The River Continuum Concept[1]

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From headwaters to mouth, the physical variables within a river system present a continuous gradient of physical conditions. This gradient should elicit a series of responses within the constituent populations resulting in a continuum of biotic adjustments and consistent patterns of loading, transport, utilization, and storage of organic matter along the length of a river. Based on the energy equilibrium theory of fluvial geomorphologists, we hypothesize that the structural and functional characteristics of stream communities are adapted to conform to the most probable position or mean state of the physical system. We reason that producer and consumer communities characteristic of a given river reach become established in harmony with the dynamic physical conditions of the channel. In natural stream systems, biological communities can be characterized as forming a temporal continuum of synchronized species replacements. This continuous replacement functions to distribute the utilization of energy inputs over time. Thus, the biological system moves towards a balance between a tendency for efficient use of energy inputs through resource partitioning (food, substrate, etc.) and an opposing tendency for a uniform rate of energy processing throughout the year. We theorize that biological communities developed in natural streams assume processing strategies involving minimum energy loss. Downstream communities are fashioned to capitalize on upstream processing inefficiencies. Both the upstream inefficiency (leakage) and the downstream adjustments seem predictable. We propose that this River Continuum Concept provides a framework for integrating predictable and observable biological features of lotic systems. Implications of the concept in the areas of structure, function, and stability of riverine ecosystems are discussed.

Key words: river continuum; stream ecosystems; ecosystem structure, function; resource partitioning; ecosystem stability; community succession; river zonation; stream geomorphology

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De la tête des eaux à l'embouchure, un réseau fluvial offre un gradient continu de conditions physiques. Ce gradient devrait susciter, chez les populations habitant dans le réseau, une série de réponses aboutissant à un continuum d'ajustements biotiques et à des schémas uniformes de charge, transport, utilisation et emmagasinage de la matière organique sur tout le

parcours d'une rivière. Faisant appel à la théorie de l'équilibreénergétique des spécialistes de la géomorphologie fluviale, nous avançons l'hypothese que les caractéristiques structurales et fonctionnelles des communautés fluviatiles sont adaptées de façon à se conformer à la position ou condition moyenne la plus probable du systkme physique. Nous croyons que les communautés de producteurs et de consommateurs caractéristiques d'un segment donné de la rivière se mettent en harmonie avec les conditions physiques dynamiques du chenal. Dans des réseaux fluviaux naturels, on peut dire que les communautés biologiques forment un continuum tempore1 de remplacements synchronisés d'espèces. Grâce à ce remplacernent continu, il y a répartition dans le temps de l'utilisation des apports énergétiques. Ainsi, le système biologique vise à un équilibre entre une tendance vers l'utilisation efficace des apports d'énergie en partageant les resources (nourriture, substrat, etc.), d'une part, et une tendance opposée vers un taux uniforme de transformation de l'énergie durant l'année, d'autre part. A notre avis, les communautés biologiques habitant dans des cours d'eau naturels adoptent des stratégies de transformation comportant une perte minimale d'énergie. Les communautés d'aval sont organisées de façon à tirer profit de l'inefficacité de transformation des communautés d'amont. On semble pouvoir prédire à la fois l'inefficacité (fuite) d'amont et les ajustements d'aval. Nous suggérons ce concept d'un continuum fluvial cornme cadre dans lequel intégrer les caractères biologiques prévisibles et observables des systèmes lotiques. Nous analysons les implications du concept quant à la structure, fonction et stabilité des éosystèmes fluviaux.

Statement of the Concept

Many communities can be thought of as continua consisting of mosaics of integrading population aggregates (McIntosh 1967; Mills 1969). Such a conceptualization is particularly appropriate to streams. Several workers have visualized streams as possessing assemblages of species which respond by their occurrences and relative abundances to the physical gradients present (Shelford 1911; Thompson and Hunt 1930; Ricker 1934; Ide 1935; Burton and Odum 1945; Van Deusen 1954; Huet 1954, 1959; Slack 1955; Minshall 1968; Ziemer 1973; Swanston et al. 1977; Platts 1979). Expansion of this idea to include functional relationships has allowed development of a framework, the "River Continuum Concept," describing the structure and function of communities along a river system. Basically, the concept proposes that understanding of the biological strategies and dynamics of river systems requires consideration of the gradient of physical factors formed by the drainage network. Thus energy input, and organic matter transport, storage, and use by macroinvertebrate functional feeding groups may be regulated largely by fluvial geomorphic processes. The patterns analogous proposed of physical energy expenditure by geomorphologists (Leopold and Maddock 1953; Leopold and Langbein 1962; Langbein and Leopold 1966; Curry 1972). Further, the physical structure coupled with the hydrologic cycle form a templet (Southwood 1977) for biological responses and result in consistent patterns of community structure and function and organic matter loading, transport, utilization, and storage along the length of a river.

