

Recolonization Dynamics of Benthic Macroinvertebrates after Artificial and Natural Disturbances in an Australian Temporary Stream

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Abstract

The effects of substratum particle size (cobbles, coarse gravel and medium-fine gravel) on recolonization by benthic macroinvertebrates after disturbance was investigated in small plots (0.05 m²) in the Finnis River, an intermittent stream in South Australia. Six weeks after flow resumed, the intermediate particle size (coarse gravel) supported the greatest densities of taxa and individuals. Experimental disturbance reduced species richness by 83% and numbers of individuals by 97%. Rapid recolonizers (e.g. mayfly and stonefly nymphs) showed little substratum specificity and attained predisturbance densities within one day. Slow recolonizers (e.g. chironomid hatchlings) favoured gravel substrata and had not reached predisturbance densities within 4 days. Recolonization of small plots appeared to be by surface movement from neighbouring intact areas. A spate on Day 7 prevented further sampling, destroying all experimental plots, but this permitted a study of macroinvertebrate recolonization following a natural disturbance at a larger spatial scale. The spate reduced species richness by 45% and numbers of individuals by 70%. Vertical migration rather than drift appeared to be the major source of recolonizing fauna. Our data show that results from small-scale experiments can not be extrapolated to large-scale disturbance because the scale of disturbance strongly influences the rate and pathways of recolonization as well as the sources and faunal composition of the recolonists.

Extra keywords: spate, substratum particle size, mobility.

Introduction

In the last two decades, stream ecologists have greatly advanced our understanding of the influence of abiotic and biotic variables on benthic macroinvertebrate assemblage structure (reviews by Minshall 1984, 1988 and Power *et al.* 1988). More recently, it has been recognized that natural physical disturbances (e.g. floods) often modify the impacts of these variables (Resh *et al.* 1988) and generate heterogeneity at a range of scales (Fisher and Grimm 1988; Grimm and Fisher 1989).

Townsend (1989) proposed three approaches to the study of disturbance in streams: phenomenological accounts of particular events, comparative studies in streams with contrasting disturbance regimes, and experimental manipulations. Phenomenological accounts of floods, although unreplicated, are vital because few such cases exist (Townsend 1989), especially for Australian streams. Experimental studies involve replication, but interpretation of their results is difficult because conclusions from manipulations conducted at small scales may be inappropriate when extrapolated to large-scale natural disturbances (Fisher 1987; Minshall 1988). Townsend suggests that the best approach involves artificially generated disturbances that coincide with a phenomenological study.

In this paper, we compare postdisturbance recolonization by macroinvertebrates of plots containing substratum particles of three different size classes. Substratum particle size has been shown to influence macroinvertebrate assemblage composition (reviewed by Minshall 1984) and is itself influenced by physical disturbances in streams. The fortuitous occurrence of a natural spate during the study enabled us to assess the realism of our experimental manipulations and to compare the recolonization patterns following artificial and natural disturbances.

Materials and Methods

Study Area

The study site is located on the Finnis River near Ashbourne, South Australia (35°18'S, 138°42'E). The Finnis River, fed primarily by Meadows Creek and Blackfellows Creek, which arise on the southern edge of the Mount Lofty Ranges, flows for 5 km through natural vegetation before entering the study site.

The site is in a shaded gully, where the stream is approximately 10 m wide. The granite slopes are covered by open woodland, tending towards low woodland/tall scrubland on the higher slopes. The principal tree species are *Eucalyptus camaldulensis*, *E. fasciculosa*, *E. obliqua* and *E. leucoxydon*. The understorey is dominated by *Olearia ramulosa*. Common riparian vegetation includes *Rubus fruticosus*, *Rosa* sp., *Fraxinus* sp. and *Pteridium esculentum*.

The highly variable discharge usually peaks in spring and ceases in late summer (Engineering and Water Supply Department, South Australia, unpublished data). During the spate that occurred in this study, discharge increased from 100 ML on Day 6 to 1200 ML on Day 8 and abated as rapidly.

Experimental Design

A preliminary survey of the study reach identified distinct patches of sand, fine and coarse gravels, and cobbles. The three most common substratum sizes (based on the classification of Wentworth 1922) were selected as experimental treatments. Experimental plots were constructed during March while the stream was dry.

To correct for potential longitudinal variation down the experimental reach, the treatments were assigned to four consecutive blocks, enabling us to analyse the data by using randomized complete-block analyses of variance (Neter *et al.* 1985). Twelve treatment plots (three substrata \times four replicates) and ten patches of natural substrata were randomly placed within each block. Treatment plots were constructed by digging holes approximately 50 cm square and 30 cm deep into the riverbed. Excavated material was shaken through a nest of sieves with mesh sizes of 50, 25, 15 and 4 mm, thereby separating out the medium-fine gravel (4–15 mm) and the coarse gravel (25–50 mm). Cobbles (100–250 mm) were chosen randomly from the dry riverbed. Intermediate particle sizes were discarded in order to accentuate the distinctions among the treatment substrata. Holes were refilled to the level of the surrounding riverbed with the appropriate size fraction.

