

Colonization by Lotic Macroinvertebrates: A Review of Processes and Patterns

Rosemary J. Mackay

Department of Zoology, University of Toronto, Toronto, Ont. M5S 1A1, Canada

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Ways in which invertebrates colonize lotic habitats are reviewed, tracing patterns in behaviour, trophic ecology, and life history that could lead to predictions concerning resilience of stream communities after disturbance. Patterns are described for small-scale experimental studies using introduced or natural substrates, for large-scale observations of new or rewatered channels, for rivers recovering from pollution, and for unstable rivers with fluctuating discharge. Colonization depends on invertebrate mobility (drift, swimming, crawling, and flight), substrate texture and associated food supplies, competition, and predation. Epilithon-browsers and filter feeders can use the resources of smooth stones; gatherers colonize as fine detritus accumulates; grazers increase as periphyton becomes established; shredders and predators tend to be late arrivals. Propagules for colonization are made more available by asynchronous and aseasonal life cycles, long oviposition periods, and refuges in the streambed or neighbouring waterbodies. Species in frequently disturbed streams benefit from these characteristics. Although disturbance may be due to stochastic factors, recovery is not due to chance. Recurring ecological patterns among early colonizers suggest that knowledge of the hydrologic regime, food resources, and dominant taxa can be used to predict the overall resilience of a stream community.

L'auteur examine les diverses manières dont les invertébrés colonisent les habitats lotiques en établissant les schèmes de comportement, l'écologie trophique et les cycles de vie qui pourraient permettre de prévoir la capacité de rétablissement des communautés des eaux courantes après qu'elles aient été perturbées. Il décrit les régimes établis lors d'expériences à petite échelle à partir de substrats nouveaux ou naturels, d'observations à grande échelle de nouveaux et d'anciens lits, ainsi que d'études de rivières après leur pollution et de rivières instables à débit irrégulier. La colonisation dépend de la mobilité des invertébrés (dérive, nage, reptation et vol), la texture du substrat et les ressources alimentaires qu'il contient, la compétition et la prédation. Les brouteurs d'épilithon et les filtreurs peuvent se nourrir à même les pierres lisses; les récolteurs s'établissent au fur et à mesure que les détritins fins s'accumulent; l'abondance des brouteurs augmente en fonction de la croissance du périphyton tandis que les prédateurs et les déchiqueteurs tendent à s'implanter en dernier. La colonisation par propagules est favorisée par des cycles de vie asynchrones et non saisonniers, de longues périodes d'oviposition et le refuge dans le lit du cours d'eau ou des bassins avoisinants. Les espèces peuplant des cours d'eau fréquemment perturbés bénéficient de ces caractéristiques. Quoique les perturbations peuvent être le résultat de facteurs stochastiques, le rétablissement ne se fait pas au hasard. Des schèmes écologiques récurrents observés chez les premiers colonisateurs portent à croire qu'une connaissance du régime hydrologique, des ressources alimentaires et des taxons dominants peut permettre de prévoir la capacité de rétablissement d'une communauté lotique.

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1. Introduction

Streambeds providing the basic habitat of lotic invertebrates are variously exposed to the forces of flowing water and, in certain climates, to drought. Because most invertebrate species are mobile or sedentary rather than sessile, many individuals are displaced during periods of high discharge when rocks may be scoured, overturned, or rolled downstream, and finer streambed substrates are stirred or shifted. Even moderate variations in flow often result in unoccupied patches of substrate. At the other extreme, drought may temporarily bare the entire streambed. In spite of such disturbances to their environment, benthic invertebrates are diverse and abundant in unpolluted running water. How do populations reestablish themselves?

According to theories developed by MacArthur and Wilson (1967), a superior colonizer in an uncrowded environment has

an advantage due to its high rate of population growth. Associated characteristics are small body size, semelparity, and short life span (Pianka 1970). These traits are shared by most stream-living macroinvertebrates (although many molluscs are exceptions); and if true to theory, at least the arthropods dominating lotic benthic assemblages should be good colonizers. They are, of course, in the sense that they maintain populations in the often-uncertain habitat of a stream. However, as this review will demonstrate, some taxa are faster colonizers than others and share features of life history and trophic ecology that give them additional advantages in the early stages of community development.

The purpose of this review is (1) to trace patterns of colonizing ability that are evident from descriptive and experimental studies in many different streams and (2) to show that these

patterns have predictive value which may be used to assess the potential resilience of streams exposed or vulnerable to unnatural disturbance. The emphasis is on insects because more information on them is available.

The need to find ways of predicting responses to disturbance is particularly urgent in the case of streams and rivers because benthic habitats are often disrupted indirectly by practices and pollutants in surrounding catchments. May (1984) doubted that any multispecies community was sufficiently well understood for confident predictions to be made about its response to disturbance. But he also acknowledged that practical decisions on environmental matters often have to be made in spite of imperfections in our knowledge. Tentative generalizations or patterns are a first step in developing guidelines for practical management problems. Moreover, the detection of natural patterns is the mission of community ecology (Wiens 1984) and forms the basis for hypotheses to explain the processes causing patterns.

In the last decade, ecologists in general have come to realize that disturbance may play an influential role in community dynamics (Sousa 1984; Strong et al. 1984). Thus, stream communities disturbed by highly variable discharge, for example, like many in Australia and New Zealand, would be kept in a nonequilibrium state and prevented from achieving ecological saturation and tight species packing, which theoretically should characterize a stable, resource-limited and niche-controlled structure (Resh et al. 1988; Townsend 1989).

A disturbed stream, then, has not been seen merely as a practical problem to be tackled by applied ecologists. A disturbance, either real or simulated, has also enabled more basic stream ecologists to explore theories on island biogeography and the relative importance of stochastic and deterministic processes in shaping community structure. As a result, a large body of literature has developed on the rates at which bare patches of stream substrate, both large and small, are colonized by invertebrates. Studies of recovery following disturbance have shown or suggested the colonization mechanisms responsible for restoring a community to its predisturbance state. Gore and Milner (1990) and Wallace (1990) reviewed many of these mechanisms, and Sheldon (1984) and Gore and Milner (1990) discussed some numerical responses of colonizing aquatic insects. No review, however, has looked for correlations between named colonizing taxa, their ecological characteristics, and the types of streams they inhabit. This review considers how, and under what environmental influences, invertebrates colonize newly available space at four different scales: small bare patches, denuded reaches, new or rewatered channels, and broadly disturbed streams. Characteristics common to early or late colonizers are examined for patterns that might lead to predictions for recovery following disturbance.

