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Abstracts of papers presented at an
AAAS Symposium. Boston, December 29, 1969

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INTRODUCTION

In recent years, a large segment of concern over our severe environmental crisis has centered on running water habitats. The formulation of suitable management practices for streams has been greatly hampered by the lack of fundamental data on the functioning of lotic systems. Since it is non-polluted streams that man wishes to maintain or reinstate, the data required necessarily involve the complex communities typical of "healthy" streams. North American ecologists have begun to provide such basic data essential for the intelligent preservation, manipulation and rehabilitation of our continental streams. The symposium stresses the state of our knowledge of stream community composition and structure together with functional aspects such as biomass production, energy transfer and the role of terrestrially produced organic matter. The intent is to summarize current concepts relative to these basic ecological data and relate them in a general way to problems of environmental quality in the hope that an exchange of information will be promoted--between those engaged in fundamental research and the formulation of ecological theory and those concerned with various phases of stream management.

The symposium is organized around selected areas of lotic research which have significant relevance to the analysis of stream ecosystem functioning. Originally it was intended that the area concerning the impact of terrestrially produced organic matter on the stream system be more completely represented. Because of the last minute withdrawal of a participant, some of this emphasis was lost.

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COMMUNITY STRUCTURE IN NATURAL STREAM SYSTEMS

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ABSTRACT

The results of both published and unpublished studies on benthic macroinvertebrate subsystems in North American Streams were analyzed to determine what, if any, fundamental features underlie the structure of various stream communities. Community composition was examined in streams of various types and sizes and located in each of the four major biomes in the United States; spatial and temporal conditions within a single stream also were considered.

Within the limits of the few suitable studies available, several suggestions were made concerning the structure of the benthic macroinvertebrate component. These are subject to modification or revision as further studies become available. But it is hoped that they will serve as a synthesis of existing information and a guide to future research.

1. There is a progressive increase in the total number of species with increase in the size of the streams. Depending on the size of the stream, the size of the species pool is somewhere between 65 and 300 species; of this, the insects account for between 70 and 90 percent.

2. Different types of streams (e.g., montane, lowland, etc.) have characteristic types of community structure.

3. Communities in streams from different biomes show certain characteristic differences in their make-up. On an interbiome basis there appears to be a relatively high degree of similarity between large streams of the Deciduous Forest biome and those of the Grassland, and, to a lesser extent, between streams of all sizes in the two forest biomes. There is a very low degree of similarity between Coniferous Forest streams and those of either the Desert or Grassland.

4. The structure of the community varies from place to place within a stream in terms of the populations represented, but apparently not in regards to the number of species (when similar biotopes are compared). The composition of the community also varies from season to season and even from month to month. In terms of specific populations this change is predictable but in terms of the number of species present it is not.

These findings indicate that the more alike two streams are in size, type, and local climate the more similar the structure of their communities will be. This suggests that community structure is environmentally controlled and that it may be possible to predict the community structure of a stream given the proper "inputs" or vice versa. As an initial step it is suggested that some measure of stream gradient and size, substrate type, mean and maximum summer temperature, and geographical location may provide sufficient input for predicting, within reasonable limits, the structure of the community.

COMMUNITY STRUCTURE IN NATURAL STREAM SYSTEMS

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ABSTRACT

The results of both published and unpublished studies on benthic macroinvertebrate subsystems in North American Streams were analyzed to determine what, if any, fundamental features underlie the structure of various stream communities. Community composition was examined in streams of various types and sizes and located in each of the four major biomes in the United States; spatial and temporal conditions within a single stream also were considered.

Within the limits of the few suitable studies available, several suggestions were made concerning the structure of the benthic macroinvertebrate component. These are subject to modification or revision as further studies become available. But it is hoped that they will serve as a synthesis of existing information and a guide to future research.

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COMMUNITY STRUCTURE OF SEMI-NATURAL STREAM SYSTEMS

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ABSTRACT

Most studies of semi-natural stream systems fall into one of two categories: studies of community metabolism or autecological studies relating the distribution of a species to some environmental factor. Examples of the study of natural or near-natural assemblages of organisms under the carefully controlled conditions permitted by a semi-natural system are quite rare. The papers of McIntire (1968) and of Brocksen, Davis and Warren (1968) are perhaps the best examples.

Apart from the biases built into a particular semi-natural system, I doubt if there are any substantive differences between the communities of natural and semi-natural systems. There are characteristics of the semi-natural stream systems reported in the literature which make them similar to a particular kind of natural stream. Most such systems are small in size; most have an autochthonous food base rather than an allochthonous one. The *raison d'etre* of a semi-natural system is to be able to reduce the number of environmental variables or to be able to manipulate environmental factors in a measurable or stepwise fashion. This should have the effect of reducing the diversity of the community relative to a natural system. By reducing the number of variables, it becomes possible to consider the response of species in a community to a simple complex of only a few environmental factors. McIntire considered the distribution of various algal species relative to time, light, and current. This could have been done by manipulating these factors and observing the response of individual species. However, it is well known that organisms respond differently within a community when forced to compete and interact with other species.

Description of Weyerhaeuser Experimental Streams

The study area covers about 2 hectares (5 acres) at an elevation of 1200 feet in the Cascades in southwestern Washington. Part of the water from a large constant-temperature (6°C) spring is diverted into a distributing pond and from there into each of three man-made stream beds. The volume of water flowing into each stream is 0.02 m^3/sec (0.75 cfs). The streams are all 1.2 m wide and range in length from 120 to 210 m. The substrate in the stream beds is homogeneous--small, smooth stones varying in size from 2 to 4 cm. The streams contain a number of riffles each separated from the other by a pool 3 m long. The riffles are alternately 8 and 15 m long. Beginning at the head, the streams have the same sequence, 8- and 15-meter riffles at 0.5%, 1.5% and 2.5% gradients. The seventh riffles is identical to the first, the eighth to the second, etc.

Description of Stream Community

To remove shading as a variable, the covering vegetation near all of the streams was removed. Consequently, primary production is very high. In the winter, the flora is dominated by several different species of moss; in the early spring, by Vaucheria sp.; and in the late spring and summer by Tribonema bombycina. The standing crop of algae varies considerably during the year with the highest values to be found between June and December. The seasonal curve of algal standing crop is very similar to that of solar radiation when one allows for a 2- to 3- month lag period.

The fauna is dominated by Baetis sp., Ephemerella spp., Nemoura spp., Rhyacophila spp., and several species of Chironomidae. The Chironomidae account for 80 to 85% of the total number of animals and 35 to 40% of the total biomass. The Trichoptera, Plecoptera and Ephemeroptera each account for about 20% of the total biomass. There are no Amphipoda and very few Mollusca in the streams. The mean total biomass is 14.1 g (wet)/m^2; the mean total number is 65,000/m^2.

Factors affecting the Spatial Distribution of Organisms

Only one variable was built into the experimental streams; the current velocity over the riffles may be 30, 42, or 53 cm/sec. Preliminary efforts at regression analysis demonstrate that most of the variation in the spatial distribution of individual populations can be explained by current velocity. Of the species which demonstrate a preference, the majority prefer the fastest current velocity. A few prefer the slowest, e.g., species of Simuliidae and Ostracoda, Paraleptophlebia spp., and Hydra sp.

There are other - biologically derived - factors which account for part of the variation in distribution. The Ephemeroptera, at a given current speed, tend to be found in greater numbers toward the foot of the stream. This appears to be due to the high rate of drift among the mayfly nymphs (ca. 8 times that of the stonefly nymphs or caddis larvae).

Due to the high rates of primary production, the concentrations of CO_2 and available nitrogen are much reduced as the water flows downstream. Consequently, the standing crop of algae is much greater at the head of the stream than at the foot. As a group, the only animal populations which consistently show a positive correlation to algal standing crop are those whose individuals have short life cycles (Chironomidae, Copepoda, etc.). A positive correlation is also apparent when comparing the temporal distribution of these multivoltine animals and algal standing crop. A few animals demonstrate a negative correlation to algal standing crop. Two of these, Hydra sp. and Simuliidae larvae, apparently cannot fare well when most of the attachment sites are occupied by filamentous algae.

