

## PERSPECTIVES

### Questions and Comments on the River Continuum Concept

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The River Continuum Concept (RCC) is a generalized conceptual framework for characterization of pristine running water ecosystems. Of the numerous tenets of the concept we particularly reevaluated the following: biological analogues of energy equilibrium and entropy in the physical system; maximization of energy consumption through continuous species replacement over a year; absence of succession in stream ecosystems, which can thus be viewed in a time-independent fashion; and maximization of biotic diversity in midreaches of streams as a result of the occurrence of highest environmental variability there together with spatial abundance shifts of insects, molluscs, and crustaceans. When emphasis is placed on rapid changes in the downstream hydraulics dependent on discharge and slope (both of which are expressed by stream order in the RCC and are key factors of the concept) and on results from tropical studies, some of these tenets are partly refuted or need extension. Some of them are in conflict with the current state of knowledge in other domains of stream ecology or are at least open to various interpretations. Therefore, we advocate modifications of the theoretical background of the RCC.

Le concept de continuum du milieu fluvial (CCMF) est un cadre conceptuel généralisé pour la caractérisation des écosystèmes lotiques vierges. Parmi les nombreux principes de ce concept, les auteurs ont réévalué en particulier les suivants : les analogues biologiques de l'équilibre énergétique et de l'entropie dans le système physique; la maximalisation de la consommation d'énergie par le remplacement continu des espèces au cours d'une année; l'absence de succession dans les écosystèmes lotiques qui peuvent donc être considérés indépendamment du temps; et la maximalisation de la diversité de la faune et de la flore dans les sections moyennes de cours d'eau, maximalisation due à la présence d'une variabilité environnementale optimale en plus de variations spatiales de l'abondance d'insectes, de mollusques et de crustacés. Certains de ces principes sont en partie réfutés ou doivent être élargis quand on met l'accent sur les variations rapides de l'hydrodynamique des eaux d'aval qui dépend du débit et de la pente (ces deux facteurs-clés du CCMF sont exprimés selon la position du cours d'eau dans le concept), et sur les résultats d'études du milieu tropical. Quelques-uns de ces concepts entrent en conflit avec les connaissances actuelles sur d'autres aspects de l'écologie lotique ou au moins peuvent être interprétés de diverses façons. Les auteurs recommandant donc des modifications des éléments théoriques du CCMF.

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**T**he question of how headwater and downstream ecosystems vary in structure and/or function was and remains a central issue of running water ecology. At the beginning of the 1970's a group of North American stream ecologists started a new approach to this question, which resulted in the River Continuum Concept (RCC) (Vannote et al. 1980). The authors of the concept consider it as a framework for a characterization of pristine running water ecosystems, "describing the structure and function of communities along a river system" in relationship to the abiotic environment. The RCC stimulated immediate comment and avid discussion (Winterbourn et al. 1981; Barmuta and Lake 1982; Culp and Davies

1982; Hauer and Stanford 1982; Taylor and Roff 1982; Winterbourn 1982; Cole 1983; Gray et al. 1983; Rounick and Winterbourn 1983; Stanford and Ward 1983; Ward and Stanford 1983; Townsend and Hildrew 1984<sup>1</sup>). Recent contributions from the RCC proponents (Cummins et al. 1983; Cushing et al. 1983; Minshall et al. 1983; Bruns et al. 1984) modify some ideas of Vannote et al. (1980), but generally support the RCC. From personal discussions and unpublished manuscripts we gather that further modifications and clarifications of the RCC

<sup>1</sup>Paper delivered at the SIL meeting in Lyon 1983. Here and in other cases we refer to the oral presentation and the abstract.

can be expected from its proponents (e.g. Sedell and Froggatt 1984; Cummins et al. 1984).<sup>2</sup>

During an analysis of the information available on the RCC we realized that some of its basic assumptions or tenets, as we interpret them, affect the domain of stream ecology to a greater degree than is evident at first glance and certainly more than is discussed in the above papers. Some tenets are at variance with our view of the current state of knowledge. Other assumptions can be interpreted in various ways and require clarification.

We will discuss some of these assumptions briefly, concentrating particularly on five tenets: biological analogues for (1) energy equilibrium and (2) entropy pattern in the physical system; (3) maximization of energy consumption through continuous species replacement over a year; (4) absence of succession in stream ecosystems, which can thus be viewed in a time-independent fashion; and (5) maximization of species diversity in midreaches of streams as a result of the occurrence of the highest environmental variability there and spatial abundance shifts of insects, molluscs, and crustaceans.

