

PERSPECTIVES

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Disturbance, patchiness, and diversity in streams

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Abstract. Perturbations in ecosystems consist of a sequence of 2 events: the disturbance, marked by the application of the disturbing forces, and the response shown by the biota to the damage inflicted by the disturbance. The disturbance must be effectively characterized, without confounding it with the response, for progress to be made in the study of the disturbance ecology of streams. A disturbance may take the form of a pulse, a press, or a ramp, and the consequent trajectory of the response may be a pulse, a press, or a ramp.

Floods and droughts are the major forms of natural disturbance in flowing waters and, although the effects of floods have been relatively well studied, those of droughts have been largely neglected. Floods accentuate downstream and lateral transport links, often with damaging consequences, whereas droughts fragment the continuity of streams. Both floods and droughts destroy and generate habitat patchiness and patchiness of the biota. During recovery, there are changes in the biotic composition and spatial configuration in patches. Resistance and resilience of the biota to disturbance may be facilitated by the use of refugia. The characterization of flood refugia is much more advanced than that of drought refugia.

Recovery from floods is marked by the rapid attainment of relatively constant levels of diversity at the local scale of individual patches. At the regional scale of streams and their catchments, several studies have reported negative correlations between diversity and levels of flood disturbance, whereas other studies have reported unimodal diversity–disturbance curves consistent with patterns expected of the intermediate disturbance hypothesis. Such a unimodal relationship may be generated in several ways that await testing. In flowing waters at the regional scale, disturbance may play a central role in regulating species diversity. A predicted increase in the severity and frequency of disturbances with global climate change requires a comprehensive understanding of the disturbance ecology of running waters.

Key words: perturbation, disturbance, response, pulse, press, ramp, streams, patchiness, floods, droughts, refugia, diversity regulation.

Disturbance is regarded by many stream ecologists as playing a central role in determining the structure of stream communities (e.g., Resh et al. 1988, Lake 1990, Fisher and Grimm 1991, Poff 1992, Giller 1996). Research on disturbance ecology in streams has concentrated on flow-generated disturbances, mostly high-flow events (floods), and has neglected low-flow events or droughts.

Natural streams and rivers have stable flows for much of the time, mostly running at base-

flow levels (Gordon et al. 1992, Poff et al. 1997). Flow-generated disturbances that periodically disrupt such stable conditions may vary greatly in duration, spatial extent, and predictability. Both floods and droughts can destroy habitat patches and create new ones that are then colonized and inhabited by biota with the return of stable flow conditions. The size of patches created by disturbance can vary greatly (Fisher and Grimm 1991). Different-sized patches are used by different biota. There may be a rich variety of habitat patches that supports the high diversity of lotic biota.

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In this paper, I explore the nature of the links between disturbance, habitat patchiness, and diversity in streams. I concentrate on flow-generated disturbance, with invertebrates being the biotic group of concern. I outline the effects of both floods and droughts and the responses of the biota to them. The effects of flow-generated disturbances on the biota can be mitigated by the use of refugia. I suggest that there is a strong link between disturbance and biotic diversity of streams at the appropriate spatial scale.

Defining Disturbance

A disturbance occurs when potentially damaging forces are applied to habitat space occupied by a population, community, or ecosystem. The magnitude of the forces may be such that organisms may be killed or displaced, consumable resources (e.g., living space and food) may be depleted, and habitat structure may be degraded or destroyed. Disturbances should be defined by the nature of their damaging (mainly abiotic) properties, especially the intensity and forms of their forces, along with parameters such as frequency, predictability, spatial extent, and temporal duration. Characterization of disturbances by their input properties has been advocated by Rykiel (1985), Lake (1990), and Poff (1992), whereas others, following the definition of White and Pickett (1985), have defined disturbances by their effects on the biota and by subsequent biotic responses. These biotic definitions have befuddled disturbance ecology. For example, Townsend and Hildrew (1994) defined a disturbance "as any relatively discrete event that removes organisms and opens up space and other resources that can be used by individuals of the same or different species". More emphatically, Bartha et al. (1997) defined a disturbance as "a multi-species, spatiotemporal pattern of mortality of non-competitive origin". If the biotic effects or the outcome of a disturbance define how it is characterized, then we do not have a standardized means to compare the impacts of different types of disturbance in the same system, or impacts of the same type of disturbance in different systems. In other areas of disturbance ecology (e.g., fires), disturbances are characterized by their intensity, season of occurrence, extent and patchiness, frequency, and type (Whelan 1995). Stream ecologists should

characterize disturbances such as floods or droughts in such a way that realistic comparisons can be made among times, sites, and rivers (Resh et al. 1988, Poff and Ward 1989). Further, in characterizing disturbances, the relevant spatial and temporal scales of the observations must be determined (Poff 1992).

I will use the following definitions of Bender et al. (1984) and Glasby and Underwood (1996): **perturbation** describes the combination of cause and effect. **Disturbance** becomes the cause of a perturbation, and **response** becomes the effect of the disturbance.

Characterization of Disturbances and Biotic Responses

Disturbances may be characterized by their temporal patterns; thus we have pulses, presses, and ramps. Pulses are short-term and sharply delineated disturbances (Fig. 1A). Floods are usually pulses, especially in constrained rivers. In lowland unconstrained floodplain rivers, floods are pulse events of extended duration. In such rivers, floods may not be regarded as disturbances but as vital resetting events—the flood pulse (Junk et al. 1989). However, floods in such systems are disturbances, even if they are predictable (Poff 1992), in that they rearrange the abiotic environment of the floodplain and the channel that in turn leads to changes in the composition of the biota.

Presses are disturbances that may arise sharply and then reach a constant level that is maintained (Fig. 1B). Natural presses in rivers may include sedimentation after landslides or after intense bushfires in the catchment. At present, most press disturbances applied to running waters are the result of human activities, e.g., the barrier effects of dams, channelization, and the persistence of heavy metal pollutants. I propose a 3rd form of disturbance, namely ramps (Fig. 1C), which occur when the strength of a disturbance steadily increases over time (and often simultaneously in spatial scale). Ramps may steadily increase in time without an endpoint, or reach an asymptote after an extended period. Droughts as "creeping disasters" (Grigg 1996) are ramps; conditions steadily get worse as droughts persist. Other examples of ramps include increasing sedimentation of a stream as its catchment is cleared, or the incremental spread of an exotic organism. Ramps

