Patch dynamics in lotic systems: the stream as a mosaic*

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Abstract. This paper applies concepts of landscape ecology and patch dynamics to lotic systems. We present a framework for the investigation of pattern and process in lotic ecosystems that considers how specific patch characteristics determine biotic and abiotic processes over various scales. Patch characteristics include: size, size distribution within the landscape, juxtaposition, diversity, duration, and mechanisms affecting patch formation. Several topics of current interest in lotic ecology are examined from a patch-dynamics perspective: (1) response of periphyton communities to nutrient patches; (2) effects of patch dynamics on nutrient spiralling; (3) riparian patch dynamics and effects of leaf litter characteristics on lotic food webs; (4) beaver-induced patch dynamics; and (5) patch dynamics of river floodplains.

We conclude that a patch-dynamics perspective coupled with a strong experimental approach can enhance the utility and predictive power of unifying concepts in lotic ecology, such as the river continuum hypothesis and nutrient spiralling, through its focus on organismal and process-specific building blocks of lotic systems. The effectiveness of a patch-dynamics approach as a framework for the study of lotic systems lies in the strength of the linkage between reductionist and whole-stream perspectives.

Key words: streams, rivers, patch dynamics, landscape ecology, communities, scale, disturbance, periphyton, floodplains.

The analysis of spatial patterns within landscapes has been widely applied in the study of terrestrial ecosystems (e.g., Forman 1983, Forman and Godron 1981, 1986, Noss 1983, Pickett and White 1985, Risser et al. 1984, Wiens et al. 1985). Landscapes have been viewed as mosaics of heterogeneous land forms, vegetation pat-

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In streams, as in intertidal zones, the distribution of both sedentary and mobile organisms is strongly influenced by the movements of overlying waters. While the unidirectional flow of water in streams can create spatial and temporal heterogeneity (in patterns of current velocity, substratum sorting, faunal habitat, etc.), mixing processes also reduce heterogeneity of other factors (e.g., spatial and temporal differences in nutrient concentrations). Surface water flow is an abiotic vector that imposes a directional flux of materials on the general background of resource concentration gradients (Forman 1983, Wiens et al. 1985).

Viewing streams as mosaics of patches provides a fresh perspective for lotic studies. Mechanisms of spatial and temporal complexity on a variety of scales can be investigated in a manageable fashion by examining interrelationships between basic building blocks of the system. For instance, unifying concepts in lotic ecology that have emphasized longitudinal linkages, such as the river continuum concept (Minshall et al. 1985, Vannote et al. 1980) and nutrient spiralling (Newbold et al. 1981, Webster 1975), can be evaluated by studying changes in characteristics of patches and interactions between specific patch types along a stream continuum. If there are net imbalances in fluxes or the spread of disturbances across boundaries in relation to within-patch processes, a directional bias to system fluxes can be established (Wiens et al. 1985). Thus, a patch dynamics approach can complement unifying theories that emphasize longitudinal continua by providing a reductionist tool for evaluation of such concepts. As stressed by Orians (1980), one of the great challenges in ecology is the bridging of the conceptual gap between micro- and macro-ecology. The study of patch dynamics with its emphasis on processes and interactions at various scales is one logical approach to making the transition.

It has long been recognized that rivers and streams are heterogeneous environments where highly clumped distributions of organisms pose severe sampling problems (e.g., Hynes 1970). Traditionally, aquatic ecologists have designated riffles, pools, runs, etc. as relatively homogeneous units for study (e.g., Hynes 1970) and, at a finer scale, patchiness has been described in terms of physical factors such as depth, width, current speed, and substratum particle size (e.g., Gorman and Karr 1978). However, patchiness within streams at scales perceived and/or exploited by stream organisms is a reality that has often been ignored. Research in lotic ecology often has been constrained by preconceived notions of what a “patch” is.

To a considerable extent, studies have stressed comparisons of conditions and/or communities within and between patches, rather than interactive processes that control form and function of patch mosaics. An instructive exception is the work on thermal effluent communities, which demonstrated the continually changing nature of these systems and the interdependence of temperature, flow, grazing, and predation (Wickstrom and Wiegert 1980). Recent descriptions of stream riffle ecosystems as open non-equilibrium systems (Peckarsky 1985) and patches in transitory equilibrium with other patches (Sheldon 1984) indicate an increasing perception of stream patches in dynamic terms.

The strength of a patch perspective to provide a better understanding of functional relationships is demonstrated by the work of Statzner (1987) and Statzner and Higler (1986). They have drawn attention to regions of hydraulic stress which are important discontinuities in river systems and influence the distribution of zoobenthos (see also Statzner et al. [1988] in this issue). Recent studies of beaver (Johnston and Naiman 1987, Naiman and Melillo 1984, Naiman et al. 1986) provide an example of how large animals can create patches in streams and act as biotic vectors that affect fluxes of energy and materials across patch boundaries. A patch perspective has been employed in lotic systems on successively smaller scales in investigations of fish (Angermeier and Karr 1984, Power 1984), sediment–fauna–leaf pack associations (Reice 1974, 1977, 1980, 1985), behavioral responses of grazing invertebrates to patchiness in algal food abundance (Hart 1981, Hart and RESH 1980, Kohler 1984, 1985), and periphyton community response to nutrient patches (Pringle 1985b, 1987, Pringle and Bowers 1984).

Our objective is to develop the concept of patch dynamics (Pickett and White 1985, Thompson 1978, Wiens et al. 1985) as a useful tool that will enhance predictive understanding of lotic systems. We present an operational definition of “patch” and discuss patch characteristics as they relate to the function of lotic ecosystems on differing scales. We then apply
a patch perspective to various ecological problems in lotic systems, ending with a series of conclusions and recommendations.

**Patch definition: what scales of variation are perceived by the organism?**

Appropriate scales in ecological studies depend upon the organism(s) of study, the time unit during which the organism(s) will be affected by environmental fluctuations and the question(s) being asked. For example, in his examination of environmental factors determining spatial and temporal heterogeneity of phytoplankton populations, Reynolds (1984) adopted the time unit of "cell generation time", asking the question, "which scales of variation are perceived by the intact cell?" Human perceptions often operate on radically different temporal and spatial scales from those of other organisms we study, contributing to the disparity between relevant and tractable scales of investigation. As stated by Allen (1977), "the ecologist is likely to measure the environment at frequencies too long and at grain sizes too large to correspond to the short frequency, fine grain actuality .... Small life forms are so far removed from human scales of perception that even the best amplifiers of our senses can't be used directly." Connell (1978) likewise noted that with long-lived organisms such as trees or corals, gradual changes in climate over several hundred years represent the same scale as season does to a phytoplankton community.

