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

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parcours d'une rivière. Faisant appel à la théorie de l'équilibre énergétique des spécialistes de la géomorphologie fluviale, nous avançons l'hypothèse 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 système 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 temporel de remplacements synchronisés d'espèces. Grâce à ce remplacement 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 ressources (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 comme 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 écosystèmes fluviaux.

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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 of organic matter use may be analogous to those of physical energy expenditure proposed 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