

The relationship between sediment mobilisation and the entry of *Baetis* mayflies into the water column in a laboratory flume

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Abstract

Mass bedload movement is thought to play a key role in initiating stream invertebrate drift during extreme flood events. However, little is known of the importance of the shear of invertebrates from stone surfaces relative to their entrainment along with bed material at different discharges. In particular, it is unclear whether so-called 'catastrophic drift' only occurs once mass bedload movement, and hence entrainment of invertebrates, occurs. We investigated the relationship between the mobilisation and transport of bed sediments and the entry of *Baetis* mayflies into the water column in a laboratory flume. Experiments quantified the percentage of *Baetis* drifting at a range of discharges that mobilised between 0 and 95% of the flume-bed sediments. Control experiments quantified drift losses from sediment fixed to the bed of the flume, such that sediments were immobile even at the highest discharges. Drift losses increased with increasing discharge and velocity in the flume. Sediment mobility contributed significantly to drift (ANCOVA, $p < 0.001$), with consistently greater drift losses in mobile sediment experiments than in those with fixed sediment. The discharge which resulted in a loss of 100% of *Baetis* from the mobile sediment bed (discharge 30 l s^{-1}) resulted in a loss of approximately 50% of individuals from the fixed bed. Results indicate that once bed sediments are mobilised, entry of *Baetis* into the drift is greater than expected from the shear of animals from stone surfaces alone. Thus, entrainment of animals along with sediment contributes significantly to drift at high flows. This implies that differences in bed stability between sites or streams, or temporal changes in sediment characteristics within a site, could influence patterns of drift.

Introduction

Disentangling the various mechanisms that influence stream invertebrate drift is an important step in improving our understanding of invertebrate distribution and abundance patterns. High discharge events are thought to represent disturbance phenomena that initiate what has been termed 'catastrophic drift' (see Brittain & Eikeland, 1988; Allan, 1995; and Giller & Malmqvist, 1998 for definitions of the various modes of drift entry).

However, despite more than half a century of drift research and renewed interest in the subject (e.g. De Crispin De Billy et al., 2002; Humphries, 2002; Elliott, 2002a, b) the mechanisms causing stream invertebrates to enter the drift during periods of high flow have yet to be fully elucidated (Faulkner & Copp, 2001).

Bond & Downes (2003) argued that in cases where the entire streambed is disturbed by a flood,

there can be little doubt as to the cause of declines in benthic abundance – both sediment and animals are mobilised and transported downstream. However, the upper limit to the velocity tolerance of invertebrates, as observed for example by Lancaster (1999), suggests that animals may sometimes be sheared from the surface of sediments before sediment mobilisation thresholds are reached. Although key to our understanding of the mechanisms causing animals to drift during hydrological disturbance events, the relative importance of the shear of invertebrates from stone surfaces versus their entrainment along with mobilised sediment at increasing discharges has not been properly quantified.

Here we present the results of an experimental study which aimed to assess the significance of sediment mobilisation for the entry of *Baetis* mayflies (Ephemeroptera: Baetidae) into the drift. We reasoned that under hydraulic conditions that are less severe than those which mobilise streambed sediments, only background drift occurs (relatively small numbers of animals entering the drift for behavioural reasons; Brittain & Eikeland, 1988). As shear forces increase, some animals may be sheared from stone surfaces, but this will depend on the availability and use of hydraulic refugia and whether invertebrate shear thresholds are reached before sediment mobilisation thresholds. We therefore hypothesised that below sediment mobilisation thresholds drift is relatively low, but once sediment is mobilised drift is greater than expected from the combined effect of background drift and

shear from stone surfaces. We tested this hypothesis by manipulating discharge in a flume and comparing the loss of *Baetis* from fixed and mobile bed sediments.

Methods

Test animals

The experiments were undertaken in an indoor, 15 m × 0.4 m, circulating glass-sided flume (Fig. 1). Mayflies of the genus *Baetis* have and continue to be the focus of much drift research (Miyasaha & Nakano, 2001; Humphries, 2002) and are known to be a numerically important component of the drift across Northern Europe (Elliott et al., 1988). Their tolerance to different water velocities has been studied, as has their use of refugia during periods of increased discharge (Lancaster, 2000). A sample of 100 Baetidae mayflies from the source stream (the Newmill Burn, Aberdeenshire, Scotland) contained only *Baetis rhodani* (Pictet), indicating that, if present, other *Baetis* species are present at low frequencies.