Our working definition of a "patch" is an operational one: A patch is a spatial unit that is determined by the organism(s) and problem(s) in question. This definition incorporates a scalar component since organisms and processes can operate within several spatial and temporal scales simultaneously. As discussed by Pickett and White (1985), patch implies a spatial pattern where patches are spatially related to each other and to the surrounding, less affected matrix. The study of patch dynamics focuses on mechanisms behind patch change and interactions between patches.

While the distinction between riffles and pools may yield patch units appropriate to some problems in lotic ecology such as factors determining fish distribution and habitat preference, such a level of spatial heterogeneity may be inappropriate for studies addressing fine-grained heterogeneity such as efficient nutrient cycling within microbial communities. In streams, patches may be determined by many interacting factors, including substratum conditions, topography, current patterns, organisms, and disturbance. Clearly, patch size and patch boundaries perceived by individual organisms vary significantly among organisms and even for the same organism at different times. As a boundary, a pond margin is impermeable to a fish, permeable and of major importance to a beaver (Castor canadensis), and not really perceived by a parasite with life history stages within both fishes and birds.

**Characteristics of patches**

The effects of patch dynamics on populations, communities, and ecosystems have been described in detail for a variety of terrestrial and marine habitats (e.g., Pickett and White 1985), often focusing on characteristics of patch types within these different systems (e.g., Sousa 1985). Here we provide a framework for application of patch dynamics to problems in lotic ecology (Table 1) by consideration of the following patch characteristics and how they affect biotic and abiotic processes over various scales: (1) size and size distribution; (2) density; (3) juxtaposition; (4) diversity; (5) duration; and (6) mechanisms affecting formation.

How do these patch characteristics affect lotic ecosystem function? All are critical determinants of both within- and between-patch dynamics. This importance is dramatically illustrated by the loss of biotic integrity that accompanies major structural modifications of stream channels. The erosive dynamics of water in meandering streams creates habitat mosaics of major consequence to the distribution of many organisms (Karr and Schlosser 1978). For instance, with respect to fish habitat, the structural simplification that results from channelization generally results in a decrease in the variance of patch sizes, patch density, the number of juxtapositions between patches, patch diversity, and even in mechanisms affecting subsequent patch formation.

Variations in patch characteristics that occur over extremes in spatial and temporal scales can influence stream structure and function. For example, the dynamics of fish populations are in-
TABLE 1. Guidelines for the application of patch dynamics in lotic systems.

I. A first step in applying a patch-dynamics perspective to a specific ecological problem is to define the conceptual patch unit(s) after consideration of the following questions:
   A. On what scales is variation perceived or exploited by the organism(s) and/or process under study?
   B. On what scale is environmental heterogeneity (patch-to-patch variation) affected by the organism or process under study?

II. Once the patch unit is determined, the following characteristics may be considered with respect to the ecological problem in question: (a) patch juxtaposition; (b) patch size and density; (c) patch size distribution; (d) patch diversity; (e) patch duration; and (f) mechanisms affecting patch formation.

III. Sampling units, sampling time frames, and/or experimental/manipulative approaches should be selected that are appropriate to the scale of the problem to be addressed.

IV. To assess system-level effects of patch-specific phenomena, one must stand back and adopt a broad focus, examining key characteristics of patches (listed above) and process-oriented interactions between patches, within the larger context of the stream landscape.

fluenced by spatial variations in habitat patch mosaics ranging in size from localized substratum patches to entire catchments. In short stream segments, the presence of instream cover or habitat patches such as undercut banks, logs, etc. are important determinants of fish biomass, species diversity, and community composition (e.g., Angermeier and Karr 1984, Fraser and Sise 1980, Hunt 1971, Sheldon 1968). Some fish populations may be composed of both sedentary and mobile groups depending upon the relative suitability of local habitats, particularly during changing environmental conditions (Fagen 1962, Harima and Mundy 1974, Karr and Dudley 1981). The physical process of fish migration, itself, presupposes the existence and/or absence of certain patch types within migratory paths. On the floodplain for instance, the presence of floating vegetation may prohibit passage of fish species that have high oxygen demands because of low oxygen concentrations under the mat. On the other hand, fishes in dewatered desert streams inhabit refugial patches under rocks or algal mats to await the next spate (Stanford and Ward 1986). Long distance migrants in rivers are frequently presented with the need to negotiate rapids and, thus, are dependent on the presence of a suitable patch structure in the form of resting pools. A serious consequence of human intervention in river systems (e.g., dam building, deforestation, channelization, etc.) is that the patch structure necessary for fish migrations may be altered, impeding upstream and/or downstream movements. Decreased habitat mosaics on a broad scale may account for declines in fish species diversity on a regional level. The observed decline in diversity of fishes from the eastern to western region of the central plains of North America is a good example (Cross 1970, Matthews 1988—see this issue). The six general patch characteristics listed above may also influence the level of system stability and resilience in response to disturbance. Disturbances are less likely to spread over a spatially heterogeneous area than through a homogeneous region. If patches are isolated in a biotically or abiotically dissimilar matrix, their response to a particular disturbance will probably differ from that when barriers do not exist (Pickett and White 1985). For instance, geomorphic heterogeneity in streams (e.g., size, density, and size distribution of patches within the stream landscape, and juxtaposition and diversity of patches, as defined by topographic characteristics) may play a major role in determining effects of disturbances, since localized areas of differing geomorphmetry may respond differently to the same disturbance regime (Pickett and White 1985). On a microscopic scale, algal cells living within hollows and indented areas of suspended sediment particles are subject to less abrasion than cells located on exposed portions of sediment grains. Algal populations inhabiting crevices on sand grains may be considered as micropatches that serve as sources of new colonists for sediment particles following the scouring effect of spates. Furthermore, algal and macrophyte communities living in topographically different substratum patches can experience different current regimes and nutrient diffusion rates, thus influencing local algal community composition and production. On a larger scale, subterranean burrows within streams may serve as refugia for fish and invertebrates during floods and during periods
when stream channels are dewatered (e.g., Glodek 1978).

There is also evidence that a high diversity of resource patches confers community stability. For example, Tilman (1982) hypothesized that diversity of plant communities may be at least partially explained by resource competition within a spatially heterogeneous environment. If individual plant species tend to maximize competitive abilities within specific and narrow ranges of resources (e.g., N:P), spatial variation in resource supplies may lead to the coexistence of many species. Evidence that dissimilarity of nutrient regimes between patches in streams can promote periphyton species diversity (Pringle 1985b) is consistent with Tilman’s hypothesis.

