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Author(s): Vincent H. Resh, Arthur V. Brown, Alan P. Covich, Martin E. Gurtz, Hiram W. Li, G. Wayne Minshall, Seth R. Reice, Andrew L. Sheldon, J. Bruce Wallace and Robert C. Wissmar
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The role of disturbance in stream ecology*

VINCENT H. RESH[1], ARTHUR V. BROWN[2], ALAN P. COVICH[3],
MARTIN E. GURTZ[4], HIRAM W. LI[5], G. WAYNE MINSHALL[6],
SETH R. REICE[7], ANDREW L. SHELDON[8], J. BRUCE WALLACE[9],
AND ROBERT C. WISSMAR[10]

[1] *Department of Entomology, University of California, Berkeley, California 94720 USA*
[2] *Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701 USA*
[3] *Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019 USA*
[4] *U.S. Geological Survey, P.O. Box 2857, Raleigh, North Carolina 27602 USA*
[5] *U.S. Fish and Wildlife Cooperative Research Unit, Oregon State University,*
Corvallis, Oregon 97331 USA
[6] *Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209 USA*
[7] *Department of Biology, University of North Carolina,*
Chapel Hill, North Carolina 27514 USA
[8] *Division of Biology, University of Montana, Missoula, Montana 59812 USA*
[9] *Department of Entomology, University of Georgia, Athens, Georgia 30602 USA*
[10] *Center for Streamside Studies, College of Forest Resources and Fisheries Research Institute,*
University of Washington, Seattle, Washington 98195 USA

Abstract. We define disturbance in stream ecosystems to be: any relatively discrete event in time that is characterized by a frequency, intensity, and severity outside a predictable range, and that disrupts ecosystem, community, or population structure and changes resources or the physical environment. Of the three major hypotheses relating disturbance to lotic community structure, the dynamic equilibrium hypothesis appears to be generally applicable, although specific studies support the intermediate disturbance hypothesis and the equilibrium model. Differences in disturbance frequency between lentic and lotic systems may explain why biotic interactions are more apparent in lakes than in streams.

Responses to both natural and anthropogenic disturbances vary regionally, as illustrated by examples from the mid-continent, Pacific northwest, and southeastern United States. Based on a generalized framework of climatic–biogeochemical characteristics, two features are considered to be most significant in choosing streams for comparative studies of disturbance: hydrologic regimes and comparable geomorphology. A method is described for quantifying predictability of the hydrologic regime based on long-term records of monthly maximum and minimum stream flows. Different channel forms (boulder and cobble, alluvial gravelbed, alluvial sandbed) have different responses to hydrologic disturbance from spates. A number of structural and functional components for comparing disturbance effects within regions and across biomes are presented. Experimental approaches to studying disturbance involve spatial-scale considerations, logistic difficulties, and ethical questions. General questions related to disturbance that could be addressed by stream ecologists are proposed.

Key words: disturbance, streams, geomorphology, hydrology, predictability.

About 2500 years ago the Greek philosopher Heraclitus presented an analogy regarding the dynamic flux of human life: "You cannot step twice into the same river" (Krumholz and Neff 1970). To stream ecologists this phrase has literal truth; spatial and temporal changes in lotic systems provide a shifting mosaic of abiotic and biotic conditions. An obvious source of this variability is the disturbance caused by rapid increases (as in spates) in the volume of water passing a point in time and the accompanying movements of substratum that result from high discharge. However, prolonged low discharge (as in droughts) and anthropogenic factors

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(which can range from abiotic stresses such as site-specific effluent releases to biotic stresses such as species introductions) may also act as disturbances.

The objectives of this paper are to: define disturbance as it applies to stream systems; review theories of disturbance as they relate to lotic communities; examine geographical differences among disturbance effects; discuss criteria for choosing streams for comparison of disturbance effects; outline the biotic and abiotic components to be measured in such comparisons; describe experimental approaches that may be used for investigating disturbance; and finally, present questions related to disturbance that can be addressed by stream ecologists.

Disturbances can vary greatly over temporal and spatial scales and have traditionally been viewed as uncommon, irregular events that cause abrupt structural changes in natural communities, thus moving them away from static, near-equilibrium conditions (Sousa 1984). This definition is not useful for streams during the relatively short terms of most studies because these systems may not be at equilibrium (Fisher 1983). As an alternative, we used a general definition of disturbance from Pickett and White (1985): a disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure, and that changes resources, availability of substratum, or the physical environment. In applying this definition, we shall be emphasizing quantification of the characteristics of the event (e.g., a spate) rather than characteristics of the response (e.g., changes in community or population structure resulting from the spate) as being the measure of disturbance. Use of the latter approach, which could be expressed as, for example, a loss of ≥50% of individuals in a community, is being considered for use in some biological monitoring programs for assessment of water quality (Jackson and Resh 1988).

We modified the Pickett and White definition to include only those events characterized by a *frequency* (rate of occurrence of events, as in recurrence intervals of spates) and *intensity* (physical force of the event per time, as in force ten gale, various seismic measurements, and flood discharge) that are outside a predictable range. Predictability must be considered in the definition of disturbance because organisms are adapted to predictable seasonal fluctuations of discharge, temperature, dissolved oxygen, etc., although this question itself deserves more research. In any event, when measured by the impact on the community, we feel that it is the unpredictable event that typically constitutes a disturbance.

Our definition of disturbance is graphically illustrated using discharge as an example (Fig. 1). Seasonal variability in the flow regime influences whether a particular rise in stream discharge would be considered a disturbance. In Figure 1, discharge (solid line) and peak flows (arrows a–d) are presented for two hypothetical streams: one in the Rocky Mountains, western USA (Fig. 1A); the other a Piedmont stream in the southeastern USA (Fig. 1B). Peak flows (a) and (c) are within the normal seasonal variation for the streams shown (i.e., they are not outside the arbitrarily chosen ±2 standard deviations of predictability, which are represented by dashed lines). In contrast, peak flows (b) and (d) are "unusual" events (i.e., they are outside ±2 standard deviations) and would be disturbances. Note that (c) and (d) are identical discharges but, using our definition, (c) is not a disturbance whereas (d) is a disturbance (Fig. 1).

There is a problem, however, with a definition of disturbance that includes statistical predictability (such as ±2 standard deviations). With this definition all streams would have the same frequency of disturbance, i.e., the 5% of the events that fall outside the two standard deviations. As a result, in a river with near constant discharge a "±2 SD" discharge would not be very different from mean conditions. This change in discharge may have a negligible effect on the ecosystem, yet it would still be defined as a disturbance. Many discussions of disturbance have been hindered by the lack of a workable definition of this term. Although we all agree that a departure from predictability should be included in the definition of disturbance, the two standard-deviation range of predictable conditions presented in Figure 1 is used only to provide a general framework for our discussion of this topic; we are not advocating that this specific criterion be used generally. Later we present an alternative quantitative method for assessing predictability in streams.

As expected from a paper with ten authors, there is a range of opinions on almost every topic. Most divergence among us probably occurs in the applicability of different disturbance theories to stream ecology; most congruence probably occurs in the importance of hydrologic regimes and comparable geomorphology as key characteristics in choosing study streams. When appropriate, alternative viewpoints have been expressed. Throughout this review, various approaches will be suggested for determining the role of disturbance in streams, and how this role might vary on a regional or a worldwide basis. We feel that the approaches proposed are applicable to: (1) basic research in the response of streams to natural phenomena (e.g., extremes in flow and temperature); (2) cross-biome comparisons of stream characteristics; (3) local, regional, or continental stream classification schemes for resource management or other purposes; (4) applied studies of the response of streams to anthropogenic disturbances; and (5) long-term monitoring of ecological phenomena in streams.