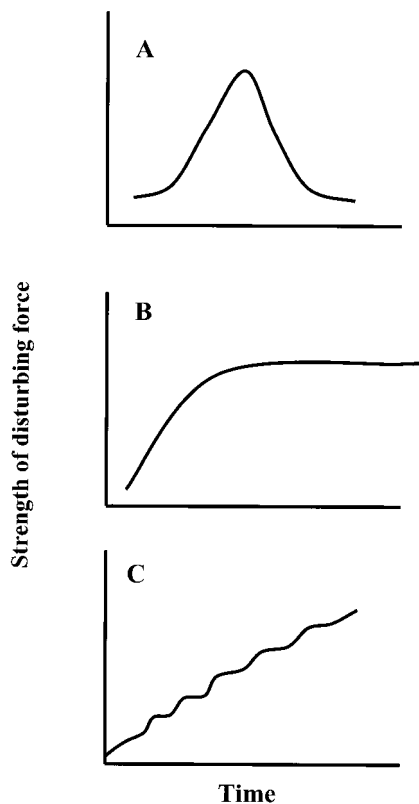


FIG. 1. Three types of stream disturbance (A.—Pulse, B.—Press, C.—Ramp) distinguished by temporal trends in the strength of the disturbing force. The disturbing force may be generated by deviations from normal conditions such as high-flow events (floods) and low-flow events (droughts, river regulation). Note that ramp disturbances may level off or increase steadily throughout the period of observation.

may also occur when the strength of a disturbance steadily declines. Thus, downward ramps may occur when stream restoration measures steadily exert their effects.

The response of the system, be it at the population, community, or ecosystem level, has often been confounded with the disturbance itself. Glasby and Underwood (1996) proposed that, in perturbations, there are press and pulse disturbances (and now ramp disturbances) to which the affected target (population, community, ecosystem) has a pulse, press, or ramp response (Fig. 2). For example, a perturbation may consist of a pulse disturbance and a pulse response (Fig. 2A), or a pulse disturbance producing a press response (Fig. 2B). The pulse disturbance

encompasses many floods, especially seasonally predictable ones, whereas the ramp disturbance with a ramp response (Fig. 2D) occurs with droughts. Until now, there has been no attempt in disturbance ecology to determine the relative frequency of different types of perturbation.

The characterization of the response is linked with the qualities of resistance, a measure of the capacity of a system to withstand a disturbance, and resilience, a measure of the capacity of the system to recover from disturbance (Lake and Barmuta 1986). Thus, invertebrates usually exhibit a pulse response to pulse floods (e.g., Yount and Niemi 1990), but massive or aseasonal floods may lead to press (e.g., Giller et al. 1991) or ramp responses (e.g., Scrimgeour et al. 1988). Clearly, if we are to progress and usefully compare both disturbance impacts and the consequential biotic responses, we need quantifiable measures of the disturbances (e.g., movement of bottom substrata with floods or reduction in habitat space with droughts), of the effects on abiotic and biotic components of the system of interest, and of the subsequent responses by the biota.

Last, the type of disturbance suffered by the biota may cause spatially and temporally scale-dependent effects and elicit different responses (Connell and Sousa 1983, White and Pickett 1985, Glasby and Underwood 1996). Thus, a flood may be a pulse to a fish population, which has a generation time of years, but it may be a press to a population of blackfly larvae with a lifetime in days. Similarly, a freshet that disrupts small patches, such as single stones, may be damaging to sedentary grazer populations with limited mobility, but may not affect highly mobile and wide-ranging grazers such as baetid mayflies.

Disturbances Caused by Excesses or Deficits in Water Movement

Perhaps because of the well-watered environments studied by most stream ecologists, floods have received much more attention (e.g., Resh et al. 1988, Yount and Niemi 1990, Fisher and Grimm 1991, Poff et al. 1997) than droughts.

Floods

The effects of floods on both the abiotic and biotic components of streams have long been

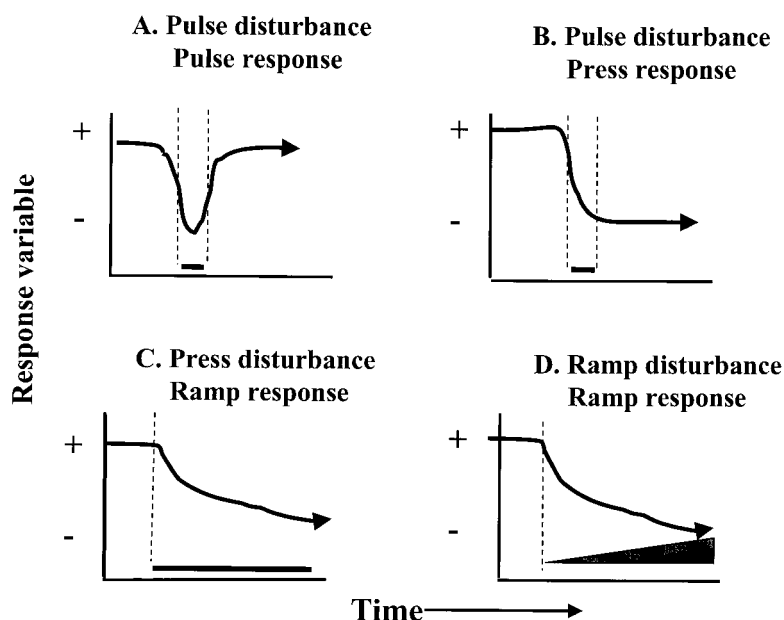


FIG. 2. Selected different forms of perturbation that are made up of the disturbance and of the response of the system affected. The duration of the disturbance is indicated by the solid bar on the X-axis; the onset and end of the disturbance are indicated by the vertical dotted lines. Four types of perturbation are illustrated. For example, a pulse disturbance may produce a pulse response (A), or a pulse disturbance may produce a press response (B), a press disturbance may produce a ramp response (C), and a ramp disturbance may produce a ramp response (D).

appreciated by hydrologists, fluvial geomorphologists, stream ecologists, fish biologists, and river managers. It has been long known that floods can deplete the biota of streams and that recovery is rapid (e.g., Moffett 1936, Mottley et al. 1939, Jones 1951, Allen 1951, Minshall 1968). Unpredictable floods were recognized as being very damaging (e.g., Moffett 1936, Hoopes 1974), whereas predictable seasonal floods were seen as a major force inducing changes in habitat structure and biota (e.g., Harrison and Elsworth 1958, Maitland 1964). However, although floods affect stream benthos, disturbance was not seen as being important in shaping stream communities (e.g., Hynes 1970). Stream communities were viewed as being deterministic rather than stochastic assemblages and equilibrium rather than nonequilibrium communities for which floods were short-term events that temporarily upset the equilibrium.

Studies of succession after floods in desert streams (e.g., Fisher et al. 1982) and on the community dynamics of stream fish (e.g., Grossman et al. 1982) led to the view that stream com-

munities are nonequilibrium assemblages largely controlled by stochastic forces, such as floods (e.g., Lake and Barmuta 1986, Resh et al. 1988). Resh et al. (1988) in their review concluded: "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".

