

When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events

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SUMMARY

1. The term 'catastrophic drift' is used to describe the large-scale displacement of invertebrates that occurs during periods of increased river discharge. However, the physical processes that lead to animals entering the water column at such times remain poorly understood. Specifically, the hypothesis that the movement of bed sediments during floods triggers a large increase in drift has lacked a rigorous field test.
2. Using a portable flume, the hydraulic conditions and rates of bedload transport associated with small, frequent floods were created *in situ* within a reach of a gravel bed river. Experiments focussed on the patches of fine sediment which are the dominant source of bed material transported during small floods. The flume produced near bed velocities of up to 2 m s⁻¹ over the patches, increasing shear stress, initiating sediment transport and causing invertebrates to enter the drift.
3. The total number of individuals lost from the bed, as well as the taxonomic composition of the drift, were influenced strongly by shear stress and bedload. The rate of loss from the bed was low at shear stresses <9 dynes cm⁻² (0–4 individuals min⁻¹ from the 0.5 m² flume bed area). Once shear stress exceeded 9 dynes cm⁻², the threshold that resulted in consistent bedload transport from the patches, the rate of loss of animals increased to a maximum of 56 individuals min⁻¹. When bedload transport rates were at their highest, the taxonomic composition of the drift was more similar to the benthos than it was to the drift observed when bed material was stable.
4. Absolute rates of bedload transport created by the manipulations were extremely low (<7 g m⁻¹ s⁻¹) and typical of those measured during small, frequent floods. Events of this magnitude do not break up the armour layer across the reach as a whole and so exposed patches of fine sediment are the principal source of bedload material. Consequently, discharge events not considered as disturbances in geomorphic terms may initiate frequent episodes of so-called 'catastrophic drift' from patches of stream bed.

Keywords: invertebrate drift, bedload transport, shear stress, portable flume, gravel-bed river

Introduction

Understanding the processes that lead to observed patterns is a central goal in ecology. Patterns of species diversity are influenced by a number of

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factors, but periodic disturbance events are now recognized as playing an important role in maintaining diversity in many ecosystems (Connell, 1979; Sousa, 1984). The potential for flood events to act as disturbances in river and stream ecosystems is self-evident. The extreme hydraulic forces that occur during high discharges (e.g. bankfull) cause mobilization and transport of sediments, scour and fill processes and, in some cases, restructuring of channel geomorphology (Leopold, Wolman & Miller, 1964). Bond & Downes (2003) argued that there can be little doubt as to the cause of declines in benthic invertebrate abundance following such events: animals are mobilized along with sediment and carried downstream.

Invertebrates are present in the water column of rivers and streams more or less constantly. Individuals may leave the bed and drift downstream as part of their normal behaviour (termed active, behavioural or voluntary drift: e.g. Huhta, Muotka & Tikkanen, 2000; Miyasaka & Nakano, 2001), while in normal flow conditions near bed shear forces occasionally dislodge individuals (termed passive or involuntary drift: e.g. Waters, 1972). Higher rates of involuntary drift occur as shear forces increase (Gibbins *et al.*, 2005), with many field studies reporting increases in drift during periods of rising discharge (reviewed by Brittain & Eikeland, 1988; Giller & Malmqvist, 1998; Callisto & Goulart, 2005). The term 'catastrophic drift' is used to describe the marked increase in drift that occurs as a result of disturbances such as floods or pollution events (Lauridsen & Friberg, 2005). However, a number of important aspects of this phenomenon remain vague or lack empirical data. First, there has been little critical analysis of whether there is a clear threshold increase above the background rate when drift can be considered to be catastrophic. Secondly, there is little empirical evidence of the physical processes that might trigger such a threshold increase in drift. Statzner, Dejoux & Elouard (1984) proposed a conceptual model of the probability of scour of invertebrates from the bed during the rising limb of a flood hydrograph. They argued that there is an initial increase in the number of animals entering the drift because of the increase in velocity (and thus shear stress), followed by a second increase once bed material becomes unstable. The increment associated with bed instability forms an important part of Brittain & Eikeland's (1988) definition of catastrophic

drift. While mass sediment movement is an obvious mechanism that could trigger catastrophic drift, there are no published field data relating rates of sediment loss from specific points on the stream bed to drift losses from these points; thus, precisely how much sediment loss is needed before drift becomes catastrophic, or whether agitation of the sediment is sufficient, remains unclear.