2. Colonization Scales and Mechanisms

Spatial and temporal scales of colonization range from biogeographic to extremely local and immediate phenomena. Vivid examples in running waters were given by Sheldon (1984). The scale of most experimental work in streams has been small (<1 m² of streambed) and has documented the establishment of macroinvertebrate assemblages following a variety of treatments that ensured an initial absence, or lowered density, of organisms. A recurring theme in such studies has been the MacArthur–Wilson model of island colonization, the islands being the bared stones or patches of substrate (or introduced substitutes) (Gore and Milner 1990). It is arguable whether such

an approach is a proper use of the model given that (1) the original theory was developed for species breeding on islands whereas residency in stream patches is transitory, (2) stream “islands” are not surrounded by a foreign and inhospitable “sea”, and (3) the species pool equivalent to the model’s mainland, which is the source of colonizers, is usually the immediately adjacent streambed. The island situation does not even resemble the modified scenario of Simberloff (1974). In spite of their imperfections in terms of the MacArthur–Wilson model, however, small-scale studies of colonization have resulted in valuable information on the mobility of lotic macroinvertebrates and their particular responses to bare patches of substrate.

Investigations of bare streambeds on a larger scale, as in a newly made stream channel, are rare; but streams exposed to severe disturbance have received more attention and share many of the drawbacks facing colonizers. A new channel with no previous inhabitants relies on somewhat distant sources for immigrants. Streams recovering from spates, drought, or unnatural chemical inputs may likewise depend on distant sources of colonizers but sometimes retain a few species or individuals in an unaffected refuge or life history stage.

Whatever the scale or cause of the uninhabited area of streambed, colonizers may reach a restored habitat in one or more ways: drifting (in the water) from upstream sources, crawling or swimming from adjacent substrates, including the hyporheic habitat, hatching from eggs laid near, on, or in the water, or flying in (amphibious bugs and beetles) and resuming an aquatic existence (Williams and Hynes 1976). Both the method and the timing of immigration by particular organisms depend on specific traits expressed in behaviour and life cycles that cause or allow a certain pattern.

3. Factors Affecting Colonization of Small Patches

3.1. Mobility of Invertebrates

Bare substrates placed in a stream have been shown to house invertebrates within 24 h, even when the substrates beforehand had been thoroughly dry or acid-scoured (and thus without epilithic growths) rather than merely brushed free of fauna (e.g. Wise and Molles 1979; Ciborowski and Clifford 1984; Lake and Doeg 1985; Boulton et al. 1988; Doeg et al. 1989b). Such rapid occupation of empty habitat shows that certain stream dwellers are extremely mobile. Some of these early arrivers may merely inspect the substrate during the course of their normal widespread foraging, and then depart just as rapidly (Giller and Cambell 1989). More sedentary organisms may be true colonizers in that they remain in the habitat until some other factor removes them or stimulates their departure some days or weeks later. Only net numerical change, rather than actual immigration and emigration, has been followed in most colonization studies; but some taxa increase in density sooner than others, reflecting both their own activity and the means by which propagules arrived.

3.1.1. Drift

When introduced substrates have been positioned to allow access from only certain sources (drift, adjacent natural substrates, air), drift seems to have provided most of the immigrants (Townsend and Hildrew 1976; Williams and Hynes 1976; Bird and Hynes 1981; Benson and Pearson 1987). Certainly those taxa most often listed among the earliest arrivals on bare substrates, such as Baetidae, *Gammarus*, Simuliidae, and Chironomidae (e.g. Waters 1964; Ulfstrand et al. 1974; Hynes

1975; Gray and Fisher 1981; Lake and Doeg 1985; Malmqvist and Otto 1987; Dudley 1988), are also known to be prominent in the drift (Waters 1972). However, Doeg et al. (1989b) found that drift contributed less than 50% of immigrants over 10 d, and they noted that the design of some substrate-holding trays hindered accessibility by crawling invertebrates in the surrounding streambed, resulting in overestimates of drift in these cases.

Minshall and Petersen (1985) claimed that drift was the primary means of redistribution of benthic organisms in streams. It is a particularly important relocating mechanism for invertebrates that do not move far under their own power such as the relatively sedentary filter-feeding caddisflies, black flies, and chironomids. Also, as discussed later with respect to large-scale events, drift from upstream reaches undoubtedly allows many taxa to recolonize disturbed reaches far downstream. Recent research employing direct observations of small patches, however, suggests that many of the extremely mobile invertebrates swim and crawl in all directions as well as drifting (Hart and Resh 1980; Wiley and Kohler 1981; Kohler 1984, 1985; Richards and Minshall 1988; Kohler and McPeck 1989).

3.1.2. Swimming

The vigorous swimming of Baetidae, Siphonuridae, and some Oligoneuriidae is familiar to anyone who has tried to pick these mayfly larvae from a live sample of stream benthos. *Gammarus* is also a strong swimmer in sheltered water, and even in riffles can use deadwater areas downstream from rocks to scuttle across a stream (Hynes 1970). Some leptophlebiid mayfly larvae swim considerable distances upstream at certain times in their life cycles (Hayden and Clifford 1974; Söderström 1987).

Swimming down to the substrate allows some drifters to leave the water column deliberately, as seen in *Baetis* and *Gammarus* (Ciborowski and Corkum 1980). Mayfly larvae use dorsoventral undulations to swim downwards, and reach the bottom far sooner than stonefly and caddisfly larvae, probably because the hair-fringed cerci form an effective paddle (Otto and Sjöström 1985). Therefore the rapidity with which many mayflies and other lotic invertebrates reach local bare substrates may be due partly to drift and partly to their swimming, either from place to place on the substrate or when leaving the drift.

Doeg et al. (1989b) inferred that swimmers were important colonizers of experimental trays of sandy substrates in slow water that were raised above the streambed and out of reach of crawlers. Although these trays could have been colonized by drift (e.g. Ciborowski (1987) has shown that drifting *Baetis* larvae are transported laterally to slow water at stream margins), the taxonomic composition of drift (collected in a drift net) in this study was different from the fauna colonizing sand.

3.1.3. Crawling

Nearly all benthic macroinvertebrates can crawl, and some do so rapidly. Giller and Cambell (1989) concluded that crawling contributed as many mayflies to the colonization of implanted natural substrate trays as drift did, and that six species of the eight mayflies in the stream reached the trays only by crawling.