In flooding streams, large volumes of rapidly moving water exert high shear forces that suspend sediments, move and redistribute bottom materials (from sand to boulders), scour and abrade the streambed, remove plants (from microscopic algae to macrophytes), move detritus, snags and debris dams, and kill, maim, and displace biota. Floods should be characterized in terms of their magnitude, duration, frequency, predictability, the rate of change of their hydrograph, and the shear forces that they exert on sections of the streambed (Poff et al. 1997). In terms of their magnitude, they can be defined as flow events that overtop the banks of their stream (Poff and Ward 1989, Gordon et al. 1992). They can be either predictable (e.g., seasonal) or

unpredictable (Poff 1992). Floods can vary from the rather frequent high-water events that entrain fine sediments and move small patches of the streambed to infrequent, catastrophic events. They vary in their effects on the stream channel, from brief spates that cause little geomorphic change to floods of long duration with extended periods of high peak stream power causing major changes to the stream channel (Costa and O'Connor 1995).

Droughts

Droughts have been greatly neglected by stream ecologists (Resh et al. 1988, Fisher and Grimm 1991, Giller 1996, Poff et al. 1997). Drought is a multifaceted term that is difficult to define (Heathcote 1969, Grigg 1996). There are meteorological, hydrological, agricultural, and economic droughts. Palmer (1965), who developed the Palmer Index for droughts, defined a meteorological drought as occurring over "an interval of time, generally of the order of months or years in duration, during which the actual moisture supply at a given place rather consistently falls short of the climatically appropriate moisture supply". Analysis of low-flow frequency curves is used to define droughts hydrologically (Gordon et al. 1992). In such curves, with decreasing discharges there is usually a break in the slope of the values and below this point drought flows occur. Thus, this point for European streams is at an exceedance probability of ~65% (Institute of Hydrology 1980), whereas for southeastern Australian streams, this point occurs at ~80% (Nathan and McMahon 1990). Droughts as detectable events may not have distinct beginnings, though they usually have sharp ends. They develop with a deficit in precipitation, which is sequentially revealed in reduced runoff, soil moisture, stream flow, and groundwater levels (Changnon 1987, Grigg 1996) (Fig. 3). Droughts vary from very reduced but persistent flow events to the complete cessation of flow (Gordon et al. 1992). In intermittent streams, drought may be difficult to separate from normal seasonal cessation of flow (Harrison 1966, Boulton and Lake 1992b). Droughts may occur regularly or unpredictably, and vary greatly in duration.

Streams undergoing droughts always show a reduction, usually dramatic, in habitat space (e.g., Hynes 1958, Larimore et al. 1959, Ladle

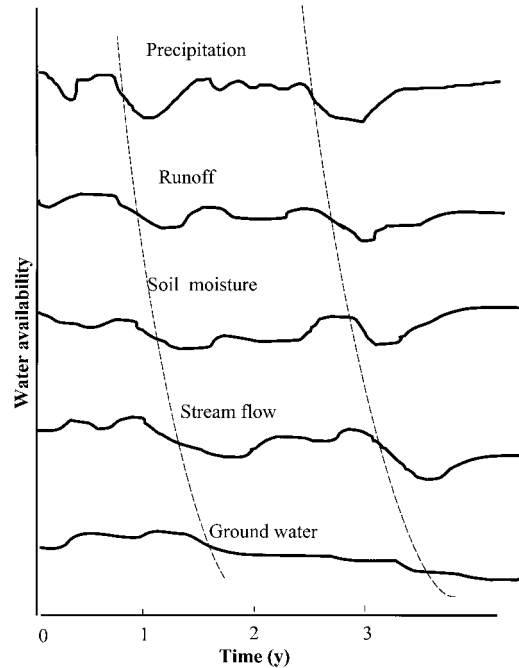


FIG. 3. The successive steps in the development of a drought, characterized by progressive decreases in water availability (Y-axis) in precipitation, runoff, soil moisture, stream flow, and groundwater. The dashed lines mark the onset of drought conditions for each environmental component (adapted from Changnon 1987). Two drought events are illustrated.

and Bass 1981, Extence 1981, Cowx et al. 1984, Smock et al. 1994, Erman and Erman 1995) (Fig. 4). Such habitat reduction also occurs regularly in systems that undergo very marked seasonal variability in flow, such as desert streams (Stanley et al. 1997) and tropical savanna streams (Douglas et al. 1995). Droughts give rise to a variety of patterns in longitudinal patchiness or in degrees of fragmentation in the normal stream continuum. Pools are formed, and larger and deeper pools downstream may persist while shallower upstream pools disappear (e.g., Lerderderg River and Creightons Creek, Victoria, Australia in 1996–1998 drought, P. S. Lake, personal observations). Alternatively, a stream may dry up for most of its length and be left with spring-fed pools at or near its source (Erman and Erman 1995; Pranjip Creek, Victoria, Australia in 1996–1998 drought, P. S. Lake, personal observations), or a stream may dry up completely throughout its length.

Droughts can exert many deleterious effects

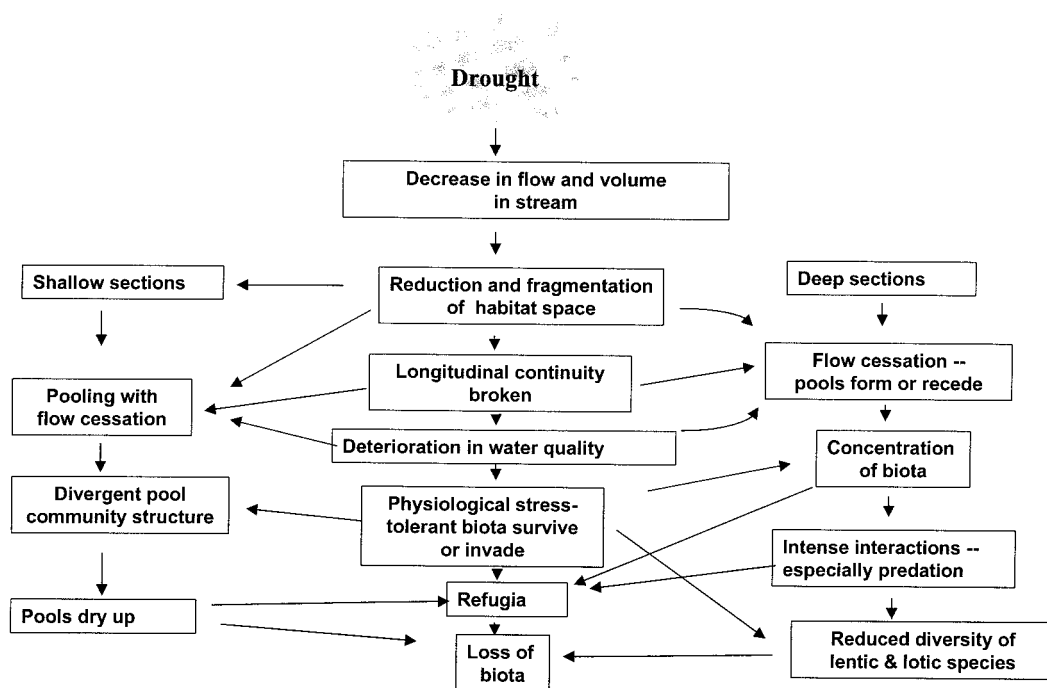


FIG. 4. A scheme of the progressive effects of drought on stream conditions and the biota. Beginning with reductions in habitat space and stream continuity (top of figure), a prolonged drought may result in great losses in habitat space and in biota (bottom of figure).