The aim of this paper is to suggest some modifications in the theoretical background of the RCC. But first we would like to stress that we accept many parts of the RCC as they stand and respect the scientific ideas that our North American colleagues have compiled in their framework.

## General Remarks on the RCC

Before we deal with the five RCC tenets mentioned above, some of the general aspects of the concept as well as the limitations contained in it will be briefly outlined and commented on.

The main goal of the RCC is to link fluvial geomorphic processes, physical structure, and the hydrologic cycle to "patterns of community structure and function and organic matter loading, transport, utilization and storage along the length of a river." This is very expressively illustrated in Vannote et al. (1980, Fig. 1), in which the influence of riparian vegetation, the status of trophy, load, transport, and the relative importance of functional feeding groups (shredders, collectors, etc.) is related to stream order (Leopold et al. 1964) as an expression of the physical component. However, as stream order is not, in any case, a meaningful description of the physical environment (Gregory and Walling 1973), it should be regarded only as an indication of the relative position of a stream reach within the entire running water system. A physical characterization of each reach under study must therefore be added.

The RCC as published in 1980 includes qualifications about certain environmental situations. Some of the criticisms of the RCC so far published are not appropriate when these limitations and modifications (Vannote et al. 1980) to the RCC are taken into account: (i) the RCC has been developed for natural, unperturbed stream ecosystems; (ii) streams at high elevations and latitudes, xeric regions, and deeply incised valleys may deviate from the general pattern with regard to autotrophy/heterotrophy; (iii) tributaries entering the main stream have localized effects of varying magnitude depending on the volume and the nature of the input.

The RCC does not particularly deal with the various types of sources (limnocrone, helocrone, rheocrone) and mouths (delta, estuary) of stream systems (see Fig. 3) nor does it mention natural lakes that occupy intermediate positions on the "river

continuum." And, a fact we regard as very important, the RCC is not restricted to a certain geographical area, i.e. we consider it a concept of worldwide applicability.

Classification of the benthic invertebrates into functional feeding groups (Cummins 1974) is a fundamental attribute of the RCC, and stresses the importance of ecological functions. We applaud this approach, which, however, poses some practical problems: the diet of a macroinvertebrate species can be varied, depending on age (e.g. Schröder 1976; Fuller and Stewart 1977) as well as on site (e.g. Martinson and Ward 1982; Williams and Williams 1982).

Special problems are posed when ecological study involves assumptions about unperturbed stream conditions, because our knowledge of the ecology of pristine headwater streams is scarce and of pristine rivers is almost nonexistent (see Horwitz 1978; Sedell and Luchessa 1982). Hence, such an approach is necessarily based to some extent on speculation. We explicitly welcome the RCC's endeavour to describe natural stream ecosystems, since in most cases this may be the most appropriate way to illustrate the deviations of our "modern" streams from their historic nature.

Today, most lower reaches of streams have been radically changed by human activities. The original condition of certain stream systems in North America have been demonstrated in a fascinating way by Sedell and Froggatt (1984) and Triska (1984): riparian trees from eroded banks formed large organic debris dams, blocking the channel, creating lakes, new side channels, and so on. A similar situation occurred in Europe. Behning (1928) described a unique biocoenosis on trees washed into the Volga. And there is historical evidence that in the twelfth century, servants on horseback had to guide ships through the Oder in order to avoid collisions with the dangerous oak trees lying in the river (Herrmann 1930). Besides the main channel, smaller ones occurred with flow characteristics resembling those in reaches further upstream (Krause 1976). Similar conditions have been described in the Amazon (Junk 1982; Sioli 1982) and the Congo (Stanley 1874-77). This "original state" of larger pristine rivers was not considered in Vannote et al. (1980): thus, we will discuss its consequences for the RCC below.

## On Five RCC Tenets

### Tenet I: Energy Equilibrium of the Physical System and Biological Analogue

In our opinion the central statement of the RCC is that "biological communities should become established which approach equilibrium with the dynamic physical conditions of the channel" (Vannote et al. 1980, p. 132). To understand this statement we must go back to Leopold et al. (1964, p. 266 ff) who discussed in detail the physical dynamic equilibrium of streams: power expended per unit length of a channel and per unit area of the bed of a channel (Table 1) are expected to tend to uniformity. A modal value of central tendency between the two will lead to a longitudinal equilibrium profile of the channel.