The principal constraint on elucidating the processes that lead to so-called catastrophic drift is that of undertaking controlled studies in river channels during the high flow events which initiate sediment transport. Consequently, indoor flumes (Ciborowski, 1983) or artificial streamside channels (Imbert & Perry, 2000) have been used extensively. While allowing for manipulation and replication, these suffer from problems related in one way or another to the simplification of the stream ecosystem, either in terms of the benthic community or the physical environment. Recreating the natural architecture of the river bed has been a perennial problem in flume studies, with a variety of artificial, simplified or randomly arranged substrata used (Young, 1992; Buffin-Bélanger, 2001; Lawless & Robert, 2001). Most recently, novel casting techniques have been used to recreate natural bed architecture in flume settings (Lancaster *et al.*, 2006). Nonetheless, a major constraint remains the limited hydraulic forces it is possible to create in laboratory flumes and artificial channels. For instance, almost none of the manipulative studies of behavioural or drift responses to discharge change have been able to create velocities exceeding 1 m s^{-1} [e.g. Walton, Reice & Andrews, 1977 (max. 0.19 m s^{-1}); Ciborowski, 1983 (max. 0.51 m s^{-1}); Lancaster, 1999 (max. 0.7 m s^{-1})]. We have been able to overcome these problems by using a portable flume *in situ* within a reach of a gravel bed river. Velocities inside the flume were sufficiently high to mobilize sands and fine gravels from patches of stream bed (maximum instantaneous near-bed velocity was 2.14 m s^{-1}) and initiate drift.

Here we present the results of manipulations in which we used the flume to address a number of questions related to the processes that initiate drift: (i) what is the statistical form of the relationship between shear stress and the entry of invertebrates into the water column? (ii) is there a clear threshold increase that represents the change from background to catastrophic drift? (iii) if so, is this threshold associated

with the sediment entrainment threshold? and (iv) what rates of sediment loss are necessary to trigger a threshold change in drift? We set the answers to these questions within the context of long-term discharge frequency/magnitude relations and associated patterns of sediment transport in the study reach. In this way, we develop a more precise understanding of the physical processes that trigger involuntary drift and the frequency with which so-called catastrophic drift occurs.

Methods

Study area

Manipulations were carried out in a reach of the Ribera Salada, an unmodified upland gravel bed river located in the Catalan Pre-Pyrenees, NE Iberian Peninsula (Fig. 1). At the study reach the Ribera Salada is a fourth order stream, with channel width varying from 5 to 10 m. The reach has a transitional pool-riffle/plane bed morphology (after Montgomery & Buffington, 1997) and an estimated median

discharge (Q_{50}) of $1 \text{ m}^3 \text{ s}^{-1}$ (Batalla, Garcia & Balasch, 2005). The median surface sediment size (D_{50-s}) in the reach is 49 mm while the subsurface D_{50} (D_{50-ss}) is 24 mm. River bed sorting, calculated using the Folk & Ward (1957) method, is 0.98 ('moderately sorted') for the surface material and 2.54 ('very poorly sorted') for the subsurface material. The armouring ratio (ratio of $D_{50-s} : D_{50-ss}$) of the study reach is 2, thus characterizing the river bed as armoured.

Manipulations using the flume focussed on patches of fine bed material distributed across the 140 m study reach (Fig. 2). These patches are meso-scale accumulations (each up to $c. 1 \text{ m}^2$ in area) of fine sediments, usually located behind obstacles or in depressions in the river bed (Laronne, Garcia & Reid, 2001). The median (D_{50}) size of sediment in the patches across the study reach ranges from 0.5 to 2 mm. Such patches are the principal source of bedload transported in gravel bed rivers at the beginning of large floods, as well as during low magnitude, high frequency events. Previous studies in the Ribera Salada have indicated that these patches are the dominant source of bedload transported during small floods (Batalla *et al.*, 2005).