on streams. The complete loss of water depletes biota trapped without refugia (Larimore et al. 1959, Iversen et al. 1978, Extence 1981, Smock et al. 1994). Other effects are the deterioration of water quality, high water temperatures, and hypoxia (Larimore et al. 1959, Ladle and Bass 1981, Cowx et al. 1984, Chessman and Robinson 1987). Longitudinal ecological processes become fragmented, limiting instream transport of resources (e.g., nutrients), harmful materials (e.g., organic leachates), and biota. Ecological processes that are stimulated include algal blooms, increased competition and predation, and invasion of the channel by terrestrial plants and animals. In short, the longitudinal and lateral linkages that depend on water movement, and that make a stream a normal flowing ecosystem become disrupted.

The intensity of biotic interactions is thought to be reduced during and immediately after floods (e.g., Peckarsky 1983, Peckarsky et al. 1990), whereas in droughts interactions may become more intense as habitat space is reduced. During droughts, there may be loss of biomass

and resources from the channel. Predatory birds very effectively harvest trapped fish, and ants may harvest dying and dried-up animals from the channel (P. S. Lake, personal observations). Droughts are very difficult to study both in the terrestrial and aquatic realms because they tend to be unpredictable and develop slowly.

Disturbance and Patchiness

The biota, their resources, and their habitats are viewed as being distributed in streams as patches (Pringle et al. 1988, Barmuta 1989, Townsend 1989, Downes et al. 1993). Patches of biota and resources are linked with other patches longitudinally (e.g., upstream-downstream), laterally (e.g., channel-floodplain, channel-riparian zone), and vertically (stream bottom-hyporheic zone) (Townsend 1996). Patches can change in position, dimensions, and sharpness of boundaries with time, the 4th dimension (Ward 1989), and thus constitute parts of an ever-changing mosaic. Patches are changed most dramatically by floods and droughts. Such

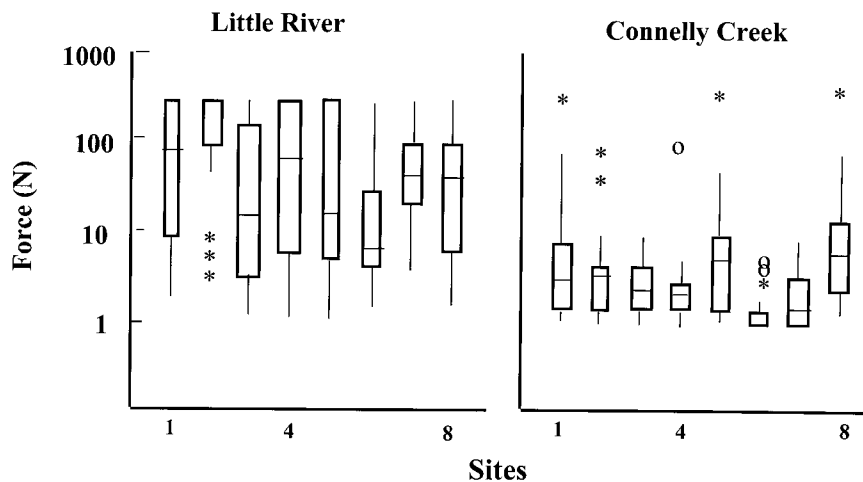


FIG. 5. High variability in the force required to shift rocks that occurs among rocks at any 1 site and between streams even when the streams are close to each other. Box plots of the force (N = Newtons) at each of 8 sites (1 = most upstream, 8 = most downstream) of 2 streams in the Acheron River system in Victoria, Australia. The boxes enclose the interquartile range, the horizontal line within the box indicates the median. The whiskers indicate 1.5 times the interquartile range, asterisks show values outside 1.5 times the interquartile range, and circles indicate values outside 3 times the interquartile range (from Downes et al. 1997).

major disturbances reconfigure patches and their linkages, setting the scene for new pathways of patch development (Fisher and Grimm 1991, Townsend 1996). However, their position and boundaries also change even under conditions of steady flow. For example, patches of the red alga *Audouiniella hermanni* developing on stones may develop a diverse and distinctive invertebrate fauna under summer low flow (Downes et al. 2000). Floods in sandbed streams, may create large patches or reaches of biota-depleted sand that are then colonized by algae and animals (e.g., Fisher et al. 1982). Substrata in stony streams may be scoured, rolled over and moved, and their biota depleted (e.g., algae: Peterson 1996, Mosisch and Bunn 1997; invertebrates: Boulton et al. 1992a, Cobb et al. 1992, Death 1996, Matthaei et al. 1997a). The degree of flood disturbance at a site is sometimes estimated by calculating the proportion of substrata that is finer than the critical particle size that can be moved by a discharge event reaching a certain depth (Cobb et al. 1992, Newbury and Gaboury 1993, Scarsbrook and Townsend 1993). Such a determination assumes a linear relationship between critical shear stress and particle size. The relationship may only apply for streambeds of uniform particle size and not for heterogeneous and steep streambeds (Wiberg

and Smith 1987, Duncan et al. 1999). Downes et al. (1997) measured the tractive force required to move rocks at 32 sites in 4 upland streams, and found considerable variability in critical force between rivers and high variability between rocks at individual sites. Intrasite variability was related to rock sizes and extent of imbrication. (Fig. 5). Such obvious interstream differences in the forces required to move stones (even within the same catchment), imply that floods, even of similar magnitude, will produce differing forms of patchiness. The results of Downes et al. (1997) confirm the doubts held by some (e.g., Andrews 1983, Wiberg and Smith 1987, Death and Winterbourn 1994, Duncan et al. 1999) on the universality of the critical tractive force-particle size correlation. High between-stone variability, and hence variability in patchiness, is also suggested by the high variability recorded for the movement in floods of marked stones placed on the streambed (Lake and Schreiber 1991, Death and Winterbourn 1994, Townsend et al. 1997b, Downes et al. 1998a). Using stones marked in situ, Downes et al. (1998a) found considerable movement of stones both on the surface and packed into the bed, not only during the wet winter season but even in the low-flow summer. Furthermore, there was considerable spatial clumping of dis-

turbed stones in both seasons as indicated by degrees of aggregation. Therefore, biota-depleted patches varying from single stones to clumps of stones can be continually produced by disturbance in stony upland streams. Downes et al. (1998a) also found that human-placed stones had disturbance frequencies $\frac{1}{2}$ those of stones marked *in situ*. This result strongly suggests that the movement of marked human-placed stones in stony streams is a poor measure of disturbance, counter to the suggestion of Townsend et al. (1997b).