Interspecific Relationships

The feeding habits of most of the invertebrate carnivores in the experimental streams have been studied. These fall into three major groups: the Rhyacophila, the setipalpian stoneflies, and certain Diptera (Tipulidae and Anthomyiidae). Many of these had considerable amounts of non-animal material in their guts and might best be characterized as omnivores. Of the three major categories of plant life in the streams: diatoms, filamentous algae, and vascular plants (particularly moss), all three were fed upon at significant levels but the diatoms were most often the dominant item.

Between 20% (Arcynopteryx curvata) and 80%(Rickera sorpta) of the diet of the setipalpian nymphs was of animal origin. A breakdown of the animal items in the diets of these nymphs showed that 85 to 95% of the animal portion of their diets was made up of chironomid larvae. These large percentages were due in part to the fact that chironomid larvae constituted 75 to 80% of the benthic fauna in the streams. However, the relative abundance of chironomids in the diets of these nymphs still exceeded the relative abundance of chironomids in the benthos.

Of the 7 species of Rhyacophila found in the experimental streams, 5 were carnivores (87 to 93% of their diets was of animal origin), 1 was an omnivore (36%), and 1 was a herbivore (2%) (Thut, 1969). Chironomidae larvae and pupae were, by far, the most important animal food source. Generally, 2 members of the microfauna, the Copepoda and Acari, were preyed upon in considerable numbers and in proportions in excess of their relative abundance in the benthos.

In the case of the Rhyacophila, the earlier stages of some species had somewhat different food preferences than did the later stages. The small early stages tended to feed more heavily on the microfauna (Copepoda and Acari). In the case of the setipalpian stoneflies, which fed almost entirely on chironomid larvae, the smaller nymphs fed upon smaller chironomid larvae.

The 6 common species of Rhyacophila in the streams demonstrated considerable diversity in their feeding habits. The feeding habits were sufficiently unlike one another that direct competition for food resources would not be expected between most species. Most species seemed to specialize (on microfauna, Chironomidae, diatoms, vascular plants, or detritus) to the extent that if food were limiting, several species of Rhyacophila could still be accommodated.

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ABSTRACT

Actions of the abiotic environment and coactions between biotic components result in a characteristic assemblage of organisms. This complex in individuals belonging to the different species in a community can be referred to as community diversity. Typically, in temperate zone communities a relatively small number of species are common and a large number of species are rare.

Data concerning community diversity of benthic macroinvertebrates has been summarized by a variety of graphic and mathematical methods. Graphic methods have included pie, bar, and line graphs. Graphic analyses are usually more difficult to prepare and may make spatial and temporal comparisons within and among communities difficult. One of the simplest and most promising mathematical methods of analysis is the diversity index. Diversity indices permit summarization of large amounts of information about numbers and kinds of organisms in a single number. A number of diversity indices have been proposed for describing the relationship between numbers of individuals and species in a community. Analysis of diversity in different communities with different models precludes comparisons among communities. Margalef (1956) proposed analysis of mixed-species populations by methods derived from information theory. Total numbers of organisms (n), number of individuals per taxon (n_i), and number of taxa (s) in the community are estimated from samples and used to estimate diversity (d) in the following expression (Patten 1962):

$$\bar{d} = - \Sigma(n_i/n) \log_2 (n_i/n)$$

The index $\bar{d}$ possesses features which makes it a useful index to summarize community diversity. The index is dimensionless and numbers, biomass units, or caloric values in any units can be used as basic data in the equation (Wilhm, 1968). The relative importance of each species collected is expressed and not merely the relationship between total numbers of species and individuals (Wilhm and Dorris, 1968). The most important requisite of a diversity index is independence of sample size. Pielou (1966) demonstrated with plant material that as sample size is progressively increased by adding new quadrats, the diversity, $\bar{d}$, of the pooled sample increases and then levels off. The leveling off of $\bar{d}$ with benthic macroinvertebrate samples was demonstrated by Wilhm (1969). Values of diversity are more difficult to obtain when using $\bar{d}$ than when using other diversity models; however, values can be obtained quickly with a computer program of only 26 steps.

The range of $\bar{d}$ varies from zero to any positive number. A value of zero is obtained when all individuals belong to the same species. The maximum value of $\bar{d}$ depends on the number of individuals counted and is obtained when all individuals belong to a different species (Table 1).

Table 1. Maximum possible values of $\bar{d}$ at different sample sizes.

Number of individuals	Maximum $\bar{d}$
100	6.64
200	7.64
400	8.64
600	9.23
800	9.64
1000	9.96
2000	10.96

A similar diversity pattern exists in benthic macroinvertebrate communities in clean water areas. Values of diversity obtained in a number of studies in unpolluted streams or in recovered areas in streams receiving pollutants is shown in Table 2. These samples were taken in a number of different areas, with a variety of sampling devices, and at different times. The samples produced from 104 to 2169 individuals and from 11 to 54 species. Despite this variability and the fact that $\bar{d}$ can vary from zero to around nine, the range of diversity was quite small. $\bar{d}$ at most stations was between three and four.

The diversity pattern is altered if pollutants are added to the stream. Values of diversity obtained in streams receiving various pollutants are shown in Table 3. Diversity of the benthic macroinvertebrate community in most cases was less than one.

In summary, a wide variety of methods exist for collecting, summarizing, and reporting data on diversity of benthic macroinvertebrates. This often precludes comparisons between studies. The collection of an adequate sample size and the summarization of data with $\bar{d}$ enables comparisons among different studies of benthic macroinvertebrate communities.

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Table 2. Data on benthic macroinvertebrate populations collected at stations in clean water streams or at recovered stations in streams receiving pollution effluents.

Source	Stream	State	Type of Sampler	Time	No. of individuals	No. of species	$\bar{d}$
Bingham (1968)	Dolores R.	Colorado	Surber	August	146	11	2.81
"	Roaring Fork	Colorado	Surber	April	117	14	2.98
"	Gunnison R.	Colorado	Surber	July	605	30	3.48
"	Castle Cr.	Colorado	Surber	April	236	29	4.00
Dambach and Olive (1969)	Olentangy R.	Ohio	Ekman	Summer	1431	38	3.91
"	Whetstone Cr.	Ohio	Ekman	Summer	221	24	3.16
Wheeling Field Station (1968)	Allegheny R.	Ohio	Artificial	Summer	104	11	2.68
"	Kanawha R.	Ohio	Artificial	Summer	163	16	3.10
Fetterolf et al. (1965)	Thunder Bay R.	Michigan	Peterson	September	128	19	3.38
Tackett (1965)	Tinker Cr.	Virginia	Surber	Fall	426	19	3.15
"	Roanoke R.	Virginia	Surber	Fall	258	16	3.01
Tackett (1963a)	N. Fork Clinch R.	Virginia	Surber	November	422	19	3.48
"	S. Fork Clinch R.	Virginia	Surber	November	711	23	3.34
"	Clinch R.	Virginia	Surber	November	529	23	3.62
Tackett (1963b)	N. Fork Shenandoah	Virginia	Surber	October	549	19	3.00
"	S. Fork Shenandoah	Virginia	Surber	October	1320	28	2.60
Mathis (1968)	Little Stony Cr.	Virginia	Surber	Summer	679	39	3.71
"	Little Stony Cr.	Virginia	Surber	Summer	1660	54	4.61

Table 2. (Cont.)

Source	Stream	State	Type of Sampler	Time	No. of individuals	No. of species	$\bar{d}$
Georgia Water Quality Control Board (1967)	South R.	Georgia	Sieves	May	211	14	2.63
"	Flint	Georgia	Sieves	May	204	29	3.42
Harrel and Dorris (1968)	Otter Cr.	Oklahoma	Ekman	Annual	2169	46	3.36
Wilhm and Dorris (1966)	Skeleton Cr.	Oklahoma	Surber	Fall	236	19	3.50

Table 3. Values of $\bar{d}$ of benthic macroinvertebrates collected at stations in streams receiving pollution effluents.

