2. THE SERIAL DISCONTINUITY CONCEPT OF LOTIC ECOSYSTEMS

river/stream/ecosystem theory/flow regulation

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ABSTRACT

Recent theoretical concepts of lotic ecosystems deal primarily with origins and fates of organic resources and inorganic nutrients as prescribed by the stream continuum and nutrient spiraling concepts. These concepts are based on gradient analysis in which stream systems are, of necessity, viewed as uninterrupted continua. Few riverine ecosystems, however, remain free-flowing over their entire course. Rather, regulation by dams has typically resulted in an alternating series of lentic and lotic reaches. The serial discontinuity concept is an attempt to attain a broad theoretical perspective of regulated lotic ecosystems. Discontinuity distance (DD), defined as the longitudinal shift of a given parameter by stream regulation, may be positive (downstream shift), negative (upstream shift), or near zero. The direction and intensity of DD vary as functions of the specific parameter examined and the position of the dam(s) along the longitudinal stream profile. The serial discontinuity concept can be applied to physical parameters (e.g., temperature summation) and biological phenomena at the population (e.g., species abundance patterns), community (e.g., biotic diversity), or ecosystem

levels (e.g., Photosynthesis/ Respiration). Regulated streams, according to the serial discontinuity concept, are viewed as large-scale experimental systems in which disruptions in continuum processes and nutrient spirals create conditions amenable to testing and developing basic theories of stream ecology.

INTRODUCTION

During the past decade two important theoretical concepts of lotic ecosystems have emerged. The river continuum concept (Vannote et al., 1980) describes the gradient of physical conditions and resulting biotic responses from the headwaters to the mouths of river systems. The nutrient spiraling concept (Webster, 1975; Wallace et al., 1977; Webster and Patten, 1979; Elwood et al., this volume) is concerned with the unidirectional and biologically mediated recycling (spiraling) of nutrients, including fixed carbon, along the river continuum. These concepts are based on gradient analysis (*sensu* Whittaker, 1967) in which stream systems are, of necessity, viewed as uninterrupted continua. Few riverine ecosystems, however, remain free-flowing over their entire course. Rather, regulation by dams has typically resulted in an alternating series of lentic and lotic reaches.

The effects of impoundments on lotic reaches immediately downstream from dams were recently summarized by Ward and Stanford (1979a). The serial discontinuity concept presented here is an attempt to attain a broad theoretical perspective of regulated lotic systems over the entire longitudinal stream profile. The concept treats physical parameters (e.g., thermal regima) and biological phenomena at the population (e.g., species abundance patterns), community (e.g., biotic diversity), and ecosystem levels (e.g., photosynthesis/ respiration). According to this concept, regulated streams are viewed as large-scale experimental systems in which disruptions in continuum processes and nutrient spirals create conditions amenable to testing and developing basic theories of stream ecology.

THE SERIAL DISCONTINUITY CONCEPT

The serial discontinuity concept, at this initial stage of its derivation, contains the following presuppositions: (1) The river continuum and nutrient spiraling hypotheses are conceptually sound and their underlying assumptions are valid. (2) The watershed is free of pollution and other

disturbance, except impoundment. (3) The remaining lotic reaches were not disturbed during reservoir construction (e.g., riparian vegetation and substrate were not modified). (4) Unless otherwise stated, the impoundments are assumed to be deep-release storage reservoirs, which thermally stratify and which do not release oxygen-deficient or gas-supersaturated waters. We intend to present the hypothesized ramifications of modifying thermal and flow regimes by impoundment as major disruptions of continuum processes, without additional complicating factors.

In Figures 1 and 2 the solid lines represent hypothetical curves of various parameters as functions of distance along the uninterrupted stream continuum. These idealized curves were derived from data contained in various sources (especially, Vannote et al., 1980; Cummins, 1975; 1977; 1979). According to such conceptualizations, natural headwater streams are characterized as heavily canopied, light-limited heterotrophic systems with low-amplitude thermal regimes and coarse substrates. Of course, not all headwater streams are canopied by terrestrial vegetation (Minshall, 1978), nor do they all receive substantial groundwater inputs to moderate temperature and flow patterns. The fact that the majority of research on natural streams in North America has been conducted in the eastern deciduous forest has fostered such generalizations since many undisturbed lotic ecosystems for which the most intensive data are available do indeed exhibit these general characteristics.

