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The River Continuum Concept: A Basis for the Expected Ecosystem Behavior of Very Large Rivers?

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Abstract

SEDELL, J. R., J. E. RICHEY, AND F.J. SWANSON. 1989. The river continuum concept: A basis for the expected ecosystem behavior of very large rivers?, p. 49–55. In D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The river continuum concept (RCC) is examined to determine its usefulness in predicting the behavior of large river ecosystems. Although some verification of RCC predictions of carbon dynamics in large rivers has been noted, most large-floodplain river systems cannot be adequately addressed using the RCC as originally defined. In the world's largest rivers, the importance of upstream carbon to the carbon utilized in downstream reaches is debatable, implying that river zones may take on a life of their own within a basin. Hydrologic interaction of a river with its streamside forest and floodplain is critical for carbon-processing and fish habitat regardless of size of the drainage basin. Our present ability to evaluate big-river biotic assemblages and ecosystem metabolic interactions is significantly limited by an inability to cope meaningfully with the complexities associated with spatial and temporal heterogeneity along the length of the river.

Résumé

SEDELL, J. R., J. E. RICHEY, AND F.J. SWANSON. 1989. The river continuum concept: A basis for the expected ecosystem behavior of very large rivers?, p. 49–55. In D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les auteurs évaluent l'utilité du concept de la continuité dans un cours d'eau (RCC) pour prévoir le comportement d'écosystèmes de grandes rivières et de fleuves. Bien que certaines prédictions du RCC concernant la dynamique du carbone dans les grands cours d'eau aient été exactes, le RCC ne peut servir, tel qu'il a été défini au départ, pour la plupart des systèmes fluviaux à larges plaines inondables. Le rapport entre le carbone des cours supérieurs et le carbone utilisé dans les cours inférieurs des plus grands fleuves du monde est discutable; cela voudrait dire que les diverses zones d'un cours d'eau peuvent être indépendantes les unes des autres. Les interactions hydrologiques entre un cours d'eau et la forêt ou la plaine inondable qui le borde sont primordiales, en ce qui concerne la dynamique du carbone et l'habitat des poissons, peu importe la taille du bassin hydrographique. À l'heure actuelle, nos capacités à évaluer les assemblages biotiques fluviaux et les rapports métaboliques dans un écosystème sont grandement limitées par notre incapacité à comprendre les complexités associées à l'hétérogénéité spatiale et temporelle le long du cours d'eau.

Introduction

Large rivers have not been as well studied from an ecosystem perspective as have small streams (Richey 1981; Naiman 1983a; Decamps 1984a). The most dramatic and predictable ecological changes occur between small streams and intermediate-sized fourth to sixth-order rivers. These changes occur within the first 200 km of river length, whereas large rivers flow for thousands of kilometres with little predictable change but with the greatest production and exploitation of fisheries resources (Welcomme 1985).

Large rivers are viewed as separate systems with a different set of ecological characteristics and management problems than upstream rivers or their valleys (Lavandier and Decamps 1983); therefore, it may not be plausible to extrapolate concepts of riverine ecosystem function applicable to upper river stretches to downstream areas. Dams, lakes, and swamps serve as "discontinuities" dividing rivers into more or less independent reaches (Ward and Stanford 1983; Decamps 1984b). Variation in the extent of large river floodplains and transverse interactions between river and floodplain forests often dominate longitudinal

characteristics of riverine ecosystems (Hynes 1985; Welcomme 1979; Junk et al. 1989; Pautou and Decamps 1985; Bravard et al. 1986; Amoros et al. 1987; Ward and Stanford 1989).

One of the most provocative concepts of longitudinal variation in riverine ecosystem characteristics is the river continuum concept [RCC] (Vannote et al. 1980; Minshall et al. 1985). The RCC treats the river network as a continuously integrated series of physical adjustments and resource gradients along which the biota and ecosystem processes are adjusted, using a hypothetical river system in a temperate forest basin as an example. River networks are viewed as longitudinally linked systems in which biotic assemblages are orderly, and ecosystem-level processes in downstream reaches are linked to those in upstream parts of the network. Subsequently, the concept has produced a great deal of lively discussion — exceptions were pointed out, new studies were initiated to evaluate its usefulness as a generalizable concept, and calls for clarifying the definition and basic tenets of the concept were heard (Statzner and Higler 1985).

