Limnol. Oceanogr., 44(4), 1999, 1091–1102

Patchy surface stone movement during disturbance in a New Zealand stream and its potential significance for the fauna

Christoph D. Matthaei,[1] *Kathi A. Peacock, and Colin R. Townsend*
Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

Abstract

A patchy movement of surface stones during disturbance in streams has been proposed from field observations, but few attempts have been made to quantify this phenomenon. If spates produce a mosaic of stable and disturbed areas, the former could serve as refugia for benthic invertebrates. We monitored the stability of surface stones at three geomorphically contrasting sites in a river with an unstable bed during three spates and one large flood. Stones were marked in situ by drilling holes in them or by scraping them with a chisel. For each stone, we determined visible surface area, embeddedness in the substratum, water depth, size of surrounding stones, and presence or absence of large stones upstream. During the first monitoring period, which covered one spate and the large flood, we marked 400 stones at each 20-m-long site in a systematic grid with 40 to 60 cm between stones. Stones were relocated after each disturbance, but each stone set was used to monitor both subsequent events. After the large flood, few marked stones were left. Therefore, additional sets of 200 stones were marked for a second monitoring period covering the remaining two spates; these stones were located at the same sites, but the distance between transects was doubled. Patchy bed movement occurred during all four disturbances, especially during the three smaller ones, which moved only 33 to 72% of marked stones. Stability of individual stones was mainly influenced by their size and embeddedness and sometimes by the water depth above the stone. Larger-scale parameters (e.g., the position of the stone across the transect) were less important. Whole-site stability differed little among sites. During the three smaller events, many stable surface stones were available as potential invertebrate refugia. In contrast, invertebrate refugia may have been restricted to the hyporheic zone and inundated flood-plain gravels during the large flood. Because patchy stone movement was observed in a river with an unstable bed, it is likely to be a feature of most rivers. Therefore, small-scale experiments may be able to simulate the effects of disturbance on the benthic community more effectively than previously thought.

Disturbance is an important organizing factor in many ecosystems (Pickett and White 1985), particularly in running waters (Resh et al. 1988). Therefore, lotic invertebrates are likely to need refugia to ameliorate the destructive effects of spates and floods (Sedell et al. 1990). These refugia include the hyporheic zone (Williams and Hynes 1974; Dole-Olivier et al. 1997; but *see* Palmer et al. 1992), inundated floodplain sediments (Badri et al. 1987), dead zones, where shear stresses on the bed are always low (Lancaster and Hildrew 1993; Robertson et al. 1995; Winterbottom et al. 1997), woody debris dams (Palmer et al. 1996), and drift from tributaries (Townsend 1989).

Little is known about the role of stable surface stones, although they are one of the most obvious potential refugia (Townsend 1989; Biggs et al. 1997). Many researchers have studied the recovery of invertebrate communities after catastrophic floods that presumably caused extensive bed movement (e.g., Fisher et al. 1982; Lamberti et al. 1991; Smock et al. 1994), but the impact of less severe disturbances is poorly understood. Recolonization after smaller spates may represent a redistribution rather than ‘‘true’’ colonization from distant sources, if the event does not disturb the whole stream bed (Townsend and Hildrew 1976). Stable surface stones could then serve as island-like refugia for invertebrates. Smaller spates may be more important for the spatiotemporal dynamics of the benthic community than large floods simply because they occur more frequently. For instance, a flood causing large-scale bed movement in a Swiss river had a return period of 5 yr (Matthaei et al. 1997), whereas a spate resulting in only partial bed movement had a return period of a mere 22 d (Matthaei et al. 1996). In these two studies, bed movement was estimated from areas where algae had been removed from surface stones. Similar observations have led other ecologists to assume the occurrence of ‘‘patchy’’ bed movements during smaller disturbances (Doeg et al. 1989; Clauss 1992).

Geomorphologists have long been aware from sediment transport studies that, even at bankfull flow, rarely is the whole bed of a river in motion (*see* reviews by Carson and Griffiths 1987; Montgomery and Buffington 1993). However, many of these studies were aimed at identifying a general threshold of mobility for the surface layer (e.g., Jackson and Beschta 1982; Andrews 1984; Carling 1988; Buffington et al. 1992), and fewer researchers focused on the fate of individual particles (e.g., Komar and Li 1986; Hassan and Church 1992). Consequently, the condition of ‘‘partial transport’’ of surface particles was defined only recently by Wilcock and McArdell (1993): Some proportion of the grains

---

[1] Present address: Department of Zoology, University of Munich (LMU), Karlstr. 23-25, 80333 Munich, Germany.

Acknowledgments

We thank the following people for assistance in the field, manufacture of equipment, statistical advice, stimulating discussions, and critical comments on earlier drafts: Chris Arbuckle, Kirsty Barr, Barry Biggs, Ian Dickson, Barb Downes, Maurice Duncan, Jim Gaw, John Harraway, Rachel Hirabayashi, Giri Kattel, Lachlan Kirk, Ian Maize, Murray McKenzie, Patrick Mulholland, Jorge Palmeirim, Dean Olsen, Marc Schallenberg, Ross Thompson, Nathan Whitmore, and two anonymous referees. Chris Matthaei was supported by a grant from the Swiss National Science Foundation.

exposed on the bed surface, regardless of size, are transported, whereas the remainder of the surface grains remain immobile. Although the existence of this phenomenon has been demonstrated in an artificial flume channel (Wilcock and McArdell 1997), there have been few attempts to quantify it in natural systems. In most ecological field studies of stone movement, researchers placed marked tracer particles in streams to investigate frequency or intensity of disturbance without considering the stability of individual particles or potential spatial patterns (e.g., Lake and Schreiber 1991; Death and Winterbourn 1995; Townsend et al. 1997). Only Downes et al. (1998) addressed these aspects using stones marked in situ, but their study did not allow definite conclusions about small-scale patchiness of stone movement because distances between randomly chosen stones were up to several meters and stone stability was not assessed after each individual disturbance.

''Micro–form bed clusters'' are bedform microunits consisting of several stones that have been described as being particularly resistant to entrainment during high-flow events (Brayshaw 1984; de Jong 1992; Biggs et al. 1997). At an even larger spatial scale, surface stone stability can be expected to be influenced by channel geomorphology. For instance, stones near the banks should be more stable than those in the line of maximum water depth, the ''thalweg'' (Leopold et al. 1964), because sediment transport rates are often highest there and decrease toward the banks (Dietrich and Whiting 1989; Laronne and Duncan 1992). Moreover, if forcing elements like bedrock outcrops are present, they can direct the main force of flow during high discharge in certain directions, causing these areas to be especially unstable (Bisson et al. 1982; Sullivan 1986). Differences in stability can also be expected when whole stream reaches are compared. For example, reaches with a wide floodplain ought to be more stable than confined channels of similar gradient and sediment size, because near-bottom shear stress increases linearly only until bankfull flow and the energy of further discharge increases is dispersed over the floodplain (Leopold et al. 1964; Richards 1982).

In the present study of surface stone movement in a New Zealand stream and the potential role of stable surface stones as invertebrate refugia, we addressed the following questions: (1) How patchy is stone movement during disturbances of different magnitudes, and what are the implications of this patchiness for the benthic fauna? (2) Which parameters influence stone stability? (3) Does stone stability differ between geomorphically contrasting sites in the same stream (an unconfined site and two constrained sites with and without forcing elements)?