The mobility of grazers has attracted particular interest because their food resources, at least in the form of algal periphyton, can be quantified. Kohler (1984, 1985) showed that the direction and extent of movement by *Baetis* were related to periphyton levels. When the quantity of algal food was low, *Baetis* larvae moved more quickly and turned more often as

they searched for a food-rich patch. Highly mobile grazers are able to cope with the patchy distribution of periphyton and find rare but preferred food items (Hart and Resh 1980; Hart 1981). Richards and Minshall (1988) estimated that 40–50% of *Baetis* larvae arriving on a single rock reached it by crawling. Ciborowski (1987) proposed that *Baetis* larvae settling out from the drift in marginal areas continued their search for food by crawling back towards periphyton in faster water.

After studying sources of colonization in a Sri Lankan river, Benzie (1984) concluded that all immigration resulted from random foraging activities over short distances. On a small scale, therefore, crawlers could colonize bare patches as effectively as drifters and swimmers.

3.1.4. Flight

At appropriate seasons, small patches of stream substrate may be colonized by flying (adult) insects. Amphibious adults (beetles and bugs) may fly in and remain. Nonaquatic adults may enter the water partly or completely to attach their eggs to submerged objects; others drop their eggs above water that provides appropriate cues. Some adults oviposit on banks or dry streambeds, providing a source of colonizers after drought. Oviposition is a means of rapid colonization, but adult activity and numbers of eggs per unit area of substrate are seldom documented.

The most important colonizing attribute of winged adults is their mobility which, together with appropriate sensory systems, allows them to search for suitable habitats. Moreover, some ovipositing adults are attracted to clean smooth substrates (Deutsch 1984; Imhof and Smith 1979) such as those often used or deliberately created for small-scale studies. Extensive oviposition was recorded on substrate trays placed in a desert stream after scouring spates in winter and summer (Gray and Fisher 1981). Total aerial colonization, including nonreproductive adults, accounted for two thirds of the taxa recolonizing the desert stream. Several species with long flight periods, and one that was iteroparous, ensured that adults could remain in the terrestrial environment until stream conditions became suitable, and that colonization could occur during most of the year (Gray 1981). In a long-term study where substrate baskets were introduced each month, Williams (1980) recorded several instances of mass colonization by first-instar larvae. He attributed their arrival to drift; however, larvae could have developed from eggs laid directly on the substrates, and an origin from egg clusters would explain the conspicuously clumped distribution of larvae.

3.2. Substrate Texture and Food

When small patches of substrate are physically disturbed, or when substrates are treated to mimic the disturbance effects, the factors most often described as having an influence on subsequent colonizers are changes in substrate texture and in the food resources associated either with the substrates themselves or with their arrangement on the streambed. As food materials and food gathering are difficult to separate from attributes of the substrate, they will be considered together.

3.2.1. Surface characteristics of substrates

Mild disturbance, such as turning a rock upside down, has little effect on grazers like baetids and glossosomatids, which will graze on periphyton on the under surface of a rock, as long as it fulfills their nutritional needs (Boulton et al. 1988). Hepatogeniids quickly move from one side of a stone to another and

graze upper and lower surfaces (B. A. Heise, University of Toronto, Toronto, Ont., pers. comm.). Grazers depending on well lit periphyton "lawns," like *Leucotrichia*, are more severely affected (McAuliffe 1984), as are sedentary filter feeders in unsuitable below-stone currents (Boulton et al. 1988). Some of these organisms may move to the upper surface if the texture is suitable, but others are unable to change their positions (McAuliffe 1984). By turning rocks over at different intervals, Robinson and Minshall (1986) maintained periphyton biomass at low levels and found that invertebrate density and species richness were reduced as disturbance frequency increased. Therefore, this kind of tumbling has a negative effect on the community as a whole, but some invertebrates can feed on any rock surface or move to the preferred one.

When disturbance is severe, resulting in the scouring of epilithon and loss of trapped detritus and invertebrates, the substrates at first offer colonizers only attachment sites and shelter. Simuliidae larvae are known to avoid substrates covered with detritus, algae, or slime and to select smooth surfaces for attachment (Chutter 1968; Gersabeck and Merritt 1979; Ciborowski and Clifford 1984; Dudley et al. 1986; Morin 1987; Hershey and Hiltner 1988; Doeg et al. 1989b). Because these larvae are filter feeders, and hence independent of food materials growing on the substrates, they can take early advantage of unoccupied space.

Hydropsychid caddisflies are among insects favouring smooth clean surfaces for oviposition. They normally lay their eggs on smooth undersides of rocks that are free of silt (personal observations) and readily respond to substitutes in the form of acrylic tiles (Deutsch 1984) or hardboard (masonite) plates (e.g. Beckett and Miller 1982). Some Simuliidae behave in a similar way (Imhof and Smith 1979). Therefore, bare patches may attract ovipositing insects at appropriate seasons even if the actual propagules are not immediately obvious.

Bare stones soon become covered with organic layers, including a polysaccharide slime produced by colonizing bacteria (Geesey et al. 1978; Rounick and Winterbourn 1983). It is possible that the dissolved organic matter adsorbed onto stones provides a source of nutrients even before bacterial colonization because Winterbourn et al. (1985) found that *Baetis* spp. removed material from ashed stones without a detectable organic layer; and another species of *Baetis* rapidly colonized stones that had been acid-scoured by Boulton et al. (1988). This behaviour suggests that at least some species of *Baetis* are adapted for removing the thinnest of epilithic films, and can thus feed like browsers before the development of an algal layer. "Browsers" is a term used for invertebrates feeding on the organic layers of stones in New Zealand streams (Rounick and Winterbourn 1983). As fine epilithic detritus begins to accumulate, gatherers are provided with recognizable food (Madsen 1972; Calow 1975). A heterotrophic epilithic community can resemble that of undisturbed substrates within 13 d (Osborne 1983).

Periphyton begins to regenerate as propagules are transported by the current, perhaps making use of more labile elements of the heterotrophic organic layer. Newly arriving *Baetis* larvae recognize relative abundance of periphyton (Kohler 1984; Richards and Minshall 1988) whose development is tracked by other colonizing grazers (McAuliffe 1983). In an ungrazed community, maximum primary productivity has been attained 21 d after exposure of bare nonstream gravel (Osborne 1983). However, like *Baetis*, not all apparently herbivorous grazers

are dependent on periphyton for colonization. Boulton et al. (1988) found that colonization patterns were similar on brushed and acid-scoured stones, although periphyton was slow to develop on the latter. A dominant scraper (*Agapetus*) was found by Lake and Doeg (1985) to be more dense in the colonizing fauna than on surrounding natural stones, perhaps because it is favoured by an early stage in periphyton succession as well as by the relative absence of silt in experimental substrates. Another example of preferential colonization of rocks with depleted periphyton was given by Ogilvie (1988) for the mayfly *Epeorus*, which she called a generalist feeder.

