, temporary storage and export.

The organic matter budget produced by Fisher and Likens (1973) is, at present, the most complete annual balance sheet published for any stream system although Sedell et al. (1973) have produced an excellent particulate budget for a stream in the Oregon Cascades. The degree to which the New Hampshire and Oregon streams compare with regard to input, processing, and export of particulate detritus is striking. These investigations entailed periodic assessments of input, standing crop, and export of organic matter, with less attention given the actual processing events.

As suggested in Figure 3, there are a number of functional groups involved in the processing of organic matter, both POM and DOM, in heterotrophic streams. After the introduction of coarse particulate organic matter (CPOM, generally greater than 1 mm in diameter), such as leaves and needles, twigs, branches, bark, nuts, fruits, and flowers, into the stream, two processes occur rapidly.

Soluble organic matter leached from the CPOM enters the DOM pool. Although coarse particulate organic matter releases soluble components during the long residence period while it is being reduced to fine particulate organic matter (FPOM, generally smaller than 1 mm in diameter), the majority of the leaching occurs within 24 hours of initial wetting, even at low temperatures (Petersen and Cummins[2]). This solubilzation can be quite appreciable; for example, leaf litter loses 5 to 30% of its dry weight in the first day, depending upon the leaf species in question (Cummins et al. 1972, Petersen and Cummins[2]). The amount of DOM produced also depends on the condition of the CPOM—that is, the degree of leaching completed in the terrestrial environment prior to introduction into the stream system.

The second rapid event is the colonization of CPOM surfaces by microorganisms in transport—cells and spores of bacteria, spores of aquatic hyphomycete fungi, and protozoans (Suberkropp and Klug 1974). A significant portion of the colonization is complete in the first week or two, again depending upon the degree of substrate preconditioning in the terrestrial soil community and the temperature regime. At warm summer stream temperatures (>15°C) the spores and hyphae of terrestrial fungi, present on the CPOM when it enters the water, play a more significant role in the fungal flora.

The leached, microbially colonized CPOM is reduced to FPOM through mechanical disruption wrought by physical abrasion in the turbulent lotic environment and two interdependent community processes—animal feeding and microbial metabolism. The rate of conversion to FPOM is dependent on temperature, extent of terrestrial preconditioning, and qualitative characteristics of the CPOM. For example, a considerable range in processing rates for different leaf species have been reported. Exponential loss rates of less than 0.5% per day are characteristic of "slow" leaf litter such as oaks and hemlock while ash and alder leaves are converted at greater than 1.5% per day (Sedell et al. 1973, Petersen and Cummins[2]).

Animals, identified in Figure 3 as shredders (coarse particle feeders), feed

[1] Cummins, K. W. Macroinvertebrates. *In* M. Owens and B. Whitton, eds. River Ecology. Blackwell Sci. Publ., England, in press.

[2] Petersen, R. C., and K. W. Cummins. Leaf processing in a woodland stream ecosystem. *Freshwater Biol.*, in press.

[3] *A.* Boling, R. H., R. C. Petersen, and K. W. Cummins. Ecosystem modeling for small woodland streams. *In* B. C. Patten, Ed. System Analysis and Simulation in Ecology, Vol. 3. Academic Press, N. Y., in press; *and B.* Boling, R. H., E. D. Goodman, J. O. Zimmer, K. W. Cummins, S. R. Reice, R. C. Petersen, and J. A. Van Sickle. Towards a model of detritus processing in a woodland stream. *Ecology*, in press.

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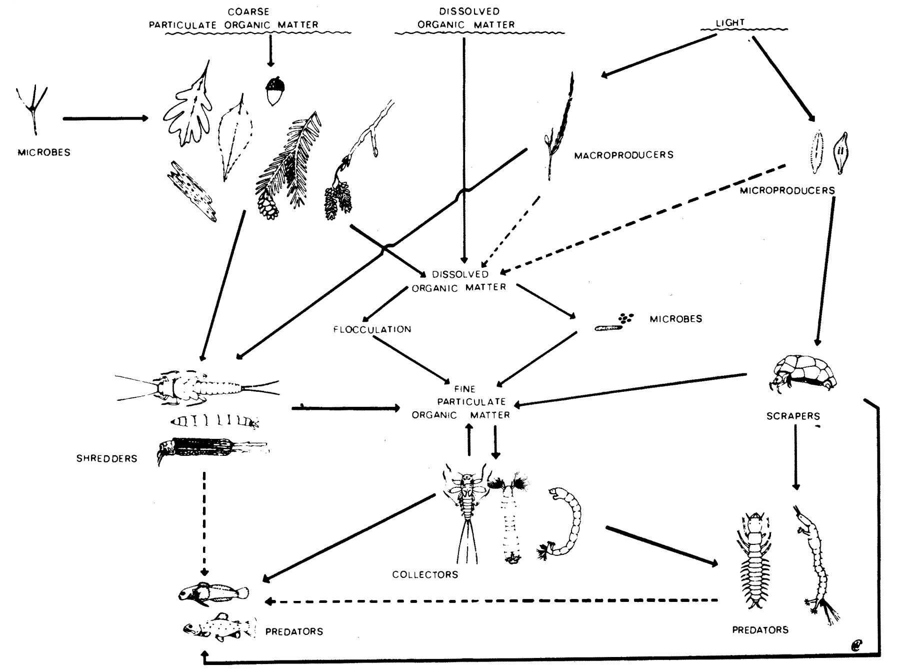

Fig. 3. A conceptual model of stream ecosystem structure and function (modified from Cummins 1973) emphasizing the processing of particulate and dissolved organic matter. CPOM is exemplified as deciduous leaves, coniferous needles, a twig, bark, nut, and flowers. Initial colonization of CPOM is represented by an aquatic hyphomycete fungal spore and the utilization of DOM by rod-shaped and spheroid bacteria. The plant community is represented by diatoms (microproducers) and moss (macroproducers). The animals shown as examples are: shredders—cranefly and caddisfly larvae and a stonefly nymph; collectors—blackfly and midge larvae and a mayfly nymph; scrapers—a caddisfly larva; predators—fishfly and midge larvae and fish (sculpin and trout).

