

Developments in Stream Ecosystem Theory¹

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Four significant areas of thought, (1) the holistic approach, (2) the linkage between streams and their terrestrial setting, (3) material cycling in open systems, and (4) biotic interactions and integration of community ecology principles, have provided a basis for the further development of stream ecosystem theory. The River Continuum Concept (RCC) represents a synthesis of these ideas. Suggestions are made for clarifying, expanding, and refining the RCC to encompass broader spatial and temporal scales. Factors important in this regard include climate and geology, tributaries, location-specific lithology and geomorphology, and long-term changes imposed by man. It appears that most riverine ecosystems can be accommodated within this expanded conceptual framework and that the RCC continues to represent a useful paradigm for understanding and comparing the ecology of streams and rivers.

Quatre importantes lignes de pensée fournissent une base pour l'élaboration d'une théorie détaillée sur les écosystèmes lotiques : (1) l'approche holistique; (2) le lien entre les cours d'eau et leur emplacement terrestre; (3) le cycle de matières dans les systèmes ouverts; et (4) les interactions biotiques et l'intégration des principes sur l'écologie des communautés lotiques. Le concept de continuum du milieu fluvial représente une synthèse de ces idées. On présente des suggestions pour l'éclaircissement, l'expansion et le perfectionnement de ce concept de façon à y inclure des échelles spatiale et temporelle plus larges. Sous ce rapport, les facteurs importants comprennent le climat, la géologie, les tributaires, la lithologie et la géomorphologie de chaque emplacement et les perturbations humaines à long terme. Il semble que la plupart des écosystèmes fluviaux peuvent être inclus dans cette structure conceptuelle élargie et que le concept de continuum représente toujours un paradigme utile pour comprendre et comparer l'écologie des ruisseaux et des rivières.

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At the beginning of this century, limnologists studying streams focused in great detail on the morphology, life cycles, behavior, and trophic relations of stream organisms (e.g. Steinmann 1907; Wesenberg-Lund 1911; Thienemann 1912). The observed diversity of the stream biota

led several researchers to seek simplifying generalities in terms of the observed fauna (e.g. Steinmann 1915; Thienemann 1925; Carpenter 1928; Needham and Lloyd 1930). These early efforts stressed observation, and although a quantitative approach was soon adopted, the approach and the investigations conducted through the 1950's were largely descriptive and autecological in nature. Since that time, the direction of stream research has changed to incorporate a more synecological and holistic approach. In the following we briefly discuss four major areas in

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TABLE 1. Major areas in which developments in stream ecosystem theory have taken place in the past decade.

1. Progression from an individualistic to a holistic viewpoint
2. Realization of the critical linkage between a stream and its terrestrial setting
3. Development of ideas about material cycling in open systems
4. Recognition of the importance of biotic interactions to the stream community

which changes in perspective regarding stream ecosystems have occurred (Table 1) and which we believe form the foundation for further advances in stream ecology. With this foundation in mind, we then propose several adjustments to our earlier concept of riverine ecosystem dynamics (Vannote et al. 1980) which have grown out of our continued interest in this area (Cummins et al. 1983; Cushing et al. 1983b; Minshall et al. 1983, 1985; Petersen 1984; Sedell and Froggatt 1984; Vannote and Minshall 1982) and out of recent studies by others.

Major Contributions in Stream Ecosystem Theory

Progression from an Individualistic to a Holistic Viewpoint

A truly holistic view of streams as ecosystems did not begin until the late 1950's, being strongly influenced by Eugene and Howard Odum (e.g. Odum 1957; Teal 1957) and Ramon Margalef (e.g. Margalef 1960). The energy budget approach of Odum for stream segments led to a flood of stream ecosystem budgets (Warren et al. 1964; Mann et al. 1972; Hall 1972; Fisher and Likens 1973; Westlake et al. 1972) for both large and small streams which has continued to the present (Cummins et al. 1983).

The past 10 yr also have seen a shift in perspective from that of viewing streams, or different stretches within a stream, as individual entities to that of a synthetic (integrated) view which seeks generalizations about streams as ecosystems (e.g. Cummins 1974; Webster 1975; Wallace et al. 1977; Newbold et al. 1982a, 1982b; Minshall 1978; Minshall et al. 1983b). The prevalent synthetic view of stream ecosystems is that of the River Continuum Concept (RCC) (Vannote et al. 1980), its antecedents (see Ide 1935; Margalef 1960; Illies 1961; Hynes 1963; Ross 1963), and correlaries (Wallace et al. 1977; Newbold et al. 1981, 1982a, 1982b; Elwood et al. 1983; Ward and Stanford 1983) which emphasize the unifying aspects of flowing water (particularly geomorphology and fluid hydraulics) in structuring stream communities and providing a template for stream ecosystem function. Historically, a number of stream ecologists have recognized shifts in community structure along the course of a river. Most focused on macroinvertebrates and fish (see papers reviewed by Hawkes 1975) and many viewed the relationship as a series of distinct zones (Illies 1961) rather than a gradually integrating continuum (but see Maitland 1966). Few attempted to treat streams and rivers holistically, and particularly to view them as ecological systems (e.g. Rzoska 1978). Margalef (1960) and Mann (1979) are noteworthy exceptions.