As epilithic growths develop, they change the texture of the substrate surface. Hydropsychid caddisfly larvae require surface irregularities for the attachment of their retreats and capture nets (personal observations). On rough-surfaced rocks, they are early colonizers (personal observations) because, like simuliids, they use seston as food. On smooth rocks, their numbers are small until algal growth or moss is well developed (Hynes 1975; McAuliffe 1983; Dudley et al. 1986). This requirement for rough texture may explain why hydropsychids are later colonizers than simuliids in a Californian stream (Hemphill and Cooper 1983; Hemphill 1988). Hydropsychid retreats, *Rheotanytarsus* tubes, simuliid pupal cocoons (resembling moss), and other structures made by sedentary invertebrates in turn facilitate the colonization of additional taxa by further increasing structural complexity and shelter (Meier et al. 1979; Deutsch 1980; Diamond 1986; Malmqvist and Otto 1987).

3.2.2. Size of substrate particles

Stones in experimental substrate trays do not offer the same range in stone size as natural substrate patches, but do mimic physically disturbed patches in that they are loose, with interstitial spaces at first free of silt and detritus. The size of substrate particle, and hence the size of interstitial spaces, affects colonization in two ways. First, large pebbles and cobbles (>40 mm in diameter) tend to be more stable and, once the surface is suitably conditioned, are more likely than finer substrates to attract clinging sedentary organisms (Khalaf and Tachet 1980; Malmqvist and Otto 1987). The interstitial spaces, however, do not provide as much shelter for small invertebrates as those in gravel, which, if silt free, attract greater densities of organisms than the surrounding substrates (Minshall and Minshall 1977; Williams and Mundie 1978; Shaw and Minshall 1980). Finer experimental substrates tend to collect a different fauna, including more burrowers such as oligochaetes, clams, and chironomine and tanytopine chironomids (Williams and Hynes 1976; Doeg et al. 1989b). A general conclusion from the literature cited is that substrate particle size has conspicuous effects on the density and taxonomic composition of the colonizing fauna.

The second effect of substrate size is on the accumulation and size of detritus particles. Gravel and small pebbles tend to trap more fine particulate organic matter (FPOM) than coarser substrates do, and are colonized by the greatest number of macroinvertebrates (Rabeni and Minshall 1977; Wise and Molles 1979; Parker 1989). In an experiment where fine and medium detritus particles were standardized and evenly distributed among several substrate sizes, Culp et al. (1983) found that invertebrate response to detritus overrode any response to substrate size; but they acknowledged that substrates may be selected by some taxa for attributes other than their detritus-trapping ability. In contrast, Peckarsky (1980) concluded that detritus did not increase colonization by invertebrates, except

in summer in a stream where natural leaf inputs were scarce. The introduced detritus in her experiment, however, was in the form of conditioned whole leaves, and may not have attracted gatherers, which are the typical detritivores of the uniform riffle habitats imitated by most experimental substrate trays or cages. Shredders that could have used whole leaves may have been rare in the riffle. Gatherers take advantage of FPOM that rapidly accumulates within the substrates, and are reported to be early (but not always the earliest) colonizers in experiments (Fisher and Gray 1983; Boulton et al. 1988; Parker 1989).

3.3. Competition

As the numbers of browsers, gatherers, filterers, and grazers grow, invertebrates begin to interact with each other. Downes and Lake (1991) have shown that *Austrosimulium torrentium* is a fugitive species, owing its early colonizing success to the absence of other stone-occupying species. Intra- and interspecific competition for space determines the densities of colonizing filterers (Hart 1986; Hemphill 1988; Matczak and Mackay 1990) and grazers (McAuliffe 1983, 1984; Hart 1985). Interactions between individual larvae often lead to density-dependent drift (Hildrew and Townsend 1980; Matczak and Mackay 1990), which is more prevalent among organisms relying on a fixed area of substrate for feeding or other purposes than among more mobile drifters (Ciborowski 1987). Besides causing emigration from the patch under consideration, competition may be occurring upstream, resulting in drift, and hence affecting the rate at which the patch receives immigrants.

3.4. Predation

Predaceous stonefly larvae on substrate patches can reduce colonization by prey taxa (Peckarsky 1985). Significant reductions in total community density as well as changes in the relative numbers of individual taxa were effected by stoneflies moving freely within a substrate cage. The same trend was found when stoneflies were confined in mesh containers and unable to feed, confirming earlier observations on avoidance of predators by prey (Peckarsky and Dodson 1980).

Early colonizers may enjoy an initial period of enemy-free space because dominant predators tend to be later immigrants (e.g. Ulfstrand et al. 1974; Allan 1975; Meier et al. 1979; Shaw and Minshall 1980; Peckarsky 1986; Boothroyd and Dickie 1989). An interesting exception among predators was in a stream where the net-spinning caddisfly *Plectrocnemia conspersa*, which has a high propensity to drift, was an early colonizer (Townsend and Hildrew 1976). Drift of net-spinners is known to result from aggressive interactions over net-spinning space (Hildrew and Townsend 1980; Matczak and Mackay 1990), and serves to distribute larvae among unoccupied habitats. The success of *P. conspersa* as an early immigrant, before a prey community had developed on the patch, could be attributed to the filter-feeding habit; by trapping drifting prey, this predator was independent of prey on the patch itself.

An extreme effect of predation on colonization was seen by Gray and Fisher (1981) in a desert stream, where 117 adult *Deronectes nebulosus* (Dystiscidae) eliminated all mayflies and chironomids in the substrate tray.

4. Timing in Small-Scale Colonization Studies

4.1. Time to Reach Equilibrium

The sequence of events during colonization of bare stream patches has been described in several ways. Classical

approaches follow the MacArthur–Wilson island biogeographic model in which community structure progresses towards an equilibrium. It is unlikely that stream communities exist in equilibrium (Lake and Barmuta 1986) although Minshall and Petersen (1985) argued that equilibrium conditions occur under certain flow regimes. Equilibrium is said to be reached on a patch when the arrival rate of new species equals the disappearance rate of other species, and thus the total number of species (strictly, taxa, owing to limitations in identification) becomes more or less constant. Alternative end points in this scheme are the stabilization of either a species diversity index or total densities (or biomass) per patch.