Response of lotic periphyton communities to nutrient patches

The turbulent nature of many, if not most, lotic environments tends to homogenize dissolved and particulate materials as they are transported downstream, at least in comparison to more sequestered supplies in lentic and terrestrial systems. Nonetheless, contiguous temporal and spatial patterns in concentrations and supply rates of resources essential to production of plant and associated bacterial communities may be identified (Meyer et al. 1988—see this issue). Little is known about the effects of such nutrient patches on algal growth and distribution in streams. Attached algae may experience variable nutrient levels over wide extremes of temporal scale: (1) seasonal (e.g., inputs of decomposing leaves and other allochthonous materials which release nutrients in a high initial pulse [Elwood et al. 1981, Howarth and Fisher 1976]); (2) hourly (e.g., following storms [Hynes 1970, Wetzel and Likens 1979]); and (3) milliseconds (e.g., when the diffusion regime experienced by a sessile cell is altered by the movement of an adjacent motile cell). Effects of nutrient patches on microbial communities are difficult to determine because ‘‘microbes are clearly scaled very differently in their ecological strategies than are humans . . . .’’ So large is the surface area of a cell (relative to its volume), that the effect of nutrient uptake might be a nutrient ‘‘draft’’ analogous to the breeze near to an air intake of a large building’’ (Allen 1977).

Algal response to variations in nutrient supplies that occur on larger scales (e.g., mass loading) are comfortably addressed according to our human sense of time and space and are the most thoroughly documented; however, little is known about effects of finer levels of temporal and spatial variation in nutrient supplies. Given that a plant a few μm in diameter is responsive to the nutrients contained in the environment immediately surrounding it (e.g., Pasciak and Gavis 1974) and that algal turnover rates are often a matter of hours, these finer levels of variation may be crucial in determining microbial distribution and abundance. It follows that such patch dynamic responses may vitally influence overall food-web complexity and pattern.

Daily measurement of ambient nutrient levels is a widely accepted way of characterizing the general nutrient environment experienced by attached microbes in streams (e.g., Peterson et al. 1983, Pringle et al. 1986, Stockner and Shortreed 1978): however, such measurements integrate information at a scale that is orders of magnitude too large to detect fine grain temporal and spatial variation in nutrient patches (e.g., Fig. 1).

A case study in point concerns the relationship between organisms in the periphyton and the surfaces to which they are attached. Macrophytes, decomposing wood, and leaf litter can be direct sources of nutrients for attached microbes. Retreats constructed by many zoobenthic species also may constitute natural nutrient-diffusing surfaces for attached algae, owing to metabolic and excretory activities of larval inhabitants (Pringle 1985a). For instance, many Chironomidae and Trichoptera larvae consolidate sand grains into tube-like retreats. In a nutrient-deficient stream in northern Michigan, significantly greater amounts of ammonia-N, ortho-phosphate, and total phosphorus were extracted from tubes of the chironomid Pagastia cf. partica in comparison with controls of unconsolidated sand (Pringle 1985b). The retreats were covered by dense mats of diatoms, supporting over 10 times the chlorophyll a than equivalent weights of control sand (Pringle 1985b) and over 12 times the diatom biomass compared with adjacent wood surfaces (Pringle 1985a). In this instance, algal community dynamics apparently respond to nutrient patches mediated by the chironomid larvae. Such efficient biophysical coupling represents a lower spatial limit within the framework of
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Hugh White Creek

Big Hurricane Branch

Ca

Na

K

Mg

CONCENTRATION (mg/L)

Na

Mg

0.00

0.50

1.00

50

40

30

20

10

0

0.30

0.40

0.50

0.60

0.70

0.80

0.90

1.00

0.30

0.40

0.50

0.60

0.70

0.80

0.90

1.00

STREAM DISCHARGE (L/s)

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Ecosystem-level nutrient fluxes may occur in patch mosaics far smaller than those generally recognized in contemporary plant ecology. For example, denitrification with biophysical aggregates in aerobic soils can be the major pathway of nitrogen loss from forests (Myrold et al. 1982 as cited by Vitousek 1985). Likewise, small localized nutrient patches around individual chironomids and their retreats may cumulatively influence ecosystem-level properties of streams because chironomids are often extremely abundant (e.g., Saether 1968, Wiley 1976). In a nutrient-poor northern Michigan stream, larval retreats of the chironomids *Microspectra* sp. and *Pagastia partica* (Fig. 2) typically covered 40–75% of submerged wood surfaces in midsummer and supported 7 to 12 times greater algal biomass than wood unmodified by larval retreats (Pringle 1985a). When present at maximum densities, a conservative estimate was that retreats of the two taxa supported over 95% of total epiphenic periphyton standing crop in the stream. Population dynamics, distribution, and feeding behavior of chironomids can have a direct effect on all characteristics of patches discussed in the previous section: juxtaposition, density, size and size distribution, diversity, and mechanisms affecting patch formation and duration. For example, when chironomid larvae emerge as winged adults, patterns of nutrient cycling in the stream may be altered owing to the loss of spatially-fixed nutrient patches previously maintained by larvae. In accordance with this prediction, Hershey et al. (1988) measured lower concentrations of chlorophyll *a* on pupal tubes than on larval tubes of the chironomid *Orthocladius rivulorum*. One might predict that effects of localized nutrient patches on streamwide patterns of algal distribution would be most pronounced in a stream with low ambient nutrient concentrations; periphyton would be found in contiguous patches in response to localized nutrient sources. In a nutrient-rich stream, however, localized patch effects are ameliorated and periphyton may be more uniformly distributed.

Viewing effects of nutrients derived from different sources as patch-specific phenomena is a prerequisite for the careful examination of interactions between nutrient sources (patches). Taking this approach, one can quantify effects of nutrient patches through experimental manipulation. For example, Pringle (1985b, 1987) developed an integrated bioassay to separate patch-specific effects of substratum and water nutrient supplies on algal growth and community structure. Experiments that enriched the water and substratum in a fully crossed design showed that nutrients derived from different sources interacted to determine periphyton growth response; periphyton responded to combined influences of water and substratum enrichment in an additive or synergistic fashion, depending on amounts and types of nutrients added from each source. In another study, algal epiphytes of *Phragmites* were found to be dependent on silicate released from host stems, when competition for silicate between planktonic and epiphytic diatoms resulted in silicate depletion in the water (Jorgensen 1957). When silica concentrations are low, epipelic diatoms obtain supplies of this mineral from the sediment and interstitial water (Happey-Wood and Priddle 1984, Werner 1977). Accordingly, a stream can be envisioned as a mosaic of nutrient micro-patches, which differ dynamically in chemical nature and, thus, may impart variable but potentially predictable biotic responses between patches.