Disturbance theory and its applications in stream communities

Disturbance is a concept long recognized in ecology, but only recently has it gained prominence as a central theme in community organization. Disturbance and its consequences challenge a dominant paradigm in ecological theory, which assumes that systems are at equilibrium (McIntosh 1985, 1987). Historically, the null hypothesis for community structure has been an equilibrium model that assumed a constant environment. This view was pervasive because of the relative simplicity of mathematical relationships based on the concept of equilibrium. The roots of this equilibrium model of communities stem from the Lotka-Volterra models of competition and predator–prey interactions derived from many studies of population ecology (Kingsland 1985). The conflict between density dependence and density independence that split ecology into competing camps in the 1950s was really a further manifestation of the dominance of equilibrium models (e.g., Andrewartha and Birch [1954] on one side and Nicholson [1954, 1958] among many others on the opposite side). Later proponents of Lotka and Volterra's equilibrium model extended the concept to include the theory of island biogeography (Cody and Diamond 1975, MacArthur 1972, MacArthur and Wilson 1963, 1967, Williamson 1981, Wilson 1969). This model typically assumes that the environment is quasi-constant and that no disturbances occur during the critical life stages of the organisms in question. However, recent studies on disturbance cast at least some doubt on the assumptions of equilibrium in natural ecosystems (Pickett and White 1985).

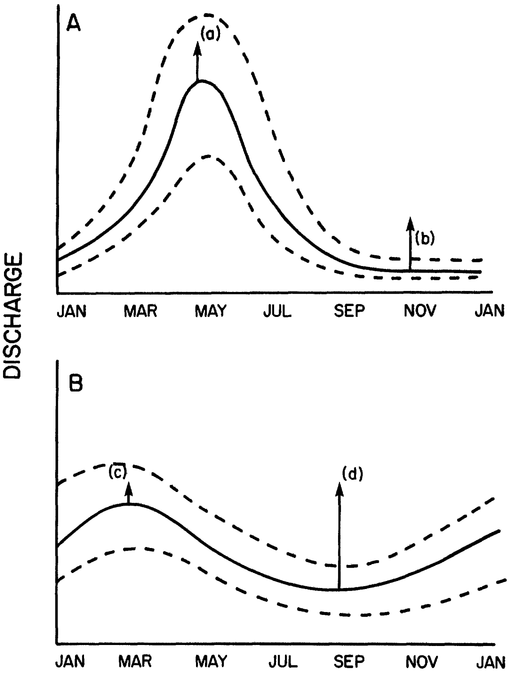

FIG. 1. Two hypothetical streams in (A) the Rocky Mountains, (B) the Piedmont in the southeastern USA. Peak flows are represented by arrows a–d. Solid line is median discharge value; dashed lines are ±2 standard deviations. See text for explanation.

The above-mentioned models assume a primacy of biotic interactions as determinants of community structure "all else being equal." This phrase implies that the environment remains "constant" or that the species are adapted to some degree of variability. In the absence of disturbance, a community is produced as the direct result of competitive, mutualistic, and trophic interactions among species. High species diversity has often been related to spatial heterogeneity or predator-mediated coexistence. Some models included variability in abiotic factors as a means for avoidance of competitive displacements (Richerson et al. 1970) but the debate over the existence and importance of equilibrium-based dynamics continues (e.g., Hutchinson 1978, Petersen 1975).

The next stage in conceptual development of disturbance theory was the intermediate disturbance hypothesis, which was proposed and developed by Connell (1978) to explain the high species diversity in tropical rainforests and coral reefs. Others had stated parts of the concept in various terms (Grime 1979) but it was Connell's article that catalyzed the current resurgence of interest in non-equilibrium models of disturbance and community structure. The intermediate disturbance hypothesis presumes a competitive hierarchy of species. In the absence of disturbance, superior competitors will eliminate inferior ones, reducing the species richness of the system. The model also presumes that the superior competitors are more efficient occupiers of space (resident species). If disturbances are too frequent or of too great a magnitude, the resident competitors will be eliminated and colonizing species (inferior competitors) will dominate the system. The absence of the resident species also lowers species richness. Under a disturbance regime that is intermediate in frequency and intensity, resident species will persist in the system along with a continuing supply of colonizing species that exploit the disturbed areas. In this manner, intermediate disturbance leads to maximum species richness.

A second important role for disturbance was suggested by Huston (1979) who discussed a "dynamic equilibrium" model. He regarded community structure as a tradeoff between growth rates, rates of competitive exclusion, and frequency of population reductions. Huston suggested that if the recurrence interval of disturbance was shorter than the time necessary for competitive exclusion, then species that were poorer competitors would persist in the system. This would serve to increase species richness, unless disturbance was severe or frequent enough to eliminate those with long life cycles. Huston concluded that diversity is determined not as much by the relative competitive abilities of the competing species as by the influence of the environment on the net outcome of species interactions.

Elements of each of these models have been applied to stream communities (e.g., Peckarsky 1983, Ward and Stanford 1983). The equilibrium model and its island biogeographic corollary was used by Minshall et al. (1983, 1985b) and by Minshall and Petersen (1985). They argued that if the period between spates in streams was long enough, then equilibrium conditions would prevail, replete with the dominance of density-dependent processes. They contrasted this rarely disturbed community with "opportunistic" community types associated with frequent disturbances.

In high elevation mountain streams such as those in the Salmon River system in Idaho, USA, that have been studied by Minshall and his colleagues, the spring spate, powered by snowmelt, is so predictable that, by our definition, it is not really a disturbance. Rather, it is a regular feature of that system. For the rest of the year, the stream flow results from relatively constant water sources (springs, glacial melting) so that a quasi-equilibrium can be established. This scenario was well documented by Hemphill and Cooper (1983) for one interspecific interaction in a California stream where larvae of the caddisfly *Hydropsyche oslari* are competitively superior to larvae of the black fly *Simulium virgatum*. However, *S. virgatum* persists in the system by exploiting space vacated by *H. oslari* during the spring spates. The black fly, being an opportunistic colonizer, quickly invades. As the water levels drop and stabilize (creating nearly equilibrium conditions), *H. oslari* again monpolizes the rock faces.

Another example comes from studies of trout in a California stream. Seegrist and Gard (1972) reported that brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*) are competitors. Brook trout spawn in the autumn and dominate in the absence of winter spates because earlier hatching confers a size advantage over spring-spawning rainbow trout. Winter spates disrupt brook trout redds and eggs; conversely spates in late spring exacerbate poor conditions for rainbow trout.

In runoff-fed streams (i.e., deciduous forest, prairie, some rainforest, and Piedmont and coastal plain streams) discharge is primarily a function of rainfall so that spates and droughts are less predictable. For example, in New Hope Creek, North Carolina (Reice, unpublished data), in Blue Beaver Creek, Oklahoma (see below), and in the Sonadora River, Puerto Rico (Covich and McDowell, unpublished data), major storms can generate spates within hours and during any season of the year. Such frequent disturbances conform to Huston's (1979) model. Reice

(1985) argued that frequent spates kept the macroinvertebrate community in perpetual disequilibrium, responding to the latest spate or drought. High species richness was attributed to disturbance that prevented competitive exclusion. Another example of this disequilibrium is given by McAuliffe (1984) who showed that the caddisfly *Leucotrichia pictipes* was prevented from developing competitive monopolies by spate-driven rock tumbling. This prolonged nonequilibrium may especially be true in streams located in anthropogenically modified catchments.

Grossman et al. (1982) argued that disturbances serve to structure fish communities in a nonequilibrium mode, and Meffe (1984) demonstrated how disturbance allows the Sonoran topminnow (*Poeciliopsis occidentalis*) to persist with an exotic predator, the mosquitofish (*Gambusia affinis*). The topminnow has innate behaviors that allow it to survive during flash floods whereas the exotic predator does not, and consequently is eliminated. In systems that have a low disturbance frequency, *Gambusia* eliminates the topminnow in one to three years through predation.