Methods

The study was conducted in the Kye Burn, Otago Province, South Island, New Zealand (NZMS 260 141 993795). Vegetation in the catchment (600–1,600 m above sea level) is mainly indigenous tussock grassland grazed by sheep, annual rainfall in the area is 600 to 1,000 mm (Otago Catchment Board 1983), and mean annual flow at the study reach is 1.1 m^3 s^{-1} (National Institute of Water and Atmospheric Research [NIWA] Dunedin unpubl. data). The reach is situated 2 km downstream of the confluence of the upper Kye Burn with Timber Creek, two tributaries with contrasting geomorphologies (Scarsbrook and Townsend 1993). Timber Creek drains a steep catchment, dominated by semischist, in which some of the mountains have highly unstable scree slopes. This provides high sediment input (Bishop 1976), resulting in an unstable, poorly armored surface layer of the stream bed (Scarsbrook and Townsend 1993; *see also* Dietrich et al. 1989). In contrast, the upper Kye Burn has a more stable geology dominated by quartzofeldspathic and pelitic schists. Because Timber Creek is the larger tributary, the Kye Burn below the confluence has the same high sediment supply and general instability of substratum. Baseflow width at the study reach is 5 to 7 m, and the stream bed consists mainly of gravels and cobbles, with some small to medium boulders (width, 256–1,024 mm) and bedrock outcrops. Continuous discharge measurements were conducted in both tributaries near the confluence from 1990 through 1997 (Scarsbrook 1995; NIWA unpubl. data) and at a gauging station in the lower Kye Burn from 1968 through 1996 (Otago Regional Council [ORC] unpubl. data).

Within the study reach of 350 m length at ~600 m above sea level, we investigated three 20-m stretches. Site 1 was a riffle in a large floodplain (width, 70–120 m) that should experience relatively low shear stress during flows exceeding bankfull discharge because part of the flow energy should be dispersed over the floodplain. In contrast, sites 2 and 3 were located in a small, steep canyon with a tightly confined channel (ratio of valley width to channel width, <2). Shear stress during above-bankfull discharges should be higher at these sites. Site 2, situated 95 m upstream of site 1 and 60 m upstream of the first bend in the canyon, was a riffle in a ''forced pool–riffle'' reach where the canyon walls and a few bedrock outcrops forced the water flow to some extent into fast-flowing areas and calmer backwaters. Site 3, another 120 m upstream, was in a ''plane bed'' section (a bedform characterized by long stretches of relatively planar channel bed; Montgomery and Buffington 1993). At this site, there were few forcing elements but more large cobbles and small boulders than at the other two sites. The downstream end of site 3 was about 40 m upstream of a sharp bedrock bend in the canyon. The slope of the water surface (measured at baseflow with a TopCon autolevel) was 1.2% at sites 1 and 3 and 1.0% at site 2. Note that the three bedforms are unreplicated; therefore, only tentative conclusions about their influence on stone stability may be drawn. Furthermore, the flow dynamics during spates at the three sites may not be entirely independent due to the proximity of the sites. However, each site was separated from the next one downstream by a bend in the canyon that broke or redirected the main force of flow during high discharge (Matthaei unpubl. observations); therefore, any effect of lack of independence ought to be quite small.

Stone monitoring—We monitored surface stone movement during two consecutive periods. For the first period, we marked 400 river stones in situ at each site from 3–6 December 1996. We either drilled holes into the stones using a battery-powered impact drill equipped with drill bit extensions, which allowed us to work in up to 60 cm of water (Downes et al. 1998), or scraped distinctive marks on them with a chisel. Ten stones were marked in a systematic grid across each of 40 transects within the 20-m sites. Distances between stones were 40 to 60 cm, and the first and last stones in each transect were 20 to 30 cm from the stream banks. Field tests had shown that this was the finest spatial grid possible that would not disturb neighboring stones during marking and relocation. The exact location of each stone in the stream bed was determined by measuring the distance from the stone to a pair of permanently marked points on the banks at the downstream end of each site. Stone area (calculated from the maximum linear and planar dimensions) was estimated under water using a viewing box with a painted-on 5-cm grid. At each point on the spatial grid, we selected for marking the first stone with an exposed length of at least 5 cm that we saw through the viewing box. In a few grid positions, we chose smaller stones because the substratum consisted without exception of small particles. The minimum length of 5 cm was selected because an associated aim was to relate stone stability to invertebrate densities, and we expected very small stones to be colonized by an impoverished fauna (*see* Douglas and Lake 1994).

For each stone, we also noted any distinguishing marks, its color, and its material. We then determined the degree of embeddedness in the stream bed using the following scale: 1 = lying loosely on top of the bed, 2 = partly covered by surrounding substratum, and 3 = well buried in the surrounding substratum or firmly wedged in by surrounding stones. In combination with the two coordinates, these parameters allowed us to reliably re-locate all stones that had not been disturbed. It should be noted that this method cannot discriminate between ''lost'' stones that have moved downstream and those that are buried. We measured water depth and estimated visually the dominant substratum size class in an area of 50 × 50 cm surrounding each marked stone using Wentworth size classes. For particles $\geq$16 mm, we used class intervals based on 1/2 phi values (16–22, 22–32, 32–45 mm, etc.; Harrelson et al. 1994), and all particles $<$8 mm were combined into a single class. Finally, we noted whether the marked stone was immediately downstream ($\leq$30 cm) of any large stone (width, $>$256 mm), because this might increase the stability of the marked stone during disturbance.

The marked stones were relocated after a spate on 21–22 December 1996 (peak discharge [Q_{max}] at study reach = 4.3 $m^3 s^{-1}$; NIWA unpubl. data), a large flood on 11–13 January 1997 (Q_{max} = 17.2 $m^3 s^{-1}$), and a spate on 18–19 January 1997 (Q_{max} = 6.9 $m^3 s^{-1}$). The large flood had a return period of 2.8 yr (ORC unpubl. data). Because water depth and turbidity never decreased sufficiently to allow the stones to be relocated between the two disturbances in January, they were treated as a single event (the ''January flood''). Apart from the disturbances, discharge remained below mean flow (1.1 m^3), and there was no bed movement between events (the estimated threshold for movement of the smallest particles in the Kye Burn is ~2 $m^3 s^{-1}$; Matthaei unpubl. observations). We did not mark any new stones between disturbances; therefore, the second event moved only stones that had remained stable during the first event, and these no longer represented an unbiased sample of the stone population at each site (*see below*).

After the January flood, few marked stones were left. On 18–19 February 1997, we marked a new set of stones as described above for a second monitoring period. Because of the information gained with the first stone set, we were able to reduce the effort involved by marking only 200 stones at each site, using 20 transects instead of 40 and increasing the distance between transects to 1 m. The second set was used to study three additional spates. The first two (on 8 and 13 April 1997) were treated as a single disturbance (Q_{max} = 5.0 $m^3 s^{-1}$), and the third occurred on 13–14 August 1997 (Q_{max} = 5.4 $m^3 s^{-1}$). Once again, there was no bed movement between events because discharge remained near or below mean flow, and we did not mark any new stones between disturbances.

The three smaller of the four studied disturbances all had return periods of $<$6 months. The shape of the flood hydrographs was quite similar during all high-flow events: a short, sharp rise to peak flow, followed by a gradual decline toward normal flow conditions.

