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Long-term effects of local disturbance history on mobile stream invertebrates

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Abstract The patchy distribution of benthic invertebrates in streams and rivers is an important and widely researched phenomenon. Previous studies on reasons for this patchiness have neglected the potential role of local disturbance history, probably because most lotic invertebrates are mobile and any effect of disturbance history was thought to be short-lived. Here we demonstrate for a New Zealand gravel-bed stream that local disturbance history can have long-term effects on the distribution of highly mobile stream invertebrates. Buried scour chains (100 at each of three 20-m sites within a 350-m reach) indicated that a spate with a return period of 5 months caused a mosaic of bed patches with different stabilities. More than 2 months after the spate, we took random, quantitative samples at each site from five patches that had experienced 4 cm or more of scour during the spate, from five patches with 4 cm or more of fill, and from five stable patches. Density of the dominant invertebrate taxon, the highly mobile mayfly *Deleatidium* spp., and densities of another three of the seven most common taxa differed significantly between patch stability categories. Larvae of *Deleatidium*, the black fly *Austrosimulium* spp. and the dipteran *Eriopterini* were most abundant in fill patches, whereas Isopoda were most abundant in scour patches. Total invertebrate densities and densities of six common taxa also differed between sites, although these were only 95–120 m apart. These results show that local disturbance history can have long-term effects on lotic invertebrates and be an important cause of invertebrate patchiness. The observed effects might have been even stronger had we sampled sooner after the spate or after a large flood. Disturbance history may influence invertebrates both directly (through dislodgement or mortality) and indirectly, through effects on the spatial distribution of their resources. Our results suggest that the role of disturbance in structuring animal communities dominated by mobile species may be more important than previously thought.

Key words Disturbance · Patch dynamics · Stream ecology · Bed stability · Mobile species

Introduction

The concept of patch dynamics, which pervades most fields of ecology, views ecosystems as highly dynamic in four dimensions: the three spatial dimensions, and time. Disturbances play a fundamental role in patch dynamics theory because they create open space and cause changes with time (Pickett and White 1985). Early research on patch dynamics was conducted on terrestrial plants (Clements 1916; Watt 1947), coral reefs (Connell 1978), and marine tidal zones (Sousa 1979). Later studies investigated ecosystems ranging from temperate and tropical forests across shrublands, prairies and desert ecosystems to subtidal marine hard substrata (Pickett and White 1985). Patch dynamics have been studied in organisms as diverse as annual grasses (Wu and Levin 1994), seagrass (Marba and Duarte 1995), forest herbs (Collins et al. 1985), woody plants (Frelich and Reich 1995; Johnson et al. 1995), marine nematodes (Lambshead and Hodda 1994), mussels (Commito et al. 1995; Denny 1995), zooplankton (Folt and Burns 1999), terrestrial insects (Schowalter 1985) and vertebrates (Crome et al. 1994; Bunnell 1995).

Stream ecologists have been discussing whether the patch dynamics concept can be applied to lotic ecosystems for more than a decade (e.g., Pringle et al. 1988; Frid and Townsend 1989; Townsend 1989; Downes 1990; Poff and Ward 1990; Dolédec and Statzner 1994; Resh et al. 1994; Townsend and Hildrew 1994). The clumped or contagious distributions of invertebrates in the stream bed have long been recognised (Scott 1958;

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Egglishaw 1964; Elliott 1971) but have recently received renewed attention in conceptual papers (Cooper et al. 1997; Crowl et al. 1997; Palmer et al. 1997). Frid and Townsend (1989) and Townsend (1989) felt that the patch dynamics perspective was well suited for the explanation of processes and patterns in lotic ecosystems. By contrast, Downes (1990) argued that, while stream studies could benefit from examining patch dynamics models in a general way, most of these models were constructed primarily for sessile communities and were therefore unsuitable for mobile stream animals. Specifically, Downes (1990) stressed the need to know more about the spatial and temporal patchiness of resources relative to the dispersal abilities and colonisation rates of stream invertebrates. She warned that species with high dispersal ability might be unaffected by resource patchiness at the chosen spatial scale of a study because they can move easily between such patches.