For both small and large basins, problems with the RCC quickly arose. River systems are not continuous physical and biological gradients to the sea (Balon and Stewart 1981; Statzner and Higler 1985), dense riparian vegetation does not exist around many headwaters at high altitudes (Ward and Stanford 1983), and biotic assemblages do not match the functionally defined progression in responses to stream order (Winterbourn et al. 1981; Benke et al. 1984; Bruns et al. 1984).

The relevance of the river continuum concept to large rivers is dependent on what characteristics or processes one is interested in — carbon flow, nutrient cycling, biotic assemblage diversity, standing crop, or fish productivity. In this paper, we : (1) examine RCC ecosystem predictions for large rivers ; (2) test these with the Moisie River, a large Canadian boreal river, the South American Amazon River, the largest river in the world and the Parana-Plata River system, and (3) consider the appropriate theoretical basis for analysis of large rivers.

Whether we view a river system as composed of a tightly integrated series of biotic and ecosystem changes from headwaters to the sea or a set of geomorphically and biotically independent reaches depends on the river system studied, the investigators' research approach, and system characteristic of interest. A river ecosystem approach must incorporate both concepts to describe adequately and account for physical and biological processes. Linking geomorphically distinct reaches functionally into a longitudinal perspective is the research challenge.

RCC Predictions of Carbon Dynamics for Large Rivers

The original RCC was not specific in its predictions of the behavior of large rivers. Most subsequent discussion focused on smaller river systems, and the complexity of large rivers was overlooked. Nonetheless, Vannote et al. (1980) and Minshall et al. (1985) addressed big rivers to make some relevant predictions of carbon dynamics. The set of carbon dynamics that can be predicted includes:

Prediction 1 — Carbon Sources

Carbon in the main channel of a large river results from various terrestrial and aquatic sources :

- a) Large rivers receive the majority of their fine particulate organic carbon (FPOC) load from upstream processing of dead leaves and woody debris because the immediate effects of adjacent riparian vegetation are minimal. Thus, the ratio of coarse to fine particulate organic carbon is expected to be very small (CPOC/FPOC < 0.001).
- b) Fine particulate detritus is also entrained from the floodplain during floods and through lateral migration of the channel.
- c) Aquatic primary production is limited by depth and turbidity, so respiration exceeds production (P/R < 1).

Prediction 2 — Carbon Processing

- a) The heterotrophic use and physical absorption of labile dissolved organic carbon (DOC) are rapid in headwater regions ; thus, DOC in the larger downstream rivers should have higher molecular weights and be more refractory. A similar pattern of increasing refractivity would be expected for POC.
- b) The rate of within-system processing increases and the rate of storage and export decreases with increasing substrate quality and duration in the river.

Prediction 3 — Stability of Energy Flow

The minimization of the variance in energy flow is the outcome of overlapping seasonal variations of detrital and primary production inputs, adjustment of functional groups over time, and the organic and inorganic matter transport and storage characteristics of rivers. As the sum of these factors, within-river oxidation is relatively constant over time and space.

Few studies on large rivers have been conducted with sufficient resolution to test these concepts. We now consider two large-river systems with sufficient data to do so (Table 1).

Moisie River

Naiman (1982, 1983a, 1983b, 1983c) demonstrated that with increasing channel size in a subarctic river of 20000 km² (Moisie River, Quebec, Canada, mean annual discharge = 470 m³s⁻¹) carbon processing could be explained by simple power functions relating the parameters of interest (community respiration, periphyton production, seston transport, DOC and POC storage) to stream order. The Moisie drainage basin has numerous lakes, bogs, and beaver dams in its upper watershed. The river system has no floodplains and is a geologically constrained riffle-pool channel. Stream order was a very useful physical parameter in the river basin because it was possible to relate stream order with great accuracy to watershed area, mean annual discharge, and channel width. This study provided unequivocal support to the RCC projections on carbon dynamics and suggested the importance of upstream carbon supply to downstream metabolism.