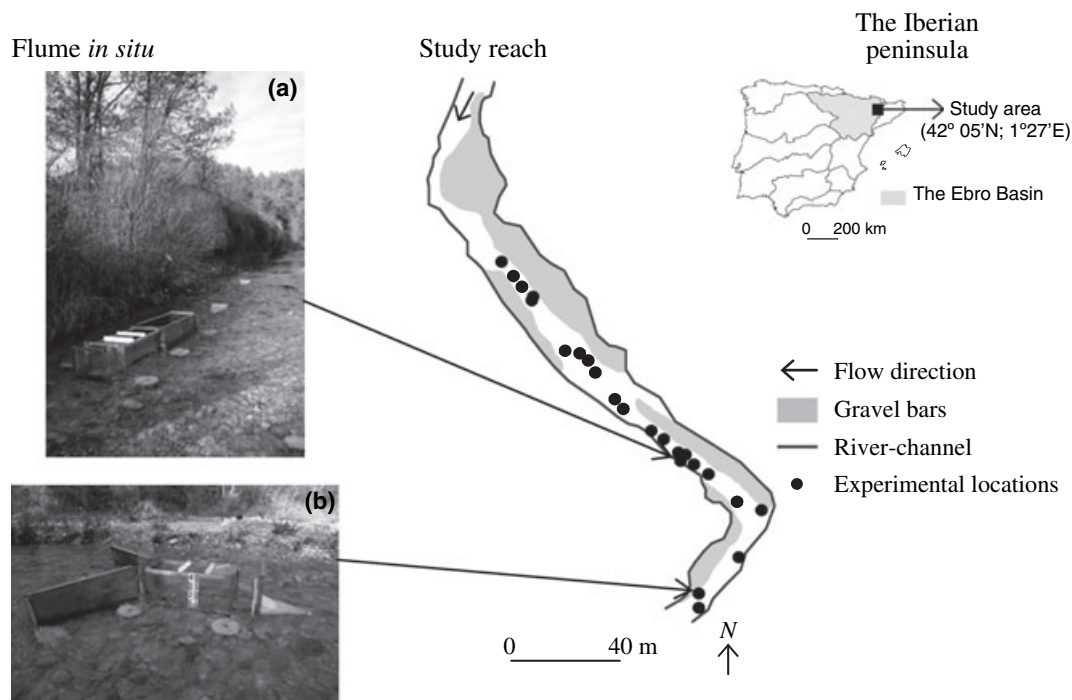


Fig. 1 Location and details of the Ribera Salada study reach, showing experimental locations and the flume *in situ*. In (a) the flume is shown with the doors in their normal position (i.e. without any manipulation of hydraulic conditions), while in (b) the doors are open (hydraulics manipulated).