Despite the high mobility of most stream animals, numerous studies of the microhabitat of lotic invertebrates have revealed correlations with local current velocity or near-bottom shear stress (e.g., Ulfstrand 1967; Peckarsky et al. 1990), water depth (Barmuta 1989; Ruse 1994), substratum size or roughness (Ulfstrand 1968; Holomuzki and Messier 1993), and physical distance between sampling locations (Barmuta 1990; Palmer et al. 1997). Others have reported the effects on microdistribution patterns of predation (Lancaster et al. 1991; Peckarsky and Cowan 1995), competition (Feminella and Resh 1990; Kohler 1992), food (Richards and Minshall 1988; Hearnden and Pearson 1991; Richardson 1992), structural elements like woody debris (O’Connor 1991), and random processes (Tokeshi and Townsend 1987; Schmid 1993).

By contrast, the potential importance of disturbance in generating patchy distributions, one of the key elements of patch dynamics theory, has been largely ignored. The results of recent studies suggest that disturbance can contribute to lotic invertebrate patchiness (Matthaei et al. 1999a, b, 2000). In many streams, physical disturbance of the stream bed occurs frequently during spates and floods. Lotic invertebrates may avoid the destructive effects of these events by sheltering in refugia. Previous work with in-situ-marked stones in the Kye Burn, a New Zealand river with an unstable bed, showed that some surface stones remain stable during smaller spates (Matthaei et al. 1999a) and serve as invertebrate refugia. Mean invertebrate densities on these stable stones were far higher than on unstable stones during the receding limb of a bed-moving spate (Matthaei et al. 2000). Consequently, invertebrate patchiness was partly caused by the “disturbance history” of each sampled stone. Fifteen days later, the mobile invertebrates had dispersed over the stream bed again, and their distribution on surface stones with different disturbance histories was far less patchy. In another study, buried scour chains revealed that most bed-moving flow events in the Kye Burn cause a complex mosaic of small (≤ 1 m^2) bed patches that experience scour, fill or remain undisturbed (Matthaei et al. 1999b). Here we present results concerning the fauna of these bed patches more than 2 months after the spate studied in Matthaei et al. (2000), and ask whether local disturbance history can have long-term effects on the distribution of mobile invertebrates in the bed of the Kye Burn.

Materials and methods

Study sites

The study was carried out in the Kye Burn in the Otago province of the South Island of New Zealand (45°58′S, 170°18′E). Vegetation in the Kye Burn catchment (600–1600 m a.s.l.) is mainly indigenous tussock grassland grazed by sheep. Annual rainfall in the area is 600–1000 mm (Otago Catchment Board 1983), mean annual flow at the study reach is 1.1 m^3/s, and baseflow is about 0.4 m^3/s (National Institute of Water and Atmospheric Research [NIWA] Dunedin, unpublished data). Stream width at baseflow was 5–7 m in the study reach, which has a high sediment supply and an unstable substratum (Matthaei et al. 1999a). The stream bed in the reach consisted mainly of gravels [sediment particles with a *b*-axis (width) of 2–64 mm] and cobbles (*b*-axis 64–256 mm), with some small to medium boulders (*b*-axis 256–1024 mm) as well as some bedrock outcrops (particle size classes from Gordon et al. 1992).