The RCC (Vannote et al. 1980) conceptualizes the entire fluvial system as a continuously integrating series of physical gradients and associated biotic adjustments. Streams are seen as longitudinally linked systems in which ecosystem-level processes in downstream areas are linked to those in upstream areas. This approach has provided useful generalizations con-

cerning 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 a river. These views are summarized by Cushing et al. (1983b) who stated, "... streams are best viewed as gradients, or continua, and that classification systems which separate discrete reaches are of little ecological value." The RCC is undergoing evolution, testing, and refinement — some aspects of which will be addressed below. However, even if nothing else were to come from it, this paradigm has served to focus attention on rivers as integrated systems and to stimulate the formulation and testing of systems-level hypotheses which have helped to move lotic ecology from a descriptive to a predictive mode.

Realization of the Critical Linkage between the Stream and Its Terrestrial Setting

Illies (1961), Illies and Botosaneanu (1963), and Ross (1963) were among the first to note similarities among stream communities over broad geographic areas. Ross in particular was struck by the association between stream macroinvertebrates and terrestrial biomes or what he termed the landscape aspect. He postulated the importance to the stream of the combination of climatic conditions necessary for the existence of such vegetation zones plus the factors imposed by the physical nature of the vegetation itself. The importance of the land-stream interaction also is implicit in the watershed approach to the study of terrestrial ecosystems (e.g. Likens et al. 1977).

Also in the early 1960's, Hynes (1963) published the first of a series of studies which drew attention to the importance of terrestrially derived (allochthonous) detritus to stream dynamics. He summarized the importance of the stream-land linkage in his paper "The stream and its valley" (Hynes 1975). Among other things, he noted that the slope of the valley, the depth and permeability of the soil, and the patterns of precipitation greatly affect the pattern of flow and dissolved organic matter content of the stream. Hynes (1975) and others have stressed the importance of the type and density of the terrestrial vegetation and of its chemical and biological dynamics once it reaches the stream. The pioneering work in this area emphasized conditions in streams draining forests and consequently, allochthonously derived organic matter. But the broader implication of these studies is clear: the terrestrial setting for the stream — be it forest, desert, taiga, or grassland — is crucial to the operation of stream ecosystem processes. Additional support for this idea has come from investigations by Fisher and Likens (1973), Minshall (1978), Cushing et al. (1980), Fisher et al. (1982), Molles (1982), Cummins et al. (1984), Minshall et al. (1983b), Naiman (1983), Strayer (1983), and others. Early research on the importance of allochthonous detritus has in turn given rise to additional major developments in the processing of this material, particularly by microbes (see reviews by Anderson and Sedell 1979 and Bird and Kaushik 1981).

Prior to a surge of interest in the role of allochthonous detritus in streams, considerable attention had been given to the primary producers (e.g. Butcher 1932, 1933, 1940, 1946; Blum 1957; Douglas 1958; Gumtow 1955) and to their role in stream food chains (e.g. Percival and Whitehead 1929; Jones 1950). With the interest generated by almost continuous breakthroughs in the area of allochthonous detritus dynamics, the important supportive or primary role of autotrophy in stream ecosystems was virtually ignored. By the mid-1970's, however, stream researchers began to direct their attention outside of forested

headwater streams. It became clear in the broader river basin and interbiome contexts, as well as in moderately shaded headwaters everywhere, that autotrophs contribute significantly to ecosystem dynamics in both the mass and quality of material they provide (Minshall 1978). Now it is generally recognized that both terrestrial plant debris and aquatic primary production are important sources of simple carbon compounds and that they commonly complement one another, both seasonally and along a river, to provide a more reliable and varied food base for lotic consumers than either would do alone (Hornick et al. 1981; Cushing and Wolf 1982; Gregory 1983).

Development of Ideas on Material Cycling in Open Systems

Webster (1975) pointed out that nutrients in a stream do not cycle in place, but are displaced downstream as they complete a cycle. He described this coupling of transport and cycling as "spiraling" and suggested that the ability of a stream to utilize nutrients is associated with the tightness and magnitude of the spirals. Webster (1975) and Webster and Patten (1979) proposed nutrient spiraling as a mechanism to account for the apparent ability of stream ecosystems to withstand and recover from disturbance. Later, Wallace et al. (1977) applied the idea in describing the role of filter feeders in streams. They suggested that filter feeders, through their capture of seston, impede the downstream transport of organic matter and serve to reduce the distance between spirals. The present state of our knowledge in this area is largely a result of the mathematical models developed by Newbold and his colleagues at Oak Ridge National Laboratories (Newbold et al. 1981, 1982a, 1982b; Elwood et al. 1983). These collective studies are termed the nutrient spiraling concept.