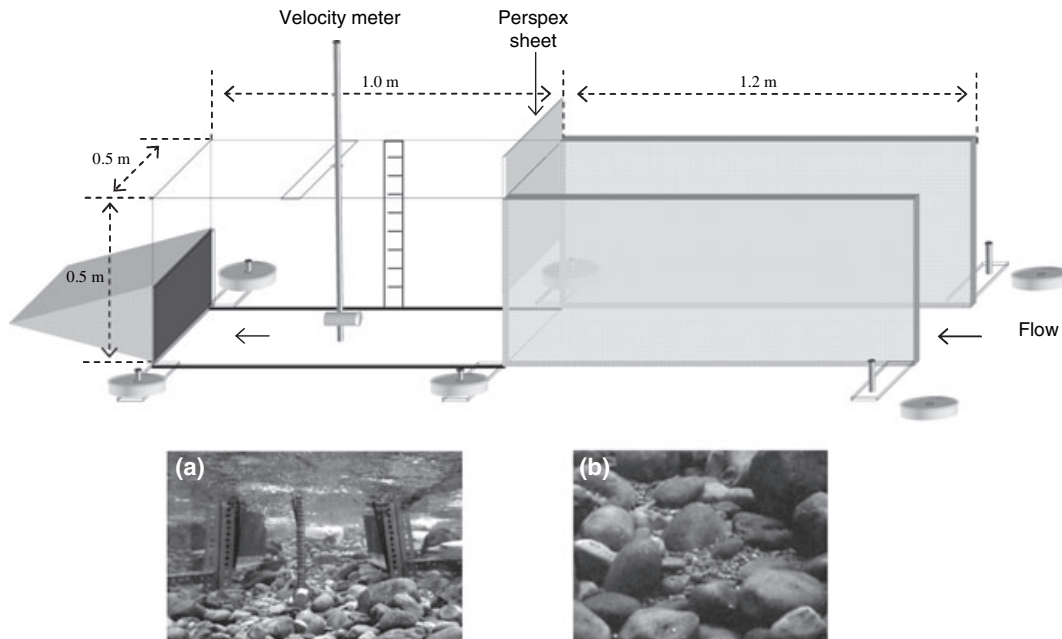


Fig. 2 The flume and patch sediments. In the flume schematic, the doors and drift net are shaded. Doors are shown in their normal position, with the area of stream bed manipulated by opening the doors situated immediately downstream from these. Further details of the flume are given in Methods. Photographs show (a) the flume from inside, located over one of the experimental patches (arrow in schematic shows the position and direction of the photograph) and (b) detail of stream bed, illustrating the relative size of fine material characteristic of a patch. Disks shown at corners of flume are weights used for anchorage.

Hydraulics and drift

To manipulate hydraulic conditions over the patches ($n = 27$), a small, portable flume was constructed (Figs 1 & 2). The flume was designed to be large enough to encompass individual patches but sufficiently small and light that it could be carried easily across the reach. The bottom was open, so that when the flume was placed at an experimental location it isolated a patch of stream bed from the rest of the channel. The downstream end of the flume was constructed so that a standard invertebrate drift net could be quickly slid in and out, at the beginning and end of each monitoring period (net 0.5-m wide, 0.25-m high and 0.5-m long; mesh 1 mm). The base of the net frame was placed on the stream bed. This net captured larger invertebrates and bed material moving downstream inside the flume.

Hinged doors were fitted to the upstream end of the flume. These doors were used in two positions. In their normal position they ran parallel to the sides of the flume (Figs 1a & 2). When opened (Fig. 1b), the doors funnelled water from a 2-m wide section of channel into the flume, increasing flume discharge

and altering hydraulic conditions over the target patch of stream bed. To increase further velocity and shear stress inside the flume when the doors were open, the flume was constructed so that a Perspex sheet could be slid vertically in and out at the upstream edge of the patch (Fig. 2). It slid down into a fixed position, leaving a gap of 15 cm between the bottom of the Perspex and the stream bed. The Perspex partially dammed the water entering the flume, with the pressure from upstream forcing water through the gap and creating a nearbed jet of water over the patch. This jet created the high velocities and shear stresses necessary for bedload movement. Once positioned at the start of an experiment, the Perspex sheet was not moved in any way.

For each experiment, water depth and velocity at two heights within the water column (at 0.2 and 0.4 of the depth) were measured at exactly the same position within the flume [Valeport electromagnetic flow meter (Model 801, Valeport Ltd., Devon, U.K.), Fig. 2a]. The flow meter recorded instantaneous velocity every second, with a mean and SD then calculated for the 1 min recording period. For each height within the water column during each experi-

ment, two consecutive means were calculated. When these differed by <10%, the average of the two was used for analysis. If they differed by more than 10%, a third measurement was taken, with the average of the two most similar readings calculated and used for analysis. During each flume experiment, water depth and velocity were also measured at a drift net positioned 2 m upstream from the flume.

The jet of water created by the Perspex sheet was relatively stable during each period of manipulation. For example, the standard deviation of the velocity measured over the 1 min recording period averaged 0.08 m s^{-1} across the 27 patch locations; this is similar to the standard deviation at the measuring points 2 m upstream of each patch (0.06 m s^{-1}). Thus, the jet did not produce highly variable pulses of water.