Within the study reach, a stream section of 350 m length at about 600 m altitude, we investigated three 20-m sites with contrasting geomorphologies. The sites were those used for monitoring spatial patterns of scour and fill in Matthaei et al. (1999b). Site 1 was a riffle in a flood plain (width 70–120 m), whereas sites 2 and 3 were in a steep canyon with a tightly confined channel (ratio valley width: channel width <2). Site 2, situated 95 m upstream of site 1, was a riffle in a “forced pool-riffle” reach where the canyon walls and a few bedrock outcrops in the upper part of the site forced the water into fast-flowing areas and calmer backwaters. Site 3, another 120 m upstream, was in a “plane-bed” section, a bedform characterised by long stretches of relatively planar channel bed (Montgomery and Buffington 1993). At this site, there were no forcing elements but the sediment was significantly coarser than at sites 1 or 2 (Matthaei et al. 1999b).

Quantification of bed movement

At each site, one hundred metal-link scour chains (Nawa and Frissell 1993) were buried in a systematic grid (five chains across each transect, with about 1 m between chains and transects) between 12 December 1996 and 20 February 1997. The chains (each about 0.5 m long) were installed vertically in the stream bed, with only the top one or two links exposed. Scour during a high-flow event exposes additional chain links, whereas fill can be measured by the thickness of the sediment layer deposited on top of the originally exposed links. The chains can also detect scour-before-fill, when a bed patch is first scoured (exposing some links that come to lie horizontally) and then subjected to sediment deposition during a later stage of the same high-flow event (though this did not occur in the current study). The exact location of each chain in the stream bed was determined by measuring distances to a pair of permanently-marked points on the banks at the downstream end of each site. For more details of the method see Matthaei et al. (1999b).

Matthaei et al. (1999b) monitored scour and fill at the three sites during six high-flow events, the last of which was used to study long-term effects of disturbance history on lotic invertebrates. This spate occurred on 13–14 August 1997, had a return period of 5 months (average from 22 years of flow data; Otago Regional Council, unpublished data), and did not exceed bankfull discharge. It caused a mosaic of patches that experienced scour, fill or remained undisturbed at the three sites (Fig. 1). Site 2 experienced the most extensive bed movements, probably due to the forcing elements in the upper part of the site that made this area particularly unstable (Matthaei et al. 1999b). The spate was followed by a long period of stable discharge and no further bed movement occurred until biological sampling.

Biological sampling and data analysis

On 21 October 1997, we collected 15 Surber samples (area 0.0625 m^2, mesh size 250 µm) at each site. A marked screwdriver was used to fix a sampling depth of 10 cm. Five samples were taken randomly from bed patches that had experienced 4 cm or more of scour during the August spate (see Fig. 1; mean scouring depth in these patches 5.3±1.3 cm (SD) at site 1, site 2: 12.0±5.6, site 3: 6.2±1.6). Another five were collected randomly from patches that had experienced 4 cm or more of fill without earlier scour (mean filling depth in these patches 9.2±3.4 cm at site 1, site 2: 6.8±2.1, site 3: 5.9±2.4), whereas the final five were taken from patches that had remained undisturbed (stable patches). In each sampling location, Surber samples were taken immediately downstream of the selected scour chain (with the frontal frame of the sampler touching the chain). Field measurements of water depths at the upstream and downstream edges of each sampled patch suggested that the amount of scour or fill in the patch (or the state of no change in stable patches) was similar to the amount of scour or fill at the corresponding chain (C.D. Matthaei, personal observations). Mean scouring depth in the sampled patches was greater at site 2 than at site 1 (P=0.03), but it was similar at sites 1 and 3 and at sites 2 and 3 (P=0.92 and 0.07, respectively; one-way ANOVA and Scheffe's post-hoc tests on log-transformed data). Mean filling depth in the sampled patches was similar across all three sites (P=0.19).

Surber samples were preserved with 70% ethanol in the field and taken to the laboratory. The invertebrates were sorted, counted and measured to the nearest millimetre (head-and-body length) under a stereomicroscope.

Total abundance, taxon richness, and abundances of the most common taxa in scour, fill, and stable patches were compared with two-way ANOVAs and Scheffe's post-hoc tests. After exploratory analysis, data were log (x) or log (x+1) transformed to improve normality and homoscedasticity.