The Newmill Burn is a small (catchment area *circa* 15 km²) canalised stream with a uniform cross-sectional shape and a channel width that ranges from 0.5 to 1.5 m. In terms of shape and dimensions, it is therefore similar to the flume (as per Fig. 1). On the morning of each set of experimental trials, *Baetis* were collected from the burn (using a hand net and kick sampling) and trans-

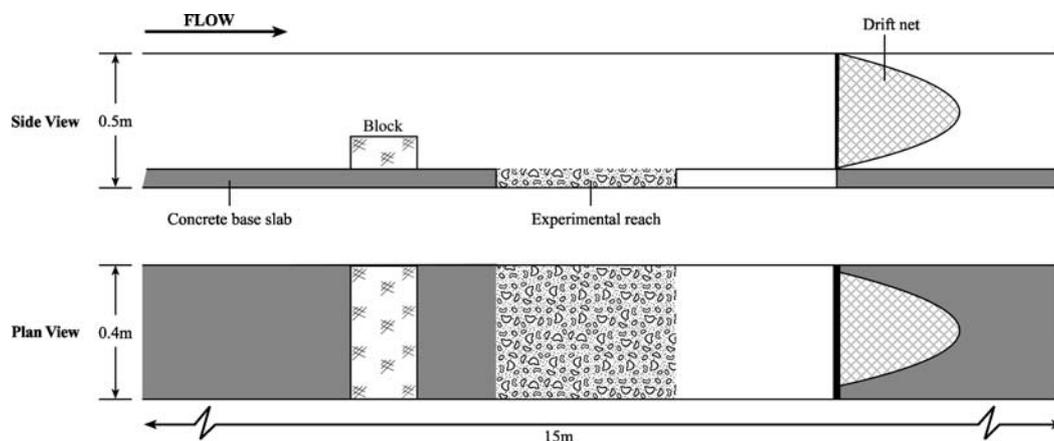


Figure 1. Plan and side views of the flume and experimental set-up.

ported back to the laboratory. Following collection of *Baetis*, water from the Newmill was pumped out and transported by tanker to the flume; mesh on the pump hoses prevented inadvertent transport of animals. Once in the flume, temperature and dissolved oxygen levels of the streamwater were monitored to ensure they remained within the daily ranges observed in the burn (Malcolm, 2002) during each period of experimentation. Experiments using *Baetis* were undertaken on 27 and 29 June and 2 July 2002, with new animals and streamwater used on each day.

Flume set-up

Experiments were conducted in a 1.0 m² reach located in the centre of the flume. This reach was filled with commercially available sediment mixed such that its size distribution (by fraction weight) was a close match to that in the Newmill Burn (Fig. 2). The largest and smallest size classes present in the Newmill were omitted from the flume mix because the largest sediments could not be mobilised in the flume and because the smallest ones resulted in clogging of the drift net and damage to the water pump. However, the largest and smallest size classes contributed only 16% (by weight) of the sediment in the Newmill; their exclusion was therefore not considered to result in an unrealistic substrate composition.

The base slab immediately downstream from the experimental reach was painted white to

improve the visibility of invertebrates washed out. At the downstream end of this slab, a net (mesh size 0.5 mm) collected all animals drifting down the flume. The drift net was held in place by metal brackets and filled tightly the entire width and depth of the flume. Any *Baetis* present in the drift net at the end of a trial were considered to have been washed out of the experimental reach and, hence, mobilised. The glass-sided flume allowed direct observation of *Baetis* during trials. Any animals present on the white base slab at the end of a trial were considered to have drifted out of the experimental reach, unless they were seen to have crawled out. The position of the net below the white base slab (i.e. 1 m downstream from the end of the experimental reach) meant that the backwater effects of the net did not influence hydraulic conditions in the experimental reach. To produce the hydraulic conditions required to mobilise sediments, a concrete block was placed 0.5 m up from the experimental reach (Fig. 1). This block produced non-uniform supercritical flow in the experimental section. Because of this it was not possible to calculate boundary shear stress; consequently, sediment mobilisation and drift were plotted with respect to discharge rather than shear.

