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Why disturbances can be predictable: a perspective on the definition of disturbance in streams

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Abstract. Resh et al. (1988, *J. N. Am. Benthol. Soc.* 7:433) assert that lotic ecosystems are unique in that disturbances are necessarily "unpredictable" events. Acceptance of this "predictability clause" in the definition of disturbance introduces problems that influence our ability to identify, describe, and discuss important aspects of disturbance in streams. I focus on four specific aspects of Resh et al.'s treatment of predictability, particularly as it relates to hydrologic disturbance (e.g., spates). First, Resh et al. offer only purely statistical criteria for identifying hydrologic disturbance, an approach that has important limitations for characterizing predictability of the disturbance regime. I suggest adoption of more physically based measures of disturbance (e.g., flow at which movement of bed is initiated) to which specific ecological responses can be determined. Second, lotic species are assumed to be "adapted" to predictable hydrological events, despite the general absence of supporting empirical evidence. I suggest that this assertion be reframed as a testable hypothesis. Third, defining disturbances as necessarily unpredictable can result in a tautology, in which biological response to disturbance and predictability of disturbance are expressed in terms of one another. Fourth, a more explicit distinction between ecological and evolutionary time scales of response to disturbance allows predictability to be properly considered as a separate (and non-tautological) component of the disturbance regime. In sum, disturbances (including predictable ones) always have ecological effects; however, the magnitude of ecological response to a particular disturbance may be constrained by evolutionary (historical) adjustments of the biota if the disturbance regime is characterized by high predictability.

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

Communication among scientists often depends on careful definition. This is certainly true in ecology, where many terms or phrases attempt to generalize across diverse systems and levels of organization. Differences in definition may arise from discernably different philosophical starting points, or they may arise more subtly from ambiguities associated with complex phenomena and frame of reference. Sometimes, ambiguities arise because terms or concepts implicit in the definition are themselves subject to variable interpretation (e.g., discussion of "niche" often relies on some common notion of "resource"). Regardless of the underlying reasons, we may speak at cross-purposes because definitional assumptions have not been adequately specified.

The word "disturbance" is becoming increasingly important in the ecologist's lexicon. The recent seminal paper by Resh et al. (1988) has played a significant role in drawing attention to this concept as applied to lotic ecosystems. Furthermore, it has greatly helped stream ecologists to focus on many basic issues relevant to the role of disturbance in structuring these systems. Produced during a workshop discussion group consisting of 10 participants, the paper by Resh et al. attempted to distil a "consensus" view on a complex issue. However, the authors expressed alternative views throughout their paper, and they invited further discussion of these views. In this paper, I wish to address a component of Resh et al.'s definition of disturbance, viz. the assertion that lotic systems are unique in that disturbances must be unpredictable. I critically examine this assertion and explore its implications to argue that acceptance of this "predictability clause" unnecessarily restricts our ability to identify, describe, and discuss important aspects of disturbance in streams, primarily because it blurs the distinction between the ecological and evolutionary time scales of biotic response to disturbance (both of which are important in disturbance studies). This is an important issue because stream ecologists need to explicitly evaluate the assumptions, ambiguities, and implications that underlie our use of the word "disturbance", a relativistic concept that changes with scale of observation (Rykiel 1985). Hereafter, disturbance will refer to hydrologic disturbance unless otherwise indicated. I will focus primarily on spates; however, similar arguments could be made relative to other types of disturbance as well (e.g., "droughts", chemical pollution, etc.).

Two widely cited general definitions of disturbance exist. Sousa (1984) defines disturbance in a population-dynamics context as "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established". White and Pickett (1985) adopt a broader definition of disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure, and changes resources, substrate availability, or the physical environment". Note that both definitions consider disturbances as "discrete" events, the impact of which can be measured in terms of ecological responses. Further, according both to Sousa and to White and Pickett, a given disturbance *regime* is characterized by the statistical distribution (based on historical record) of individual events in terms of such attributes as frequency, intensity (magnitude), duration, and predictability.