Source	Stream	State	Pollutant	$\bar{d}$
Wheeling Field Station (1967)	Tuscarawas R.	Ohio	Chlorides	0.42
"	Black Fork	Ohio	Acid	0.49
"	Wills Cr.	Ohio	Acid	0.49
"	Conottom Cr.	Ohio	Domestic	0.75
Dambach and Olive (1969)	Olentangy R.	Ohio	Domestic	0.59
"	Whetstone Dr.	Ohio	Oil	1.18
"	West Branch	Ohio	Coal	0.87
Tackett (1965)	Roanoke R.	Virginia	Wood	1.32
"	Roanoke R.	Virginia	Oil	1.01
"	Tinker Cr.	Virginia	Mining	0.76
Tackett (1963a)	Clinch R.	Virginia	Domestic	0.53
Tackett (1963b)	South R.	Virginia	Plating	1.25
"	South R.	Virginia	Fiber	1.42
"	Shenandoah R.	Virginia	Pharmaceutical	1.60
Georgia Water Quality Control Board (1967)	South R.	Georgia	Domestic	1.02
"	Flint R.	Georgia	Industrial	1.54
FWPCA (1966)	Arkansas R.	Oklahoma	Oil	0.99
"	Pole Cat Cr.	Oklahoma	Domestic	0.69
"	Bird Cr.	Oklahoma	Domestic	0.78
Harrel and Dorris (1968)	Otter Cr.	Oklahoma	Brines	1.37
Wilhm and Dorris (1966)	Skeleton Cr.	Oklahoma	Oil, domestic	0.84

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THE STREAM ECOSYSTEM: TERRESTRIAL-LOTIC COMMUNITY INTERACTIONS[1]

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ABSTRACT

The input of organic and inorganic materials to streams arises on the landscape and it is largely the events in the terrestrial environment that determine what materials streams receive. These losses from the landscape are a relatively insignificant quantity of material as far as the terrestrial environment is concerned and are treated by terrestrial ecologists as such. However, the organic and inorganic materials represent a tremendous resource to the aquatic environment. On a long term basis the loss of these materials represents the gradual lowering of land masses by erosional processes. Over short time periods the inorganic material determines water quality and represents a nutrient material for autotrophic organisms. The organic matter is the primary food source for heterotrophic organisms and most streams behave as heterotrophic communities (Hynes 1963). In this brief discussion I wish to review sources of materials carried in streams, the effect of geologic type, time dependency of inputs to streams, and the movement of some specific ions into water courses.

A convenient starting point for discussion of inputs is the graded stream concept. This concept has been used in developing theories of stream succession (Nelson and Scott 1962; Minckley 1963; Minshall 1967). The effect of physiographic region is important because streams grow by headward erosion and according to theory will eventually produce a peneplained land surface. Only when a stream reaches the so-called base level will it come into equilibrium with the surrounding landscape. The input and output of streams is essentially in equilibrium over short time periods because streams have limited capacity to store materials in their beds and usually do not have the capability of daming themselves. Thus, the stream load at any one time is very closely correlated with events on the landscape, particularly with respect to the addition of water, sediment, organic matter and dissolved materials.

The stream load consists of dissolved and particulate materials carried in the flowing water which is the vehicle by which the substances are moved from the landscape. Rates of transport of materials from landscapes to the oceans have received considerable attention because of geochemical interest in rates of chemical denudation. Modern work started with Clarke's estimate in 1924 and the estimate has been refined in various ways since then. More recent estimates include those of Durum, Heidel and Tison (1960) and Livingston (1963). The mainstem rivers are considered integrative in that their chemical content reflects inputs from various physiographic regions.

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Stream biologists are particularly interested in allochthonous and autochthonous organic materials and these may even be of importance in lakes (McConnell 1968). The origin of organic matter is of considerable importance because organic matter of different origins can be distinguished and separated. Further, the source of the organic matter has an important effect on functional aspects of streams, particularly with respect to oxygen balance and energy sources for consumer organisms. Since most streams behave as heterotrophic systems, more organic matter is oxidized or consumed than is produced. Odum (1956) pointed out the significance of oxygen balance in aquatic habitats and suggested that it may be an indicator of a steady state condition or a climax community.

Inorganic matter can come from the stream bed itself, from ground water, or from erosional processes on the landscape. In actual practice I suspect that the dissolved inorganic materials are determined as the percolating ground water moves vertically and then laterally through the soil profile. By the time ground water enters a stream its chemical quality has been established. Particulate inorganic materials are derived from the stream bed during normal discharges and during storm events come from the landscape as well as the stream bed. From the functional standpoint with respect to the mineral nutrition of aquatic organisms, it does not matter where these inorganic materials originated. This is not to deny that it would not be of interest to know where a particular atom of a chemical element comes from, but from a realistic standpoint I do not think we have the capability of distinguishing the sources of these atoms. Thus, the source of the organic matter is of biological significance for processes within the stream but we cannot claim this same significance for inorganic matter.

Miller (1961) studied solutes in small streams draining single rock types in New Mexico. It should be emphasized that the areas he studied were essentially devoid of human activities although cattle and sheep grazed most of the area. Rock types included quartzite, granite and sandstone. One of his major conclusions was that water quality of a stream was rather uniform regardless of the size of the drainage basin. This again suggests that water quality is determined on the landscape and not in the water course. The areas studied by Miller varied in rainfall, elevation, soil, vegetation and hydrology. The constancy of water quality originating from different geologic types indicated that weathering mechanisms were relatively constant regardless of the other environmental factors. When Hynes (1969) referred to increases in dissolved solids in a downstream direction, he was referring to rivers under the influence of cultural activities and consequently pollution. We know that human activities are an important factor in determining the dissolved solid load in surface streams.

Different parent materials result in different basic chemical compositions of streams draining watersheds. In Miller's studies the quartzite was most resistant followed by granite and sandstone. However, in the case of sandstone most of the solute content of the water was derived from a carbonate cement and thin limestone which contributed less than one percent to the total parent material. In current studies of dissolved element content of water draining experimental watersheds we also see some sharp contrasts depending upon rock type. The Hubbard Brook (Thornton, N. H.) and Coweeta (Franklin, N. C.) watersheds have relatively soft water. In fact most of the streams draining Coweeta watershed have a Ca content of less than 1 ppm. These watersheds are located on crystalline rocks. The Walker Branch watershed at Oak Ridge, Tennessee, is located on dolomitic limestone and the calcium content varies somewhat with rainfall but usually is within the range of 20 to 30 ppm.

Research on rivers relating stream load to stream discharge is particularly pertinent with respect to instantaneous inputs of material to surface waters from the surrounding watershed. Leopold and Maddock (1953) studied an extensive series of load-discharge relationships and concluded that the best mathematical model relating these parameters was usually of the type $Y = aX^b$ where Y is load and X is stream discharge. When the slope, b, equals one, the relationship is actually arithmetic. Slopes of one are characteristic of streams where each added increment of discharge is accompanied by an equivalent increment of load. This condition is typical of very well-regulated landscapes such as heavily vegetated watersheds. The Hubbard Brook watershed responds in this way to dissolved cations (Likens, et al., 1967). Slopes greater than one are characteristic of stream load-discharge relationships during periods of heavy rainfall when surface runoff occurs. Surface runoff occurs either as gulley-type or sheet erosion. In either case high water velocities pick up a large load. Suspended sediment and orgnnic debris accrue to the stream at a rate greater than the accrual of water. Slopes less than one are typical of situations where there is a dilution of materials in the stream by incoming water. Nelson (1970) suggested that the slope of the regression of particulate organic matter on stream discharge could be used as an indicator of the relationship between autochthonous production and allochthonous organic matter in streams.