Fig. 4. 1000x scanning electron microscope picture of the surface of a 1-week-old oak leaf incubated in Augusta Creek (Kalamazoo Co., Mich.) from 17 Aug. 73 to 20 Aug. 73. The long fungal spores on the right half of the photograph are the aquatic hyphomycete *Clavatospora tentacula;* the short ones at the upper left are *Lunulospora curvula.* The small ovoid and short rod-shaped bodies are bacteria; microcolonies are particularly visible at the upper left corner. The large diatom frustule shown at the lower left is a *Cymbella* species. (Photograph courtesy of K. F. Suberkropp, Kellogg Biological Station; see also Suberkropp, K. F., and M. J. Klug. Decomposition of deciduous leaf litter in a woodland stream. I. A scanning electron microscopic study. *Microbiol. Ecol.*, in press.)

upon the CPOM converting only about 40% of what they ingest to their own tissues and respiratory CO_2 (Welch 1968). The remainder is egested as feces. This process of reduction in CPOM particle size constitutes a significant contribution to the FPOM pool—approximately 2 to 7 mg of feces per large shredder individual per day (McDiffett 1970, Cummins et al. 1973). During colonization and growth the microbial community also attacks the CPOM which, after leaching, constitutes a high carbon (about 30% cellulose and lignin), low nitrogen substrate. Using the CPOM as a carbon source and dissolved inorganic and organic nitrogen the microflora metabolizes the substrate and grows (Fig. 4), also producing FPOM in the form of fragments and sloughed microbial cells. The microbial biomass associated with CPOM is reflected by increased nitrogen content of stream leaf litter through time (Kaushik and Hynes 1971).

Considerable evidence has accumulated indicating a nutritional dependence by the shredders on the microbial flora of the CPOM rather than the substrate itself (Kaushik 1969, Wallace et al. 1970, Triska 1970, Kostalos 1971, Liston 1972, Mackay and Kalff 1973, Bärlocher and Kendrick 1973a, 1973b). One might liken the microbial tissue to "peanut butter" which only occurs on nutritionally unsuitable "crackers," so that "cracker" ingestion is always a prerequisite to obtaining "peanut butter." Although the microflora can reduce leaf litter coarse particulate organic matter to FPOM in the absence of shredders (Triska 1970, K. F. Suberkropp, Kellogg Biological Station, pers. comm.), the presence of the large particle feeders results in a 20% increase in the conversion of CPOM to FPOM at normal fall-winter stream temperatures (Petersen and Cummins[4], Boling et al.[5]). Also, there can be little doubt that shredder feeding enhances CPOM substrates as microbial colonization sites—for example, in the process of skeletonizing leaves (Fig. 5) by increasing exposed edges and surface areas.

Thus, the FPOM pool is created through physical and biological (shredder and microbial) reduction in CPOM particle size. In addition, FPOM enters directly from the watershed; about 4% of the particulate organic matter input to Bear Brook was estimated to be

[4] See footnote 2, p. 632.
[5] See footnote 3A, p. 632.

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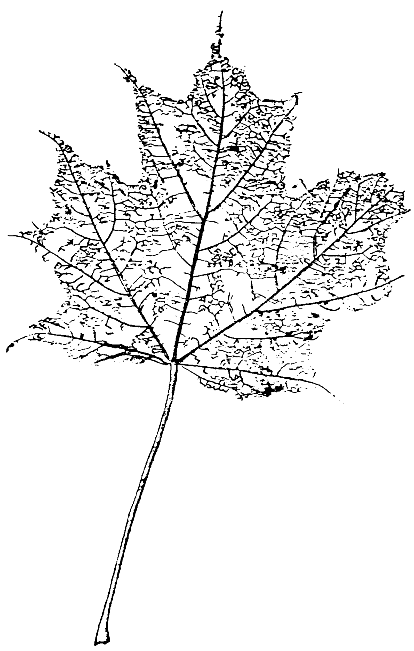

Fig. 5. A photocopy of a sugar maple *(Acer saccharum)* leaf skeletonized by the shredder *(Tipula abdominalis* : Diptera : Tipulidae) feeding at 5°C.

FPOM by Fisher and Likens (1973). A significant amount of small particles enters the FPOM pool through activities associated with the DOM pool. Leachate from CPOM as well as DOM from the terrestrial system entering via surface runoff and subsurface groundwater (and aquatic plant and microbial excretions) are converted to FPOM by physical flocculation and microbial assimilation—the microbes themselves being, by definition, fine particles. Physical flocculation of DOM to FPOM can be quite significant and is dependent on such parameters as turbulence, temperature, pH, and various ion concentrations (Lush and Hynes 1973). Cummins et al. (1972) showed the rapid and dramatic effect that bacteria in transport can have on DOM in the form of leaf litter leachate.

Animals feeding on FPOM are referred to in Figure 3 as collectors because of the reaggregation of small particles resulting from their ingestion activities. Various food collecting mechanisms are employed either to filter FPOM from transport in the water or gather fine organic particles from the sediments (Cummins 1973). Collector feeding may increase or decrease particle size within the FPOM pool, but often the feces are similar in size to the ingested particles. The fate of the FPOM is recycling through collector populations, with the associated respiratory loss (25-30% of ingestion [Welch 1968]), microbial metabolism to CO_2, and export.