Derivation of the Concept

As the cyclic theory for explaining the evolution of land forms and streams (young, mature, ancient) proved unsatisfactory, the concepts gradually were replaced by a principle of dynamic equilibrium (Curry 1972). The concept of the physical stream network system and the distribution of watersheds as open systems in dynamic ("quasi") equilibrium was first proposed by Leopold and Maddock (1953) to describe consistent patterns, or adjustments, in the relationships of stream width, depth, velocity, and sediment load. These "steady state" systems are only rarely characterized by exact equilibria and generally the river and its channel tend toward a mean form, definable only in terms of statistical means and extremes (Chorley 1962); hence, the idea of a "dynamic" equilibrium. The equilibrium concept was later expanded to include at least nine physical variables and was progressively developed in terms of energy inputs, efficiency in utilization, and rate of entropy gain (Leopold and Langbein 1962; Leopold et al. 1964; Langbein and Leopold 1966). In this view, equilibration of river morphology and hydraulics is achieved by adjustments between the tendency of the river to maximize the efficiency of energy utilization and the opposing tendency toward a uniform rate of energy use.

Based upon these geomorphological considerations, Vannote initially formulated the hypothesis that structural and functional characteristics of stream communities distributed along river gradients are selected to conform to the most probable position or mean state of the physical system. From our collective experience with a number of streams, we felt it was possible to translate the energy equilibrium theory from the physical system of geomorphologists into a biological analog. In this analysis, producer and consumer communities characteristic of a given reach of the river continuum conform to the manner in which the river system utilizes its kinetic energy in achieving a dynamic

equilibrium. Therefore, over extended river reaches, biological communities should become established which approach equilibrium with the dynamic physical conditions of the channel.

Implications of the Concept

It is only possible at present to trace the broad outlines of the ways the concept should apply to stream ecosystems and to illustrate these with a few examples for which reasonably good information is available. From headwaters to downstream extent, the physical variables within a stream system present a continuous gradient of conditions including width, depth, velocity, flow volume, temperature, and entropy gain. In developing a biological analog to the physical system, we hypothesize that the biological organization in rivers conforms structurally and functionally to kinetic energy dissipation patterns of the physical system. Biotic communities rapidly adjust to any changes in the redistribution of use of kinetic energy by the physcial system.

STREAM SIZE AND ECOSYSTEM STRUCTURE AND FUNCTION

Based on considerations of stream size, we propose some broad characteristics of lotic communities which can be roughly grouped into headwaters (orders 1-3), medium-sized streams (4–6), and large rivers (>6) (Fig. 1). Many headwater streams are influenced strongly by the riparian vegetation which reduces autotrophic production by shading and contributes large amounts of allochthonous detritus. As stream size increases, the reduced importance of terrestrial organic input coincides with enhanced significance of autochthonous primary production and organic transport from upstream. This transition from headwaters, dependent on terrestrial inputs, to medium-sized rivers, relying on algal or rooted vascular plant production, is thought to be generally reflected by a change in the ratio of gross primary productivity to community respiration (P/R) (Fig. 2). The zone through which the stream shifts from heterotrophic to autotrophic is primarily dependent upon the degree of shading (Minshall 1978). In deciduous forests and some coniferous forests, the transition probably is approximately at order 3 (Fig. 1). At higher elevations and latitudes, and in xeric regions where riparian vegetation is restricted, the transition to autotrophy may be in order 1. Deeply incised streams, even with sparse riparian vegetation, may be heterotrophic due to side slope ("canyon") shading.