The dashed lines in Figures 1 and 2, which synthesize our present understanding of regulated streams, indicate hypothesized modifications of those parameters when dams are placed on upper, middle, and lower reaches. Impoundments are viewed as theoretical dimensionless points on the longitudinal stream profile (i.e., only the modification of the downstream lotic ecosystem is shown; the limnological dynamics within the reservoir are not). It must be stressed that the curves presented are highly idealized. The vertical axes are intentionally presented without scales. It is probably not possible to quantify precisely any of the parameters along the entire stream continuum. The best data are available for stream orders 1 through 5. Much additional research is needed to confirm or refute even the relative changes postulated here as resulting from impoundment. Further refinements will be required to account for geographical differences and synergistic effects engendered by other disturbances to watersheds.

The differential effects of dam position on parameter modification are illustrated in Figures 1 and 2. We postulate that a parameter that may be greatly modified in the lotic reach below a dam placed at one point on the longitudinal stream profile may be little affected by impounding a different reach. A major impoundment at any position on a river system
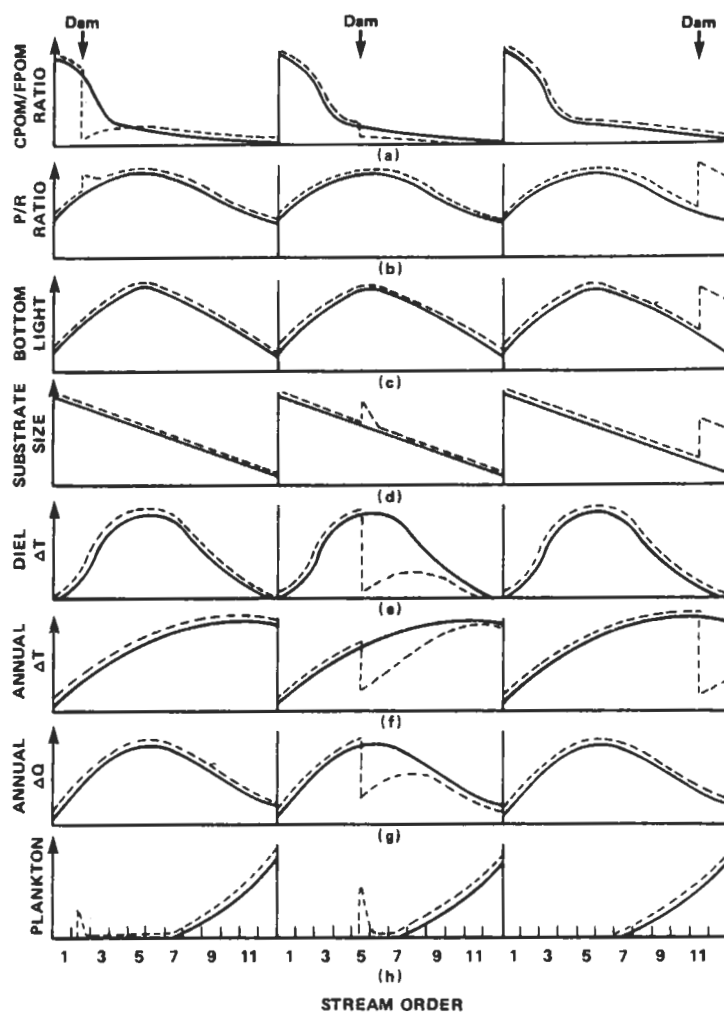
Figure 1. Relative changes in various parameters as a function of stream order, based on our interpretation of natural stream continua theory (solid lines) and postulated effects (dashed lines) of damming headwaters (left column), middle reaches (center column), and lower reaches (right column) of a river system. See text for further explanation.

