INTERBIOME COMPARISON OF STREAM ECOSYSTEM DYNAMICS¹

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Abstract. Studies were conducted in four distinct geographic areas (biomes/sites) in northern United States to examine changes in key ecosystem parameters: benthic organic matter (BOM), transported organic matter (TOM), community production and respiration, leaf pack decomposition, and functional feeding-group composition along gradients of increasing stream size. Four stations ranging from headwaters (1st or 2nd order) to midsized rivers (5th to 7th order) were examined at each site using comparable methods. The results for each parameter are presented and discussed in light of the River Continuum Concept of Vannote et al. (1980). The postulated gradual change in a stream ecosystem's structure and function is supported by this study. However, regional and local deviations occur as a result of variations in the influence of: (1) watershed climate and geology, (2) riparian conditions, (3) tributaries, and (4) location-specific lithology and geomorphology. In particular, the continuum framework must be visualized as a sliding scale which is shifted upstream or downstream depending on macroenvironmental forces (1 and 2) or reset following the application of more localized "micro"-environmental influences (3 and 4). Analysis of interactions between BOM and TOM permitted evaluation of stream retentiveness for organic matter. Headwaters generally were most retentive and downstream reaches the least. Estimates of organic matter turnover times ranged between 0.2 and 14 yr, and commonly were 1-4 yr. Both turnover times and distances were determined primarily by the interaction between current velocity and stream retention. Biological processes played a secondary role. However, the streams varied considerably in their spiraling of organic matter due to differences in the interplay between retentiveness and biological activity. Differences in the relative importance of retention mechanisms along the continuum suggest that headwater stream ecosystems may be functionally more stable, at least to physical disturbances, than are their intermediate river counterparts.

Key words: benthic organic matter; carbon cycling; community metabolism; Idaho; invertebrate functional groups; Michigan; Oregon; Pennsylvania; River Continuum Concept; seston; spiraling; stream ecosystems; transported organic matter.

INTRODUCTION

From the time biologists first began to examine streams there has been a tendency to look at communities or organisms and their associated abiotic factors. The periphytic, macroinvertebrate, and fish com-

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munities have received particular attention. However, there have been few attempts to treat streams and rivers holistically, and particularly, to view them as discrete ecological systems. It has been only within the last 25 yr that knowledge of the organization and functioning of streams has reached a stage that allows generalizations to be made about these ecosystems. Such advances have been built on the early ideas about longitudinal succession and community structure (Mar-

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FIG. 1. Simplified models for two hypothetical stream ecosystems. Stream A is characteristic of most forest streams, while Stream B is characteristic of large rivers and uncanopied small streams. The components are the same in both cases but their relative importance (as reflected by the size of the boxes) differs in the two systems.

galef 1960); the role of riparian vegetation in structuring stream communities (Ross 1963); generalizations about ecosystem structure and function (Cummins 1974, McIntire and Colby 1978); autotrophic production (Minshall 1978); and nutrient cycles in streams (Newbold et al. 1981). However, few unifying concepts have been proposed that can serve as a foundation for stream ecosystem research.

One reason for this missing foundation is the complex and diverse nature of flowing-water ecosystems. It is more difficult to visualize streams of different size in the same drainage as belonging to the same ecosystem than to visualize a pond or a forest, no matter how large, as being a discrete ecosystem. For example, a reach of a large river such as the Mississippi typically has not been included in the same ecosystem as its headwater streams. The reluctance to view flowing waters as ecosystems (Rzóska 1978) may be due partly to the difficulty in defining the term ecosystem (Mann 1979), but is more likely attributable to the way streams or their entire drainage system (all streams and rivers that are linked together) are visualized. This conceptualization is even more difficult without some general unifying principles that apply to all flowingwater ecosystems.

Recently, Vannote et al. (1980) proposed that the coalescing network of streams in a river drainage system is a continuum of physical gradients and associated biotic adjustments. This approach leads to useful generalizations concerning the magnitude and variation through time and space of the organic matter supply, the structure of the invertebrate community, and resource partitioning along the length of the river. The River Continuum Concept views streams as longitudinally linked systems, i.e., those in which system-

level processes (cycling of organic matter and nutrients, ecosystem metabolism, net metabolism) in downstream areas are linked to in-stream processes in upstream areas; the concept provides a general framework for dealing with streams as spatially heterogeneous systems (O'Neill et al. 1979).

The utility of visualizing an entire river system as a continuum of communities and material processes with their associated abiotic factors may be illustrated as follows. Consider a simplified six-component model of a small woodland stream and larger sized reach farther downstream, as shown in Fig. 1. The relative size (e.g., dry mass in grams per square metre) of each component is illustrated by the size of the boxes. Both systems have the same functional components, even though the species present may be different; that is, general structure and function are the same. The difference between the two systems is in the relative magnitude of the components, the rates and amounts of transfer between components, and the actual species engaged in the transfers. But the two systems are essentially modifications of the same basic plan, and the entire stream-to-river complex can be viewed as one ecosystem composed of a series of communities along a continuum.

Four sets of hypotheses can be generated from the conceptualization of streams as a continuum of communities. The hypotheses may be grouped under the following sets of assumptions:

- If the particulate organic matter at one location in a stream is determined by what occurs upstream, and if the biological community exploits this resource, then:
 - a. there will be a gradual reduction in particle size as the material is metabolized and fragmented;
 - b. there will be a decrease in the organic content of those particles in transport (seston); and
 - c. there will be a downstream reduction in the fraction of a particle that is readily metabolized.
- 2) If the relative contribution of organic matter from the riparian zone decreases downstream as compared to that present in a stream, and given the assumptions in (1), then:
 - a. there will be a reduction in coarse-to-fine particle size ratios; and
 - b. there will be a relative increase in particulate organics generated by in-stream processes.
- If stream channel morphology changes from narrow, shallow, and heavily shaded to wide, deep, and open, then:
 - a. there will be a shift from benthic metabolism dominated by heterotrophic processes to a dominance of photosynthesis, but shifting again to heterotrophic processes with increasing river depth and sediment load which interferes with benthic primary production; and

- b. there will be a shift from community metabolism dominated by benthic processes to metabolism dominated by water column processes.
- 4) If the assumptions concerning food resources of the invertebrates in (1) and (2) above are valid and the channel morphology changes as in (3), then:
 - a. there will be a reduction from the headwaters to the lower reaches in the relative abundance of organisms dependent on coarse particle detritus; and
 - b. there will be a shift in the animal community structure from those animals obtaining their food from the stream bottom (shredders, grazers, deposit feeders) to organisms feeding on particles in the water column (filter feeders).

The approach used in this study was to view the entire stream-river system as an ecosystem and to investigate changes in ecosystem-level parameters at different locations along headwater-downstream gradient. Historically, there has been considerable attention paid to changes in communities along a watercourse (e.g., Minckley 1963, Cushing 1964, Bishop 1973) with special attention being given to benthic invertebrates (Ide 1935, Sprules 1947, Jonasson 1948, Illies 1953, Harrison and Elsworth 1959, Maitland 1966, Harrel and Dorris 1968, Ulfstrand 1968, Minshall and Kuehne 1969, and others); fish (Trautman 1942, Huet 1949, 1954, Kuehne 1962, Harrel et al. 1967, Whiteside and McNatt 1972, Tramer and Rogers 1973, Horowitz 1978, Platts 1979); and special groups such as mussels and freshwater gastropods (Goodrich and van der Schalie 1944) and Trichoptera (Wiggins and Mackay 1978). However, the effort required to examine a complete river ecosystem with a full complement of parameters has restricted the scope of such research.

The design of this study included the selection of ecosystem-level parameters that were general enough to apply to all streams and rivers and precise enough to make information on these components meaningful. These were examined during four seasons of one year (1976) at four locations of different stream size in each of four different river systems across the United States. The response of these stream systems was examined with the same sampling procedures to facilitate comparison of results. The data were collected to test the hypotheses listed above, to evaluate the utility of the continuum concept, and to gain further insight into the ecology, behavior and dynamics of lotic ecosystems. Between-station comparisons at each site allow independent testing of the hypotheses while between-site comparisons permit testing of the generality of the findings.

The four stream systems selected for study consisted of two in the Western Coniferous Forest Biome and two in the Eastern Deciduous Forest Biome: (1) a tributary system of the McKenzie River, Oregon; (2) the Upper Salmon River, Idaho; (3) a tributary system of the Kalamazoo River, Michigan; and (4) White Clay Creek and Buck Run, Pennsylvania (Figs. 2, 3, 4). More detailed results and site-specific analyses for each stream system (including Naiman and Sedell 1979a, b, 1980, Cummins et al. 1981, Hawkins and Sedell 1981, Minshall et al. 1982) and comparative analyses of selected variables (including Sedell et al. 1978, Moeller et al. 1979) are being published elsewhere. The purpose of this contribution is to examine the results for all parameters collectively in an effort to synthesize our findings and to seek general trends that may apply to a majority of streams despite the inherent variability typical of these systems. Specifically we wish to test hypotheses derived from the River Continuum Concept over a range of stream sizes extending from headwaters through intermediate-sized rivers.