In four stream systems studied in an interbiome test of the RCC (Minshall et al. 1983b), all first-through third-order stations had "tight" spirals associated with a high retention capacity; the larger stream locations (fifth- to seventh-order) all had long distances between spirals. Rate of recycling was considered "fast" for about half of both the small- and large-sized streams, indicating differences in degree of biological influence (Minshall et al. 1983b). But in all streams studied, spiraling distance was determined primarily by current velocity and the presence and effectiveness of physical retention devices; biological processes played a lesser quantitative role. Thus, in many cases, the retentive capacity of the stream exerts a significant influence on ecosystem dynamics. In another study, Wallace et al. (1982) have shown that experimental reduction of the lotic insect fauna reduces the breakdown, utilization, and subsequent downstream transport of organic matter, indicating that consumers are important in regulating energy flow and nutrient cycling in stream ecosystems (see also Brock 1967; Elwood et al. 1983). Thus, physical retention and macroinvertebrate processing are important mechanisms, along with the microbial action mentioned earlier, for closing or tightening the recycling process in streams and preventing the rapid throughput of materials.

Together, the RCC and nutrient spiraling concepts point to a shift from the view of streams as discrete segments to one of a continuous, interacting set of biological and physical processes along the stream gradient (Newbold et al. 1982b; Cushing et al. 1983b). This shift should lead to a reevaluation of the idea that streams are conduits that simply transport materials from the land to the sea, and hence to a greater appreciation of the metabolic and retention roles streams play.

Recognition of the Importance of Biotic Interactions within the Stream Community

One of the underlying biases of research in lotic ecology has been that streams are highly variable and hence unpredictable. Consequently, stream communities often are regarded to be dominated by physical factors and highly individualistic (e.g. Winterbourn et al. 1981; Grossman et al. 1982). However, we suggest that while stream communities are not strictly deterministic, neither are they a hodgepodge of organisms resulting solely from stochastic events (see e.g. Barnes and Minshall 1983). The probability theory of fluvial geomorphologists (Leopold and Langbein 1962), and the thermal equilibrium theory (Vannote 1978; Sweeney and Vannote 1978; Vannote and Sweeney 1980), clearly suggest that there is a high degree of predictability (and hence opportunity for determinism) embedded in the apparent stochasticity of streams. Also, as pointed out by Turelli (1981) and Schoener (1982), relatively small amounts of environmental fluctuation have small biological effects so that the simpler deterministic approach often is adequate. In addition, not only does the opportunity for density-dependent (deterministic) phenomena exist in streams (Horwitz 1978; Shiozawa 1983; Minshall et al. 1985) but, in fact, biotic determinants are operable (e.g. Hildebrand 1974; Hildrew and Townsend 1976; Bohle 1978; Peckarsky 1979, 1980, 1981; Peckarsky and Dodson 1980a, 1980b; Hart 1981, 1983; Wiley and Kohler 1981; Allan 1982; Fisher et al. 1982; Bruns and Minshall 1983; McAuliffe 1983, 1984).

The RCC is primarily a deterministic model to some (Winterbourn et al. 1981; Winterbourn 1982; Grossman et al. 1982); others view it as largely stochastic (Barmuta and Lake 1982; Fisher 1983). Actually it lies somewhere in between (see e.g. Levins and Lewontin 1980). For example, the RCC focuses on physical features of the environment as providing much of the habitat template (*sensu* Southwood 1977) for stream communities, but it also is founded on trophic responses that are generally considered to be largely deterministic (Richardson 1980; Fisher 1983; Gorman and Karr 1978; Matthews 1982).

In addition to the relative spatial (longitudinal) and temporal predictability now believed to exist in stream environments, certain characteristics of the biota allow them to recover quickly from environmental fluctuations and thereby minimize the effects of what commonly are viewed as significant perturbations. In particular, the mobility, short life cycles, high reproductive rates, and ability to encyst or to burrow into the substratum allow stream organisms to avoid or adjust quickly to regular variations in the stream environment (e.g. flood resets) and to treat these variations essentially as *time constants* (see Hutchinson 1953) (e.g. Lehmkuhl and Anderson 1972; Minshall et al. 1985; Winget 1984). Studies of invertebrate colonization on introduced substrata (Minshall 1984) or following "catastrophic" flood and dewatering (Minshall et al. 1983a) also support the idea that rapid recovery from physical disturbance in streams is commonplace. Thus, these reset events are not really "stress," at the system level at least, and community structure is dependent on them in order to persist. Further, within the periods of physical variation (e.g. between spates) there commonly are sufficient time spans to permit the establishment and maintenance of equilibrium conditions. There seem to be certain periods during the year when equilibrium (hence deterministic or density dependent) conditions may prevail.

