

Physical Habitat Template of Lotic Systems: Recovery in the Context of Historical Pattern of Spatiotemporal Heterogeneity

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ABSTRACT / Spatial and temporal environmental heterogeneity in lotic ecosystems can be quantitatively described and identified with characteristic levels of ecological organization. The long-term pattern of physicochemical variability in conjunction with the complexity and stability of the substratum establishes a physical habitat template that theoretically influences which combinations of behavioral, physiological and life history characteristics constitute appropriate "ecological strategies" for persistence in the habitat. The combination of strategies employed will constrain ecological response to and recovery from disturbance. Physical habitat templates and associated ecological attributes differ geographically because of biogeoclimatic processes that constrain lotic habitat

structure and stability and that influence physicochemical variability and disturbance patterns (frequency, magnitude, and predictability). Theoretical considerations and empirical studies suggest that recovery from natural and anthropogenic disturbance also will vary among lotic systems, depending on historical temporal variability regime, degree of habitat heterogeneity, and spatial scale of the perturbation. Characterization of physical habitat templates and associated ecological dynamics along gradients of natural disturbance would provide a geographic framework for predicting recovery from anthropogenic disturbance for individual streams. Description of lotic environmental templates at the appropriate spatial and temporal scale is therefore desirable to test theoretical expectations of biotic recovery rate from disturbance and to guide selection of appropriate reference study sites for monitoring impacts of anthropogenic disturbance. Historical streamflow data, coupled with stream-specific thermal and substratum-geomorphologic characteristics, are suggested as minimum elements needed to characterize physical templates of lotic systems.

Stream ecologists have long recognized that physical environmental heterogeneity influences species richness and abundance (Thienemann 1954, Hynes 1970). This viewpoint is reflected in contemporary synthetic theories of lotic ecosystem structure and function, which emphasize the importance of spatial habitat heterogeneity and temporal environmental variability (Vannote and others 1980, Elwood and others 1983, Ward 1989). In the past several years, a growing number of lotic ecologists have argued that physical disturbance plays a dominant role in structuring lotic communities (Peckarsky 1983, Stanford and Ward 1983, Ward and Stanford 1983a, Lake and Barmuta 1986, Power and others 1988, Resh and others 1988, Reice and others this volume), and a "consensus" may have emerged on the general impor-

tance that disturbance plays in constraining the types of ecological processes and patterns observed in streams (see Resh and others 1988). Furthermore, since the intensity and temporal distribution of physical selective forces differ between streams according to regional biogeoclimatic constraints, lotic community structure and ecological response to disturbance are recognized to have a geographic pattern as well (Fisher 1983, Peckarsky 1983, Fisher and Grimm 1988, Minshall 1988, Resh and others 1988, Poff and Ward 1989). The long-term regime of natural environmental heterogeneity and disturbance may be considered to constitute a physical habitat template (*sensu* Southwood 1977, 1988; cf. Minshall 1988) that constrains the types of species attributes appropriate for local persistence. Thus spatial and temporal characteristics of the physical environment may predetermine the type and range of ecological response mechanisms available following natural and anthropogenic disturbances.

The importance of the spatiotemporal scale employed in an investigation is a current focal point of ecology (e.g., Wiens 1989), including stream ecology (Minshall 1988) and has direct consequences for de-

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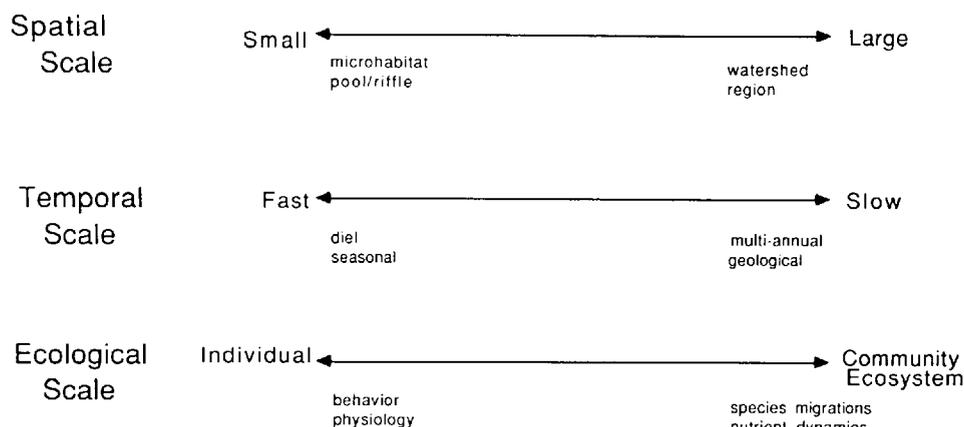


Figure 1. General scaling relationships in lotic ecosystems. As habitat spatial scale increases from small to large, frequencies of associated temporal phenomena decrease, leading to a small–fast to large–slow gradient, along which different levels of ecological organization and associated response characteristics are generally arrayed. (See text for further discussion.)

etecting recovery in disturbed streams and rivers (see Kelly and Harwell this volume). In lotic ecosystems, spatial and temporal environmental heterogeneity occurs at many scales that can be associated with characteristic levels of ecological organization (Figure 1). The detection of recovery from natural or anthropogenic disturbance depends on selection of the appropriate spatial and temporal scales for the ecological response variable(s) of interest. Frequently, detection of a system's return to some end point approximating a predisturbance state is a primary research and regulatory objective (see Yount and Niemi this volume, Niemi and others this volume). However, the prediction of the time required for recovery to occur requires an understanding of the ecological processes or mechanisms through which recovery is effected. This understanding must include not only characterization of the disturbance at the appropriate spatial, temporal, and ecological scales, but also knowledge of the biota's "preadaptedness" to a particular disturbance.

In this article, we argue that biological resistance to, and recovery from, anthropogenic disturbance is a function of the biota's experience with historical, natural spatiotemporal variation. Lotic environments presenting substantially different physical templates will have "selected" for correspondingly different ecological response characteristics to natural disturbance in such a way as to influence a variety of responses to anthropogenic disturbance. The characterization of physical habitat templates is not only of basic scientific interest but also has valuable management implications for understanding how individual lotic systems respond to, and recover from, anthropogenic disturbances over broad geographic scales. We consider the long-term temporal pattern of physical variability (de-

scribed primarily by streamflow and thermal regimes), in conjunction with substratum heterogeneity and stability, to constitute the minimal elements necessary for the description of lotic physical habitat templates.

Individual sections of this article will be used to address the following objectives: (1) identify, in a hierarchical context, the relevant scales for evaluating spatio-temporal heterogeneity in lotic systems; (2) address the importance of specific patterns of environmental variation in space and time in establishing the physical habitat template of lotic systems, and suggest techniques through which lotic environmental templates might be identified; (3) describe how templates of natural environmental heterogeneity and disturbance can be related to characteristic ecological processes and patterns; and (4) explore how ecological response to, and recovery from, anthropogenic disturbance reflects predisturbance regime of environmental heterogeneity and disturbance.