Large rivers receive quantities of fine particulate organic matter from upstream processing of dead leaves and woody debris. The effect of riparian vegetation is insignificant, but primary production may often be limited by depth and turbidity. Such light attenuated systems would be characterized by P/R < 1. Streams of lower order entering midsized or larger rivers (e.g. the 3rd order system shown entering the 6th order
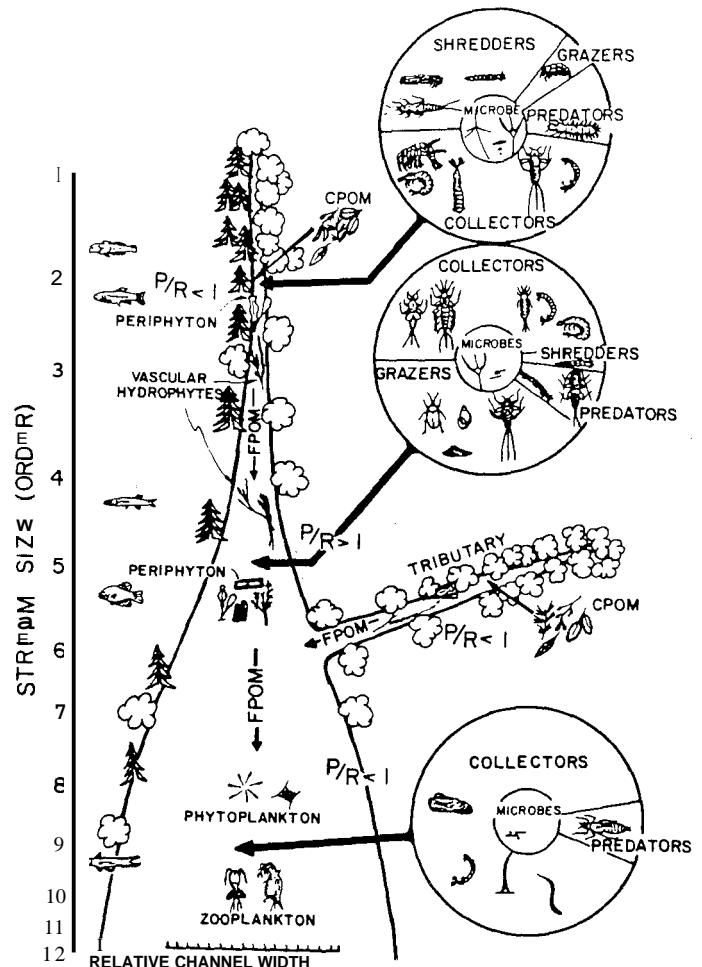

FIG. 1. A proposed relationship between stream size and the progressive shift in structural and functional attributes of lotic communities. See text for fuller explanation.

river in Fig. 1) have localized effects of varying magnitude depending upon the volume and nature of the inputs.

The morphological–behavioral adaptations of running water invertebrates reflect shifts in types and locations of food resources with stream size (Fig. 1). The relative dominance (as biomass) of the general functional groups — shredders, collectors, scrapers (grazers), and predators are depicted in Fig. 1. Shredders utilize coarse particulate organic matter (CPOM, >1 mm), such as leaf litter, with a significant dependence on the associated microbial biomass. Collectors filter from transport, or gather from the sediments, fine and ultrafine particulate organic matter (FPOM, 50um-1 mm; UPOM 0.5–50 um). Like shredders, collectors depend on the microbial biomass associated with the particles (primarily on the surface) and products of microbial metabolism for their nutrition. Scrapers are adapted primarily for shearing attached algae from surfaces. The proposed dominance of scrapers follows shifts in primary production, being maximized in midsized rivers
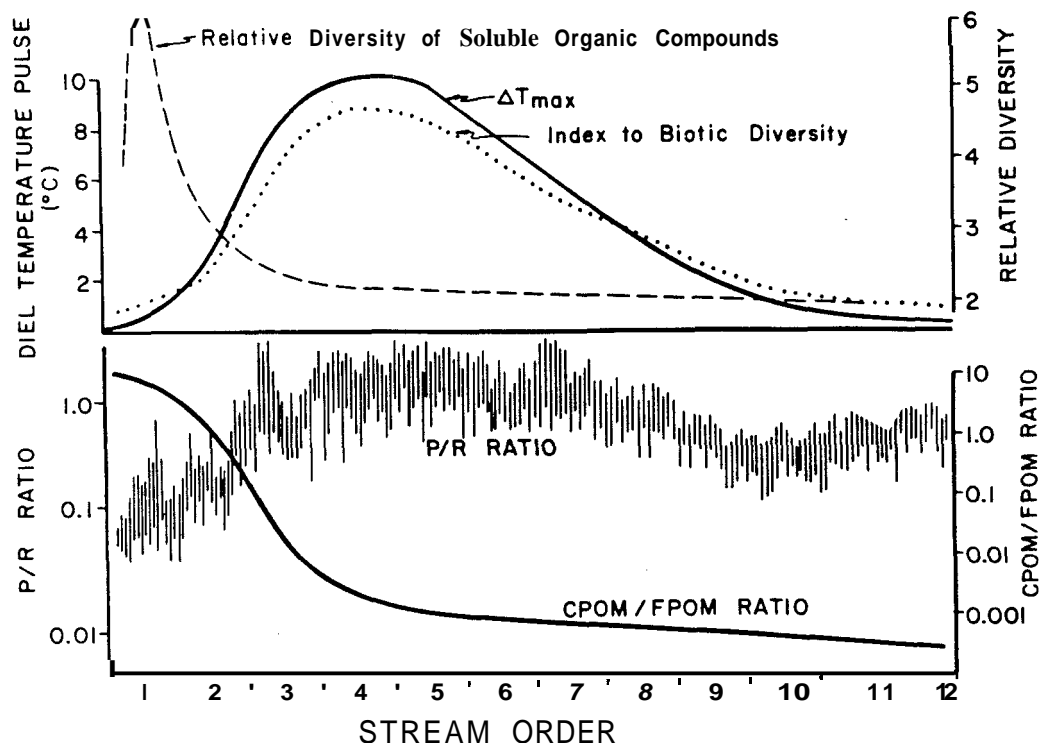
FIG. 2. Hypothetical distribution of selected parameters through the river continuum from headwater seeps to a twelfth order river. Parameters include heterogeneity of soluble organic matter, maximum diel temperature pulse, total biotic diversity within the river channel, coarse to fine particulate organic matter ratio, and the gross photosynthesis/respiration ratio.