Most lotic consumers are trophic generalists or selective omnivores (Hutchinson 1981) that feed in proportion to the

broad kinds and amounts of foods available. Thus, the belief that competition for food is not a major factor in structuring stream communities is related to the widely held view that streams are highly variable and hence stochastic in nature. The RCC (and the data subsequently collected to test it: Hawkins and Sedell 1981; Minshall et al. 1982, 1983b; Cushing et al. 1983a) suggests that food relationships are important in structuring stream communities (see also Mackay and Wiggins 1978; Molles 1982). Lotic consumers also show morphological specialization with respect to food-gathering structures (Cummins and Klug 1979; Hale 1981; Merritt and Cummins 1978) resulting in considerable partitioning of food resources based on particle size, palatability, particle type, and constituents (Cummins 1973; Wallace et al. 1977; Anderson and Cummins 1979; Cummins and Klug 1979; Sheldon 1980; McAuliffe 1983). Ongoing competition for food has been demonstrated by Hart (1983) and McAuliffe (1983, 1984) whereas in other cases, resource partitioning (resulting in the "controlled" avoidance of competition) is evident (Minshall 1968; Mackay and Kalff 1969; Vannote 1978; Bruns and Minshall 1983).

Another important step in the development of stream ecosystem theory is the integration of certain principles of community ecology within the broader geomorphic/ecosystem context. The RCC, in conjunction with recent developments in population and community ecology (e.g. Cody and Diamond 1975; Southwood 1977; Anderson et al. 1979; Brown 1981; May 1981), suggests that the organization of lotic macroinvertebrate communities can be explained by the mean state of environmental variables and their degree of temporal variability and spatial heterogeneity. The gradient from headwaters to high-order reaches may be viewed as a spectrum of differentially variable habitats, and the patterns of species diversity for the total community and for specific functional groups appear to be interpretable within the context of habitat templates (see Southwood 1977). For example, we have found that components of community organization of lotic macroinvertebrates (e.g. species richness, niche breadth and overlap, and community complexity and stability) can be explained by the degree of temporal variability and spatial heterogeneity (D. A. Bruns, A. B. Hale, and G. W. Minshall, unpubl. data; Minshall et al. 1985). This structural approach complements previous RCC studies which emphasized ecosystem function. It also serves to introduce a conceptual basis for understanding lotic communities which in the past have been studied predominately from a descriptive aspect. And finally, it points the way for experimental investigations whereby mechanisms of community organization can be addressed directly.

Expansion of the River Continuum Concept to a Broader Geographic and Historical Model

The RCC defines a standard for natural, unperturbed lotic systems against which existing streams can be compared. The utility of the RCC lies in its identification of a set of general conditions and relationships that can be used to study and compare stream systems. In this context, the RCC provides a framework for understanding the ecology of streams and rivers and is not intended as a description of biological components of all rivers in the individualistic context (i.e. it is an abstraction in the sense of Levins and Lewontin 1980). The RCC defines a general condition and in so doing explains the interrelationships between sets of unique conditions. Regional and local devia-

tions from the general pattern are a predictable result of specific variation in climate and geology, tributary influence, and location-specific lithology and geomorphology, as well as of long-term changes imposed by man. These factors are discussed more fully below.

Climate and Geology

Many geologists have accepted for sometime the idea that climate and geology are the ultimate determinants of river morphology through their effect on discharge and sediment load (e.g. Leopold and Wolman 1957; Gregory and Walling 1973; Lotspeich 1980). Together, climate and geology provide many factors influencing the characteristics of a river basin or watershed ecosystem. This has been accentuated by (1) the realization that river morphology and discharge can provide the template for stream ecosystem structure and function (Curry 1972, 1976; Horwitz 1978; Vannote et al. 1980), (2) examination of stream ecosystem dynamics over different North American biomes (Minshall et al. 1983b), (3) efforts to classify watersheds as ecosystems (Warren 1979; Lotspeich 1980), and (4) attempts to evaluate streams outside the north-temperate region in a broader context (Winterbourn et al. 1981). Climate, of course, affects the type and density of vegetation (Kuchler 1964; Bailey 1978; Garrison et al. 1977) and the effect of climate on the stream is in turn intimately bound up with the pattern of vegetation (Ross 1963; Gregory and Walling 1973; Hynes 1975). For example, precipitation and vegetation interact to affect runoff and erosion and hence sediment yield and organic matter loading. In other words, the action of flowing water, and hence such things as bed form and stability and organic matter storage and transport, varies with climate (e.g. Peltier 1950; Gregory and Walling 1973; Minshall et al. 1983b).