Data analysis—We first plotted the presence and absence of marked stones during the four disturbances to identify general patterns of bed stability. Because stones were marked in a systematic grid, there was a chance they did not represent the ''true'' sediment composition at the sites. Therefore, we calculated the percentage of overall bed movement at each site for a random subsample made up of 25% of the marked stones during the first disturbance monitored with each stone set. Such a subsample was not possible for the second disturbance monitored with each stone set, because all stones moved by these events represented ''survivors'' of the first events. To determine which parameters influenced stone stability, we calculated stepwise logistic regressions (Aldrich and Nelson 1984) using SPSS, with presence or absence of stones as a binary *y* variable and the different parameters measured for each stone as independent *x* variables. Inspections of the correlation matrices showed no strong collinearities between *x* variables. After exploratory data analysis, stone area and size of surrounding stones (using mean values of the dominant particle size class, e.g., 27 mm for the 22–32-mm class) were log-transformed to meet the assumption of normality. Presence of large stones upstream and embeddedness were treated as categorical variables, the latter in the form of two binary dummy variables, with embeddedness category 3 serving as the standard embeddedness. The first variable compared embeddedness category 1 with the standard, whereas the second compared category 2 with the standard (for details on use of dummy variables in regression, *see* Kleinbaum et al. 1988; Harraway 1995). To allow for a potential dependency of bed stability at a larger spatial scale, we included position of the stone across the transect (1–10) and distance of the stone from the nearest river bend downstream as additional *x* variables. In all but one stepwise regression, forward and backward procedures produced identical results, indicating the robustness of the analysis due to our large data sets. In Fig. 3, comparisons between stable and unstable stones were performed using two-sided *t*-tests (stone area, log-transformed data) and Mann–Whitney *U*-tests (embeddedness; *see* Potvin and Roff 1993). The sequential Bonferroni technique (Rice 1989) was used to adjust the significance levels for the two comparisons within each stone set.

Results

Stability patterns of marked stones—Overall stone stability differed considerably between the four disturbances (Figs. 1, 2), even between the two events monitored with complete stone sets, which had similar maximum discharges (Table 1). During these events, 33 to 72% of the marked surface stones disappeared. The second disturbances monitored with each stone set moved 37 to 85% of the stones that remained.

After the spate in December 1996, stable stones were relatively evenly distributed at site 1, except for smaller areas with few remaining stones (Fig. 1a). In contrast, the stones in the downstream third of site 2 were more unstable than those in the other two-thirds (Chi-square test between thirds, $P < 0.001$). At site 3, particles in the first two transect positions were particularly stable, and few marked stones remained along the whole site at positions 7 and 8 (Chi-square test between longitudinal site fifths, $P < 0.001$). These site-specific spatial patterns were not repeated during the other three disturbances. After the January flood, few stones were left at any site (Fig. 1b), whereas the opposite was the case after the event in April (Fig. 2a). After the spate in August 1997, all sites had several smaller areas from which all marked particles had disappeared (Fig. 2b).

Overall stability of the marked stones also differed little between sites (Table 1). Furthermore, calculations of overall stability using the stones marked in a systematic grid differed by just a few percentage points from calculations using the random 25% subsamples from the two complete stone sets.

Parameters influencing stone stability—Models produced by stepwise logistic regression correctly predicted presence or absence after disturbance for 62 to 90% of the marked stones (Table 2). Stone stability was mainly influenced by properties of the stones themselves or by local parameters. Stone area (12 of 12 cases) and degree of embeddedness in the surrounding substratum (9 cases) were the most important parameters, always showing positive relationships with stone stability. Water depth above the stone had an effect in 6 cases (5 negative and 1 positive). The presence of large stones upstream or the dominant particle size class surrounding the marked stone had occasional significant positive effects. Larger-scale parameters were less important than local ones. Thus, the distance of the marked stones from the next river bend downstream and/or position across the transects significantly influenced their stability in only 7 cases (5 positive and 2 negative relationships).

Except for the spate in December 1996 at site 2, the correlation matrices calculated for the stepwise regressions showed only weak relationships (Pearson's $r_p \leq 0.3$) between stone surface area or size of surrounding stones and position across the transect or distance from the nearest bend downstream. This implies that the two particle size–related parameters were largely independent of the position of the marked stones within each site (i.e., the sediments at our sites were well sorted). During the spate in December 1996 at site 2, stone area and the size of surrounding stones were correlated significantly with the distance from the nearest bend downstream ($r_p = 0.47$ and 0.52, respectively; $P < 0.001$). The more unstable downstream third of the site consisted of smaller stones than the other two-thirds (one-way ANOVA between thirds, $P < 0.001$).

The important parameters stone area and embeddedness were analyzed in further detail. First, we compared the average stone area of the complete stone sets and their average embeddedness with those of the stones that remained stable or disappeared during the four disturbances (Fig. 3). Unstable stones were generally significantly smaller and less deeply embedded than stable stones. Within stone sets, area and embeddedness of stable stones increased from first to second disturbance in most cases. Area and embeddedness of unstable stones also increased, because all stones present before the second event were survivors of the first. These findings illustrate the bias introduced by studying two subsequent disturbances with the same stone set, because the stones used to monitor the second events were larger and more deeply embedded than the average particles in the complete stone sets. All the same, this bias probably did not have a strong effect on the overall nature of the parameters contributing to stone stability, because stone area and embeddedness were the most important parameters in both the complete and incomplete stone sets (Table 2).

For stones that remained stable during the four disturbances, frequency of changes in visible surface area and embeddedness varied somewhat between sites but not in any consistent manner (Table 3). Visible surface area remained constant for at least 80% of marked stones at each site during most of the disturbances, except for sites 2 and 3 during the spate in December 1996. Several of the existing area changes were <30% of the area of the stone in question. Stone embeddedness changed somewhat more often than stone area during the last two disturbances. However, direct changes from loose to well embedded (or vice versa) occurred for <10% of marked stones in 10 of the 12 data sets and never for more than 16%.

Discussion

Our first objective was to determine whether a patchiness of surface stone movement occurred during disturbances of different magnitudes. We had expected the degree of patchiness to be high during minor spates and to decrease with increasing discharge. Our results fully support these predictions and confirm in detail what previously had been only suspected from field observations (e.g., Doeg et al. 1989; Matthaei et al. 1996) and recently has been shown at a more general level by Downes et al. (1998). During the two smaller disturbances in the Kye Burn, monitored with complete stone sets, only 33 to 72% of marked surface stones were disturbed, leaving many that could have acted as refugia for invertebrates. Overall bed movement during the second event monitored with each stone set was probably higher