When equilibrium is equated with a plateau in number of species, the apparent colonization period has been as short as 4–6 d in some experiments (Townsend and Hildrew 1976; Lake and Doeg 1985), but more usually is in the range of 10–25 d (Wise and Molles 1979; Lake and Doeg 1985; Minshall and Petersen 1985; Peckarsky 1986). Total invertebrate densities in these experiments seem to have levelled off more slowly in 10–30 d. The times taken for various kinds of introduced substrates to develop equilibrium communities (or stable population densities) were tabulated and discussed by Rosenberg and Resh (1982) who concluded that even when comparisons were limited to rock-filled containers in riffles, colonization times varied according to experimental design, season, and geographic location. Short-term (less than 2 wk) experiments may be unrealistic because an “equilibrium,” as defined earlier, cannot develop while substrates are still experiencing changes in epilithic texture and interstitial deposition, which affect the attractiveness and extent of living space. High early departure rates (“extinction”) as a result of inhospitality are at odds with the classical model. Some sampling intervals may miss the “colonization” and “extinction” of certain species; and at some seasons, mass immigration or emigration may be occurring in the stream as a whole as a result of egg hatching and emergence.

4.2. Numbers of Individual Taxa

A second method of timing colonization events is to follow changes in numbers of individual taxa. This method shares a problem with the classical one: samples of the “island” fauna usually cannot differentiate between colonists truly exploiting the resources of the patch and individuals that are merely exploring the potentials and moving on. For example, the often recorded early rise in numbers of *Baetis* (e.g. Ulfstrand et al. 1974; Shaw and Minshall 1980; Ciborowski and Clifford 1984; Lake and Doeg 1985; Dudley 1988) probably includes much coming and going while larvae test periphyton resources before eventually staying longer to feed. On the other hand, the equally sharp rise in Simuliidae (e.g. Ulfstrand et al. 1974; Lake and Doeg 1985) is more likely to reflect true colonization of bare sites for filter feeding. A later decline in simuliid densities has been explained as part of the colonization sequence as larvae avoid growing densities of algae and other filter feeders (Lake and Doeg 1985; Hemphill 1988; Downes and Lake 1991) or simply as due to emergence (Khalaf and Tachet 1977).

In spite of uncertainties as to true colonization versus exploration, the individual-species approach reveals which types of organisms are available and able to take advantage of changing resources. Using this approach, colonization may be described as complete either when number of individuals per taxon becomes stable or when final densities and relative proportions

of the various taxa match those in the community surrounding the patch being studied. If colonization is being used as a measure of recovery, then comparing assemblages on experimental substrates with those surrounding them is the better guide. Rather few small-scale studies have done this in a systematic way. Short-term experiments have found inconsistencies in the comparisons when early colonizers were overrepresented by drifters from upstream habitats (Ciborowski and Clifford 1984). Longer studies (e.g. Boothroyd and Dickie 1989; Doeg et al. 1989a) allow time for immigration by less mobile species and show how certain unexpected changes in experimental patch densities may be explained by similar changes in natural substrates. Lake and Doeg's (1985) comparison of different equilibrium criteria in the Acheron and Toorong rivers showed that the numbers of colonizing species over time levelled off conspicuously over 8 d but took 16 or 32 d, respectively, to reach the numbers found in the surrounding riffles.

4.3. Effects of Season and Life History

Timing of events is heavily dependent on season. In yearlong or multiseasonal studies, colonization has been reported as being faster in summer and early fall in perennial temperate streams (Shaw and Minshall 1980; Williams 1980; Doeg et al. 1989a). In most temperate streams, recruitment in general is higher at these seasons for many species. Dispersal (drift, crawling) from crowded egg-hatching sites, oviposition directly on experimental substrates, and greater activity at higher temperatures all increase chances of invertebrates being recovered on the newly available introduced space. Faster periphyton development in summer increases the rate at which epilithic growths attract and sustain grazers. In Australia, where summer is the season of peak riparian litter fall (Bunn 1986; Lake et al. 1986), benthic organic matter accumulated faster in experimental patches in summer than in winter (Doeg et al. 1989a) and may have attracted colonizers. The more colonizing mechanisms that are available at any one time, the faster colonization will be at that time.

The effect of invertebrate life history on colonization is more complex than the simple seasonal recruitment mentioned above. If colonizing propagules for a species are limited to a particular life history stage, e.g. gravid females ovipositing directly, or age-restricted drifters, then at times when propagules are unavailable, fewer colonizers can be expected on experimental substrates even though the species is present in the surrounding benthos. This limitation might explain why substrates in Lake and Doeg's (1985) Acheron II experiment, which was carried out in winter, never matched natural substrates in number of species and why chironomids, which were known to be mainly summer drifters, were slow to colonize substrates in another winter experiment in the Acheron River (Doeg et al. 1989a). When propagules are produced more frequently or are active over longer periods, colonization is completed more quickly. For example, rapid colonization in intermittent desert streams has been attributed to nearly year-round oviposition by some insects owing to long-lived females or to wide-ranging flight from asynchronous populations in permanent habitats (Gray 1981). Asynchrony and the lack of seasonality in life cycles of many New Zealand stream-living insects mean that emergence and oviposition can take place over many months (Winterbourn 1978; Towns 1981). Australian populations also seem to be poorly synchronized (Marchant 1986). Insects are not the only invertebrates with asynchronous development. *Gammarus*, too,

is often seen in a wide range of size classes so that appropriate sizes for scavenging among bare patches are always available, as well as reproductive stages (Ulfstrand et al. 1974).

5. Small-Scale Studies of Disturbance Intensity and Frequency

The basic supposition, when introducing experimental substrates into streams, is that the particular treatment mimics some level of natural disturbance. Thus, rocks that are picked clean of invertebrates, but not dried or scraped, are equivalent to stream substrates subjected to some tumbling or shifting, which washes away associated animals and interstitial silt but leaves rock texture intact, together with attached microbial and algal growths. Scrubbing and drying remove live epilithon, but may leave some regenerating material. Disturbances severe enough to scour away basal epilithic structures and marl have been simulated by substituting quarry stones, or by exposing natural stream rocks to acid or mechanical abrasion.

During a month-long colonization experiment, Lake and Doeg (1985) found considerably fewer species on quarry stones than on previously brushed and dried river stones, except on the final day. Invertebrate density on quarry stones levelled off after 15 d whereas density on river stones continued to rise, with conspicuously higher numbers of scraper-grazers. Even brushed and dried river stones were quickly able to generate a sustaining epilithon for scrapers. In a similar comparison, Bolton et al. (1988) scoured stones from another Australian river in 2 N nitric acid to mimic severe disturbance. Epilithon recovery, as expected, was slow, and scraper densities were far lower than those on control rocks. However, *Baetis* densities rose rapidly to match control rocks within 8 d, and colonization curves for several other taxa and total densities, although somewhat lower, were similar in shape to control curves despite poor epilithic development. These comparative experiments demonstrated consistent patterns of colonization, with the same sequence of early and late taxa even though densities were different.