The carbon fixed in the stream, as indicated previously to be typically less than 1% of the total stream community energy supply, is shown in Figure 3 as photosynthesizing organisms (primary producers) such as algae (usually diatoms) and mosses. Animals specially adapted for removing firmly attached algae from exposed surfaces in running waters are designated scrapers. Available evidence suggests that mosses (and rooted aquatic macrophytes, if they occur) enter the community processing mechanisms as CPOM at times of dieback, being subject to very little animal feeding while alive (Cummins 1973).

The predator category (Fig. 3) functions as a major source of shredder, collector, scraper, and, also, predator mortality. In this view, all nonpredatory mortality is considered physiological death.

FUNCTIONAL GROUPS AND ORGANIC MATTER PROCESSING

Heterotrophy-Autotrophy and Import-Export Relationships

Determination of the rates and efficiencies at which organic matter is processed (converted to CO_2 and nutrients) in running water systems and the factors regulating such rates and efficiencies probably constitutes the primary goal of the present stream research effort. One basic distinction to be made in comparing stream communities is the ratio of heterotrophy to autotrophy; that is, a comparison between organic matter processing (community respiration: O_2 consumption and CO_2 production) and organic matter elaboration (photosynthesis: CO_2 consumption and O_2 production). Of course, the ratio will change with stream order—from first order headwater streams through higher order major rivers, as well as over diurnal and seasonal cycles. The use of a ratio of gross photosynthesis to respiration, placing running water communities on a scale to determine if they are predominantly in a processing (consumption) or producing mode (Fig. 6), was suggested by Odum (1956). Fisher and Likens (1973) expanded the system to include import to and export from the stream system, combining the two ratios in a three dimensional coordinate system.

It appears that organic matter import-export phenomena in streams are subject to considerable interpretation with regard to inclusion in community processing budgets. Obviously, during a spate, organic matter measured in a stream is primarily in an export mode. Quantities transported, particularly CPOM, will depend upon the degree of flooding, or percent bankfull discharge (Leopold et al. 1964). However, the material transported during these short periods, which may constitute the major portion of particulates exported over an entire annual cycle, is often dominated by organic matter from the bank that has been subjected to little or no stream processing and is simply moved through at a rate less than the biological response times.

For example, if a dry leaf that falls on the stream surface and floats on top through a section of stream in a matter of minutes is to be included in an organic matter budget for the section, considerable qualification is necessary with regard to definitions of such terms as annual budget, processing, and efficiency. Methods such as direct micro-

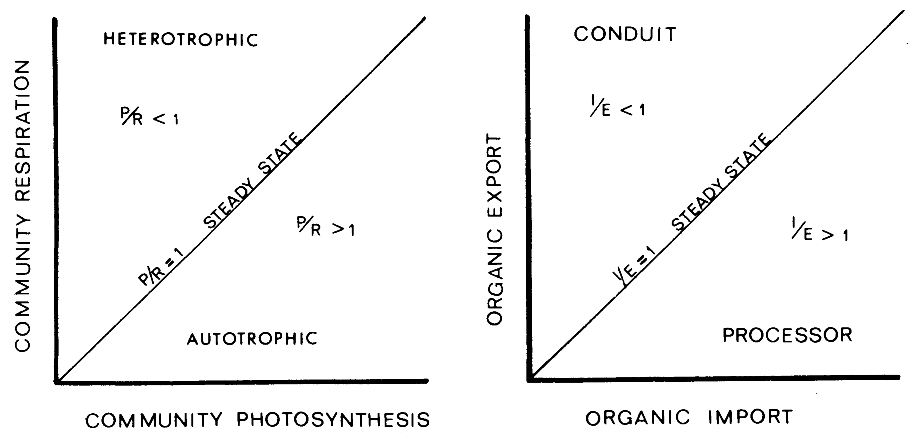

Fig. 6. The relationship between photosynthesis (autotrophy) and respiration (heterotrophy) and import (processor) and export (conduit) of organic matter in stream ecosystems (for a single combination figure see Fisher and Likens 1973).

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scopical examination for aquatic hyphomycete fungal spores (Triska 1970), measurements of community respiration per unit organic weight of detritus (Boling et al.[6]), or estimations of microbial biomass using bioluminescent-ATP methods (Chappelle and Levin 1968) could be employed as indices of the percent of such transport material actually subjected to in-stream processing—particularly if such measurements were compared to reference standards incubated in the stream for known periods.

A combination of techniques can be effectively utilized to evaluate the relative importance of heterotrophic vs. autotrophic processes as well as the organic matter storage capacity in streams. Periodic assessment of the average detritus standing crop in a section of stream, primary production (in-stream photosynthesis), and community respiration constitute lotic, process-oriented measurements. When stream community function is to be the focal point of investigations, perhaps such process data should assume priority over watershed-oriented budgets in which the major effort is directed at estimating inputs (import) and outputs (export). In stream process studies, changes in detritus standing crop not accounted for by predicted increases due to primary production, or decreases due to respiration, can be attributed to import or export. The relationships are summarized in Table 1 and some representative data for a small Michigan woodland stream are given in Figure 7. The difference in autotrophy at an open vs. a shaded section of the stream is apparent.

[6] See footnote 3A and B, p. 632.

Undoubtedly the ratio of heterotrophy to autotrophy is controlled by light, temperature, organic and inorganic inputs, and flow, with lesser localized effects by invertebrate grazers (scrapers). Shifts from heterotrophy to autotrophy in streams usually involve conversion from the typical diatom-moss (e.g., *Fontinalis*) community and, in some streams, also watercress (*Nasturtium*) beds around the springs, to filamentous green algae (e.g., *Cladophora, Stigeoclonium, Ulothrix,* etc.) and/or beds of rooted aquatic plants. The correlation between maximum light income to streams in the autumn just after leaf-fall and in the spring just prior to leaf-out, and photosynthetic maxima was shown by Hall (1971).