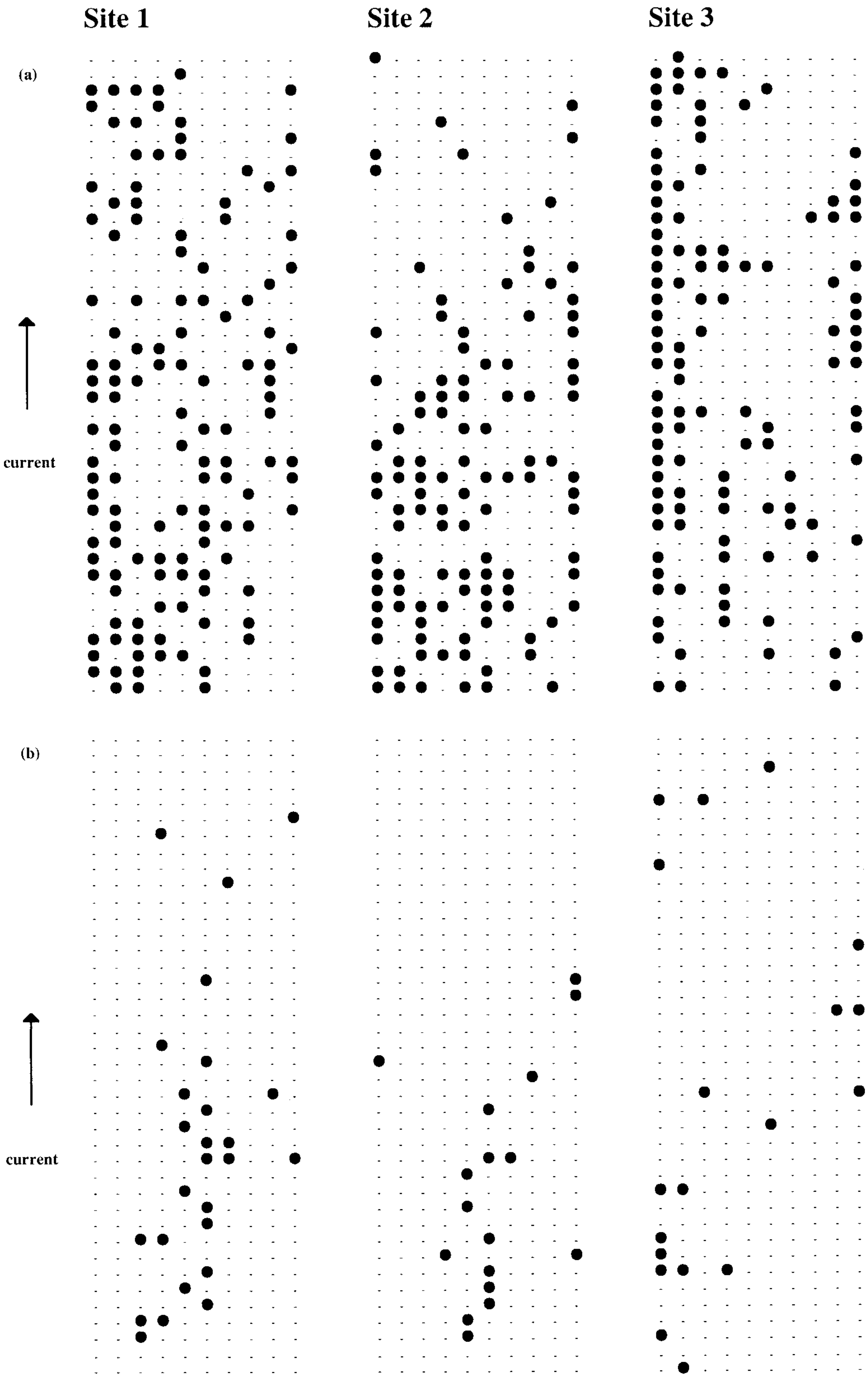

Fig. 1. Spatial patterns of presence (●) or absence (−) of marked stones after the disturbances in December 1996 (a) and January 1997 (b).

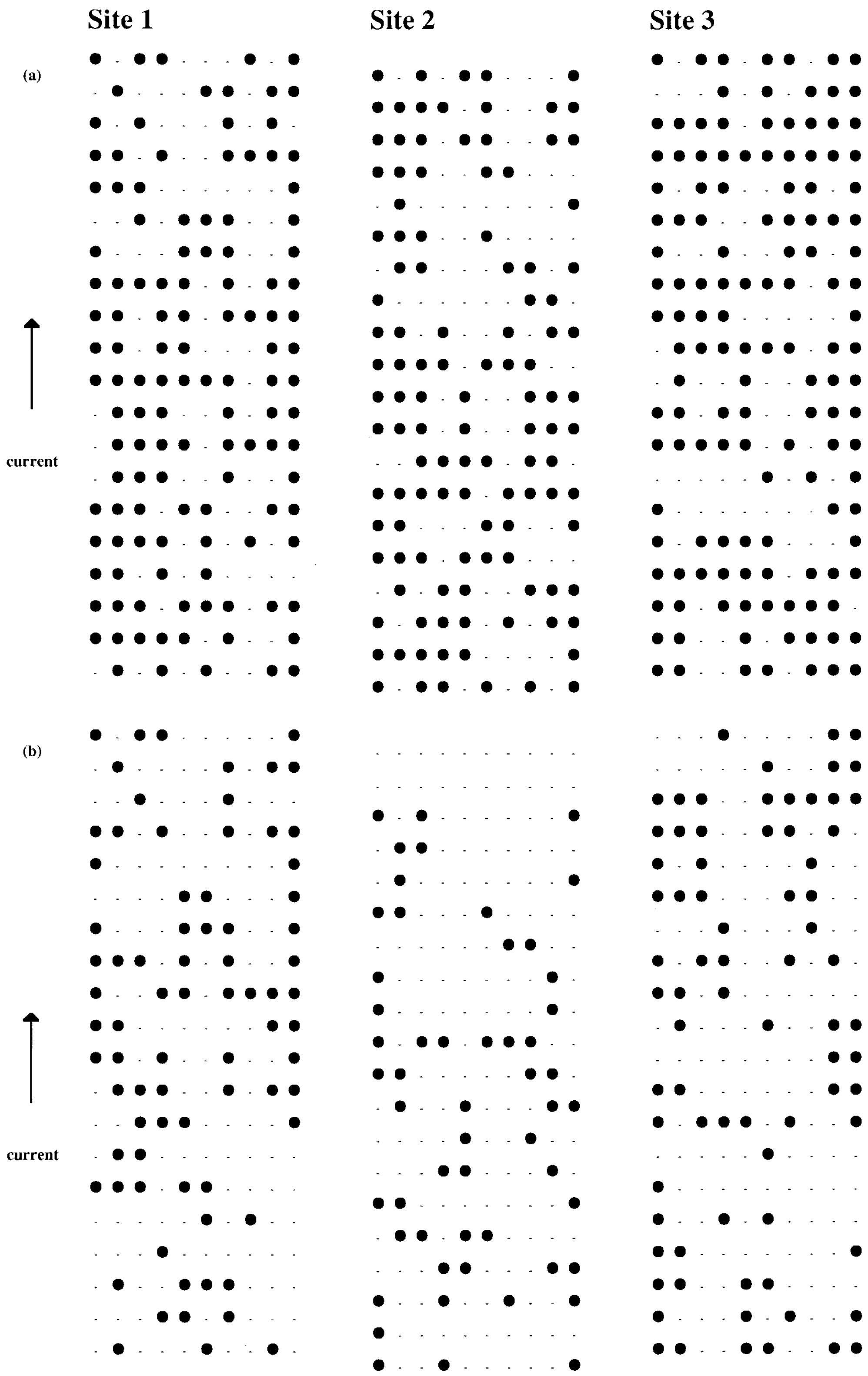

Fig. 2. Spatial patterns of presence (●) or absence (−) of marked stones after the disturbances in April 1997 (a) and August 1997 (b).

Table 1. Movement of surface stones at the three sites during the four disturbances (as % of stones that had been present before each individual event). The stability of a random 25% subsample of the systematically marked stones is given for the two events that affected complete stone sets.

	Date and site of disturbance											
	Dec 96			Jan 97			Apr 97			Aug 97		
Parameter	1	2	3	1	2	3	1	2	3	1	2	3
Q_{max}, m^3 s^{-1}		4.3			17.2			5.0			5.4	
Stones present before disturbance, *n*	400	400	400	128	111	114	200	200	200	123	116	135
Stones moved during disturbance, %	68.0	72.2	71.5	79.7	84.7	84.2	38.5	42.0	32.5	36.6	54.3	43.7
Stones of random 25% subsample moved, %	73.0	73.0	66.0		No complete stone set		44.0	44.0	34.0		No complete stone set	

* Q_{max} = maximum discharge during each disturbance.

than estimated on the basis of the incomplete sets of stones that survived the first event. Therefore, it is likely that <15 to 20% of surface particles remained stable during the large January flood with its return period of 2.8 yr. Here, other types of refugia may assume more importance, such as the hyporheic zone (Williams and Hynes 1974; Dole-Olivier et al. 1997) or the inundated floodplain (Badri et al. 1987).