Use of the intermediate disturbance hypothesis (Connell 1978) has been advocated for stream ecosystems (Stanford and Ward 1983, Ward and Stanford 1983). In research that supported this hypothesis, Robinson and Minshall (1986) manipulated disturbance frequency by turning over experimental brick substrates at intervals of 0, 3, 9, 27, and 54 days. Invertebrate species richness and density declined as disturbance frequency was increased. The effects on H′ diversity were variable (no effect in the autumn; reduced H′ at high-disturbance frequency in the summer). This study produced some data that are consistent with the intermediate disturbance hypothesis, notably the reduced species richness at high frequencies of disturbance. In contrast, Reice (1984) found that species richness and H′ diversity did not respond to minor rock tumbling disturbances. Furthermore, colonization by rare species did not increase in the more disturbed patches (Reice 1985), as predicted by that model. Reice inferred that the intermediate disturbance hypothesis did not apply to streams because of the lack of a general demonstration of predictive competitive displacements in streams (however, see Hart 1981, 1983, 1985, 1987, and Lamberti et al. 1987 for examples of competitive interactions among grazers in streams).

Of the three major hypotheses about the role of disturbance in lotic community structure (i.e., the equilibrium model, the dynamic equilibrium model, and the intermediate disturbance hypothesis), the dynamic equilibrium model seems to be the most generally applicable hypothesis. However, there is some disagreement as to whether the limited pool of available data supports it (e.g., Minshall et al. 1985b). The key to this model, as applied to stream communities, is that the recurrence interval of disturbance events (spates, droughts, anthropogenic inputs, etc.) is shorter than the time necessary for competitive or predator–prey interactions to lead to the elimination of species. However, the remarkable faunal diversity of many streams still demands explanation. Since natural disturbances occur less often in the lentic benthos, differences in disturbance frequency may contribute to the high species richness of stream benthos when compared with most lakes and ponds. Likewise, disturbance frequencies may explain why biotic interactions seem to be much more evident in lentic than lotic communities (but for examples where both "stochastic abiotic" and "deterministic biotic" processes are coacting, see Power et al. [1988] in this issue, Karr and Freemark [1985], and Schlosser [1985]). The intermediate disturbance hypothesis (Connell 1978) also has applicability, but its acceptance in stream ecology is contingent upon further demonstration of competitive hierarchies and ordered dominance sequences among stream organisms. Most of us feel that the null hypothesis of a constant, disturbance-free environment can be rejected in most stream ecosystems but some spring-fed streams seem to have communities that fit these equilibrial predictions of biotic interactions (Minshall et al. 1985b).

Geographical patterns of disturbance: natural activities

Given a theoretical basis for viewing disturbance in stream communities, are there general patterns of disturbance effects that apply to streams in different regions or even to all streams within a region? In an attempt to generate hypotheses related to this idea, we initially constructed a disturbance matrix that incorporated the spatial extent, temporal scale, and severity (i.e., the impact on organisms) of various disturbances on stream ecosystems for three well-studied regions of the United States: mid-continent, Pacific northwest, and southeast. However, identification of general patterns was not possible for several reasons: (1) disturbances differ greatly among regions and among geological provinces within regions; (2) events that constitute a disturbance in one region may, in another, be considered a regular phenomenon that is critical to stream ecosystem function, e.g., high rainfall and damaging spates in high-gradient streams vs. large lowland rivers that depend on river–floodplain interactions (see Lowe-McConnell 1988 and Welcomme 1988 in this issue); (3) some events occur with such low frequencies in certain regions that it is questionable whether they should be considered in all regions; e.g., vulcanism is far more important in the Pacific northwest (Bretz 1964, Bretz et al. 1956, Li et al. 1987) than in the mid-continent and southeastern United States; and (4) data on the frequency, intensity, and severity of distinct events are generally lacking, even in well-studied areas of the United States.

Unusually high discharge was considered to be a natural phenomenon common to all areas. However, the impact of spates may vary considerably among regions and among provinces within regions. In high-gradient streams of all areas, spates may be devastating, resulting in massive slope failures, bank erosion, substrate scouring, and loss of habitat and biota. In contrast, large lowland rivers in the mid-continent and southeastern region have extensive forested floodplains, and have annual or seasonal flooding that may be beneficial (i.e., flood-induced nutrient and energy transfers between the river and floodplain, which may be critical for aquatic biota [Cuffney 1988]).

Drought can influence stream ecosystems in all regions as well. Drought has a direct influence on all inputs and outputs that are dependent upon discharge, e.g., dissolved and particulate organic matter (T. F. Cuffney and J. B. Wallace, University of Georgia, unpublished data). Animal and plant communities may be altered because of changes in wetted channel area. As stream biota become concentrated into smaller areas or isolated pools, predation by vertebrates (e.g., herons, raccoons) may increase in importance. In many areas, headwaters often become intermittent and even hyporheic flow through riffles can cease if the water table drops sufficiently low. The effect on biota of these habitats can be extreme and longterm (Resh 1982). On the Southeastern coastal plain, low-order (first through third) streams frequently cease flowing during the summer or are reduced to a series of isolated pools (A. C. Benke, University of Alabama, personal communication), and the species that inhabit such systems are very different from species in headwater streams fed by permanent springs.

Episodic natural events such as vulcanism and major earthquakes tend to occur with low frequencies (often centuries apart) in all regions; however, recent examples such as the New Madrid earthquakes of 1811 and 1813 and the 1980 eruption of Mt. St. Helens attest to their importance. For example, approximately 40% of the native fish fauna of Pacific northwest stream-systems can be anadromous, and some resident freshwater fishes are capable of limited salt water excursions. Li et al. (1987) speculated that this pattern resulted from repeated flooding (from 6 to 40 times) caused by the breaking of ice dams produced by retreating continental ice sheets (19,000–12,000 B.P., Bretz 1964, Bretz et al. 1956). Allen (1984) has expressed the energy released by these broached ice dams as equivalent to one hydrogen bomb exploding every 36 hours for 10 days! As a result of these significant changes, many fish species of the Pacific northwest have adapted to colonizing areas affected by glaciation. For example, as the continental glacier has retreated in Glacier Bay, Alaska, anadromous fish have been observed invading streams in that area (R. Garrett, U.S. Fish and Wildlife Service, personal communication; Milner 1987).

Besides the above-mentioned forces, several other factors can be disturbances in stream ecosystems, including fire (e.g., Minshall et al. 1981), beavers (e.g., McDowell and Naiman 1986), and snow and debris avalanches (J. R. Barnes, Brigham Young University, personal communication; G. W. Minshall, personal observation). The effects of these disturbances, however, have been less studied than the effects of flooding.

Geographical patterns of disturbance: anthropogenic activities

In the previous section we discussed how the effects of natural disturbance events vary regionally. Human activities have almost universally played an important role in shaping and disturbing stream ecosystems (Petersen et al. 1987, Resh and Grodhaus 1983); but how does the severity and relative importance of human impact on stream ecosystems vary across regions? Clearly, the impact of humans on streams can vary in spatial scale from affecting extremely localized microhabitats (e.g., displacement of an individual rock) to affecting large regions (e.g., acidic precipitation). The temporal span of these disturbances also can vary greatly, ranging from days (e.g., some toxins and localized removal of gravel and sand from streams) to centuries (e.g., dam construction, desnagging of large rivers, construction of levees). Mills et al. (1966) give an excellent account of the long-term human influences on the Illinois River.

Although the same anthropogenic disturbances may occur in all regions, their severity, frequency, and intensity may vary greatly even in local geographical areas. For example, in the John Day River Basin in northcentral Oregon, major anthropogenic disturbances ranked in descending order of impact include: (1) cattle grazing; (2) forestry and logging practices; (3) dredge mining; (4) beaver removal through trapping; (5) urban usage such as domestic consumption and sewage discharge; and (6) management practices involved with the restoration of riparian habitat and the use of poisons to remove undesirable fish species. Moving west to the Willamette River Basin, major anthropogenic influences would be ranked as: (1) agricultural practices; (2) urbanization and desnagging for barge commerce; (3) forestry practices; (4) beaver removal through trapping; and (5) introduction of exotic fish species. Finally, moving to the Coastal Range streams of the Pacific northwest, major anthropogenic disturbances would be ranked as: (1) forestry practices (e.g., clearcut logging), and concomitant activities including road building, creation of splash dams, and pesticide usage; (2) fish management practices; (3) urbanization and sewage outfalls, desnagging of streams, and modification of estuaries; and (4) agriculture, which includes dewatering of streams, dairy cattle usage, and practices that result in acceleration of stream bank erosion. These rankings are based on studies by Bottom et al. (1985), Hjort et al. (1981, 1984), Li et al. (1984), Murphy and Hall (1981), Murphy et al. (1981), Raymond (1979), Ryman and Stahl (1980), Sedell and Luchessa (1982), Swanson et al. (1982), Wendler and Deschamps (1955), and Winegar (1977).