The frequency as well as the intensity of disturbance has been tested in small-scale experiments. In a Rocky Mountain stream, bricks that were turned over at frequent intervals supported less periphyton and had lower invertebrate species richness and density than bricks turned less often (Robinson and Minshall 1986). This kind of high-elevation mountain stream normally experiences a predictable major rise in discharge only at snowmelt, which is so predictable that Resh et al. (1988) did not consider it to be a real disturbance. Rather, it is a seasonal event to which organisms are adapted in terms of life history and behaviour. In such a stream, spates at other seasons are indeed disturbances; and the more frequent the occurrence, the more severe the impact, as shown by experimental overturning of rocks at these seasons (Robinson and Minshall 1986).

In contrast, colonization experiments in streams exposed to irregular spates throughout the year do not show clear correlations between disturbance frequency and community recovery. In a southeastern USA stream, Reice (1984, 1985) showed that recovery of riffle invertebrates after experimental rock tumbling was the same in terms of species richness and diversity whether tumbling had occurred only once or twice (after a 2-wk interval). Stream substrates raked three times over 20 d in the Acheron River recovered as quickly as patches raked only once (Lake et al. 1989). In this Australian river, individual species were also unaffected by disturbance frequency, suggesting

that all taxa were well able to cope with repeated disruptions of the streambed.

6. Disturbance and Colonization on a Larger Scale

The small-scale studies reviewed so far are reasonable simulations of the colonizing events that might follow local disruptions and minor spates. Natural rocks surrounding an experimentally denuded patch are like sheltered bays and the hyporheic zone following moderate increases in discharge: both harbour potential colonizers. The proximity of so many colonizers, however, means that colonization rates are probably far higher in small-scale experiments than in situations when more of the streambed is affected. Manipulative experiments on whole streams are understandably rare, but studies of new channels and of streams recovering from drought, extreme spates or floods, and certain types of pollution have all provided information on colonization or recovery rates.

6.1. Disturbed Reaches

Where disruption is severe but local, as in the case of polluting inputs, the substrate is occupied by stream invertebrates as soon as it is able to provide shelter and food. For example, in a stream polluted by a gasoline spill, invertebrates recovered from a 2–25% reduction in densities within 7 mo (with reference to an upstream site) and reached full species richness within 16 mo (Pontasch and Brusven 1988). The sequential downstream recovery of study sites, as well as the lag in restoration of species richness, suggested that drift was the most important colonizing mechanism. Normal drift by organisms immediately upstream was probably occurring during the severely polluted period, but settling was not permanent until the habitat became hospitable. Habitat recovery was aided partly by mechanical agitation 1 mo after the spill to remove hydrocarbons, and partly by dense periphyton blooms (Pontasch and Brusven 1987) which provided abundant food not only for grazers but also, perhaps, for gatherers as sestonic FPOM was trapped and the algae later decayed. In contrast, a stream relocated along a uniformly wide, flat-bottomed channel filled with gravel and silty sand provided neither interstitial habitats for riffle macroinvertebrates nor suitable structures for periphyton development and leaf-pack accumulations (Narf 1985). Instead, silt flushed out of the new channel was a pollutant. Not until 5 yr later, when cobbles had been washed free of silt, did the colonizing fauna match the upstream reference site. A similar pollutant, volcanic ash from the 1980 eruption of Mt. St. Helens, was blamed for the slow (>5 yr) recovery of the caddisfly fauna in streams within the blast zone (Anderson and Wissemann 1987).

Another example of recovery after severe local disturbance was given by Lamberti et al. (1991) who described the effect of a catastrophic debris flow on a forested stream. Vagile herbivores like chironomids and baetids matched upstream densities within 1 yr, and less mobile herbivores (glossosomatids and pleurocerid snails) did so within 2 yr. Shredders and predators were late colonizers. Rapid recoveries were attributed to increased primary production in the disturbed reach, which provided food-rich habitat for colonizers arriving by drift and oviposition.

6.2. New Channels and Recovery from Drought and Washouts

Examples of colonization on a truly large scale were provided by a newly opened 0.6-km channel that rerouted the

Tongue River, Wyoming, across nonriverine substrates (Gore 1979, 1982) and by the rewatering of the North Fork of the Teton River, Idaho, after exposure first to catastrophic discharge, and then to 3.5 mo (August–December) without flow following deliberate diversion upstream (Minshall et al. 1983).

In both cases, the river upstream from the new or dewatered channel was clearly the chief source of colonizers because the rate at which sequential study sites were colonized was directly related to distance from this source. The colonization site near the lower end of the Tongue River new channel received later immigrants from the recognizable established community in the river downstream, presumably by upstream crawling. Aerial colonization was also possible during at least the first 3 wk of the study (August). In the Teton River, the distance (>20 km) of the study sites from the Snake River downstream, and the December opening of the North Fork, meant that drift was probably the only colonizing mechanism there for the first few months; dewatering had destroyed resident populations, at least within the top 50 cm of streambed. During the first 5 mo of the Tongue River rerouting, the station closest to the source of colonizers approached equilibrium more rapidly than the two more distant stations, which were similarly staggered. This was true whether equilibrium was measured in terms of invertebrate densities, number of taxa, or a community structure resembling the upstream source of colonizers. A similar sequence was seen in the Teton River. Both sets of data were in accordance with the predictions of the island biogeographic theory of colonization from a single “mainland” source, although Gore (1982) recognized that the strict MacArthur–Wilson model, with its continued isolation of islands, would no longer apply once the new channel became continuous with the source area in substrate texture and food.

The time taken to reach “equilibrium” in the Tongue and Teton rivers depended on the way equilibrium was defined and measured. In the Tongue River new channel, densities and community similarity comparable with the river upstream were reached within 70 and 125 d, respectively, but species richness did not become constant until ~300 d after the new channel was opened (Gore 1979, 1982). In the Teton River, total numbers recovered in ~375 d and cumulative species richness in ~700 d (Minshall et al. 1983). In both rivers, the number of taxa per collection (species richness) lagged behind number of individuals. This lag contrasts with small-scale studies where numbers of taxa tended to level off early; it may be explained by the importance of drift in the newly watered channels and the fact that certain species are far more prevalent than others in the drift. If other colonizing sources had been available, then more species might have been represented sooner. Indeed, in the Tongue River new channel, where upstream movement and aerial colonization were possible from nearby sources (<1 km away), the lag was not as pronounced as in the Teton River.