Geology affects the relative erosiveness of the parent material in a drainage basin and, consequently, watershed topography, chemical load, bed composition, and the like. Geology gives each physiographic region its distinctive appearance. Within each region, geologic structure, acted on by processes controlled by climate, gives shape to each land form (Lotspeich 1980). Recently, Strayer (1983) has shown that stream size and surface geology are the major factors controlling mussel distribution in the streams of southeastern Michigan. Others (e.g. Minshall and Minshall 1978; Magdych 1984) have demonstrated how differences in water quality mitigated or caused by the underlying geology can profoundly affect major segments of the benthic invertebrate community. In fact, as noted by Magdych (1984), these findings suggest the need to modify the RCC to allow for multiple gradients if it is to be useful in the generation of ecological models in regions where abnormal (nongradient) chemical inputs are important.

The riparian system (Swanson et al. 1982) can override the effects of climate and geology to some extent, especially in small (first to fourth) order streams below the tree line. The riparian vegetation is seen as a "ribbon of continuity" that makes many headwater streams look very similar worldwide (Cummins et al. 1984). Within rather broad climatic limits undisturbed headwater streams have temporally stable accumulations of large woody debris. Also, there seem to be biochemical equivalents along these streams in terms of riparian plant inputs that show fast, intermediate, and slow rates of decomposition (K. W. Cummins, pers. obs.). Thus, shading, geomorphic structuring by woody debris, and biochemically analogous inputs from the riparian system result in similar functional group assemblages in spite of differences in geology and climate.

Further, it is evident that even in larger stretches of a river (greater than fourth-order) the floodplain or riparian zone cannot be uncoupled from the stream channel itself. The RCC (Vannote et al. 1980) stressed that the influence of the terrestrial system on a stream diminishes as the stream becomes larger and that autochthonous carbon inputs to higher order streams (seventh- to tenth-order) should increase while allochthonous inputs of carbon decrease. However, Sedell and Froggatt (1984) have shown that many rivers in pre- and early settlement times also were heavily subsidized by their local flood plains. This subsidy took several forms including local litter fall from extensive riparian forests and carbon inputs from sloughs and side channels. In addition, Triska (1984), in his review of the Red River, reported that between 1828 and 1876, woody debris from the riparian zone of this eighth-order stream was enough to cause log jams along a 400- to 500-km stretch of the river. Besides being a direct carbon input to the river, the logs acted as a physical retention device that caused flooding of the riparian zone, drowning of trees, and a further addition of material to the river.

Tributary and Related Influences

Tributary additions to master streams have a significant influence on the continuum pattern. Where tributary inputs deviate from their usual summative influence on river water quality, expected (*sensu* Vannote et al. 1980) trophic and community patterns may be altered. The magnitude of change depends on tributary size (Fig. 1), regional drainage density, vegetation cover, land use, and lotic versus lentic source of inputs. A variety of effects may be envisioned. Concentrations of nutrients and/or food items in the tributaries may be higher than in the mainstream and serve to increase the mainstream levels. This could lead to increases in algal production or filter feeder densities if limiting concentrations were exceeded. Alternatively, a tributary may serve to dilute the mainstream concentrations or to provide a sustained input of coarse materials to a mid- or high-order master channel which could result in a biotic structure and function similar to upstream reaches. These postulates have been substantiated by the studies of Bruns et al. (1984) in the Middle Fork of the Salmon River. Not only were tributary influences demonstrated but the differing effects of small and large tributaries were contrasted.

A corollary to the RCC has recently been developed which emphasizes the impact of man-made dams on stream dynamics (Hauer and Stanford 1982; Ward and Stanford 1983). Ward and Stanford (1983) visualized the effect of relatively high dams as producing a shift in stream ecosystem structure and function in either an upstream or downstream direction depending on the size of the stream on which the dam is located and the position of outflow relative to the thermocline. The expected effects are similar to those postulated for tributaries. Extensive pools, whether generated by dams or associated with low gradient (Brown and Brown 1984), appear to have predictable impacts on stream conditions which represent local modifications to the trend expected for rivers in general (Vannote et al. 1980; Magdych 1984).

Local Lithology and Geomorphology

Here the focus is on location-specific variations in local geology and in the morphology of the river channel (perhaps most evident in flow patterns and substratum composition). The classic view of a river system is one of progressive change from