At the Kellogg Biological Station we have demonstrated in paired artificial stream channels that temperature elevation (5°C) can produce a heavy growth of filamentous green algae in one channel when the general fall-winter stream community, light, nutrients, flow, and grazers are the same in both systems. R. L. Vannote and coworkers (pers. comm.) at the Stroud Water Research Center have shown in their superb experimental stream facility that flow-discharge regimes exert important controls on the dominance of primary production in running waters. It appears that spates prevent the establishment of a filamentous algal system, and the attendant reduction in animal diversity, over the annual cycle. Obviously, the "switch" that initiates the trend from heterotrophy to autotrophy is a complex set of interactions and not merely a light controlled change.

Primary Producers

The organisms that contain chlorophyll and are capable of photosynthetic carbon fixation constitute a separable, functional group in stream communities since they collectively represent the internal energy supply for the system. However, within such a category there are two functionally distinguishable components—algae, or microproducers, and vascular plants, or macroproducers (Fig. 3). As stated above, stream vascular hydrophytes (mosses and flowering plants) enter the community processing machinery almost exclusively at the time of dieback, following the same general CPOM pathway as terrestrial plant tissue inputs, probably at faster rates due to their aquatic beginning and more fragile nature. The typical stream microproducers (nonfilamentous algae)

TABLE 1. Summary of relationships between detritus standing crop, photosynthesis, respiration, and organic matter import and export over a specified time interval (t).

Evaluation system	Measurements			Increase (+) or decrease (-) in g/m² over interval t (t_1 to t_2)	Change in detritus standing crop not accounted for by evaluation system	Conclusions about system not evaluated
	Initial instantaneous (t_1)	Rate estimated for	Final instantaneous (t_2)			
P/R ratio and detritus standing crop	Detritus standing crop	Photosynthetic production Community respiration	Detritus standing crop	+, - or 0	No change	Import = Export (or both = 0)
				+	Positive	Import > Export
				-	Negative	Export > Import
I/E ratio and detritus standing crop	Detritus standing crop	Import of organic matter Export of organic matter	Detritus standing crop	+, - or 0	No change	Photosynthesis = Respiration
				+	Positive	Photosynthesis > Respiration
				-	Negative	Respiration > Photosynthesis

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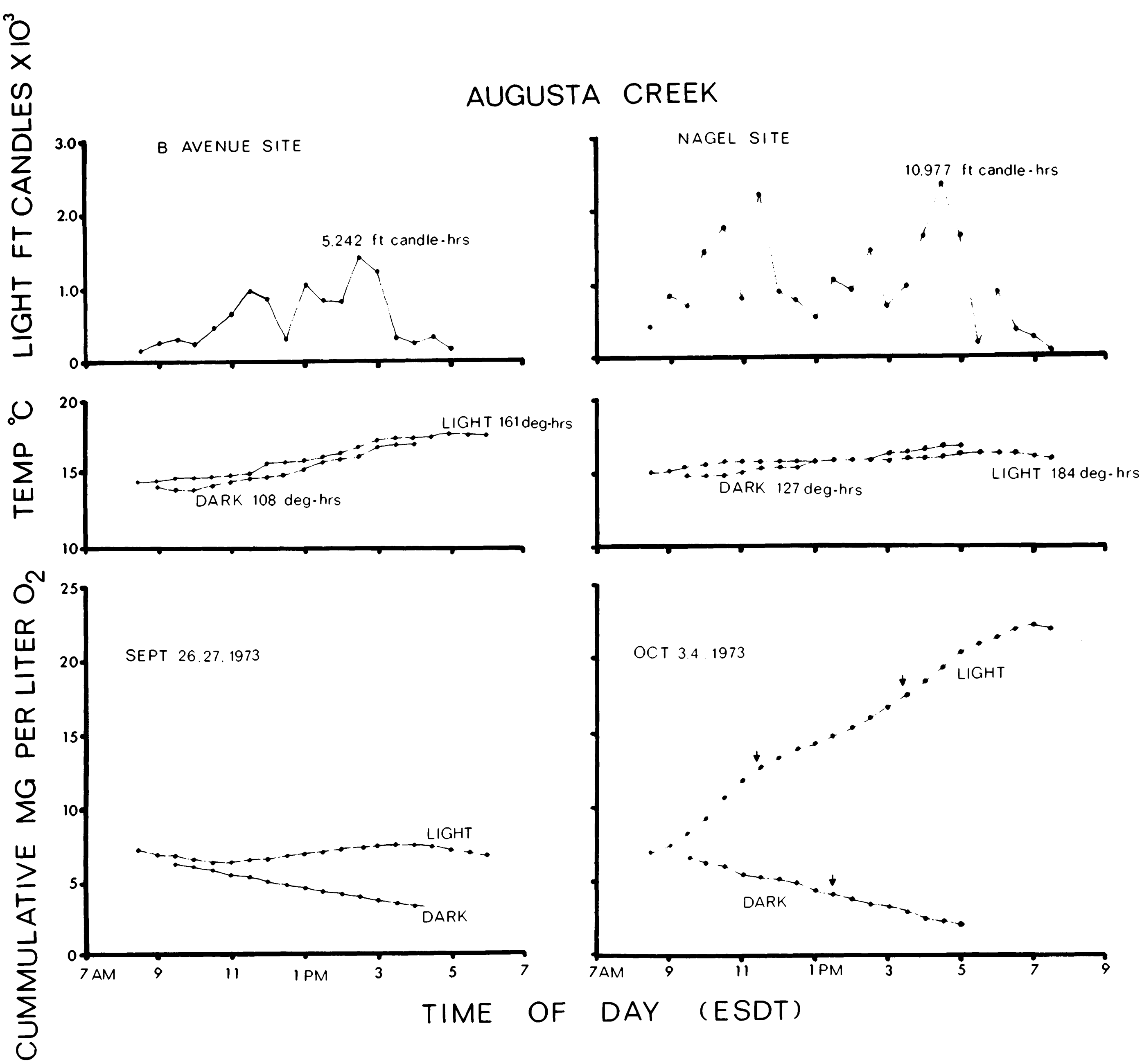