Field Sampling

When flow began, all experimental plots were inundated simultaneously. Six weeks later (Day 0), each treatment plot and two plots of natural substrata in each block were sampled to examine the influence of substratum particle size on the assemblage composition of benthic macroinvertebrates. Samples were collected from the centre of each plot with a flow-independent suction sampler (Boulton 1985) that enclosed 0.05 m² (22.5 \times 22.5 cm) of substratum, which was scrubbed and stirred to a depth of 10 cm. Suspended material was pumped for a fixed time (45 s) through a 50- μ m-mesh collecting net and preserved in 4% formalin for transport to the laboratory.

After sampling, each treatment plot was experimentally disturbed by vigorous shuffling and kicking in the plot for 2 min. On Day 0, postdisturbance samples were taken from two plots of each substratum particle size in each block immediately after the disturbance in order to ascertain the efficiency with which the combination of sampling and artificial disturbance reduced macroinvertebrate abundance. One plot of each substratum particle size in each block was sampled on Days 1, 2 and 4. Plots sampled on Day 1 were immediately redisturbed, allowing them to be resampled on Day 4 to give macroinvertebrate density data after 3 days of recolonization. These samples were taken from plots disturbed twice, whereas other samples were collected from plots disturbed only once. These data are included in the analysis because the experimental disturbance removed nearly all individuals (see later). Two

plots of natural substrata in each block were sampled on Days 0, 1, 2 and 4 to document background variation.

A spate prevented sampling on Day 7 and destroyed all experimental plots on Day 8. Although the experiment was thus prematurely truncated, the spate effectively demonstrated the process under investigation and permitted a study of macroinvertebrate recolonization following a natural disturbance that denuded a much larger area of the streambed. Ten benthic samples were taken from natural substrata on Day 11, the earliest opportunity at which the depth and current velocity of the river permitted sampling. A further 10 samples were taken 4 days later (Day 15) to compare 4-day recolonization after the spate with recolonization after the small-scale experimental disturbances.

On Day 15, two 50- μm -mesh drift nets were placed in the stream approximately 2 m from each bank and 20 cm above the riverbed to examine invertebrate drift as a potential source of recolonists. Each 2-m-long conical net was 50 cm in diameter and was attached to a 30-cm-long aluminium headpiece with a square intake (10 \times 10 cm). This headpiece prevented a pressure cone of water from forming across the opening and reducing the filtration efficiency (Boulton, unpublished data). Samples were collected every 2 h for 24 h except at dusk and dawn, when samples were collected hourly.

Laboratory Processing

Macroinvertebrates retained on a 250 μm sieve were identified as far as possible and enumerated. Oligochaetes were separated into 'large' specimens retained on a 1000 μm sieve and 'small' specimens retained on the 250 μm sieve. Individuals too small to classify beyond family were placed into artificial categories (e.g. chironomid hatchlings) and considered as separate taxa in the analyses.

Data Analysis

Macroinvertebrate abundance is not proportional to the surface area of substrata because the combined surface area of the particles is unlikely to reflect the area available when the particles are packed together *in situ* (Chutter 1968; Khalaf and Tachet 1980; Culp *et al.* 1983; Barmuta 1990). Therefore, references below to the abundance or density of taxa are to the number of individuals per substratum sample of 0.005 m³ (0.05 m² sample area \times 10 cm depth).

Abundance data were transformed using $\log_{10}(x + 1)$ (Elliott 1977), and the suitability of the transformation was confirmed by using χ^2 goodness-of-fit tests. Percentage data were arcsine-transformed (Zar 1984) prior to analysis. Mean numbers of taxa were normally distributed and thus not transformed.

To examine the influence of substratum particle size on macroinvertebrate assemblage composition 6 weeks after flow resumed, Model I one-way analyses of variance (ANOVAs) (Zar 1984) were performed on the mean number of taxa, the mean number of individuals (with and without small oligochaetes), and the mean densities of common taxa in samples collected from plots of different substratum particle sizes. 'Common' taxa were regarded as all taxa that occurred in more than 75% of the replicates of any one treatment with a density greater than five individuals per sample. To investigate the influence of time since last disturbance concurrently with substratum particle size, Model I two-way ANOVAs were performed on the mean number of taxa, the mean number of individuals (with and without small oligochaetes), and the mean densities of common taxa. In both sets of analyses, the overall error rate for multiple species in samples was adjusted by using the Bonferroni procedure (Neter *et al.* 1985). With this procedure, the nominated significance level (here 0.05) is divided by the number of nonindependent tests. This makes the tests more conservative to account for the lack of independence between tests. When interaction terms were not significant, Tukey's honestly significant difference procedure (Zar 1984) was used to locate sources of significant differences.