Recently, Mangelsdorf and Scheurmann (1980) took a physical-analytical approach to the question of the equilibrium profile, giving examples and discussing the situation in streams that have almost reached or are far from their equilibrium profile. They stress that tectonics, lithology, and climate determine the longitudinal profile of each running water in a characteristic way. Thus, for example, the Rhine has three base

<sup>2</sup>See also Minshall et al. in this issue (Ed.).

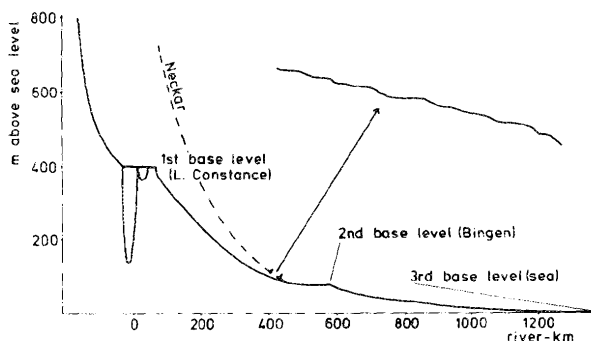


FIG. 1. Rough slope curve of the Rhine and the Neckar (according to Mangelsdorf and Scheurmann 1980). The Rhine has three base levels: lake level of Lake Constance (its depth is indicated by the two loops), slate formation at Bingen, and sea level at the mouth (indicated by the thin straight line). The arrow points to a detail in the slope curve of the Neckar above Heidelberg (according to Wilser 1937).

levels (Fig. 1): Lake Constance, Bingen (due to slate), and, finally, the sea, i.e. at present the Rhine is approaching an equilibrium profile in three sections. This is due to the very "turbulent" history of the Rhine, into which other basins were incorporated (Quitow 1976–77). The Neckar is included in Fig. 1. If we take a closer look at its profile above Heidelberg, in an area with a high tectonic diversity, the influence of location-specific events on a stream profile can be demonstrated. These two examples show that empirical-statistical models of the physical state of a stream system cannot be used without checking if the models are valid for these streams.

System-characteristic runoff patterns, which are assumed to modify the progressive and predictable change in the physical system (Minshall et al. 1983), will further complicate the RCC. In Europe, 60 different types of runoff patterns are characterized (Grimm 1968), which can be altered on the microscale by basin shape and relief (Gregory and Walling 1973, fig. 5.10).

In principle, however, it can be stated (Mangelsdorf and Scheurmann 1980, p. 148) that a stream does tend towards that profile at which, for a given discharge, the material imported will be transported. If material input and transport capacity are not in equilibrium the stream starts to erode or to accumulate. Generally, a stream with a source in the mountains and no additional base level along its course to the mouth can then be divided into three sections: an upper reach, where erosion is dominant; a middle reach, which represents a zone of transition; and a lower reach, where accumulation prevails. Since the ratio of material input to transport capacity is not constant at a given point of the stream over time — in addition to more regular annual variations, irregular episodic changes occur (Bergstrom 1982; Kelsey 1982) — the limits between these three reaches shift upstream and downstream according to discharge and material load. Hence, the reach with the highest dynamics is the middle one where the slope levels off. In this area natural streams are frequently braided at first and then start to meander. Where a stream is braided, there is a frequent decrease or increase in channel number and a variety of channel characteristics, depending on the discharge (Mosley 1982).

We are not sure whether biological consequences of the dynamic equilibrium of a stream discussed by Curry (1972, p. 13), in a paper cited in the RCC under the heading "Derivation of the concept," are implicitly included in the RCC or not. Curry considered that the energy of the physical system,

which is expended as frictional heat energy, is "of great importance as energy input in biologic communities." Therefore the tendency toward uniformity of energy expenditure in river systems will help to explain the stability and diversity of stream communities. Are these ideas covered by the following RCC statement: "The tendency of the (physical) river to maximize the efficiency of energy utilization and the opposing tendency toward a uniform rate of energy use" (Vannote et al. 1980, p. 131), which is another way to express the dynamic equilibrium condition of a channel, has an analogue in the trade-off of the biological system between the tendency "to make most efficient use of energy inputs" (e.g. through resource partitioning of *temperature*) and the tendency "towards a uniform rate of energy processing throughout the year" (Vannote et al. 1980, p. 134)? And what is the meaning of "a tendency for reduced fluctuations in energy flow" of "river ecosystems" (p. 133) or a tendency of "stream ecosystems ... towards uniformity of energy flow on an annual basis" (p. 134) (Vannote et al. 1980)? Does this imply an energetic unity of the physical and biological system? If so, the annual variations in physical energy flow (e.g. discharge) must be counterbalanced by the biological energy flow in order to reach uniformity on the ecosystem level (= abiotic + biotic energy flow tend to uniformity).