with $P/R > 1$. Shredders are hypothesized to be codominant with collectors in the headwaters, reflecting the importance of riparian zone CPOM and FPOM-UPOM derived from it. With increasing stream size and a general reduction in detrital particle size, collectors should increase in importance and dominate the macroinvertebrate assemblages of large rivers (Fig. 1).

The predatory invertebrate component changes little in relative dominance with stream order. Fish populations (Fig. 1) show a shift from cool water species low in diversity to more diverse warm water communities (e.g. Huet 1954). Most headwater species are largely invertivores. Piscivorous and invertivorous species characterize the midsized rivers and in large rivers some planktivorous species are found — reflecting the semi-lentic nature of such waters.

The expected diversity of soluble organic compounds through the continuum is shown in Fig. 2 (dashed line). Headwater streams represent the maximum interface with the landscape and therefore are predominantly accumulators, processors, and transporters of materials from the terrestrial system. Among these inputs are heterogeneous assemblages of labile and refractory dissolved compounds, comprised of short- and long-chain organics. Heterotrophic use and physical absorption of labile organic compounds is rapid, leaving the more refractory and relatively high molecular weight compounds for export downstream. The relative importance

of large particle detritus to energy flow in the system is expected to follow a curve similar to that of the diversity of soluble organic compounds; however, its importance may extend further downstream.

Thus the river system, from headwaters to mouth, can be considered as a gradient of conditions from a strongly heterotrophic headwater regime to a seasonal, and in many cases, an annual regime of autotrophy in midreaches, and then a gradual return to heterotrophic processes in downstream waters (Fisher 1977). Major bioenergetic influences along the stream continuum are local inputs (allochthonous litter and light) and transport from upstream reaches and tributaries (Fig. 1). As a consequence of physical and biological processes. the particle size of organic material in transport should become progressively smaller down the continuum (reflected by CPOM:FPOM ratio in Fig. ?, except for localized input of lower order tributaries) and the stream community response reflect progessively more efficient processing of smaller particles.

RIVER ECOSYSTEM STABILITY

Stability of the river ecosystem may be viewed as a tendency for reduced fluctuations in energy flow, while community structure and function are maintained. in the face of environmental variations. This implicitly couples community stability (sensu Ricklefs 1979) to the instability ("noise") of the physical system. In

highly stable physical systems, biotic contribution to ecosystem stability may be less critical. However, in widely fluctuating environments (e.g. stream reaches with lage fluctuations in temperature), the biota may assume critical importance in stabilizing the entire system. In this interpretation, ecosystem stability is achieved by a dynamic balance between forces contributing to stabilization (e.g. debris dams, filter feeders, and other retention devices; nutrient cycling) and those contributing to its instability (e.g. floods, temperature fluctuations, microbial epidemics). In systems with a highly stable physical structure, biotic diversity may be low and yet total stability of the stream ecosystem still be maintained. In contrast, systems with a high degree of physical variation may have high species diversity or at least high complexity in species function which acts to maintain stability.