Spatiotemporal Heterogeneity

Hierarchical Spatial Scales

Streams and rivers reflect the landscapes they drain (Hynes 1975). The spatial relationship of any lotic ecosystem to its landscape setting can be viewed in terms of lateral (channel–riparian), longitudinal (channel–channel) and vertical (channel–groundwater) linkages (Ward 1989), the relative importances of which vary in both space and time. Although vertical linkages can assume great importance in some riverine reaches (see Stanford and Ward 1988), longitudinal and lateral linkages (*sensu* Vannote and others 1980) will be emphasized here.

In hierarchy theory, natural systems often are

viewed as series of sequentially nested functional levels with the behavior of any system level constrained by the level above it (Allen and Starr 1982, Urban and others 1987). The rates of system processes vary inversely with the spatial extent of the level, thus leading to a general small–fast to large–slow gradient (see Figure 1). Frissell and others (1986) have developed a spatially nested hierarchical system for stream classification. Levels are physical habitat systems that reflect watershed geomorphologic constraints and that are amenable to regional, higher-order biogeoclimatic classification. Although based on the prototype of a second- to third-order mountain stream, the system is general enough to allow extrapolation to other lotic settings as well. This approach emphasizes the watershed-dependent nature of lotic systems and the importance of physical habitat in controlling biotic organization within regional biogeoclimatic constraints.

The *stream* (= *watershed*) *system* places the entire drainage network in a watershed context. Watershed characteristics reflect geologic and climatic history of the drainage basin and biogeoclimatic region. Infrequent, high-magnitude geologic or climatic events (e.g., volcanism, glaciation) contribute to change at this spatial scale. *Segment systems* are portions of streams bounded by such major discontinuities as tributaries or changes in underlying bedrock. Within segments, *reach systems* are defined by breaks in channel slope, bank material, floodplain characteristics, substratum character, or riparian canopy cover. Reaches extend up to hundreds of meters of channel length. *Pool–riffle systems* are characterized by breaks in bed topography and water surface slope, depth, and velocity patterns. Many classes of pool–riffle systems are possible, depending largely on morphogenetic features (e.g., bedrock outcrop or treefall) with which they are characteristically associated (see Frissell and others 1986). Finally, *microhabitat systems* are components of pool–riffle systems that are similar in such morphometric features as substratum type, water depth, and water velocity. Discontinuities in these features delineate boundaries for microhabitat patches, which typically scale on the order of fractions of a meter, depending on substratum properties and heterogeneity. Temporal persistence of microhabitat patches depends on the frequency with which disturbances (e.g., scour, spates) occur and on patch susceptibility to disturbance.

This physical habitat hierarchy is appropriate for lotic ecosystems, where all organisms are in intimate contact with the substratum for at least some stage(s) of their life cycles. Availability and persistence of substrata thus have the potential for directly influencing

successful life cycle completion and persistence of all lotic species. Moreover, habitat change at any higher level in the hierarchy has a downward-cascading effect on all subordinate nested levels. According to the river continuum concept (Vannote and others 1980) and its modifications (e.g., Minshall and others 1985), biotic attributes vary both longitudinally within a stream and geographically among streams. Thus, the spatial framework of Frissell and others (1986) is further embedded in larger landscape units that can be delineated according to geological, geomorphological, climatic, or ecogeographic criteria (Leopold and others 1964, Bailey 1976, Lotspeich and Platts 1982, Brussock and others 1985, Frissell and others 1986, Omernik 1987).

Hierarchical Temporal Scales

Temporal variability in major physicochemical conditions (e.g., temperature, current and/or streamflow, dissolved gases) is best viewed in a hierarchy that corresponds directly to periodic climatic events that have functioned as exogenous evolutionary forces structuring patterns of biological activity and life cycle schedules. Several temporal levels can be delineated. The *geological* level scales from decades up to thousands of years. Although the occurrences of geologic catastrophes inevitably have immediate ecological consequences (e.g., the eruption of Mount St. Helens), many geologic events occur as gradual long-term changes (e.g., glaciation) and can be viewed as contributing to biogeographic patterns and driving speciation through geographic isolation (e.g., Zwick 1981). The *multiannual* scale corresponds to climatic phenomena that recur with periodicities on the order of up to decades. Examples would be the El Niño/southern oscillation (ENSO) events (Cane 1983) and the Sahalian drought cycle (Faure and Gac 1981). ENSO events may lead to associated periodic streamflow patterns in some tropical (Richey and others 1989) and temperate (Molles and Dahm 1990) regions. This scale represents a transition between evolutionary (many generations) and ecological (few generations) time, and variability at this scale may contribute to ecological “crunches” (sensu Wiens 1977). The *annual*, *seasonal*, and *dial* temporal levels reflect periodic climatic phenomena of increasingly high frequency. Ecological activity budgets and life cycle schedules probably have evolved using environmental information provided at these high frequency temporal scales (cf. Ward and Stanford 1982; Sweeney 1984). Consequently, many ecological processes and patterns occur at frequencies that correspond to these temporal scales. The degree of natural variability in physicochemical conditions at these high

frequency temporal levels often reflect climatic, geologic, and ecogeographic constraints. Thus, for a geographically diverse group of lotic settings, this high frequency variability can range from great to small and from predictable to unpredictable. The specific pattern of this temporal variability has important ecological consequences.

Rationale for Physical Habitat Template in Lotic Ecosystems

Southwood (1977, 1988) viewed the temporal persistence of habitat to be a significant selective determinant of the appropriate "ecological strategies" adopted by species. In lotic ecosystems, physical habitat structure is of critical importance to the distributions and abundances of organisms. In general, greater spatial heterogeneity at the scale of organisms results in greater microhabitat and hydraulic diversity and hence in greater biotic diversity. The intimate association between lotic organisms and the substratum confers special ecological importance upon the spatial heterogeneity at the microhabitat scale. For example, surface roughness affects algal colonization dynamics and diversity (Tuchman and Stevenson 1980); insect diversity is positively correlated with substratum surface complexity and particle size heterogeneity (see Minshall 1984); and larger substratum structures provide cover for fish, the abundance of which increases with increasing cover (Saunders and Smith 1962, Hynes 1970).

The temporal persistence of microhabitat quantity (and quality) represents an interaction between microhabitat characteristics (e.g., quantities and distributions of various particle sizes) and exogeneous, climatically driven physical events that act to disrupt habitat. Disruptions occur either through physical disturbance (e.g., spates that scour or move the substratum) or through rendering the habitat physiologically undesirable (e.g., extreme thermal conditions or dissolved oxygen reductions associated with low flow periods). The time course of microhabitat availability and persistence, relative to the specific life cycle requirements of the organisms utilizing those microhabitat types, can be viewed as constituting a physical habitat template that constrains the types of "ecological strategies" that can be locally successful (i.e., persist over the long term). For example, species requiring stable substrata for successful growth and development are not likely to persist in habitats where substrata are frequently disturbed (cf. McAuliffe 1984).