Downes et al. (1998) found that disturbed stones were aggregated in space in three Australian rivers, indicating that some parts of the stream bed were more likely to be moved than others. Despite significant variation in the force required to move rocks in these rivers (Downes et al. 1997), all three have a relatively well-armored layer of surface stones (Lake pers. comm.) that is not easily disrupted even during large increases in discharge (e.g., *see* Brooks 1997). According to Dietrich et al. (1989), inactive zones (bed areas where no particle movement occurs during disturbance) are most likely to develop in such well-armored rivers because

Table 2. Parameters influencing stone stability.†

Date of disturbance	Site 1		Site 2		Site 3	
	Parameter	*P*	Parameter	*P*	Parameter	*P*
Dec 96	Stone area	***	Stone area	***	Embeddedness (1 vs. 3)	***
	Position across transect	***	Embeddedness (1 vs. 3)	***	Stone area	***
	Embeddedness (1 vs. 3)	***	Embeddedness (2 vs. 3)	**	Water depth	***
	Distance from next bend	***	Water depth	**	Presence of large stones upstream	**
	Embeddedness (2 vs. 3)	**	Distance from next bend	*	Embeddedness (2 vs. 3)	**
	Water depth	*	% correct	80.3	% correct	84.5
	% correct	79.8				
Jan 97	Stone area	***	Stone area	***	Stone area	**
	Distance from next bend	**	Water depth	*	Presence of large stones upstream	*
	Position across transect	*	% correct	85.6	Position across transect	*
	Embeddedness (1 vs. 3)	*			% correct	86.0
	% correct	89.8				
Apr 97	Stone area	***	Embeddedness (1 vs. 3)	***	Stone area	***
	Embeddedness (1 vs. 3)	***	Stone area	***	Embeddedness (1 vs. 3)	***
	Size of surrounding stones	*	Water depth	***	Size of surrounding stones	**
	Presence of large stones upstream	*	% correct	79.0	% correct	84.0
	% correct	82.0				
Aug 97	Stone area	**	Stone area	***	Stone area	***
	Distance from next bend	**	Embeddedness (1 vs. 3)	***	Embeddedness (1 vs. 3)	**
	% correct	71.5	Water depth	**	Embeddedness (2 vs. 3)	**
			% correct	70.7	% correct	62.2

* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.
† % correct is the percentage of marked stones at each site for which the logistic model correctly predicted presence or absence after each individual disturbance. Stone embeddedness consisted of two binary component variables: loose (1) vs. well embedded (3) and intermediate (2) vs. well embedded. For each regression, the significance levels of all parameters are given to illustrate their relative importance.

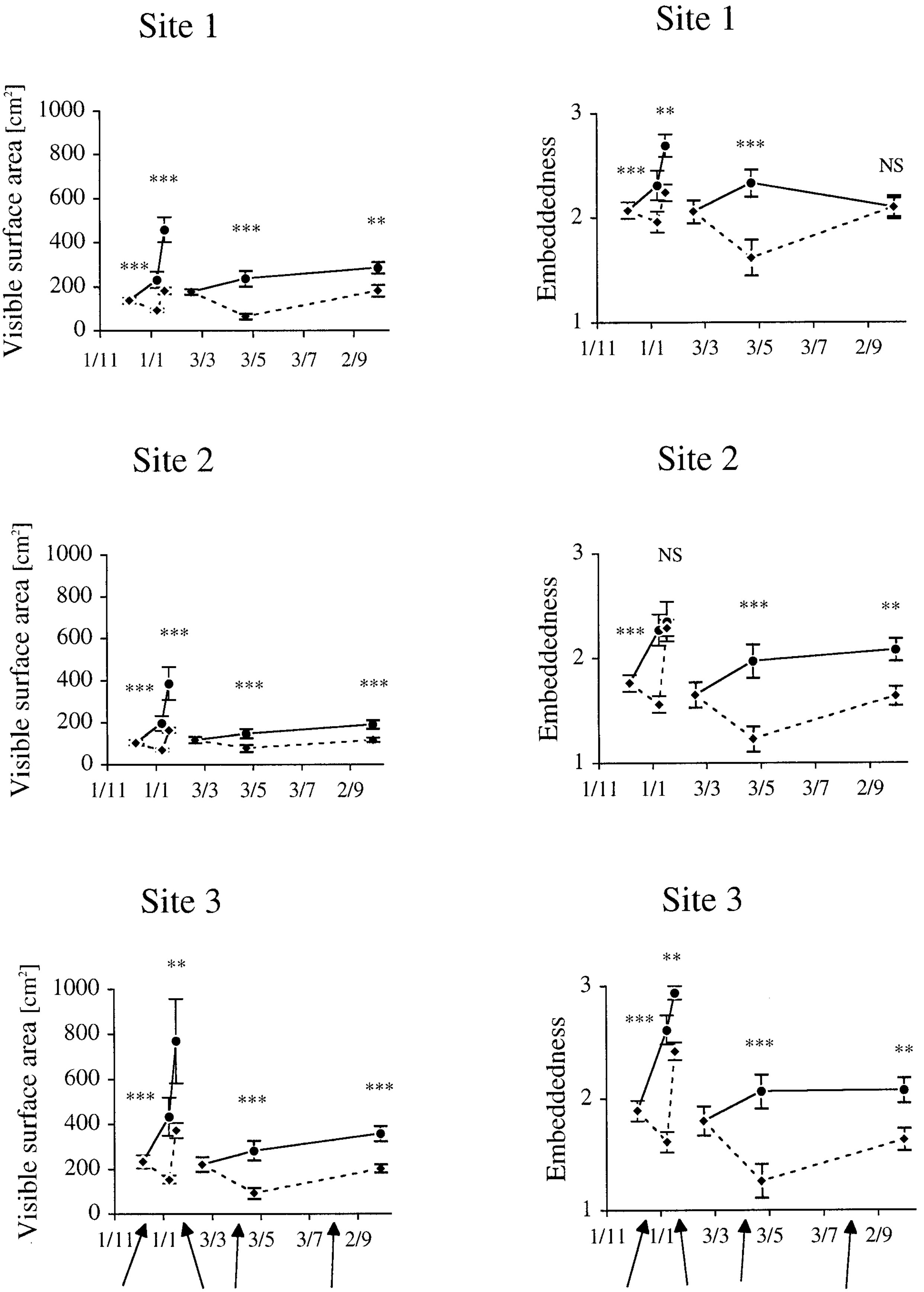
Site 1
Visible surface area [cm²]
1000
800
600
400
200
0
1/11
1/1
3/3
3/5
3/7
2/9
***
***
***
**
Site 1
Embeddedness
3
2
1
1/11
1/1
3/3
3/5
3/7
2/9
***
**
***
NS
Site 2
Visible surface area [cm²]
1000
800
600
400
200
0
1/11
1/1
3/3
3/5
3/7
2/9
***
***
***
***
Site 2
Embeddedness
3
2
1
1/11
1/1
3/3
3/5
3/7
2/9
***
NS
***
**
Site 3
Visible surface area [cm²]
1000
800
600
400
200
0
1/11
1/1
3/3
3/5
3/7
2/9
***
**
***
***
Site 3
Embeddedness
3
2
1
1/11
1/1
3/3
3/5
3/7
2/9
***
**
***
**

Table 3. Frequency of changes in visible surface area (increase or decrease) and degree of embeddedness in the surrounding substratum of the stones that remained stable during each of four different disturbances (expressed as % of total number of stable stones for each event).