For example, in stream zones experiencing wide diel temperature changes, organisms may be exposed to suboptimum temperatures for significant portions of the day, but over some range in the diel cycle each organism encounters a favorable or optimum temperature range. Under these conditions an optimum temperature will occur for a larger number of species than if the thermal regime displayed minimum variance. Also, in the thermally fluctuating system, many populations have an opportunity to process energy, and as temperatures oscillate around a mean position, various populations may increase or decrease their processing rates. Thus, an important aspect of the predictably fluctuating physical system is that it encompasses optimum conditions for a large number of species. This interplay between physical and biological components can be seen in terms of ecosystem stability by considering the response of total biotic diversity in the river channel as balanced against the maximum diel temperature range ($^\wedge$T max) (Fig. 2). Headwater streams in proximity to groundwater supply or infiltration source areas exhibit little variation in AT max. With increased distance from subsurface sources and separation of the forest canopy, $^\wedge$T max will attain its widest variance because of increased solar input. The $^\wedge$T max amplitude is greatly diminished in high order streams due to the buffering effect of the large volume of water in the channel (Ross 1963). In headwater springs and brooks, diversity may be low because biological communities are assembled from those species which can function within a narrow temperature range on a restricted nutritional base; the stability of the system may be maintained by the low amplitude of diel and annual temperature regimes. Total community diversity is greatest in medium-sized (3rd to 5th order in Fig. 2) streams where temperature variations tend to be maximized. The tendency to stabilize energy flow in midsized streams may be aided by high biotic diversity which mitigates the influence of high variance in the physical system as characterized by $^\wedge$T max; i.e. variation due to fluctuating thermal regimes should be offset by a high diversity of biota. In large rivers,

stability of the system should be correlated with reduction in variance of diel temperature. We wish to emphasize that temperature is not the only factor responsible for the change in community structure; it is simply one of the easiest to visualize. Other factors such as riparian influence, substrate, flow, and food also are important and change in predictable fashion downstream both absolutely and in terms of the relative heterogeneity of each.

TEMPORAL ADJUSTMENTS IN MAINTAINING AN EQUILIBRIUM OF ENERGY FLOW

Natural stream ecosystems should tend towards uniformity of energy flow on an annual basis. Although the processing rates and efficiencies of energy utilization by consumer organisms are believed to approach equilibrium for the year, the major organic substrates shift seasonally. In natural stream systems, both living and detrital food bases are processed continuously, but there is a seasonal shift in the relative importance of autotrophic production vs. detritus loading and processing. Several studies (Minshall 1967; Coffman et al. 1971; Kaushik and Hynes 1971; MacKay and Kalff 1973; Cummins 1974; Sedell et al. 1974) have shown the importance of detritus in supporting autumn-winter food chains and providing a fine particle base for consumer organisms during other seasons of the year. Autotrophic communities often form the major food base, especially in spring and summer months (Minshall 1978).

Studies on headwater (order 1-3) streams have shown that biological communities in most habitats can be characterized as forming a temporal sequence of synchronized species replacement. A a species completes its growth in a particular microhabitat, it is replaced by other species performing essentially the same function, differing principally by the season of growth (Minshall 1968; Sweeney and Vannote 1978; Vannote 1978; Vannote and Sweeney 1979). It is this continuous species replacement that functions to distribute the utilization of energy inputs over time (e.g. Wallace et al. 1977). Individuals within a species will tend to exploit their environment as efficiently as possible. This results in the biological system (composite species assemblage) tending to maximize energy consumption. Because some species persist through time and because new species become dominant, and these too are exploiting their environment as efficiently as possible, processing of energy by the changing biological system tends to result in uniform energy processing over time. Thus, the biological system moves towards equilibrium by a trade-off between a tendency to make most efficient use of energy inputs through resource partitioning of food, substrate, temperature, etc. and tendency toward a uniform rate of energy processing throughout the year. From strategies observed on small to medium-sized streams (orders 1-5), we propose that biological communities, developed in natural streams

in dynamic equilibrium, assume processing strategies involving minimum energy loss (termed maximum "spiraling" by Webster 1975).