Attributes of the physical habitat template elicit biological responses at the individual, population, and

community levels. Slobodkin (1968) provided a homeostatic framework for describing how individuals and populations respond to environmental variability that is noncatastrophic (i.e., which does not induce random mortality). The first response to noncatastrophic environmental change occurs at the level of the individual through the mechanism of *behavior*. Avoidance of stressful conditions is commonly observed among lotic organisms (e.g., Edington 1968, Martin and Gentry 1974, Matthews 1987). If the environmental change cannot be avoided, the organism will be forced to make a *physiological* adjustment to the new conditions (presuming conditions are not lethal). Change in oxygen consumption rate as a function of dissolved oxygen concentration is a typical example (Hynes 1970). If the environmental change persists only briefly, the organism can return to its previous physiological state. However, if the change endures, physiological acclimation to the altered environmental condition(s) may occur, and the individual's new physiological state confers enhanced resistance to further change. The range of physiological tolerance can vary among individuals within a population, among local populations, and among species (e.g., Matthews 1987). Where environmental change is too severe for individual behavioral or physiological maintenance of homeostasis—frequently the case for disturbance—biological response occurs through a *genetic* change at the population level. Variation among individuals in ability to tolerate environmental fluctuations and survive disturbance (e.g., through behavioral and physiological avoidance or through timely attainment of a resistant life history stage), results in an alteration of gene frequencies in the next generation. Thus, selection has occurred for phenotypes "resistant" to some component(s) of disturbance.

The temporal distribution of physical selective forces in an environment provides a framework for interpreting how species persist under particular templates. Persistence can be viewed as occurring in evolutionary (= geological) or in ecological (= multianual or faster) time. Theoretically, any environmental variation marginally affects fitness of at least some individuals and thus provides a potential selective pressure on the population (Levins 1965). Environmental variation that demonstrably affects fitness (e.g., by damaging or killing) can be defined as a physical disturbance (Sousa 1984), and the statistical characteristics of the distribution of disturbances over the long term can be referred to as the disturbance regime. The statistical pattern and temporal autocorrelation of environmental variability and disturbance were postulated by Levins (1965) to provide specific environ-

mental information that is reflected in "optimum genetic systems" (Levins 1965) of populations (i.e., local adaptation to prevailing physical environmental selection regimes). Thiery (1982) generalized the relationship between environmental variation and species adaptation and indicated that the most important selective forces associated with a disturbance regime were the disturbance frequency (relative to species generation time), the degree of deviance from mean conditions, and the contingency or predictability of the deviations. Thus, different disturbance regimes provide different selective pressures. For example, the more deviant and unpredictable a temporal variability regime, the fewer the individuals within a species capable of tolerating and persisting under it and, therefore, the stronger the selective pressure for specific homeostatic responses. Generalized responses to such an environmental selection regime would be small size coupled with rapid growth and development (Slobodkin 1968).

While local adaptation to specific environmental selection regimes may occur for genetically isolated populations, it is not necessary to invoke this mechanism to explain differential species success under different physical habitat templates. Species that do not possess the "ecological strategies" (physiological, behavioral, and/or life history characteristics) necessary to accommodate the prevailing pattern of environmental variability and disturbance in a locale may invade it but will not persist there. In this sense, the dynamics of the physical habitat template act as a bottleneck or "filter" on community assembly (cf. the wetland vegetation model of Van der Valk 1981).

This theoretical framework as applied to lotic ecosystems is illustrated in Figure 2, where a regime of temporal heterogeneity and disturbance is characterized by fluctuations in the magnitude of an environmental "intensity signal" representing the summation of all physicochemical environmental factors (current and/or streamflow, temperature, dissolved oxygen, desiccation stress, etc.) that affect species performance and fitness. Disturbances, which can be considered as signal intensities that exceed the species-specific tolerance limits of individuals, include such environmental extremes ranging from periods of low flow, low dissolved oxygen, and high temperature to high flow events that move substrata in suspension or along the bed. Temporal physicochemical variability and disturbance are distributed with some statistically definable magnitude, frequency, and periodicity, which can be expressed relative to individual species' life cycle phenologies (Figure 2). Species may persist under a given signal if they are tolerant of the range of condi-

tions present or if they possess the behavioral or life history characteristics that allow them to avoid the occurrence of lethal conditions. The effective tolerance range for a species (indicated by the extended scale bars in Figure 2) can be increased not only by the possession of appropriate behavioral or life history attributes, but also where habitat structure and heterogeneity provide refuge from disturbance. For example, large, stable substrata can resist displacement during extreme flows, and hyporheic zones may provide refuge from the danger of desiccation during low flows. Thus, in addition to the temporal distribution of the physicochemical environmental signal, habitat structure contributes to the dynamics of physical habitat template. Although not illustrated in Figure 2, species tolerance ranges can change with development, such that identification of sensitive temporal bottlenecks might be important in understanding species persistence under a given physicochemical variability regime. Similarly, long periods of disturbance or "adverse" environmental conditions (see Southwood 1988, cf. Minshall 1988) may reduce the effective tolerance ranges of species and thus provide an additional constraint on successful ecological strategies. In Figure 2, "adverse" conditions could be expressed as high-intensity, long-duration environmental signals.

For several theoretical reasons, ecological process and pattern are expected to be more persistent with respect to disturbance in lotic systems experiencing wide spatiotemporal heterogeneity than in less variable systems. First, frequently disturbed, noncontingent environments exert consistent selective or "filtering" pressure for species having some combination(s) of behavioral flexibility, physiological eurytopy, and "opportunistic" life history characters (e.g., Sanders 1969, Pianka 1970, Menge 1976, Menge and Sutherland 1976, Schlosser 1987, this volume). All these characters can be viewed as homeostatic responses to frequent disturbance (cf. Slobodkin 1968). Assemblages of insects (Siegfried and Knight 1977) and of fish from both flood-prone (Harrell 1978) and intermittent (Larimore and others 1959; Schlosser 1987) streams have been accorded these attributes. Second, spatiotemporal heterogeneity may encourage maintenance of genetic polymorphism (Levins 1965, Chesson 1985, Lynch and Gabriel 1987), which theoretically contributes to greater population homeostatic potential (Slobodkin 1968, see Quattro and Vrijenhoek 1989). Third, habitat complexity mediates the impact of disturbance because stable refuges are likely to exist in heterogeneous habitats (see Sedell and others, this volume, for an extended treatment). This is similar to the notion that disturbance in homogeneous habitats