Since these energy statements have a great impact on the theoretical background of stream ecology, they require clarification by its authors.

From the above it is evident that the energy expenditure of the physical system plays an important role in the RCC. However, recent contributions on the RCC have not concentrated on hydraulics. For example, only a short sentence in Minshall et al. (1983, p. 18) was devoted to this subject. Thus, we used the data from the 16 stations investigated in that study to calculate some simple physical parameters such as power expended per unit of length and area, shear stress, and Froude number, which gives an indication of turbulence in streams (streaming or shooting flow; see Table 1 for formulae). No modal value of central tendency between power/reach and power/area is indicated by the downstream pattern of these parameters (Fig. 2). Neither do Froude number and shear stress exhibit uniform tendencies (Fig. 2). The causes of this may be that (i) available discharge data are annual means and not bankfull discharges, (ii) the streams studied were not within the limits set by the dynamic equilibrium theory of streams, (iii) in three of the four study sites the lowermost stations did not receive water from the upper stations, and (iv) the location-specific lithology and geomorphology modified the general tendency expected at several stations; such a tendency is, of course, difficult to discern at only four stations over stream reaches 35–57 km long.

To demonstrate the relationship between stream geomorphology (e.g. slope), the physical properties of flow near the stream bottom, and aquatic invertebrate ecology, we will introduce another parameter here: the thickness of the laminar sublayer above the stream bottom. Distribution patterns of benthic invertebrates are related to this indicator of the actual forces acting at the stream bottom, i.e. "hydraulic stress" (Statzner 1981a, 1981b). This sublayer equation (formula 5 in Table 1) incorporates, in principle, the same parameters as the Manning formula (6 in Table 1), which can be transformed into the sublayer equation and vice versa (Smith 1975). If the Manning formula is written differently (6') and compared with formula 5, it becomes evident that the thickness of the laminar sublayer is

TABLE 1. Formulae used for the expression of physical patterns along the course of streams (note that the Manning formula (6) is written for wide channels with a simplified roughness parameter).

$$\begin{aligned}
 (1) \quad P_1 &= QgSp & (2) \quad P_2 &= \frac{QgSp}{w} \\
 (3) \quad \tau_0 &= gDS\rho & (4) \quad Fr &= \frac{U}{\sqrt{gD}} \\
 (5) \quad \delta' &= \frac{11.5\nu 5.75 \log \left( \frac{12D}{r_p} \right)}{U} \\
 (6) \quad U &= \frac{\text{const.}}{r_p} D^{2/3} S^{1/2} & (6') \quad \frac{1}{S} &= \left( \frac{\text{const. } D^{2/3}}{\frac{r_p}{U}} \right)^2
 \end{aligned}$$

NOTE:  $D$  = channel depth (m),  $Fr$  = Froude number,  $g$  = acceleration due to gravity ( $\text{m/s}^2$ ),  $P_1$  = power per unit length of a channel ( $\text{W/m}$ ),  $P_2$  = power per unit area of a channel ( $\text{W/m}^2$ ),  $Q$  = discharge ( $\text{m}^3/\text{s}$ ),  $r_p$  = roughness of channel bottom (m),  $S$  = slope (m/m),  $U$  = mean current velocity (m/s),  $w$  = channel width (m),  $\delta'$  = thickness of laminar sublayer (m),  $\nu$  = kinematic viscosity ( $\text{m}^2/\text{s}$ ),  $\rho$  = density of water ( $\text{kg/m}^3$ ),  $\tau_0$  = shear stress ( $\text{N/m}^2$ ).

also related to slope (Statzner 1981a): an increase in slope should reduce the thickness of the laminar sublayer, hence raising the hydraulic stress on the stream bottom and vice versa. We have thereby linked a central tendency of microhabitat characteristics in a reach ("hydraulic stress") to a macrohabitat characteristic ("slope"): the latter "are major determinants of the types of microhabitats," to which fish as well as invertebrates respond (Bovee 1982, p. 3). It should be noted here that these formulae (5, 6, 6') as written in Table 1 are not applicable to all hydraulic situations found in natural streams (Bovee and Milhous 1978; Statzner 1981a), and they are used here as vehicles to elucidate some of the physical patterns one can expect along a stream course.