SITE DESCRIPTIONS

All four study streams are located at approximately the same latitude (Fig. 2) in relatively undisturbed watersheds in which the headwaters are forested. The uppermost station (number 1) at each site was established near the headwaters (1st and 2nd order) and the lowermost station (number 4) was chosen to be the largest stream in the basin unaffected by pollution or impoundment (except the Salmon River, which is not impounded over its entire 650 km length). The four locations at each site (except Pennsylvania) were in the same basin, though not necessarily on the same contiguous body of water, and were representative of a particular size and order of stream for a given watershed.

Physical features

Data for a number of morphological features are presented in Fig. 3. Stream size is given in terms of order (Strahler 1957), external link number (Shreve 1966), and mean annual discharge. The streams are most comparable in terms of orders represented; all other parameters varied more widely as dictated by local climatic and topographic conditions. First, 2nd, and 3rd order streams are represented at three of the four sites; 5th order at all sites; and 4th, 6th, and 7th order at one site each. The number of external links was similar for all the headwater stations and reasonably comparable for the second stations, but showed wide divergence at the two downstream locations, attaining 59 in Pennsylvania and over 800 at Idaho. Greatest range of discharges was found at the Oregon site $(0.002-55 \text{ m}^3/\text{s})$ and the smallest range $(0.006-2.83 \text{ m}^3/\text{s})$ m³/s) in the Pennsylvania system. Mean discharges for all the headwater stations were within an order of magnitude of each other; values for the other stations differed widely between sites.

The streams were chosen to represent widely different climatic and geomorphic settings. These differ-



FIG. 2. Runoff in cubic feet per second (cfs) and cubic metres per second, air temperature, and precipitation patterns for the study sites during the 1975–1976 water year. Runoff is from United States Geological Survey records, and temperature and precipitation are from United States Weather Bureau records for regularly monitored locations nearest the most downstream station at each site. $\bar{x} = mean$; m = mode.

ences are illustrated by patterns of temperature, precipitation, and runoff (Fig. 2); channel morphology (Fig. 3); and longitudinal profile (Fig. 4).

Oregon showed the widest range in total precipitation, from ≈ 292 cm/yr in the mountain headwaters to ≈ 168 cm near station 4; for Idaho the range was from 90 to 40 cm/yr. Values for the other two streams were much more constant over the extent of their study stations and correspond to those calculable from Fig. 2. In Idaho the precipitation accumulates from November through March as snow and enters the stream during May–July. This results in a hydrograph (Fig. 2) characteristic of mountain-fed streams in semi-arid regions and sharply contrasts to west-coast mountain streams in wetter regions dominated by maritime climate, as exemplified by western Oregon. A major portion of the total precipitation in Oregon occurs from January through April as rain. Precipitation is spread more throughout the year at the two eastern sites, resulting in highly variable hydrograph fluctuations. Precipitation at the two locations differed considerably— Michigan reflecting a continental climate and Pennsylvania, a marine storm influence. During the period of this study, there were no major storms or floods in the watersheds studied and all annual hydrograph recurrence intervals were between 2 to 4 yr.

Stream channel morphology is represented in terms of width, depth, slope, configuration, and density of large wood debris (Fig. 3). All variables but large wood and slope show a progressive increase downstream within each stream system, but between streams it is difficult to generalize. Widths of headwater and farthest downstream stations were generally similar except for the downstream Pennsylvania site, which was

FIG. 3. Comparison of physical parameters for the 16 sites used in the study. A section of each site is drawn to the scale shown on the left of the figure or as indicated; location and size of large wood debris are included. Longer sections than shown were used in the sampling program and were either 100 m or three riffle-pool units, whichever was longer. Q is the measured mean annual discharge during 1976. Width and depth are averaged over the entire site and measured at base flow. Slope is an average for the entire stream section used.



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FIG. 4. Longitudinal profiles for the study site showing locations of the study reaches in terms of elevation and distance from the source. The absolute elevations at the lowest station of each site were: Idaho 1867 m; Oregon 364 m; Michigan 226 m; and Pennsylvania 75 m. The lowermost station at Oregon and Michigan is actually upstream from the mouth of the tributary on which the other stations are located and that of Pennsylvania is in an adjacent watershed, but each is plotted as if it were situated an equivalent distance downstream.

about one-third the size of the others. Mean depths were reasonably similar at all stations, except the 3rd and 4th Oregon and Michigan stations were notably deeper than the others. Slopes were much greater (Fig. 3) and longitudinal profiles (Fig. 4) steeper for the two Western streams. Density of large wood debris was highest in the headwaters of all streams and greatest at the Oregon site.

Water chemistry

Several chemical variables were measured. Emphasis here is on those which broadly characterize the four sites (Fig. 5). Since differences among the sites in alkalinity, hardness, and total dissolved solids were similar, only alkalinity is discussed.

Mean alkalinities (CaCO₃ concentrations) in Michigan (mean of all four stations and seasons 219 mg/L) were approximately three times those in Pennsylvania (75 mg/L), with the latter about equal to those in Idaho (50 mg/L). Alkalinity levels in Oregon (14 mg/L) were less than a third of those in Idaho and an order of magnitude less than those in Michigan. The low levels in Oregon are related mainly to high precipitation and low soil contact time in this region, since both Oregon and Idaho streams were underlain with igneous rock. Concentrations of total-N in Pennsylvania generally were about two times those in Idaho and Michigan and two orders of magnitude greater than total-N levels in Oregon. Total-P concentrations were about three-fold higher in Pennsylvania than at any of the other sites.

METHODS

At each of the 16 locations used in the study, a length of stream (reach) was chosen for the sampling



FIG. 5. Seasonal water chemistry values expressed as means of the four stations at each site. NA indicates samples were not analyzed for this component.

program. The length depended on the size (width and depth) of the stream and was defined as either three riffle-pool sequences or 100 m, whichever was longer. This ensured that in small streams (1–2 m wide), long sections would be available to reduce the effects of the sampling on subsequent samples, while in wide streams (10–25 m), enough riffles and pools would be sampled to be representative. Each reach was measured and mapped to the nearest metre (e.g., Fig. 3), and each metre was designated to permit random selection for sampling. Habitats were assigned to one of two types, being either erosional (riffle, run, chute, rapids) or depositional (alcove, pool, drop zone, backwater) even though there are many areas which are in between the two habitat types. Measurements of par-

TABLE 1. Percent of erosional (riffles, runs) habitat, by area, in the study reaches.

	Stream								
Station	Oregon	Idaho	Michigan	Pennsyl- vania					
		Erosiona	al area (%)						
1	50	94	80	76					
2	80	98	70	44					
3	75	92	65	36					
4	95	92	65	30					



FIG. 6. Flow chart of the methods used for the determination of transport, storage, invertebrates, and community metabolism.

ticulate organic matter, community metabolism, and population density were weighted for percent erosional and depositional habitat in each reach based on the relative areas of each type (Table 1) obtained from the maps.

A summary of the specific methods used in measurement of the main ecosystem parameters is presented in Fig. 6. Particulate organic matter transport and storage, community metabolism, and benthic invertebrate standing crops plus basic water quality and hydraulic features and solar radiation were measured during four seasons in 1976 (Fig. 7) to represent the periods of midwinter, leafout, midsummer, and leaffall.

Except for Idaho, transport was sampled before or after major runoff events in order to avoid relatively short-term conditions of little biological activity. In Idaho, the runoff period was much more extended (Fig. 2), and so was included in the transport sampling regimen. Transport samples were collected at 0.6 m depth in the region of mean velocity. Measurements of transported organic matter (transport) and community metabolism were made over several days. Benthic particulate organic matter and invertebrates were sampled on a single date in each season, with a minimum of three replicates per season in each of the two habitat types, but invertebrate data for only two seasons were analyzed.

Samples for transport and storage were fractionated in the field by a series of monofilament (Nitex) nets or Taylor, United States Standard screens into a series of eight particle size categories (Fig. 6). Each category was assigned an acronym and subscript with seston or transport detritus assigned TOM for transported organic material, and benthic organic, BOM. The subscript then signifies the lower boundary of each category, as in BOM₁₆, the benthic organic matter in the <20 cm >16 mm category. In addition, three additional superclasses were constructed by collapsing various categories together. The 16, 4, and 1 mm categories were collapsed into coarse particulate organic matter (CBOM or CTOM), the 500, 250, 100, and 50 μ m collapsed into the fine particulate organic matter (FBOM or FTOM), and the remaining category was called ultrafine (UBOM or UTOM).

Community metabolism was measured using oxygen changes within in situ plexiglass chambers (Bott et al. 1978). Measurements lasted 20–30 h and chambers were

SITE	WINT	ER	Ι	SF	RING		SU	MER		AL	JTUM	N
PA				C								
MI												
ID												
OR		C]									
	J F	- '	М	Α	M	J	J	Α	S	0	N	D

FIG. 7. Sampling periods used by the four River Continuum study sites during 1976. Periods were adjusted at each site to correspond to four seasonal periods within the constraint of accessibility.

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FIG. 8. Annual means of transport and benthic organic matter by particle size category (coarse [CPOM], fine [FPOM], ultrafine [UPOM]) and totals for all sites and stream sizes.

flushed as required to avoid supersaturation; this procedure also reduced possible problems of nutrient depletion and metabolite accumulation. The type of stream substrate determined the type and collection of material for the chamber. In loose unconsolidated or fine-grained substrates, such as at the Pennsylvania, Michigan, and upper Idaho stations, precolonized, substrate-filled plastic trays were used. In consolidated and coarse-grained substrates where plastic trays could not be buried, such as at the Oregon and lower Idaho stations, rocks and organic debris accumulations were placed in the chamber. Weighted estimates of BOM respiration were obtained using measured values of respiration for coarse and fine detritus and standing crops of these size fractions on the stream bottom.