	Date and site of disturbance											
	Dec 96			Jan 97			Apr 97			Aug 97		
Parameter	1	2	3	1	2	3	1	2	3	1	2	3
Stable stones left after disturbance	128	111	114	26	17	18	123	116	135	78	53	76
Visible surface area of stones												
Change of 15–30%	1.6	7.2	10.5	3.8	11.8	11.1	2.4	2.6	1.5	0	3.8	1.3
>30–50%	0.8	6.3	8.8	0	5.9	5.6	1.6	2.6	2.2	0	0	1.3
>50%	5.5	9.0	11.4	15.4	0	0	2.4	3.4	4.4	0	1.9	3.9
Total changes in area	7.8	22.5	30.7	19.2	17.6	16.7	6.5	8.6	8.1	0	5.7	6.6
Degree of embeddedness*												
1 → 2	0.8	0.9	0.9	0	11.8	0	3.3	5.2	3.7	1.3	3.8	6.6
1 → 3	0	1.8	2.6	3.8	0	0	0	0.9	0.7	0	1.9	3.9
2 → 3	0.8	0	0.9	7.7	5.9	0	5.7	6.0	0.7	11.5	1.9	0
3 → 2	0	1.8	4.4	0	0	11.1	7.3	16.4	8.1	10.3	3.8	9.2
3 → 1	0	0	6.1	0	0	0	4.1	3.4	3.7	15.3	1.9	7.9
2 → 1	0	0	1.8	3.8	0	0	5.7	4.3	8.9	9.0	5.7	3.9
Total changes in embeddedness	1.6	4.5	16.7	15.4	17.6	11.1	26.0	36.2	25.9	47.4	18.9	31.6

* 1, loose; 2, intermediate; 3, well embedded.

of a low local sediment supply from upstream (less than the transport abilities of the river). However, the results of the present study show that patchy bed movement occurs even in a river with a high sediment supply and an unstable substratum. It seems likely to be an important feature of most rivers.

Note that we use the term patchiness primarily to describe the phenomenon of partial transport (sensu Wilcock and McArdell 1993) of individual surface stones. The spatial patterns in Figs. 1 and 2 suggest that stones tended to be disturbed in clumps, with large areas of stream bed moving in their entirety while others remained stable. However, this conclusion is tentative because our stones were marked in a systematic grid and our bed stability data were not continuous. Although the spatial grid of stones was the finest possible for practical reasons, there were always several unmarked stones between each adjacent pair of marked ones, and we do not know whether these moved during disturbance. Consequently, we did not use specific techniques for the analysis of spatial point patterns (e.g., Diggle 1983; Manly 1997). On the other hand, our systematic design is unlikely to have introduced a substantial bias relative to random marking, because overall stone stability differed little between the originally marked stones and the random 25% subsamples (Table 1).

Our findings are relevant for the interpretation of stream disturbance experiments (e.g., Reice 1985; Boulton et al. 1988; Englund 1991), the value of which has been questioned because of the smallness of the area disturbed relative to a natural event (Minshall 1988; Lake 1990; Mackay 1992). Few researchers have physically disturbed patches larger than the size of individual stones (Clifford 1982; Doeg et al. 1989; Matthaei et al. 1996), and almost none have disturbed entire stream reaches. However, Matthaei et al. (1997) were able to confirm the realism of their experiments by showing that the degree of reduction and recolonization patterns were similar for common invertebrates in a large flood versus experimental disturbance of 9-m^2 plots in a Swiss river. In our study, individual stones moved while others nearby remained undisturbed during the same high-flow events, lending more weight to the validity of conclusions drawn from small-scale disturbance experiments, especially those conducted in streams with a more stable bed than the Kye Burn.

The fact that smaller spates caused only partial but nonetheless significant movement of surface particles in the Kye Burn is intriguing from a geomorphological perspective as well. Gravel and cobble bed channels have often been described as ‘‘bankfull threshold channels’’ because little bed movement is thought to occur below this critical discharge (e.g., Henderson 1963; Jackson and Beschta 1982; Richards 1982; Carling 1988). Return periods for bankfull discharge can vary depending on basin area, sediment character, channel slope, and entrenchment, but commonly used figures

---

←

Fig. 3. Average visible surface area (left) and embeddedness (right) of the complete stone sets and of stones that remained stable (—●—) or disappeared (- - ♦ - -) during the four disturbances (indicated by arrows on the *x* axis at site 3). Results for the two stone sets are shown separately, with each first average representing the complete stone set. ** = difference between stable and unstable stones was highly significant after Bonferroni adjustment. *** = very highly significant. Error bars are standard errors, some of which are too small to be visible.

range from 1 to 3 yr (Leopold et al. 1964; Richards 1982; Poff and Ward 1989). The smaller spates studied in the Kye Burn had return periods of <6 months and therefore probably did not reach bankfull discharge. This conclusion gains weight from shear stress estimates calculated for our three sites during these spates (Matthaei et al. in press), because near-bottom shear stress differed little between the floodplain site and the constrained sites. Nevertheless, these below-bankfull events managed to disturb 33 to 72% of our marked surface stones. In addition, stone stability varied considerably between the three events, although they all had a similar peak discharge, a similarly shaped flood hydrograph, and roughly the same duration (1–2 d). These results do not support the idea of a bankfull threshold or any other threshold for general mobility of the surface layer in the Kye Burn. However, they correspond well with Wilcock and McArdell's (1993) concept of partial transport, which assumes gradually increasing grain mobility over a range of near-bed shear stresses.

Parameters influencing stone stability—Our logistic models predicted presence or absence of the marked stones after disturbance with considerable accuracy (62–90% correct). We had expected properties of the stones themselves, local parameters, and larger-scale parameters related to channel geomorphology to be influential. All three categories contributed to stone stability, but stone area and embeddedness in the surrounding substratum were the most important parameters at all sites. Water depth above each stone was the third most important parameter. In comparison, larger-scale parameters related to channel geomorphology were less relevant. Nevertheless, significant relationships between stone stability and their position in the systematic spatial grid existed in 5 of the 12 data sets.

Our findings of the consistent importance of stone area and embeddedness for stone stability agree with those of Downes et al. (1998), although, in a more general way, geomorphologists have known for years that these two parameters influence surface particle stability. Shields (1936) derived a formula in which the ''critical'' shear stress for general mobility of the surface layer is a function of median particle diameter. Similarly, several studies have shown that particle embeddedness affects bed movement at this threshold flow (Fenton and Abbott 1977; Komar and Li 1986; Buffington et al. 1992). The negative influence of water depth on stone stability in the Kye Burn is probably related to near-bottom shear stress, a parameter that increases with water depth (Carson and Griffiths 1987). This result is also consistent with field data showing that sediment transport rates are often highest in the thalweg, the line of maximum water depth (Dietrich and Whiting 1989; Laronne and Duncan 1992).

Mean size and embeddedness of the two complete stone sets hardly changed at all from the first to the second monitoring period (Fig. 3), indicating that even the large flood did not alter the overall composition of the surface layer. For most stones that remained stable during a disturbance, visible surface area was constant before and after the event. Stones also changed only rarely from loosely to well embedded or vice versa. Because stone area and embeddedness were the most important parameters influencing stone stability, the stability of individual Kye Burn stones during the previous disturbance (relative to each other) can probably be reconstructed reasonably well by simply determining their size and embeddedness. Similarly, it should be possible to predict the relative stability of individual stones during the next disturbance. Several studies have reported a significant positive correlation between stone surface area and invertebrate species richness (Trush 1979; Clements 1987; Douglas and Lake 1994) or total number of individuals (Clements 1987; Downes et al. 1995). Our findings suggest that these correlations may be partly due to the greater stability of larger stones, which allows development of a more diverse and abundant invertebrate assemblage.