Taxa were classified according to their rate of recolonization during this experiment. 'Fast' recolonizers achieved predisturbance densities within 1–2 days in all substrata. Taxa with 'moderate' rates of recolonization attained predisturbance densities in at least two of the three treatment substrata within 4 days. Remaining taxa were classified as 'slow' recolonizers.

Abundances of common taxa were ranked and tested for concordance among substrata by using Kendall's coefficient of concordance, W (Zar 1984). This nonparametric procedure compares the ranking of species in samples with the null hypothesis of randomness. Kendall's W ranges between 0 (no concordance) and 1 (complete concordance). A stable assemblage would be more consistent in the ranked abundance of its constituent taxa than would a fluctuating assemblage (Meffe and Minckley 1987).

Drift rates over 24 h (24HDR; *sensu* Allen and Russek 1985) were calculated for the 10 most common taxa in the drift. This equation estimates the total number of organisms drifting past the

sampling point in 24 hours. It was assumed that the 24HDR of each taxon would be positively correlated with the potential of each taxon to recolonize the substratum plots. This assumption is admittedly simplistic and ignores behavioural preferences for specific substrata, but at least it provides some indication of the importance of this postflood recolonization pathway in this study.

Results

Assemblage Composition 6 Weeks after Resumption of Flow

One block of treatments and natural substrata had to be discarded from the analyses because it was different from the other three blocks in width, flow regime and substratum

Table 1. Summary of one-way analyses of variance on means of numbers of taxa, densities of individuals with and without small oligochaetes, and densities of the 19 most common taxa among substrata

MFG, medium-fine gravel; CG, coarse gravel; C, cobble; NAT, natural substrata. Adjusted 0.05 Bonferroni significance level = 0.0023 (n.s., not significant; * $P < 0.0023$). Densities that are not significantly different ($P > 0.0023$) are underlined

	Significance	Density			
		Highest	Lowest		
Mean number of taxa	*	CG	<u>MFG</u>	<u>NAT</u>	<u>C</u>
Mean number of individuals	*	MFG	<u>CG</u>	<u>NAT</u>	<u>C</u>
Mean number of individuals excluding small oligochaetes	n.s.				
Nematoda					
Nematoda spp.	n.s.				
Oligochaeta					
Small oligochaetes	*	<u>MFG</u>	<u>CG</u>	<u>NAT</u>	<u>C</u>
Large oligochaetes	*	<u>CG</u>	<u>MFG</u>	<u>NAT</u>	<u>C</u>
Gastropoda					
<i>Physastra gibbosa</i>	*	CG	<u>C</u>	<u>MFG</u>	<u>NAT</u>
Amphipoda					
<i>Afrochiltonia australis</i>	n.s.				
Insecta					
Ephemeroptera					
<i>Atalophlebia australasica</i>	n.s.				
<i>Nousia inconspicua</i>	*	<u>CG</u>	<u>C</u>	<u>MFG</u>	<u>NAT</u>
Mayfly hatchlings	*	<u>MFG</u>	<u>CG</u>	<u>C</u>	<u>NAT</u>
Plecoptera					
<i>Dinotoperla evansi</i>	n.s.				
<i>Newmanoperla thoreyi</i>	n.s.				
Stonefly hatchlings	n.s.				
Diptera					
Chironomidae					
<i>Riethia</i> sp. 1	*	CG	<u>MFG</u>	<u>NAT</u>	<u>C</u>
<i>Cricotopus</i> sp. 1	*	CG	<u>MFG</u>	<u>C</u>	<u>NAT</u>
<i>Cricotopus</i> sp. 3	n.s.				
<i>Cricotopus</i> sp. 5	n.s.				
Chironomid hatchlings	*	<u>CG</u>	<u>MFG</u>	<u>NAT</u>	<u>C</u>
Ceratopogonidae					
<i>Bezzia</i> sp. 1	n.s.				
<i>Culicoides</i> sp. 1	n.s.				
Tricoptera					
<i>Hellyethira simplex</i>	n.s.				

composition. At this block, the river was 13 m wide with many large cobbles (diameter > 300 mm). Flow, divided by a large log-jam directly upstream, converged turbulently in the centre of the block. This was not foreseen when the river was dry. Variance associated with this block obscured the variance due to the treatments. The other three blocks were similar in width (mean = 9 m) and particle size distribution, having a mixture of particle sizes spanned by the experimental treatments, with uniform flow across each block.