Measurement of leaf decomposition followed the procedure of Petersen and Cummins (1974). Approximately 10-g oven-dry-mass packs of mockernut hickory (*Carya tomentosa*) leaves were sewn together with nylon monofilament, attached to bricks, and placed in riffles at each of the 16 stations in fall 1975. At least

three packs from each station were removed after 3, 30, and 60 d incubation. The 3-d packs were used to correct the results for leaching and handling losses. Upon removal the leaf packs were gently rinsed to remove fine particulate sediments, oven dried for 24 h at 50° C, and reweighed.

Samples for water chemistry analyses were filtered in the field, and either analyzed the same day or frozen and stored for future analyses. Total dissolved solids were measured after evaporation of a filtered sample (American Public Health Association [APHA] 1975) at Pennsylvania, or by comparing conductance against the evaporation method at Michigan, Idaho, and Oregon. Total alkalinity was measured by Standard Methods (APHA 1975) using either methyl purple (Pennsylvania, Idaho) or bromcresol green-methyl red (Michigan, Oregon) as endpoint indicators. Hardness was measured by atomic absorption (for Ca and Mg) (APHA 1975) at Pennsylvania and Idaho, and by the EDTA titrimetric method (APHA 1975) at Michigan and Oregon. Total-N was obtained by the Kjeldahl method after prereduction at Oregon and Idaho, and by summation of NO₃-N, NO₂-N, and NH₄-N at Michigan and Pennsylvania. At all sites total-P was determined using the ascorbic acid method (APHA 1975) after perchloric digestion.

RESULTS AND DISCUSSION

Benthic organic matter (BOM)

Benthic particle sizes.—Results of the benthic organic matter sampling are summarized in Figs. 8 and 9. The eight particle size groups, when combined into the three categories mentioned earlier, respond differently among stations and seasons (Fig. 8).

For each of the three major detritus categories and for the total amount, a four-way analysis of variance (ANOVA) was performed with site, station, habitat (i.e., erosional and depositional areas), and season as the four factors. Since there was a significant relationship (P < .001) between the variance and means of this rather large data set (n = 598), the data were transformed using the Taylor transformation (Thöni 1967). The results of the four-way ANOVA showed significant ($P \ll .001$) differences for site, station, and habitat for the three organic particle categories and all four factors for total BOM. These significant differences merely indicate an association between the factors and the dependent variable, because in large data sets, trivial associations may achieve statistical significance (Kirk 1969). The strengths of the statistical associations are reported in Table 2. Except for CBOM, the greatest amount of variability in storage was associated with site. This reflects such differences as the dominance of woody coarse particulate matter in the Oregon streams and the great abundance of FBOM in the Michigan streams (also see Fig. 8). Seasonal effects are relatively small as judged by the amount of variance explained. Habitat type generally accounted



FIG. 9. Total concentration of transported and benthic particulate organic matter by season at each of the study sites and stations. Values are weighted to reflect relative importance of the different habitats sampled.

for more variation in benthic organic matter than did stream size (order).

While there was significant association between stream size and storage, this represented only 10% of the variation in total BOM. There also was no consistent trend in the ordering of stored detritus at the four locations at each site (Fig. 9). In Oregon, the headwater stream stored very large quantities of organic matter (AFDM annual mean 1420 g/m²; CV = 23%) as compared to the other three downstream sites (234, 81, 78 g/m²). However, this downstream decrease in BOM was not repeated at any of the other three sites. Michigan, as mentioned above, showed a consistent but small downstream increase in total storage, with fine particulates (<1 mm) accounting for 78-94% of the total. This can be explained in part by the retention of fine particulates in the much lower gradient stream due to filtration by dense beds of macrophytes.

Thus, local geomorphic factors which determine de-

TABLE 2. Percent of variance explained by factors grouped for each particle size category and total of benthic particulate organic matter.

	Particle size category							
Factor	СВОМ	FBOM	UBOM	Total BOM				
	Percent variance explained							
Site (biome)	8	36	48	31				
Station (stream size)	17	9	7	10				
Habitat (riffle, pool)	15	24	9	18				
Season (W, S, S, F)	NS	NS	NS	2				

position in a stream were more important in explaining the variance of detritus standing crop than either relative stream size (order, link, etc.) or season. Part of the explanation for the lack of association between storage and seasons is that benthic organic material, throughout the year, is predominantly fine (<1 mm) and ultrafine (<0.05 mm) particulates. Coarse particulate input does have a strong autumnal peak, but this is not reflected in our results for BOM for a variety of reasons, including:

- 1) the timing of the inputs relative to when some of the samples were taken,
- accumulation in relatively rare depositional areas, and
- the fact that freshly fallen leaves do not enter the storage compartment as readily as weathered leaves transported into the streams in spring.

A general prediction of the River Continuum Concept is that the detrital base shifts with increasing stream size such that a decrease in coarse particulates (CPOM) is accompanied by a relative increase in fine particulate organic matter (FPOM, UPOM). This prediction was based on the observation that most large particle detritus of terrestrial origin enters headwaters where it is retained and processed. The headwaters are the location of maximum interface between stream and landscape and support the highest densities of retention devices (Bilby and Likens 1980). Larger streams, being under less direct terrestrial influence and having fewer retention mechanisms, are more dependent on tributary inputs and the products of in-stream primary production.

As shown in Fig. 10, the first three stream sizes generally show this downstream shift in benthic organic matter particle sizes. However, in the largest sized rivers studied (orders 5, 6, and 7), the ratio tends to be smaller than expected, relative to the upstream stations, at all but the Oregon site (Fig. 10). A major reason is the contribution of CPOM derived from tributaries, macroalgae, and vascular hydrophytes, in midsized rivers. For Oregon station 4, the FBOM/ CBOM ratio may be lower than expected because the substrate tends to be armored and less retentive of FBOM than at upstream stations. Also, CBOM at the

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FIG. 10. Trends in benthic organic matter particle sizes expressed in relation to the coarse fraction and mean absolute amounts (AFDM, g/m^2) of coarse material; based on mean annual values. The shaded curve shows predictions of the River Continuum Hypothesis.

lowermost Oregon station is largely wood caught between boulders. Calculating the ratio of fine-to-coarse particulates with and without the ultrafines (UBOM) shows the latter's importance (Fig. 10). The ultrafines always were greater than the fines, and the general effect is to increase the ratio about 1.5-fold (range 1.1 to 10.4). The fundamental pattern is for an increase in fine particulates with increasing stream order up to 3rd or 5th order. Thereafter, the ratio is relatively constant. The ratios were lowest for the wood-dominated Oregon streams and highest for the fine-particle-dominated 1st through 3rd order Michigan and 5th through 6th order Idaho streams.

While the ratio of fine to coarse organic matter showed only a weak tendency to increase in a downstream direction, the absolute amount of coarse particulate estimated for each location showed an exponential decrease downstream (Fig. 10). The only divergence in the latter trend is at Idaho where additional local inputs may be occurring or a change in gradient may be causing a general buildup of coarse



FIG. 11. Mean chlorophyll a concentrations at each site by station and season.

material. The largest stream in Michigan holds more coarse particulate than would be predicted even though it is less than the smallest Michigan stream studied. There does not appear to be any simple correlation between gradient and amount of coarse material because the two streams that have the strongest downstream decrease in concentration have both the highest (Oregon) and lowest (Pennsylvania) gradient (see Fig. 4).

Benthic chlorophyll a.—One of the predictions of the Continuum Concept is that there will be an increase in autotrophic processes in a downstream direction as channel morphometry changes to allow increased light penetration. While autotrophic processes are best described by direct metabolism measurement (see Stream Metabolism section), they also may be indicated by the standing crop of the autotrophic community.

Chlorophyll *a* concentrations on rock substrates were used to indicate standing crops of benthic primary producers. Concentrations usually varied widely by reach during each season; over half of the 62 data sets had a coefficient of variation greater than 50%. Mean chlorophyll *a* concentrations were lowest in the headwater reaches and were greatest in intermediate or farthest downstream reaches at Michigan and Oregon sites (Fig. 11). At Idaho, this expected trend generally was reversed. Chlorophyll *a* tended to be lowest at the Pennsylvania site. Trends in a downstream di-

rection were least pronounced there, and statistically significant differences between stations were observed only in winter. Seasonal mean solar radiation and precipitation leading to scour of benthic algae were generally more uniform at Pennsylvania stations than elsewhere. At Idaho, for example, high flow was concentrated in spring and early summer and at Oregon in late fall through early spring.