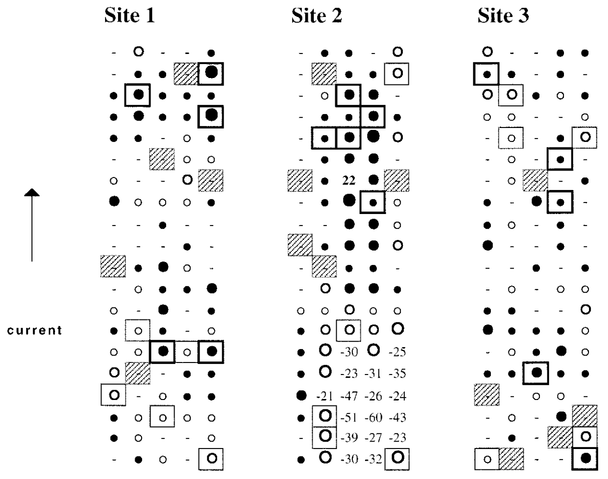

Fig. 1 Spatial patterns of scour (○), fill (●), or stable patches (–) during the spate. The *square frames* indicate the randomly chosen locations where the Surber samples were taken. "*Stable*" is equivalent to ≤1 cm scour or fill. The first chain row at each site was at the downstream end of the site, and left and right in the figure represent true left and right in the stream. Symbols: scour ○ >1–5 cm, ○ >5–10 cm, ○ >10–20 cm; and fill • >1–5 cm, ● >5–10 cm, ● >10–20 cm. Values >20 cm are specified in the figure (negative for scour and positive for fill)

Results

Samples were dominated by larvae of the mayfly *Deleatidium* (65.8% of the mean invertebrate total in all 45 samples). Other common taxa were larvae of Chironomidae (8.9%), black flies *Austrosimulium* spp. (8.8%), the beetle *Hydora* spp. (5.2%), Oligochaeta (3.5%), Isopoda (2.1%), and the dipteran *Eriopterini* (1.8%). These seven taxa comprised 96% of the invertebrates in the samples.

Taxon richness and total invertebrate density were similar across patch history types (Fig. 2, Table 1). However, the marginally non-significant result for total density (P = 0.06) may be partly a consequence of the fairly low statistical power of the analysis. Densities of *Deleatidium*, *Austrosimulium*, *Eriopterini* (all more abundant in fill patches), and Isopoda (more abundant in scour patches) differed significantly between patch types (Table 1). For *Deleatidium* and Isopoda (Fig. 3), these patch density patterns were fairly consistent across sites. By contrast, *Austrosimulium* and *Eriopterini* showed a significant site by patch type interaction, indicating that effects of patch type differed across sites. Chironomidae and *Hydora* (Fig. 4) showed no effects of patch type (but site by patch type interactions were close to significant; statistical power below 0.8). Densities of Oligochaeta were similar across patch types and showed no site by patch type interaction.

The invertebrate faunas also differed markedly between sites (Table 1). Mean total invertebrate density and densities of *Deleatidium*, Chironomidae, *Austrosimulium*, and Oligochaeta were highest at site 1. Isopoda were most abundant at site 2, and *Eriopterini* densities were similar at sites 1 and 2 but significantly lower at site 3.

For the four most common taxa, we also analysed whether densities of small (head-and-body length ≤3 mm) and large individuals (>3 mm) differed between sites and patch stability categories (Table 2). These size classes