TABLE 1. Summary of carbon dynamics for two large rivers, subarctic Moisie River, Canada, North America, and tropical Amazon River, Brazil, South America.

| | Moisie River ($2 \times 10^5 \text{ km}^2$) | Amazon River ($6 \times 10^6 \text{ km}^2$) |
|----------------------------|--|--|
| Carbon Sources | upstream refractory carbon and river inchannel autotrophs | allochthonous vascular plants from lowland areas, no river channel carbon, |
| Carbon Processing | annually high due to autotrophs, geomorphic areas not examined for carbon processing, spiral length longer than 9th order reach length | refractory carbon processing over 100's km, respiration rapid in distinct geomorphic regions (10's km) from undetermined channel margin sources. |
| Stability of Carbon Energy | upstream carbon subsidy and large river summer autotrophic production in channel. Temperature controlled in winter | relatively uniform in composition and amount, 2 fold annual variability in respiration. |

Moisie River Carbon Sources

Naiman (1983a) and Connors and Naiman (1984) found an unequivocal transition between streams dominated by allochthonous inputs (orders 1–3) and those dominated by autotrophic inputs (> order 4). As channel size increased, there was the predicted decrease in allochthonous inputs and an increase in gross production by mosses, macrophytes, and periphyton. The 9th order river segment received a large input from in-channel moss production.

Moisie River Carbon Processing

Naiman (1983a, 1983b) found that respiration rates increased with stream-size increase. Most of the respiration came from autotrophic respiration. Within-stream processing increased with increasing substrate quality derived from the autotrophs. Storage of organic material decreased with stream-size increase.

Moisie River Stability of Energy Flow

From the published accounts of the carbon dynamics of the Moisie River, it is not yet possible to determine if within-river oxidation is constant over time and space. From the respiration data, it appears as if the upstream reaches subsidize the downstream reaches to a certain extent (Naiman et al. 1987).

Moisie River Summary

This large, subarctic river with negligible floodplain areas but with many bogs and lakes in its basin follows the RCC predictions on carbon processing (Table 1). A problem with

extrapolating to other rivers is that the length of the 9th-order river reach is less than 100 km and floodplains does not exist along the river. Nonetheless, the Moisie River represents one of the best studied large-river ecosystems to date. The 9th order Salmon River in Idaho (Minshall et al. 1983) is a geologically constrained, clear water, pool-riffle channel. It also exhibits similar carbon characteristics as the Moisie River.

Amazon and Parana-Plata River Systems

The CAMREX (Carbon in the Amazon River Experiment) project measured the distributions and composition of carbon as a function of geomorphology and hydrology over a 2 000-km stretch of the Amazon River on nine cruises at different stages of the hydrograph. On the basis of reported results (Ertel et al. 1986; Hedges et al. 1986a, 1986b; Richey et al. 1986; Devol et al. 1987) we can examine the RCC (Table 1).

Amazon Carbon Sources

The POC has an almost constant composition over time and space in the Amazon mainstem. The fine particulates ($< 0.063 \text{ mm}$) are predominantly degraded, N-rich soil organic matter, whereas the coarse fraction ($> 0.063 \text{ mm}$) is recent, diagenetically unaltered vascular plant material (about 80% leaf and 20% wood). Stable carbon isotopes indicate that some of this material is probably derived from within the lowland basin and not in the headwaters. The DOC — about 50% of the total organic carbon — averages 60% humic materials (balance unknown), with the fulvic and humic acid fractions having distinct compositions and residence times within different parts of the basin. Dissolved humic acids introduced by blackwater tributaries are preferentially adsorbed onto mainstem fine particulates. Macrophyte remains constitute no more than 10% of the total organic matter. There is no consistent downstream increase in refractory organic components or simplification of organic composition in the particulates.