Some clear trends are obvious in the Tongue and the Teton studies which confirm patterns seen during small-scale experiments. In the Tongue River new channel, early colonizers were *Baetis* species, simuliid (first) and hydropsychid (second) filter feeders, and chironomids (Gore 1979), which Gore (1982) categorized as collector-gatherers and collector-filterers. Scrapers arrived a few days later. Minshall et al. (1983) provided few data on individual taxa in the Teton, but noted that *Baetis* and chironomids colonized within days of rewatering. *Baetis*, at least, seems to have been termed a grazer in the Teton River, for grazers were generally predominant during the early

stages of recolonization, but were soon replaced by collectors (presumably including gatherers as well as filterers). In both rivers, predators and shredders were late arrivals and low in abundance.

The Tongue and Teton River studies of newly watered channels dealt only with true colonization because the existence of resistant stages in the dry channel was virtually impossible in the Tongue River and unlikely in the Teton. When drought occurs regularly, perhaps on a seasonal or annual basis, returning water revives survivors as well as attracting colonizers from elsewhere. Some survivors (e.g. certain species of mayflies, chironomids, and simuliids) hatch from drought-resistant eggs (Hynes 1958; Williams 1977). Others venture from refuges in the hyporheos, damp spots under rocks and organic debris, and isolated stream pools (Clifford 1966; Hynes 1975; Boulton 1989).

Where streams are too sunbaked to allow survival in the streambed, as in some African streams during drought (Harrison 1966; Hynes 1975), colonization is most likely from eggs laid by aerial adults when flow resumes, followed by rapid hatching and growth. Mature baetid (*Centroptilum*) nymphs and chironomid pupae developed within 18 d in a tributary to the Pawmpawm River in Ghana (Hynes 1975). In the Pawmpawm River itself, the first colonizers included simuliids as well as baetid and chironomid gatherers; baetid and hydropsychid predators were later.

Even streams recovering from catastrophic washouts may be recolonized by survivors, these being either exceptionally deeply buried — such as tabanid larvae in a desert stream (Gray 1981) — or sheltered in debris on the edge of floodwaters from which they return as floods recede (Cushing and Gaines 1989). More often, recovery is through oviposition by aerial insects (Siegfried and Knight 1977; Gray and Fisher 1981) that either emerged from the stream before disturbance and were long lived (Gray 1981) or immigrated after emergence from neighbouring streams (Resh 1982). Colonization rates obviously will be faster if the disturbance occurs at a time when insects are most likely to be on the wing. The recovery of Burns Run, a normally stable stream in Pennsylvania, after Hurricane Agnes caused a 150-fold increase in discharge (Hoopes 1974), probably owed much to the early date (June) of the storm, which meant oviposition was possible over the rest of the summer. Summer, however, is not always a favourable season. Contrasting effects of winter spates (regular events to which the fauna was assumed to be adapted) and an unexpected and severe spate in summer were described by Giller et al. (1991) for an Irish stream. In this tributary of the River Araglin, recovery was relatively rapid after the winter spates, but was much slower (>3 yr) after the summer spate.

6.3. Unstable Rivers

Rivers that experience frequent fluctuations in discharge, much bed movement, and high loads of suspended sediment inflict the most difficult conditions on their benthic faunas, and consequently provide interesting information on tolerance and resilience. Recent studies of such large unstable rivers in New Zealand (Sagar 1986; Scrimgeour et al. 1988; Scrimgeour and Winterbourn 1989) showed that although invertebrate densities are severely reduced after major spates, mainly through abrasion of algal food as well as direct damage, certain taxa are able to recover quickly. These taxa are mostly collector-browsers, such as the leptophlebiid mayfly *Deleatidium* and chiron-

omid larvae, filter-feeding hydropsychids (*Aoteapsyche*), and predatory hydrobiosid caddisflies. Larvae avoid spates to some extent by burrowing into the substrate (even normally sedentary hydropsychids do this: Poole and Stewart 1976; R. J. Mackay, unpublished data) or by surviving in sheltered segments of these braided rivers (Scrimgeour et al. 1988; Scrimgeour and Winterbourn 1989). Denuded braids are recolonized either by drift (Sagar 1983) or by ovipositing adults coming from refuge braids (Scrimgeour et al. 1988). Most of these colonizing species are present in a wide range of size classes throughout the year, and thus have the potential to mature and multiply rapidly during stable flow regimes.

In unstable New Zealand rivers, *Deleatidium* species seem to be particularly resilient. Part of their success may result from their habit of browsing the rapidly regenerating organic layers on stones, which are important food materials in New Zealand rivers (Rounick and Winterbourn 1983; Collier and Winterbourn 1990). In the Inangahua River, New Zealand, bed materials are continually being abraded by fine sediments, and algal growths are unable to become well established. Even though other invertebrates apparently feed on fragments of allochthonous materials that are alternately mobilized in spates and trapped in depositional sites, Winterbourn et al. (1984) found that *Deleatidium* probably derives much of its carbon from dissolved organic material taken up by the epilithic microbial layer.

After reviewing the literature on spatial and temporal heterogeneity in streambeds, Poff and Ward (1990) concluded that streams with a greater historical record of such heterogeneity will express greater persistence, resistance, and rate of recovery than less variable systems, largely because the biota is adapted to cope with the conditions.

7. Colonization Patterns

7.1. Taxa and Trophic Groups of Primary Consumers

When colonizers of experimental patches, disturbed reaches, newly watered channels, and disturbed rivers are compared around the world, taxa recur with remarkable concordance at the family level and are often identical (or close relatives) at the generic level. Among the mayflies, Baetidae (mostly *Baetis*) are abundant and early colonizers in most parts of the world (e.g. Ulfstrand et al. 1974; Hynes 1975; Gore 1979; Gray and Fisher 1981; Minshall et al. 1983; Lake and Doeg 1985; Boulton et al. 1988; Parker 1989; Lamberti et al. 1991). Certain Leptophlebiidae are similarly recorded, such as *Deleatidium* in New Zealand (Sagar 1986; Scrimgeour et al. 1988) and *Atalonella* and *Atalophlebiodes* in Australia (Lake and Doeg 1985; Boulton et al. 1988). *Baetis* may share the browsing habit of *Deleatidium* if it is capable of removing thin organic films. The other leptophlebiids could be browsers too, or they may be gatherers as they are in North America (Lamberti and Moore 1984; Merritt and Cummins 1984). Chironomidae are consistently recorded among the first colonizers (most studies of new or disturbed substrates), especially after scouring spates and washouts (McElravy et al. 1989). When chironomids have been identified beyond family (e.g. Gray and Fisher 1981; Sagar 1986; Doeg et al. 1989a; Parker 1989), orthocladiine gatherers are predominant. The early arrival of all the above browsers and gatherers is consistent with their ability to exploit the earliest food materials on and among bare substrates. Fisher et al. (1982) found that gatherers composed 87% of numbers and 85% of biomass in the invertebrate community of a desert

stream disturbed by flash floods. Later in the recovery of streams, a grazing habit may be adopted by browsers, and additional herbivorous taxa contribute to colonization.