Patch size and shape for particular biota may vary with time and season, with discharge, and with position in the stream channel. New patches created by disturbance, such as individual stones in a riffle (Death 1996, Downes et al. 1998a), may differ in their distinctiveness in relation to their surroundings, and this difference may fade as the patch is colonized and comes to resemble its surroundings. At the other extreme, a flood that disturbs and moves the entire streambed may create large patches with diffuse boundaries. This effect is encountered in sandbed streams, but may occur in any stream with disturbances having high shear forces (e.g., Fisher et al. 1982, Palmer et al. 1992). This description is partly speculative because there is little information on the size and spatial aggregation of biota-depleted patches in streams with different levels of disturbance.

Drying events can generate new patterns of patchiness at different spatial scales (Stanley et al. 1997) (Fig. 4). For example, at the reach scale, riffles dry up much more rapidly than pools (Boulton and Lake 1990, Stanley et al. 1997), and pools themselves may become a series of small isolated pools before drying up completely. Pools can persist and may undergo major changes in community composition and densities. Such pools may become controlled by local rather than longitudinal processes. Thus different populations, especially fish, may diverge markedly as differing forms and strengths of top-down control come into play (Power et al. 1985). The fragmentation process caused by drying may exert powerful and lingering effects on the ecology of streams (Boulton and Lake 1992b, Stanley et al. 1997).

Disturbance and Refugia

The effects of a disturbance generated by changes in water movement may be ameliorated

if the biota use refugia (Sedell et al. 1990). Refugia in stream ecology have been largely defined in the context of floods, although low-flow refugia have been recognized (Lancaster and Hildrew 1993a). Refugia are either places or "temporal synchronisms between the heterogeneity of flow and the organisms' life cycle, life history or habitude" that reduce disturbance-dependent mortality (Lancaster and Hildrew 1993a, Lancaster and Belyea 1997). Lancaster and Belyea (1997) described 4 classes of mechanisms of refugium use. Two, which apply between generations and between habitats are "refugia through complex life cycles" and "between-habitat refugia". The 1st class may apply, for example, to the biota with desiccation-resistant life stages that live in temporary streams (e.g., Clifford 1966, Boulton 1989) and possibly those animals in the "seed" or egg bank of the streambed (Zwick 1996). The 2nd class may apply to biota in a stream system that is only partly damaged by disturbance; the biota in undisturbed sections could potentially colonize the depleted sections (Stanley et al. 1994). Two other mechanisms apply to biota within generations and at small spatial scales—"refugia through changes in habitude" and "within-habitat refugia" (Lancaster and Belyea 1997). The former occurs when biota normally dwelling in a habitat survive disturbance through changes in habitat use. For example, 1st-instar insects may dwell in the hyporheic zone and recolonize the surface after a disturbance. Within-habitat refugia occur when a habitat patch has areas in which the effects of a disturbance are reduced. This refugium is the most common type that has been studied. During a disturbance, animals actively move or are passively carried into the refugia. In a structurally heterogeneous channel, there may be many obstacles, holes, interstices, or pieces of debris that offer protection from disturbance.

Flood refugia

Both descriptive studies (Lancaster and Hildrew 1993b, Robertson et al. 1995, Dole-Olivier et al. 1997, Brooks 1998) and experimental studies (Palmer et al. 1992, 1995, Winterbottom et al. 1997) have reported biota using within-habitat refugia during spates. Brooks (1998) found evidence for the passive movement of organic matter, chironomids, and mayflies into pools during

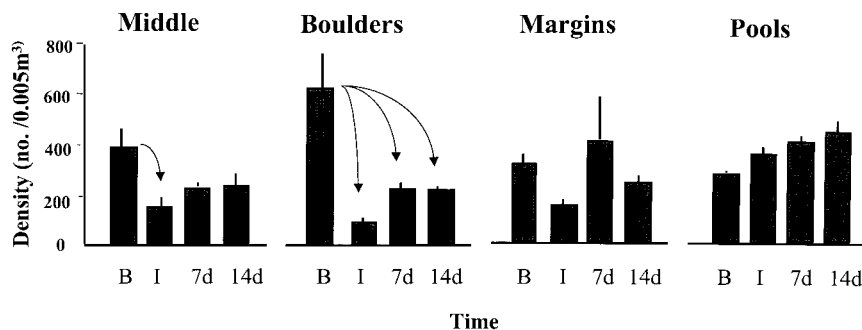


FIG. 6. Changes in the total abundance (mean \pm SE, $n = 128$) of macroinvertebrates in 4 habitats (middle of the channel, behind boulders, at channel margins, and in pools) before (B) and after a major flood (duration = 2 d) in the Lerderderg River, Victoria. I = immediately after the flood, 7 d = 7 d after the flood, 14 d = 14 d after the flood. Arrows indicate statistically significant ($p < 0.05$, 2-way [time by habitat] ANOVA followed by post-hoc before- and after-contrast tests) departures from preflood densities. (Adapted from Brooks 1998.)

a large flood in a temporary river, the Lerderderg River, Australia. In contrast several species in the middle of the channel were not depleted by the flood, including the glossosomatid *Agapetus kimminsi*. Experimental channel studies showed that with either increasing turbidity or velocity (both mimicking flood conditions), *A. kimminsi* actively sought refuge by moving from the tops of stones to the sides. This finding corroborates the observations of Cobb et al. (1992) that *Glossosoma intermedium* resides under cobbles and boulders during spates.

In Brooks's (1998) study, areas downstream of large, protruding boulders had a rich and diverse fauna before the flood and were hypothesized to be flood refugia. However, during the flood, water rose over the boulders and changed the downstream zones into areas of great turbulence and scouring that removed most of the fauna and organic matter. Thus, areas downstream of large boulders may be disturbance-dependent refugia, safe at 1 depth and sites of denudation at higher levels (Fig. 6). The major refugium in the Lerderderg River is provided by interstitial spaces between the rocks in the stream channel (Brooks 1998). These rocks are tightly imbricated and will only move in massive floods.

The availability of suitable refugia in streams may be a critical measure of the levels of resistance and resilience to disturbance. Recolonization after floods is usually rapid in streams with a bed composed of large, tightly imbricated rocks and, hence, many refugia (e.g., Brooks 1998, Matthaei et al. 1996, 1997a). The impact of

floods may be great and recovery of macroinvertebrates relatively slow in streams with a loosely structured sand bed and few refugia (Fisher et al. 1982, Grimm and Fisher 1989). Aerial colonization over a considerable distance may be the major form of recruitment (Gray and Fisher 1981).