Amazon Carbon Processing

The riverine carbon pools have a significant component of recent carbon, indicating carbon cycling times within the Amazon basin of $< 150 \text{ yr}$ for all but the fine particulate fraction ($< 600 \text{ yr}$). High rates of respiration occur within the river, supported by organic material of an as yet undetermined lateral source and composition. These exchanges take place most actively in several distinct geomorphological regions where floodplain waters interact with mainstream water, and are characterized by carbon and water mass balance anomalies. Most respiratory CO_2 is lost to the atmosphere, which is a major sink for riverine carbon.

Amazon Stability of Energy Flow

Deciding whether in-river oxidation in the Amazon basin is constant over time and space is subjective. Respiration per unit volume varies over the annual hydrograph by a factor of two. Attainment of equilibrium depends on the various time and space scales of water routing, sediment transport, and chemical cycling. The systematic variability of water

and element distributions is observable on the order of weeks. According to the properties of each substance, relevant length scales range from hundreds of kilometres up-and down river (conservative substances) to tens of kilometres (less conservative substances) to lateral exchange with the varzea (more labile substances).

Clearly, the Amazon does not conform precisely to the original tenets of the RCC. However, the principal distributions of carbon are controlled by the geomorphology and hydraulics of the system, which are central points of the RCC. Lateral exchange with the floodplain has a significant effect on the mainstem carbon abundance and oxidation. Big rivers can be divided up into metabolically discrete zones or patches. They do not form a simple, direct spatial continuum of organic processing from headwaters to the sea, because of discontinuities in landforms and hydraulics that constrain river–forest–varzea interactions.

Parana–Plata River System

The Parana–Plata River system, the neighboring drainage basin south of the Amazon, is the only major floodplain river where a longitudinal relationship of fish biomass with river organic material and nutrients has been demonstrated. Quiros and Baigun (1985) regressed fish biomass and catch per unit effort against total organic nitrogen and against total organic carbon and found that much of the spatial variability in fish abundance in the Parana River is explained by the content of organic matter in the water column. Island lagoons under greater influence from the main river channel showed smaller fish biomass than those near the margins of the floodplain, where they are influenced by secondary channels and lateral tributaries with more organic matter. In aquatic environments with low nutrient concentrations, the positive relationship between levels of organic matter in the water column and fish abundance might not be found.

Quiros and Cuch (1989) found a longitudinal increase in nutrients, zooplankton, benthos, fish, and organic matter both in the water column and bottom sediments in the main channel of the upper Parana. Thus the Plata River appeared to be spatially structured along a longitudinal continuum as well as a lateral one across the floodplain.

Amazon/Parana–Plata Summary

These results are not viewed by us as a verification of the RCC. They do point out the common theme of distinct reaches within big-river systems that vary in structural complexity, nutrient richness, and fish biomass. The most productive areas are those most interactive with the floodplains, and geomorphic features determine the extent and duration of this interaction in predictable ways.

RCC, Geomorphology, and River–Forest Interactions

From these and other studies (Minshall et al. 1983, and Naiman et al. 1987) we observe that the RCC provides the most useful predictions of longitudinal lotic ecosystem characteristics for river systems with geological constraints on the extent of forest–river interactions. In unconstrained areas with extensive river–floodplain forest interaction, such as in the Amazon and other large rivers (Welcomme 1979; Bayley and Petrere 1989; Junk et al. 1989; and

Quiros and Cuch 1989), productivity of the riparian forest and processes distinctive to the flooded forest environment can greatly modify the longitudinal patterns of ecosystem processes predicted by the RCC.

We agree with Welcomme (1979) and Bravard et al. (1986) that ultimately the significance of floodplain forest effects on river ecosystems can be predicted based on geomorphic and hydrologic constraints on the duration and areal extent of these interactions. A useful approach may be to delineate river reaches on the basis of the lateral extent of floodplain scaled in relation to channel width (floodplain width/bankfull channel width). One might expect a progressive decrease in constraint on floodplain width in a downstream direction. This would follow from the typical decrease in gradient and increase in sediment deposition in downstream areas. However, the distribution of constrained and unconstrained reaches does not vary uniformly along river systems. For example, in the Zaire River system in Africa lower river reaches are highly constrained by bedrock and the river course follows fault lines (Savat 1975; and Balon and Stewart 1983).