Fig. 7. Comparative data on light, temperature, and oxygen production (light chamber) and oxygen utilization (light and dark chambers) at two sites on Augusta Creek, a small, hardwater brown trout stream in southern Michigan (Kalamazoo and Barry Counties; Manny, B. A., and R. G. Wetzel. Diurnal changes in dissolved organic and inorganic carbon and nitrogen in a hardwater stream. *Freshwat. Biol.*, in press). The B Avenue site is a first order, headwater, heavily shaded section (P/R = 0.5); the Nagel site is a third order, more open stream section about midway along the drainage (P/R = 1.7). Measurements of oxygen concentration were made in closed chambers (holding about 3 liters stream water) using oxygen probes (Yellow Springs Instruments) equipped with a vibrator to maintain water circulation. The chamber bottoms (3.186×10^{-2} m^2) were filled with natural stream sediments ($\bar{x}$ of 1.5 liters) and allowed to incubate in situ for 3 months. The chambers contained 114.1 g (B Ave. Site) and 117.3 g (Nagel Site) organic matter (550°C ash free dry wt). (Data from Donna K. King, Kellogg Biological Station. Autotrophic-heterotrophic relationships in a woodland stream, Ph.D. thesis in preparation.)

are either grazed by scrapers or enter the FPOM pool.

Methods are available for assessing the contribution of primary producers to stream ecosystem metabolism. Changes in dissolved oxygen levels over 24-hour cycles at two points along a stream (upstream-downstream method, e.g., Hall 1971) or in light and dark closed, circulating (Fig. 7) or open flow-through chambers (Hansmann et al. 1971) are frequently measured. Tracer (^{14}C, ^{32}P) techniques are also available either for use in closed systems or for direct applications of small doses to streams (rapidly disintegrating ^{32}P, [Elwood and Nelson[7]]). Standing crop measurements of rooted vascular plants just prior to winter dieback probably provide the best estimate of their contribution to stream organic matter budgets.

Primary production should be measured against a background of light,

[7]Elwood, J. W., and D. J. Nelson. Measurement of periphyton production and grazing rates in streams using a ^{32}P material balance method. *Oikos*, in press.

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TABLE 2. A scheme for partitioning stream detritus according to particle size ranges. (Modified from Boling et al. 1974a.)

Detritus Categories: General	Detritus Categories: Specific	Acronym	Approximate size ranges (mm)	Dominant Constituents	Dominant animal detrital feeding group (see Fig. 7)
Coarse particulate organic matter (CPOM)	Large resistant particulate organic matter	RPOM	> 64	Logs, branches, large twigs large sections of bark (processing times > 1 year)	Detritus shredders
	Whole leaf organic matter	LVOM	> 16 < 64	Leaf litter (leaf packs)	Detritus shredders
	Leaf fragment organic matter	LFOM	> 4 < 16	Large leaf, twig, and bark fragments, fruits and nuts, large seeds, buds and flowers, conifer needles	Collector - macrogatherers
	Large particulate organic matter	LPOM	> 1 < 4	Small fragments of plant (and animal) parts	Collector – Macrogatherers Collector – macrofilterers
Fine particulate organic matter (FPOM)	Medium particulate organic matter	MPOM	>0.25 < 1	Plant and animal fragments, feces of large invertebrates	Collector - macrofilterers Collector - microgatherers
	Small particulate organic matter	SPOM	>0.075 <0.25	Plant, animal, and fecal fragments of large invertebrates and feces of small invertebrates	Collector - microfilterers Collector - microgatherers
	Very small particulate organic matter	VPOM	>0.0005 <0.075	Very small detrital fragments and free microorganisms	Collector - microfilterers
Dissolved organic matter		DOM	<0.0005	Organic matter in solution – leachate from plant and animal detritus, microbial and producer excretions	Little or none

temperature, and nutrient (especially P and N) data to permit intersystem comparisons. Cumulative measures of light and temperature, e.g., foot- or meter-candle-hours or days (1m-cand. = 1 lumen/m^2) and degree days, should prove more useful than calendar time intervals. If lower light or thermal limits can be demonstrated, time intervals below these levels should be excluded from the cumulations.

Given that the prototype, first to third order stream is a cool, heavily shaded, heterotrophic system, in-stream photosynthesis normally contributes very little to the total annual energy flux—for example, less than 1% in the New Hampshire stream studied by Fisher and Likens (1973). Larger running waters (fourth order and above) should exhibit a trend toward autotrophy, although nonperturbated prototypes of these larger systems are virtually nonexistent in the temperate zone because of massive man-engendered alterations in watershed vegetation cover, nutrient inputs, and flow (by impoundment).

Microconsumers

Since the nonliving organic matter substrates and the metabolizing microorganisms are never isolated from one another in streams, consideration of these components as functionally separate compartments seems merely academic. At present, compartmentalization of organic substrate and associated microbes by particle size, which is clearly related to processing time, seems to be the most tractable approach.

Inasmuch as a seasonal sequence of reduction in the particle size of organic matter can be demonstrated (Boling et al.[8]), changes in the biochemical nature of particulate organic matter (POM) and in the associated microbial functions associated with particulate degradation would be expected—expectations supported by particle size-dependent respiration measurements (Boling et al.[9] Hargrave 1972). For this reason, it seems fruitful at present to treat detritus particle size classes as functional units, even though organic matter obviously forms a continuum from logs through fine particles, large molecular aggregates and complexes to small molecules. A scheme for which some data have been collected (Boling et al.[8]) is summarized in Table 2.