The time dependency of inputs to streams is an important characteristic and is closely correlated with rainfall. While there are seasonal effects, the most striking changes occur during storm flows. Storm flows account for a large proportion of the particulate material carried in streams. The proportion of stream load carried in storm events varies with the watershed and type of stream but data from several rivers shows that 50% of the annual load may be carried in from 4 to 95 days (Leopold, et al. 1964). The watersheds with better vegetative cover required more days to attain the 50% value. Kennedy (1963) studied the Broad River, Georgia, in some considerable detail. In this case 90% of the annual load was discharged in 20% of the year and 50% of the load was carried within 2% of the year. These relationships were obtained during conditions of normal high discharge and not during catastrophic events. The uneven addition of materials to a stream from a watershed is of importance for subsequent processes in the stream such as temporary storage, and downstream transport.

The relationship between stream discharge and P and N additions to water were discussed recently by Biggar and Corey (1969). The comparative movement of these nutrient elements is dependent on whether they are included in surface runoff or whether they percolate through the soil profile to enter ground water. Nitrogen forms such as NO_3 and NH_4 are quite soluble. When rain first falls, the nitrogen compounds on the soil surface are dissolved and carried into the soil. Runoff which occurs later encounters very little available N and as a result, runoff waters contain little soluble N. Measurements show that runoff waters have less nitrogen than the initial rainfall which also includes NO_3 scavenged from the atmosphere. Nitrates which enter the ground water, move with it in true solution. In the soil the N compounds are subject to assimilation by plants but otherwise N compounds move into surface streams.

The behavior of P is different, primarily because of chemical reactions in soil to form poorly soluble compounds. Inorganic P occurs as calcium phosphate in alkaline soils and as iron and aluminum phosphate in acidic soils. Phosphorus applied to the surface of soil saturates available sites and the concentration of PO_4 in the soil solution will tend to rise. An equilibrium situation will develop and runoff water can carry the equilibrium concentration of P. Phosphorus that enters percolating ground water becomes adsorbed. Comparative values show the phosphates in ground water are in the neighborhood of 10 ppb on undisturbed areas. Runoff water may contain as much as one ppm or slightly more.

These relationships between N and P content of the Palouse River water were observed by Buscemi (1969) who studied changes in the elemental composition of river water as a function of rainfall and snow melt. He also noted that Fe and Mn behaved much the same as P in that minimum elemental concentrations occurred during peak runoff periods.

We can expect the input of Ca and Mg into streams to be dependent on CO_2 in the soil profile because these elements will move in solution as bicarbonates. The CO_2 is derived from decaying organic matter and respiration of plant roots. This is one of the direct but subtle interrelationships between aquatic and terrestrial environments. Streams are passive with respect to the materials they carry and the importance of terrestrial and meteorological processes to stream inputs is quite apparent.

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DETRITAL CONSUMERS IN NATURAL SYSTEMS

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ABSTRACT

The importance of plant detritus as an energy substrate for aquatic organisms is widely documented in both published and non published studies. The role of detritus in nutrition was recognized largely by analysis of the stomach contents of a broad spectrum of aquatic invertebrates and fish. The accumulation of recent evidence suggests that in woodland streams, the allochthonous detritus input may support up to two-thirds of the annual energy requirements of primary consumer organisms. Evidence also presented cites the importance of fungi and bacteria in conditioning detritus prior to consumption by stream invertebrates.

Our recent studies have been directed towards quantitative evaluation of the input-output and the utilization of allochthonous detritus by stream invertebrates and microflora. Deciduous leaf input to study streams was a function of forest canopy density, gradient of adjacent stream-side slopes, and the duration of snow cover on the forest floor. Following the large detrital input during the autumn leaf shed period, wind was an important transport mechanism translocating leaf litter from the forest floor to the stream system. High gradient streams with steep slopes had the largest leaf input and retention. The gravitational effect was apparently important in the downhill movement of wind blown leaf litter on steep slopes. On an annual basis leaf input ranged between 200 to 800 $g/m^2/yr$ (dry weight) on three study streams located in SE Pennsylvania.

The resident time, and subsequently the degree of biotic utilization of deciduous leaf accumulations in streams varied widely in different streams and in different years. Detention time was related to stream gradient, the frequency and intensity of fall and winter rains, and the number of riffles or other entrapment features in the stream.

Initial studies were conducted to quantify the rate of insect colonization in recently formed leaf packs and to determine the progressive changes in community structure, biomass, and growth rates throughout the winter and spring months. The study involved sampling both naturally occurring leaf pack accumulations and specially constructed leaf packs. Constructed leaf packs were sewn together loosely with monofilament, weighed about 25 grams, and were tethered in rocky riffles. We placed 120 artificially constructed leaf packs in riffles in order to study the colonization rate and subsequent changes in community structure.

Three functionally active groups of insects invaded leaf packs. The groups recognized were (1) species feeding directly upon deciduous leaves, (2) species feeding on microdetrital particles entrapped between layers of leaves, and (3) predator insects. Genera in the first group included Tipula, Peltoperla,

Pteronarcys, and Limnephilus. Micro-detrital grazers included Ephemerella, Paraleptophlebia, Taeniopteryx, Isonychia, and midge larvae. The principal predator genera were Acroneuria, Phasganophora, and Isoperla nymphs.

Early instar Ephemerella dorothea and E. deficiens nymphs invaded leaf packs within a few hours of formation. Population densities peaked by mid winter at about 600 nymphs per 25 gram leaf pack. The nymphs, feeding upon micro-detrital particles, grew at a constant exponential rate from the time of initial invasion until emergence in late spring. Leaf packs were effective water filtering structures. A 25 gram leaf pack accumulated approximately 8 to 10 grams ash free dry weight of organic detritus in a size range less than 500 microns diameter. The micro-detrital component consisted largely of diatoms and fecal material of detritus feeding insects. Mid winter invasion of leaf packs by predator insects rapidly reduced the density of Ephemerella nymphs to about 10 to 20 nymphs per 25 grams leaf pack by late winter.

Species of insects which fed directly upon deciduous leaves generally entered leaf packs at the time of formation. Leaf consuming species had definite feeding preferences and actively consumed preferred leaf species before changing to less preferred diet items. The feeding preferences were highly predictable and growth rates were directly correlated to the order of feeding preference. The growth rates of insects with strong feeding preferences were dependent upon population densities within leaf packs. The composition of the contemporary forests in the region studied (American beech - northern red oak) was judged not to be optimum for the feeding preferences of detritus consumers.

Table 1 presents the annual energy budget for the cranefly larva Tipula abdominalis when reared on a diet of mixed species of deciduous leaves. The calorific content of the diet ration was 4655 cal/g dry weight.

Table 1. Average annual energy budget for Tipula abdominalis larvae reared on mixed species ration of deciduous leaves. Values are g cal/larva /yr.

	Male	Female
Ingestion	5339	9803
Assimilation	1764	3235
Growth	400	735
Egestion	3575	6568

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PRODUCTION IN NATURAL STREAM SYSTEMS

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ABSTRACT

The trophic structure of streams consists essentially of three trophic levels: periphytic algae and other attached or rooted plants as primary producers, invertebrates such as insects and crustaceans as the primary consumers, and fishes as secondary consumers. A fourth level may be said to exist if carnivorous invertebrates are present and constitute the third level, while fish make up the fourth.

Although several estimates of primary production rate have been made in certain types of streams, no generally applicable method appears to be available; allochthonous leaf detritus accounts largely for the primary organic matter in many, if not most, streams. On the other hand, good methods for the estimation of fish production rate have been developed and have been applied most successfully to salmonid populations (Ricker, 1946; Allen, 1949, 1951; others).

The mathematical and graphical methods of Ricker and Allen, developed for fish, are of course valid for any organism (including plants: Mathews and Westlake, 1969) when the necessary input data can be obtained. The methods can thus be applied to invertebrates in certain cases (Neess and Dugdale, 1959; Waters, 1966). In the mathematical method, the mean standing crop and the instantaneous growth rate are required; in the graphical method, periodic measurement of the mean individual weight and density in numbers for a discrete cohort are required. These required data may be obtained in the field for some stream insects, particularly those with short emergence periods and non-overlapping generations, but probably not for most stream invertebrates.