Shear stress can normally be calculated using the gradient of the vertical velocity profile at the point of interest (Gordon, McMahon & Finlayson, 2004). However, the jet created by the Perspex sheet affected the velocity profile inside the flume and rendered this method inappropriate. Instead, shear stress was calculated using an inverted form of the law of the wall formula which, along with a number of constants and a measure of bed roughness, requires only a value of nearbed velocity (notations are given in the Appendix):

$$\text{Shear stress}(\tau_b) = \rho(v_z k)^2 [\ln(10z/D_{84})]^{-2}$$

Velocity measured at $0.2 \times d$ inside the flume was used in the calculations, fulfilling the recommendation of Whiting & Dietrich (1990). This formula was tested by Whiting & Dietrich (1991) in a stream where conditions were similar to the flume (increased nearbed velocity, with little variation through the vertical profile and similar bed roughness). They found that in these conditions it yielded more convincing results than using the vertical profile. Following Whiting & Dietrich (1990), we use units of dynes cm^{-2} for flume shear stress calculated using this formula; note that dynes cm^{-2} are equivalent to Nm^{-2} ($1 \text{ dyne cm}^{-2} = 1 \text{ Nm}^{-2}$).

The drift net at the downstream end of the flume permitted assessment of the number of animals present in the drift over the course of an experiment. This drift was comprised of animals entering the flume from upstream (less any which settled within the flume), together with those mobilized from the bed of the flume during a period of

manipulation. To be fully confident about the impact of the manipulations on drift losses from the bed of the flume, it would be necessary to stop all animals entering from upstream. However, trials indicated that the use of a complete blocking net across the upstream end of the flume reduced flume velocities by 40–50% and so limited sediment entrainment. To provide an estimate of the number of animals entering the flume from upstream during each period of manipulation, drift was measured using a net placed 2 m directly upstream of the flume. This was the closest that a net could be placed without reducing velocity in the mouth of the flume. For each period of manipulation, the number of animals lost from the flume bed was calculated by subtracting the drift recorded in the upstream net (u/s net) from that in the net at the downstream end of the flume. Thus, it is important to note that, rather than a direct measure of the number of animals leaving the bed, we have an estimate of this based on the difference between 'drift-in' and 'drift-out'.

To address the possibility that the upstream net stopped some animals from entering the flume (and therefore biased the estimate on the number lost from the bed), we ran a trial to assess drift distances. One hundred animals (random mix of benthic taxa) were released into the upstream end of the flume. Animals were released into the water column 10 cm from the bed and those remaining in the drift were captured in the net at the downstream end of the flume. Exactly 66% of animals released in this trial regained the bed within the 1 m distance between their release point and the net. Townsend & Hildrew (1976) found that most drifting invertebrates were derived from <2 m upstream of the sampling point. Elliott (2002) found that, at velocities $<0.3 \text{ m s}^{-1}$, the drift distance of *Baetis* was typically <2 m. This taxon was a numerically dominant component of the drift in the Ribera Salada, comprising 49.5% of all animals captured during the manipulations. As velocity at the upstream measuring points in the Ribera Salada averaged 0.24 m s^{-1} (0.1 SD), the majority of this numerically dominant animal were, therefore, most likely to be drifting only short distances. We concluded that the upstream net did not markedly reduce the number of animals entering the flume, as most of those captured by this net would have returned to the bed before reaching the flume.