In the southeastern United States, anthropogenic influences differ among the Appalachian, Piedmont, and Coastal Plain Provinces. In the Appalachian Mountains, heavy rainfall combined with dense forest cover gives rise to many clear streams, which serve municipalities, and manufacturing, recreational, and energy generation (hydroelectric) interests. These diverse demands on water resources, combined with forest management practices, place severe stresses on these streams. Major anthropogenic disturbances include: sewage and industrial effluents (e.g., Kondratieff et al. 1984, Kondratieff and Simmons 1982, Tarter 1976); clearcut logging (Silsbee and Larson 1983, Tebo 1955, Webster et al. 1983) and associated road-building (Lenat et al. 1981); mining practices (Tarter 1976), which often result in acid drainage problems (Samuel et al. 1978); dam construction; and potential susceptibility to acidic precipitation (Lynch and Dise 1985). In the southeastern Piedmont, major anthropogenic disturbances include: urbanization (Benke et al. 1981); channelization; agriculture and grazing; logging, including associated road construction (Lenat et al. 1975); and dam construction for hydroelectric generation, recreational use, and water storage. In low-gradient streams of the Southeastern Coastal Plain, major anthropogenic disturbances include: removal of woody debris from high-order rivers, a process that was begun in the early 1800s and has resulted in the loss of both invertebrate and fish habitat (Wallace and Benke 1984); extensive large-scale agriculture, which also has resulted in extensive deforestation (Odum and Turner 1987); logging, which on low-gradient flood plain and wetland forest since the early 1800s has occurred at the rate of 100,000 acres per year (Odum and Turner 1987), and hydroelectric projects. Dams and hydroelectric projects represent important disturbances in all regions of the Southeast. In Georgia, the surface area of land covered by impoundments increased by approximately 100 times between 1900 and 1980. By 1980, most of the pristine stream and river sites had been impounded (Odum and Turner 1987).

Factors influencing the effects of disturbance

A variety of factors may influence the intensity, frequency, and severity of a disturbance. For example, the geomorphology of a stream may determine the response of its biota to a disturbance such as sedimentation, in that some depositional habitats may be more susceptible to sedimentation than swift, shallow, high-gradient reaches (Gurtz and Wallace 1984, Moon 1939). In contrast, massive sedimentation, such as that resulting from the eruption of Mt. St. Helens, may obliterate almost all stream biota and drastically alter habitats.

Susceptibility to toxic agents varies with species. Because it is unlikely that any two communities within the same geographical area are constituted of equal proportions of the same species, it is equally unlikely that the community-level response will be the same for any one toxin. Likewise, the influence of acidic precipitation on stream biota will vary, depending on the composition of the biota and characteristics of local soil and underlying bedrock (Record et al. 1982).

The life cycles of the organisms that constitute a given community must also be considered in relation to the frequency and type of disturbance. In many cases, community structure may be strongly influenced by disturbance. For example, in two California coastal streams that are influenced by a Mediterranean-type climate (wet winters, dry summers) annual differences and similarities in the post-wet season benthic community have been associated with above-average, average, and below-average rainfall and discharge years (McElravy et al. 1989; Resh, unpublished data). Likewise, in warm desert streams of the southwestern United States where flash flooding (spates) may eliminate up to 95% of the insect abundance, species that inhabit these streams tend to have short life cycles and continuous emergence, which ensure rapid recolonization by adults from adjacent riparian areas (Fisher et al. 1982, Gray 1981, Gray and Fisher 1981). Prior exposure, and the frequency and type of disturbance, influence species composition and the response of a given community to the disturbing force. Without prior exposure there is no evolutionary basis (e.g., life history or physiological resistance [Wallace et al. 1986]) upon which either a specific or a community response can be framed.

Since disturbances vary with respect to type, frequency, and severity among and within regions, studies emphasizing effects of disturbance should concentrate on the following: (1) What factors influence community structure at local (reach, segment, and stream order) levels? (2) What factors influence community structure within different geologic provinces within regions? (3) Are there factors, such as local geomorphology, that influence community structure among regions? (4) Are there common adaptations and life history patterns within regions? (5) Do stream communities in different regions respond in a similar way to a given disturbance? These questions are next discussed in the context of choosing streams for inter- and intra-biome comparisons.

Choice of comparable study streams and components to be measured

To assess disturbance regimes in the context of factors that may control community structure and function in streams, we developed a schematic representation of stream's basic climatic-biogeochemical characteristics (Fig. 2).

In broadest terms, latitudinal regions with similar climates will have similar types of lotic systems, but numerous variants correspond to local differences in underlying rocks, topography, plants, and animals (e.g., Rohm et al. 1988). We can depict the climate of any lotic system as having three basic features: light and temperature regimes, atmospheric chemical cycles, and precipitation. The climate and geology of the region combine to control the hydrologic, geomorphic, and geochemical character of the system. The resulting fluvial geomorphic, chemical (both water and soil), and terrestrial features, along with local and regional land use (with timber harvest and road construction being two of many possible examples), influence biotic structure and function of the stream (Fig. 2).

Every lotic ecosystem has many levels of organization, for instance: (1) system size; (2) habitat structural characteristics (i.e., diversity, quality, quantity in terms of animal use); and (3) physicochemical and biotic compositional properties. The physicochemical properties of the third level of organization demonstrate how the levels can be further scaled, for example: coarse, fine, and colloidal inorganic particles; water chemistry; gaseous composition; coarse and fine particulate organic matter; and dissolved organic matter.

In choosing streams for comparison, it is best to minimize variation among as many of the

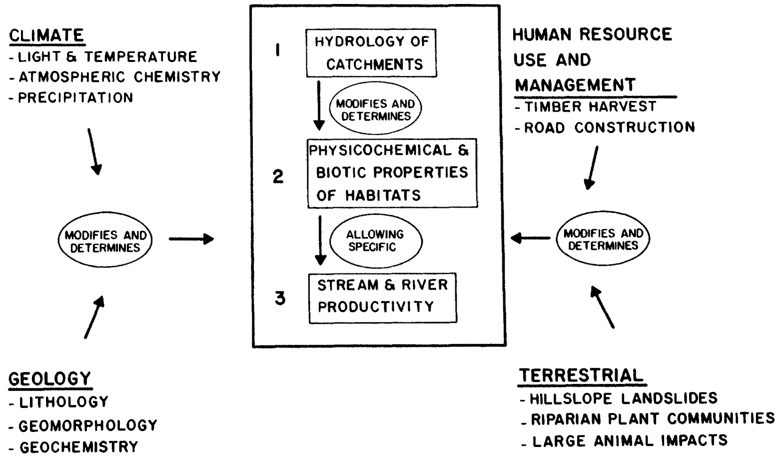

FIG. 2. A generalized representation of abiotic and biotic factors affecting stream productivity within a catchment.

features in Figure 2 as possible. However, we feel that two characteristics are most important: (1) comparable hydrologic regimes, in terms of frequency, intensity (both relative and absolute), and predictability of extreme flows; and (2) comparable geomorphology and substratum. In the next sections, approaches for comparing stream ecosystems based on these characteristics will be presented.

Once such study streams are chosen, what biotic components should be examined in making comparisons and examining disturbance effects? Structural and functional components that we view as essential are presented in Table 1. These focus on the biota as synthesizers of disturbance impacts and reflect sensitive and crucial ecosystem components.