Retention capacity of depositional vs. erosional areas.—The benthic detritus sampling scheme took into account rather obvious differences between depositional and erosional habitats at each station. We have termed riffle-run habitats "erosional" and pool-alcove areas "depositional." These categories do not necessarily apply throughout the year. At high flow, pools generally are erosional and riffles depositional (Keller 1971, Lisle 1979). While it can be generalized that erosional habitats possess less detritus than depositional ones, there is by no means a constant relationship between the amounts stored in the two. In Fig. 12, ratios of riffle to pool BOM are presented for the annual averages for the 16 locations. Total BOM riffle-pool ratio ranged from 0.07 at Oregon station 2 to a high of 0.83 at Pennsylvania station 2. Erosional habitats had a median value of 27% as much total detritus as depositional areas. The CBOM ratio also had a median value of 0.27, but had a much wider range of values with a high of 1.33 at Idaho station 2 to a low of 0.06 at Oregon station 2. UBOM had a higher median value (0.35) but there also were locations (Oregon stations 3 and 4, Pennsylvania station 2) in which riffles stored more organic matter than pools or alcoves on an annual basis. At all 16 locations pools stored more fine material than riffles, and this ranged from 33 to 1.3 times as much. Even though depositional areas generally store more particulate organics than erosional areas, there are differences in the various particle categories. The fine particulates generally accumulate selectively in depositional zones while coarse and ultrafine particulates are more evenly distributed over the stream bottom.

Differences in standing crops and particle size distribution of BOM between erosional and depositional habitats indicate the importance of stratified sampling and the value of adjusting means for a given reach by habitat weighting. The effect of weighting is to reduce the standard error of the estimate by about half. This is because depositional zones tended to be more variable in amount of detritus, but occupied less area in the study reaches.

Transported organic matter

Transport concentration.—Transported organic matter (TOM) for all four biomes, stream sizes, and seasons (Figs. 8, 9) was dominated (84% of total) by the ultrafine particle sizes (UTOM), which had an average AFDM value of 1886 (range 230–12 000) mg/m³. This study was among the first to reveal the predom-



FIG. 12. Comparative retention and storage by erosional vs. depositional habitats at the 16 locations. Box and whisker plots of annual data (Tukey 1977). The lines ("whiskers") connect the extremes. In case of more than one "extreme" value, only the first in the group is connected by the line. The line within the boxes denotes the median while the ends of the boxes ("hinges") delimit values midway (rank-wise) between the median and the extremes.

inance of ultrafine particles in the organic component of transport (see also Sedell et al. 1978). These and subsequent findings (e.g., Wallace et al. 1982) clearly indicate the need for finer fractionation and better understanding of the material comprising this size class. In particular, subtle downstream changes in particle sizes may be hidden using methods which do not adequately separate the smaller size fractions. Coarse particulate organic matter (CTOM) comprised 2% of the total with an average AFDM of 36 mg/m³ (range of 1-340); the maximum generally corresponded to high discharge conditions and movement of wood or decaving vascular hydrophytes. The 4-1 mm size class most frequently dominated the CTOM transport. Fine particulate organic matter (FTOM) generally accounted for 14% of the total AFDM and averaged 328 mg/ m³ (range 20-3200). In most instances, UTOM and FTOM for Michigan were significantly higher than at all other sites.

Ratios between the different particle sizes were relatively constant between seasons at most stations. With one exception (Pennsylvania station 4), UTOM did not exceed FTOM by a factor of more than 35 to 1 ($\bar{x} =$ 26:1; mode = 1.5–2.0:1). On the average (\bar{x}), UTOM exceeded CTOM by a factor of \approx 200:1 (mode = 65– 70:1), whereas FTOM was \approx 15 times more abundant than CTOM (mode = 1.5–2.5:1). The UTOM:CTOM and FTOM:CTOM patterns were inconsistent. Generally the largest river examined in a given system was the most dissimilar with respect to the ratio of fine: coarse organic matter transport. Based on annual means, the largest of our stations in the Pennsylvania, Michigan, and Oregon systems showed a relative decrease in fine particulates, but an increase was ob-



FIG. 13. Trends in transported organic matter particle sizes expressed in relation to the coarse fraction. Based on mean annual values. Shaded curve shows predictions of the River Continuum Hypothesis.

served in the Idaho system (Fig. 13). With the inclusion of ultrafines, an increase relative to coarse particulates in the largest river sites was indicated for Pennsylvania and Michigan, but the pattern for Idaho and Oregon rivers was unchanged.

We predicted that fine organic particulates should increase relative to coarse material from headwaters through increasing stream size. However, the ratio of fine : coarse particles in transport did not increase with stream size as hypothesized except in the Idaho system (Fig. 13). Variance from the prediction probably reflects CTOM derived from tributaries, from aquatic macrophytes, from debris accumulation, and from locally heavy leaf fall. Wallace et al. (1982) found a downstream decrease in the FTOM/CTOM ratio, similar to that noted for three of our sites, over orders 1-4 of a southern Appalachian stream. They also found that the ratios did not reflect downstream reductions in mean particle size. The general pattern observed for our sites was for similar ratios of fine:coarse organic matter in transport in stream orders 1 through 5, particularly with the ultrafines included. The unpredicted dominance of coarse particulates transported in the 7th order Oregon river was likely dependent on local riparian and upstream inputs of wood, alder leaves, and aquatic macrophytes, since all of our large stream sites lacked major retention devices.

Following Taylor transformation to stabilize the variance, the transport data for all sites (4), seasons (4), and stations (4) were submitted to a three-way ANOVA. We did not focus on significant associations between factors and dependent variables, since these

TABLE 3. Percent of variance explained by factors grouped for each particle size category and total of transport particulate organic matter.

	Pa	article siz	ze catego	ry			
Factor	СТОМ	FTOM	UTOM	Total TOM			
	Percent variance explained						
Site (biome)	34	35	11	8			
Station (stream size)	9	12	NS	NS			
Season (W, S, S, F)	11	10	17	9			
Multiple r^2	54	57	28	17			

may be an artifact of the analysis, but concentrated on the relative strength of these associations (Table 3). When the entire data set is viewed in this factorial design, very little (17%) of the variance in total transport organic matter can be explained. The three factors taken together explain 54 and 57% of the variance in CTOM and FTOM but little of the ultrafine transport. Of the three factors, differences among sites (biomes) seem to make up most of the explained variance but still only account for 34 and 35% of the coarse and fine transport. Differences among stations (stream size) seem to have the least importance in explaining the variance in any of the transport fractions or the total amount and in fact are insignificant for UTOM and FTOM. Seasonal effects, while statistically significant (P < .0001), explain little of the variance, and the differences among the four categories in terms of explained variance do not warrant further description.

Based on the ANOVA, transport of ultrafine particulates is rather independent of the examined factors while the transport of coarse and fine particulates shows differences depending on biome. Thus, the concentration of UTOM appears to be a dominant and relatively invariant parameter having little dependence on stream system, size, or season. Geographic location (biome) also affects the amount of coarse and fine particulates but season and stream size have relatively little effect. The results of the ANOVA also suggest that, since stream size did not explain much of the difference in transport, the expected change in particle size ratio would not be seen. (Although if the UTOM fraction, which contained 84% of the total TOM, had been further partitioned, this trend might have been revealed.) What was not predicted was the almost insignificant amount of coarse material that was transported as compared to fine and ultrafine material. These results attest to the retentiveness and/or efficiency of processing of CPOM inputs by streams regardless of geographic location.

Stream metabolism

Benthic community metabolism.—Measurements of benthic primary production and respiration were made at the four sites to determine spatial and temporal vari-

ations in utilization of solar and reduced chemical energy along the stream continuum. Because detailed analyses will be presented elsewhere, only generalizations that relate to interbiome comparisons are given here.

One of the hypotheses tested concerning stream system function was that community metabolism would change predictably downstream. Published studies have shown that headwater reaches generally are dominated by respiratory metabolism and are dependent on allochthonous dissolved and particulate energy inputs. Community function is expected to shift from a dominance of respiration (heterotrophy) to a dominance of photosynthesis (autotrophy) in downstream reaches in response to increased solar energy as a result of widening of the streambed and separation of the tree canopy. Further downstream, a return to dominance of respiration should occur as solar radiation is attenuated with increased depth and greater turbidity (Vannote et al. 1980).

1. Gross primary productivity.—Gross productivity data (estimated by summing net community primary productivity and photoperiod community respiration) are presented in Fig. 14. The coefficients of variation associated with individual data sets were usually 20–70%, although values as low as 5% and as high as 80% were obtained.

In most seasons, gross primary productivity increased with downstream direction in all biomes. The number of statistically significant differences (Scheffé Multiple Range Test, P = .05) occurring between the most upstream reach and the other reaches increased with downstream distance; i.e., reaches 1 and 2 differed in only 4 of 14 instances, 1 and 3 in 7 of 14 instances, and 1 and 4 in 10 of 14 instances. However, the farthest downstream reach did not invariably have the greatest productivity. For example, at Idaho in the summer and autumn, primary productivity was significantly greater in the third reach than in the fourth.

Primary productivity at one or both of the eastern sites was usually significantly greater than at either one or both of the western sites. However, in summer and fall, activity at some Idaho stations did not differ significantly from stations at the eastern sites. Oregon stations usually had lowest gross primary productivity at all seasons.

2. Community respiration.—Community respiration had fewer statistically significant differences between stations within a region than gross primary productivity; between-station differences occurred in only half the data sets. The CV associated with data sets for a given station/season ranged from 8–96% but most (52 of 62) were between 11–70%. Respiration usually increased with downstream direction, but not invariably (Fig. 14). In general, respiration was significantly greater in both eastern stream systems than in the western sites except in the autumn, when respiration at Idaho 1 was significantly greater than at Michigan



TABLE 4.	Loss of	leaf pack A	AFDM	expressed	as mean	percentage	per day	y (d) (or per	degree-day	(Dd) by	y station	and site.
CV = c	coefficient	of variatio	n.										