Indeed, results of integrated bioassays employed by Pringle (1985b) showed that periphyton species diversity was highest where

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**Fig. 1.** Data illustrating short-term temporal variation in ambient concentrations of calcium, sodium, potassium, and magnesium as a function of discharge in Hugh White Creek and Big Hurricane Branch during a storm on 30 June 1981. Both streams are located at Coweeta Hydrologic Laboratory in southwestern North Carolina, USA. Hugh White Creek drains an undisturbed hardwood forest watershed and Big Hurricane Branch drains a watershed that was logged in 1977. The arrows show the time sequence of samples over the total sampling period of about three hours. Samples from Hugh White Creek were taken every 15 minutes. Samples from Big Hurricane Branch were taken even more frequently when the hydrograph was rising. The time between the onset of the storm and peak discharge was 50 minutes in Big Hurricane Branch and 65 minutes in Hugh White Creek. Data from J. R. Webster and S. W. Golladay, Virginia Polytechnic Institute and State University.
substratum chemistry and water chemistry were markedly different. This supports Tilman's (1982) prediction that the level of spatial heterogeneity (or variance in resource availability between patches) may determine species richness. Moreover, Pringle's data also support the complementary suggestion of Naiman et al. (1988—see this issue) that boundaries between adjacent patches (ecotones) play an important role in maintaining biotic diversity. The fact that epipelic communities are located at the interface of two often very dissimilar, chemical patches (i.e., water and substratum) may help explain Hutchinson's (1975) observation that the species diversity of algae is frequently greater on sediments than in the open water of lakes and ponds.

Effects of patch dynamics on nutrient spiralling

Characteristics of patches along the longitudinal continuum of a stream determine how chemical nutrients are transported. As nutrients move downstream, they are taken up, used, and subsequently released by stream organisms. This coupling of downstream movement with patterns of immobilization and mineralization has been described as nutrient spiralling (Webster 1975, Webster and Patten 1979), a concept which can be usefully evaluated from a patch perspective. Spiralling length is defined as the average downstream distance traveled by a nutrient atom (or ion) as it completes a cycle (Elwood et al. 1983). It has two components that are directly influenced by patch dynamics: (1) uptake length, defined as the distance an inorganic dissolved nutrient atom (or ion) travels before being incorporated into a benthic particle; and (2) turnover length, the distance it then travels in particle form before being again released into solution.

Nutrient spiralling lengths (e.g., Mulholland et al. 1985, Newbold et al. 1983) have usually been measured over fairly long reaches (ca. 100 m), not in ignorance of the habitat variability or patchiness over this distance, but rather to use spiralling length as an integrative measure of ecosystem function. Viewing the whole river continuum as described by Vannote et al. (1980), nutrient spiralling processes are affected by stream patches on at least three levels: substratum patches, riffle-pool sequences, and larger, stream order variability.

The abiotic and biotic retention of nutrients is largely determined by patch characteristics discussed in the previous section and their interactions over various scales. For instance, Meyer (1979) has found differences in phos-
phosphate sorption on silty versus sandy substrata. Most stream segments or reaches are mosaics of different substratum types (e.g., gravel, sand, silt, and organic accumulations) that may differentially affect abiotic uptake of nutrients. Therefore, the relative size of different physical substratum patches, their size distribution and density within the stream landscape, combined with their juxtaposition, diversity, and duration, all interact to affect the overall nutrient retention of the reach and will determine, in part, the dynamics of nutrient cycling within the drainage network.

Nutrient dynamics are often mediated by both autotrophic and heterotrophic biota (e.g., Elwood et al. 1981, Gregory 1978, Lock and Johns 1979) which may be distributed in fairly discrete, but non-uniform patches. For example, Pringle (1985a, 1987) found dense patches of diatoms on the nutrient-rich retreats of chironomids and on artificial substrates enriched with nutrients. Also, Hart (1985) has shown that grazing caddisflies can create patchy distributions of attached algae, and thus influence nutrient cycling. On somewhat larger scales, vascular macrophytes have highly patchy distributions in streams and can be major components of nutrient cycles (e.g., Hill 1979, Meyer 1979, Vincent and Downes 1980). Even when plant distributions appear to be fairly uniform, their activity may have considerable spatial variability related to current patterns. Several studies have shown that periphyton production and nutrient uptake is significantly affected by current velocity (Lock and Johns 1979, McIntire 1966, Whitford and Schumacher 1964). Moreover, attached algae possess a variety of characteristics and adaptations that maximize their ability to exploit patch-specific variations in nutrient availability, hence increasing the overall retentiveness of the system and shortening nutrient spiralling lengths. Such characteristics include cell permeability, cell motility, presence of mucilage and/or enzymes that facilitate nutrient uptake (e.g., alkaline phosphatase), mode of enzyme release, heterotrophic capabilities, luxury consumption, and storage. Virtually nothing is known about how these factors interact to determine nutrient cycling processes operating over a range of scales.

In many streams, especially small shaded headwater streams, nutrient uptake by heterotrophic organisms associated with decaying organic matter may be considerably more important than autotrophic processes. For example, in their studies of a small Tennessee stream, Newbold et al. (1983) and Mulholland et al. (1985) found that phosphorus spiralling length was inversely correlated with the abundance of large particulate detritus on the streambed. In fall, when this material was abundant, spiralling length of phosphorus was short. In summer, once most of this material had decayed, phosphorus spiralling length was longer. A similar situation probably exists for other nutrients, especially nitrogen, as many studies have demonstrated nitrogen immobilization by decaying leaves (e.g., Kaushik and Hynes 1968, Triska and Buckley 1978) and wood (e.g., Aumen et al. 1985, Melillo et al. 1983). Although leaf fall may initially distribute leaves uniformly over a streambed, these leaves are quickly rearranged by the current into a highly clumped distribution (Fisher and Likens 1973). For example, fine and coarse particulate organic matter in samples taken from five first- and second-order streams in North Carolina was significantly clumped in every case (Table 2).

In addition to immobilizing dissolved nutrients, decaying organic material may also be a site for denitrification. Several studies (e.g., Kaushik and Robinson 1976, Swank and Caskey 1982) have suggested that denitrification is a major pathway of nitrogen loss from streams. Swank and Caskey (1982) found that rates of denitrification were highly variable over the streambed and tended to be correlated with sediment organic matter and the presence of intermittent seeps.

At a larger scale, woody debris has been shown to be an important component of many streams (e.g., Triska and Cromack 1980). The distribution of this material is extremely patchy and usually occurs in debris dams. These woody debris dams are major sites for nutrient transformations associated with the decomposition of wood, nutrient uptake, and nitrogen fixation (e.g., Triska et al. 1984). These dams also slow water velocity, thus shortening nutrient spiralling; but, their greatest effect on nutrient spiralling probably is that they retard transport of organic and inorganic particles and their associated nutrients (e.g., Bilby 1981).