will directly and indirectly affect all ecological aspects of the downstream lotic ecosystem at some level of resolution. Some, however, will be more severely influenced than others, and gross measurements may be little affected in some instances. For example, a headwater dam (Figure 1a) will greatly depress the ratio of coarse particulate to fine particulate
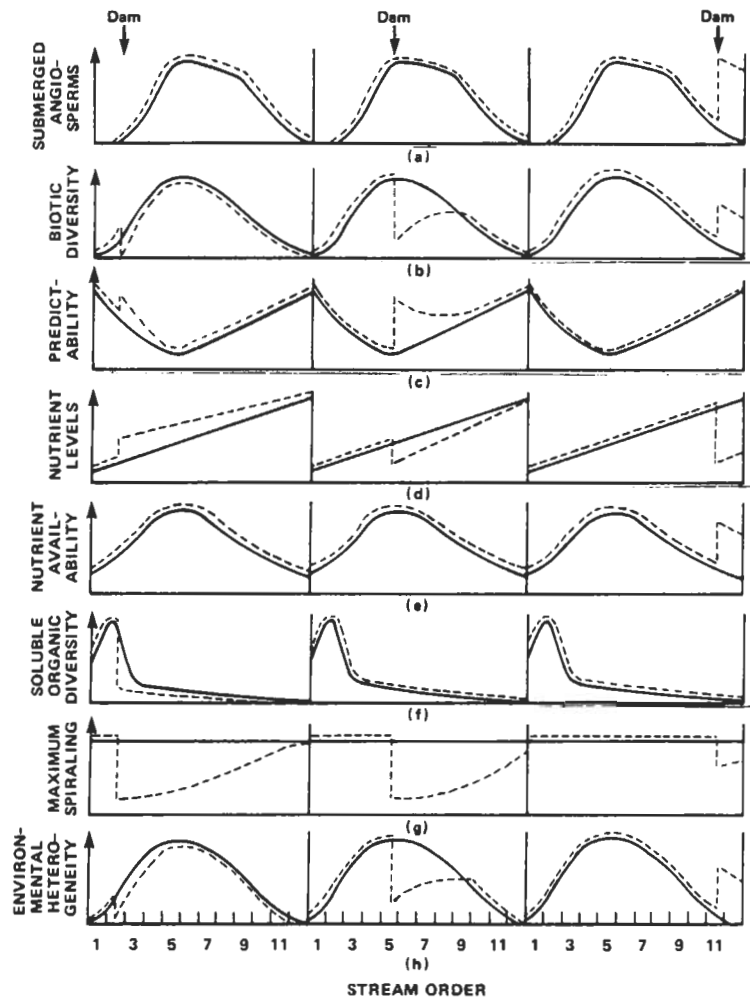
Figure 2. Relative changes in additional parameters (see Fig. 1 legend).

organic matter (CPOM/FPOM) below the impoundment because instream transport of detritus is blocked, whereas impounding the lower reaches of a river system will have little effect on the size composition of detritus. Invertebrate functional feeding groups will reflect changes in the CPOM/FPOM ratios (Short and Ward, 1980). Because of the importance of direct allochthonous inputs (primarily leaf litter) in the energy budgets of the upper reaches of forested streams, a headwater dam would be expected to modify functional composition most severely (shredders

would be greatly reduced). In contrast, a dam on the lower reaches may not greatly alter the trophic relationships of the receiving stream.

Light intensity at the stream bottom (Figure 1c) will not be greatly changed by a headwater impoundment unless the downstream riparian vegetation is disrupted, but the clarification effect of impounding a formerly turbid river will greatly increase light penetration. This accounts for the hypothesized increase in photosynthesis-to-respiration ratio below dams in lower reaches (Figure 1b), especially if water clarity is accompanied by increased substrate stability. Clear water released from dams creates a hydrodynamic disequilibrium resulting in removal of fine sediment particles (see Simons, 1979). The effect on substrate size composition would be greatest in lower reaches (Figure 1d) where the majority of particles are small. Damming the Brazos River in Texas changed a sand-bottom stream into one with a predominantly rubble substrate (Stanford and Ward, 1979). Although few data are available, the effect of impoundment on the composition and quality of sedimentary detritus of downstream reaches (see Webster et al., 1979) may be biologically significant at all points on the stream profile.