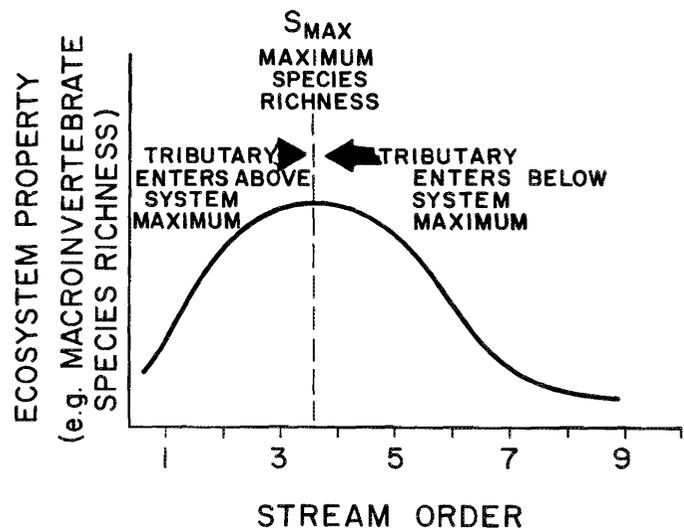


FIG. 1. The effect of a tributary on stream ecosystem parameters depends on where the tributary enters the larger stream. If a tributary enters above the point of system maximum it will drive the stream to that maximum. If it enters below it will move it back to reset that parameter. In this example, species richness reaches a maximum in third- to fourth-order streams. Tributaries entering above this cause the community to reach its maximum sooner. Tributaries entering below the peak increase richness by driving the system back.

high-gradient, turbulent, rocky headwaters to low-gradient, sluggish, mudbottomed rivers, and with a channel pattern progressing from straight, through braided, to meandering. Further reflection indicates that the ideal rarely is so clearly achieved. For example, in the Salmon River the steep-gradient headwaters descend immediately to a low-gradient glacial valley, and channel pattern varies from straight to meandering to braided and back to meandering, then straight, then braided. In addition to differences in hydraulic dynamics associated with these changes, one may expect major shifts in such factors as riparian inputs, channel storage of organic matter, and interchange with the flood plain (Fig. 2).

Studies on the distribution of *Gonidea angulata* and *Margaritifera falcata* in relation to substrate and periodic temporal variations in runoff amply demonstrate the influence of local lithologic and geomorphic processes on the relative abundance and population size structure of these organisms (Vannote and Minshall 1982). *Gonidea angulata* was predominant and possessed high population densities on stabilized sand and gravel bars; *M. falcata* was predominant in cobble and boulder areas. On cobble areas unprotected by block boulders, most *Margaritifera* populations were relatively young (20–40 yr) and had an approximately normal size distribution. On boulder controlled substrates, the size frequency was skewed towards the larger, old (100 yr) age-classes. Periodic floods, perhaps approaching a 50- to 100-yr return period, apparently cause high mussel mortality by bed scour in most canyon habitats. This periodic scour keeps populations relatively young with an approximately normal size distribution. In contrast, where mussel beds are protected by a field of large block-boulders, the dissipation of kinetic energy during floods is primarily through turbulence within the water column rather than bed shear. In these rare but highly stable habitats, *M. falcata* attains maximal density, old age, and a population structure that is skewed towards large individuals. Thus, local (site specific) conditions may alter both community and population structure and con-

GEOMORPHIC FEATURES			
	CANYON	BRAIDED	MEANDERING
PARAMETER			
Stream Surface Area : Discharge	LOW	HIGH	MEDIUM
Riparian Inputs	LOW	HIGH	MEDIUM
Detrital Storage	LOW	HIGH	MEDIUM-HIGH
Area Flooded	SMALL	LARGE	MEDIUM

FIG. 2. Shifts in important ecosystem parameters in response to changes in geomorphic features resulting from differences in hydraulic dynamics at different points in a stream reach.

found efforts to obtain an accurate holistic view unless they are taken into account.

Long-Term Effects of Man

Townsend (1980) contended that the spatial aspect of streams can be viewed without regard to the temporal. However, recent research (Molles 1982; Cummins et al. 1983, 1984) suggests that both a spatial and a temporal scale must be employed to obtain an understanding of stream dynamics. This is particularly important, since our concept of aboriginal conditions presently is so poor (at least 100 yr of nonendemic, man-made effects in South America and Africa, up to 400 yr in North America, and 1000 yr or more in Europe).

The impact of man on the structure of ecological communities is a common theme running through modern environmental science and pollution biology. However, man's greater responsibility for wholesale alteration of communities and extinction of species over the entire historical record has only recently been suggested (Goudie 1981; Lewin 1984) and may be a much larger effect than thought. In stream research the intimate connection between the stream and the adjacent terrestrial environment has focused attention on how man-caused disturbances such as fire (Minshall et al. 1981), silviculture (Molles 1982), riparian control (Cummins et al. 1984; Sedell and Froggatt 1984), and tree debris removal (Triska 1984) have potential for long-term changes in stream systems. This awareness has been accentuated by the need for resource managers to know the natural, presettlement conditions of areas under their supervision (Romme 1982; Romme and Knight 1982; Sedell and Luchessa 1982). Various postsettlement alterations likely to have had major impacts on the nature of stream ecosystems include the following: urbanization; deforestation; tillage; irrigation; dam construction; channel alteration for navigation, logging, mining, and flood control; virtual extermination of beaver, bison, and other large mammals including aboriginal man; grazing by

domestic animals; and fire suppression. These changes, many of them so subtle as to go unnoticed, have made it difficult for modern stream ecologists to place their findings in perspective with reference to natural, pristine conditions or to obtain meaningful measurements of certain aspects such as carbon budgets (Cummins et al. 1983). Nevertheless, incorporation of a broad temporal perspective has begun to aid substantially in the understanding of stream ecosystem structure and function both past and present (Molles 1982; Romme and Knight 1982; Sedell and Luchessa 1982; Sedell et al. 1982; Cummins et al. 1983; Fremling and Claffin 1984).