Comparisons of standing crop biomass (e.g., per m^2) of the main ecosystem constituents (Table 1, component 1) may provide the most immediate and direct assessment of disturbance. Ideally, measurements should be made before and after quantified disturbance events but comparisons of mean annual standing crop values among frequently and infrequently disturbed streams in an array of climatic regions also would be valuable. To provide a complete picture of the influence of disturbance on the individual biotic and benthic organic matter compartments, simultaneous estimates of the import/export capacity cf. the water volume of each stream should be obtained through measurements of transport/drift (Table 1, component 2). We anticipate that in most situations, streams that are more frequently disturbed will show lower standing crop biomass than less frequently disturbed streams. Also, on both evolutionary and short-term time scales, a similar relationship should hold for the recent history of disturbance. That is, more recently disturbed sites will have lower standing crops than those that have not been disturbed for some time. Higher transport/drift rates in disturbed streams than in undisturbed ones could compensate for benthic standing crop losses or provide for rapid recovery following disturbance.

In contrast to the expected deleterious influ-

TABLE 1. Structural and functional components of the stream biota recommended for comparing disturbance effects on stream systems. See text for explanation.

1. Standing crop biomass (by group: algae, macrophytes, invertebrates, fish, benthic particulate organic matter)
2. Transport/drift (total dissolved organic carbon, total particulate organic carbon, invertebrates, fish)
3. Primary and secondary production
4. Taxonomic richness
5. Trophic-functional diversity
6. Nutrient-cycling functional dynamics
7. Patterns of life history tactics: reproductive, physiological, and behavioral responses
8. Size spectra
9. Biotic interactions (e.g., competition, parasitism)

ence of most disturbances on standing crops, some disturbances, especially those involving physical removal of individuals or nutrient enhancement, may be reflected in enhanced growth rates of the remaining organisms (Table 1, component 3); other disturbances (e.g., toxic substances) may have an inhibitory influence. For comparisons among stream systems, such effects are most readily and meaningfully made at the level of whole systems or representative component primary (Bott et al. 1985) and secondary production (e.g., Benke et al. 1984, Huryn and Wallace 1987; see also Benke et al. 1988 in this issue). Assessment of primary production should be done in such a manner that values for net ecosystem metabolism can be obtained for use in component 5. Thus, implicit in this recommendation is that measurements will be made in such a way that estimates of community respiration (also needed for component 5) will be obtained concurrently.

The response of a stream community to disturbance and its ability to recover are expected to be related to the diversity of its constituents, both structurally (taxonomic) and functionally (Table 1, components 4 and 5). Degree of recovery from a disturbance must be measured, at least in part, in terms of species richness (component 4). A stream with a diverse predisturbance biota should have more species available as potential recolonists for community recovery. However, if the spatial extent of the disturbance is large, more species would have to be restored to its community than to a community having initially low diversity (assuming that the disturbance left both communities with equally low numbers of species). Any differential influence of disturbance on the underlying food-base (autogenic vs. allogenic) should be reflected by measures of trophic-functional diversity (component 5). Such measures also would provide evaluation of the widely accepted (Cairns 1977), but untested, assumption that compensatory functional responses may occur following disturbance, even though structural attributes, such as species richness, may be adversely affected. The intensity, frequency, and predictability of disturbance should be reflected by differences in the autotrophic/heterotrophic nature of the streams at both the whole system (e.g., community P/R ratios, export/import ratios; Cummins et al. 1983, Rosenfeld and Mackay 1987) and functional feeding group levels (Cummins 1973, 1974, Cummins and Merritt 1984). However, the specific measures are in need of further refinement and testing (Cummins et al. 1983, Minshall 1988—see this issue).

In general, disturbance may be expected to alter the nutrient cycling dynamics (reservoirs, pathways, flux rates) in a manner related to the kind and extent of upheaval and changes in functional roles of the biota as grazers, detritivores, etc. (Table 1, component 6). In particular, measurement of nutrient-spiralling lengths and turnover times appear to provide useful indices of the effect of disturbance (Elwood et al. 1983, Newbold et al. 1981, 1982). The information for determining these measures for carbon are already contained in components 1, 2, and 3, when they are combined with measures of stream discharge and morphology (mean channel width, depth). Comparable estimates could be made for phosphorus or nitrogen through quantification of biologically incorporated amounts in the benthos and water by determining appropriate P or N to ash-free dry-mass conversion factors for components 1 and 2 and through measurement of P or N uptake and release rates.

Life history tactics of constituent populations and their pattern for the entire community (Table 1, component 7) are expected to vary among streams depending on the intensity, frequency, and predictability of disturbance. A variety of reproductive, physiological, and behavioral responses may be elicited, modified, or selected for or against in response to disturbance. Reproductive responses include fecundity, length of life cycle (or time to first reproduction), type of reproduction, and kind of propagules. Entrance into a resistant stage such as diapause, and timing and duration of germination, hatching, and pupation are possible physiological responses. Behavioral responses include avoidance through emigration, hiding, location of egg deposition, and vagility. One would anticipate that certain tactics may tend to predominate, depending on the type and extent of disturbance. For example, high vagility is often linked to high fecundity, and small size among species. As a result, streams with a greater preponderance of "fugitive species" should recover faster from a disturbance.

Shortening of the time required for development to the pivotal age of reproduction may be critical for organisms that live in frequently disturbed habitats. This results in rapid life cycles and small sizes for the semelparous organisms, the forms that predominate among stream invertebrates. A few stream organisms (e.g., bivalve molluscs) have the contrasting strategy of long life, large size, and iteroparity, coupled with resistance to short-term stresses. But iteroparity is seldom linked to significant storage of energy for future residual reproductive effort among stream organisms, as it is for some terrestrial species, because survival in streams is too tenuous. Streams with the greatest predominance of organisms with short life cycles, and least conservation of energy for future reproduction (like chironomids), may be expected to recover most rapidly following disturbance. Thus, comparison of the size composition of the communities in various streams (Table 1, component 8) should yield a useful means of evaluating the effects of disturbance.

Finally, conventional ecological theory suggests that disturbance will decrease or eliminate the extent and importance of biotic interactions in a community (Table 1, component 9). Determination of the kind and degree of these interactions among stream communities will provide valuable insight into the importance of disturbance in structuring lotic communities. One would expect to see a greater degree and role of biotic interactions in relatively undisturbed stream environments than in more highly impacted ones. This topic is discussed at length by Power et al. (1988) in this issue.

Hydrologic regimes and disturbance

All ecological phenomena in lotic ecosystems are affected to some extent by extremely high or low flows. Effects of extreme flows often have been observed as loss of numbers or biomass of certain taxa through flood scour or desiccation. In addition, hydrologic history has a strong influence on ecosystem structure and function (e.g., organic matter dynamics). However, until recently, ecological research has seldom been placed in a context that considers past hydrologic conditions or other disturbances (Cummins et al. 1983, Minshall et al. 1985a). This is unfortunate because although recent events may dominate observed patterns, the long-term record of extreme flows imposes constraints of an evolutionary nature on the biota.

Frequency and intensity of extreme flow events are disturbance characteristics that must be considered together. For example, high intensity events may occur so infrequently with respect to life spans of the dominant species that these organisms cannot adapt to these hydrologic events. Although lower intensity events may have significant effects on certain ecosystem components or phenomena, they may occur frequently enough that they can be considered part of the normal behavior of the system. In a prairie stream, for example, storm flows of sufficient intensity to remove mats of filamentous algae may occur many times during a single year, whereas a spate that causes significant displacement of macroinvertebrates has a longer recurrence interval. Timing of an extremely high or low flow is also important with respect to many factors, including seasonal litterfall peaks, life history stages of certain taxa, or the sequence of extreme flow events. The spatial extent of disturbance (e.g., widespread flooding due to a hurricane compared with the localized effect of an intense thunderstorm) may control recovery rates by affecting the distances that recolonizers have to traverse.

We assume, therefore, that predictability of hydrologic regime is important with respect to evolution of behavior, life history strategies, and competitive interactions (Gray and Fisher 1981). There have been few attempts to quantify predictability in relation to ecological phenomena in streams, although Horwitz (1978) showed a relationship between fish community structure and temporal variability of discharge using the coefficient of variation of daily discharge.