						Stat	ion						
	1				2			3			4		
Site	d	$\overline{\mathrm{Dd}}$	(CV)	d	$\overline{\mathrm{Dd}}$	(CV)	d	\overline{Dd}	(CV)	d	$\overline{\mathrm{Dd}}$	(CV)	
						Percenta	age lost						
Oregon	.35	.06	(28)	*			*			*			
Idaho	.37	.15	(27)	.16†	.05		.10	.03	(51)	.17	.05	(15)	
Michigan	1.06	.13	(18)	.55	.06	(19)	.77	.08	(24)	.69	.08	(11)	
Pennsylvania	1.53	.13	(1)	.95	.08	(30)	1.19	.11	(14)	.78	.06	(10)	

* Leaf packs lost.

† Only one pack recovered.

1, and Idaho 3 was greater than Pennsylvania 3. As with primary productivity, Oregon stations tended to possess lowest community respiration throughout the year.

3. Net daily metabolism.—The balance between gross primary productivity and 24-h community respiration is defined as net daily metabolism (NDM). This parameter provides information concerning the dominance of autotrophic or heterotrophic processes in a reach. It is analogous to the community P/R ratio but reveals absolute magnitude in grams per square metre per day.

Except for Oregon in spring (NDM = 0.02), all headwater reaches were heterotrophic in all seasons (Fig. 14). Autotrophy predominated at the farthest downstream reaches (station 4) at Michigan and Oregon at all times, at Idaho in all seasons but autumn, and at Pennsylvania during winter and summer. The balance between autotrophic and heterotrophic processes favored autotrophy with increasing downstream distance in all seasons. While the farthest downstream station was not always the most autotrophic, the across-biome comparison does indicate a downstream trend towards increased autotrophy at all sites. At Michigan and Pennsylvania, gross productivity tended to peak at the farthest downstream reach, but in the western sites, maximal productivity sometimes was obtained in intermediate reaches. Seasonal differences in metabolic activity within a reach were sometimes statistically significant. Across-biome comparison of reach function at this point presents difficulties. While in some seasons eastern sites differed from western sites in system function, in other seasons eastern and western sites grouped together. Thus, although trends with downstream direction often were evident, it appears that multiple local influences combined to regulate community activity.

Leaf decomposition.—Leaf packs of mockernut hickory (*Carya tomentosa*) collected at one location in Pennsylvania were placed at all 16 study reaches to estimate the processing of leaf material. The experiment was designed to test the hypothesis that headwater streams were able to process leaf material faster than higher order streams where leaf material is relatively rare. If there is a shift in community structure and if this shift is caused in part by the relative abundance of allochthonous detritus (Vannote et al. 1980) then a shift in processing ability should also occur. It also can be hypothesized that all 1st order streams have about the same ability for this processing, having evolved mechanisms to exploit this resource, and that this should be stronger than regional or watershed differences.

The results were subjected to ANOVA, but since the leaf packs at all but one of the Oregon stations were lost, the analysis could be made only for three of the sites. ANOVA showed that there was a significant difference (P < .001) among biomes but that there was no significant difference (.25 > P > .1) among stream sizes for percent AFDM lost per day for the 12 stations. There was also a significant interaction term (P < .001). The results are presented in Table 4 as the mean and coefficient of variation of the percentage lost for the 12 stations used in the ANOVA plus the 1st order stream in Oregon that had packs remaining. At each of the three sites, the fastest rate of leaf processing was seen at the smallest sized stream. This result appears to validate the hypothesis that small headwater streams process leaf material faster than downstream reaches. However, this only holds within a particular watershed; not all 1st order streams process faster than all higher order streams. In fact, some 3rd order streams process faster than a 1st order stream from another biome.

There was no consistent downstream trend of lower processing as the stream becomes larger (Table 4). While the hypothesis that 1st order streams have a greater ability to process leaf litter may be true, as soon as the stream gets larger a variety of mechanisms come into play causing local differences in the observed rate of processing. In general, the combination of these factors seems to be dependent on watershed character. Some characters seem to be associated with 1st order streams but little can be said about predicted changes in 2nd through 7th order streams where local conditions determine much of the behavior.



FIG. 15. Spatial distribution of benthic invertebrate functional groups, expressed as a percent of the total number of each group collected (given on the figure), at each of the four stations of each site during summer (Su) and autumn (A) or winter (W).

As mentioned elsewhere, the four sites represent a rather large range of physical environments. This diversity is especially evident in terms of thermal regime. While the leaf pack experiment was conducted during a 2-mo period in the fall, average water temperature differed substantially among sites, ranging from 13°C at Pennsylvania to 4° at Idaho. Continuously recorded temperature data, expressed on a degree-day basis, was used instead of time to express the leaf pack mass loss. As can be seen from Table 4 (and also supported by a two-way ANOVA) maximum processing again occurred at the smallest stream in each series, and there is the same inconsistent downstream trend. The disparity between 1st order streams and the other orders is now greater but the disparities among three of the 1st order streams have been removed. Oregon's 1st order stream had much lower processing even when corrected for degree days.

We conclude that temperature was responsible in part for the differences in processing in 1st order streams, but that it had little to do with the differences among higher order streams at one site, or with the fact that 1st order streams process leaves faster than those higher orders. If we assume that microbial processing is controlled primarily by temperature, then factors other than microbial decomposition must be causing the differences, probably invertebrate leafshredders and physical fragmentation.

Functional groups

At each station the invertebrates were assigned to a particular functional group following the definitions presented by Cummins (1974) and Merritt and Cummins (1978). These assignments were, however, modified depending on local differences and based on the experience and observations of the researchers at each site.

The hypothesis to be tested was that the relative importance of the functional groups would shift in concert with downstream changes in food resources. Specifically, shredders were expected to be codominant with collectors in the headwaters and then rapidly to diminish in importance; collectors were expected to increase in importance, becoming the predominant



FIG. 16. Percent composition of the total numbers of benthic invertebrates per square metre (given in parentheses) collected at each station during summer (Su) and autumn (A) or winter (W).

macroinvertebrate component in large rivers; grazers were predicted to follow the anticipated shift in the abundance of primary producers (see Stream Metabolism above). The predatory invertebrate component was seen as changing very little in relative dominance with stream size (Vannote et al. 1980).

As predicted, shredders generally were most abundant in the headwaters and rapidly declined downstream (Fig. 15). The importance of collectors in the headwaters varied with site and season, but there was a general tendency to increase in relative abundance with distance downriver. Grazers showed a tendency to be most abundant in the lower reaches during autumn (winter for Idaho) and in the upper reaches during summer, but did not strongly follow the expected pattern. The longitudinal distribution of predators was variable with no consistent pattern among sites or seasons.

At all sites except Oregon 1 and 2 (Devil's Club and Mack Creek), collectors tended to be the predominant functional group. Grazers generally ranked second, except in the headwaters where shredders replaced the grazers in importance (Fig. 16). At each station, the proportion of the community made up by predators generally was less than that of either collectors or grazers and rarely exceeded 30% of the total abundance.

Total abundance at the four sites was similar in autumn (winter in Idaho) ranging between 1500–2500 invertebrates/m² (Fig. 16). Notable exceptions were the low values (\approx 200) at the two upper stations in Idaho and the high values (\approx 7000–8000) at the bottom two stations in Michigan. Summer invertebrate densities were more variable but Michigan stations generally were the highest (\approx 3500–9000) and three of the Idaho sites were among the lowest (\approx 350–750). The high Michigan invertebrate total abundances coincide with similar maxima in benthic organic matter. In Michigan, the high summer primary production in the largest stream consisted largely of macrophytes, which were a poor food resource for grazers but produced additional high-quality fine particulates for collectors.

Synthesis

Until recently there were few generalizations about stream ecosystems. Failure to develop a unified theory of structural and functional organization in these ecosystems is due, in part, to lack of information concerning the levels and ranges of ecosystem variables from an array of streams in different geographical and vegetational settings. In addition, there has been a lack of attention to differences in terms of geomorphology, quality and quantity of inputs, and the potential for autotrophic production. The present study provides an opportunity for direct comparison of stream ecosystem properties because a range of watershed types is represented and standarized methods were used.

As an initial evaluation of interactions within this large data set, Pearson product-moment correlation coefficients incorporating data from all seasons, sites,

TABLE 5. Correlation matrix (r values) for selected ecosystem parameters. Correlation coefficients >.38 are significant (P < .01); NS indicates values were not significant. Only those parameters for which at least one significant correlation value was obtained are reported but data for all parameters examined in this study were analyzed (except macroinvertebrates). Subscripts designate the particle size classes (in micrometres).