ECOSYSTEM PROCESSING ALONG THE CONTINUUM

The dynamic equilibrium resulting from maximization of energy utilization and minimization of variation in its use over the year determines storage or leakage of energy. Storage includes production of new tissue and physical retention of organic material for future processing. In stream ecosystems, unused or partially processed materials will tend to be transported downstream. This energy loss, however, is the energy income, together with local inputs, for communities in downstream reaches. We postulate that downstream communities are structured to capitalize on these inefficiencies of upstream processing. In every reach some material is processed, some stored, and some released. The amount released in this fashion has been used in calculating system efficiency (Fisher 1977). Both the upstream inefficiency (leakage) and the downstream adjustments seem predictable. Communities distributed along the river are structured to process materials (specific detrital sizes, algae, and vascular hydrophytes) thereby minimizing the variance in system structure and function. For example, materials prone to washout, such as flocculant fine-particle detritus, might be most efficiently processed either in transport or after deposition in downstream areas. The resistivity of fine particle detritus to periodic washout is increased by sedimentation in depositional zones or by combination in a matrix with the more cohesive silt and clay sediments. Thus, enhanced retention results in the formation of a distinct community adapted to utilize this material. The minimization of the variance of energy flow is the outcome of seasonal variations of energy input rates (detritus and autotrophic production), coupled with adjustments in species diversity, specialization for food processing, temporal expression of functional groups, and the erosional–depositional transport and storage characteristics of flowing waters.

TIME INVARIANCE AND THE ABSENCE OF SUCCESSION IN STREAM COMMUNITIES

A corollary to the continuum hypothesis, also arising from the geomorphological literature (Langbein and Leopold 1966), is that studies of biological systems established in a dynamically balanced physical setting can be viewed in a time independent fashion. In the context of viewing adaptive strategies and processes as continua along a river system, temporal change becomes the slow process of evolutionary drift (physical and genetic). Incorporation of new functional components into the community over evolutionary time necessitates an efficiency adjustment towards reduced leakage. In natural river systems community structure gains and loses species in response to low probability cataclysmic events and in response to slow processes of channel development.

The concept of time invariance allows integration of community structure and function along the river without the illusion that successional stages are being observed at a given location in a time-dependent series. The concept of biological succession (Margalef 1960) is of little use for river continua, because the communities in each reach have a continuous heritage rather than an isolated temporal composition within a sequence of discrete successional stages. In fact, the biological subsystems for each reach are in equilibrium with the physical system at that point in the continuum. The concept of heritage implies that in natural river systems total absence of a population is rare, and biological subsystems are simply shifting spatially (visualize a series of overlapping normal species-abundance curves in which all species are present at any point on the spatial axis but their abundance differs from one point to the next) and not in the temporal sense typical of plant succession.

On an evolutionary time scale, the spatial shift has two vectors: a donwstream one involving most of the aquatic insects and an upstream one involving molluscs and crustaceans. The insects are believed to have evolved terrestrially and to be secondarily aquatic. Since the maximum terrestrial–aquatic interface occurs in the headwaters, it is likely that the transition from land to water first occurred here with the aquatic forms then moving progressively downstream. The molluscs and crayfish are thought to have developed in a marine environment and to have moved through estuaries into rivers and thence upstream. The convergence of the two vectors may explain why maximum species diversity occurs in the midreaches.

Conclusion

We propose that the River Continuum Concept provides a framework for integrating predictable and observable biological features of flowing water systems with the physical–geomorphic environment. The model has been developed specifically in reference to natural, unperturbed stream ecosystems as they operate in the context of evolutionary and population time scales. However, the concept should accommodate many unnatural disturbances as well, particularly those which alter the relative degree of autotrophy:heterotrophy (e.g. nutrient enrichment, organic pollution, alteration of riparian vegetation through grazing, clear-cutting, etc.) or affect the quality and quantity of transport (e.g. impoundment, high sediment load). In many cases, these alterations can be thought of as reset mechanisms which cause the overall continuum response to be shifted toward the headwaters or seaward depending on the type of perturbation and its location on the river system.

A concept of dynamic equilibrium for biological communities, despite some difficulties in absolute defini-

tion, is useful because it suggests that community structure and function adjust to changes in certain geomorphic, physical, and biotic variables such as stream flow, channel morphology, detritus loading, size of particulate organic material, characteristics of autotrophic production, and thermal responses. In developing a theory of biological strategies along the river continuum, it also should be possible to observe a number of patterns that describe various processing rates, growth strategies, metabolic strategies, and community structures and functions. Collection of extensive data sets over the long profile of rivers are needed to further test and refine these ideas.

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