A total of 90 735 individuals representing 109 taxa was collected in six samples from natural substrata and from three blocks of experimental plots (36 samples) 6 weeks after flow resumed. In all, 19 taxa were classified as common. The mean number of taxa, mean number of individuals and mean densities of eight of the 19 common taxa differed significantly among substrata ($5.9 < F_{3,38} < 13.0$, $P < 0.0020$) (Table 1). There were significantly more taxa in plots of the intermediate particle size, coarse gravel ($F_{3,38} = 9.9$, $P < 0.001$) (Table 1).

Small oligochaetes comprised 75% of the number of individuals in coarse gravel and cobbles and 85% in medium-fine gravel and natural substrata. The mean number of

Table 2. Percentage reductions in abundance after experimental disturbance and after the spate Rate-of-recolonization classifications (Table 3) are included (F, fast; M, moderate; S, slow). Significant increases in density are shown by asterisks (adjusted 0.05 Bonferroni significance level = 0.0022, * $P < 0.0022$). Percentage changes in density after experimental disturbance are means of the density changes in the three experimental substrata. Changes in density after the spate are percentages of densities in natural substrata taken on Day 4; dashes indicate mean densities of <2 individuals per 0.005 m³

	Experimental disturbance		Natural disturbance (spate)	
	Reduction in density after disturbance (%)	Increase after 4 days ^A (%)	Reduction in density after disturbance (%)	Increase after 4 days ^A (%)
Mean number of taxa	83	80*	45	78*
Mean number of individuals	97	38*	70	112*
Mean number of individuals excluding small oligochaetes	97	69*	83	33
Nematoda spp. (M)	97	59*	99	54*
Small oligochaetes (S)	97	31*	67	133*
Large oligochaetes (M)	94	43*	—	—
<i>Physastra gibbosa</i> (M)	98	120*	—	—
<i>Afrochiltonia australis</i> (F)	99	177*	33	117*
<i>Atalophlebia australasica</i> (F)	99	47*	52	28
<i>Nousia inconspicua</i> (F)	99	109*	89	7
Mayfly hatchlings (S)	97	15*	—	—
<i>Baetis soror</i> (F)	100	81*	91	23
<i>Dinotoperla evansi</i> (F)	96	48*	91	11
<i>Newmanoperla thoreyi</i> (F)	99	99*	80	18
Stonefly hatchlings (S)	99	22*	—	—
<i>Riethia</i> sp. 1 (M)	100	36*	—	—
<i>Cricotopus</i> sp. 1 (M)	96	91*	74	23
<i>Cricotopus</i> sp. 3 (S)	100	28*	83	23
<i>Cricotopus</i> sp. 5 (S)	95	26*	—	—
Chironomid hatchlings (S)	95	45*	82	39*
<i>Bezzia</i> sp. 1 (M)	87	54*	90	45*
<i>Culicoides</i> sp. 1 (M)	89	114*	—	—
<i>Hellyethira simplex</i> (M)	94	64*	91	12

^A Expressed as a percentage of the predisturbance density.

individuals was significantly greater in coarse and medium-fine gravel than in cobbles ($F_{3,38} = 6.3$, $P < 0.001$) (Table 1), reflecting the high density of small oligochaetes. The mean number of individuals excluding small oligochaetes was analysed separately in order to examine the patterns of the other taxa. Densities of these individuals did not differ significantly among substrata.

The densities of common mayflies (*Atalophlebia australascia* and *Nousia inconspicua*) and stoneflies (*Dinotoperla evansi*, *Newmanoperla thoreyi* and hatchlings) did not vary significantly among treatment substrata, whereas mayfly hatchlings were significantly more abundant in coarse gravel and medium-fine gravel ($F_{3,38} = 7.8$, $P < 0.001$). The gastropod *Physastra gibbosa* and the chironomids *Riethia* sp. 1 and *Cricotopus* sp. 1 were significantly most abundant in coarse gravel ($8.6 < F_{3,38} < 12.9$, $P < 0.001$) (Table 1). Numbers of chironomid hatchlings were also greater in coarse gravel than in cobbles or natural substrata.

The ranked abundances of common taxa were highly concordant among substrata (Kendall's $W = 0.75$, $\chi^2 = 54.2$, $P < 0.001$) and the null hypothesis of randomness was rejected, indicating that the compositions of the assemblages colonizing each substratum particle size were similar.

Recolonization of Substrata after Experimental Disturbance

The experimental disturbances reduced species richness and numbers of individuals by 83% and 97% respectively (Table 2). There was no significant difference among substrata in the arcsin-transformed percentage reduction of taxa ($F_{2,15} = 2.2$, $P = 0.15$) or numbers of individuals ($F_{2,15} = 0.46$, $P = 0.67$).