Drought refugia

Very little is about known refugia from drought. When flow ceased in 2 intermittent Australian streams, Boulton (1989) identified 8 types of refugia for 91 taxa of macroinvertebrates. These refugia are used seasonally and may not all persist through a long drought. Receding pools contained most of the taxa, whereas the hyporheos and the pholeteros (fauna of crayfish burrows; Lake 1977) contained only a few taxa. Almost $\frac{1}{2}$ of the taxa used refugia without free water, such as under stones, litter, and coarse woody debris in the dry streambed. In contrast, Sycamore Creek, Arizona, had only 3 types of onsite refugia: dried litter, the hyporheic zone, and the dry streambed. Recolonization of the stream was controlled by aerial sources (Boulton et al. 1992b), and from upstream sites of permanent water linked with the downstream dry sites when flow returned (Stanley et al. 1994). Space under stones in intermittent streams is a multipurpose refugium used to survive floods, to evade fish predation (Closs 1996), and to survive dry periods. Clearly, as is the case with floods, there may be a great variety of refugia during droughts, each type with

its own pattern of patchiness. Unfortunately, we still know little about the influences of the patchiness of different refugia on the spatial patterns of stream community recovery after floods, let alone after droughts (Palmer et al. 1996, Stanley et al. 1997). A further complication in studying any recovery is that, in Australia at least, droughts are often broken by severe floods.

Resilience: Recovery after Disturbance

Floods

Although resistance to floods (a pulse disturbance) by stream biota is low, the resilience or capacity to recover is typically high (a pulse response). The rate of substrate recolonization is usually rapid, and depends on the intensity of the disturbance, the spatial extent of the area disturbed, the availability of colonists, and the composition of the biota (Sheldon 1984, Lake 1990, Wallace 1990, Yount and Niemi 1990, Mackay 1992). However, there are exceptions. Recovery may be slow or prevented (a press or ramp response) where flooding is very severe (e.g., Scrimgeour et al. 1988), or occurs out of season (e.g., Giller et al. 1991). It is unclear how strongly postflood recovery depends on the availability of refugia (Lancaster and Belyea 1997). Palmer et al. (1995, 1996) found that the rapid recovery of biota in a sandy stream was unrelated to the use of refugia, whereas Brooks (1998) found that faunal recovery was related to both the availability and use of refugia.

The high mobility of most stream animals contributes to the high rate of recovery. Mobility allows many animals to use refugia and to recolonize after disturbance (Mackay 1992, Winterbottom et al. 1997). Recolonization of disturbed streambeds may occur by drift, surface movements, movement from the hyporheic zone, swimming, and flight (Williams and Hynes 1976, Mackay 1992). Drift appears to be a major avenue in perennial streams (Williams and Hynes 1976, Matthaei et al. 1997b), whereas aerial recolonization may be the major route in temporary streams (Gray and Fisher 1981). Recolonization strategies differ among biota (Khalaf and Tachet 1977, Lake and Doeg 1985, Winterbottom et al. 1997). Some species, notably simuliids, colonize bare patches rapidly and may disappear as quickly (Ciborowski and Clifford

1984, Downes and Lake 1989), whereas others, notably grazers and predators, are slow and steady colonizers (McAuliffe 1984, Hart 1985, Lake and Doeg 1985, Mackay 1992). In both cases, success may depend on the availability of resources. Patch characteristics, such as species composition, change with time after disturbance. Two important features of the colonization process are 1) that the return to pre-flood abundance levels is generally rapid and precedes species richness, and 2) the return of species richness usually follows a smooth trajectory to an asymptote, suggesting that, in spite of the disturbance (Minshall and Petersen 1985), species richness at both the patch and site levels is fairly constant and well regulated.

The amount and extent of patchiness of streambeds disturbed by high water events varies greatly from single rocks being rolled (Downes et al. 1998a) to entire streambeds in motion (e.g., Molles 1985, Sagar 1986). Small but detectable spates create small disturbed patches in an otherwise intact streambed that may harbor a normal fauna (e.g., Brooks 1998). In contrast, big floods may reduce the fauna greatly over a considerable area (e.g., Hoopes 1974, Smock et al. 1994).

It has been argued (e.g., Brooks and Boulton 1991) that experimentally disturbing small patches of streambeds poorly equates with natural flood conditions. However, the similarity between natural and experimental conditions may vary with flood magnitude. Matthaei et al. (1997a) were able to compare the effects on the fauna of a large natural flood with the experimental disturbance of small patches in a Swiss river. They found, surprisingly, that there was a great similarity between the faunal patterns and dynamics of the natural and experimental disturbances. This result needs testing elsewhere but is encouraging for future experimental studies. Matthaei et al. (1997b) correctly argued that small-scale studies of benthic recolonization notably by drift (e.g., Doeg et al. 1989b) do not simulate the large-scale, faunistically depleted conditions that follow large floods. However, small-scale studies do simulate the conditions prevailing after the much more common small spates that create small depleted patches surrounded by large intact patches. Floods of different magnitudes may create patches of different sizes and configurations, and both rates and routes of colonization by the biota of the patches

may vary greatly. By generating such patch heterogeneity, floods may strongly influence both the levels and maintenance of diversity in streams.

Droughts

In contrast with the information on flood effects, there have been relatively few studies of stream faunal dynamics after droughts (e.g., Hynes 1958, 1961, Larimore et al. 1959, Harrison 1966, Iversen et al. 1978, Extence 1981, Ladle and Bass 1981, Griswold et al. 1982, Resh 1982, Cowx et al. 1984, Morrison 1990, Boulton and Lake 1992a, 1992b, Boulton et al. 1992b, Smock et al. 1994, Erman and Erman 1995). Most reports are from mesic, temperate regions; only 4 of the above references (Harrison 1966, Boulton and Lake 1992a, 1992b, Boulton et al. 1992b) concern areas regularly subject to severe droughts. In all of these studies, the droughts were defined in relation to local normal conditions and, consequently, varied tremendously in severity. Duration ranged from ~10 wk (Hynes 1958) to >2 y (Larimore et al. 1959).

In general, recovery from drought by invertebrates and fish takes more time than recovery from floods (Griswold et al. 1982, Niemi et al. 1990, Boulton and Lake 1992b, Boulton et al. 1992b). Colonization of drought-affected streams or stream sections may occur by 5 avenues: 1) movement from subsurface (hyporheic) refugia, 2) hatching or reactivation of drought-resistant stages, 3) upstream movement, 4) downstream migration notably by drift, and 5) aerial recolonization either by adults (e.g., beetles and water bugs) or through oviposition (Williams and Hynes 1976). The avenues used vary. In some drought-affected Scottish streams, recolonization of insects was mostly from drought-resistant eggs or from eggs laid by flying adults (Morrison 1990), whereas upstream movement and aerial recolonization were the major avenues of recolonization in a South Carolina stream after drought (Smock et al. 1994). As for floods, abundance levels return more rapidly than levels of species richness in recovery from droughts (Hynes 1961, Iversen et al. 1978, Cowx et al. 1984).