Side channels, braided channels, and off-channel backwaters (seasonal) may have an effect similar to that of tributaries. However, the massive snag removal that took place on essentially all North American rivers in the late 1800's and early 1900's, together with large-scale channelization efforts, has converted the majority of streams greater than fourth- to sixth-order from heavily braided or meandering systems to single, relatively straight channels (see e.g. Cummins et al. 1984; Fremling and Claffin 1984; Sedell and Froggatt 1984; Triska 1984). Thus, instead of a single fifth-order channel there might have been five third-order channels. Among other things, this would mean that the riparian effect was much different prior to such alterations. Wood, removed by man, probably produced a very different channel form in mid-sized rivers than that found today. Braids, off-channel backwaters, and side-channel streams probably caused many mid-order rivers to behave more like headwaters. However, intensive beaver activity prior to the mid-1800's may have had a countereffect in that the extensive impoundments the beaver created would have made headwater streams wider, slower, and more mid-order in character.

Implications to Stream Ecology

Deviations in regional and local conditions (associated with such things as climate and geology, tributaries and related

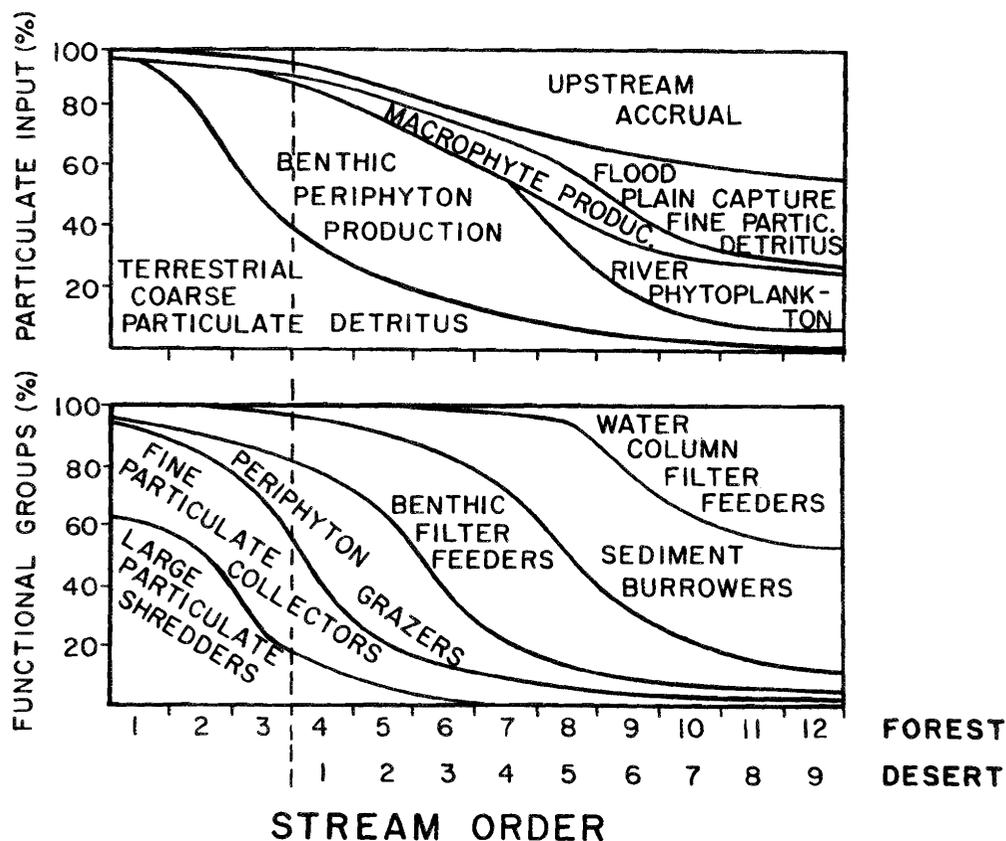


FIG. 3. Expected changes in particulate organic matter inputs and functional feeding group relationships along a river system (after Vannote et al. 1980). The abscissa is shown as a "sliding scale" to emphasize the fact that different streams enter the continuum at different points. In the two cases illustrated, forest streams begin with a strong terrestrial influence (reflected by a predominance of allochthonous organic matter and detrital processors) whereas desert streams, due to the lack of shading and reduced influx of allochthonous detritus, enter the sequence at a point displaced to the right and equivalent to a more downstream position of the forest stream.