A comparison of predictability of temporal flow patterns among streams requires a quantitative technique that assesses the temporal distribution of flows according to their intensity, and takes into consideration the relative contribution of seasonal phenomena to the annual runoff pattern. Colwell (1974) presented a technique for assessing predictability of ecological phenomena using indices based on information theory. The parameter of interest is assigned to "states" (e.g., flowering stages or categories of precipitation amounts in Colwell's examples) for each time class (e.g., season or month). A frequency matrix is constructed in which the occurrences of the parameter are assigned according to state (as horizontal rows) and to time class (as vertical columns) for the time period

TABLE 2. Frequency matrix of monthly maximum flows for Blue Beaver Creek near Cache, Oklahoma, for the period 1967–1984. Flow classes represent the upper limit of the logarithm (base 2) of the range of flows in the class, so that class i (where i ranges from 0 to 20) includes flows $>2^{i-1}$ and $\leq 2^i$ L/s. For example, class 1 represents flow greater than 1 (2^0) but less than or equal to 2 L/s; class 0 includes all flows ≤ 1 L/s. Each number in the body of the matrix [the intersection of flow class and month from October (O) to September (S)] is the frequency of occurrence (number of years) of monthly maximum flows in each flow class for the period of record (18 yr in this example).

Class	O	N	D	J	F	M	A	M	J	J	A	S	Row Total
0	4	4	3	2	2	1	0	0	0	4	9	7	36
1	1	1	0	1	0	1	1	0	0	0	1	0	6
2	1	0	3	1	2	0	0	0	0	3	0	0	10
3	1	1	0	0	0	1	0	0	2	0	1	0	6
4	0	1	1	1	0	0	0	0	1	0	2	0	6
5	1	1	1	2	2	2	0	1	1	2	2	1	16
6	2	1	2	2	0	0	0	1	1	2	0	2	13
7	2	1	2	1	2	2	1	1	1	2	0	1	16
8	0	0	3	2	2	1	1	0	1	0	1	0	11
9	0	5	2	1	1	0	2	1	2	2	1	1	18
10	1	1	0	1	1	1	5	1	1	1	0	2	15
11	1	0	0	1	2	1	1	1	1	0	0	0	8
12	0	2	1	2	2	6	1	2	0	1	0	2	19
13	2	0	0	0	2	0	6	3	2	1	0	0	16
14	1	0	0	1	0	1	0	3	4	0	0	2	12
15	0	0	0	0	0	1	0	3	1	0	1	0	6
16	0	0	0	0	0	0	0	1	0	0	0	0	1
17	1	0	0	0	0	0	0	0	0	0	0	0	1
18	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0

of interest. Predictability, as calculated using Colwell's equations, ranges from 0 (minimum predictability, when all flow classes are equally probable for all months) to 1 (maximum predictability, when there is only one non-zero value per column). Predictability can be expressed as the sum of two components: constancy and contingency. Constancy is maximum if the state is the same for all time classes in all years (i.e., all horizontal row totals except for one are zero). Contingency represents the degree to which time determines state and is minimum if all vertical columns are homogeneous (i.e., there is no seasonal pattern). An example of a frequency matrix is discussed below.

The above frequency matrices and indices of predictability have been used for many ecological applications, including stream temperature (Vannote and Sweeney 1980) and reservoir water level (Stearns 1981). Applicability of Colwell's indices for streamflow data was suggested by Stanford and Ward (1983), although they did not present any examples. Bunn et al. (1986) reported predictability of several Australian streams using these indices but did not indicate how flows were assigned to classes.

Gurtz (unpublished data) has applied these indices to flow data from streams in the United States Geological Survey (U.S.G.S.) Hydrologic Benchmark Network. This network presently consists of 58 stations in relatively small catchments (70% are in basins smaller than 200 km^2) throughout the United States. These streams were selected because they had minimal human influences on their hydrologic or water-quality characteristics and they were relatively protected from anthropogenic change (Cobb and Biesecker 1971).

An example of a frequency matrix used by Gurtz for calculating predictability is shown in Table 2. Months were selected for the time classes (vertical columns) to provide a seasonal representation of the annual flow pattern. Flows were assigned to classes (horizontal rows) according to a logarithmic progression. For each of the stations, separate frequency matrices were derived for monthly maximum and monthly minimum flows. In each case, the input data were the daily mean discharge values available in the Water Data Storage and Retrieval System (WATSTORE) files maintained by U.S.G.S.

Differences in predictability among streams can be seen in three examples selected from the U.S.G.S. Hydrologic Benchmark Network. Blue Beaver Creek, in southwestern Oklahoma, is an intermittent stream draining a catchment of mostly native grassland located within the Wichita Mountains Wildlife Refuge and Fort Sill Military Reservation. Halfmoon Creek is a high-elevation steep-gradient stream on the eastern slope of the Continental Divide in central Colorado, located entirely within the San Isabel National Forest. Dismal River is located in the sandhills of central Nebraska and drains mostly rangeland.

Temporal variability in flow can be compared visually among these streams by examining the distribution of monthly maximum flows for a common 18-yr period of record (Figs. 3A–C). Blue Beaver Creek (Fig. 3A) has the most highly variable flow regime. The means of the monthly maximum flows for the 18-yr period follow a seasonal pattern with highest monthly values in May and lowest monthly values in August. Monthly maximum flows have high variance throughout the year as seen in the width of the standard deviations in Figure 3A, although high flows are less predictable (higher variance) in September and October than at other times. In this example of low predictability, extremely high flows may occur in any month. Halfmoon Creek (Fig. 3B) has a more regular pattern, with a peak in late spring and early summer that corresponds to the period of snowmelt, which shapes the annual hydrograph. The width of the standard deviations of monthly maximum flow is not as wide as for Blue Beaver Creek (Fig. 3B cf. 3A). Dismal River has a constant flow pattern, with little seasonality and very narrow standard deviations of the monthly maximum flows (Fig. 3C).

Colwell's predictability indices provide a quantitative tool for comparing the hydrologic regimes of these streams (Table 3). Predictability (P) of monthly maximum flows is least for Blue Beaver Creek, highest for Dismal River, and intermediate for Halfmoon Creek; Constancy (C) follows the same pattern for these streams. Contingency (M) is highest for Halfmoon Creek, and least for Dismal River, reflecting the seasonal patterns apparent in the graphical comparison (Fig. 3). Monthly minimum flows are typically more predictable than max-

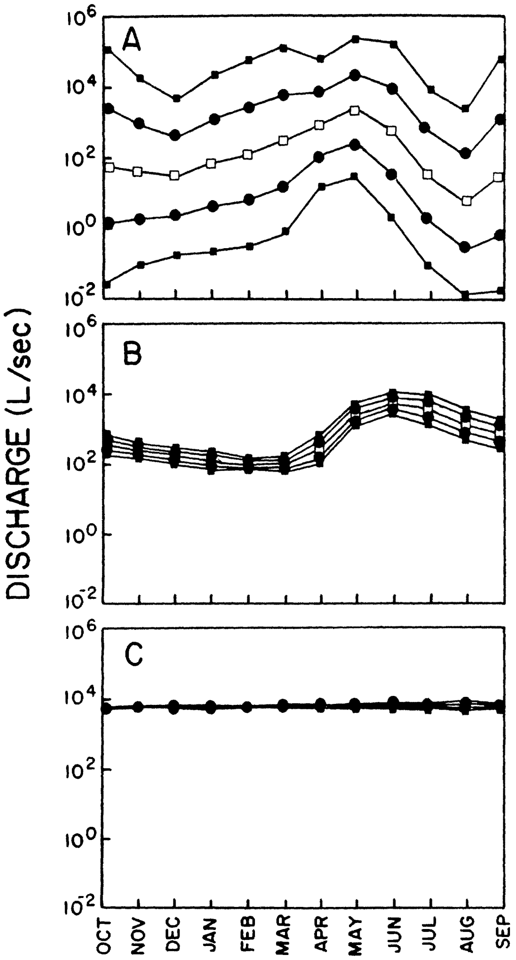

FIG. 3. Temporal variability of monthly maximum flows for the period 1967–1984 in three streams in the U.S. Geological Survey Hydrologic Benchmark Network: (A) Blue Beaver Creek, near Cache, Oklahoma (U.S.G.S. Sta. No. 07311200); (B) Halfmoon Creek, near Malta, Colorado (U.S.G.S. Sta. No. 07083000); and (C) Dismal River, near Thedford, Nebraska (U.S.G.S. Sta. No. 06775900). In each graph the middle line represents a mean of 18 monthly maximum flow values, one for each year of the record. The lines from top to bottom represent: +2 standard deviations (SD), +1 SD, mean, −1 SD, −2 SD.