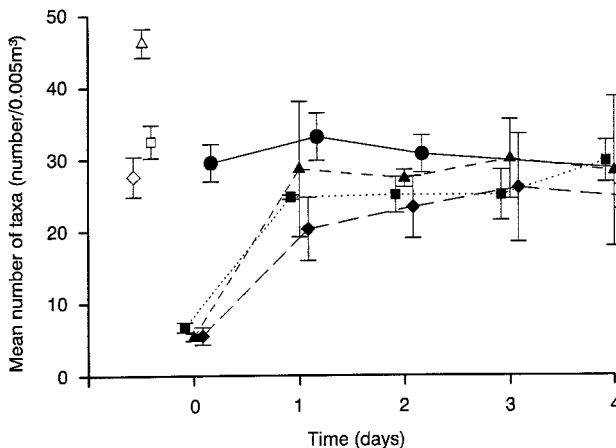


Fig. 1. Increase in mean number of taxa in medium-fine gravel (■), coarse gravel (▲), cobbles (◆) and natural substrata (●), with standard error bars ($n = 3$). Open symbols represent densities prior to experimental disturbance.

A total of 183 814 individuals was collected (including those collected 6 weeks after the resumption of flow), representing 115 taxa of which 20 were deemed common. The mean number of taxa, mean number of individuals (including and excluding small oligochaetes) and mean densities of 15 of the 20 common taxa varied significantly among substrata ($6.1 < F_{3,71} < 15.4$, $P < 0.001$) or with time ($6.7 < F_{3,71} < 20.2$, $P < 0.001$) over 4 days. No substratum-time interactions were significant. The mean number of taxa increased significantly only on the first day in all substrata (Fig. 1). The number of taxa in coarse gravel remained below predisturbance levels. Predisturbance densities of taxa were achieved by Day 2 in cobbles and Day 4 in medium-fine gravel.

Recolonization trajectories for the mean number of individuals primarily reflected recolonization by large numbers of small oligochaetes. The mean number of individuals excluding small oligochaetes attained predisturbance densities after 2 days in medium-fine gravel and cobbles (Fig. 2). Predisturbance densities in coarse gravel were not reached in 4 days.

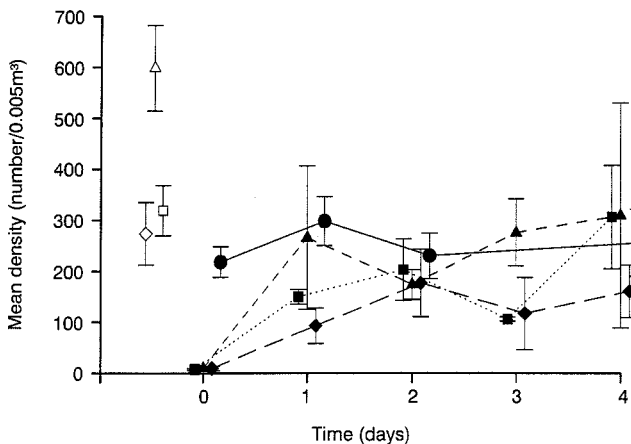


Fig. 2. Increase in mean number of individuals (excluding small oligochaetes) in medium-fine gravel (■), coarse gravel (▲), cobbles (◆) and natural substrata (●), with standard error bars (n = 3). Open symbols represent densities prior to experimental disturbance.

Table 3. Classification of taxa according to their rate of recolonization of substratum plots

MFG, medium-fine gravel; CG, coarse gravel; C, cobble

Classification	Time taken to recolonize to predisturbance densities (days)		
	MFG	CG	C
Fast			
<i>Baetis soror</i>	1	1	1
<i>Afrochiltonia australis</i>	1	1	1
<i>Atalophlebia australasica</i>	1	1	2
<i>Nousia inconspicua</i>	2	1	2
<i>Dinotoperla evansi</i>	1	2	1
<i>Newmanoperla thoreyi</i>	1	2	2
Moderate			
<i>Hellyethira simplex</i>	3	1	2
<i>Physastra gibbosa</i>	3	—	3
<i>Riethia</i> sp. 1	—	1	1
<i>Cricotopus</i> sp. 1	3	—	2
Nematoda spp.	4	—	1
Large oligochaetes	1	1	—
<i>Bezzia</i> sp. 1	4	1	1
<i>Culicoides</i> sp. 1	4	—	3
Slow			
Mayfly hatchlings	—	—	—
Stonefly hatchlings	4	—	—
Chironomid hatchlings	—	—	4
Small oligochaetes	—	—	—
<i>Cricotopus</i> sp. 3	—	—	2
<i>Cricotopus</i> sp. 5	4	—	—

Large stonefly and mayfly nymphs and the amphipod *Afrochiltonia australis* attained predisturbance densities in all substratum particle sizes within 2 days and were classified as fast colonizers (Table 3). Eight of the common taxa colonized the substrata at moderate rates, whereas hatchlings, small oligochaetes and *Cricotopus* spp. were classified as slow colonizers (Table 3).