As there was only one flume, it was not possible to run simultaneous replicate trials. Within a single flume, an alternative to the current design would have been to run replicate trials simultaneously in a number of experimental reaches distributed along the flume. However, the backwater effects of the block and the downstream effects of the drift net meant that this was not possible within the

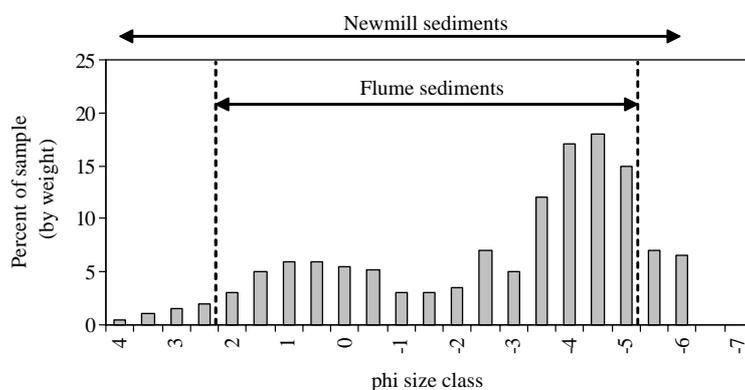


Figure 2. Sediment size characteristics in the Newmill Burn and the flume bed. Newmill sediments covered phi classes 4 to -6 while those in the flume extended from classes 2 to -5.

15 m length of the flume. Thus, given the constraints imposed by the flume, the current experimental design was considered optimum.

Sediment mobilisation trials

Before any animals were put in the flume, a series of trials were conducted to establish the percent (by weight) of sediment mobilised from the experimental reach at different flume discharges. Thirty such trials, each at a different discharge, were conducted. Any sediment present on the white base slab or in the drift net at the end of a trial was considered to have been mobilised. Each trial lasted 15 mins and at the end of each period, sediment was collected from the base slab and the drift net, weighed and expressed as a percentage of that at the start.

The time period for all subsequent experiments was set at 15 mins. This was because the sediment mobilisation trials showed that (a) at high flume discharges more than 95% of the sediment could be mobilised and transported out of the experimental reach within 15 min, while (b) at low discharges the sediment remained entirely stable (i.e. 0% mobilisation) over a 15 mins period. Velocity was measured during each trial using an electromagnetic flow meter located in the centre of the experimental reach. Velocity was measured at 0.6 of the water depth and so approximated the mean water column velocity.

It proved possible to manipulate discharge in the flume over an approximately sevenfold range

(0.5–32 l s⁻¹). This range equated to a change in velocity from 0.044 to 1.44 m s⁻¹ within the experimental reach. There was no visible or measurable movement of the flume-bed sediments at discharges less than 8 l s⁻¹ (Fig. 3). The smaller, surface sediments began to agitate at this threshold, with finer material saltating out of the experimental reach at discharges of 8–10 l s⁻¹. Beyond this point the percent of sediment mobilised increased rapidly, with 50% of sediment mobilised and transported out of the reach at a discharge of 15 l s⁻¹ and 95% mobilised at 30 l s⁻¹.

Invertebrate mobilisation trials

Further trials were conducted to establish the relationship between flume discharge and the loss or mobilisation of *Baetis* from the experimental reach. For each trial the sediment in the experimental reach was populated with *Baetis* equivalent to the mean density found in the Newmill Burn (259 m² ⁻¹, established from five replicate surber samples). Animals were introduced at a low flow (zero water column height; i.e. water only inundating sediments) because animals released into the water column with any moving water were immediately carried out of the reach. Individuals that were physically injured (e.g. missing body parts) or clearly less mobile than their congeners were not used in the experiments. No attempt was made to sort animals by size; hence they were a random sample of those collected from the Newmill.

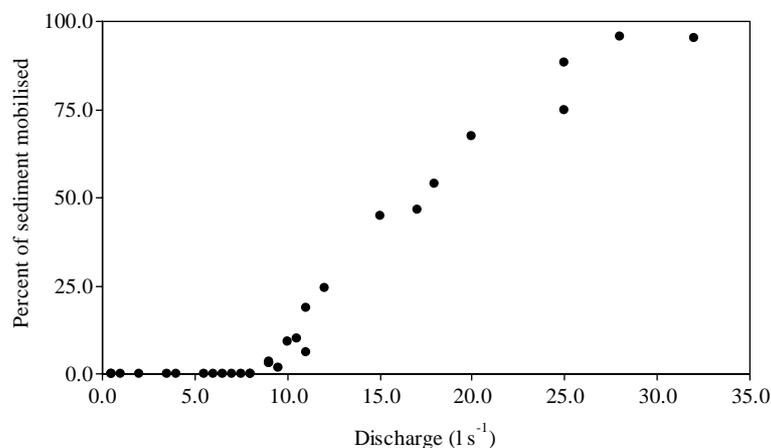


Figure 3. Relationship between discharge and the loss of sediment from the experimental reach.