If colonists cannot browse or gather, the alternative early feeding strategy is filtering, making use of suspended fine detritus which is nearly always present in disturbed streams. Simuliidae, Hydropsychidae, and some chironomine chironomids (*Rheotanytarsus*) are reported repeatedly. Because the hydropsychids can only establish retreats on rough-surfaced rocks, they are not always the earliest filterers. Nevertheless, they have some characteristics of opportunists in that the genera most often reported (*Aoteapsyche*, *Asmicridea*, *Cheumatopsyche*, *Hydropsyche*, and *Symphitopsyche*) are in the subfamily Hydropsychinae. Larvae in this subfamily tend to have unspecialized nets and a broad diet (Fuller and Mackay 1980), and they can feed on drifting animals as well as detrital seston (Lamberti and Moore 1984).

Shredder-dominated communities, such as those in first-order forested streams, are rather slow to recover after disturbance (Wallace 1990), and shredders have often been reported as later colonizers than other detritivores and herbivores (Gray and Fisher 1981; Gore 1982; Minshall et al. 1983; Boulton et al. 1988; Doeg et al. 1989a; Lamberti et al. 1991). Many shredders have poor dispersal abilities (Wallace et al. 1986). With the exception of *Gammarus*, shredders are rather rare in the drift (Waters 1972), so they are not routinely transported to disturbed reaches from upstream sources. Coarse particulate organic matter (CPOM) concentrations tend to be more seasonal than FPOM, and may not be immediately supplied to a disturbed patch or stream. Shredder life cycles tend to be long (Wallace et al. 1986) and tied to seasonal inputs and decay of CPOM. Many life cycles are synchronous. Therefore, colonizing stages may not be available following an unexpected disturbance. The relatively few numbers of shredders among early colonizers of introduced substrates could be the result of a low shredder density in the study riffle (a possible explanation for Peckarsky's (1980) results) and the slow rate of CPOM accumulation. When CPOM did collect on substrate trays in a suitable stream, many shredders were among the colonizers (Ulfstrand et al. 1974).

7.2. Mobility and Life Cycles

The recurring taxa include many of those that were described earlier as drifters, swimmers, and rapid crawlers. Some adult insects are strong fliers, like the beetles that may be conspicuous in streams recovering from drought. Some adults are short-lived; but asynchronous life cycles, as seen in Australian and New Zealand streams, mean that propagules could be available for colonization at all times, especially if headwaters, side channels, or nearby streams provide refuges from which propagules can disperse to restored habitats. In fluctuating environments, successful colonizers have life cycles that allow them to take advantage of temporary benign periods in disturbed streams, and at the same time to benefit from such features in these streams as unsilted substrates and early successional stages in periphyton development.

Temperatures supporting maximum growth rates will obviously provide the fastest regeneration of populations. Usually these are warm temperatures (annual mean $> 15^{\circ}\text{C}$) which, in the southern USA at least, allow development times as short as 6–15 d for chironomids (Gray 1981; Stites and Benke 1989), 9 d for black flies (Hauer and Benke 1987), and 10–19 d for

Baetis (Gray 1981; Benke and Jacobi 1986). However, Hauer and Benke (1991) found that high growth rates recorded for chironomids in the Ogeechee River were related not only to temperature but also to high discharge ($> 20 \text{ m}^3/\text{s}$). They attributed the growth response to the higher seston concentration associated with high discharge. High growth rates in cool-adapted species, too, allow them to be pioneers in new or disturbed streams. One of these species is *Orthocladus calvus*, with a development time in southern England (52°N) of 16 d. This species not only colonized a new gravel channel with remarkable rapidity, but was so specialized for this kind of virgin habitat that it was not known from typical stream communities in the area (Ladle et al. 1985).

7.3. General Predictions

Benthic communities will develop and stabilize sooner if the disturbance that originally denuded the substrate is a local rather than a regionally extensive catastrophe. If upstream reaches, side channels, and neighbouring drainages are unaffected, the surviving benthos and ovipositing adults soon provide colonizers. Recovery will be faster if the colonization period coincides with reproductive periods in the benthos. Colonization by shredders that are closely tied to allochthonous organic inputs could be restricted by season. Likewise, certain algal scrapers have a limited period of activity dependent on the productivity of epilithic algae. Such seasonally bound life cycles in streams that normally experience only regular climatic events could limit colonization when the biota is damaged by an unexpected disturbance.

Streams most likely to recover quickly are runoff streams, in which discharge is often irregular and unpredictable (Poff and Ward 1990). They include perennial and intermittent upland streams in Victoria (Lake et al. 1985, 1988) and agricultural Ontario (Mackay 1979) as well as the more flashy flows typical of New Zealand (Winterbourn et al. 1981), coastal California (McElravy et al. 1989), and deserts (Fisher et al. 1982). Many of these streams are in a climate that allows long periods of oviposition, asynchronous life cycles, and high growth rates, all of which favour the availability of propagules and the rapid exploitation of newly available or restored habitats.

Recurring ecological patterns are seen in the repopulating species. Many of the same taxa and functional groups are involved. Lotic invertebrate communities likely to be resilient after disturbance will include substantial proportions of baetid, leptophlebiid, and sometimes heptageniid mayflies, multivoltine black flies, especially fugitive species, opportunistic orthocladine browsers and gatherers, clinging chironomine filterers like *Rheotanytarsus*, and Hydropsychine caddisflies. Where periphytic algae regenerate quickly, grazers will colonize soon after detritivores.

In the nonequilibrium conditions of disturbed streams, communities are thought to be controlled in a stochastic manner (Wallace 1990). However, although a disturbance may indeed occur by chance, the same cannot be said of the ability of the disturbed community to "bounce back." There is some degree of predictability if the fauna is known. Depending on hydrologic regime and season, predictions can be made on the likely responses of lotic invertebrates to disturbance, according to their ecological traits and dynamics. The ability of a stream to cope with disturbance could be assessed. This kind of information could be invaluable to planners debating the necessity of protecting a stream. For although our ecological knowledge

at the species level is still incomplete, some recognition of typical faunal patterns can provide the constructive advice needed in environmental decision-making.

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