Experimental design

The flume was placed on the stream bed such that the area hatched in Fig. 2 covered the target patch of fine material. This ensured that the area to be manipulated was dominated by the fine material which characterized the patch. The area of stream-bed between the flume doors was always upstream of the patch, and so was comprised larger and more stable material. Loss of animals and sediments from each patch was quantified under two different flow conditions. The first was with the flume doors in their normal position, where there was no manipulation of velocity or other hydraulic conditions inside the flume. Drift and bedload were sampled over a 15-min period at each patch location. At the end of each 15-min period, the drift net was removed and its contents emptied into a sorting tray. Any sediment present in the net was retained for analysis and invertebrates were preserved in alcohol for subsequent identification and enumeration. Data from these manipulations were coded velocity 1 (V1). The drift net was then replaced (always within 1 min), the flume doors opened and the vertical Perspex sheet fixed into position. Drift and bedload were then measured over a 5 min period; these data were coded velocity 2 (V2). A shortened time period was used to avoid clogging of the net. After the manipulation, the flume was moved to a new location.

All manipulations were conducted between 09:00 and 17:00 hours (daylight) on three dates between February and April 2006. This minimized the possibility of artefacts resulting from daytime/night-time patterns of behavioural drift or differences resulting from seasonal changes in benthic abundance. On each date, flows were low and stable (discharges always less than the reach median flow). Fourteen benthic samples were collected from random locations across the reach over the period of the manipulations. Samples were collected using a Surber sampler (base frame of 0.1 m², net mesh 1 mm), with the substratum inside the base frame disturbed to a depth of approximately 10 cm using a garden hoe. In the laboratory, all invertebrates from the drift and benthic samples were counted and identified to family, genus or species level.

Characterization of river bed and bedload sediments

Sediments in patches had previously been sampled (January 2003) using the area-by-weight method (Kellerhals & Bray, 1971). Surface and subsurface bed material across the study reach was sampled in December 2005. No significant floods occurred in the Ribera Salada between either of these sampling occasions and the flume manipulations. The surface material was characterized using the pebble count method (Wolman, 1954). For this, 500 particles were randomly selected and measured by passing them through a template with square holes scaled at 1/2 ϕ intervals. This method produces a grain size distribution (GSD) curve which is truncated at 8 mm and, therefore, underestimates the proportion of the bed comprised of finer material. However, it gives a robust indication of the GSD of the surface material of the reach as a whole. The subsurface material was sampled using the volumetric method (Lane & Carlson, 1953). An area of an exposed low gravel bar was sprayed with paint so as to identify the surface material. This layer was then removed to expose the subsurface material, which was then excavated, sieved and weighed to determine GSD. The total weight of the subsurface material sampled was 150 kg, with the largest particle being 160 mm and weighing 2.5 kg. Thus, the weight of the largest particle was 1.7% of the total sample weight. According to the criteria discussed by Church, McLean & Wolcott (1987), this weight of material produced an acceptable accuracy for the estimate of the subsurface GSD.

A small flood occurred in the Ribera Salada on 30 January 2006. Discharge during the flood peaked at 5 m³ s⁻¹, a discharge equalled or exceeded 10% of the time. Bedload was sampled during the flood 1.5 km upstream from the study reach by means of two automatic, continuously recording Birkbeck-type pit traps. Weights and GSDs of these samples were determined and related to the flume data to compare hydraulics and the rates and size characteristics of bedload material.

Bedload samples collected during the flume manipulations were dried, sieved and weighed to obtain a total weight and GSD for each sample. Although the net mesh was 1 mm, material finer than this was retained (up to 50% of the bedload in individual samples comprised material finer than 1 mm). Thus,

the drift net was relatively efficient at capturing fine material and any underestimate of material smaller than 1 mm is considered minimal.

Statistical treatment of data

The statistical relation between the number of animals lost from the flume bed and shear stress was assessed by means of spline analysis and regression (using NLOGIT software, version 3.0, Econometric Software Inc., New York, U.S.A.). Spline analysis looks for different relationships (splines) between dependent and independent variables across a data range; the point where the relationship changes represents a breakpoint. The analysis iteratively tests different values of the independent variable (shear stress) to determine the position of the breakpoints that result in a marked change in values of the dependent variable (number of animals lost from bed). The validity of a given model is assessed using the maximum likelihood value, combined with the significance value (P) of each spline.