Common taxa were highly concordant over time and among substrata (Kendall's $W = 0.73$, $\chi^2 = 531$, $P < 0.001$).

Recolonization of Natural Substrata after a Spate

It is difficult to determine when a natural spatte begins and ceases to be a disturbance to resident stream invertebrates. However, the spatte that occurred in this study appeared to be a less intense disturbance than the experimental manipulation (cf. percentage reductions in density after experimental and natural disturbances, Table 2). However, recolonization was generally faster after experimental disturbances (cf. percentage increases in density, Table 2).

The spatte reduced the densities of all common taxa (Table 2). Mayfly and stonefly hatchlings, large oligochaetes, *Physastra gibosa*, *Riethia* sp. 1, *Cricotopus* sp. 5 and *Culicoides* sp. 1 were too rare in natural substrata (mean density < 2 individuals per 0.005 m^3) to allow valid comparisons of pre- and postspatte densities. In the 4 days after the spatte, the densities of only five taxa (small oligochaetes, chironomid hatchlings, *Afrochiltonia australis*, nematodes and *Bezzia* sp. 1) increased significantly ($P < 0.001$) (Table 2). Densities of remaining taxa did not increase significantly (Table 2).

There was no significant difference in the extent to which densities of fast, moderate or slow recolonizers (Table 2) were reduced by the spatte ($F_{2,10} = 1.1$, $P = 0.37$).

Table 4. Comparison between the 10 most common taxa in the drift and the 10 most common taxa in the benthos after the spatte
Rate-of-recolonization classifications (Table 3) are included (F, fast; M, moderate; S, slow)

Drift	Benthos
Small oligochaetes (S)	Small oligochaetes (S)
Chironomid hatchlings (S)	<i>Nousia inconspicua</i> (F)
<i>Cricotopus</i> sp. 1 (M)	Chironomid hatchlings (S)
<i>Afrochiltonia australis</i> (F)	<i>Atalophlebia australasica</i> (F)
<i>Hellyethira simplex</i> (M)	<i>Dinotoperla evansi</i> (F)
<i>Dinotoperla evansi</i> (F)	<i>Cricotopus</i> sp. 1 (M)
Stonefly hatchlings (S)	<i>Hellyethira simplex</i> (M)
<i>Corynoneura</i> sp. 1	<i>Newmanoperla thoreyi</i> (F)
<i>Polypedilum</i> sp.	Nematoda spp. (M)
<i>Dicrotendipes</i> sp. 2	<i>Afrochiltonia australis</i> (F)

Drift

Seven of the 10 most common taxa in the drift were common in the benthos, representing fast, medium and slow colonizers (Table 4). The 10 most common taxa in the drift differed from the 10 most common taxa in the benthos (Table 4). Only three of the five taxa that increased in density after the spatte (small oligochaetes, *Afrochiltonia australis* and chironomid hatchlings) were present in the drift.

Discussion

Assemblage Composition in Experimental Substrata 6 Weeks after Resumption of Flow

Six weeks after flow resumed, most taxa and individuals were found in plots of intermediate-sized particles (coarse gravel). This has been observed often (Rabeni and Minshall 1977; Williams and Mundie 1978; Wise and Molles 1979) and may reflect the efficiency with which intermediate-sized particles trap fine particulate detritus (Rabeni and Minshall 1977; Parker 1989). Fast interstitial currents and a lack of organic matter in cobble plots may

provide little incentive for animals other than filter-feeders to recolonize. In addition, the interstices of natural substrata and medium-fine gravel contained many inorganic particles that limit space and the diffusion of gases (Minshall 1984). Thus, the lower densities in these substrata may reflect the limited availability of different resources.

Many workers have used replicate substratum treatments to examine the influence of substratum particle size on macroinvertebrates (e.g. Rabeni and Minshall 1977; Wise and Molles 1979; Khalaf and Tachet 1980; Reice 1983). However, the flow environment of replicates in different positions in the stream is likely to be quite different at a scale relevant to invertebrates due to natural variation in micro-scale flow patterns produced by a heterogeneous streambed profile (Davis 1986; Casey and Clifford 1989). Barmuta (1990) examined the interaction between the effects of substratum particle size, current velocity and location on stream benthos, concluding that location in the riverbed influenced the fauna more than the interaction between current velocity and substratum particle size. Reice (1983) also noted inexplicable patchiness in the distributions of macroinvertebrates among standardized substratum baskets.