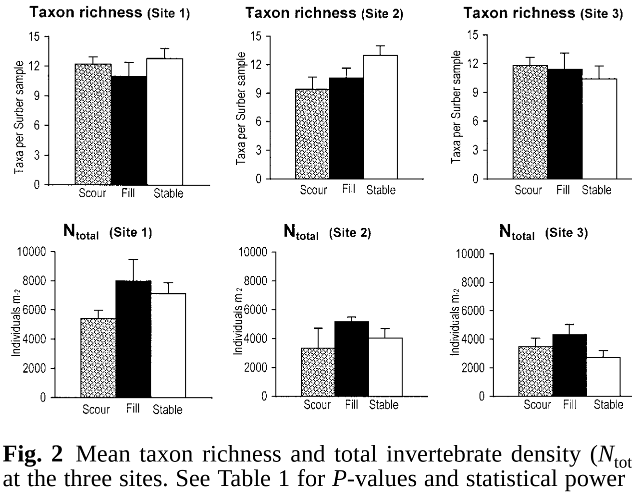

Fig. 2 Mean taxon richness and total invertebrate density (N_{total}) at the three sites. See Table 1 for P-values and statistical power of two-way comparisons between sites and patch types. *Error bars* represent standard errors

were chosen because they divided the populations of each taxon roughly in half. Densities of large *Deleatidium* and Chironomidae (P=0.05) differed between patch types but not between sites, whereas the opposite was the case for small individuals of the two taxa. These patterns differed from those for the entire populations of each taxon (compare with Table 1). Densities of small *Hydora* were similar across sites and patch types but large individuals were most abundant at site 1, and also more abundant in stable than in scour patches. The pattern for large individuals contrasted with that of the entire population, whereas the pattern for small individuals was similar to that of the entire population. Large and small *Austrosimulium* showed the same general density patterns as the entire population (patch type effects were not quite significant for the former but the corresponding statistical power values were below 0.8, see Table 2).

Discussion

Our research in the Kye Burn shows that local disturbance history can have both short- and long-term effects on the microdistribution of lotic invertebrates. In a previ-

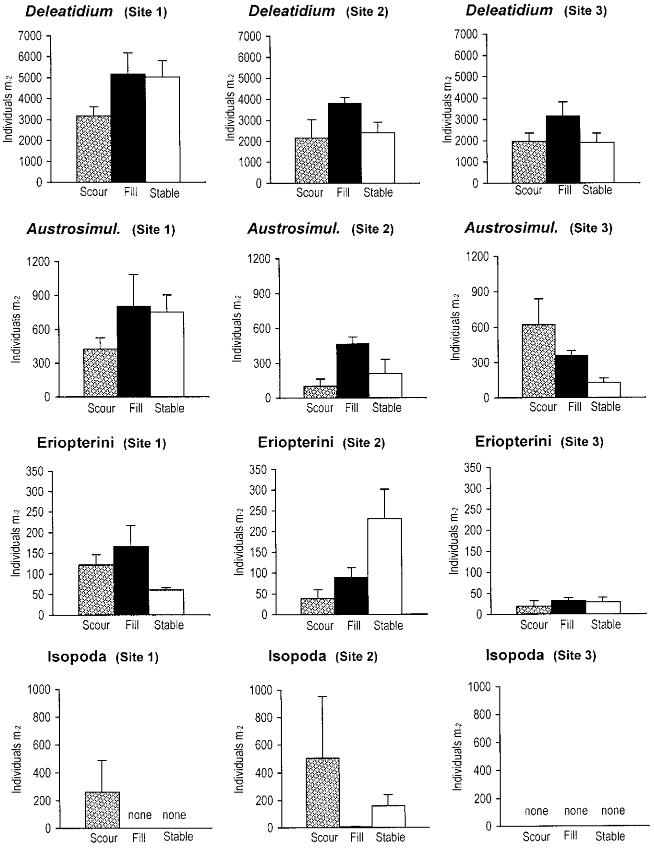

Fig. 3 Mean densities (±SE) of *Deleatidium* spp., *Austrosimulium* spp., *Eriopterini*, and Isopoda at the three sites. See Table 1 for *P*-values and statistical power of two-way comparisons between sites and patch types