The DOM size range is primarily in transport while POM size fractions, especially CPOM, are usually concentrated in the sediments. There is evidence that the transport and sediment systems can operate semi-independently (Cummins et al. 1972). Successional changes in biochemistry (Kaushik and Hynes 1968, 1971, Hynes and Kaushik 1969) and microbial flora (Triska 1970,

[8] See footnote 3A and B, p. 632.

[9] See footnote 3A, p. 632.

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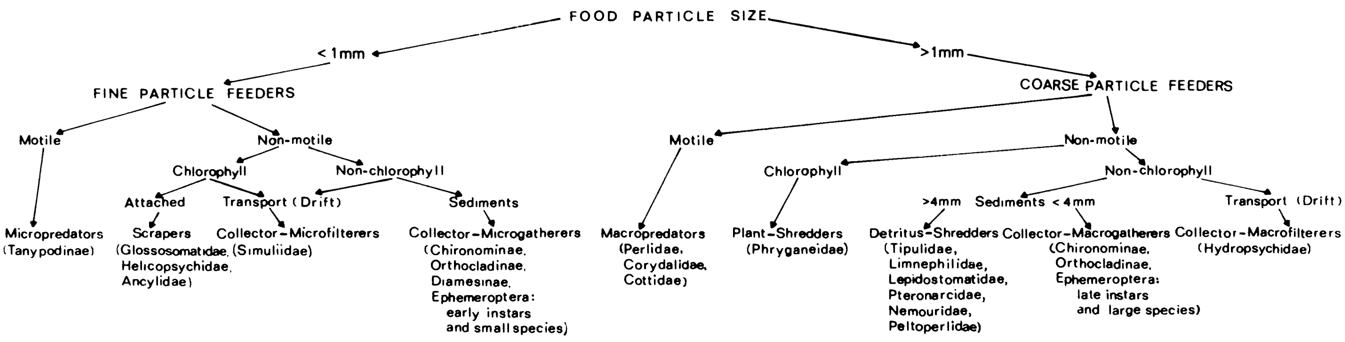

Fig. 8. Functional categorization of stream animals according to particle size and character of food with some selected examples of taxa that, in general, would have representatives included in a given functional category. Trueflies (Diptera)—Midges, Tanypodinae, Chironominae, Orthocladiinae, Diamesinae; blackflies—Simuliidae; craneflies—Tupulidae. Caddisflies (Trichoptera)—Glossosomatidae, Helicopsychidae, Phryganeidae, Limnephilidae, Lepidostomatidae, Hydropsychidae. Mayflies—Ephemeroptera. Stoneflies (Plecoptera)—Perlidae, Pteronarcidae, Nemouridae, Peltoperlidae. Dobson—and fishflies (Megaloptera)—Corydalidae. Limpets (Mollusca, Gastropoda)—Ancylidae. Fish—Cottidae (sculpins).

K. F. Suberkropp and M. J. Klug, Kellogg Biological Station, pers. comm.), termed "conditioning," have been shown for the CPOM category. These initially involve minimal particle size conversion. Similar successional sequences (conditioning) have yet to be detailed for other detritus size fractions.

Although it is true that remarkable amounts of biological activity proceed in streams at low temperatures (late fall through early spring), the processing rates are still under general thermal control. For example, leaf litter processing, taken broadly to include conversion to smaller particles and CO_2, progresses at a rate approximately 20% faster at 10°C than 5°C, as determined in experimental channels populated by the same micro- and macrobiota (Cummins and coworkers, Kellogg Biological Station, unpubl. data). The evolution of much of the stream biota has been largely in response to the major inputs of POM in the autumn, primarily in the form of deciduous leaf litter (Hynes 1963, Ross 1963). The resultant capability to metabolize effectively at temperatures well below normal thermal optima is unparalleled in temperate terrestrial systems.

As new techniques are developed and more data gathered, microbial and biochemical differences which transcend particle size categories will certainly become apparent. In addition to direct observation of microorganisms (especially epifluorescence and scanning electron microscopy, Fig. 4), the isolation and identification of biochemical capabilities of microbial elements will provide critical additional resolution of functional roles. For example, identification and quantification (probably through microcosm and tracer uptake studies) of cellulolytic and/or lignolytic activity of detrital bacteria and fungi in natural streams under *normal* stream temperature regimes should constitute a prime objective for lotic researchers. Fractionation of DOM by molecular weight should permit recognition of microbes associated with certain fractions and concomitant processing rates (Bretthauer 1971, M. J. Klug, Kellogg Biological Station, pers. comm., T. L. Bott and R. A. Larson, Stroud Water Research Center, pers. comm.). Again, if stream studies are process-oriented, new microbial data will be most useful if related to rates at which conversions of coarse particulate to fine particulate to dissolved organics to CO_2 occur.

The presence of microconsumers other than bacteria and fungi in stream detritus is often noted but seldom quantified: for example, protozoans, diatoms, rotifers, microcrustaceans, nematodes, and water mites (the last three overlap in size with early life stages of organisms usually considered macroconsumers [Cummins[10]]). In most instances, only the protozoans and diatoms might constitute significant biomass and metabolic activity relative to the bacteria and fungi. Protozoans serve primarily as particle aggregators functioning both as collectors and, like other microorganisms, as FPOM. Diatoms function as microproducers, although densities on the surfaces exposed to light are usually low, and probably as facultative microconsumers of DOM since they are often found deep in CPOM detrital accumulations in a viable condition. At present, there is little choice but to include protozoans and diatoms along with fungi and bacteria as the processing microbiota of a given detritus fraction.