A third method for invertebrates, termed here a "removal-summation" procedure, is included in both the earliest and most recent attempts to estimate production rate. Essentially, the method involves summing the weight of all the organisms that die or are otherwise removed; for a given complete cohort, this sum is equal to the cohort's production. Additionally, it may be used for any population over a given period of time if the change in standing crop is also taken into account. The "removal-summation" method may be used in two ways: (1) summing successive losses as determined by a series of standing crop measurements (Anderson and Hooper, 1956; Hynes and Coleman, 1968); and (2) summing independent estimates of various forms of removal (such as predation, emergence, drift, etc.) from a given area (Borutsky, 1939; Waters, 1962).

Current work at the University of Minnesota is concentrating on the attempt to estimate production rate of the stream amphipod, Gammarus pseudolimnaeus. This species was selected because of its quantitative significance in many streams of the upper Mississippi River region, particularly in some of the more productive trout streams. Furthermore, other species of Gammarus are similarly

important in streams of other regions. Available methods are not readily applicable to an amphipod, because it does not occur in discrete cohorts, nor can growth rates be determined effectively from field sampling. Essentially, the approach being used is that of the mathematical method, obtaining standing crops from field bottom samples and growth rates from laboratory cultures with partial confirmation from the field data.

The life cycle of G. pseudolimnaeus includes two major periods of reproduction: early spring and mid-summer. Those hatched in early spring (at just under 2 mm in length and 0.2 mg in weight) reach maturity in about three months (7 mm in length, 6 mg in weight) and constitute the main breeding population for the mid-summer period. Those hatching in mid-summer overwinter to provide the main breeding population for the following spring. Maximum length of life is about one year, at about a length of 18 mm and a weight of 60 mg. From this information, and a series of size frequency diagrams constructed from field samples, instantaneous growth rates may be approximated for certain periods of the year and certain size groups.

Laboratory cultures include a series of flowing-water aquaria in which daily temperature cycles and photoperiods are produced similar to those obtaining in the field; food is provided in the form of leaves taken from the actual field area. Replicated cultures are set up for three size groups: young (2 to 7 mm), mature (7 to 11 mm), and old (11 to 18 mm), and growth rates are determined separately for each size group by periodic measurements.

Data being obtained from the field are also suitable for analysis by the Hynes-Coleman procedure (modified by Hamilton 1969) to obtain additional production rate estimates for comparison.

Drift rates of G. pseudolimnaeus are also being measured periodically, with the hope of elucidating the possible relation between production and drift rates. The field procedure includes a new "drift-block" technique to estimate production rates, to be used for comparison with the estimates obtained from the other methods; the technique is a modification of the "removal-summation" procedure.

Calculation of the annual turnover ratio (i.e., ratio of annual production to mean standing crop) ultimately will be possible, leading hopefully to increased precision in knowledge of general levels of turnover ratios.

Estimate of fish production rate are concurrently being made in the study stream, using the Allen curve method; since G. pseudolimnaeus constitutes by far the major portion of the fish diet, comparison of the production rate of the two trophic levels may provide approximations of the ecotrophic coefficient.

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MINERAL CYCLING IN SEMI-NATURAL SYSTEMS[1]

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ABSTRACT

Emphasis on mineral cycling in aquatic ecosystems generally has been focused on the elements, C, P, and N. This is because carbonaceous material is the end product of photosynthesis, and phosphorus and nitrogen are usually regarded as the elements most likely to limit algal growth. Production of organic matter by photosynthesis and subsequent elaboration of new tissue and organisms also involves incorporation of other elements; hence, mineral cycling proceeds with production.

Two developments which have contributed to a relatively recent increase in our knowledge of cycling in lotic systems are (1) the development of workable semi-natural microcosms which adequately reproduce natural systems while lending themselves more readily to manipulation and analysis, and (2) the availability of a wealth of radionuclides with which investigators can more easily trace the movement of extremely small amounts of various elements through aquatic food-webs. Simulated lotic ecosystems described in the literature can be broadly grouped into those developed to study community metabolism, including productivity and specific mineral cycling, and those used to investigate organism-substrate relationships. This paper deals with the cycling of specific radioactive minerals in artificial lotic ecosystems.

Garder and Skulberg (1966) studied the accumulation of several radionuclides in the biotic and abiotic media of an experimental stream in Norway. As expected, there were gross differences in amounts and specificity of uptake by the various components of the ecosystem. Watts and Harvey (1963), Harvey and Patrick (1967), and Harvey (1969) utilized a continuous flow system to investigate the uptake and retention rates of several radionuclides by algae. They related uptake rates to different ambient concentration, temperature, and community morphology. Whitford and Schumacher (1961) established the presence of an "inherent current demand" in lotic algae using phosphorus-32.

Recent work in our laboratory, using the lotic microcosm described by Cushing and Porter (1969), has revealed several facets of the cycling of zinc-65 by natural periphyton communities.[2] Experiments with a recirculating water system have shown that zinc-65 uptake is mainly adsorptive since uptake is

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[2] In cooperation with Dr. F. L. Rose, Idaho State Univ., during his appointment on an AEC Post-doctoral Fellowship at Battelle-Northwest. A full account of these studies is under preparation for publication.

essentially the same for living communities in continuous light or darkness, or for killed communities. A 12-hour photoperiod produces alternating periods of uptake and loss most likely related to pH changes at the cell surfaces. Zinc-65 uptake is directly related to the ambient zinc-65 concentration and emphasizes the importance of controlling the ambient concentration in these types of studies, especially when reporting concentration factors (radioactivity in algae/radioactivity in water). Experiments using varying concentrations of stable cations (Zn and Mg) with identical zinc-65 concentrations illustrated the competition for binding sites among the different elements. Increasing stable cation concentrations proportionally reduced the uptake of zinc-65. Experiments with a one-pass water system, where ambient zinc-65 concentration is constant, have revealed a much different pattern of uptake from the closed system. No indication of approaching equilibria is seen in the one-pass system, during comparable time periods, although it is apparent in the closed system where it is undoubtedly related to the decreasing ambient zinc-65 concentration.

In summary, our work has shown that (1) closed system "equilibria" are related to physico-chemical changes as the ambient zinc-65 concentration decreases and, perhaps, metabolic by-products interfere, (2) zinc-65 uptake is predominately adsorptive in nature with direct competition for binding sites with other divalent cations, and (3) caution is advised in using and interpreting concentration factors, a widely used and mis-used term in the literature.

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* Denotes papers applicable to radionuclide cycling studies in semi-natural lotic systems. This is a partial bibliography and no attempt was made to list all papers describing various continuous flow culture devices.

ENERGY BUDGETS[1]

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ABSTRACT

Introduction

Assuming that the functioning of ecosystems can best be described in terms of energy flow and nutrient cycling, it is prediction and manipulation relative to these two functional aspects which holds the greatest promise in the area of ecosystem management. Energy budgets for ecosystems--that is, how much energy is required per unit time to operate a system and how is the energy apportioned between the various components--can be prepared by summation of data at the level of populations. Such assessments seem more useful than monitoring total energy flow, e. g. light income = heat output. Even though our apparent goal is the management of ecosystems, there will probably be no instances in which this will be of interest independent of manipulations of specific populations within the system.

The energy flow diagram shown in Fig. 1 illustrates some of the summations and rate functions to be determined in estimating a budget at the ecosystem level. The model shown is for a semi-controlled stream, but the essentials of the macroconsumer portions would be the same for all natural lotic systems. The herbivore, detritivore and carnivore categories shown in Fig. 1 would be calculated by summation of all populations (or portions of populations - see below) fitting each of the three designations. Fig. 2 represents a budget for a natural population of a benthic stream macroconsumer. Both the summation of energy expenditures in various "compartments" and the transfer rates between components are depicted.