Distinct signs of succession characterize recovery from drought. Recolonization in an intermittent Zimbabwean stream was marked by a transient boom in simuliids and chironomids, which were replaced by "more permanent

members of the fauna, such as *Baetis harrisoni*" (Harrison 1966). A long lag in the recovery of the biota and the elimination of some species are characteristic of faunal dynamics after drought, in contrast to floods (e.g., Hynes 1961, Ladle and Bass 1981, Boulton and Lake 1992a). Ladle and Bass (1981) found a variety of common taxa (e.g., *Polycelis felina*, *Herpetocypris reptans*, *Agapetus fuscipes*) greatly reduced in abundance in a small chalk stream after drought, whereas the common amphipod *Gammarus pulex* was "practically eliminated". Like the simuliids in Harrison's (1966) study, some taxa appear to be favoured by drought. Two plecopteran and 1 ephemeropteran species steadily increased in abundance, possibly as a result of reduced competition and predation, after a drought that greatly reduced the abundance of up to 11 common insects (Hynes 1961). In summary, recovery after drought may take considerable time, species may be greatly depleted if not eliminated, and faunal dynamics may be somewhat unpredictable because the effects of drought are very species-specific compared to recovery after floods.

Disturbance, Patchiness, and Diversity

Floods and droughts in natural stream systems vary both in intensity and duration. Although overall changes in the fauna and its use of refugia with disturbance have been described, few studies that have investigated the changes in patchiness induced by disturbance, and that occur during recovery. The flood studied by Brooks (1998) (Fig. 6) disrupted the substrata of pools and channel margins, but the fauna recovered rapidly. The fauna living behind boulders was abundant before the flood, but flooding greatly depleted these areas, and they had not recovered by the end of the study (Fig. 6).

The variable flow patterns of most streams and rivers generate the marked spatial and temporal heterogeneity that characterizes these systems (e.g., Poff and Ward 1990, Giller 1996, Palmer and Poff 1997, Poff et al. 1997, Puckridge et al. 1998). Thus, disturbance-related variables such as the multivariate instability index of Death and Winterbourn (1995) and a range of hydrological variables, especially FRE3 (frequency of floods >3 times the median flow, Clausen and Biggs 1997), are strongly correlated

with both invertebrate species richness and total abundance. Increasing disturbance levels negatively correlate with species richness.

Given the heterogeneity of perennial streams, it is not surprising to find that abundance may fluctuate greatly and there is continuous species turnover (Lake et al. 1985, Minshall et al. 1985, Flecker and Feifarek 1994). However, species richness at the local habitat scale may be surprisingly constant (e.g., Lake et al. 1985, Giller et al. 1991, Death and Winterbourn 1994). Furthermore, there is a strong species-area relationship for invertebrates on stream stones (local habitat scale), not generated by passive sampling (Hart and Horwitz 1991, Douglas and Lake 1994), suggesting strong local regulation of species richness (Downes et al. 1998b, 2000). The strong regulation of species richness occurs even though there is a continual change in species composition, a situation very much at odds with the equilibrium conditions integral to island biogeography theory (MacArthur and Wilson 1967). Strong regulation of species richness at the local habitat scale is also suggested by the rapid yet predictable species recolonization of disturbed substrata (e.g., Lake and Doeg 1985, Doeg et al. 1989a, Death 1996, Matthaei et al. 1996, 1997a) in which species richness rapidly reaches an asymptote. Downes et al. (1998b) demonstrated that manipulation of surface structure (pits, cracks, and rough or smooth surfaces) and macroalgae, while holding surface area constant, strongly influenced species richness; the former 2 variables were strongly correlated with area (Downes et al. 1995). Further, Downes et al. (2000) showed that surface structure and macroalgae acted independently in regulating species richness. Thus, even under highly nonequilibrium conditions, species richness appears to be tightly regulated at the local habitat scale, and this regulation operates on new or disturbance-depleted patches. Colonization is rapid and predictable even after repeated disturbance (Clifford 1982, Death 1996, Lake et al. 1989).

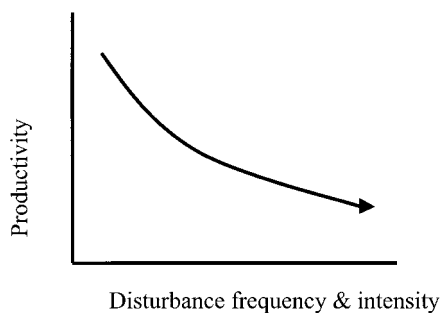
It appears that there is strong regulation of species richness at the habitat level, and that the species in each habitat are drawn from a regional pool. The idea of a regional species pool is linked with the concept of regional species richness, and leads on to the relationships between local and regional species richness (Connell and Lawton 1992). The distinction between local

(habitat-specific) and regional scales of species richness is currently unclear, especially in streams (Angermeier and Winston 1998). One definition of region is the particular stream and its catchment ("watershed" of Frissell et al. 1986, "drainage" of Grimm and Fisher 1992, "HP region" of Angermeier and Winston 1998). This regional unit harbors the species pool that provides the species that colonize, at a small local scale, habitat patches in that stream.

Most theories of species diversity regulation are not scale-specific. Indeed, scale has rarely been considered in this context. Thus, the keystone species concept may operate at the local scale of a rock platform, whereas the intermediate disturbance hypothesis may operate at the scale of a very large area of rainforest (Connell 1978, Collins and Glenn 1997). Ward and Stanford (1983) detected a pattern of species diversity among separate river systems that was consistent with the intermediate disturbance hypothesis. However, experiments involving multiple disturbance at sites within a single stream have not supported the hypothesis (e.g., Reice 1985, Lake et al. 1989). These 2 studies were probably executed at scales that were both inappropriate spatially and temporally inappropriate. Furthermore, Wootton (1998) has argued that the intermediate disturbance hypothesis may not apply to multitrophic systems such as stream communities, which have usually 2 food chains, 1 based on detritus and 1 based on algae, and each with at least 3 trophic levels. Townsend et al. (1997a) found evidence for the intermediate disturbance hypothesis in a correlational study. Streambed disturbance (stone movement) was "by far the best at accounting for variation in taxonomic richness" across the 27 monitored tributaries of the Taieri River, New Zealand.