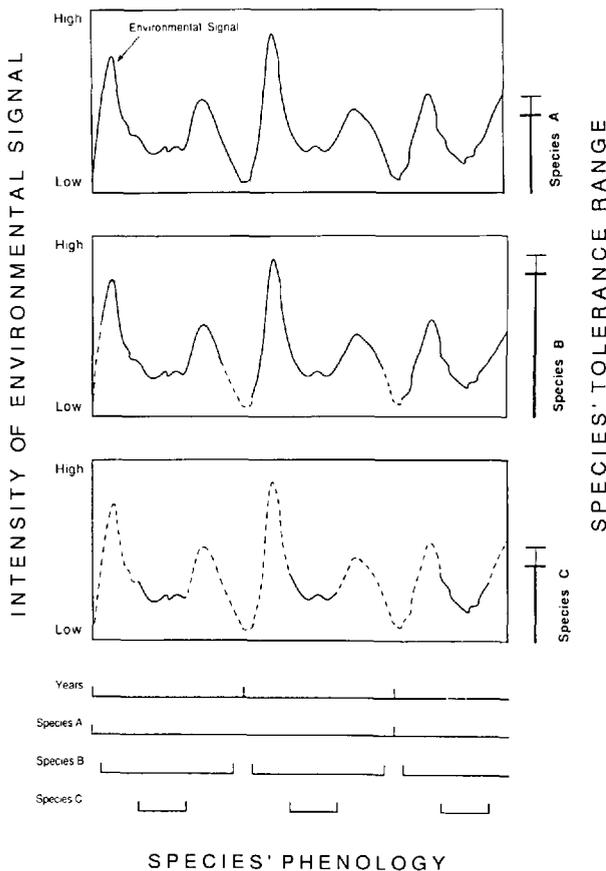


Figure 2. Conceptual model of how environmental heterogeneity provides a physical template for species persistence. Variability in all environmental conditions produces a composite, time-distributed "intensity" signal that ranges from low to high. The hypothetical pattern of temporal variability presented here represents fluctuation in a composite environmental signal with high magnitude and regular seasonal periodicity of intensity. Signals of high magnitude that exceed the physiological tolerance ranges of a species (bold scale bars along vertical axes) constitute a disturbance for that species. Frequency of disturbance is scaled to species generation time (species phenology scale bars along time axis). Species can potentially persist under the given physical template if tolerance ranges are not exceeded by environmental fluctuations or if characteristic population phenologies are in phase with the pattern of temporal variability. Spatial heterogeneity may increase the effective tolerance ranges (indicated by vertical extensions of tolerance scale bars) for some kinds of environmental signals by providing refuges. In this example, species A is a perennial resident of the stream with a biennial generation time. Its tolerance range is insufficient to allow persistence under a regime of frequent (relative to generation time) disturbance. The species cannot persist in this environment unless it migrates or finds refuge during the periodic extremes. Species B has an annual life cycle (gaps in the scale bar indicate periods of absence from the environment, e.g., insect emergence) and would normally persist, given its broad tolerance range. Occasional extreme environmental fluctuations might drive it toward local extinction; however, spatial heterogeneity and/or "opportunistic" life history characteristics would facilitate rapid recovery. Species C has a narrow tolerance range, but it can persist in this predictable environment by altogether avoiding disturbance conditions (e.g., through diapause, emergence, migration), as indicated by the gaps in the phenology scale bars. Refer to text for additional discussion.

changes patches "in phase" (Abugov 1982), while disturbance in spatially complex habitats results in a "mosaic of successional patches" (Levin and Paine 1974).

In predictable environments, physical selective pressures are temporally autocorrelated and thus provide a periodic signal to which species may adapt or from which species may escape (cf. Levins 1965, Thiery 1982). Predictable environments without substantial variability are considered constant and are characterized theoretically by selective pressures that favor species that have sacrificed (over evolutionary time) physiological eurytopy for fine-tuned biological competitive ability (Connell and Orias 1964, Sanders 1969). Because variation in the environmental intensity signal (cf. Figure 2) is infrequent relative to the life-span of the resident organisms, selective pressure for disturbance-generated life history adaptations is weak. In streams with more constant signals, biotic structuring forces may thus attain importance (cf. Power and others 1988, Resh and others 1988, Poff and Ward 1989). Accordingly, populations and communities from more constant environments are relatively susceptible to a disturbance of some absolute magnitude when compared to populations and com-

munities from more variable, unpredictable environments (Slobodkin 1968, Holling 1973, Connell and Sousa 1983, cf. Resh and others 1988). Another kind of temporal predictability is represented by periodicity (contingency) in environmental variation. Here, the strong periodic signal provides a strong physical selective pressure to which species have presumably adapted in ways similar to constant environments (Slobodkin and Sanders 1969, Inger and Colwell 1977). Species assemblages in contingent environments are thought to be particularly susceptible to unpredictable (nonperiodic) disturbance (Levins 1965, Slobodkin and Sanders 1969, Menge 1976, Resh and others 1988) (cf. Figure 2).

Several aquatic studies have emphasized the behavioral, physiological, and life history characteristics possessed by local populations or species that are "adapted" to temporal streamflow or thermal regimes. In the desert Southwest, spates and intermittency are frequent, relatively seasonal, and act as strong selective forces. Meffe (1984) demonstrated an innate, adaptive flood-avoidance behavior in individuals of a native poeciliid fish species. John (1963) found native cypripinids inhabiting intermittent streams to spawn in response to late-summer, but not early-summer,

flooding. For invertebrates, Gray (1981) and Fisher and others (1982) documented a variety of behavioral and life history attributes that allow lotic insects to persist in a desert stream characterized by both spates and intermittency.

Examples for nondesert systems also exist. Some insects have been reported to avoid spates (e.g., Zahar 1951) and desiccation (Larimore and others 1959, Williams and Hynes 1977) by migrating downward into the substratum. Martin and Gentry (1974) showed that dragonfly larvae could avoid lethal thermal conditions by migrating temporarily into the deeper, cooler substratum. Fish physiological tolerances have been found greater in thermally variable vs more constant environments both within and among species (Matthews and Styron 1981, Feminella and Matthews 1984, Matthews 1987). Matthews (1987) also showed that individuals from "harsh" environments were more adept than those from "benign" environments at finding the least stressful microhabitats as physicochemical conditions deteriorated. Peterson (1987) found that algal assemblages from variable current velocity regimes resisted desiccation more effectively than did those from more constant regimes. Poff and Matthews (1985) argued that frequent, unpredictable anthropogenic thermal variation in a stream eliminated all mayfly species except one that is both eurythermal and asynchronously multivoltine.

The work of Vepsäläinen (1978) on aquatic hemipterans showing that long-winged morphs (dispersers) dominate in temporary habitats, whereas short-winged morphs (nondispersers) dominate in more permanent (i.e., predictable) habitats provides strong correlative evidence for physical environmental selection of appropriate phenotypes. Leggett and Carscadden (1978) provide compelling correlative evidence that anadromous Atlantic shad vary latitudinally from Florida to Nova Scotia in degree of iteroparity depending on home river thermal harshness, a temporally predictable environmental characteristic that directly affects likelihood of juvenile survivorship. Examples consistent with the hypothesis of adjustment of life history schedules to local environmental predictability exist for non-freshwater systems as well (e.g., Foster and Moreton 1981, Zammuto and Millar 1985, Etter 1988).