Resh et al. (1988:434) modify the White and Pickett definition for streams to include events that are only ". . . outside a predictable range . . . [because] . . . organisms are adapted to predictable seasonal fluctuations of discharge, temperature, dissolved oxygen, etc. . . .". Further, they state that ". . . when measured by the impact on a community, we feel that it is the unpredictable event that typically constitutes a disturbance". Although intuitively appealing on its face, this "predictability clause" introduces significant methodological and conceptual problems that deserve discussion.

How predictability of disturbance can be non-arbitrarily determined

Resh et al. link disturbance and predictability using two statistical approaches. First, they present graphical arguments (figs. 1, 3) that hydrological events may be considered disturbances if they are extreme *relative to* the expected long-term mean value for some specified time interval. In their example, monthly means ± 2 standard deviations (SD) are used to represent the "predictable range" included in their definition (though they caution against general use of this specific criterion). While their approach appropriately considers the impact of disturbance in the context of normal environmental variation, I wish to emphasize some specific limitations associated with such a purely statistical approach to defining predictability of disturbance. Resh et al. indicate that any purely statistical definition of disturbance is arbitrary because, in their example, all months would have the same expected disturbance frequency (i.e., 5% assuming a normal distribution) given a sufficiently long period of record. However, because all months have equal disturbance frequencies, disturbances would also be equally likely for each month, leading to the unexpected conclusion that disturbances (as defined) have no seasonal predictability (i.e., they are uniformly distributed throughout the year). Thus, using this (or other) arbitrary statistical criterion to define "disturbance", one could argue that *all streams* are similar in having no seasonal predictability of disturbance.

Resh et al. partially address this issue in their second approach, where they apply a formal measure of predictability (Colwell 1974) to monthly maximum and minimum daily discharges. They show convincingly that temporal distribution of these extreme flows varies among streams (fig. 3, tables 2, 3). However, maximum or minimum monthly extremes are arbitrary insofar as they do not necessarily represent actual hydrologic disturbances, so calculated predictability scores do not necessarily describe predictability of disturbance *per se* (a point not explicitly addressed by the authors). Resh et al. appropriately conclude that such a quantitative analysis is useful both for considering temporal hydrologic constraints on the biota and for site-matching in comparative studies. However, similar arguments can be made about formal measures of predictability for other arbitrarily selected levels of flow (e.g., mean daily flow—Poff and Ward 1989). Thus, I would argue that arbitrarily chosen hydrographic statistics (e.g., mean or SD of flow defined over any arbitrary time interval) can be used to characterize predictability of *streamflow* generally (and thus facilitate among-stream hydrographic comparisons); however, they cannot necessarily be used to characterize the predictability of *disturbance* specifically.

Non-arbitrary criteria for disturbance are needed to characterize the statistical predictability of a disturbance regime. Objective measures are needed to identify events that satisfy the criteria provided in the Sousa (1984) or White and Pickett (1985) definitions (viz., resource loss, mortality, etc.). In streams, flows that move substrata (spates) are events that clearly satisfy these conditions. Different approaches can be taken, depending on the frame of reference. For example, bankfull discharge could be considered as a *channel-wide* measure of disturbance, because this level of flow is often correlated with active channel formation and significant sediment transport (e.g., Richards 1982) and therefore directly and indirectly modifies many levels of ecological organization. Poff and Ward (1989) used this approach and showed that seasonal predictability of an index of bankfull flow varies greatly among streams across the USA. Some streams experience bankfull discharge with a relatively fixed periodicity (e.g., in spring during snowmelt), while in others bankfull flow occurs without seasonal pattern (i.e., at any time of the year). Importantly, some streams do not have a clear pattern of predictability using this criterion, indicating a gradient in disturbance predictability across lotic ecosystems.

A finer-grain approach for identifying disturbance in a particular stream might be tailored by determining at what level of flow *patch-specific* disruptions occur. Indeed, Resh et al. emphasize differential susceptibility of substratum types to disturbance as an important mediator of biotic responses to hydrologic disturbances. Biota inhabiting a particular type of substratum (e.g., sand) may be "disturbed" by a given hydrologic event, whereas biota on another patch type (e.g., gravel) may not be. Sediment transport processes are sufficiently well understood for us to estimate when substratum movement will occur (given data on median particle size, channel geometry, gradient, and discharge). This habitat-specific approach has been adopted by researchers working on a variety of organisms, from meiofauna (Palmer et al. 1992) to macroinvertebrates (McElravy et al. 1989, Rader and Ward 1989, cf. Feminella and Resh 1990) to fish (Erman et al. 1988) and cave fauna (Poulson and Culver 1969).