After a 30 min settling period, flows were increased to the required trial discharge; discharge ramp-up was via by a hand wheel controlling a valve and took *circa* 30 s. Once the trial discharge was reached, animals present on the base-slab or in the drift net (i.e. animals which had moved out or been mobilised during the ramp up phase) were counted and removed from the experiment. This meant that density varied slightly between individual trials and differed from the mean density in the Newmill. However, differences were always less than 10% and within the range of variability established for the Newmill. The trial discharge was then maintained for 15 mins. At the end of each 15 min period, the number of drifting *Baetis* was expressed as a percentage of the start number. Any individuals remaining in the experimental reach were then removed, mobilised sediment was replaced and a new set of animals introduced for the next trial.

Behavioural drift in *Baetis* is predominantly nocturnal (Waters, 1962; Huhta et al., 2000). To control for diel variability in behavioural drift, all trials were conducted during daylight hours between 1100 and 1600 h. This consistency of timing also helped control for the effects of diel variability in susceptibility of *Baetis* to spates (as observed by Lancaster, 1992). Trials were conducted under natural, ambient light conditions. In total, 33 invertebrate mobilisation trials were completed, covering the range of discharges determined from the previous trials to result in 0–95% of the flume-bed sediments being mobilised. Discharge magnitude was randomised between trials.

Control, fixed sediment trials

Once the sediment mobilisation and invertebrate drift trials had been completed, the flume-bed sediments were fixed by placing them on concrete spread across the base of the experimental reach. In the same way as described above, invertebrates were then introduced onto this fixed bed and 20 trials were run across the experimental discharge range. These trials provided data on the mobilisation and drift of invertebrates with the same mix of sediment sizes but in the absence of any substrate movement.

ANCOVA was used to determine the influence of discharge on the percentage of *Baetis* lost from

experimental trials with fixed and mobile bed sediments. Sediment stability was incorporated into the model as a covariate, allowing its influence on *Baetis* loss to be determined. Fisher's *F* test, conducted as part of the ANCOVA, determined whether the null hypothesis (no influence of discharge or sediment stability on drift) should be rejected.

Results

In the mobile bed trials there was a significant linear relationship (df 16, $F = 169.7$, $p < 0.0001$) between the percent of sediment mobilised and transported out of the experimental reach and the percent of *Baetis* lost from the reach (Fig. 4). The *y* intercept of the line was 14.03, suggesting that even in the absence of sediment mobilisation, approximately 15% of *Baetis* entered the water column and drifted out of the reach during the 15 min trials.

ANCOVA indicated that both discharge (Fisher's $F = 234.5$, $p < 0.0001$) and sediment stability (Fisher's $F = 68.2$, $p < 0.0001$) exerted a significant influence on the percent of *Baetis* lost from the experimental reach (Fig. 5). For any given discharge, ANCOVA model parameters indicated that *Baetis* loss was increased by the mobilisation of sediment (parameter value for sediment mobility = 21.03). The slopes of the lines representing the relationship between discharge and percent *Baetis* lost from the reach in fixed ($y = 1.529x - 0.26$; $R^2 = 0.764$) and mobile ($y = 3.35x - 0.71$; $R^2 = 0.888$) differed significantly

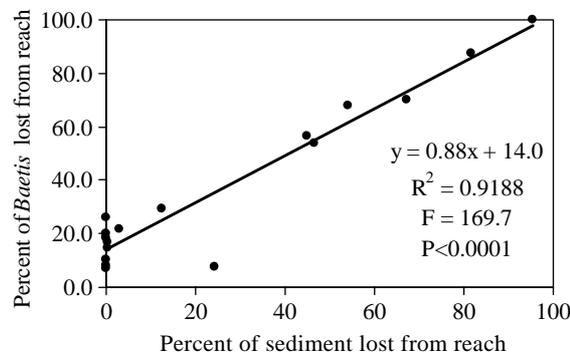


Figure 4. Relationship between the loss of sediment and *Baetis* from the experimental reach.