Toward a Description of Stream Habitat Templates

Lotic systems vary in patterns of spatial and temporal heterogeneity. At very coarse spatial scales, differences reflect climatic constraints (e.g., mesic vs arid regions). However, differences also can exist at finer

levels of spatial resolution (e.g., within mesic regions). The frequency, magnitude, and predictability of temporal environmental variation and disturbance constitutes an important component of the physical habitat template that constrains ecological expression at a variety of spatial scales. Therefore, a quantitative description of how patterns of temporal heterogeneity in streams vary within and among large landscape units is of both theoretical and managerial importance.

Unfortunately, lotic environmental templates are not easily quantifiable (but see Bournard and others 1987a,b for an attempt) because they represent not only physical habitat structure, but also historical patterns of physicochemical variability, for which data are rarely directly available. However, by identifying major environmental variables for which long-term records exist or can be reasonably inferred, it may be possible to describe physical habitat templates at least qualitatively. The minimum elements to be considered in such an approximation would be substratum, thermal regime, and streamflow pattern. Indeed, these three variables have been variously emphasized in conceptual models that predict patterns of natural diversity (Stanford and Ward 1983) and ecological adjustments to anthropogenic disturbances (Ward and Stanford 1983b) along river longitudinal profiles.

Substratum Characteristics

Spatial heterogeneity at the microhabitat level will mediate the impact of a particular physicochemical variability regime and thus should provide an initial level of focus in describing the habitat component of the physical template. Methods exist for quantitative description of substratum heterogeneity in lotic systems (see Minshall 1984), such that spatial habitat heterogeneity could be compared among lotic settings. With information on stream slope, substratum particle size (e.g., median diameter), and stream depth, coupled with discharge characteristics, empirical hydraulic relationships (e.g., see Dingman 1984, Newbury 1984) could be used to estimate the temporal stability of the substratum, including spatial refuges, where these have been identified. Movement of bed material under high flow events has been used as a measure of disturbance in a few studies (e.g., Erman and others 1988, McElravey and others 1989, Rader and Ward 1989), and more widespread utilization of this objective measure would allow the within-stream (longitudinal) and among-stream variation in substratum characteristics (see Brussock and others 1985) to be cataloged with respect to habitat stability.

Thermal Characteristics

The role of thermal variability and disturbance has

been considered from a theoretical perspective (Vannote and Sweeney 1980, Ward and Stanford 1983a) and shown to explain various aspects of species performance (Beitinger and Fitzpatrick 1979, Ward and Stanford 1982). Biologically relevant components of thermal regimes, such as annual extremes, seasonal rates of change, and diel fluctuations, are under gross climatic control and vary with both latitude and altitude (Vannote and Sweeney 1980, Ward and Stanford 1982, Lake and others 1985, Ward 1985). Even though local conditions such as groundwater contributions can modify the general geographical patterns, thermal regimes are probably relatively predictable on a seasonal to annual basis within given streams (Vannote and Sweeney 1980). Such predictability implies that reasonable inferences on long-term thermal characteristics for lotic systems may be possible by coupling short-term thermal data (e.g., annual thermograph data) with corresponding atmospheric records and then extrapolating historically. Physical water–air heat-exchange models (e.g., Theurer and others 1984) might be used in conjunction with temperature-dependent oxygen saturation relationships to characterize the frequency, duration, timing, and predictability of temperature extremes and dissolved oxygen deficits, both important aspects of species tolerance.

Streamflow Characteristics

Flow is strongly correlated with most important physicochemical factors in lotic systems (e.g., current, water depth, desiccation potential, thermal stress, resource renewal rates), although the exact relationship will vary both among streams and longitudinally within streams. More variable streamflow conditions thus imply more variable rates of ecological processes. The flow regime not only plays a dominant role in regulating channel complexity and stability (Leopold and others 1964) and hence habitat attributes, but also regulates the import and export of allochthonous organic material that serves as both habitat and food resource (e.g., Gurtz and others 1988). Because flow regimes, unlike thermal regimes, can be highly unpredictable over short time scales, inferences about