Summing up the above, we suggest the following characterization of an "ideal" or "standard" pristine running water course (Fig. 3) to which real streams can be compared. The source and the first part of its effluent are frequently characterized by relatively low hydraulic stress. A transition zone is followed by a reach of high hydraulic stress, which, after the next zone of transition at the break-point of the slope curve (we regard the values of bed slope, hydraulic slope, and energy slope as identical), is then followed by a zone of lower hydraulic stress. Further downstream, numerous large-scale discontinuities of the hydraulic stress occur. How the mouth of a stream system entering the sea is developed depends mainly on the material exported by the stream and the transport capacity of the marine component, including tidal amplitude and other currents (Mangelsdorf and Scheurmann 1980). The role of the stream in this context has been illustrated in "large-scale experiments": reduction of material transported by the stream due to artificial dams reduces the area of the original delta (Baxter 1977). The main types of mouths are estuaries and deltas (Fig. 3), and it is important to note that the physical characteristics of the stream influence in part the salinity at the mouth of the stream.

We conclude that the pattern of physical parameters as

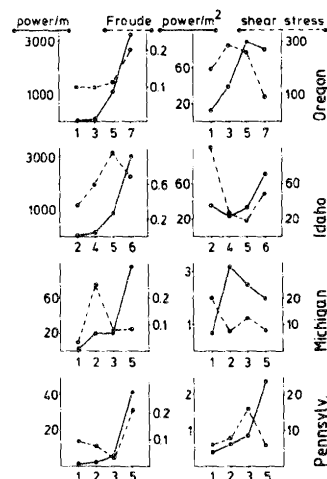


FIG. 2. Parameters for energy expenditure (see Table 1 for formulae and units) at the 16 RCC stations considered by Minshall et al. (1983). Note that no uniform patterns emerge on the way downstream (x-axes: stream orders), if the complete set of data is considered.

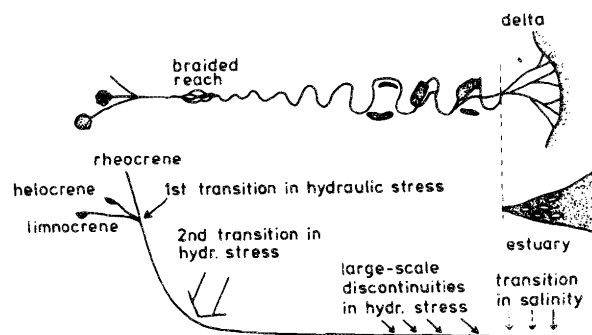


FIG. 3. Some typical changes in the central tendency of habitat characteristics from the source to the mouth in a hypothetical pristine stream. Not all of the components shown here can be or must be present in a stream system.

proposed in Fig. 3 obviously does not represent a "continuous" or "intergrading" gradient as dictated by the RCC (Vannote et al. 1980; Cushing et al. 1983), and variations on the microscale as well as lakes and other additional base levels will complicate matters much more. Thus, the analogies between the physical and the biological equilibrium of streams cannot be as simple as suggested by the RCC.

## Tenet II: Entropy Patterns

In addition to energy statements discussed above, some clarification is required about a statement on entropy: from headwaters to the mouth there is a constant gain in the physical variable "entropy." Vannote et al. (1980, p. 132) postulate that "the biological organization in rivers conforms structurally and functionally to kinetic energy dissipation patterns of the physical system."

Does this imply a characteristic tendency in biological entropy from the source to the mouth of a stream? The longitudinal organization of the gross photosynthesis/respiration ratio in the stream (thermodynamic concept of entropy) or the species diversity (e.g. Shannon index: entropy concept of information theory) can serve as indicative parameters. Both are considered in the RCC (Vannote et al. 1980, fig. 2), and in contrast with

the constant entropy gain in the physical system, both show increasing as well as decreasing tendencies on the way downstream.

Or does the entropy statement imply that the biological communities will adjust to the physical entropy pattern through energy consumption and processing, resulting in similar tendencies in the biological entropy in every reach of the stream? This is, of course, a usual tendency of organisms, since "living systems" are "negentropic" (Fränzle 1978).