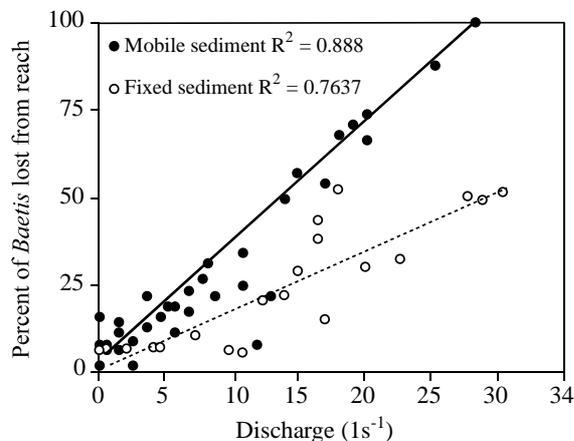


Figure 5. Mobilisation and drift of *Baetis* from trials with fixed and mobile flume-bed sediments. Both fitted regression lines are significant at $p < 0.0001$ (mobile sediment trials $y = 3.35x - 0.71$, $df = 33$, $F = 253.9$; fixed sediment trials $y = 1.529x - 0.26$, $df = 19$, $F = 58.2$).

(ANCOVA, $p < 0.001$). There was a significant interaction between discharge and sediment mobilisation (ANCOVA: Fisher's $F = 37.13$, $p < 0.0001$).

Discussion

The flume experiments indicated that once bed sediments are mobilised, the drift of *Baetis* mayflies increases above that expected from the combined effect of background drift and the shear of animals from stone surfaces. Seen in a different way, the experiments suggest that sediment stability may help limit the effects of extreme hydraulic forces on benthic invertebrates. The work contributes to our understanding of the circumstances under which high discharge events may lead to catastrophic drift; more specifically, it suggests that the point on the flood hydrograph where sediment mobilisation is initiated may represent an important disturbance threshold. These points are discussed below.

Allan (1995) argued that the difficulty of measuring bed movement has prevented ecologists from having a full understanding of how substrate stability affects organisms. Cobb et al. (1992) found that rivers with unstable substrates were characterised by low invertebrate species diversity, but it was unclear from their work whether the low

diversity was because of indirect effects (e.g. animals moved away from unstable patches because there was little deposition of organic food material) or because substrate instability resulted directly in increased drift. By controlling flume discharge and substrate mobilisation, it proved possible to address this question in the current work. Sediment mobility proved a significant covariate (ANCOVA; $p < 0.0001$), indicating that substrate instability can influence the total drift flux. This suggests that substrate instability can influence benthic community structure. Previously, the relative importance of the shear of invertebrates from stone surfaces and substrate mobilisation in initiating drift proved difficult to quantify (Allan, 1995). In the current experiments, drift losses from the trials with mobile sediment were approximately double those from trials where the bed was immobile.

It is necessary to be cautious when interpreting the results of flume experiments and, in particular, when comparing results with stream studies. Where possible, conditions in the flume were similar to those in the Newmill Burn, the source of the test organisms. Newmill Burn water was used in the experiments, so limiting water chemistry artefacts. The size and shape of the flume and the flume-bed sediments were also similar to the Newmill Burn, so experimental artefacts resulting from differences in channel scale, geometry or bed architecture were limited. However, sediments in the flume were arranged randomly rather than being sorted by moving water, as occurs in natural streams. It therefore remains possible that *Baetis* behaviour was affected by the lack of natural sediment sorting. While in theory the absence of a food supply in the flume could initiate artificially high rates of behavioural drift, individual animals were in the flume for a period of no more than 90 mins so this seems unlikely. Overall, drift losses from the 33 mobile and 20 fixed sediment trials were very different, so the sediment stability effect is considered to represent a real phenomenon. With care, some general inferences concerning processes in natural streams can therefore be drawn from the experiments.