influences, local lithology and geomorphology, and long-term effects of man) suggest that adjustments need to be made in the RCC if it is to be applied across biomes, especially when environmental extremes or unusual situations are involved. For example, in some wooded parts of Africa (e.g. Zimbabwe), large amounts of coarse particulate leaf detritus do not reach the stream. Most leaf material is processed by terrestrial detritivores during the dry season, and by the time the rains come, the coarse material has already been reduced to fine particles (R. C. Petersen, pers. obs.). Consequently, an important functional feeding group (shredders) is reduced or absent from such streams, and a sequence of adjustments in invertebrate trophic structure results (Fig. 3). The absence of large-particle shredders also appears to be typical of unstable, poorly retentive headwater streams in disturbed watersheds (Rounick and Winterbourn 1983a, 1983b). As another example, there are many areas of the world in which, for one reason or another, headwater streams (first-order woodland streams) simply do not occur. In areas dominated by porous calcareous geology such as in Florida (Odum 1957) or the western mountains of Jamaica (Petersen 1984; pers. obs.), the rivers begin as larger sized systems. In these rivers it still is expected that the basic sequential model will be followed but the river will skip the upper small-order categories and the effect that those small systems have on the downstream reaches will be removed. In Jamaican springs, which begin with a width of 30–40 m, the

streams below the springs are dominated by primary production (macrophytes and periphytic algae). The grazer functional group, consisting of snails, dominates the macrobenthos, and due to a lack of particulate organics, filter feeders are rare but collector–gatherers feeding on decomposing macrophytes are abundant. In short, the system structure is similar to a midorder woodland river but without the filter feeders that normally feed on the upstream losses of particles. The need to accommodate these sorts of changes are explicit in the original formulation of the RCC (Cummins 1975; Minshall 1978; Vannote et al. 1980) but the point has been missed by some investigators (e.g. Winterbourn et al. 1981; Rounick and Winterbourn 1983a).

Because streams are ecosystems with numerous linkages and feedback loops, care must be taken in developing and testing stream ecosystem theory that critical interrelations are not excluded or unconsciously left uncoupled. For example, some investigations have taken the absence of macroinvertebrate shredders from certain headwater streams as failing to support the RCC (e.g. Winterbourn et al. 1981). But the various facets of organic matter processing cannot be viewed in isolation. For one thing, it is unreasonable to expect macroinvertebrate shredders to be present if the coarse particulate organic matter supply is inadequate or unreliable. Also, various trade-offs may occur in which the macroinvertebrate shredders may be replaced or supplemented by other size-reducing mechanisms (microbes, beaver, physical fragmentation). The important point in terms

of the RCC is that when coarse particulate organic matter enters a stream it will be reduced to fine particulate organic matter and that this phenomenon generally is quantitatively most significant in the headwaters of a river system. It is only when these features are shown to be unimportant or absent that this aspect of the RCC can be shown not to hold. Furthermore, abnormal (often anthropogenic) factors may obscure or obliterate the expected response such as when the entrance of geothermal waters or other adverse environmental conditions selectively eliminates certain components of the community. Sometimes such influences may occur on a large scale (e.g. acid rain), further obscuring the relationship and giving the impression that the general presettlement pattern is being examined. This is especially true if the event is a temporally distant one where the cause is separated from its present-day effect by time as well as space. Examples include acid rain in Europe which began with the Industrial Revolution and deforestation of large tracts of land which in parts of England may date back 3000 yr to the Bronze Age (Dr. W. Pennington, Botany Department, University of Leicester, U.K., pers. comm.).

Since stream ecosystem dynamics also are coupled closely to the fluvial geomorphic conditions, these conditions must be taken into account when testing the RCC or devising alternative explanations. This suggests that, in examining conditions along a river system, samples should be taken so that the mean or most characteristic geomorphic conditions in each stretch are represented. For example, collections of organisms taken only from riffles along the course of a river may provide an erroneous view of general patterns of distribution, since the characterizing geomorphic properties of the stream reach may be being overridden by the sampling procedure and a depositional rather than an erosional biota may actually be the appropriate representative. Here, too, the long-term temporal perspective is an important one. Due to flow regulation, many stream channels, particularly in lowland areas, are over- (e.g. due to channelization) or under-fit (e.g. due to sedimentation) or otherwise managed in ways that alter the natural conditions (e.g. weed cutting). While these represent deviations, the extent of which can be measured against the RCC, they do not provide evidence of conditions that invalidate the concept.

Conclusion

Stream ecosystem theory has seen a number of important advances, especially in the past decade. The RCC is consistent with these views and has served to synthesize most of them into a workable general hypothesis. Although the worldwide generality of the model remains to be further evaluated, it appears that most riverine ecosystems generally can be accommodated within the current conceptual framework. In this regard, it appears that even systems identified as "exceptions" (e.g. Winterbourn et al. 1981) represent no more than variations on a central theme (e.g. if coarse particulate organic matter is not there, neither will shredders or large-wood geomorphic control, etc.).

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