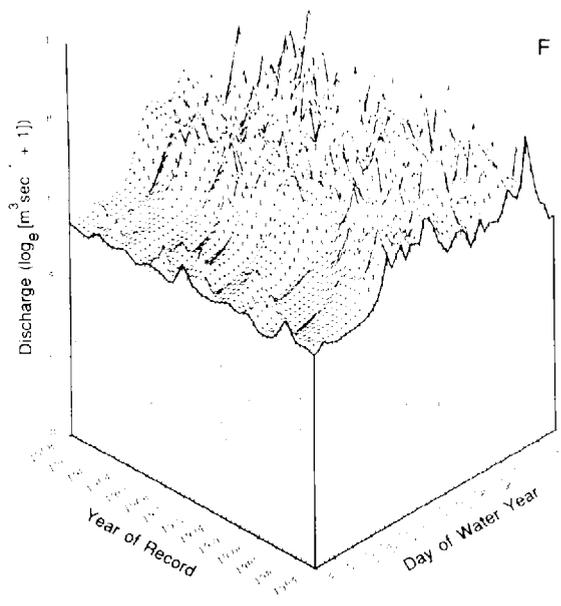
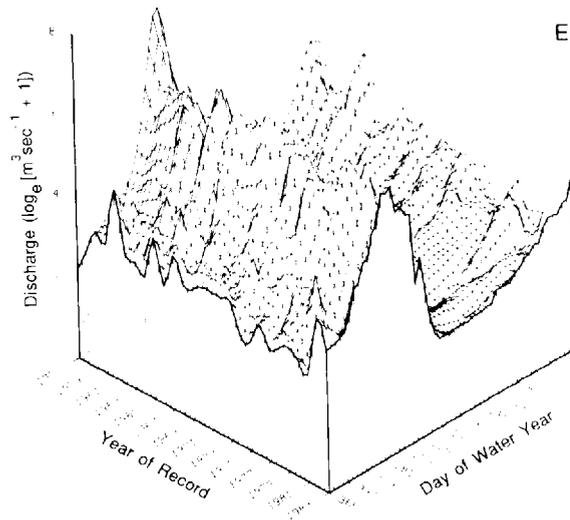
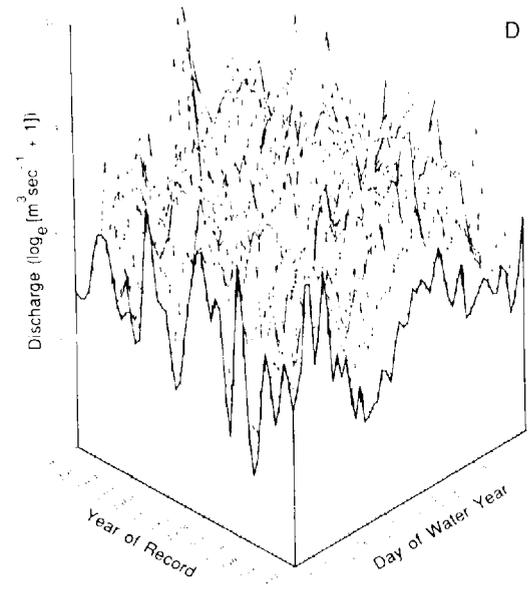
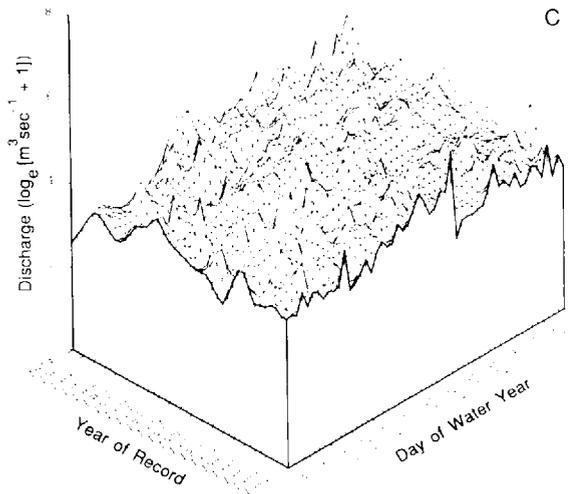
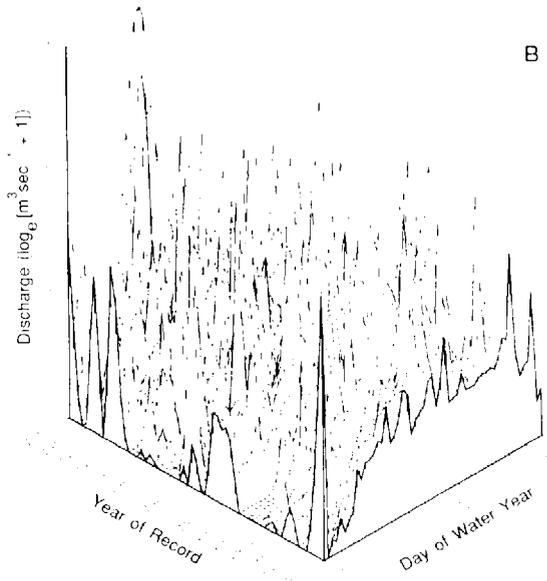
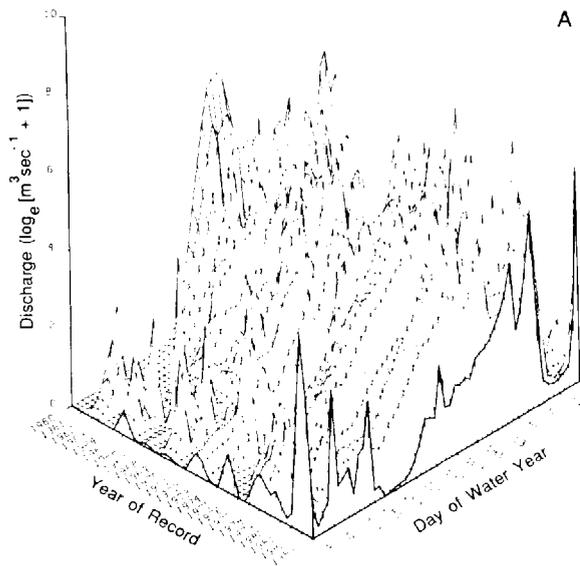
long-term flow regimes (including disturbance) from short-term hydrological observations are inadvisable.

No standard methodology for ecologically relevant characterization of streamflow data currently exists, although some techniques that describe the range and temporal distribution of flow have been proposed (e.g., Resh and others 1988, Poff and Ward 1989). Poff and Ward (1989) evaluated ecologically relevant flow characteristics for 78 streams across the United States using long-term, daily mean discharge records. Criteria were developed for detecting hydrologic disturbance (intermittent flows and flows exceeding an index of bankfull discharge), and patterns of hydrologic similarity among the streams were examined statistically based on measures of flow variability and disturbance regimes. At ecologically relevant temporal scales (e.g., multiannual and less), a wide range of among-stream variability and predictability in flow was found. Similarly, disturbance regime (frequency, predictability, duration, timing) varied among streams. With cluster analysis, streams were grouped into one of nine categories, which demonstrated some expected geographic separation. However, some geographically proximate streams did vary hydrologically, suggesting caution with regard to making broad-scale regional extrapolations.

Figure 3 shows the dynamic temporal variability in streamflow for a group of nonrandomly selected streams from six of the nine categories proposed by Poff and Ward (1989). Extremes in annual conditions, characteristic rates of change, trends in seasonal contingency, and within- and among-year variation in flow are revealed. Many of the streams illustrated in Figure 3 have fundamentally different flow regimes, which, in conjunction with climatically constrained thermal characteristics and geologically constrained substratum characteristics, presumably contribute to correspondingly different physical templates for their respective biotas.

The methods of Poff and Ward (1989) provide a technique for roughly estimating temporal distribution of physical streamflow disturbances where long-term daily flow data are available. Beyond that, systematic

Figure 3. Streamflow histories based on long-term, daily mean discharge records for six gauged stream stations showing within- and among-year temporal flow variability. Year of record is water year, 1 October–30 September, and discharge is \log_e ($\text{m}^3\text{sec}^{-1} + 1$). Stream category designations are from Poff and Ward (1989) to which reference should be made for additional details. **(A)** “Intermittent flashy” Sycamore Creek, Arizona, USA (USGS station 09510200); **(B)** “harsh intermittent” Dry Creek, Oklahoma, USA (07213000); **(C)** “mesic groundwater” Augusta Creek, Missouri, USA (04105700); **(D)** “perennial flashy” Satilla River, Georgia, USA (02226500); **(E)** “snowmelt” Colorado River, Colorado, USA (09010500); **(F)** “winter rain” South Fork of the McKenzie River, Oregon, USA (14159200).



attempts to couple temporal flow patterns with corresponding thermal characteristics are needed to describe the temporal distribution of the physicochemical "signal" (see Figure 2) for particular lotic settings. Moreover, explicit incorporation of substratum characteristics (e.g., size distributions of substrata, including occurrence of refuges) is needed to provide detailed information on habitat stability and quality, important mediators of the actual effect a particular physicochemical variability regime will have in a given lotic setting.

Biotic Responses to Anthropogenic Disturbances

One general effect of human modification of ecosystems is alteration of the temporal regime of natural variation and disturbance (Urban and others 1987). In lotic systems, many anthropogenic disturbances alter temporal pattern of environmental variability (e.g., thermal constancy below hypolimnetic release dams, high frequency flow fluctuations below hydroelectric dams, nutrient inputs from point and nonpoint sources). These anthropogenic disturbances may exceed tolerance thresholds for certain biota (e.g., lethal thermal releases), although they do not necessarily represent novel physical or physiological stressors. The release of toxic substances into waterways, however, typically introduces novel physiological stressors to the biota in the receiving stream. Organisms must attempt to detoxify these substances via existing physiological pathways (Levins 1968, Fisher 1977). These stressors often prove biochemically intractable and result in substantial morbidity and mortality.