Stone stability at three geomorphically contrasting sites—We had predicted site 1 in the floodplain to be more stable than the two constrained sites, but overall stone stability was quite similar at all three sites. This unexpected result may be explained by the return periods of the four disturbances and the shear stress estimates for these events at our sites. Peak discharge during the three smaller spates was below bankfull, and near-bottom shear stress differed little between sites. Even during the January flood, which exceeded bankfull, shear stress was not lowest at site 1 because of its relatively steep energy slope (Matthaei et al. in press).

Spatial patterns of presence and absence of marked stones, and the parameters affecting stability, also differed little between sites. Only the spate in December 1996 caused site-specific spatial patterns (Fig. 1a). The instability of the downstream third of site 2 during this spate can be explained again in terms of stone size; the particles in this area were significantly smaller than elsewhere. Stones near the left bank at site 3 in the December spate may have been particularly stable because they were on the inside of a slight bend, whereas only a few particles remained near the right bank because of forcing of the water flow by the stream bend. All the same, it remains unclear why these stability patterns were not repeated during any other disturbance. We are aware that we have no replication at the bedform level, because we studied only a single site in each category. However, there are two additional reasons why we may have been unable to detect substantial differences between the three sites. First, our sites were much shorter than the survey reaches in most geomorphological studies (about 20 times the channel width at bankfull discharge; Harrelson et al. 1994). We wanted the finest possible spatial grid of marked stones and had to limit the total effort involved. Second, the baseflow surface slopes at all three sites were quite similar (1.0–1.2%), whereas plane bed channels are often steeper (up to 3% slope; Montgomery and Buffington 1993) and steeper plane beds may have a different stability.

Our results suggest that patchy stone movement is likely to be a feature of most rivers. Therefore, many stable surface stones are likely to be available as potential refugia for benthic invertebrates during spates. It remains to be tested whether invertebrates use these refugia.

References

ALDRICH, J. H., AND F. D. NELSON. 1984. Linear probability, logit, and probit models. Sage.

ANDREWS, E. D. 1984. Bed material entrainment and hydraulic geometry of gravel-bed rivers in Colorado. Geol. Soc. Am. Bull. **95:** 371–378.

BADRI, A., J. GIUDICELLI, AND G. PRÉVÔT. 1987. Effects of flood on the benthic macroinvertebrate community in a Mediterranean river, the Rdat (Morocco). Acta Œcol. Œcol. Gen. **8:** 481–500.

BIGGS, B. J. F., M. J. DUNCAN, S. N. FRANCOEUR, AND W. D. MEYER. 1997. Physical characterisation of microform bed cluster refugia in 12 headwater streams, New Zealand. N. Z. J. Mar. Freshwater Res. **31:** 413–422.

BISHOP, D. G. 1976. Geological map of New Zealand 1:63360, sheet S126, Mt Ida, 1st ed. Department of Scientific and Industrial Research.

BISSON, P. A., J. L. NIELSON, R. A. PALMASON, AND L. E. GORE. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low stream flow, p. 62–73. *In* N. B. Armantrout [ed.], Acquisition and utilization of aquatic habitat information. American Fisheries Society.

BOULTON, A. J., G. M. SPANGARO, AND P. S. LAKE. 1988. Macroinvertebrate distribution and recolonization on stones subjected to varying degrees of disturbance: An experimental approach. Arch. Hydrobiol. **113:** 551–576.

BRAYSHAW, A. C. 1984. Characteristics and origin of cluster bed forms in coarse-grained alluvial channels. Memo. Can. Soc. Petrol. Geol. **10:** 77–85.

BROOKS, S. S. 1997. Impacts of flood disturbance on the macroinvertebrate assemblage of an upland stream. Ph.D. thesis, Monash Univ.

BUFFINGTON, J. M., W. E. DIETRICH, AND J. W. KIRCHNER. 1992. Friction angle measurements on a naturally formed gravel streambed: Implications for critical boundary shear stress. Water Resour. Res. **28:** 411–425.

CARLING, P. 1988. The concept of dominant discharge applied to two gravel-bed streams in relation to channel stability thresholds. Earth Surf. Processes Landforms **13:** 355–367.

CARSON, M. A., AND G. A. GRIFFITHS. 1987. Bedload transport in gravel channels. J. Hydrol. N. Z. **26:** 1–151.

CLAUSS, K. 1992. Horizontale 'patch'-Verteilung in der Schotterfauna eines alpinen Baches 2. Ordnung. Diploma thesis, Univ. of Regensburg.

CLEMENTS, W. H. 1987. The role of rock surface area on distribution and abundance of stream insects. J. Freshwater Ecol. **4:** 83–91.

CLIFFORD, H. F. 1982. Effects of periodically disturbing a small area of substratum in a brown-water stream of Alberta, Canada. Freshwater Invert. Biol. **1:** 39–47.

DEATH, R. G., AND M. J. WINTERBOURN. 1995. Diversity patterns in stream benthic invertebrate communities: The influence of habitat stability. Ecology **76:** 1446–1460.

DE JONG, C. 1992. A reappraisal of the significance of obstacle clasts in cluster bedform dispersal. Earth Surf. Processes Landforms **16:** 737–744.

DIETRICH, W. E., J. W. KIRCHNER, H. IKEDA, AND F. ISEYA. 1989. Sediment supply and the development of the coarse surface layer in gravel-bedded rivers. Nature **340:** 215–217.

———, AND P. J. WHITING. 1989. Boundary shear stress and sediment transport in river meanders of sand and gravel, p. 1–50. *In* S. Ikeda and G. Parker [eds.], River meandering. Water Resour. Monogr. 12. American Geophysical Union.

DIGGLE, P. J. 1983. Statistical analysis of spatial point patterns. Academic.

DOEG, T. J., P. S. LAKE, AND R. MARCHANT. 1989. Colonization of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. Aust. J. Ecol. **14:** 207–220.

DOLE-OLIVIER, M-J., P. MARMONIER, AND J-L. BEFFY. 1997. Response of invertebrates to lotic disturbance: Is the hyporheic zone a patchy refugium? Freshwater Biol. **37:** 257–276.

DOUGLAS, M., AND P. S. LAKE. 1994. Species richness on stream stones: An investigation of the mechanisms generating the species–area relationship. Oikos **69:** 387–396.

DOWNES, B. J., A. GLAISTER, AND P. S. LAKE. 1997. Spatial variation in the force required to initiate rock movement in four upland streams: Implications for estimating disturbance frequencies. J. North Am. Benthol. Soc. **16:** 203–220.

———, P. S. LAKE, A. GLAISTER, AND A. WEBB. 1998. Scales and frequencies of disturbances: Rock size, bed packing and variation among upland streams. Freshwater Biol. **40:** 625–639.

———, ———, and E. S. G. Schreiber. 1995. Habitat structure and invertebrate assemblages on stream stones: A multivariate view from the riffle. Aust. J. Ecol. **20:** 502–514.

ENGLUND, G. 1991. Effects of disturbance on stream moss and invertebrate community structure. J. North Am. Benthol. Soc. **10:** 143–153.

FENTON, J. D., AND J. E. ABBOTT. 1977. Initial movement of grains in a stream bed: The effects of relative protrusion. Proc. R. Soc. Lond. **352:** 532–537.

FISHER, S. G., L. J. GRAY, AND N. B. GRIMM. 1982. Temporal succession in a desert stream following flash flooding. Ecol. Monogr. **52:** 93–110.

HARRAWAY, J. A. 1995. Regression methods applied. Univ. of Otago Press.