Both channel-wide and patch-specific approaches attempt to identify threshold flows that potentially constitute ecologically meaningful physical events. The disturbance is thus defined in terms of the physical event (a cause), not in terms of the biotic response (an effect) (see Rykiel 1985, also cf. Resh et al. 1988). However, the specification of a disturbance is scale-dependent and is guided by the ecological question(s) of interest. For example, less flow is required to remove surface benthos than to scour deep hyporheos, leading to fundamentally different perceptions of what intensity of physical disruption constitutes a disturbance for these two different ecosystem compartments. That a physical event may constitute a disturbance at one level but not another indicates the hierarchical nature of disturbances (cf. Allen and Starr 1982, Frissell et al. 1986). Therefore, it is critical that a researcher clearly specify the scale of observation, both with respect to the characteristics of the physical disturbance (i.e., magnitude, duration) and to the ecological level(s) of response. In principle, once a particular threshold disturbance flow is established, the statistical properties of a disturbance *regime* (e.g., predictability, frequency) can be determined, if hydrologic data are available. This approach forces us to link specific hydrologic events explicitly to specific system characteristics (e.g., substratum movement) and to specific ecological responses, thereby facilitating non-arbitrary descriptions of disturbance regimes. Information provided by this approach would allow us to contrast spatial and temporal differences in ecological responses to specific hydrological events both within and among streams. It would also encourage us to examine differences and similarities of response from both ecological and evolutionary perspectives (see below).

Why organisms are not necessarily "adapted" to predictable disturbances

Let us assume that disturbance predictability can, in fact, be measured for a system. We are still left with Resh et al.'s assertion that, because organisms are "adapted" to predictable environmental fluctuations, only unpredictable events count as disturbances. This argument introduces important issues and problems. Initially, we ought to ask ourselves under what conditions adaptation to environmental variation can be expected. Thiery (1982) identified three general properties of a given set of environmental conditions that collectively justify the cost of adaptation. (This argument presupposes that species have the potential to adapt to the set of conditions to begin with.) If the environmental selection regime consists of extreme events that are *frequent* in their occurrence (relative to organism life span), not too *deviant* (relative to normal conditions), and *contingent* (i.e., predictable), then organisms may adapt, e.g., by modifying life cycles to minimize exposure to extremes. An important point, however, is that different combinations of these properties lead to different expectations about whether adaptation would be favored and what form it might take (Slobodkin 1968, Slobodkin and Sanders 1969, Thiery 1982). For example, adaptation may be possible where a set of conditions is simultaneously deviant, infrequent, yet predictable, or where it is deviant, frequent, yet unpredictable. But if extreme events are infrequent and unpredictable, or if they are simply very rare (regardless of predictability), then appropriate selective pressures for maintaining adaptation would presumably be absent.

These arguments indicate that just because an environment is predictable does not mean that organisms are adapted to it; potential adaptation to disturbance predictability is itself contingent upon other attributes of the disturbance regime. In north temperate streams, highly periodic seasonal changes in temperature or resource inputs (which are extreme and frequent relative to population turnover times for many lotic species) may arguably result in evolutionary adjustments of biota (e.g., Vannote et al. 1980). However, the frequency and seasonal predictability of hydrologic disturbances can vary widely in many streams across a range of values (Poff and Ward 1989), leading to presumably noisy environmental selective forces that may not promote local adaptation.