Investigators which have produced energy budgets for invertebrate macroconsumers (e.g. Richman, 1958; Kuenzler, 1961; Phillipson, 1963; Comita, 1964; Woodland *et al*., 1968; Cummins *et al*., 1969) have not dealt with lotic organisms except for the work of Trama (1957).

Methods for Determining Energy Budgets for Lotic Macroconsumers

Since population energy budget determinations require the processing of extensive amounts of diverse data and a great many populations must be analyzed before a useful budget estimate at the system level can be obtained, automation

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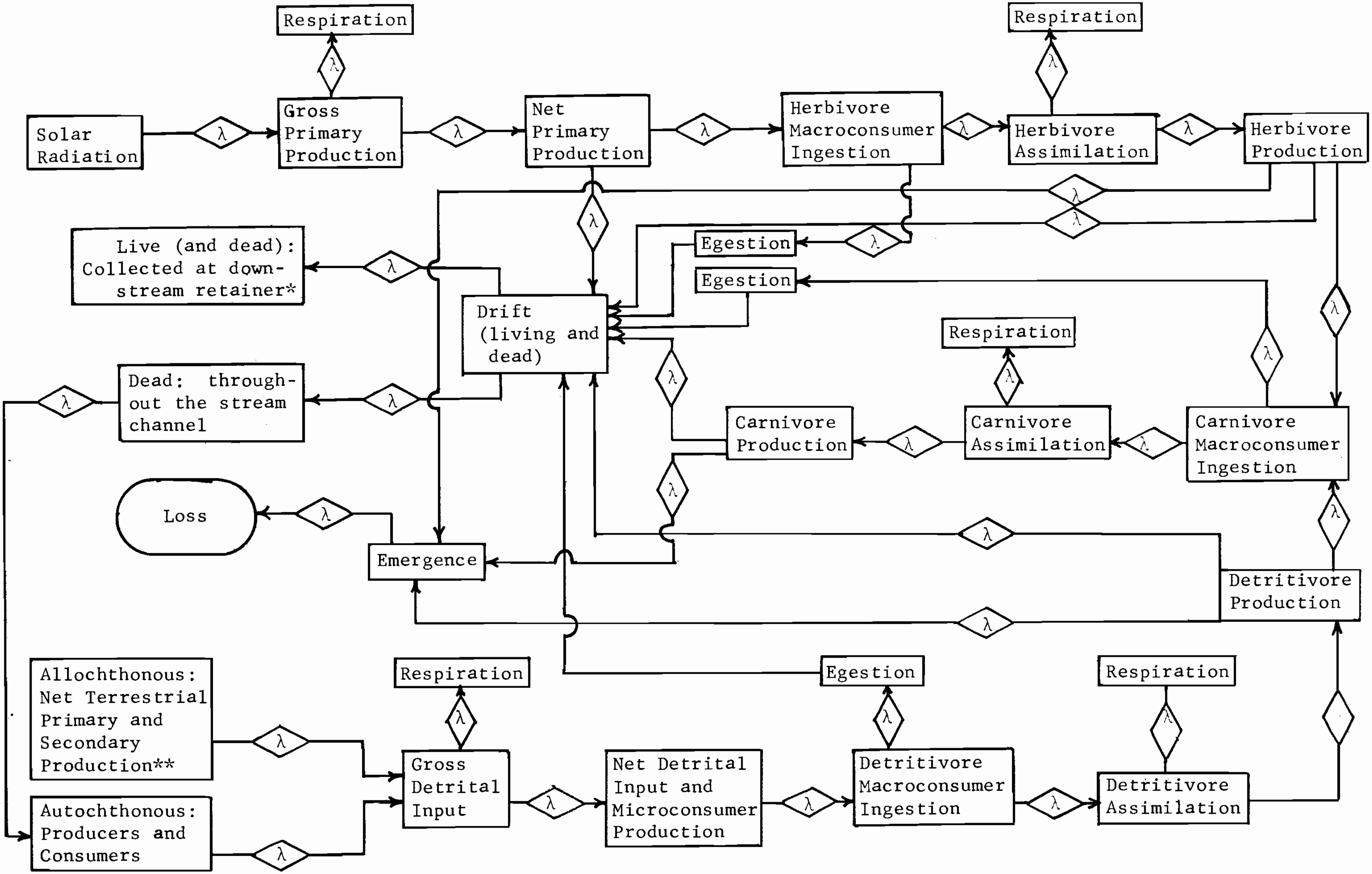


Fig..1. Components of an annual energy budget for a semi-controlled stream ecosystem. The symbol λ stands for transfer rates. *Retainer contents reintroduced at upstream position on a regular schelude. **Added to system in known amounts.

of data gathering and analysis is critical. We are attempting to establish a standard processing package for determining such energy budgets, as summarized in Fig. 3. The aim is to obtain data output in the form of punch tape which can be processed by computer terminal utilizing standard routines kept on file. Reduced handling of the data and computer manipulation not only increases the volume of data that can be processed, but significantly reduces errors. Particularly useful are subroutines that sort out aberrant pieces of data which violate previously set limits.

Ingestion and Egestion

In order to determine instantaneous ingestion, representatives of each size class of a given species are dissected and the gut contents concentrated on Millipore filters for counting. Enumeration is in three categories, algae, detritus (including the microbial biota) and animals. The final result is an estimate, on a per individual basis, of the calorie content of the algal, detrital and animal components of the food in the gut.

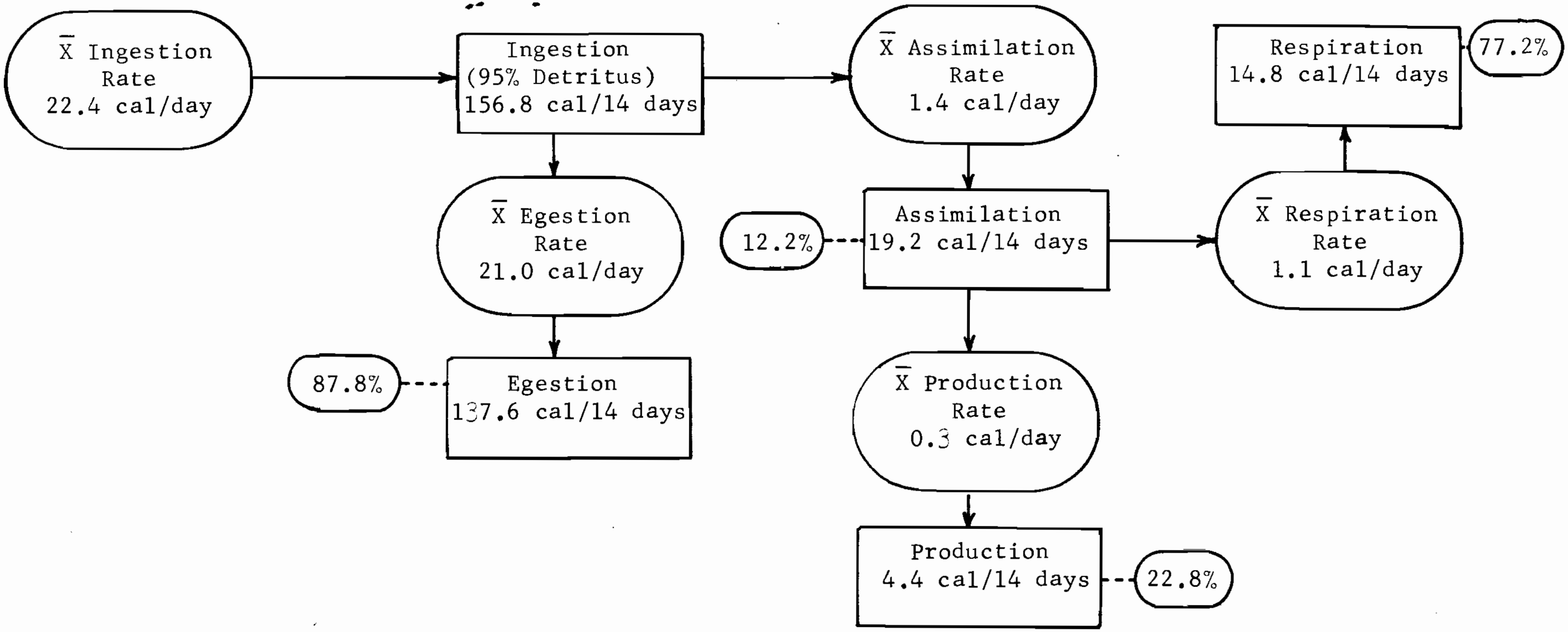
Based on these relative caloric ingestion of the three food categories, portions of the standing crop of each age class of a given species are assigned to herbivore, detritivore and carnivore trophic categories. Thus, organisms are placed in trophic categories on the basis of tissue support.