	TOM_{45}	TOM_{50}	TOM ₁₀₀	TOM ₂₅₀	TOM 500	$TOM_{1 \times 10^3}$	BOM_{45}	BOM_{50}	BOM ₁₀₀	BOM ₂₅₀	BOM ₅₀₀	$BOM_{1 \times 1}$	03BOM4×105
TOM ₅₀	.75												
TOM 100	.77	.90											
TOM ₂₅₀	.65	.74	.90										
TOM 500	.57	.64	.84	.98									
$TOM_{1 \times 10^3}$.49	.49	.71	.91	.94								
$TOM_{4\times 10^3}$	NS	NS	.47	.63	.69	.66							
BOM ₄₅	.44	.59	.53	.43	NS	NS							
BOM ₅₀	.62	.75	.72	.53	.43	NS	.73						
BOM ₁₀₀	.55	.65	.62	.49	.39	NS	.91	.89					
BOM ₂₅₀	.41	.55	.48	.39	NS	NS	.78	.73	.85				
BOM 500	.46	.55	.52	.47	.40	.43	.83	.69	.84	.93			
BOM1×103	NS	NS	NS	NS	NS	NS	.66	NS	.57	.75	.82		
BOM _{4×103}	NS	NS	NS	NS	NS	NS	.54	NS	.39	.62	.60	.88	
BOM _{16×103}	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.63	.80
Hardness	.65	.66	.67	.56	.51	.46	.58	.82	.71	.53	.59	NS	NS

and stations were calculated for all possible parameter pairs (except macroinvertebrates). No significant correlations (P <.01) between independent parameters were found for gross primary productivity, net primary productivity, community respiration, net daily metabolism, BOM, TOM, alkalinity, hardness, NO₃-N, NH₄-N, total-P, chlorophyll *a*, temperature, photosynthetically active radiation (PAR), stream power, or discharge except as follows:

- (1) gross primary productivity vs. TOM_{.45}, hardness, temperature, and PAR,
- (2) net primary productivity vs. PAR,
- (3) community respiration, same as for GPP plus BOM₅₀, BOM₁₀₀, BOM₅₀₀, and alkalinity, and
- (4) TOM₁₆ vs. stream power.

In all of the latter cases, the correlation coefficient was between 0.44 and 0.56, except for community respiration vs. temperature, where it was 0.64. However, of the 420 possible pairwise correlations, several groups of significant relationships were observed (Table 5).

Particle sizes (BOM or TOM) were more closely correlated with adjacent size classes than with less related sizes. This supports the idea that detritus processing is a stepwise phenomenon involving small decreases in median particle size at each step (Boling et al. 1975) rather than large-scale changes in particle size. High correlations also were found between hardness (primarily calcium in these streams) and particulate organic matter. Highest correlations were with the smaller par'cle sizes (≈ 0.45 through 500 μ m) and may reflect a relationship between concentration of cation nuclei (e.g., Al, Ca, Fe, Mg) and conversion of DOM to UPOM (e.g., Lush and Hynes 1978, Dahm 1981).

Ultrafine and fine transport particulate concentrations tended to be correlated with benthic detrital standing crops (Table 5) suggesting considerable exchange between the suspended and deposited fractions. However, in general only 40–65% of the variance can be explained by this interrelationship; the remainder undoubtedly is due to physical and biological conversion of particle sizes, local terrestrial inputs, and physical features of the channel. An example of such a physical modifier is the retentiveness of the smaller Oregon streams, which is largely a consequence of accumulations of woody debris (Fig. 3) but shows up in both coarse and fine particle categories (Fig. 8).

Comparison of BOM and TOM—ecosystem retention

The relationship between detritus in storage and transport was examined by calculating their ratio after transport was multiplied by average depth to convert it to a square metre basis. This ratio is a relative measure of reach retention (RR);

$$\mathbf{RR} = \frac{\mathbf{BOC}}{\mathbf{TOC} \times d}$$

where BOC is benthic particulate organic carbon, TOC is transport particulate organic carbon and d is depth (data and units as in Table 7 and Fig. 3).

The more retentive nature of the headwater streams is apparent from our results (Table 6), particularly in the wood-dominated headwater Oregon stream. The larger streams are less retentive, presumably because of the reduced number and effectiveness of geomorphic and hydraulic controls affecting deposition. Idaho station 2 does not fit the pattern largely because of the highly erosive flow and armored, poorly retentive nature of the channel bottom. Oregon station 1 had the highest value of reach retention with 29 848 times as much material in the benthos as in transport. Pennsylvania had the lowest value for RR of all locations at its station 4 with 80 times more organic matter in the benthos than in transport. TABLE 6. The ratio of storage to transport as a measure of reach retention (RR) for the 16 locations used in this study. See text for calculation. Regression constants (α , β) and coefficients of determination (r^2) for the relationship between ln reach retention and ln link number also are given.

		Static	on				
Site	1	2	3	4	α	β	r^2
		RR (storage/	transport)				
Oregon	29 848	2302	176	192	10.0568	-0.9258	0.9540
Idaho Michigan	923	427	310	215	6.1898	-0.0937 -0.1704	0.8436
Pennsylvania	3037	1494	595	80	8.2126	-0.8654	0.9594

In order to investigate further the relationship between stream size and retention capacity, we regressed the natural log of reach retention against the natural log of link number (data from Table 6 and Fig. 3). There was a significant relationship (P < .01) for the entire data set of 16 locations taken together. When analyzed separately the relationship was also significant (P < .01) for Oregon, Michigan, and Pennsylvania with coefficients of determination higher for the three individual sites than for the entire data set (Table 6, Fig. 17). Reach retention and stream link number also were correlated for Idaho but the relationship was not significant (P > .05).

As mentioned above and shown by the slopes in Table 6 and Fig. 17, there was a general rate of change from small headwater streams to larger downstream areas in terms of retention character. The Oregon headwater stream, located in a dense coniferous forest, shows dramatic retention owing mainly to the sheer mass of woody debris. The size and bulk of this material rapidly becomes less important as the channel becomes wider and deeper in the downstream direction. At the other three sites woody debris also creates retention devices, but its relative importance compared to channel size is less. Reach retention is, therefore, moderately low as compared to Oregon. However, in Pennsylvania the rate of decrease in the retentive capacity of the stream is very close to that found in Oregon, whereas in Idaho and Michigan it is much less.

While headwater streams are more retentive than downstream reaches, each watershed has its own relationship between stream geomorphology and retention. In this study we have shown that stream size as measured by link number is inversely correlated with reach retention. However, the decrease in retentiveness depends on a combination of many factors. Most of those factors will be autocorrelated with link number, such as watershed area, discharge, depth, width, and channel roughness. However, there are other retention factors, such as riparian vegetation type, that will not be autocorrelated to stream size. The combination of these factors acting in concert creates a substrate retention capacity that is distinct for each of the watersheds studied.

While in most streams there may be an orderly

progression of decreasing retention, this is not the case in all streams, as illustrated by the Idaho data. It can still be concluded that retention is a more dominant factor in the headwaters, but the decrease may not always be uniform in the downstream direction. This is because the downstream shifts in retention factors may not be continuous. For example, Idaho did not show a continuous decrease in slope downstream. In addition, the river shows a rather dramatic riparian vegetation shift, going from coniferous forest in the headwaters to sagebrush in downstream sections.

Some authors (e.g., Naiman and Sedell 1979b) have suggested that the amount of organic material associated with the benthos is strongly influenced by stream power. Extension of this logic suggests an inverse relationship between reach retention and stream power. When we calculated unit stream power, using the equation given by Naiman and Sedell and data given in Fig. 3, we found no correlation between unit stream power and benthic organic matter for the four study sites individually or the 16 stations combined. Thus, it appears that the factors controlling the retention of organic matter in streams involve much more than just the force of flowing water, and that efforts to explain the standing crop densities of BOM must incorporate measures of material input, processing, and channel rugosity as well as of water transport mechanisms.

Stream metabolism

To allow comparison between benthic and transport metabolic processes, the transport estimates originally measured in milligrams per cubic metre were first converted to grams per square metre by multiplying by depth, and then, using an average respiration rate of 0.5%/d (R.C. Petersen, *personal observation*), the transport respiratory metabolism (TRC) was derived. The consumption of organic matter, measured as respired C, was considerably (1000-fold) higher on the stream bottom (0.10–0.96 g·m⁻²·d⁻¹) than that estimated for the water column (0.1–10.5 × 10⁻³ g·m⁻²·d⁻¹) (Table 7) even though a relatively high respiration coefficient was used for calculating water column activity.

Net daily metabolism (NDM) reflects the interplay between community production and decomposition. Since metabolism in the water column of the study



FIG. 17. Least squares linear regression $(y = \alpha + \beta x)$ of reach retention (defined in the text) on stream size (as link number). Coefficients of determination (r^2) and regression coefficients (α, β) given on graph.

streams was minimal (Table 7), conditions in the benthos explain the major observed metabolic responses. On a mean annual basis, benthic net daily metabolism shifted from a strongly heterotrophic state in the headwaters to reduced deficits and eventual autotrophic conditions at the downstream sites (Table 7). At Oregon and Idaho sites, autotrophic conditions began to predominate at station 3, while at the Michigan site autotrophic predominance was delayed until station 4. Annually, Pennsylvania NDM never attained a positive value, probably because the terrestrial canopy never opened sufficiently to permit significant autotrophic production. Stream width at Pennsylvania station 4 was only \approx 17 m, whereas at the most downstream station of the other sites it was 40–45 m. However, periphyton standing crops at Pennsylvania station 4 also were low because of frequent scour by storms. While turbidity differences may have existed between stations and sites, pronounced turbidity was not encountered for long periods and probably had minor influence in the shallow water column.