There are at least 2 ways that a unimodal curve of species richness against disturbance frequency/intensity could be generated. The usual explanation is that high levels of disturbance create harsh conditions that permit only a limited fauna of highly mobile opportunists to survive (Connell 1978). Conversely, in streams with low levels of disturbance, competition may be so intense that only a limited fauna of strong competitors survives. A mixture of the 2 faunal types persists, yielding increased diversity at intermediate levels of disturbance. Although there is evidence for opportunists, it is difficult to

A. Disturbance and productivity



B. Productivity and species richness

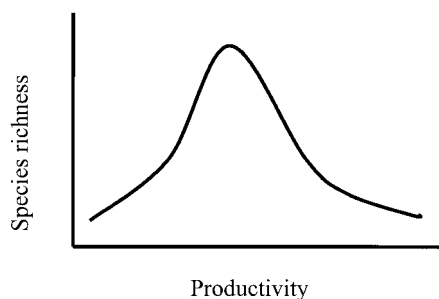


FIG. 7. Suggested relationship between disturbance, productivity, and species richness at sites within a region. A.—Large scale hydrological factors generate a pattern in which productivity for a range of sites is negatively correlated with increasing levels of hydrological disturbance. B.—A unimodal relationship between productivity and species richness (Rosenzweig 1995) is generated across this range of sites with different productivities, with low species richness at both the high and low productivities, and high levels of species richness at sites of intermediate productivity.

gather unequivocal evidence for competition as a powerful community structuring force, especially in streams.

Alternatively, invertebrate species richness may be linked to productivity (Rosenzweig 1995). Disturbance could generate a linear gradient of low primary productivity with high disturbance and high productivity with low disturbance (Fig. 7A). This productivity gradient then gives rise to the well-known unimodal curve relating productivity and species richness

(Rosenzweig and Abramsky 1993, Rosenzweig 1995) (Fig. 7B). Nine hypotheses have been proposed to explain the decline in species richness with high productivity (Rosenzweig 1995), one of which involves disturbance. The interaction between productivity and disturbance, and in turn with species richness, has also been modeled by the dynamic-equilibrium model of Huston (1994). This model has been applied successfully to riparian plants subjected to a range of flood regimes (Pollock et al. 1998). Species richness was low at sites subject to either high and low flood frequencies and with low productivity, whereas species richness was high at sites of both intermediate productivity and flood frequency. It will be difficult to test these hypotheses by experimental manipulation given the large spatial scale required. Rather, evidence may need to be accumulated in descriptive studies relating disturbance to species diversity across gradients of sites.

A hierarchically nested pattern of mechanisms may operate in streams to regulate species richness (Fig. 8). The interactions between climate and geomorphology at the regional level generate a flow regime with a distinctive disturbance regime. The disturbance regime, especially frequency and intensity, may be a major regulating influence on species richness at this regional scale and may generate pools of potential colonists for the various types of habitat patch (Fig. 8A). Thus, the fauna for each type of habitat patch may be drawn selectively from a regional pool (Fig. 8A). At the local scale of a particular type of habitat patch, strong interactions, such as competition for resources, may regulate local diversity (Fig. 8B). It may be difficult to carry out experiments at the large regional scale required to test this hypothesis, although advances may be made with experiments carried out at the local scale across regional gradients. It would be most instructive to ascertain how selectively species at the local habitat level are drawn from regional pools, and to determine the nature and strengths of interspecific interactions and their role in diversity regulation at the local scale. Needless to say there is a dearth of information on both of these important problems.

Conclusions

Natural disturbances caused by variations in water movement and flow volume exert a major

A. DIVERSITY AT REGIONAL SCALE (S_R)

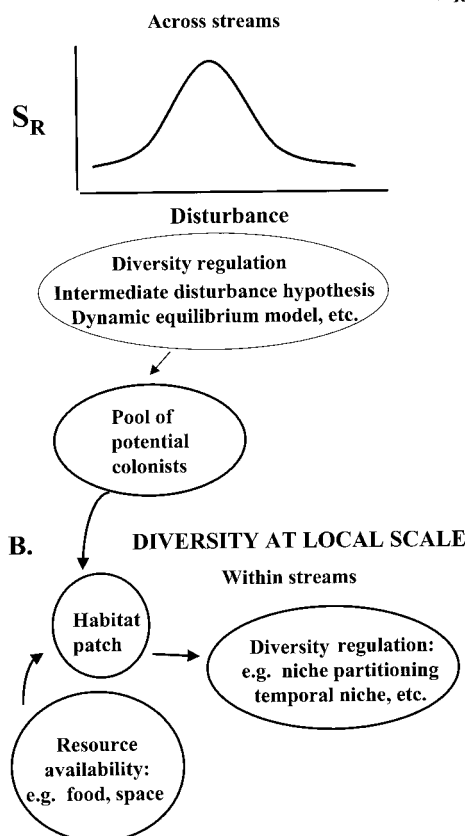


FIG. 8. Scheme of suggested relationships between the regulation of diversity at the regional scale of streams (A) and at the local scale of habitat within streams (B). I suggest that, for sites within a region, hydrology interacting with stream geomorphology produces the disturbance regime that then determines species diversity of potential habitat colonists. At the local scale of a habitat patch (B), species diversity is a function of the interaction between the pool of colonists and resource availability. The determining interaction may operate by mechanisms such as niche partitioning.

influence on ecological structure and function in streams across a range of scales from local to regional. For progress to be made in understanding the disturbance ecology of streams, there is still the need to quantify the abiotic properties of disturbance to allow meaningful comparisons between disturbance events and between streams. Disturbances differ in their temporal nature—pulse, press, and ramp—and, in turn, the responses of the biota differ. Floods

and droughts differ greatly in their effects on the abiotic environment of streams and, in turn, on the biota. Most floods have short-term effects but some may cause major changes in species composition. In contrast, droughts may generate a marked lag effect on diversity. Floods may re-establish or augment upstream–downstream continuity, whereas droughts generate fragmentation. The impacts of droughts on stream habitats and biota are poorly understood.

The effects of disturbance on the biota (resistance) and the subsequent response of the biota (resilience) are both mediated by the availability of a variety of refugia. A disturbance creates a new pattern of patchiness, which subsequently changes as the biota recover from the impact of the disturbance. The species diversity at the habitat patch level is strongly regulated, with the availability of resources being a major avenue of regulation. At the catchment level, disturbance caused by floods and by droughts may regulate diversity. Thus, the evidence is steadily accumulating for many streams to show that extreme events (disturbances) exert strong and even persistent effects on community structure and functioning.

Future global climate change caused by forces such as the greenhouse effect will undoubtedly have strong effects on the ecological structure and functioning of stream communities (Firth and Fisher 1992, Arnell et al. 1996). Steady changes in temperature, precipitation, and stream hydrology will influence stream biota, but such effects may be minor compared to the impact of extreme events. It is now generally accepted that major impacts of global warming on streams, especially aridland streams, are likely to be experienced through changes in the frequency of extreme events—floods and droughts (Whetton et al. 1993, Fowler and Hennessey 1995, Arnell et al. 1996). Thus, faced with this future, it becomes essential that we gain a clear understanding of the links between stream patchiness, function, and diversity, an understanding that incorporates disturbance as a major driving force.

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