It is unlikely that damming either the headwaters or lower reaches will have much effect on the maximum diel temperature range (diel ΔT) of the receiving stream (Figure 1e). The suppression of the diel range will be considerable below a dam in the middle reaches, where the greatest daily thermal range is normally exhibited, and will profoundly influence the biotic community structure (Ward and Stanford, 1979b). The annual thermal range (Figure 1f) would remain similar below a deep-release dam in the headwaters but would be reduced by impounding middle, and especially lower, reaches. Interpretation is complicated by shifts in latitude. The Mississippi River, for example, is exposed to quite a different climatic regime at its origin in Minnesota than at its mouth in Louisiana. Since water near 4° C is discharged from deep-release dams in winter and summer, the annual thermal amplitude may be greatly constricted. Surface-release reservoirs, especially if shallow, may significantly modify the receiving stream biota by raising summer temperatures (Fraley, 1979). Other thermal modifications engendered by stream regulation and their biological implications are discussed in detail in Ward (1976a) and Ward and Stanford (1979b).

In a pattern not unlike temperature, the flow regime of natural streams often exhibits maximum variation in middle reaches. The relative flow constancy of headwaters is attributed to their spring-fed nature and the moderation of precipitation by terrestrial watershed processes, whereas the discharge pattern of large rivers is dampened by the cumulative variations of many tributaries (Hynes, 1970). The middle reaches are most

influenced by local meteorological events and hence exhibit the most variable and unpredictable flow regimes.

Storage reservoirs may moderate flow fluctuations (ΔQ) in the middle reaches (Figure 1g) by storing water during spates and major runoff periods and releasing additional water during periods of normally low flow. Storage reservoirs have a lesser influence on the already relatively constant flow regime of headwaters and lower reaches. The downstream flow regime is largely a function of the purpose of the reservoir. See Ward (1976b) for a discussion of the types of flow regulation and effects on stream biota.

True plankton communities (Figure 1h) occur only in the lower reaches of river systems except below impoundments and natural lakes. Plankton released from surface-release impoundments typically result in greatly enhanced populations of filter-feeding stream invertebrates immediately below the dam (Simmons and Voshell, 1978; Ward and Short, 1978). Lentic plankton are rapidly eliminated downstream, with concomitant major shifts in the invertebrate functional feeding-group composition. Plankton are also released from deep-release dams, but apparently not in sufficient numbers or with sufficient temporal predictability to greatly influence the trophic structure of the receiving stream biota (Ward, 1975).

Impoundment will not allow development of submerged angiosperms (Figure 2a) in the headwaters unless the canopy is disrupted, nor will major changes occur in the middle reaches where dense populations normally occur. In contrast, damming lower reaches may greatly enhance rooted aquatic plants, since the high nutrient levels can be used in the clear water and more stable substrate below the dams. High-gradient mountain streams lacking angiosperms may develop dense beds in regulated sections (Ward, 1976c). Attached algae exhibit a similar response (see Lowe, 1979).

It is postulated that biotic diversity, relative to unregulated lotic systems, will be modified irrespective of the position of the impoundment along the stream profile (Figure 2b). Regulation of the headwaters will suppress the biotic diversity in the receiving stream, primarily because of the disruption of detrital transport and the spiraling of nutrients and organic matter. The severe reduction of biotic diversity induced by damming middle reaches has been attributed primarily to the altered thermal regime. For example, it has been suggested (Ward, 1976a; Ward and Stanford, 1979b; Vannote et al., 1980) that daily variation in temperature, which is suppressed below dams in middle reaches, is partly responsible for maximizing species diversity in natural lotic systems by providing a wide range of thermal optima, even though suboptimal conditions occur over a portion of the diel cycle for each species.

Although few biological data are available for lower reaches, enhanced environmental heterogeneity below dams would likely lead to an increase in biotic diversity. The only known record of enhanced zoobenthic diversity below a dam occurs in a river that exhibited increased substrate and thermal heterogeneity in the regulated section (Ward and Stanford, 1979b).