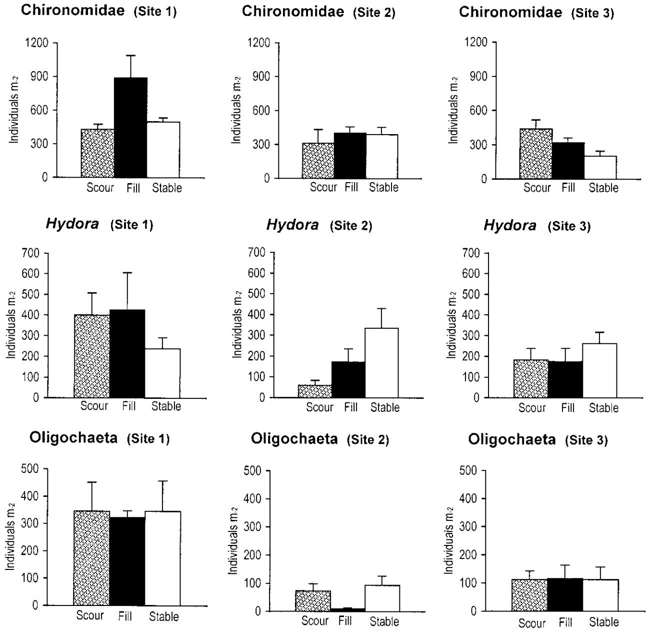

Fig. 4 Mean densities (±SE) of Chironomidae, *Hydora* spp., and Oligochaeta at the three sites. See Table 1 for *P*-values and statistical power of two-way comparisons between sites and patch types

Table 1 Summary of two-way ANOVAs comparing the invertebrate fauna between sites and patch types (log-transformed data; site or patch type rankings determined with Scheffe's *F*-tests. Where only two sites or patch types are named in the rankings, the other two pairwise comparisons showed no further significant differences). Statistical power (1–β is given and all α <0.05 and β <0.20 are shown in italics. For means and SEs see Figs. 2,3,4

	Site effects			Patch type effects			Site × Patch type	
	P	Power	Ranking	*P*	Power	Ranking	*P*	Power
Taxon richness	0.50	0.16	No difference	0.52	0.15	No difference	0.21	0.43
Total invertebrates	*0.004*	0.88	S1>(S2 = S3)	0.06	0.55	(Fill > scour)	0.36	0.32
Deleatidium	*0.01*	0.71	S1>(S2 = S3)	*0.02*	0.80	Fill > scour	0.55	0.22
Chironomidae	*0.004*	*0.87*	S1>(S2 = S3)	0.15	0.39	No difference	0.05	0.67
Austrosimulium	*0.001*	*0.97*	S1>S2	*0.03*	0.67	Fill > stable	*0.005*	*0.91*
Hydora	0.09	0.48	No difference	0.13	0.41	No difference	0.07	0.62
Oligochaeta	*<0.0001*	*1.0*	S1>(S2 = S3)	0.36	0.22	No difference	0.38	0.30
Isopoda	*0.008*	*0.82*	S2>S3	*0.04*	0.62	Scour > fill	0.20	0.44
Eriopterini	*<0.0001*	*1.0*	(S1 = S2) >S3	*0.048*	0.59	Fill > scour	*0.01*	*0.86*

Table 2 Summary of two-way ANOVAs comparing densities of large (>3 mm) and small (≤3 mm) individuals of the four most common taxa between sites and patch types (log-transformed data; site or patch type rankings determined with Scheffe's *F*-tests. Where only two patch types are named in the rankings, the other two pairwise comparisons showed no further significant differences). Statistical power (1–β) is given and all α <0.05 and β <0.20 are shown in italics