We believe that the absence of this theoretical background will not mean a loss in significance of the RCC; thus, we suggest omitting the above statement on entropy.

#### Tenet III: Temporal Sequence of Species Replacement and Utilization of Energy Inputs

After a species has completed its growth "it is replaced by other species performing essentially the same function ... It is this continuous species replacement that functions to distribute the utilization of energy inputs over time" and results in a composite species assemblage tending to "maximize" energy consumption (Vannote et al. 1980, p. 134). This tenet may be applicable only to stream systems in geographical zones subject to distinct seasonal variations in abiotic factors.

A temporal sequence of species replacements, such as postulated by the RCC based on experience from North America, has already been rejected by Winterbourn et al. (1981) and Towns (1983) for streams in New Zealand. In equatorial regimes, all principal species of a stream system are present over the whole year. This is clearly demonstrated by emergence data of four insect groups from a stream situated 2°S in Zaire (Zwick 1976; Statzner 1976; Lehmann 1979; Kopelke 1981): no complete temporal replacement occurs, although several species show cyclic patterns. The terrestrial vegetation in this latitude does not exhibit a distinct phenology comparable with that of temperate zones, but periodic patterns obviously do occur (Dieterlen 1978). This suggests some seasonality in the input of coarse organic material into the stream communities, which is probably processed faster in the tropics than in temperate climates (Dudgeon 1982). The question is whether such stream communities near the equator have developed other possibilities to "maximize" energy consumption. Fittkau (1973) suggests that the high efficiency of energy utilization is linked to a high species number and a relatively low abundance of each species in Central Amazon streams which are scarce in nutrients.

Another question is whether the species assemblage of a stream reach really plays the role postulated by the RCC. Minimization of leakage (export of organic compounds) from a stream reach is another way to express maximization of energy consumption. Recent studies have shown that leakage is reduced under normal discharge conditions if the invertebrate fauna is destroyed in experiments or in computer simulations (Wallace et al. 1982; Webster 1983; see also Meyer and O'Hop 1983), i.e. macroinvertebrates decrease the efficiency of stream ecosystems.

#### Tenet IV: Time Invariance and Absence of Succession in Stream Ecosystems

Vannote et al. (1980, p. 135) stated that the temporal change of the biological system of a stream "becomes the slow process of evolutionary drift" and the community "gains and loses species in response to low probability cataclysmic events and in response to slow processes of channel development." As a result

of this, succession in stream ecosystems is absent and these systems can be viewed in a time-independent fashion.

If we accept cataclysmic events as a factor that causes gains and losses of species, then we might expect that the biological community in the stream is reestablished afterwards by means of succession (see Fisher 1983) parallel to that in the terrestrial environment (e.g. after landslides, wildfires, or volcanism).

In our opinion, succession cannot, therefore, be rejected in stream communities. As a consequence, stream ecosystems cannot always be viewed in a time-independent fashion. And we have evidence from long-term studies that time invariance does not occur: this is demonstrated for insects (Illies 1978, 1982) and fish (Grossman et al. 1982). While discussing organic matter budgets for stream ecosystems, some authors of the RCC drew a similar conclusion in a recent paper (Cummins et al. 1983).

#### Tenet V: Pattern of Biological Diversity

This tenet of the RCC, discussed at some length, states that high environmental variation results in high biotic diversity. This concept was actually first formulated early in this century by Thienemann in one of his biocoenotic principles (see Hynes 1972, p. 234).

In Vannote et al. (1980) the variation of the environment is discussed using the example of the diel water temperature amplitude, which is certainly highest in the midreach of a natural stream in temperate climates. The RCC indicates that the biological diversity is therefore also highest in the midreach (Fig. 4D). However, if we include the annual amplitude of the water temperature (i.e. as a second environmental factor), the highest variability no longer occurs in the midreach of our stream. And it is very improbable that all other factors mentioned by the RCC, such as riparian influence, substrate, flow, and food, show their highest variability exactly in the midreaches of streams (see also the conclusion at the end of tenet I). The latter holds especially true if we include non-temperate climates. Tropical streams may have very low diel and annual temperature amplitudes in their middle and even lower reaches (e.g. Sioli 1975; Statzner 1975).