In fluvial systems ranging from small streams to large rivers we observe great variation in this floodplain width index resulting from constraints imposed by bedrock outcrops, fans and deltas constructed at the mouths of tributaries, landslides, and other features. In steep, mountain rivers unconstrained reaches may be only 0.5–10 km in length. In contrast, the entire lower 2 000 km of the Amazon River is unconstrained, although there is significant variation in river pattern and interaction with floodplain forest over this part of the river system (Mertes 1986). Unconstrained river reaches typically have multiple secondary channels and extensive area of forest–river interaction caused both by high bank coefficient ratio of streambank:valley floor length and by a broad area of inundation during floods.

The concept of a “bank coefficient” or perimeter index (Gosse 1963) is very useful to river ecologists. This ratio is high where there are many islands and irregular banks. Gosse (1963), with particular reference to the central basin of the Zaire River, suggests that fish production is strongly related to the number and sizes of forested islands present in a given reach. Gosse stresses the importance of island development in improving habitat heterogeneity (depth, substrate, current) and enhancing trophic conditions. For the lower 2 000 km of the Amazon River, Mertes (1986) found that areas containing the largest number of islands corresponded with the areas of highest lateral migration. Sedell and Froggatt (1984), Minshall et al. (1985), and others have noted that in these areas carbon storage and riparian inputs, as well as area inundated, are greater than in single channels, implying greater productivity.

River reaches with a high “bank coefficient” index or perimeter index usually occur in hydraulic transition zones, such as changes in gradient. Neither studies of ecosystem production parameters (respiration, allochthonous inputs, gas dynamics, nutrient production) nor of fish fauna have been matched to such a zone of hydraulic change or intense interaction with the riparian vegetation in large floodplain rivers. River ecologists first need to partition the river into broad geomorphic characteristics of a segment, reach, or zone of a river (Amoros et al. 1987) and then determine the biotic community and carbon processing response for channel and floodplain reaches within these reaches.

The interaction of the stream channel with vegetated stream banks or floodplain is important for fish communities regardless of size of stream or river. This interaction represents a factor in both forested and savannah areas that is generally overlooked in large rivers because of the diminished inputs of leaf litter, shading, and stability of a downed tree or snag.

On large floodplains of rivers the hydrologic connectedness of the floodplain to the main river channel and area inundated may determine its productivity. The rate at which water moves onto or off of the floodplain helps determine the type and extent of the nutrient cycling regime (anaerobic to aerobic). Junk et al. (1989) described river pulsing or the seasonal flood wave as the driving force for the river-floodplain complex, maintaining the complex in a dynamic equilibrium. The flood pulse, preventing permanent stagnation, allows for rapid recycling of organic matter and nutrients, and results in a productivity which is hypothesized to be greater than if the interflood zone were either permanently inundated or dry.

The geomorphic structure and biology of river systems viewed in this way exhibit interesting similarities and differences between headwater streams and large rivers. Both constrained and unconstrained reaches can occur at any drainage area within a basin, but agents leading to their formation may vary. In small and intermediate sized channels, for example, large woody debris can locally raise base level, forming a broad unconstrained reach upstream. Landslides are common agents of constraint in fourth- and fifth-order channels in unstable mountain areas. Constraints along major river valleys are principally bedrock outcrops. Very broad, unconstrained areas with extensive channel development can form at intrariver system deltas.

The hydrology and hence biology of unconstrained reaches varies significantly between headwater streams and river mainstems. Small drainage areas and steep hillslope and channel gradients typical of headwater streams limit the duration of overbank flooding. Under these conditions particulate organic matter can be exchanged between the channel and floodplain forest, but the dominant effects of streamside forests are shading and input of litter and large woody debris directly to the stream channel.

In headwater areas flooding generally does not last long enough for certain floodplain processes to occur. Where floodplain forests, lakes, and secondary channels are flooded for weeks and even months, high levels of aquatic primary and secondary production can occur (Welcomme 1979; Junk et al. 1989). This is possible along large rivers in which exceptionally large drainage areas and low transit time of water can sustain flooding of long duration. Consequently, much of the forest-river interaction in these settings occurs in the flooded forest environment.