The high biotic diversity in the middle reaches of natural streams may result not only from spatial heterogeneity but also from temporal heterogeneity (i.e., low predictability, Figure 2c). Lind (1971), for example, contrasted the relatively constant supply of organic matter discharged from a reservoir in Texas with the seasonal variations in organic transport which typify unregulated streams. Within limits, low predictability (high temporal heterogeneity) in flow and temperature regimes (and other factors) may enhance species packing of lotic organisms by several mechanisms (Patrick, 1970; Ward, 1976a); increased predictability resulting from impoundment may contribute to the reduced biotic diversity of regulated streams in middle reaches.

Although total nutrient levels (Figure 2d) generally increase along the stream continuum (Cummins, 1977), availability (Figure 2e) is probably greatest in middle reaches where the light regime and substrate are most suitable for plant growth. If the residence time of headwaters is increased, deep-release impoundments could conceivably raise nutrient levels downstream, but availability would not be altered. In middle and lower reaches, reservoirs generally act as nutrient sinks, but nitrate may be greater in outflowing than inflowing water (see Soltero et al., 1973). Greater nutrient availability induced by impoundment in lower reaches, because of increased clarity and substrate stability, may compensate for reduced levels in the receiving stream.

The relative diversity of soluble organic compounds (Figure 2f) is highest in headwaters of natural streams (Vannote et al., 1980), and impoundment of upper reaches would likely exert the greatest effect on this parameter. If residence time is increased, limnological phenomena within the reservoir (including biotic uptake and transformations) may reduce the chemical diversity below a headwater dam. Such a conclusion must, however, remain highly speculative at this time.

The homeostatic feedback mechanisms which control in situ nutrient cycling in autotrophic ecosystems (the "circular causal systems" of Hutchinson, 1948) are not directly applicable to stream ecosystems because of the unidirectional movement of water. If we view the stream on a spatio-temporal scale, however, a storage–cycle–release phenomenon, termed "nutrient spiraling" (Webster, 1975; Wallace et al., 1977; Webster and Patten, 1979, Elwood et al., this volume), becomes apparent. As

stated by Cummins (1979), "communities in each successive stream order are dependent upon the inefficiency or 'leakage' from the preceding orders."

Vannote et al. (1980) emphasized the adjustments made by the biotic community along the river continuum which "are structured to process materials . . . thereby minimizing the variance in system structure and function." They further "propose that biological communities, developed in natural streams in dynamic equilibrium, assume processing strategies involving minimum energy loss. . . ," which is equated with maximum spiraling. From this we have deduced that maximum spiraling is maintained throughout the natural stream continuum (Figure 2g) by biotic adjustments to continually changing physical conditions. We propose that the disruption of nutrient spiraling by impoundment will be severely manifested in upper and middle reaches but less severely altered in large rivers where dissolved and particulate matter entering the reservoir will not differ greatly from that passed through the dam. There is some indication that the "food quality" of detritus may vary as a function of stream order (Naiman and Sedell, 1979). It is probable that limnological phenomena within reservoirs alter the food quality (as well as the amount and the chemical and size composition) of detritus, but no data are available.

Finally, we propose that environmental heterogeneity (viewed broadly to include both spatial and temporal components) exhibits a pattern along the stream profile (Figure 2h) which is similar to biotic diversity (see, e.g., Hedrick et al., 1976) and that the response to regulation will also be similar.

Multiple Impoundment

Figures 1 and 2 consider the differential effects on a given parameter of single dams positioned in the headwaters, the middle, or the lower reaches of a river system. Many river systems, however, are alternating series of lentic and lotic reaches because of multiple impoundment. For example, eleven main-stem dams have been constructed on the Snake River, a tributary of the Columbia (Robinson, 1978). The few data available on cumulative effects of multiple impoundment (e.g., Denisova, 1971) deal primarily with physico-chemical changes within the reservoirs. Virtually nothing is known regarding cumulative effects of multiple impoundment on the remaining lotic segments. If, for example, a factor modified by an upstream impoundment has not been returned to normal levels before reaching the next reservoir, will the interaction be neutral, cumulative, or ameliorative, and to what extent? Not only are precise answers to such

questions generally unknown but the questions themselves have rarely been asked.