In those mobile sediment trials where no sediment movement occurred (i.e. at flume discharges less than 8 l s^{-1}), an average of 9.5% (SD 5.7) of *Baetis* entered the water column. This percentage

equates to the background drift rate in the flume. Many studies have attempted to quantify background drift rates (Townsend & Hildrew, 1976; Williams, 1980; Cibrowski, 1983; Miyaska & Nakano, 2001; Humphries, 2002) but because of different approaches and equipment, comparison between these studies and the current flume experiments is unwise. Drift is known to increase above the background rate during high discharge events. Lancaster (1992) found that spates representing a three-fold increase in discharge resulted in increased drift and reduced benthic densities of *Baetis* in natural streams. In the flume it was possible to manipulate discharge over a much larger range than this ($0.5\text{--}32\text{ l s}^{-1}$), increasing mean column water velocity by more than an order of magnitude and mobilising up to 95% of sediment. Sediment mobilisation of this scale, at least as dramatic as that which is known to have initiated catastrophic drift in natural streams, has rarely been achievable in flumes. Results from the flume trials suggest that where it occurs, sediment mobilisation is likely to contribute significantly to drift in natural streams during high discharge events.

McLay (1968) found that approximately 50% of benthic invertebrates in a New Zealand stream were washed downstream during spring snowmelt spates. However, in a recent manipulative study, Bond and Downes (2003) found that neither substrate movement nor high suspended sediment levels during spates were necessary to illicit a drift response. Data from the fixed sediment flume trials, where up to 50% of animals were lost at high discharges, is further evidence that increased drift can occur in the absence of substrate movement.

In the mobile sediment trials there was a clear sediment mobilisation threshold, above which the percentage of sediment lost from the experimental reach increased dramatically. This point may be considered as a physical disturbance threshold, a threshold that marks the boundary between catastrophic and non-catastrophic drift. However, no such threshold was apparent in the *Baetis* drift data. Because the flow control valves on the flume were relatively imprecise, it was difficult to repeatedly run *Baetis* trials at discharges immediately above and immediately below the sediment mobilisation threshold. Thus, the apparent absence of a threshold in the *Baetis* data may simply

reflect an inadequate number of data points in the key discharge region. Conversely, it may be that *Baetis* did not respond in the same way as the inorganic bed material; i.e. a behavioural response at this threshold point mediated the impacts of flow change. One such response would be for individuals to move to interstitial areas as the first surface sediments begin to agitate and become mobile. While this is an attractive explanation, the current data do not permit assessment of whether the lack of a threshold in the *Baetis* data reflects this sort of behavioural response or simply poor data resolution around the key discharge.

Conclusions and implications

The precise nature of relationships between discharge, shear forces, sediment mobilisation and the drift of *Baetis* are specific to the flume used in the current experiments. For this reason, results need to be interpreted with caution and inferences concerning controls on drift in river channels made only with care. Nonetheless, the effects of discharge and sediment mobility on *Baetis* drift in the flume experiments were clear; consequently the general conclusion that sediment stability/instability plays a key role in determining the impacts of a given high flow event is well founded. Bed stability in river channels is influenced by both the size and sorting of sediments; thus changes to sediment characteristics may affect the likelihood that a hydrological event of a given magnitude will result in invertebrate drift. Changes in sediment characteristics may occur when channels are modified to aid flood conveyance (when large sediments are removed) or when rivers are impounded (when sediments downstream from the reservoir become coarse and stable relative to pre-impoundment conditions). Data from the flume experiments suggest that drift from such areas may be altered as a result of changes in sediment stability.

In the fixed bed trials 50% of *Baetis* were lost from the experimental reach at a discharge of 30 l s^{-1} . This percentage loss is equivalent to what has been classified as catastrophic drift in field studies (e.g. McLay, 1968), a type of drift usually associated with flood conditions during which the substrate is physically disturbed (Brittain &

Eikeland, 1988). Despite the clear role that sediment mobilisation plays in initiating drift, an important conclusion from the fixed bed experiments is that considerable drift can also occur in absence of sediment movement.

At relatively high flume discharges, entrained animals were observed to saltate violently down the channel along with mobilised sediment. Individuals transported in this way may be more likely to sustain injury than those sheared from stone surfaces and carried downstream in a water column free of sediments. This difference may affect their subsequent fitness. Our understanding of the impacts of floods would benefit from studies which are able to assess the relative frequency of injury during events which do and do not result in mass bedload movement. By linking event magnitude to measures of injury or fitness, such studies could improve our understanding of the implications of hydrological disturbance for invertebrate population dynamics.

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