In addition to the tracer methods discussed below, ingestion and egestion rates are determined in the laboratory under controlled temperature conditions and with known diets. Leaf detritus from the stream (including the microflora) cut into discs with a cork borer, dried and preweighed, attached algae grown on preweighed cover slips and preweighed pellets made from prey species can be used as food material. Weight loss of food, weight gain of feeding animals and weight of feces produced, all per unit time, are measured directly. Collection of fecal pellets is particularly easy for species which produce a peritrophic membrane.

Assimilation (Tissue Incorporation)

The measurement of tissue incorporation using carbon-14 as a tag must take into account the nutritional history of the feeding organism and the biochemical composition of the food. In the normally functioning stream macroinvertebrate, assimilated products of carbohydrate digestion are probably utilized rapidly for respiration (maintenance cost), where as fatty acids and glycerol from lipids, and amino acids from proteins are probably incorporated more permanently. That is, fat bodies and structural protein would result from anabolic processes, the energy expenditure of which is part of the maintenance cost. Animals which have been starved before the initiation of the experiment would be expected to behave differently with respect to incorporation and respiration of carbohydrate, fats and proteins.

Regardless of the method the intent is to measure the rate at which material entering the anterior end of the "plumbing" becomes incorporated into the tissues, or the assimilation rate as calories per time, and the efficiency of this incorporation per unit of ingested material. The latter allows for the conversion of ingestion data to an assimilation base. This is particularly important since



Stable Age Distribution

Sample	Age Class (%) 1	2	3	4	5	Prepupae	Pupae	Total Number of animals measured
7/23/69	0	0.56	5.08	14.40	27.68	24.29	27.96	354
8/6/69	0	1.17	8.23	14.11	27.12	23.50	27.05	85

Fig. 2. Components of an energy budget for a benthic stream macroinvertebrate, *Glossosoma nigrior* (Trichoptera)

various food substances are undoubtedly assimilated with different per unit weight efficiencies.

Respiration (Maintenance Cost)

Maintenance cost for the population is estimated by gathering age and temperature specific data on individuals in the laboratory (e.g. with a Gilson differential respirometer) and projecting it to the entire population under a given set of conditions. Unfortunately, the literature is saturated with oxygen consumption values that are essentially useless to ecologists; they represent animals under stress conditions. It is probably accurate to assume that at any given temperature, unless the animals are dying, the lowest oxygen consumption value measured is the best representation of the natural condition. The age and nutritional state of the animals, the substrate available, water movement and light conditions are among the more important factors to be considered., all of which bear on the locomotory behavior of the organism.

Also, it is of little use for energy budget determinations to measure respiration rates at temperatures to which the organisms are never naturally exposed. Evidence is accumulating that many freshwater invertebrates exhibit maintenance cost plateaus. That is, over the range of temperatures normally encountered, the energetic cost to the organism is essentially constant.

Production (Growth and Reproduction)

The problem of production has already been discussed as part of this symposium. Suffice it to say that there are several ways of estimating biomass increments through time. Certainly of critical importance is the adjustment of the population census schedule so that it is equal to or less than the biomass turnover time. Our approach has been to determine numerical shifts in population age structure and utilize age-specific mean weights per individual in estimating production.

There are two components of production to determine: 1) the weight gain per individual between time 1 and time 2 multiplied by the number of individuals surviving to time 2 and, 2) the weight gain made by individuals not surviving the entire time 1 to time 2 interval. With regard to the second component, if all individuals are lost the instant following the initial census at time 1 the production to be added to the estimate, obtained as the first component, is zero. If all individuals are lost the instant before the census at time 2, the additional production would be the weight gain per individual over the period multiplied by the number of individuals lost (i.e. the number per unit area at time 1 minus the number per unit area at time 2). Actually, the loss is undoubtedly spread over the time interval, so that some median point may serve as a reasonable estimate. Thus production might be calculated as follows:

N_1 = number/unit area at time 1*
N_2 = number/unit area at time 2*
wt = weight gain/individual from time 1 to time 2

$$\text{Production} = (N_2)(wt) + \tfrac{1}{2}\Big[(N_1 - N_2)(wt)\Big].$$

(*Assuming no new recruitment over the period)

If "natural" or physiological death is negligible and the loss to predators has been assessed independently, then a more accurate estimate is possible. This sort of analysis can only be attempted when all major macroconsumer components of a stream system are receiving close scrutiny--a rare occurrence.

A Representative Short-Term Energy Budget (Glossosoma nigrior:Trichoptera)

The intra-instar weight gains can be determined directly if a stable age distribution is approached, as shown for the 14 day Glossosoma nigrior budget in Fig. 2. Each census was based on three 900 cm^2 bottom samples in a small cold water Michigan stream (Augusta Creek, Barry County).

The rapid and accurate determinations of energy budgets for stream macroconsumers should form a critical facet of lotic ecosystem investigations. Such data, together with energy budgets for primary producers and microconsumers will allow for the assessment of ecosystem functioning necessary for predictive manipulation of stream communities.

A great deal remains to be done in the development and refinement of techniques (e.g. see Fig. 3), but particular attention should be directed toward standard methods for determining ingestion and assimilation rates. In order to obtain realistic rates and efficiencies of tissue incorporation, a great deal of information is needed on nutritional biochemistry of benthic stream macroconsumers and feeding habits under natural conditions.

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SUMMARY OF FACTORS AFFECTING THE STRUCTURE OF BENTHIC COMMUNITIES IN STREAMS

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ABSTRACT

Benthic communities in streams are composed of algae, protozoa, rotifers and various macroinvertebrates including insects. These organisms live on or in the bed or shores of streams attached to aquatic plants, debris or inorganic substances and floating or swimming in the water close to the bed of the stream.

A community is usually thought of as a group of organisms that interact. In a stream we have many relatively small communities. However, some organisms interact to form larger communities--for example, estuary fish that swim upstream to the headwaters to spawn and rear their young.

The kinds and numbers of species composing benthic communities vary with the chemical and physical conditions of the stream and the invasion rate. For example, in an oligotrophic stream where the nutrient level is very low, we typically have rather high diversity but extremely small populations. These benthic communities typically consist of many species with varying life histories. For example, in diatoms, we have many species that reproduce once a day, once every three days, once a week or sometimes once in several weeks. Variation in the generation time for various species is great, although a total generation time for even the longest species is very short compared to some plants and animals.

The strategy of survival that has been adopted by most of these species is a short generation time, a high reproductive rate, and many offspring together with the ability to produce resting cells, spores, or over-wintering eggs, or the ability to pupate or to lower the metabolic rates in order to withstand the rigorous changes of the environment.

The energy and nutrient sources are quite different for benthic stream communities than for such communities in lakes or for terrestrial communities. In streams nutrients--dissolved, suspended, and organismal--are continually entering a given area from upstream or from the watershed either by direct runoff or through ground water. There is a continual renewal of dissolved nutrients rather than the recycling of nutrients which is so characteristic of lakes and terrestrial communities. Typically, these benthic communities have four or five stages of energy transfer. In each such community we have decomposers, primary producers, herbivores, and primary and sometimes secondary carnivores. Of course, omnivores which graze on two or three of the groups are always present. In each of these groups of organisms, performing these various functions, there are a great many species representing many different genera, orders, and systematic groups.