Evidence for the importance of the substratum in determining the distribution of benthic invertebrates has been conflicting because generalizations are sought from a wide variety of taxa that are studied using different experimental procedures (Minshall 1984), and these generalizations are often confounded by an inappropriate scale of investigation. Changes in substratum characteristics (e.g. size, shape, roughness, orientation, heterogeneity) alter interstitial and surface flow patterns and the degree to which organic matter is trapped (Minshall and Minshall 1977; Rabeni and Minshall 1977; Davis 1986; Statzner *et al.* 1988; Barmuta 1990). The interstitial environment must be quantified at a finer, more appropriate scale if we are to determine successfully the abiotic factors influencing the distribution of taxa and hence macroinvertebrate assemblage composition.

Recolonization of Experimental Substrata after Disturbance

In our study, we classified as rapid recolonists those highly mobile taxa (e.g. mayfly and stonefly nymphs, amphipods) that recolonized all treatments within 2 days and were substratum generalists (*sensu* Minshall 1984). Moderate recolonizers were also substratum generalists but were less mobile. For example, larvae of the hydroptilid caddisfly *Helyethira simplex* are restricted by their purse-shaped cases. Other taxa (nematodes, large oligochaetes and the ceratopogonid larvae *Bezzia* sp. 1 and *Culicoides* sp. 1) are common in the hyporheic zone (Gray and Fisher 1981; Williams 1984) and apparently sacrifice some mobility in favour of physical modifications for an interstitial existence.

Slow recolonists were usually small individuals (e.g. mayfly, stonefly and chironomid hatchlings). In contrast to older nymphs, mayfly and stonefly hatchlings did not recover from disturbance in 4 days, demonstrating that the size of a species can have a major effect on its rate of postdisturbance recovery. For smaller taxa, the distance that must be covered to recolonize a patch is larger in proportion to body size. Thus, smaller individuals may tend to be less mobile than larger ones. The degree of variation in drift rates for different sizes of individuals is not known. Disturbances during the first few months of flow in a temporary stream may have a greater short-term effect on faunal assemblages than do disturbances in early summer, when many taxa are older, larger and perhaps less vulnerable to disturbances and can recolonize patches rapidly. However, these larger taxa may be less able to seek refuge in the interstitial spaces of the hyporheic zone.

Recolonization of Natural Substrata after a Spate

It is difficult to determine the start and end of disturbance for episodic discharge events in streams. There are no data to indicate when high discharge becomes a disturbance to the invertebrate taxa. It is difficult to determine the timing and amount of streambed particle movement relative to discharge and to assess the influence of this movement on the resident

macroinvertebrates. Sustained high discharge restricted the first sampling opportunity to Day 11, 3 days after peak flow. At this time, most of the streambed appeared to have been disturbed.

Taxa that swiftly recolonized natural substrata after the spate differed from those classified as rapid recolonists on the basis of results from the small-scale experiment. After the spate, the densities of only one rapid recolonist (the amphipod *Afrochiltonia australis*) increased significantly. This result highlights the risks involved in extrapolating classifications of mobility based on small-scale experiments to predictions of trends following natural disturbances, especially given the inevitably different time frames between experiments and natural phenomena.

Only two of the 115 taxa collected in this study were sedentary (the freshwater limpet *Ferrissia* sp. and the bivalve *Sphaerium tasmanicum*). Both of these taxa were rare. In intermittent streams that are frequently disturbed by spates and droughts, the fauna must be highly mobile to escape or recolonize rapidly (e.g. Fisher *et al.* 1982; Boulton 1989; Grimm and Fisher 1989) or be capable of resisting the disturbance (e.g. Boulton *et al.* 1991). *Afrochiltonia australis* was the only taxon that appeared capable of resisting the spate in the present study. This amphipod is a competent swimmer and may have been able to resist the current in turbulent near-bed flow. Highly mobile taxa may seek refuges away from fast current velocities more quickly than less mobile taxa and therefore avoid much of the disturbing force of the spate. We found no significant difference among the percentage reductions in density of fast, moderate or slow recolonizers after the spate, possibly because our samples were taken in midchannel in a riffle where the substratum had been completely reworked and was at least 50 m from potential refuges (e.g. debris dams). *Afrochiltonia australis* may have recolonized denuded substrata from the water column as the spate subsided.

The densities of only five of the 20 common taxa increased significantly after the flood. Four of these taxa (small oligochaetes, nematodes, the ceratopogonid *Bessia* sp. 1 and chironomid hatchlings) are typical of the hyporheos (Williams and Hynes 1974; Gray and Fisher 1981; Williams 1984; Marchant 1988; Boulton *et al.* 1991). As discharge increases, some taxa (especially chironomids, ceratopogonids and other Diptera) migrate downward (Williams and Hynes 1974; Marchant 1988) and may rapidly move back to the surface when flow subsides (Morris and Brooker 1979). Recolonization after the spate in the present study may represent active vertical migration from deeper substrata that were not disturbed. Densities of six taxa (Nematoda spp., *Nousia inconspicua*, *Baetis soror*, *Dinotoperla evansi*, *Bezzia* sp. 1, *Helyethira simplex*) were reduced by similar degrees (within 10%) by the spate. Of these, only the numbers of nematodes and *Bezzia* sp. 1 (two hyporheic taxa) increased significantly after 4 days. Slower recolonization by the other taxa (all surface dwellers) may have been due to their depletion from the upper zones by the spate.