A second explanation of the RCC for the maximum of species diversity in the midreach of streams is the convergence of two vectors that illustrate shifts in spatial distribution (Vannote et al. 1980, p. 135): insects are believed to have become aquatic first in headwater streams, while molluscs and crustaceans have reached streams from the marine environment through the mouth of streams. Later, insect abundance shifted downstream and mollusc and crustacean abundance shifted upstream.

The confluence of these migratory vectors might cause high diversity (e.g. Shannon index) in the midreach only if insects shifted at the same speed downstream as molluscs and crustaceans shifted upstream, but not during the phase of complete overlap of the abundance patterns (Fig. 4A-4C). We see no evidence to suggest that these conditions are fulfilled in nature, especially not in most streams. On the other hand, existing evidence shows that, excluding effects of pollution, diversity in streams may change drastically bearing no relation to the "order" of that stream (Statzner 1981c) or that diversity is almost constant throughout different "orders" (Minshall et al. 1982).

A large part of the discussion of this topic dealt with benthic macroinvertebrates, which, of course, contribute only part of the complete community diversity. It is, for example, a well-known fact (and also shown by Vannote et al. 1980, fig. 1)

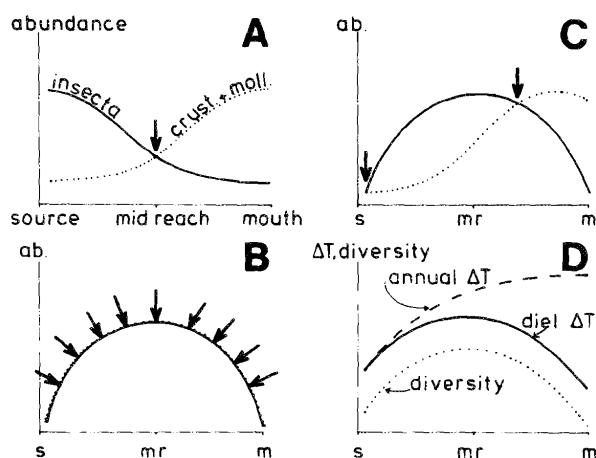


FIG. 4. (A–C) Hypothetical abundance distribution of Insecta, Crustacea, and Mollusca shifting downstream or upstream, respectively, and the consequences for a diversity index (e.g. Shannon), which is highest (arrow) where the abundance of all species is the same. (A) Beginning of shift, both groups shifting with the same speed; (B) complete overlap, both groups shifting with the same speed; (C) Insecta shifting faster downstream than Crustacea and Mollusca upstream. (D) Development of the diel and annual water temperature amplitude and the diversity, as suggested by the RCC, from the source to the mouth of a stream. See text for discussion of these patterns.

that plankton develops mainly in the lower reaches of streams, and the number of fish species increases there also. This will, of course, influence the diversity pattern of the complete community, which is probably at its highest in the lower reaches of streams, where the large-scale discontinuities in hydraulic stress occur (Fig. 3). Furthermore, the environmental variability of a particular physical structure may influence the diversity of one group (e.g. insects) in a different way than that of other groups (e.g. fish) (Schlosser 1982).

## Conclusion

The five tenets of the RCC discussed above are open to various interpretations, need extension, or are unexpected or refuted by the current state of knowledge. The physical parameters in streams obviously do not exhibit a continuous or intergrading gradient (tenet I) in the downstream direction (Fig. 3). Thus, biological analogues of the energy equilibrium in the physical system are more complicated than suggested by the RCC. It is not clear how the RCC relates entropy patterns of the biological to the physical system (tenet II). Since we do not see an essential need for the statement on entropy in the RCC, we recommend its omission from the concept. This will reduce the theoretical ballast of the RCC. Maximization of yearly energy utilization through species replacement (tenet III), lack of succession and time invariance in stream communities (tenet IV), and specific mechanisms leading to high biotic diversity in midreaches of streams (tenet V) are either rejected (IV), unexpected (V), or restricted to particular geographical areas (III). We therefore suggest modifying the original RCC by excluding tenets III–V from the concept. This will result in a higher flexibility and larger applicability of the RCC.

In our opinion, these modifications will hardly conflict with projects relating to the RCC that have been realized up till now (see Minshall et al. 1983 and references therein; Cummins et al. 1983; Cushing et al. 1983; Bruns et al. 1984). These projects

placed emphasis on gross photosynthesis and respiration and on the status of organic matter and the corresponding functional organization of the community, i.e. on points that we evaluate as major objectives of the RCC. None of these is directly restricted by the recommended modifications.

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