Community respiration could be expected to exhibit a reverse pattern from primary productivity and be greatest in headwater reaches with associated larger detrital standing crops. Since this did not occur (Fig. 14, Table 7), increased respiration either is linked to reduction in detrital particle sizes or is related to increases in periphyton and associated heterotrophic microbes and meiofauna.

Material cycling

The characteristic unidirectional flow of stream ecosystems adds another dimension to carbon and other nutrient cycles by downstream displacement of the materials involved. In a broader perspective, cycling still occurs, but the introduction of this additional spatial dimension (distance downstream) results in partially open cycles or "spiraling" (Webster 1975, Wallace et al. 1977, Newbold et al. 1981, 1982, Elwood et al. 1982).

Material spiraling in flowing waters is a function of both physical and biological processes. This is an important distinction between the situation in streams

TABLE 7. Mean estimates of transported (TOC) and benthic (BOC) particulate organic carbon, respiratory metabolism in the transport (TRC) and benthos (BRC), and net daily metabolism (NDM) for the four study sites. Heterotrophic reaches (negative NDM) are indicated by underlining; autotrophic reaches (positive NDM) are indicated by boldface numbers.

Station number					
size)	Carbon measure	Idaho	Oregon	Michigan	Pennsylvania
1	$\begin{array}{c} TOC \ (mg/m^3) \\ BOC \ (mg/m^2) \\ TRC \ (mg \cdot m^{-2} \cdot d^{-1}) \\ BRC \ (mg \cdot m^{-2} \cdot d^{-1}) \\ NDM \ (mg \cdot m^{-2} \cdot d^{-1}) \end{array}$	$ \begin{array}{r} 1056 \\ 97 451 \\ 0.5 \\ 291.9 \\ -83.4 \end{array} $	476 710 371 0.1 113.7 -57.3	2748 303 005 3.4 225.3 -127.8	1105 201400 0.3 443.7 -224.1
2	TOC	1896	231	3402	518
	BOC	68 079	116 993	435 814	92 883
	TRC	2.2	0.2	5.1	0.3
	BRC	257.1	133.9	652.8	441.7
	NDM	125.0	-29.1	-44.0	-101.4
3	TOC	594	255	2226	784
	BOC	161 625	40 348	482 437	126 005
	TRC	1.2	1.1	7.8	1.1
	BRC	400.6	170.6	667.7	352.4
	NDM	84.1	15.3		-1.0
4	TOC	663	339	2333	1522
	BOC	105 709	38982	451461	48 608
	TRC	1.5	2.7	10.5	3.0
	BRC	188.1	162.2	918.5	693.1
	NDM	59.6	30.1	85.1	86.6

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	Mecha Retention	nism Biologica	Effect on Nu Il Rate of	itrient Cycling Distance Between	Ecosystem Response to Nutrient Addition	Ecosystem	Cate	gorization study
A	нісн	Activity HIGH	Recycling FAST	Spiral Loops SHORT STREAM FLOW	CONSERVATIVE (I>E)	HIGH	MI PA	2,3 1,2,3
В.	HIGH	LOW	SLOW	SHORT	STORING (I>E)	нібн	OR ID MI	1,2 1 1
C.	LOW	HIGH	FAST		INTERMEDIATELY CONSERVATIVE < A but > D	LOW	ID MI PA	3 4 4
D.	LOW	LOW	SLOW		EXPORTING (I=E)	LOW	OR ID	3,4 2,4

FIG. 18. Postulated effects of different interactions between distance of downstream movement (e.g., $v \times time$) and biological activity (such as BRC or k) on organic matter ("nutrient") cycling in streams and their relationships in the streams of this study (ID—Idaho, MI—Michigan, OR—Oregon, PA—Pennsylvania). I = import, E = export. In the schematic representation of "spiraling," rate of recycling reflects the biological activity. The smaller the diameter of a loop the faster the rate. Distance between spiral loops represents the extent of downstream displacement of a cycle by the unidirectional flow of water. The effect of flow can be offset by retention mechanisms so that the higher the retention the shorter the distance between loops (i.e., the more nearly complete the cycle at any one point in the stream). The quantity of material being cycled is represented by the thickness of the spiraling line.

and that occurring in most other ecosystems. Downstream displacement is primarily a function of physical mechanisms. Thus, the degree of displacement of the cycle from its conventional closed form is determined largely by water flow, and in general, the greater the flow, the greater the distance between the "loops" of the spiral (Fig. 18). Stream ecosystems exhibit a number of mechanisms for offsetting the effects of unidirectional flow (Table 8). These mechanisms have the effect of reducing the distance between the loops of the spiral by slowing the rate of downstream transport of materials. The actual recycling of materials in streams, as in other ecosystems, is controlled largely by biological activities and hence is largely a function of the biota and temperature, oxygen, and basic nutrient conditions. Rate of organic matter recycling can be measured by the rate of community respiration (Newbold et al. 1982). Because of the completely different roles played in material spiraling by physical and biological factors, we believe that it is important to distinguish continually between displacement and recycling in any attempts to understand stream ecosystem dynamics.

Elwood et al. (1982) and Newbold et al. (1982) use community respiration, divided by the standing crop of organic matter, for estimating rate of recycling (=k). Calculation of these values (as BRC/BOC, from Table 7) showed a general tendency for k to increase downstream at all sites but Idaho, though each responded at a different rate (Table 9, Fig. 19). Values range from 0.07/yr at Oregon station 1 to 5.22 at Pennsylvania station 4, but most were between 0.26 and 1.75. Benthic respiratory metabolism (BRM) showed a similar tendency to increase downstream at all sites but Idaho (reported as BRC in Table 7 and Fig. 19). However, distinctions between sites were much clear-

TABLE 8. Mechanisms for slowing the rate of loss of organic materials in stream ecosystems and their modes of action.

Retention mechanism	Mode of action
 Physical storage: wood debris, boulders, macro- phyte beds, pools and al- coves, and deep sedi- ments. 	 Retain materials near points of origin and delay their movement down- stream.
 Biological uptake and storage: primarily as plant and animal tissue but also as secretions (commonly found in shells, cases, and nets), fecal pellets, etc.* 	2) Reduce rate of down- stream loss as a result of capture, utilization, and (partial) conversion to biomass.
 Reduced gradient and/or flow velocity. 	3) Reduce rate of transport.

* Organisms, especially invertebrates, may also increase the rate of downstream loss by reducing particle size, dislodging material, and increasing leaching rates (Newbold et al. 1982). But we believe that their net effect will be to slow the downstream progression of organic matter.

TABLE 9. Estimates of rate of downstream movement (v), recycling rate (k), turnover length (S), and turnover time (T) for the four study sites.

v n/d)	<i>k</i> (yr ⁻¹)	S (km)	T (yr)
0.19	0.07	1.0	13.9
5.23	0.40	4.8	2.5
66.3	1.53	39.6	0.7
33	1.53	246	0.7
32.3	1.10	10.8	0.9
90	1.39	129	0.7
31	0.91	92.3	1.1
50	0.66	200	1.5
7.3	0.26	10.4	3.9
89.2	0.55	59.5	1.8
56.3	0.51	40.2	2.0
00.9	0.73	50.4	1.4
1.9	0.80	0.9	1.3
4.7	1.75	1.0	0.6
7.7	1.02	2.8	1.0
40	5.22	30.8	0.2
	7.3 89.2 56.3 00.9 1.9 4.7 7.7 40	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$



er for BRM than for k and the BRM values for each site were more closely related to water temperature than were those of k (Fig. 19). We are not certain of the reason for the differences in the relationships of BRM and k with temperature; both were expected to show similar patterns. However, it is likely that the metabolically reactive portion of the BOM varies from one location to another and that dividing BRM by BOM to get k obscures the actual conditions by not taking these differences in quality into account. For example, Michigan, which on the basis of temperature would be expected to have high recycling rates (and does when BRM is considered), has some of the lowest k values. This probably is due to the large masses of BOM found there, a large proportion of which is undergoing anaerobic decomposition (K. W. Cummins, personal observation). If it were possible to distinguish only the metabolically more active (aerobic) portion of this material in calculating k, the values would be much higher. Therefore, in order to summarize conditions at each of the study locations with respect to material cycling (Fig. 18), we used absolute values of benthic community respiration rather than k. For example, on this basis Michigan stations 2, 3, and 4 are considered to have high biological activity and therefore to have "fast" rates of recycling. Half of the study stations were categorized as having fast rates of recycling and half were characterized as being slow. All of the "fast" locations, except Idaho station 3, were in eastern, deciduous forest streams and all of the "slow" locations, except Michigan station 1, were in western, coniferous forest streams.

FIG. 19. Community respiration (both as k and as BRC) and annual mean temperature in relation to stream order at each study site.