Based upon the drift entry model of Statzner *et al.* (1984), the existence of two breakpoints (= three splines) in the relation between shear stress and the number of animals lost from the flume bed was first tested for. If, at the highest maximum likelihood value, one of the splines had a P -value exceeding 0.05, the three spline model was rejected. In this circumstance, the single line best representing the relation was fitted to the data. Spline analysis was then used to look for a breakpoint across this relation. In some V1 manipulations, more animals were captured in the u/s net than in the flume; this resulted in the computed value of the number lost from the flume bed being negative. To fit and test exponential models, data were transformed by adding a constant of 3 so as to remove negative values. Such an upward movement of the dependent variable does not influence the marginal effects of changes in the independent variable, or any other statistical property of the model.

Drift and benthic samples were analysed using non-metric multidimensional scaling (NMDS). Prior to analysis, abundance data were transformed to proportions, so that the NMDS depicted patterns in species composition and relative abundance. Multi-response permutation procedure (MRPP) was used to test whether *a priori* defined groups of samples differed in their position on the NMDS ordination

plot. MRPP is a nonparametric procedure for testing the hypothesis of no difference between two or more groups across multi-dimensional space. NMDS and MRPP were undertaken using PC-ORD version 2.0 (McCune & Mefford, 1995).

Results

Hydraulics and sediment transport

Data on hydraulic changes resulting from the manipulations are summarized in Table 1. Averaged across all patches, the increments in mean column and nearbed velocity were 80% and 120% respectively. Shear stress and sediment transport changed consistently between the V1 and V2 data sets (Table 1 and Fig. 3). The increment in shear stress between respective V1 and V2 manipulations averaged almost 400% and reached a maximum value of 40.57 dynes cm^{-2} . Depth changed little once flume doors were opened: the maximum depth increment observed in any one location was 4 cm, but in most cases was not measurably different. Thus, the increases in

Table 1 Summary of hydraulic and bedload characteristics before (V1) and during (V2) flow manipulations. Values are computed from the 27 patch locations

	V1	V2
Velocity at $0.4 \times$ depth (m s^{-1})		
Average	0.53	0.96
SD	0.19	0.41
SE	0.04	0.08
Velocity at $0.2 \times$ depth (m s^{-1})		
Average	0.39	0.86
SD	0.16	0.44
SE	0.03	0.08
Local boundary shear stress (dynes cm^{-2})		
Average	2.13	10.59
SD	1.59	9.94
SE	0.33	1.84
Bedload rate ($\text{g m}^{-1} \text{s}^{-1}$)		
Average	0	1.21
SD	0	2.01
SE	0	0.42
Median grain size of bedload (mm)		
Average	N-A	1.40
SD	N-A	0.29
SE	N-A	0.05
Sorting index (calculated using Folk & Ward, 1957)		
Average	N-A	0.80
SD	N-A	0.18
SE	N-A	0.03