HARRELSON, C. C., C. L. RAWLINS, AND J. P. POTYONDY. 1994. Stream channel reference sites: An illustrated guide to field technique. Gen. Tech. Rep. RM-245. U.S. Department of Agriculture.

HASSAN, M. A., AND M. CHURCH. 1992. The movement of individual grains on the streambed, p. 159–176. *In* P. Billi, R. D. Hey, C. R. Thorne, and P. Tacconi [eds.], Dynamics of gravel-bed rivers. Wiley.

HENDERSON, F. M. 1963. Stability of alluvial channels. Trans. Am. Soc. Civil Eng. **128:** 657–686.

JACKSON, W. L., AND R. L. BESCHTA. 1982. A model of two-phase bedload transport in an Oregon coast range stream. Earth Surf. Processes Landforms **9:** 517–527.

KLEINBAUM, D. G., L. L. KUPPER, AND K. E. MULLER. 1988. Applied regression analysis and other multivariate methods. Kent.

KOMAR, P. D., AND Z. LI. 1986. Pivoting analyses of the selective entrainment of sediments by size and shape with application to gravel threshold. Sedimentology **33:** 425–436.

LAKE, P. S. 1990. Disturbing hard and soft bottom communities: A comparison of marine and freshwater environments. Aust. J. Ecol. **15:** 477–488.

———, and E. S. G. Schreiber. 1991. Colonization of stones and recovery from disturbance: An experimental study along a river. Verh. Int. Ver. Limnol. **24:** 2061–2064.

LAMBERTI, G. A., S. V. GREGORY, L. R. ASHKENAS, R. C. WILDMAN, AND K. M. S. MOORE. 1991. Stream ecosystem recovery following a catastrophic debris flow. Can. J. Fish. Aquat. Sci. **48:** 196–208.

LANCASTER, J., AND A. G. HILDREW. 1993. Flow refugia and microdistribution of lotic macroinvertebrates. J. North Am. Benthol. Soc. **12:** 385–393.

LARONNE, J. B., AND M. J. DUNCAN. 1992. Bedload transport paths and gravel bar formation, p. 177–202. *In* P. Billi, R. D. Hey, C. R. Thorne, and P. Tacconi [eds.], Dynamics of gravel-bed rivers. Wiley.

LEOPOLD, L. B., M. G. WOLMAN, AND J. P. MILLER. 1964. Fluvial processes in geomorphology. Freeman.

MACKAY, R. J. 1992. Colonization by lotic macroinvertebrates: A review of processes and patterns. Can. J. Fish. Aquat. Sci. **49:** 617–628.

MANLY, B. J. F. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Univ. of Otago Press.

MATTHAEI, C. D., K. A. PEACOCK, AND C. R. TOWNSEND. In press. Scour and fill patterns in a New Zealand stream and potential implications for invertebrate refugia. Freshwater Biol.

———, U. Uehlinger, E. Meyer, and A. Frutiger. 1996. Recolonization of benthic invertebrates after experimental disturbance in a Swiss prealpine river. Freshwater Biol. **35:** 233–248.

———, ———, and A. Frutiger. 1997. Response of benthic invertebrates to natural versus experimental disturbance in a Swiss prealpine river. Freshwater Biol. **37:** 61–77.

MINSHALL, G. W. 1988. Stream ecosystem theory: A global perspective. J. North Am. Benthol. Soc. **7:** 263–288.

MONTGOMERY, D. R., AND J. M. BUFFINGTON. 1993. Channel classification, prediction of channel response, and assessment of channel condition. Rep. TFW-SH10-93-002. Washington State Timber/Fish/Wildlife Agreement. U.S. Dept. Nat. Res.

OTAGO CATCHMENT BOARD. 1983. The Taieri River: A water resource inventory. Allied.

PALMER, M. A., P. ARENSBURGER, A. P. MARTIN, AND D. W. DENMAN. 1996. Disturbance and patch-specific responses: The interactive effects of woody debris and floods on lotic invertebrates. Oecologia **105:** 247–257.

———, A. E. BELY, AND K. E. BERG. 1992. Response of invertebrates to lotic disturbance: A test of the hyporheic refuge hypothesis. Oecologia **89:** 182–194.

PICKETT, S. T. A., AND P. S. WHITE. 1985. The ecology of natural disturbance and patch dynamics. Academic.

POFF, N. L., AND J. V. WARD. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. Can. J. Fish. Aquat. Sci. **46:** 1805–1818.

POTVIN, C., AND D. A. ROFF. 1993. Distribution-free and robust statistical methods: Viable alternatives to parametric statistics? Ecology **74**: 1617–1628.

REICE, S. R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. Oecologia **67:** 90–97.

RESH, V. H., AND OTHERS. 1988. The role of disturbance in stream ecology. J. North Am. Benthol. Soc. **7:** 433–455.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution **43:** 223–225.

RICHARDS, K. 1982. Rivers: Form and process in alluvial channels. Methuen.

ROBERTSON, A. L., J. LANCASTER, AND A. G. HILDREW. 1995. Stream hydraulics and the distribution of microcrustacea: A role for refugia? Freshwater Biol. **33:** 469–484.

SCARSBROOK, M. R. 1995. Disturbance and spatial refugia in stream communities. Ph.D. thesis, Univ. of Otago.

———, AND C. R. TOWNSEND. 1993. Stream community structure in relation to spatial and temporal variation: A habitat templet study of two contrasting New Zealand streams. Freshwater Biol. **29:** 395–410.

SEDELL, J. R., G. H. REEVES, F. R. HAUER, J. A. STANFORD, AND C. P. HAWKINS. 1990. Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. Environ. Manage. **14:** 711–724.

SHIELDS, A. 1936. Applications of similarity principles and turbulence research to bedload movement. *In* W. P. Ott and J. C. Uchelen [translators], Mitt. Preuss. Versuchsanst. Wasserbau Schiffsbau. Cal. Inst. Technol. Rep. 167.

SMOCK, L. A., L. C. SMITH, J. B. JONES, AND S. M. HOOPER. 1994. Effects of drought and a hurricane on a coastal headwater stream. Arch. Hydrobiol. **131:** 25–38.

SULLIVAN, K. 1986. Hydraulics and fish habitat in relation to channel morphology. Ph.D. thesis, John Hopkins Univ.

TOWNSEND, C. R. 1989. The patch dynamics concept of stream community ecology. J. North Am. Benthol. Soc. **8:** 36–50.

———, AND A. G. HILDREW. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. J. Anim. Ecol. **45:** 759–772.

———, M. R. SCARSBROOK, AND S. DOLÉDEC. 1997. Quantifying disturbance in streams: Alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. J. North Am. Benthol. Soc. **16:** 531–544.

TRUSH, W. J. JR. 1979. The effects of area and surface complexity on the structure and formation of stream benthic communities. Master's thesis, Virginia Polytech. Inst.

WILCOCK, P. R., AND B. W. MCARDELL. 1993. Surface-based fractional transport rates: Mobilization thresholds and partial transport of a sand/gravel sediment. Water Resour. Res. **29:** 1297–1312.

———, AND ———. 1997. Partial transport of a sand/gravel sediment. Water Resour. Res. **33:** 235–245.

WILLIAMS, D. D., AND H. B. N. HYNES. 1974. The occurrence of benthos deep in the substratum of a stream. Freshwater Biol. **4:** 233–256.

WINTERBOTTOM, J. H., S. E. ORTON, A. G. HILDREW, AND J. LANCASTER. 1997. Field experiments on flow refugia in streams. Freshwater Biol. **37:** 569–580.

Received: 29 April 1998
Accepted: 17 November 1998
Amended: 11 February 1999