TABLE 3. Basin characteristics and predictability of monthly maximum and minimum stream discharge for three streams in the U.S.G.S. Hydrologic Benchmark Network. Mean annual discharge (Q) and Predictability are for 1967–1984. Predictability indices are those of Colwell (1974): P = Predictability, C = Constancy, M = Contingency, and M/P is the proportion of Predictability due to Contingency.

	Drainage Area km²	Q L/s	Basin Elev. m	Channel Slope m/km	Predictability							
					Maximum				Minimum			
					P	C	M	M/P	P	C	M	M/P
Blue Beaver Creek near Cache, Oklahoma	64	295	370–730	5–11	0.31	0.12	0.19	0.60	0.57	0.42	0.15	0.26
Halfmoon Creek near Malta, Colorado	60	813	2970–4400	19–379	0.73	0.35	0.37	0.51	0.74	0.44	0.31	0.41
Dismal River near Thredford, Nebraska	2486[a]	5475	850–1220	ca. 1	0.99	0.98	0.01	0.01	1.00	1.00	0	0

[a] Only about 78 km² contributes directly to surface runoff.

imum flows (Gurtz, unpublished data). This is true especially for Blue Beaver Creek, which has a much higher predictability (as a result of constancy) for minimum flow than for maximum flows (Table 3). Monthly minimum flows for the Dismal River all occurred in the same flow class, so both predictability and constancy equal one. Monthly minimum flows in Halfmoon Creek had higher constancy and lower contingency than monthly maximum flows, although predictability was about the same.

In the introduction to this paper, we defined disturbance as an event that falls outside a predictable range, arbitrarily selected as ±2 standard deviations. Figure 3 shows that, using this criterion, the intensity of flow considered to be a disturbance varies considerably among the three streams shown and, as illustrated by Blue Beaver Creek, varies seasonally as well. The severity of any event also depends on changes in hydraulic factors (see Statzner et al. 1988 in this issue), the channel morphology of the stream (see next section), and other factors. However, the temporal pattern of recurrence of stream flows of different intensity, as shown above using Colwell's indices of predictability, may also impose constraints that have significant consequences for stream organisms. Although the general applicability of arbitrarily defining predictability is not clear, we agree that comparative studies of disturbance effects should include temporal patterns of the hydrologic regime, and that these indices provide a useful, quantitative approach for assessing applicability of study sites.

Comparable geomorphology and substratum

Channel form is a fundamental variable that summarizes most physical attributes of stream ecosystems. Primarily these attributes are geology, gradient, runoff, and climate, but they also include width, depth, discharge, velocity, substrate size and character, flooding and stability, and bedload sediments. Collectively, these parameters may be useful as predictors of stream biotic communities. Channel form changes systematically from the headwaters downstream and is predictable across broad geographic regions (Brussock et al. 1985, Schumm 1977). Minshall et al. (1983) attributed much of the regional variability in the River

Continuum Concept to local variations in this physical factor.

The generalized physical model of streams depicts a watercourse that originates in the mountains and flows onto an alluvial valley with decreasing slope, canopy cover, and particle size, and increasing flow, depth, and turbidity (e.g., Vannote et al. 1980). Three distinct channel forms could occur along this longitudinal profile: (1) a bedrock, boulder, and cobble, debris-regulated reach in the headwaters (hereafter called a boulder and cobble channel form); (2) an alluvial gravelbed with distinct riffle and pool structure in the mid-reaches (hereafter called a gravelbed channel form); and (3) an alluvial sandbed farther downstream (hereafter called a sandbed channel form). Streams that originate in regions of only moderate relief (i.e., low gradient) may have little or none of the boulder and cobble channel form but instead have a gravelbed channel form in their headwaters. Similarly, streams originating in lowlands generally will have a sandbed channel form throughout their lengths. The occurrence and longitudinal progression of stream channel forms is a product of relief, climate, and lithology, and is therefore predictable for broad geographic regions.

Brussock et al. (1985) further characterized these three channel forms and, based on variations in longitudinal patterns of channel-form succession, described seven rather distinct stream regions in the United States. Other approaches to regional characterization of streams include the identification of aquatic "ecoregions" (Hughes and Omernik 1981, Larsen et al. 1986, Omernik 1987) based on patterns that reflect spatially variable combinations of causal factors, which include climate, mineral availability (soils and geology), vegetation, physiography, and land use. These approaches may be useful for characterizing streams in terms of resource management (e.g., Frissell et al. 1986, Hughes et al. 1986, Rohm et al. 1988).

An additional modification, braided channels, is often superimposed on the three distinct channel forms mentioned above. Braided channels occur in places where the stream channel has more bedload entering it than the stream is competent to remove. Braided channels often occur in intermontane reaches where there is a sharp transition from high to low gradient. These braided channels may correspond to transitions between the three basic channel forms, and to the zones of hydraulic stress transition described by Statzner and Higler (1986). Braiding is common in areas of mass deposition of glacial till and in areas where excess bedload is accrued as a result of some physical disturbance, e.g., slope failure or anthropogenically induced erosion (Carling 1988, Knox 1977).

Disturbance and channel form

Disturbance varies among channel forms and substratum types in rather predictable ways. For example, moderate increases in discharge have relatively little effect in a boulder and cobble channel. Increasing flow causes little, if any, shift among areas of erosion and deposition because flow reversal (sensu Richards [1982] wherein fast flow areas become slow and vice versa) does not occur. Rather, erosional areas become more intensely erosive and depositional areas decrease in size and degree. Severe flooding in boulder and cobble channel forms that cause mass slippage of banks into the stream channel and mud and debris flows, however, can be devastating to biota (S. V. Gregory and G. A. Lamberti, Oregon State University, personal communication).

We speculate that biotic communities in gravelbed channels generally are affected most by variation in discharge. The difference in cross-sectional profile results in different responses between the boulder and cobble channel form and the gravelbed channel form. In the former, which has no floodplain, increased discharge continues to exert increased force on the stream bed. In the latter, the discharge spills over the banks into the floodplain where the residual energy is spent. Flow reversal occurs in the gravelbed channels, which scours the pools and alternately aggrades and degrades the riffles on the ascending and descending side, respectively, of a flood hydrograph. We presume that pools are areas of greatest physical disturbance during flow reversal events (which are bed-forming flows) and that the upstream slopes of the riffles, including the highest point in the longitudinal profile, may be the least intensely disturbed. If true, this variability of disturbance intensity may partially explain the upstream-biased distribution of most invertebrates within riffles (Brown and Brown 1984, Godbout and

Hynes 1983, Lamberti and Resh 1978, Mason 1976; see also Statzner et al. 1988).

Owing to the inwardly spiralling flow patterns in riffles and the outwardly spiralling flow patterns in pools (see Richards 1982), presumably the centers of riffles (in cross section) receive less disturbance, and centers of pools the most disturbance during increased discharge. Impacts of spates are most diverse in gravelbed channels because the physical habitat is more diverse. A variety of types of substratum, ranging from bedrock to silt, form microhabitats in riffle-pool reaches, some of which are virtually absent from the other channel forms.

We presume that biological communities in sandbed channels probably are affected least by physical disturbances such as increased discharge because even slight flows are able to move sand, and the biotic community, which has had to adapt to these conditions, is less affected by increased movement of this type of substratum (Reice 1985).