Synthesis

Longitudinal variation in river ecosystems can be viewed from several perspectives: (1) the RCC view emphasizes change in carbon processes and invertebrate communities in relation to controls on food resources, (2) a more traditional drainage basin ecosystem approach focuses on the flows of carbon and biogeochemical cycling, (3) fisheries perspectives concern species distributions and productivity in various habitats. The very significant reach-scale variation of

river-forest interactions, discussed in this paper, is an integral part of carbon and biogeochemical cycling systems and of the fisheries ecology of rivers of all sizes. However, this type and scale of river ecosystem behavior is not addressed by the RCC. As such, the RCC is of limited value for predicting large river ecosystem function.

Geomorphic conditions in unconstrained river reaches promote interaction of rivers with floodplain forests with potentially dramatic impacts on aquatic processes. The original statement of the RCC recognized along-stream variation in the effect of streamside forest on the channel environment, but did not consider the effect of the flooded forest environment. The ideas of Welcomme (1979), Decamps (1984b), Bravard et al. (1986), and Junk et al. (1988), thus provide concepts that lead to a more robust conceptual view of a river-floodplain system.

Future analysis of river ecosystem structure and function must integrate the RCC to floodplain-forest interactions of the whole hydrosphere (groundwater included). The river floodplain system has already been addressed. What has not been addressed is the linking of individual reaches along the river. What are the ecosystem consequences of different longitudinal arrangements of various hydrologic and geomorphic reaches? Ecosystem dynamics of carbon and nutrients will be affected if adjacent reaches are radically different, e.g., the river flowing from a floodplain reach into a geologically constrained reach. A framework which allows us to examine both the hydrologic and geomorphic settings of the individual reaches and their longitudinal arrangement will make it possible to distinguish the relative merit of viewing a particular river ecosystem as a continuum or as a series of independent reaches. The appropriateness of either of these alternative views is likely to vary with river system structure and with the ecological attribute of interest. For some very conservative attributes of the river ecosystems, reach-scale variation in system structure is of little consequence. Some system attributes, such as fisheries productivity, may vary greatly from reach to reach and within a reach.

Approaches to hierarchical classification (Lotspeich 1980; Frissell et al. 1986; Amoros 1987) help in delineating elements of the system and their relative scales, but stop short of elucidating ecosystem dynamics. The large river system is a sequence of patches of varying lengths and widths, and not a simple continuum. The large river is an accumulation of materials and gases experiencing differing transient times on and off the floodplains to the atmosphere or the sea. The next important step in understanding river ecosystems is to quantify and determine the controls on reach-to-reach interactions of materials, energy, and organisms.

The drainage basin ecosystem approach is accepted for a variety of river studies (Odum 1957; Fisher and Likens 1973; and Hynes 1975). Even in large basins unidirectional flow makes the river dependent upon its headwater streams and integrated subbasins. The distinctive reaches of a big river are also dependent on upstream water, sediment, and some nutrients. An ecosystem approach to large rivers cannot be avoided.

The ecosystem approach to rivers is not as concerned about biotic communities and physical habitat as about energy or carbon flow, nutrient dynamics, and biogeochemical processes linking terrestrial-lotic systems. This is an

important point of divergence with the more community and population biologist's approaches to stream and river systems. The ecosystem approach favors mass balance of carbon or nutrients to help identify areas needing study and identifies a set of ecosystem metabolic or nutrient cycling processes used to compare river systems in different geographical regions. Chemistry is the key interface discipline providing a common language for communication and for coordination of concepts and experiments. This approach has been used at the macroscale of the earth to examine linkages between continents, oceans, atmosphere, lakes, and rivers (e.g., global carbon cycling as it is affected by deforestation, agriculture, industrialization, acid rain, and effects of climatic shifts).

The challenge for future research will be to determine how ecologically important processes at the reach levels can be meaningfully aggregated to large river system wide and global-scale responses. How the different spatial and temporal scales can be integrated between and among disciplines (ecosystem scientists, fisheries scientists, biogeochemists, atmospheric scientists, engineers, geomorphologists, and others) is the present challenge.

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