Macroconsumers

Stream macroconsumers are generally considered to be those animals, dominated by invertebrates, that attain a size of at least 3 to 5 mm at termination of growth (Cummins[10]). The general classification of macroconsumers, primarily according to food particle size shown in Figure 3, has been expanded in Figure 8. As stated previously, the primary role of nonpredator macroconsumers is viewed as particle size conversion—hence the recognition of functional groups on the basis of particle size fractions eaten and method of feeding. Predators are seen as both particle converters, the "particles" being the prey, and as controllers of nonpredator populations. The fortuitous ingestion of animals by shredders, collectors, and scrapers during detrital or algal feeding and detritus and algal intake by predators, primarily as prey gut contents, exemplify inconsistencies resulting when attempts are made to define functional roles beyond the simplistic level of food particle size only (Coffman et al. 1971, Cummins 1973).

Although such inconsistencies may represent little error in estimating the processing rates of organic matter in streams, they suggest that other qualifiers of a particle size classification should be sought. M. J. Klug and coworkers of the Kellogg Biological Station Stream Research Group have been investigating other critera for evaluating macroconsumer functional roles in organic matter processing. A combination

[10] See footnote 1, p. 632.

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of data on microbial gut flora, related macroconsumer gut morphology, and food gathering apparatus, together with general food type, constitute promising criteria. Radiotracers can also be used for the rapid, approximate determination of the trophic role of stream animals (e.g. Ball and Hooper 1963, Sedell 1971, Cummins[11]).

Temperature is viewed as controlling the general dimensions of macroconsumer life cycles through influence on metabolism–respiration, feeding, and growth rates. These relationships can be conveniently summarized in terms of cumulative temperature (degree-days) over the growth period (Table 3). Within the overall limits set by temperature, growth rate, and, to some extent, survivorship (excluding predator-engendered losses) are controlled by food quality and quantity. As an example, the effect of in-stream conditioning time (i.e., microbial colonization and growth) and leaf species on feeding by a shredder is shown in Figure 9. There is about a 1 week time lag (at 15°C) before the "slow" leaf species (aspen) is fed upon at the same rate as the "fast" species (ash), but 2 weeks are required before maximum feeding rate is obtained on both types of leaves.

[11] See footnote 1 p. 632.

Management Strategies

The fundamental problem in stream management is clearly "water quality," in the broad sense meaning system quality. Regardless of definition, here lies the challenge–interfacing, in compatible fashion, the self-perpetuating structure and function of running water ecosystems with selfish, "natureless" human goals. Water quality is, in fact, always defined in reference to these goals. For example: Will the system support a particular sport fishery? Will it be a habitat where noxious and pathogenic organisms will flourish? Will it decompose organic wastes or serve merely as an export conduit?

From the data at hand, two points seem clear. First, the maintenance of water quality necessitates the continuance of certain relationships between CPOM, FPOM, and DOM together with the involvement of critical functional ecological groups of both micro- and macroorganisms. Second, unless about one third of the total organic matter input (about one half of the POM) is processed, i.e., converted to CO_2, annually by the stream system and unless in-stream plant growth remains subservient to terrestrial organic matter as the "fuel" to drive the system, the stream in question probably has impaired water quality.

In general, the differences between relatively undisturbed woodland

TABLE 3. Functional categorization of stream animals according to life cycle characteristics with some examples of trophic (by food particle size) and taxonomic groups that would be in each category. For placement of taxonomic groups see Fig. 7.

Generation time (egg to egg)	Designation	Growth period	Approximate degree days	Fine particle feeders (FPF)	Coarse particle feeders (CPF)
Multiple generations per year	Autumnal (Fall-Winter) and Vernal (Spring-Summer)	Sept–March April–August	1300 2500	Baetidae Heptageniidae Leptophlebeidae Glossosomatidae Helicopsychidae Hydropsychidae Chironominae Orthocladiinae Simuliidae	Hydropsychidae Lepidostomatidae
Full year (no "shut-down")	Annual	(Sept–August or April–March	3800	Gastropoda Pelecypoda (Amphipoda)	Perlidae* Tanypodinae* (Amphipoda)
Full Year (with "shut-down")	Annual–Autumnal (Summer "shut-down")	Sept–March	1300	Ephemerellidae Neophylacinae Orthocladiinae	Tipulidae Limnephilidae, e.g. *Pycnopsyche* Lepidostomatidae Nemouridae
	Annual–Vernal (Winter"shut-down")	April–August	2500	Ephemerellidae Brachycentridae Chironominae Orthocladiinae	Limnephilidae, e.g. *Hydatophylax*
More than one year (usually more than 2) (no "shut-down")	Biannual	Autumn–Autumn or Spring–Spring	3800/yr		(Cottidae*)
More than one year (usually 2) (with "shut-down")	Biannual–Autumnal (Summer "shut-down")	Fall–Winter seasons	2600		Pteronarcidae (Peltoperlidae)
	Biannual–Vernal (Winter "shut-downs")	Spring–Summer seasons	5000		Decapoda Corydalidae* Corduligasteridae* Gomphidae*