	Size class	Percentage of all individuals	Site effects			Patch type effects			Site × Patch type	
			P	Power	Ranking	*P*	Power	Ranking	*P*	Power
Deleatidium	Large	40%	0.19	0.34	No difference	*0.02*	0.75	Fill > scour	0.19	0.44
	Small	60%	*0.001*	*0.97*	S1>(S2 = S3)	0.13	0.42	No difference	0.50	0.25
Chironomidae	Large	33%	0.34	0.23	No difference	0.05	0.58	(Fill > stable)	*0.04*	0.70
	Small	67%	<*0.0001*	*0.99*	S1>(S2 = S3)	0.31	0.25	No difference	0.13	0.52
Austrosimulium	Large	34%	*0.001*	*0.96*	(S1 = S3) >S2	0.09	0.49	No difference	*0.03*	0.76
	Small	66%	*0.001*	*0.95*	S1>(S2 = S3)	0.05	0.58	(Fill > stable)	*0.003*	*0.93*
Hydora	Large	44%	*0.03*	0.65	S1>(S2 = S3)	*0.049*	0.59	Stable > scour	0.09	0.58
	small	56%	0.23	0.30	no difference	0.47	0.17	No difference	0.17	0.47

ous study, stable surface stones sampled during the receding limb of a bed-moving spate harboured far more invertebrates than unstable stones (Matthaei et al. 2000). In the present research, we sampled the invertebrates in bed patches of known disturbance history more than 2 months after the same spate. In spite of a long period of stable flow between the spate and animal sampling, densities of the dominant taxon *Deleatidium*, and of *Austrosimulium*, *Eriopterini*, and Isopoda differed significantly between scoured, depositional (fill), and stable bed patches. These effects of disturbance history on the invertebrate community might have been even stronger had we sampled sooner after the spate, or had we studied a large flood instead of a rather small spate with a return period of 5 months. To our knowledge, our study is the first to provide evidence for such long-term effects of local disturbance history on lotic invertebrates.

The study is also among the first to show long-term effects of a patchy disturbance on an animal community dominated by organisms that are highly mobile relative to the spatial scale of the disturbance. Scoured, depositional, and stable bed patches were separated by just a few metres (Fig. 1). *Deleatidium* is a rapid crawler and good swimmer, and black flies can cover long distances by drift (see review by Mackay 1992). Both taxa are well-known as abundant and early colonisers of disturbed reaches (Mackay 1992) and could have easily dispersed between the different patch types within a few days or less. The two taxa comprised 75% of the entire invertebrate community in our samples. The lasting effect of local disturbance history on these mobile taxa contrasts with the expectations of Downes (1990) and lends support to the opinion of Frid and Townsend (1989) and Townsend (1989) that patch dynamics models may be applied to lotic ecosystems. The possibility that patchy disturbances can affect the long-term distribution of mobile stream organisms has recently gained some theoretical support, as well. Nisbet et al. (1997) modelled invertebrate grazer dynamics in lotic grazer-algae systems and showed that patches can develop persistent differences in grazer densities depending on the initial conditions in the patch and grazer immigration from adjacent patches.

The observed long-term effects of disturbance history on the invertebrates in the Kye Burn were not simply a direct consequence of differential dislodgement/mortality during the spate because high mobility should have permitted rapid recolonization of disturbed patches. Moreover, if density patterns were caused by losses during the spate, invertebrate densities should have been highest in stable patches if these served as refugia during the event (as did stable surface stones; Matthaei et al. 2000). In fact, none of the common taxa was most abundant in stable patches 2 months after the spate. Densities of *Deleatidium*, *Austrosimulium* and *Eriopterini* were highest in depositional patches, and Isopoda were most abundant in scoured patches. Therefore, we believe the observed density differences were an indirect effect of the spate; scoured and, especially, depositional patches seemed to provide a more suitable habitat for invertebrates than the stable patches.