Channel modification by large woody debris varies among channel forms. Large woody debris (or snags) in sandbed channel forms are generally stable and provide the physical substratum that accounts for considerable production of macroinvertebrates (Benke et al. 1984) and cover for many fish. In a boulder and cobble channel, large woody debris may partially block stream flow and form a pool upstream; in a sandbed channel, however, flow is diverted and a pool forms downstream from the woody debris obstruction. The greatest channel modification by woody debris may occur in the gravelbed channel form (Bisson et al. 1987). In contrast to what occurs in a sandbed channel form, the wind-thrown tree may have more far-reaching effects in a gravelbed channel. Gravelbed channel forms have rather predictable sinuosity patterns, and riffles occur at about every five to seven stream widths (Leopold et al. 1964). If the wind-thrown tree falls across, or lodges at, the head of a riffle, it will cause local increases in flow during the next spate, which will occasionally cause movement of the riffle downstream, dig a pool, and thereby disrupt the pattern of spacing. The stream will spend considerable energy, and cause extensive rearrangement of substratum downstream (perhaps several kilometers for several years), to return to a normal riffle and pool spacing pattern (A. V. Brown, personal observation). Of course, this process may be interrupted and complicated by the entry or movement of other large debris items, and as a result the stream channel never stabilizes.

Braided channels always form where there is more bedload than the stream can move during high flow. The deep unconsolidated layer of material covers the bedrock and affords protection for stream biota by providing interstitial refugia. Streams with sparse bedload are more severely affected by high and low discharge events. Rivers with a deep hyporheos of coarse particles, like the Flathead River, Montana (Stanford and Gaufin 1974), offer the greatest protection from disturbances. Such substrata offer more interstitial space, flow, and resistance to washout.

Experimental approaches for investigating disturbance

The ability to make independent, replicated contrasts is the essence of the experimental method. Observation and "natural experiments" can suggest and support hypotheses but properly designed manipulations are required to disentangle the array of confounding factors that influence ecological processes. Experimentation dealing with disturbance effects in streams is constrained by ethical and practical difficulties but, nonetheless, such experiments have provided especially valuable understanding of stream processes.

Small-scale (<1 m^2) mechanical disturbances, such as turning over substratum, are easily applied (Clifford 1982, Reice 1985), have little lasting impact, address fundamental questions in stream ecology, and can be adequately replicated. When applied to a somewhat larger scale (10–100 m^2), disturbances of substratum (Thomas 1985) or channel form (Heede 1985) are laborious, which limits replication and may have more persistent effects. Shading experiments (Towns 1981) and manipulation of woody structure (Angermeier and Karr 1984) also provide examples of disturbance that have been done at this scale.

Most studies involving experimentation on still longer sections of streams (>100 m^2) have used chemical stressors, such as acids (Hall et al. 1980), nutrients (Elwood et al. 1981), or insecticides (Wallace et al. 1982). With inputs of chemicals it is often difficult to produce localized effects; conversely, it is quite possible to affect hundreds of meters of stream with a single chemical drip-tank. In what seems to be the sole example of physically manipulating a substantial length of stream without modifying the surrounding landscape, Bilby and Likens (1980) experimentally removed debris dams from an entire stream.

Entire small drainages of streams have been experimentally altered (Bormann and Likens 1979) more frequently than proportionate lengths of streams. Even so, such experiments are few and the usual perspective has been to view stream properties as the diagnostic equivalent of a blood test for the terrestrial ecosystem. For example, measurement of stream nutrients has been done to determine nutrient loss from soils rather than as a manipulation of nutrient levels in streams. Until fairly recently, interest in stream processes (Webster and Waide 1982) has been secondary to terrestrial processes.

The decision to apply severe disturbance or to conduct large-scale experiments on streams involves ethical as well as scientific issues. Thus far, restraint has been the rule. For example, the limited application of an insecticide (methoxychlor) by Wallace et al. (1982, 1986) to remove certain components of the benthic community is far less extensive than the use of the same compound to control larvae of biting black flies. Such experiments, however, should be done only after consideration of alternative methods. In addition, experiments involving severe degradation should meet high standards in statistical design and measurement procedures to minimize the number of inconclusive studies and the need for repetition. Many poorly replicated experiments could yield no information and cause far more damage than a single, adequately replicated study.

Experimentation in streams presents special statistical problems. Hurlbert (1984) coined the term "pseudoreplication" to describe experiments in which a single treatment is applied but error statistics are generated by replicated subsampling within the treated unit. Stewart-Oaten et al. (1986) should be consulted for further discussion. Many stream experiments, especially the large-scale ones, are pseudoreplicated. Likewise, a serious constraint on stream studies arises from the directional flow and downstream "carry" of treatment effects, which require that control or low-dosage sections be located upstream (Elwood et al. 1981, Hall et al. 1980). Wallace et al. (1982, 1986) used a parallel drainage as a control, the only way to avoid upstream-downstream confounding effects.

Improvements in experimental studies on streams can be achieved in many ways. An adequate array of experimental streams can provide adequate replication, as can systems of artificial channels fed by stream water. More selective agents of disturbance such as the bacterium *Bacillus thuringiensis israelensis*, which is apparently specific to black fly and other dipteran larvae, could be considered for use. Improvements in sampling design and measurements techniques could reduce the number of replicates needed. However, beyond the issues of replication and precision is the issue of comprehensiveness. Small-scale experiments can focus on single questions but large-scale experimental disturbances should be investigated by interdisciplinary teams testing multiple hypotheses at all levels, from microbial activity to geomorphic processes. Clearly, response mechanisms and not just endpoints need to be elucidated. Since large disturbances have longer recovery times, the planning of such experiments, if not the immediate commitment of resources, must be for the long term.

Future research on disturbance

Once comparable streams are chosen, what topics related to disturbance could be addressed by stream ecologists? We have prepared a series of general questions (which could easily be rephrased as hypotheses) regarding disturbance effects that we feel are testable and should be considered further.

(1) In streams that are different in some set of general characteristics such as hydrographs and shear stress, will the communities respond to a unit disturbance in fundamentally similar or different ways?

(2) Will rates and sequences of recovery by a community be faster in frequently disturbed streams than in rarely disturbed streams because the community composition will have been previously influenced by disturbance events?

(3) Will community responses to anthropogenic disturbances such as pesticides, dams, and exotic species introductions be fun-

damentally different from responses to natural disturbance?

(4) To what extent will rates of recovery vary with intensity of disturbance?

(5) To what extent does the spatial scale of disturbance affect recovery?

(6) In terms of timing of a disturbance, will the biota of strongly periodic (e.g., highly seasonal) and less periodic environments have different recovery sequences?

(7) What is the hierarchy of severity among physical, chemical, and biological disturbances?

(8) Are biological communities in highly retentive streams less affected by disturbances than communities in poorly retentive streams?

(9) Does temporal variability in biological communities reflect variability in frequency and predictability of disturbance?

(10) In frequently disturbed streams, will life histories of organisms include effective dispersal or resistant stages? Will life histories tend toward short life spans and high fecundity or a bet-hedging tactic of long life and iteroparity? Will growth rates and age structure be influenced? Will highly mobile species capable of using rapidly changing spatial/temporal refugia be favored?

This review opened with an analogy comparing the flux of human life to the natural variability that we see in streams. It may be appropriate to note that some of the followers of Heraclitus believed the universe to be in a flux so rapid that "you cannot step into the same river once" (Fuller 1945:50–51). This view may parallel the beliefs of researchers who emphasize the stochastic nature of stream processes, or of others that find inherent bias in field experimentation. However, at whatever position along a stochastic-deterministic spectrum a researcher lies, several points are clear. Disturbance is an important topic in stream ecology. It can be responsible for a host of temporal variations in spatial patterns. The frequency, intensity, or severity of disturbance will determine when, if ever, a community will reach equilibrium. Disturbance will have major impact on productivity, nutrient cycling and spiralling, and decomposition. In fact, to some of us, disturbance is not only the most important feature of streams to be studied, it is the dominant organizing factor in stream ecology.

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