Common taxa in the drift were not representative of taxa that recolonized after the spate. Two of the five taxa that increased in density over the 4-day sampling period (nematodes and *Bezzia* sp. 1) were absent from the drift. Although *Afrochiltonia australis* may have recolonized via drift in this study, drift is probably a less important source of recolonists after major disturbances because upstream reaches are also denuded. In a Canadian temporary stream, macroinvertebrates tended to colonize substrata from hyporheic environments and via upstream movement rather than by drift (Williams 1977).

Comparison of Experimental and Natural Disturbances

The size of the disturbed area relative to the size of the system affects the rate and dynamics of the recovery process (Fisher 1987; Minshall 1988). Recolonization was rapid in small plots due to the proximity of colonists in the surrounding riverbed. Mobile animals had only to move 25 cm onto the plot to be within sampling range the next day. This is a drawback of studies that disturb individual rocks or small patches of substratum (e.g. Lake and Doeg 1985; Boulton *et al.* 1988) to simulate disturbance by floods. However, minor

spates may affect only small areas of riverbed, creating denuded patches rather than a complete reach or stream section (Peckarsky 1987; Doeg *et al.* 1989). Recolonization of these patches represents a redistribution of the benthos (Townsend and Hildrew 1976) rather than colonization after a catastrophic flood (e.g. Fisher *et al.* 1982).

Conclusions derived from studies at different scales of resolution may not be commensurate. We concur with Minshall (1988) that manipulative experiments conducted at small spatial scales provide considerable insight into the recovery dynamics of individual stones or patches of substratum and aid in explaining the spatial heterogeneity of local habitats. However, such experiments tell us little of the effects of disturbances, such as spates, on a whole stream. Responses to larger-scale disturbances are likely to depend on factors such as the percentage and depth of the sediments disturbed, how far the substratum moves, and the degree of mortality and extent of displacement of organisms (Minshall 1988). However, the unpredictability and large spatial scale of spates makes controlled and replicated experiments difficult. Comparisons such as ours reflect sheer good fortune in timing.

Assemblage Composition

The stability of rank abundances of taxa after disturbances suggests a stable assemblage structure. Stability refers to the ability to return to an 'equilibrium' state after a temporary disturbance, and it may be attained either through resistance (to deflection of state variables) or through resilience (swift recovery to the predisturbance state) (Holling 1973; Connell and Sousa 1983). Our data are insufficient to assess the resilience or resistance of macroinvertebrates to the spate. However, the assemblage composition of common benthic invertebrates in the Finnis River appears to be stable through resilience to small-scale disturbances. High resilience of macroinvertebrate communities has been documented in other Australian streams (e.g. Boulton *et al.* 1988; Doeg *et al.* 1989; Lake *et al.* 1989). It is incorrect to conclude that disturbances have little effect on stream macroinvertebrate communities because, even though the rankings were stable, individual abundances fluctuated widely (cf. Meffe and Minckley 1987). However, the major role of disturbances in streams may be in reorganizing and maintaining the spatial heterogeneity of resources (Resh *et al.* 1988; Lake *et al.* 1989) rather than direct impacts on faunal abundances.

Such spatial and temporal heterogeneity of resources is critical to maintaining the high species richness and rapid turnover of energy typical of streams subject to frequent natural disturbances. Aquatic macroinvertebrate assemblages in these streams are characterized by large numbers of substratum generalists (*sensu* Minshall 1984) that are highly mobile and capable of seeking refuge from spates or droughts. Deterministic hypotheses formulated to explain structure in communities of relatively sedentary individuals (e.g. tropical rainforests, coral reefs) that compete hierarchically for some limiting resource (e.g. light) are unlikely to account for patterns observed in the structure of lotic macroinvertebrate assemblages (cf. Frid and Townsend 1989).

We will make progress only by choosing models, variables and experiments that are appropriate to the scale of investigation and breadth of question (Wiens 1989). This approach is exemplified by studies of ecosystem responses to natural disturbances in desert streams (e.g. Grimm and Fisher 1989); at the finer level of responses by assemblages (communities), different approaches must be used. We have demonstrated that results from small-scale experiments cannot be extrapolated to predict successfully the effects of large-scale disturbances, even when the temporal component is minor, because the scale of the disturbance strongly influences the rate and pathways of recolonization and the sources and faunal composition of the recolonists.

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