Using data from Table 7 and Fig. 3, the rate of downstream movement (v) of material at the different stations may be calculated (Table 9) (Newbold et al. 1981, 1982, Elwood et al. 1982). v equals the product of TOC (in grams of carbon per cubic metre) and discharge (Q in cubic metres per day) divided by the product of BOM (in grams of carbon per square metre) and mean width (in metres). Rate of downstream movement ranged from about 20 cm/d at Oregon station 1 to >1 km/d at Oregon station 4. For the purposes of categorizing the study streams, distance of downstream movement in a day was obtained by multiplying by t (=1d); values ≤ 100 were considered "short" and those >100 were classed as "long" (Fig. 18). Thus at all of the headwater stations 1 and 2 (except Idaho station 2) materials moved relatively short distances as a result of physical processes. At Pennsylvania, a relatively low rate of particle movement persisted through station 3. But at station 4 at all of the sites, and at the station 3 locations in Oregon and Idaho, the downstream movement of materials increased perceptibly.

The ratio of downstream velocity (v) to rate of recycling (k) yields the organic matter turnover length (S). S (=v/k) is defined as the average travel distance

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of an atom of nutrient between its entry or fixation in the stream and its loss through respiration (Elwood et al. 1982). Turnover lengths for the study streams (Table 9) showed the same tendency to change (increase) with distance downstream seen for many of the other ecosystem attributes in this study (Idaho and Michigan stations 2 seem to be exceptions in this case). The shorter turnover lengths found in the headwaters were almost totally due to the slow velocity of materials, since respiration rates were uniformly low (often lowest) at the upstream stations. Pennsylvania stations 1 and 2 and Oregon station 1 had the shortest carbon turnover distances but still required ≈ 1000 m of stream for processing of organic matter. Greatest turnover distances (100 to 250 km) were found at Idaho stations 2, 3, and 4 and Oregon station 4. However, turnover lengths do not give the full story because the time required for the passage of an atom through a section of stream is not apparent. Sections with short turnover distances may actually have longer retention times than regions with long turnover distances. Turnover times, calculated as:

$$T = \frac{1}{v} \cdot S$$

ranged from 0.2 to 14 yr, but most of the values were between 1 and 4 yr (Table 9). Highest values generally were found in the headwaters, again emphasizing the greater capacity of these small tributaries for physical retention of organic matter.

CONCLUSION

The postulated gradual change in ecosystem structure and function along a stream (Vannote et al. 1980) is supported by this study. Deviations from the expected pattern are explainable largely on the basis of variations imposed by: (1) watershed climate and geology, (2) broad scale riparian determinants (e.g., extensive tree cover or open meadowland), (3) tributaries, and (4) location-specific lithologic and geomorphic features (e.g., a large block boulder or a braid in the channel). These forces are superimposed on the overall tendency for physical conditions within a river system to change progressively and predictably with increasing stream size.

Climatic and geologic controls affect nutrient supply, runoff pattern and amount, and general geomorphic responses (e.g., Figs. 3 and 5). Riparian determinants control light and litter inputs, physical storage via the presence and absence of debris accumulations, etc. Tributaries may differentially alter temperatures, particle concentrations and types, and nutrient loads with their entrance into the main stream. Locationspecific features cause the disruption of general geomorphic patterns within a stream reach. Watershed and riparian characteristics interact to regulate detrital transport and storage dynamics and determine the relative importance of autotrophy and heterotrophy in a given stream reach. For example, although Oregon headwater streams were the highest gradient systems investigated (Fig. 4), they are highly retentive physically mainly due to large accumulations of wood debris (dry mass 10–30 kg/m²). Metabolic parameters, such as net daily metabolism and community respiration, reflect the general geologic–hydrologic controls, but they are significantly modified by characteristics of riparian vegetation, which largely determine light regime and allochthonous inputs and modify temperature.

The four factors listed above also tend to produce gradient effects downstream from their point of initial impact on the stream. Thus the idea of an overall continuum response is valid, but the framework must be visualized as a sliding scale which is shifted upstream or downstream depending on macroenvironmental forces (factors 1 and 2) or reset following the application of local, "micro"-environmental forces (factors 3 and 4). For example, the point along the continuum at which there is positive net daily metabolism on an annual basis varies from order 2 in Idaho to 3 in Oregon and 4 in Michigan, and is still not observed by order 5 in Pennsylvania. As an example of a microenvironmental effect, in Idaho local factors account for an increase in coarse organic matter at the 5th order station, which serves to set conditions for this component back to levels expected for a 3rd order stream (Fig. 10c). However, in general the "resets" are expected to be rather transient due to the size of the main stream relative to the factor being imposed.

An especially important aspect revealed by this study is the critical role played in ecosystem structure and stability by retention devices in streams. It is clear (see Comparison of BOM and TOM—Ecosystem Retention, and Material Cycling) that material turnover distances and times are determined primarily by current velocity and the presence and effectiveness of physical retention devices. Biological processes played a lesser quantitative role in the systems studied here.

Retention devices can take a variety of forms (Table 8), occur at a wide range of frequencies, and perform at varying levels of efficiency. Log jams and other wood debris accumulations probably provide especially effective means of reducing material losses from small streams because of their high filtering capacity and high frequency of occurrence along the stream (see Swanson and Lienkaemper 1978, Bilby and Likens 1980, Bilby 1981). Such devices and/or reduction of stream gradient should enhance the productivity of stream ecosystems by shortening spiraling length (see also Elwood et al. 1982). They will also serve to reduce scouring, sloughing, and downstream drift and permit the buildup of microbial and invertebrate processors. But recycling is primarily a biotic process, so any enhancement of the rates of processing of organic matter

or of the exchange of nutrients beyond some existing potential probably will require manipulation of temperature, oxygen supply, and/or limiting nutrient supplies.

Even barring major restructuring caused by large storms or channelization, the response of stream ecosystems to dissolved and particulate matter inputs differs depending on the interaction between physical retention and biological activity (Fig. 18, center column). For example, systems with short increments of movement downstream and relatively fast rates of recycling (i.e., relatively short time delays in moving from the biotic to the abiotic compartments and back again, as in streams such as Pennsylvania stations 1, 2, and 3) will tend to process large amounts of organic matter and nutrients and will be classed as "conservative." In contrast, systems with slow rates of recycling and long distances between spirals (such as cold, fast-flowing streams that have few retention mechanisms, e.g., Idaho stations 2 and 4) tend to be more conduit-like and export a large proportion of the material they receive and produce. Streams with relatively high retention and slow-to-moderate rates of biological acitivity (e.g., Oregon, Idaho, and Michigan stations 1) will store relatively large amounts of organic matter.

Ecosystem stability in streams may be achieved by a dynamic balance between forces contributing to stabilization (e.g., retention mechanisms) and those contributing to its instability (e.g., floods) (Vannote et al. 1980). In this context, we expect small streams in unperturbed watersheds to be more stable ecosystems than intermediate-sized streams. This generalization tends to be borne out by the present study (Fig. 18, last two columns). Under natural, vegetative-climax conditions, small streams will maintain a more constant or predictable food base, more favorable substratum conditions, and more moderate and reliable flow than intermediate streams because of their greater physical retentiveness. Such systems are highly resistant to change, but once perturbed (e.g., through clearcutting and removal of wood debris from the streambed) they may require decades or centuries to recover. In contrast, midsized streams constantly undergo change as reflected by their wide range of discharges, largescale bed movements, and lack of storage and its attendant buffering capacity in terms of food resources. Large rivers may show a tendency toward increased stability because of reduced turbulence near the streambed, off-stream (flood plain) storage of water and materials, and the tendency for smoothing out large upstream fluctuations in flow.

Major characteristics of the ecosystems of small headwater streams and larger rivers within a given geological-climatic unit (biome) are compared in Table 10. Actually, the two types of characteristics intergrade with progressive change in size of the stream and, for a given system, the scale will shift between TABLE 10. Comparison of some major ecosystem characteristics at the two extremes of the river continuum.

	Headwater streams	Rivers (>7th order)
A)	Biological processes are co- dominant with geomorphic- hydrologic controls of sys- tem dynamics.	Same
B)	System dominated by ripar- ian processes for inputs of organic matter; wood, if present, is usually a stable structural element, although its location is random.	System dominated by up- stream processes; large wood debris is a tran- sient structural element but the location of its occurrence is predict- able.*
C)	Biological processes quali- tatively well matched to in- puts but quantitatively in- sufficient.	Biology matched to both quantity and quality of inputs.
D)	Physical turnover (e.g., v) low.	Physical turnover high.
E)	Biological turnover (e.g., <i>R</i> or BRM/BOM) low.	Biological turnover high.
F)	Processing occurs mainly on the bottom.	Processing occurs mainly in the water column.

* Prior to 1880 wood probably was an important structural element in most North American rivers, especially in the crossover areas between meanders, but these "snags" were systematically removed for navigation purposes by the United States Corps of Engineers.

the two sets as explained above. In the headwaters, the characteristics tend to result in the long-term accumulation of organic matter; proceeding downstream, the system becomes more balanced to its inputs until, in the large rivers, inputs and outputs are about equal (see Fig. 18 center and final columns for results from our streams).

In order to address the expanded view of the River Continuum Concept elaborated in this section, we are currently studying a single, relatively unperturbed river ecosystem extending well beyond (15 000 links) the upper size limits considered in the present study (800 links). In addition to providing a further test of the River Continuum Concept and extending its application from mid- to large-size streams, the project is expected to help resolve questions concerning the relationship of stream size to retentiveness and ecosystem stability, and to permit detailed examination of the influence exerted by tributaries and local geomorphic features. Study of this large river system, coupled with the regional comparisons presented here, should provide a solid base for understanding stream ecosystem dynamics.

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