A higher level of patchiness in streams is associated with the alternation of riffles and pools. Because of differences in slope and hence water
TABLE 2. Clumping of fine and coarse particulate organic matter (FPOM and CPOM) taken from five streams at Coweeta Hydrologic Laboratory, Macon County, North Carolina. Samples were collected with a 0.071-m² pot sampler in July 1985. The ratio of the variance to the mean \( \frac{s^2}{\bar{x}} \) is an indication of the dispersion of the material. A ratio greater than one indicates clumping. In all cases the ratio was significantly greater than one (chi-square test, Cox 1985). Data from S. W. Golladay, Virginia Polytechnic Institute and State University.

<table>
<thead>
<tr>
<th>Stream</th>
<th>( \bar{x} ) (g/m²)</th>
<th>n</th>
<th>( \frac{s^2}{\bar{x}} )</th>
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<tbody>
<tr>
<td>FPOM</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Sawmill Branch</td>
<td>156.0</td>
<td>30</td>
<td>387.7</td>
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<tr>
<td>Big Hurricane Branch</td>
<td>46.1</td>
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<td>30.5</td>
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<td>Carpenter Branch</td>
<td>499.6</td>
<td>30</td>
<td>407.9</td>
</tr>
<tr>
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<td>102.2</td>
<td>60</td>
<td>47.4</td>
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<tr>
<td>Grady Branch</td>
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<td>30</td>
<td>23.9</td>
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<tr>
<td>CPOM</td>
<td></td>
<td></td>
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<td>97.2</td>
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<td>63.9</td>
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<tr>
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<td>Grady Branch</td>
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velocity, riffles and pools differ in substratum type, particulate organic matter accumulation, and plant distribution. These factors all affect nutrients in ways similar to the smaller scale patterns discussed previously. Meyer (1980) found significant differences between the phosphorous dynamics of pools and rapids and Naiman et al. (1986) discussed the differences between nutrient processes in undammed and beaver-dammed streams.

Patchiness at a comparative spatial scale occurs when treefall creates a canopy gap over a woodland stream, increasing light penetration to the streambed. Primary production in many woodland streams appears to be limited by available sunlight (e.g., Triska et al. 1983). Canopy gaps may create patches where autotrophic processes temporarily dominate nutrient dynamics (S. W. Golladay, Virginia Polytechnic Institute, personal communication).

Finally, over the length of an entire river, nutrient spiralling efficiency or length may differ dramatically between reaches. In shaded, headwater streams, heterotrophic processes and particle retention dominate. In somewhat larger streams, that are open to sunlight but are still shallow, autotrophic nutrient uptake, release of dissolved organic compounds, and plant decay are probably the most important processes affecting nutrient dynamics. Farther downstream, in deep turbid rivers, heterotrophic nutrient processes may again predominate, owing to decomposition of relatively higher organic carbon loads. Minshall et al. (1983) and Naiman et al. (1987) showed that carbon turnover lengths increased several orders of magnitude in downstream reaches of large rivers. However, neither study was extended to the near lentic conditions of very large rivers where floodplain dynamics may be very important.

When viewed from a landscape perspective, nutrient spiralling is controlled by a shifting mosaic of patch-specific biotic and abiotic processes existing on various spatial scales. We have attempted to discuss typical patterns of patchiness and how they affect nutrient spiralling. Perhaps more interesting than some of the typical patterns discussed, may be the variability in patch-specific nutrient cycling processes within and between biomes and ways in which natural and anthropogenic disturbances (such as volcanoes, major storms, clear-cutting, and dam building) affect patterns of patchiness and related nutrient transport.

**Riparian patch dynamics and effects of leaf litter characteristics on lotic food webs**

Streams and rivers are like threads traversing the shifting patchwork of terrestrial landscapes. Some patches are obvious (e.g., fires and agricultural or urban areas), whereas others are more subtle. Impacts of terrestrial patches on streams are often buffered and/or obscured by dilution and downstream transport of nutrients and organic materials. The extent to which each terrestrial patch imposes ecological changes upon its drainage system depends upon both spatial (terrestrial patch size in relation to stream size) and temporal (longevity of the patch) scales.

Few studies have investigated stream riparian zones from a patch-dynamics perspective, and such an approach may be beneficial since landscape interactions are so complex. Riparian vegetation acts as both a source and filter for energy and materials entering stream ecosys-
tems. It influences water temperature by shading, although the effect varies seasonally in relation to the deciduous versus evergreen nature of the flora. Shading may also limit instream primary production; and streamside vegetation is a major source of particulate detritus used by zoobenthos in headwater streams. As discussed above with respect to nutrient spiralling, both of these influences, in turn, may affect lotic nutrient cycling processes and trophic structure. A desert stream with limited riparian vegetation may be predominately autotrophic, whereas a stream of similar size in the deciduous biome may be dominated by heterotrophic processes, owing to allochthonous leaf fall from the riparian canopy (Minshall 1978, Minshall et al. 1983). Riparian vegetation also influences channel form by limiting bank and bank erosion. It acts as a moderator of run-off volume (Jackson 1987), decreasing sediment, nutrient, and water transport from adjacent disturbed areas (e.g., Karr and Schlosser 1978, Peterjohn and Correll 1984).

The ability of catchments as a whole to retain nutrients may be addressed from the perspective of patch dynamics (Vitousek 1985). A catchment composed of a mosaic of vegetation patches may be more retentive than catchments dominated by climax or uniformly distributed vegetation. But how do riparian vegetation patches interact to affect the relative importance of allochthonous versus autochthonous energy sources, nutrient and sediment inputs, discharge fluctuations, habitat requirements for adult stages of “aquatic” insects, the quantity and quality of allochthonous food sources available to stream organisms, and consequently the trophic structure of stream communities? Clearly these are complicated questions because of the interacting effects of many different factors. We suggest that a patch-dynamics perspective, coupled with a strong experimental approach, is particularly useful in identifying and quantifying key factors that have heretofore been obscured by interrelated effects.

How do riparian patch characteristics affect the lotic food webs in terms of quantity and quality of leaf litter? Diversity, species composition, and successional stage of riparian vegetation is clearly important. Patches of reduced vegetational diversity (e.g., monocultures such as orchards or intensive silviculture) may not provide quantity or quality of leaf litter in a time sequence that favors high diversity of stream organisms. Processing rates of leaf litter vary by tree species (Anderson and Sedell 1979). Thus, sustained availability to shredders of microbially conditioned leaf detritus is presumably dependent upon a suitable mix or patchiness of riparian tree species (Golladay et al. 1983). Experiments by McArthur et al. (1985) indicate that within stream reaches, resident microfloras can be adapted to use dissolved organic compounds derived from particular groups of riparian plants. Likewise, Molles (1982) demonstrated how benthic community structure (taxonomic composition and abundance of functional feeding groups) was influenced by structural and decompositional characteristics of the riparian vegetation at different stages of forest succession; his temporal model focuses attention on streams as both patchy and dynamic environments.