The extent to which different types (novel vs non-novel) of anthropogenic disturbances affect ecological process and pattern in receiving lotic systems has been established in a general way (e.g., Cairns and others 1971). The present general theory of biotic response is based largely on the assumptions of equilibrium, deterministic (i.e., predictable) theory of biotic organization (see Lake 1985 for a critique). Allowance must be made, however, for the likelihood that biotic response to disturbance will vary in a substantial manner among receiving systems, depending on historical patterns of natural environmental variability and disturbance. Such a history-dependent framework has long been proposed for estuarine response to disturbance (Cope land 1970) and is, to some degree, implicit in the recent regionalization approaches to aquatic resources management in streams (see Hughes and others this volume).

Theory suggests that lotic populations and commu-

nities from more naturally variable and disturbed systems should respond less dramatically than those from less variable environments to nonnovel (Sanders 1969, Slobodkin and Sanders 1969, Holling 1973) and perhaps novel (Levins 1965, 1968) disturbances because species inhabiting unstable environments are adapted to varying environmental conditions and high rates of mortality. Thus, relatively greater resistance and persistence (*sensu* Connell and Sousa 1983) can be *hypothesized* to characterize biota from more variable and disturbed lotic environments.

Several experimental and comparative studies from the marine literature indicate that organisms from variable environments are more persistent when confronted with both natural and novel stressors than are those from more constant habitats. The mechanisms involved can be placed into four non-mutually exclusive categories: behavioral, physiological, life history, and genetic. For example, Boesch and others (1976) found that estuarine benthic communities from more constant salinity habitats showed poor persistence following nonnovel hurricane-induced disturbance (salinity reduction) relative to fauna from nearby variable salinity habitats. Similarly, communities from more variable salinity habitats were found to persist more successfully under organic pollution (Rosenberg 1973). A few studies bear on novel stressors. Hyland and others (1985) experimentally added fuel oil with toxic constituents to sediments from relatively constant and inconstant infaunal habitats. The community from the more variable habitat exhibited greater persistence with respect to, and recovery from, the simulated oil spill. Similar findings in marine macrobenthic communities were noted by Boesch and Rosenberg (1981) for toxic pollutants. Fisher (1977) showed that clones of certain phytoplankton species from estuarine populations were more resistant (maintained higher growth rates) than were clones from oceanic populations when experimentally subjected to a novel chemical (PCB) stressor. Tedengren and others (1988) compared the resistance of two species of gammarid isopods to additions of diesel oil and cadmium and found respiration rate (a correlate of resistance) of the "physiologically broad-niched" species less affected than that of the more stenotopic species. Individual behavioral mechanisms that allow species to minimize environmental stresses in variable environments may contribute to similar avoidance of some kinds of anthropogenic disturbances. Such behavior in lotic organisms inhabiting variable environments has been documented (e.g., Martin and Gentry 1974, Meffe 1984, Matthews 1987).

Fisher (1977) explored the physiological basis for

his observations on responses of phytoplankton to PCBs. He suggested that, because pelagic algae live in predictably (i.e., constantly) nutrient-poor waters, selection has acted to bring their membrane-bound active transport systems into more direct contact with the external environment to reduce energetic cost of nutrient acquisition. The pelagic "specialists" are thus more vulnerable to chemical disturbance than their estuarine counterparts. Greater physiological eurytopy among individuals in a population (or species) can increase the tolerance ranges for novel toxins that exert stress along some physiological pathway(s) for which the individuals are already broadly tolerant. For example, tolerance to anoxia could enhance tolerance to exotic cytochrome *c* poisons (Levins 1968). However, physiological eurytopy might not provide this advantage to populations occurring at the margins of a species range, where individuals may already be at the limits of their physiological tolerance ranges (see Tedingren and others 1988). The evidence for increased thermal tolerance for lotic fishes from more variable environments (e.g., Matthews and Styron 1981, Feminella and Matthews 1984, Matthews 1987) suggests that physiological homeostatic responses may indeed be more fully developed under increasing environmental variation in streams.

Life history traits enhancing survival in variable environments have been observed for lotic insects (Siegfried and Knight 1977, Vepsäläinen 1978, Gray 1981) and for fish (John 1963, Harrell 1978, Matthews 1987, Schlosser 1987). "Opportunistic" life history characteristics also can contribute to species persistence and recovery (e.g., Boesch and Rosenberg 1981, Hyland and others 1985). However, for high initial resistance to disturbance, other mechanisms (e.g., physiological tolerance) must also be involved.

Finally, populations from more variable or stressful habitats may possess relatively more variable phenotypes and genotypes, the presence of which contributes to long-term persistence in the unpredictable environment (Levins 1965, 1968, Grassle and Grassle 1974, Danks 1983). Some empirical evidence exists for increased genetic variation in populations from relatively more variable environments (Powell 1971, Koehn and others 1980, Zimmerman 1984, Groeters and Dingle 1987, Quattro and Vrijenhoek 1989, but see Futuyama 1986). The presence of extreme phenotypes and/or greater population genetic variability should increase the likelihood that disturbances, including physiologically novel ones, will be survivable by at least some individuals. Insect resistance to novel toxins such as DDT demonstrates the potential for adaptation to novel stressors. That "opportunistic"

species tend to develop resistance most quickly (Georghiou 1972) is consistent with the hypothesis that populations occurring in variable environments possess greater adaptive potential to novel stressors. Anthropogenic disturbances of varying magnitude and frequency can be conceptually viewed as contributing to the composite environmental signal in Figure 2. In this context, disturbances that cause the signal to exceed species' tolerance limits lead to local extinction. Disturbances that occur coincidentally with periods of low physical or physiological stress (low-magnitude signal) or with resistant life stages would be less directly damaging (cf. Wallace and others this volume, Resh and others 1988).

Summary and Research Needed

Appropriate spatial and temporal scales are required to detect the effects of disturbance on a given biological response variable. In general, high-frequency biological phenomena (e.g., behavior, physiological acclimation) are appropriate for assessing recovery potential from disturbances of small spatial extent or of short temporal duration (see Figure 1). Behavioral or physiological resistance (often the subject of toxicological studies) generally requires a small temporal scale. Changes in foraging activity or respiratory acclimation can be observed in a matter of hours, but detection of altered reproductive behavior or physiology could require a temporal scale approaching the organism's lifetime. Lower-frequency phenomena such as population or community persistence would be appropriate for large spatial disturbances (e.g., clear-cutting), which will result in disruption of all hierarchical habitat levels down to the microhabitat scale (e.g., Gurtz and Wallace 1984). Indeed, large-scale anthropogenic disturbances may alter the nature of the physical habitat template itself. For example, dramatic changes in land use practices can alter sediment and woody debris inputs and/or outputs and precipitation-runoff relationships, in turn affecting channel morphology and microhabitat distribution and persistence, thereby imposing new physical environmental constraints on the resident biota, some of which may subsequently be "filtered" from the system. Extensive disruption of many system variables (e.g., temperature, runoff, nutrient budget) may overload the available response potential of many resident populations and push the system into another "domain" from which recovery may not be possible (cf. Holling 1973).