In a more pragmatic context, the imbroglio of the last two decades concerning the "adaptationist programme" and the "just-so stories" (Gould and Lewontin 1979) should caution us from over-interpreting the limited data suggestive of local adaptation to hydrologic regimes. While there is some evidence that populations inhabiting separate locales (where environmental selective pressures differ) may be characterized by different life history strategies (Leggett and Carscadden 1978, Crowl 1990) or behaviors (Flecker 1992), we cannot yet say whether any of these patterns result from genetic isolation or phenotypic flexibility. Indeed, it is not necessary to invoke local adaptation at all if the environment simply "filters out" species that lack appropriate mechanisms for persisting under a given disturbance regime (see Poff and Ward 1990). Even if lotic organisms are globally adapted as "weedy" (fugitive) species inhabiting relatively variable, disturbed systems (see Townsend 1989), different degrees of "weediness" may be favored under different environmental regimes (e.g., stable vs. flashy streams) (cf. Minshall 1988, Resh et al. 1988, Townsend 1989). The main point is that we just do not know generally whether "adaptation" or "filtering" (or both, or neither) occurs, and it probably does not really matter for many ecological questions. So, rather than asserting a priori that organisms are "adapted" to the "predictable" portion of the environmental spectrum, this thought can be recast in terms of testable hypotheses such as the following: organismal attributes (e.g., life history tactics) or ecosystem attributes (e.g., primary or secondary production) will vary among streams depending on the predictability or various interactive components of the disturbance regime (cf. Resh et al. 1988). Data are needed to test these hypothesis.

Linking disturbance and predictability can result in a tautology

Accepting the assertion that disturbances *must* be unpredictable also involves the risk of relying on the magnitude of ecological response to define disturbances—something Resh et al. state they wish to avoid. As an extreme and hypothetical example, suppose a stream is sampled only twice: once prior to and once shortly following a "major spate". Was the spate a disturbance? If resources and biota were severely depleted by this spate, it would indeed be disturbance according to Sousa (1984) or White and Pickett (1985). But the *stream* definition (Resh et al.) apparently requires some knowledge of "predictability", and, unfortunately, hydrologic details for this hypothetical stream are lacking (often the case in the real world). According to the Resh et al. definition, the biota respond only to unpredictable events; therefore, we might deduce, tautologically, that this was a (unpredictable) disturbance because the biota responded. Had the ecological response been less dramatic (e.g., 50% or 10% of the observed value), we might be tempted to conclude that it was not a disturbance and thus "predictable". This example is intentionally exaggerated to make the point that strict adherence to the "unpredictability clause" in the definition of disturbance introduces ambiguity that can place us in the uncomfortable position of documenting disturbance depending on the magnitude of biological response(s). As argued above, specifying a physical threshold for disturbance with the *potential* to alter specified ecological or ecosystem properties allows one to define predictability of disturbance independent of ecological response to the event. Admittedly, ecological responses to such threshold flows may vary spatially or temporally, but this variation itself is of prime ecological and evolutionary interest.

Why disturbances can be predictable: ecological vs. evolutionary perspectives

With the above arguments, I have attempted to illustrate what I view as methodological and conceptual ambiguities associated with including predictability in a definition of disturbance. Yet I agree with the authors of the Resh et al. paper that "unpredictable" disturbances typically have substantially greater impact on lotic ecosystems than "predictable" ones of similar magnitude. This seeming contradiction can be resolved, I believe, by making explicit what in the Resh et al. paper is a largely implicit yet very important distinction about the time scale of biotic response to disturbance. Resh et al. state (p. 443) that the "effects of extreme flows often have been observed as loss of numbers or biomass of certain taxa through flood scour or desiccation". In considering the importance of predictability of hydrologic events, they say, "We assume, therefore, that predictability of hydrologic regime is important with respect to evolution of behavior, life history strategies, and competitive interactions". The authors are distinguishing between two very different scales of biotic responses to disturbance: ecological and evolutionary. In *ecological* terms, the consequences of disturbance are clear: resources are exported, population densities are reduced, etc. These are, in fact, the criteria by which one identifies disturbance according to definitions of Sousa (1984), White and Pickett (1985) and Resh et al. (1988). Therefore, in ecological time, disturbances can clearly be predictable because, for example, no population can be perfectly "adapted" to a hydrological event that disrupts habitat or exports resources. By contrast, in *evolutionary* terms, the loss of some individuals from a population during an extreme event may be irrelevant because it is a normal component of species population dynamics. This evolutionary perspective is related to the views of Lewontin (1969) and Holling (1973) that higher-level system relationships (e.g., species persistence as opposed to maintenance of population densities) may resist displacement by disturbance from a "basin of attraction" due to high system stability (for recent discussions see Connell and Sousa [1983] and Sutherland [1990]). In this view, a system incorporates its disturbance history, such that only unexpected events (in magnitude or timing) have the potential to "push" the system beyond its "stable" boundaries. This appears to be what Resh et al. have in mind when they state that disturbances can only be events occurring "outside a predictable range". This is certainly a valid and important perspective, and one that is particularly applicable to perturbation-dependent ecosystems (e.g., fire-driven forest and grassland systems), where organisms and communities have become dependent on, and actually contribute to, the disturbance factors that are inherent to the system (see Vogl 1980).