A variety of poorly understood environmental factors interact at different time scales to produce a diverse array of patch characteristics exhibited by riparian vegetation. We have little perspective, for example, of how life histories of stream organisms that are dependent on riparian leaf litter may be linked to evolutionary processes in riparian vegetation. Plants have evolved numerous strategies for defending their tissues from herbivory and microbial attack. Among these defenses are physical barriers (e.g., tough cuticle, spines, or trichomes) and secondary metabolites that act as feeding deterrents or are toxic (e.g., Feeny 1976, Harborne 1982, Janzen and Rosenthal 1979, Levin 1976, Rhodes and Cates 1976). Insect herbivores have, in turn, often developed the ability to tolerate or detoxify plant defensive chemicals, frequently using the chemical deterrent as a feeding cue or attractant (Ehrlich and Raven 1965, Futuyma 1983). This action and reaction has been likened to a coevolutionary “arms race” but direct evidence for long-term stepwise adaptations of interacting herbivorous insects and plants is meager (Futuyma 1983). Shredder insects in streams consume the same leaf material that has evolved defenses against terrestrial herbivory and microbial attack (Fig. 3). There is, of course, no selective pressure on plants to evolve defenses against these shredders. However, shredder stream insects have presumably adapted to changes in chemical characteristics of leaf detritus in both evolutionary time (responses of
Fig. 3. Schematic diagram illustrating how plant chemical defenses and soil nutrient availability may affect the quality of riparian leaf litter available to shredder invertebrates in streams.

Riparian plants to terrestrial herbivores and microbes) and ecological time (successional changes in species composition of riparian vegetation).

Nutrient availability within soils or groundwaters may also influence riparian patch dynamics and the nutritional quality of stream leaf litter (Fig. 3). Increased availability of soil nutrients to riparian vegetation (e.g., through agricultural runoff) should increase the nutrient content of detrital inputs into the stream. Nitrogen (or protein) is of critical nutritional importance to both terrestrial herbivores (Mattson 1980) and stream detritivores (Cummins and Klug 1979). Leaf nitrogen content declines with senescence and abscission so that nitrogen content of leaf detritus may be especially critical to detritivores. Changes in nutrient status may also cause shifts in plant tissue concentrations of carbon-based (e.g., phenolics) and nitrogen-based (e.g., alkaloids) defensive chemicals (Bryant et al. 1983, Chew and Rodman 1979, del Moral 1972).

While patchiness in the quantity of leaf litter available to a stream system is likely to be obvious (e.g., loss of riparian vegetation during land development), patchiness in leaf litter quality is likely to be widespread, complex, and not at all obvious. Catchment management must include an understanding of how qualitative patchiness of riparian vegetation affects leaf litter characteristics and hence detrital food webs in streams.

A recent study by Irons et al. (1988) provides an example of how changes in the species composition and nutrient status of riparian vegetation might affect consumption of leaf litter by shredders. Four species of Alaskan trees common in riparian areas (alder, birch, willow, and poplar) were fertilized with nitrogen, phosphorus, nitrogen + phosphorus, or given no fertilizer (control). Senescent leaves were offered to a shredder, Hydatophylax variabilis (Trichoptera:Limnephilidae). Consumption of leaf material was compared among nutrient treatments (within tree species) and among tree species (within nutrient treatments). Alder was preferred over other tree species in all nutrient treatments. Larvae preferred leaf material treated with nitrogen + phosphorus for all species except poplar. Poplar leaves fertilized with nitrogen were highly preferred whereas fertilization with nitrogen + phosphorus apparently rendered leaf material nearly inedible. Nutrient
(N, P) and tannin content, and leaf toughness differed among tree species and nutrient treatments. Consumption of leaf litter was positively correlated with nitrogen content and negatively correlated with tannin content but was uncorrelated with leaf toughness. A next step is to assess consequences of these qualitative differences in leaf detritus in terms related to shredder fitness (growth, mortality, reproduction) for a wide range of shredder organisms. But the work of Irons et al. (1988) suggests that the benefits of riparian vegetation as buffer zones (e.g., decreasing nutrient runoff into the stream by means of nutrient uptake by riparian plants) may be offset if stream organisms dependent on leaf litter cannot use it efficiently because of excessive nutrient content, or inappropriate ratios, or both (i.e., as derived from “fertilized” riparian trees). Thus, ecosystem-level repercussions of patch-specific phenomena in the riparian zone need to be addressed. For instance, how does species composition of riparian patches interact with the nutrient status of the vegetation to affect the trophic structure of stream communities? Do these interactions vary along tropical–temperate gradients?

**Beaver-induced patch dynamics**

In North America, beaver (*Castor canadensis*) have a strong influence on patch dynamics in stream ecosystems. Since near extermination at the beginning of this century, the population size of North American beaver has increased dramatically. Although current beaver populations have reached only 10–15% of the population size before the arrival of Europeans, changes in stream patch dynamics over the last 80 years have been substantial as beaver recolonize areas where habitat and food resources have not been used for many decades (Naiman and Melillo 1984, Naiman et al. 1986).

Long-term population dynamics, in combination with feeding and dam building activities, act to produce a startling array of patch characteristics within the drainage network. In Quebec, Naiman and Melillo (1984) and Naiman et al. (1986) found that beaver ponds had a density averaging 10.6/km² in second- and fourth-order streams, while in northern Minnesota the number of beaver ponds on the Kabatogama Peninsula increased from 0.15/km² in 1940 to 1.9/km² in 1981 (Naiman, unpublished data). These patches have significantly different standing stocks and fluxes of carbon and nitrogen (Naiman and Melillo 1984, Naiman et al. 1986), a different community composition (McDowell and Naiman 1986), and alternative pathways for carbon metabolism (Ford and Naiman 1988) compared with the original stream. Beaver have once again become a key component in the structure and function of stream ecosystems in the boreal forest. The overall influence of beaver-created patches on the drainage network needs to be considered in terms of mechanisms of patch formation and patch size, distribution, density, juxtaposition, diversity, and longevity. In combination, these factors interact to influence the overall biogeochemical economy of the drainage network.