* Predators

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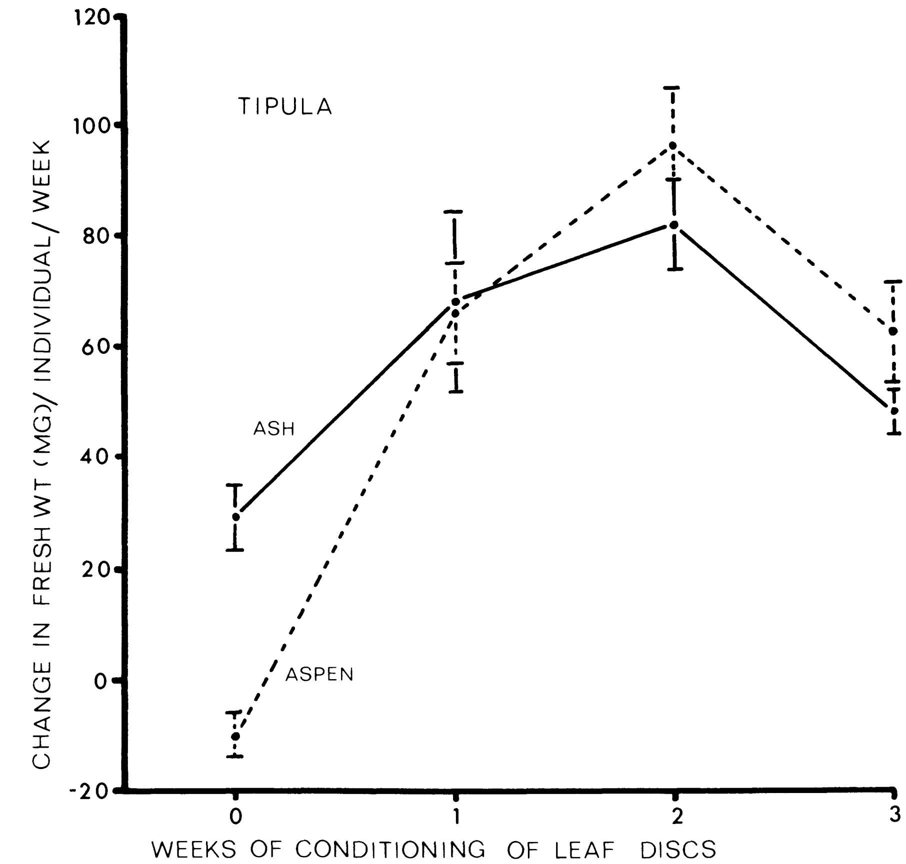

Fig. 9. Effect of in-stream conditioning time and leaf species on feeding by the cranefly larva shredder *Tipula abdominalis* (Diptera : Tipulidae) at 15°C. Each point represents the mean (± 1 SD) of five larvae held individually in tubes (screened at both ends through which water circulated) containing discs of either ash or aspen leaves conditioned 0, 1, 2, or 3 weeks in Augusta Creek. The decline in growth on the 3-week conditioned leaf discs was the result of food limitation. (Data from G. L. Spengler, Kellogg Biological Station.)

streams, characterized by high processing efficiency, and "organically enriched" or "polluted" running water systems of similar dimensions are the size distribution of the organic particles that enter the stream, timing of the inputs, POM retention characteristics of the system, temperature and nutrient regimes, and the presence of key functional groups of organisms. Where appropriate options exist, management strategies should be developed and implemented based on available stream ecosystem theory (Fig. 1). "Water quality" status should be monitored through recognition of the continued appropriate relationships between CPOM, FPOM, DOM, and micro- and macroorganisms.

It is not presently known whether the efficiency with which organic matter is processed in streams can be increased above reported levels (Fisher and Likens 1973, Sedell et al. 1973). Since so few systems have been studied in a fashion permitting comparison, the range of natural efficiencies has yet to be established—clearly, comparison of streams at opposite ends of such a spectrum would be most instructive.

Three general management strategies, singly or in various combinations, seem promising:

(1) changes in the physical nature of the running water system—light (e.g. artificial shading), temperature, aeration, POM retention characteristics, etc.;

(2) changes in organic inputs, particularly particle size distribution; and

(3) changes in the biota, for example shredder population densities.

If, as Fisher and Likens (1973) report for Bear Brook, the general input pattern is for at least half the organic matter to enter as POM, dominated by CPOM, then waste water treatment procedures that produce effluents high in DOM with particulates dominated by FPOM are unlikely to contribute positively to the maintenance of stream "water quality" defined in terms of "natural" organic matter processing rates. The use of retention structures (e.g., rods driven into the stream bottom) to reduce movement and export of CPOM, especially leaf litter, in and through a section of stream should increase total processing, particularly if shredder populations are supplemented by stocking.

Potentially, model development constitutes an important aspect of management strategies, although none, including biological processing, have been utilized in relation to streams. Initial models are currently available which simulate primary production (McIntire 1973) and particulate detritus processing (Boling et al.[12]).

CONCLUSIONS

In summary, the basic features of stream ecosystem structure and function are now established and various functional ecological components and their interrelationships have been defined and initially dimensioned for some representative streams. The search continues for additional or alternative functional criteria to replace partially or totally the previous dependence on classical taxonomic units. Attention is now focused on two apparently generalizable conditions in nonperturbated running waters: The efficient conversion of organic matter, especially particulates, to CO_2 and the maintenance of a minor role played by in-steam plant growth. Clearly the time is at hand to infuse the "new stream ecology" into management strategies directed at our precious running waters.

ACKNOWLEDGMENTS

Contribution No. 256 of the Kellogg Biological Station. The original research and synthesis were supported by National Science Foundation Grant GB-36069X and U.S. Atomic Energy Commission Contract AT(11-1)2002. This paper was possible only through the interchange of ideas with a great many stream ecologists, particularly: Robert C. Petersen, Michael J. Klug, and Keller F. Suberkropp, Kellogg Biological Station; Robin L. Vannote and Thomas L. Bott, Stroud Water Research Center; and James B. Sedell, James D. Hall, Oregon State University, and R. H. Boling, Michigan State University. I am also

[12] See footnote 3A and B, p. 632.

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grateful for data and helpful suggestions provided by Robert H. King, Donna K. King, G. Milton Ward, George L. Spengler, and Virginia I. Holt of the Kellogg Biological Station.

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