The introduction of novel physiological or lethal nonnovel stressors to lotic systems generally alters the natural small-fast to large-slow gradient by reducing

Table 1. Summary of relative ecological recovery time (to arbitrary end point) and biological recovery mechanisms as related to type and spatial extent of disturbance and to degree of natural background spatiotemporal heterogeneity^a

Disturbance characteristics	Spatial extent	Example	Relative recovery time	Biological recovery mechanisms
I. Natural disturbance				
	Small	Spate	Very fast ^b	Behavioral avoidance, recolonization; increased growth among survivors Population, community adjustments to new template; species migrations
	Large	Watershed fire	Slow ^b	
II. Anthropogenic disturbance				
A. Nonnovel				
1. Acute				
a. Sublethal	Small	Thermal point source	Very fast ^b	Behavioral, physiological avoidance; rapid recolonization Behavioral avoidance; rapid recolonization
b. Lethal	Small	Thermal point source	Fast ^b	
2. Chronic				
a. Sublethal	Small	Thermal point source	Fast ^b	Physiological acclimation
	Large	Erosion nonpoint source	Slow ^b	Population, community adjustment
b. Lethal	Small	Thermal point source	Very slow ^b	Selection for increased physiological tolerance
	Large	Channelization	Very slow ^b	Population, community adjustments to new template; species migrations
B. Novel				
1. Acute				
a. Sublethal	Small	Short-lived toxicant	Fast ^b	Physiological acclimation; behavioral avoidance; recolonization Physiological acclimation; behavioral avoidance; recolonization
	Large	Short-lived toxicant	Slow ^b	
b. Lethal	Small	Short-lived toxicant	Slow ^b	Recolonization
	Large	Short-lived toxicant	Very slow ^b	Recolonization; selection for tolerant genotypes
2. Chronic				
a. Sublethal	Small	Residual toxicant	Slow ^b	Physiological acclimation; colonization by tolerant genotypes Physiological acclimation; colonization by tolerant genotypes
	Large	Residual toxicant	Slow ^b	
b. Lethal	Small	Residual toxicant	Very slow ^b	Regional recolonization by rare resistant genotypes
	Large	Residual toxicant	Very slow	Regional recolonization by rare resistant genotypes

^aRelative recovery times are expressed relative to other examples in the group with the same arabic numeral and should be compared to the recovery times for natural disturbances of similar spatial extent.

^bIndicates faster expected relative recovery time for systems with greater historical spatiotemporal heterogeneity.

response time for recovery (Table 1). The result is a shift toward population- and community-level processes and patterns as the appropriate ecological scale

of response following such disturbance. However, in some instances it may be possible to use high-frequency biological data to assess large-scale spatial dis-

turbances. The correlation between caddisfly net-building behavior and species diversity in some polluted streams is promising in this regard (Petersen and Petersen 1983, 1984).

In almost all cases of anthropogenic disturbance, it is *hypothesized* that systems having greater historical spatial and temporal heterogeneity will express greater persistence, resistance, and rate of recovery relative to less variable systems (Table 1). This is because biotic recovery is effected through individual and population behavioral, physiological, life history, and genetic mechanisms, all of which are influenced to some extent by historical patterns of temporal and spatial heterogeneity (i.e., the physical habitat template). However, the prediction of precise recovery trajectories following disturbance depends on two further considerations. First, measures of ecological performance in the face of anthropogenic disturbance must be separable from natural variation in ecological dynamics from year to year (cf. Stewart-Oaten and others 1986). Unfortunately, the natural range of environmentally variable parameters (both biotic and abiotic) is rarely known because of the paucity of long-term studies (Likens 1983, Schindler 1987). Second, successful prediction of recovery is dependent on definition and can range from the qualitative (e.g., species persistence) to the quantitative (e.g., return to pre-disturbance population densities). Without long-term ecological–environmental data, a strictly quantitative expectation would appear unrealistic. A goal of qualitative recovery (e.g., species persistence) would serve to maintain system relationships and perhaps provide more achievable management guidelines (Holling 1973, Connell and Sousa 1983).

Several important questions need to be addressed in order to relate historical environmental heterogeneity to biotic recovery potential. Are ecological processes and patterns in historically variable lotic environments more resistant and persistent with respect to anthropogenic disturbance than those from less variable systems? Does the importance of timing of the disturbance vary among systems as well? Are species or populations from historically variable environments more resistant to toxic novelties? These questions could be addressed experimentally *in situ* either by whole-stream manipulation or, alternatively, by subjecting organisms from differentially heterogeneous lotic systems to standard toxicity testing. Care must be taken not to select organisms or lotic systems that have a disturbance history, because chronically exposed populations already may have undergone several generations of selection for resistant genotypes (cf. Swarts and others 1978, Kaufman 1982, Blanck and Wäng-

berg 1988, Klerks and Levinton 1989). In any event, the present method of using nonnative or nonlotic bioassay organisms for stream toxicity testing (US EPA 1985) cannot answer these questions.

Can data that exist for disturbance at one scale (e.g., microhabitat) or one level of biological response (e.g., physiological acclimation) be translated to higher levels or are there discreet “domains of scale” (*sensu* Wiens 1989) across which one may not generalize? How dependent are such linkages to spatial heterogeneity across levels? Does recovery potential have a detectable regional component that reflects large-scale differences in geomorphology, temperature, and stream-flow characteristics? If so, how does one define the boundaries between such regions? How does one identify potentially important, fine-scale differences in local conditions (e.g., precipitation–runoff patterns, contribution of groundwater, thermal regime, etc.) within regions? Answers to these questions will require intensive and extensive basic research on the relationship between environmental variation and lotic community structure and function (see Resh and others 1988, Poff and Ward 1989, other papers in this volume). Studies examining many spatial levels simultaneously are needed for many different “regions,” where study streams are chosen with explicit reference to their physical habitat templates. Although streams with sufficient hydrologic and thermal data should be preferentially considered for selection, techniques for evaluating hydrologic properties in ungauged watersheds (e.g., Cunnane 1988) might allow sites lacking hydrologic data but having historical biological data to be examined as well. The cataloging of hydrologic, thermal, and substratum and/or geomorphological characteristics for a variety of representative lotic systems would provide a quantitative framework for predicting recovery from natural and anthropogenic disturbance across broad geographical scales. Coupled with biological data, this framework would serve both to advance an important research area and to facilitate sound site-specific management decisions.

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