An evolutionary perspective on disturbance is inherent in statements such as only unpredictable events are disturbance (Resh et al. 1988, Reice et al. 1990), or the absence of hydrologic disturbance following river impoundment is itself a disturbance (cf. Ward and Stanford 1983). But, use of Sousa's (1984) or White and Pickett's (1985) definitions compels us to view disturbances as "discrete" events that always have ecological impacts, though the ecological responses may well be constrained by evolutionary (historical) events. Therefore, as suggested by Resh et al., populations may be adjusted to a particular disturbance regime such that high discharge occurring at an unusual time of the year (in evolutionary or historical terms) indeed would have a much greater impact (in ecological terms) on community structure than that same spate occurring at the usual time of year (as illustrated in Resh et al.'s fig. 1). The possibility of evolutionary adjustments to hydrologic disturbance itself generates important insights and hypotheses. For example, we could hypothesize that under a particular disturbance regime, biological mechanisms or attributes (e.g., mobility, behavior, physiology, life history, morphology) that confer differential survival and persistence under that environmental selection (or filtering) regime should be favored. Across a gradient of disturbance regimes within or among streams, we would expect to find statistical associations between patterns of physical environmental variability and appropriate biological attributes (e.g., Lake et al. 1985, Minshall 1988, Resh et al. 1988, Poff and Ward 1989, 1990, Townsend 1989, Reice et al. 1990, Wallace 1990).

Concluding remarks

In summary, I see four limitations in Resh et al.'s assertion that disturbances are necessarily unpredictable. First, use of arbitrary hydrological statistics may be appropriate for characterizing predictability of streamflow generally but not of disturbance specifically. Physically based criteria for disturbance (e.g., flows initiating bed movement) with clear ecological consequences (e.g., faunal or resource displacement) are needed to quantify differences in predictability of disturbance *per se*. Second, the assertion that lotic biota are "adapted" to "predictable" hydrologic disturbances lacks a firm empirical basis and should be regarded as a hypothesis to be tested. Third, defining disturbances as necessarily unpredictable can result in a tautology, wherein response to disturbance and predictability of disturbance are expressed in terms of each other. Fourth, the important distinction between ecological and evolutionary time scales of response to disturbance, though implicit throughout Resh et al., should be made explicit. Doing so allows us to consider predictability as a separate component of the disturbance regime. Disturbances are, by definition, ecological events, but if their temporal distribution is "predictable enough", ecological responses may be small because organisms and communities have adjusted to them in evolutionary (historical) terms. Differences within or among streams with respect to ecological responses to specified disturbance intensities can be *hypothesized* to reflect differences in disturbance regimes (predictability, frequency) among sites, but data are needed to test such hypotheses.

Ecologists are ultimately concerned with how disturbance contributes to stream ecosystem structure and function (Resh et al. 1988). We want to know what ecological and evolutionary mechanisms contribute to species success and persistence in lotic systems characterized by hydrologic events of variable intensity, frequency, duration *and* predictability. Clearly, these issues go far beyond the narrow concern over definition of terms, and differences in perspective will persist and should be encouraged. But it is worthwhile to explore the assumptions that underlie our concepts and perspectives, so we do not communicate at cross-purposes while attempting to discern nature's web.

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