Beaver create patches in two primary ways: by dam building and by foraging both in the impoundment and in the adjacent riparian zone. Dam building alters the hydrologic regime, accumulating material in the stream channel and creating extensive anaerobic zones as oxygen availability to the deep sediments is decreased (Naiman et al. 1986). Foraging by beaver is selective (Jenkins 1979), changing the vegetative community composition and the nature and amounts of allochthonous inputs to the aquatic environment (Conners and Naiman 1984). Both mechanisms of patch formation have long-term consequences for the stream depending upon the hydrologic regime, the response of the riparian vegetation to foraging, and the ability of beaver to maintain activity at the site. The ontogeny of a beaver pond, from its formation to its eventual decay, may range from a year to many centuries, with the physicochemical characteristics shifting during the aging process. When viewed in a landscape perspective, the distribution of beaver ponds becomes a dynamic mosaic of constantly shifting environmental situations reflecting pond age and size, degree of community maturity, substratum, hydrological characteristics, and resource inputs. This shifting mosaic of beaver-created habitat, a dominant part of the landscape for tens of thousands of years (Hays 1871, Jenkins and Busker 1979), overlies the natural development of the drainage network driven by climate and geology. The changing pattern of beaver ponds has both spatial and temporal components. Since all ponds along a reach of stream are not identical, specific ecosystem parameters are not spa-
entially constant. The result is a dynamic habitat where the relative importance of an ecosystem parameter varies along the channel. For example, one pond may have a primary production rate typical of a third-order stream, another the rate of a ninth-order stream, while the connecting riffles have rates of the normal second-order stream. This assumes that primary production, as well as other parameters, are not significantly affected by upstream ponds. Further, since beaver populations are known to wax and wane over time, the changes they cause will similarly have temporal variations in density and diversity. These changes may be manifested by changes in the internal biogeochemical economy of the watershed or, in addition, by changes in the total watershed budget for a particular parameter. Historically, this shifting mosaic, both spatially and temporally, was undoubtedly an important determinant of biogeochemical economies for pristine watersheds. This complex situation is analogous to the present variety of human-induced perturbations subjected upon stream systems. The concept of a shifting patch mosaic offers a convenient and essential approach for quantifying patch dynamics when biotic parameters continually adjust to abiotic gradients, such as those naturally occurring along stream–river continua.

The density of beaver-created patches is a response to beaver population dynamics, with a sufficient lag time to account for the return to normal stream conditions after the habitat is abandoned. This lag time may range from decades to centuries depending upon local conditions (Rudemann and Schoonmaker 1938). At present, for most of North America, cyclic changes in patch density are not well known nor are the long-term consequences well understood. Beaver populations in many areas are continuing to increase with the virtual absence of natural predators and an abundance of early successional forage along stream channels. Consideration of the large-scale consequences of habitat abandonment on stream stability and long-term productivity can only be speculative at present.

**Patch dynamics of floodplains**

Patch dynamics have yet to be formally applied to explain the functioning of the flood plains of the potomon, mainly because such systems have been less studied than other types of fluvial systems. Sufficient information does exist, however, to show the potential of the concept in explaining the distribution and abundance of fish and other biota in the lower reaches of rivers and to suggest future avenues of exploration.

The potomon of most large, unmodified rivers can be thought of as existing in two major states: (1) a low flow state in which aquatic components of the system are confined to channels and residual water bodies distributed over a relatively flat alluvial plain; and (2) a high flow state where aquatic components of the system fill the valley of the river to a greater or lesser extent. This means that a large proportion of the system alternates between a wet and a dry state at least once per year. Between these two states are periods, usually relatively brief, during which water levels rise or fall.

Floodplains may be considered to be subject to temporal events of four orders:

1. Annual (or twice a year in some equatorial rivers) cycles of flood and low water;
2. Periods of $10^4$–$10^5$ years during which erosional and depositional processes produce a slow evolution and succession in the various components of the system. Meanders migrate laterally reworking the sediments of the plain. New water bodies are created on the floodplain, and existing ones age through siltation and eventually disappear;
3. Periods of $10^7$–$10^8$ years during which disturbance events, in the form of greater than average floods or droughts, locally reform the river and its floodplain; and
4. Longer geological periods of $\geq 10^8$ years when landform processes may substantially alter the nature of the river basin by river capture, flow reversals, etc.

To these natural processes should be added effects of dams, deforestation, agriculture, and other human disturbances, which have substantially changed the nature of the world's rivers.

Erosional and depositional processes combine over time to impart a distinct texture to the river and its floodplain (Amoros et al. 1982, Bravard et al. 1986, Saio et al. 1986) that can be described in terms of patches. Individual patches can be remarkably persistent even though they
typically undergo a successional process that may consist of: (1) a slow transition from one state to another, as in the silting of individual water bodies; (2) a rapid change followed by a relatively steady state, as in the silting of the upper end of a channel transforming it into a dead arm; or (3) a local catastrophic event, such as the collapse of an eroded bank or the lateral displacement of a channel into a new bed. G. H. Copp (Université Claude Bernard [Lyon], personal communication) has pointed out that some changes in patch structure that appear to evolve slowly, in fact proceed through a series of critical threshold events. Thus an anabranch (a stream leaving a river and joining it lower down) that supports a certain community of organisms will switch rapidly to a different phase that supports a totally different community as soon as its upper end is closed and it becomes a dead arm. A similar transition to an isolated water body occurs when the lower end is closed.

Large river systems characteristically exhibit an orderly succession of features that repeat themselves for considerable distances, often thousands of kilometers along the river channel. Depending on slope and silt loadings, these can take the form of braided anabranches and islands or meanders which tend to change slowly with downstream progression. Some of these features are complex. In the case of a meander bend, at least three distinct patches can be identified: (1) the deepwater at the outer edge of the meander; (2) the point bar; and (3) the slack downstream of the point bar. Several workers (Araujo-Lima et al. 1986, Junk et al. 1983) have identified fish community structures associated with such habitat patches. The nature of these features can change downstream as mean particle size decreases. For instance, levees are reduced and finally disappear. Sandy point bars are gradually replaced by mud banks. Patch structures in the main channel can be remarkably subtle. In the lowest reaches of the river, where the bottom sediments appear to be a homogeneous cover of fine particulate substrata, differences in nutrient content can be sufficiently great to be detected by illiogphagous fish such as Prochilodus which feed on the organic compounds absorbed onto particles. Differences in concentrations of such compounds largely explain the patchy distribution of populations of this fish taxon (Quiros and Delfino 1986). Mud-feeding fish of this type can locally exhaust nutrient-rich patches (Bakare 1970), and patch structure is determined by a feed-back mechanism between depositional processes and fish feeding dynamics.

Mats of floating vegetation tend to produce strong vertical gradients in temperature and dissolved oxygen in underlying waters that can significantly affect the distribution of fish and other organisms. Many fish species are intolerant of low dissolved oxygen and will tend to move to zones of higher flow and better aeration. Other species are equipped with auxiliary breathing organs and may actively seek regions of low dissolved oxygen. Thus, patches of floating vegetation may segregate other biota or processes. The larger the patch, the greater its tendency to act in this way. Floodplain pools blocked with large masses of vegetation will often be populated only by species that are able to penetrate the barrier of the deoxygenated water under the mat. Smaller patches are less stable and are more readily dislodged by current and carried out into the main stream.