Local depositional events without earlier scour are common in the Kye Burn (Matthaei et al. 1999b), and we suggest that colonists of the freshly deposited sediments are derived partly from individuals in the original surface substratum (now buried), and partly from individuals that crawl or drift from elsewhere. Scoured patches are more likely to have lost animals at or near the substratum surface (though some may have moved down as the spate arrived), and colonisation by crawling and drifting is probably more important. We can only speculate about the reasons for the greater attractiveness of disturbed patches compared with stable ones because microhabitat parameters were not quantified. Both scoured and depositional patches offer clean substrata for new colonists, and depositional patches may also provide more interstitial living space and fresher particulate organic matter for detritivores (Metzler and Smock 1990; Naegeli et al. 1996) than stable bed patches. Larvae of black flies are well-known to have a preference for bare substrata as an attachment site from which to filter feed (e.g., Doeg et al. 1989; Matthaei et al. 1997), and *Deleatidium* is capable of browsing the thin microbial layers on stream stones, which regenerate much more rapidly than benthic algae after a disturbance

(Rounick and Winterbourn 1983; Winterbourn et al. 1984). The overall patterns in the use of patch types by *Deleatidium* were a consequence of distributional differences of larger individuals (Table 2; note also differences for larger Chironomidae and *Hydora*), implying that local disturbance history may be more important for the later developmental stages of these taxa, perhaps because older/larger larvae have more specific habitat preferences.

We took our samples more than 2 months after a spate with an average return period of 5 months. This means that after almost half the expected stable period (before the next high-flow event of similar magnitude), significant effects of the previous spate on invertebrate densities were still detectable. These observations imply that the imprint of hydrological disturbance on the invertebrate community in the Kye Burn will be observed over a large proportion of the stream bed and almost continuously. Just like the conifer forest in a fire-prone region (Johnson et al. 1995) or seaweeds on the boulders of a storm-battered shore (Sousa 1979), much of the stream bed of the Kye Burn appears to be always in a state of recovery from the last disturbance. The invertebrate density patterns that we observed in the Kye Burn may represent an earlier stage in a reasonably predictable succession (pioneer species arrive in a patch soon after a disturbance, to be replaced by others as algal resources and physical conditions change with time), as opposed to the unpredictable lottery of species replacement characteristics of founder-controlled communities (Yodzis 1986). The nature of the successional mosaic can be expected to contrast in rivers with different levels of productivity and disturbance regimes. Thus, algal growth in the Kye Burn is quite slow and visible mats require several months of stable flow to become established (C.D. Matthaei, unpublished data); perhaps larval black flies and *Deleatidium* would benefit from denuded substrata for shorter periods in more productive streams with faster algal colonisation and growth. Conversely, in flood-prone rivers like the Swiss River Necker where spates causing at least partial bed movement occur as often as once a month (Matthaei et al. 1996), the importance of disturbance history for invertebrate patchiness and community structure may be even greater than in the Kye Burn.

Total invertebrate density and overall densities of several common invertebrate taxa differed significantly, for undetermined reasons, between sites (Table 1), emphasising the point made by Downes et al. (1993, 1995) that even sites in close physical proximity in the same stream can be quite unlike in their invertebrate fauna. Of most relevance to the present study is the fact that effects of local disturbance history on invertebrates were not always consistent across sites. *Austrosimulium* and *Eriopterini* showed a significant site by patch type interaction, and the interaction term was almost significant for Chironomidae and *Hydora* (Table 1, Figs. 3,4). Whatever the precise habitat effects of hydrological disturbances turn out to be, it is clear that these effects and/or their consequences for invertebrates can differ between sites with contrasting geomorphologies. Substratum composition (e.g., Ulfstrand 1968, Holomuzki and Messier 1991), availability of food resources (Hearnden and Pearson 1991; Reed et al. 1994), local current velocity (Ulfstrand 1967; Osborne and Herricks 1987), and water depth (Barmuta 1989; Ruse 1994) are known to influence the microdistribution of lotic invertebrates. If these parameters are themselves influenced by local disturbance history, then history could turn out to be the most pervasive cause of the patchy distribution of lotic invertebrates. In the absence of a full understanding of the historical details of the patchy mosaic that is the stream bed, stream ecologists may be missing much of the plot.

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