Benthic organisms composing benthic communities interact in various ways. Among the more important of these are the predator-prey relationships. The density and competition resulting from the saturation of an environment with specimens and/or species have also been observed in benthic communities.

Of similar importance are the effects of density independent factors on the structure of these communities. The environment in the streams is often very rigorous and very changeable. As a result populations of species are continually being cut down by unpredictable changes in the environment. It is the affect of a rigorous and unpredictable environment that is probably largely responsible for the low equitability and low diversity of benthic communities.

Various workers have attempted to characterize an orderly sequence in the development of various types of communities. Margalef has characterized young communities as having species with widely fluctuating populations, sizes, high metabolic rates, short life cycles and high reproductive rates producing large numbers of offspring. In contrast, mature communities are characterized by species which have more stable population sizes, longer life cycles, lower metabolic rates, and fewer offspring which are more protected. Benthic communities by these criteria and those set forth by Hutchinson are relatively young or immature communities for they are characterized by small, rapidly reproducing species with short life cycles.

The effect of pollution or perturbation on these communities, if it is nutrient enrichment or substances of very low toxicity, is generally to first cause some change in the sizes of the populations of species present. In some cases reproduction is inhibited by the pollutant whereas other species may be very tolerant of the pollutant and have increased reproductive rates. Also we sometimes see changes in the age classes present--for example, a pollutant's effect may be more severe on the very young or very old individuals and thus we see within a species a shift in relative numbers of individuals in various age classes. A more severe change usually brings about a change in kinds of species. More intense perturbation such as very toxic pollutants actually bring about a severe reduction in numbers of species and often a reduction in food pathways in the community. Another effect of toxic pollution is a repressing of reproduction resulting in reduced biomass. We have found that various kinds of pollution produce various combinations of these effects.

SUMMARY

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ABSTRACT

Community Structure and Diversity

As Minshall showed convincingly, definite patterns of benthic macroinvertebrate stream community structure are associated with general environmental regimes in North America. Consistency of pattern is apparent when structural components of similar sized streams are compared along the length of their drainage. Basic similarities are also associated with terrestrial biome type and a direct relationship exists between number of species and stream size.

This consistency of stream community composition, manifest as structural correspondence between environmentally similar running water habitats, allows for prediction about structure in artificially created streams. As Thut reported, artificial or semi-natural streams can be a powerful tool in the analysis of community structure and energy flow through a lotic system. The three replicated Weyerhaeuser streams, consisting of alternated riffles and pools of homogeneous substrate, have been employed to study the trophic partitioning of stream communities and distribution patterns relative to current, substrate and drift. Of particular interest are the consistent trophic differences between seven species of the caddisfly genus *Rhyacophila* occurring in the experimental streams.

Wilhm demonstrated that the dimensionless index $\bar{d}$ provides a concise and, importantly, comparable index of community diversity. Values theoretically range from zero, when all individuals are of the same species, to a maximum value equal to the number of individuals collected, i.e. all individuals belonging to a different species. Except at very small numbers of samples, $\bar{d}$ is independent of sample size. There is no question that characterization of stream community diversity (as $\bar{d}$) can be a powerful tool for comparing communities and assessing changes. Unfortunately, in many studies our taxonomic capabilities lag far behind the demand for the use of this tool.

Interactions with the Terrestrial Biome

As more attention continues to be focused on the importance of allochthonous organic matter on autochthonous stream productivity, the dominant role of terrestrial primary production becomes more apparent. Vascular plant tissues, trapped by the running water system acting as a sink, probably already contain fungal spores destined to initiate the decomposition sequence. Definite successional patterns can be observed involving initial fungal infection followed by bacterial invasion and interrupted periodically by detritivore ingestion. The rate of plant tissue degradation is species specific, for example willow (Salix) leaves being broken down quickly and oak (Quercus) leaves slowly. The differing decomposition rates may involve varying successional rates rather than actual microfloral species differences. The detritivore macroconsumers apparently respond to, and probably derive their primary nutrition from, the microbial flora and fauna which use the leaf as a physical and nutritive substrate.

The critical importance of terrestrially produced organic matter to lotic ecosystem functioning was discussed by Nelson. In emphasizing the need to distinguish between allochthonous and autochthonous organics, he stressed that neither the investigator nor the organisms can make such a distinction relative to inorganic constituents. Since rainfall and stream discharge are not distributed evenly throughout the year, the 50% level of annual discharge load is carried in one quarter of the year or less; the better the cover the more time required to reach the 50% level. Because of atmospheric and land surface stripping, maximum stream concentrations of many elements are reached in the early stages of peak runoff periods, in later stages absolute amounts are lowered by dilution.

Productivity

As described by Vannote, the combination of an experimental flowing water system and a natural stream are being employed to investigate lotic ecosystem dynamics. A wide variety of studies are incorporated in a broad ecosystem approach including experiments aimed at delineating the importance of detritus as a food base. Specific assemblages and successional patterns are typical of leaf packs produced artificially to simulate those that accumulate naturally in the stream. Rapidly growing mayfly nymphs and tipulid larvae are followed by stonefly predators. Although food conversion efficiencies are fairly constant for a variety of leaf species, certain ones are selected by tipulid larvae for ingestion. Such "compartments" of detritivore-predator activity insure the rapid and efficient utilization of primary production of terrestrial origin in the stream ecosystem.

After briefly reviewing trophic theory for lotic systems and production models for stream macroconsumers, Waters discussed detailed estimates being made on production rates of the amphipod Gammarus pseudolimnaeus. The production estimates are based on field standing crop information and instantaneous growth rates calculated from laboratory culture data. By combining life history and age structure data from the field, confirmation of laboratory rates is possible at certain times of the year. One main objective is to calculate turnover ratios (annual production ÷ mean annual standing crop) and compare amphipod production to that of brook trout which depend upon them as a major dietary item.

Following a review of periphyton-related lotic mineral cycling studies, Cushing reported on investigations of zinc-65 cycling by natural periphyton communities measured in an ingenious recirculating laboratory system. The critical problem of the concentration factor was discussed, particularly with regard to closed systems and the problem of spike introduction vs continuous introduction of isotope. Zinc-65 uptake has been shown to be primarily adsorptive in nature and involved with competition for binding sites with other cations. Clearly the complicated and interrelated problems of adsorptive and absorptive uptake by periphyton need to be investigated in relation to nutrient cycling throughout trophic levels in stream ecosystems.

Cummins reviewed some studies of energy budgets of invertebrates including one stream mayfly. After considering the investigation of budgets at both the system and population level, a series of procedures was outlined for determining budgets for natural populations of stream macroconsumers. Ingestion, egestion and assimilation can be determined by tracer techniques or direct food weight loss-animal weight gain-fecal weight production laboratory studies. Temperature-, age-, and nutritional state-specific respiration (maintenance cost) is determined in the laboratory and applied to the field population under given environmental conditions. Production (growth) can be determined over periods when the population approaches a stable age distribution (with no recruitment) by increases in the mean weight per individual over the period and an estimated loss factor determined from changes in the standing crop. As an example, a short term energy budget for a stream caddisfly (Glossosoma nigrior) was presented.

Patrick presented an extensive review of stream studies. In the first phase of the discussion a background concerning stream ecosystem structure and function was laid. This included consideration of the uniqueness of energy and nutrient sources for lotic waters and organizational stability of stream communities derived from species diversity and trophic interactions. Competition for microhabitats and very specific food requirements probably maintain the diversity of community structure. Many streams may be characterized as immature communities in which "opportunistic" species continually invade microhabitats that become available due to the flow-related physical instability of the environment.

The second phase of the discussion by Patrick centered on the effects of perturbations in stream communities. The result of such alterations as organic pollution is a species replacement of many "specialists" with a few "generalists". That is, a general reduction of complexity, diversity and stability. At the base of the community alteration may be food chain blockage. The effects vary in relation to the intensity of the perturbation but in the initial phases of the alteration the changes may be species specific, age specific or involve a repressing of growth and reproductive rates.