We have developed a hypothetical framework to visualize the basin-wide effects of impoundment (Figure 3) in an attempt to attain a broad theoretical perspective of regulated lotic ecosystems. The approach is applicable to smaller drainage basins (e.g., fifth-order systems) or portions of larger watersheds. The framework may also be used as a sub-model to investigate the effects of individual dams in a series.

Two components are apparent (see Figure 3). Discontinuity distance (DD), defined as the longitudinal shift of a given parameter by stream regulation, has a length variable (X), which is the displacement of the parameter in stream-order units (kilometers may be more useful than stream-order units, especially in xeric regions). An upstream shift is indicated by X_{neg} and a downstream shift by X_{pos}; X_o indicates that no major longitudinal shift is apparent. The theoretical example in Figure 3 shows a downstream shift of the parameter A maximum by five stream orders (DD = +5).

The second component is parameter intensity (PI), defined as the difference in absolute parameter units between the natural and the
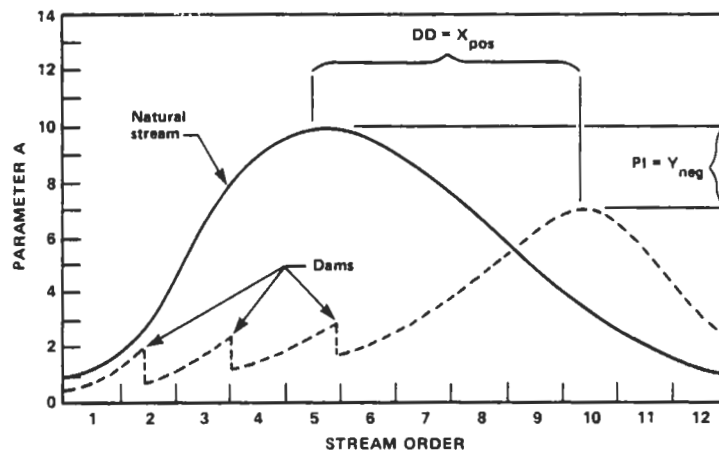

Figure 3. Theoretical framework for conceptualizing the influence of impoundment on ecological parameters in a river system. Discontinuity distance (DD) is the downstream (positive) or upstream (negative) shift of a parameter a given distance (X) due to stream regulation. PI is a measure of the difference in the parameter intensity attributed to stream regulation. See text for further explanation.

regulated lotic system. Parameter intensity can be elevated (Y_{pos}), depressed (Y_{neg}), or unchanged (Y_o) in comparison with the natural lotic system. For parameter A (Figure 3), PI is –3.

We contend that the conceptual framework exemplified in Fig. 3 provides a structure for designing and interpreting research on regulated lotic ecosystems. It is intentionally simplistic and general in this initial formulation, not only as a reflection of our inability to quantify precisely the effects of regulation but also so that it may be applicable to a variety of physical and biological parameters at different levels. For example, regulation of a river system may cause the distribution pattern of a lotic species to shift three stream orders downstream where mean annual abundance is depressed from 3000 to 2000 organisms/m^2 (DD = +3 and PI = –1000 organisms/m^2), or the position of the maximum photosynthesis-to-respiration ratio may not shift longitudinally but may be elevated from 1.1 to 1.3 at that point (DD = 0 and PI = +0.2).

One contribution of the model may be simply to focus conceptually on the basin-wide ramifications of stream regulation. The temporal shift of maximum temperatures in the Columbia River as additional dams were constructed (Jaske and Goebel, 1967), for example, could have been predicted and the biological implications better understood given a comprehensive view of the watershed. From a preliminary analysis of the distribution of hydropsychid caddisflies over nearly 300 km of a river with four mainstream impoundments (Stanford and Ward, 1981), it appears that the thermal regime and particulate organic carbon dynamics have undergone major downstream shifts since regulation of the river system. A simple mathematical model incorporating a variable number of reaches and impoundments should be initially developed and tested to examine trends in single parameters before attempting to apply this framework to the interactions of multiple factors. We hesitate to speculate further on the potential utility of the model without the results of experimental field research designed specifically within this framework. The ultimate goal of such a scheme is to stimulate research leading to the causal relationships essential to a fuller understanding of basic and applied aspects of stream ecology, and its success should be judged by that criterion.

ACKNOWLEDGMENTS

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