The effect of increasing size of floodplain water bodies (FAO/UN 1971) is also closely linked to the capacity of vegetation mats to lower dissolved oxygen. Small residual water bodies on the floodplain are often completely covered with floating vegetation, and underlying waters are typically completely devoid of oxygen. As a result, the few fish species that populate them are those which are adapted to breathe atmospheric oxygen. Somewhat larger water bodies in the patch become less homogeneous and areas of open water appear in which oxygen levels are high enough to support a number of more resistant species. Further increases in the size of water bodies introduce a hierarchy of patches of floating, emergent and submersed vegetation, and open water. This diversity of habitat patches, and the improved oxygen conditions arising from the effect of wind, enable a greater variety of species to survive. Further expansion in the size of water bodies is accompanied by an equivalent increase in habitat and species diversity.

Few fluvial ecosystems have escaped the activities of man. Dahm et al. (1987) point out that historical reconstructions have shown repeatedly that many floodplain landscapes were more complex and heterogeneous in space and time than is now the case. They suggest that recon-
structions are prerequisites for understanding contemporary patterns. Modifications of floodplain patch dynamics can be considered as proceeding in three main phases: (1) colonization, (2) utilization, and (3) destruction. Originally most floodplains appear to have been heavily wooded (at least with gallery forests), even in drier parts of the world. This condition still exists in some equatorial basins where the subtle interactions between trees and fish communities (Goulding 1980) or the adaptations to colonize dead wood lying in river channels (Lowe-McConnell 1964) attest to the complexities of patch structure in unaltered environments.

Early in the colonization process, human activities progressively reduced the forest cover and replaced much of the woodland with the savannah plains that are so typical of African and South American rivers today. This process led to drastic changes in the ecosystems which were aggravated as the size of woodland patches decreased (e.g., Alho et al. 1988). Greater instability was introduced into the physical system with an acceleration of erosion-deposition cycles. More long-lasting and stable structural patches (trees) were replaced by mosaics of floating, emergent, and submerged vegetation. Increased insolation led to higher temperatures and to more rapid recycling of organic matter. Phyto- and zooplankton increased in abundance and floating grasses became the dominant form of primary production. These changes were probably accompanied by changes in fish population structure that have not been documented. However, more recent observations (e.g., Goulding 1980) indicate the types of changes that may have occurred. Decreases in the size of woodland patches leads to the decline in the number of frugivorous species. Likewise, the disappearance of wood from streambeds leads to a diminution of species dependent on such habitats for refuge.

During the utilization phase, river channels and floodplains are subject to intensive rural use involving agriculture, fisheries, cattle rearing, and even human occupation (e.g., Alho et al. 1988). Use of the plain can be highly organized while the flood pattern is maintained. Traditional values of human communities at this level of use often show a deep understanding of the role of patch structure of floodplains and many features are adapted to maximize production. Examples include plantations of floating rice, patches of floating vegetation that are used as devices to concentrate fish for later capture, and floodplain water bodies that are adapted as drains in fish ponds. Further modifications to the structure of floodplain systems have resulted from the introduction of new organisms. The introduction of floating weeds such as Salvinia, Azolla, and Eichhornia have frequently led to changes in nutrient cycling, with massive repercussions throughout the system. On a smaller scale, introduction of a fish such as the grass carp (Ctenopharyngodon idellus) can eliminate patches of submerged vegetation resulting in a disappearance of water bodies, or conversion in primary production to phytoplankton and shifts in the species composition of communities of aquatic fauna.

During the destruction phase, the characteristics of the river and its floodplain are so altered by channelization, drainage, poldering, and urbanization that few of the original features of the system remain. The breakdown of patch structures essential to the breeding and feeding of many species results in a simplification of the fish community and greatly lowered productivity.

An understanding of various elements of fluvial ecosystems and the way in which they relate to one another is crucial to effective management. Such knowledge is needed both at the utilization level, where maintenance of the correct balance of water level and water use can permit sustained harvesting of a number of aquatic and terrestrial food organisms, and at the destruction level, where similar information is needed to mitigate changes and restore what has been lost.

Studies on energy flow and structural dynamics of biota between and among terrestrial, riparian, and riverine patches, as superimposed on the floodplain surface, are needed. Comparisons of temporal dynamics of floodplain processes in desert, forested, and savannah (i.e., transition between forested and drier biomes) environments may be most instructive. In particular, it is vital to document how floodplain-dependent fishes are influenced by intensity and duration of flood periods. Conservation of the few remaining pristine big river floodplains cannot occur without this information (Wel-
comme 1988—see this issue). A patch dynamics approach may offer a new synthesis for such studies.

Conclusions and recommendations

In addition to specific recommendations presented with the preceding discussion topics, we offer the following conclusions and recommendations in hopes of facilitating the application of a patch-dynamics perspective to problems in lotic ecology, and stimulating ideas and approaches for future study:

1. A patch dynamics approach has the potential to yield information central to the effective management and long-term survival of lotic systems by increasing our understanding of the role of various elements in streams and the way in which they relate to one another.

2. The effectiveness of a patch-dynamics approach as a framework for the study of lotic systems lies in the strength of the linkage between reductionist and whole-system perspectives.

3. Examination of patch-dynamics can enhance the utility and predictive power of unifying concepts in lotic ecology such as the river continuum hypothesis (Vannote et al. 1980) and nutrient spiralling (Newbold et al. 1981) through its focus on organism and process-specific building blocks of lotic systems. Examination of patches and process-oriented interactions between patches will allow quantitative comparisons to be made within and between stream systems.

4. Patch-to-patch variability in lotic systems should be viewed as information, rather than statistical noise to be overcome with adequate sample size. This concept needs to be applied over extremes in spatial and temporal scales, from the response of microbial communities to nutrient patches on a scale of μm and milliseconds, to differences between catchments in different biomes.

5. With respect to tropical–temperate comparisons, more data are necessary from a variety of lotic systems within given geographical areas; variability within biomes must be examined before cross-biome comparisons can be made. Broad and often inaccurate generalizations regarding properties of tropical ecosystems have generated restrictive assumptions regarding functional characteristics of tropical streams.

6. A patch perspective is recommended as an ideal framework to test Tilman’s (1982) consumer resource theories as they apply to lotic systems. The study of patch dynamics, with a landscape perspective, also provides a useful perspective with which to examine little-understood biotic/abiotic interactions in streams (e.g., Power et al. 1988—see this issue).

7. A greater emphasis should be placed upon those characteristics of a study organism that allow it to perceive and affect patch-specific phenomena or variation in its environment.

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