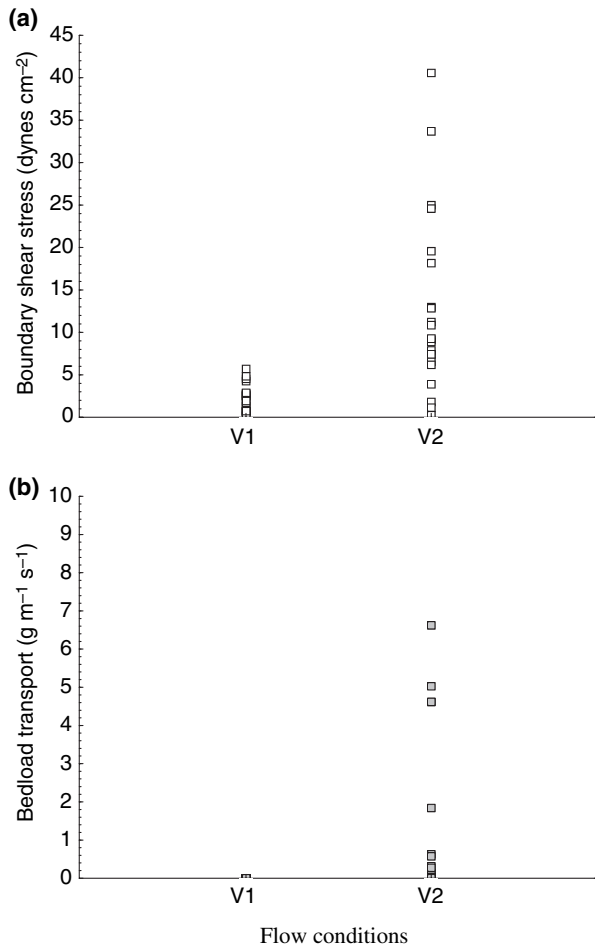


Fig. 3 Range of (a) shear and (b) bedload recorded in unmanipulated (V1) and manipulated (V2) flow conditions.

flume discharge created by opening the doors resulted primarily in increases in velocity.

No bedload transport was recorded in the V1 samples but was found in 23 (85%) of the V2 samples. Once shear stress exceeded 9 dynes cm⁻², bedload transport was recorded consistently. In the 23 V2 samples which contained sediment, bedload rates ranged from 0.001 to 6.62 g m⁻¹ s⁻¹. Sediment present in the bedload was mostly in the range of coarse sand (Fig. 4). The low SD values for the bedload D_{50} (Table 1) indicate highly size-selective transport of bed material. The bedload sorting index varied from 0.6 to 1.3, indicating moderately sorted material. The envelope of the GSD for the bedload fell almost wholly (75% of sizes) within that of the patches, indicating that the patches were the dominant source of material. These GSDs were distinctly finer than the surface material of the reach overall, even allowing for

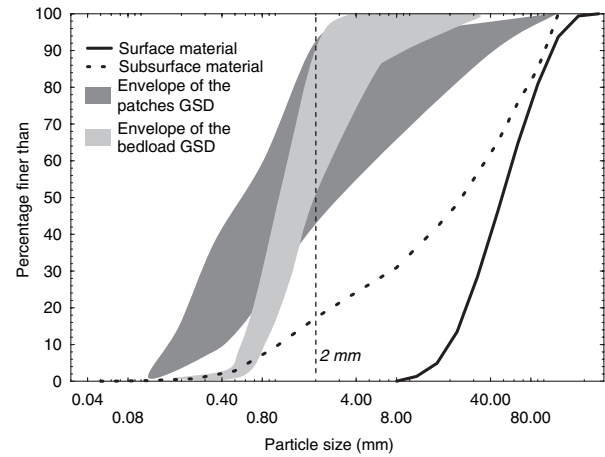


Fig. 4 Grain size distributions for the study reach (surface and subsurface material), sediment patches and bedload samples. The vertical line positioned at 2 mm shows the upper size limit of sand.

any underestimate of finer material in the bedload samples.

During the flood of 30 January, discharge was competent to mobilize sediments of the size found in the experimental patches for a period of 9 h. Over this period, mean velocity was 1.5 m s⁻¹ compared with velocities of 0.5–2.1 m s⁻¹ in the V2 manipulations in which sediment was entrained (velocities at $0.4 \times d$). Mean bedload rates during the 9-h period were 0.97 (trap 1) and 2.04 (trap 2) g m⁻¹ s⁻¹, with D_{50} sizes of 1.17 and 4.62 mm respectively. These values, as well as data given in Batalla *et al.* (2005), indicate that velocities and the rates and sizes of bedload resulting from the flume manipulations are broadly representative of small floods (c. 5 m³ s⁻¹) that occur frequently in the study reach.

Relations between drift, hydraulics and bedload

In total, 41 invertebrate taxa were found in the 95 samples collected from the study reach (14 benthic and 81 drift samples). The most abundant taxa in the samples were the mayflies *Baetis* and *Ecdyonurus* and caddisflies of the family *Hydropsychidae*. The number of animals lost from the bed varied as a function of shear stress and rates of sediment transport (Fig. 5). The two breakpoint (three spline) model was rejected because at the highest maximum likelihood value, the P -value for one of the splines exceeded 0.05. A simple exponential curve provided the best fit for the relation between shear stress and the number of animals lost

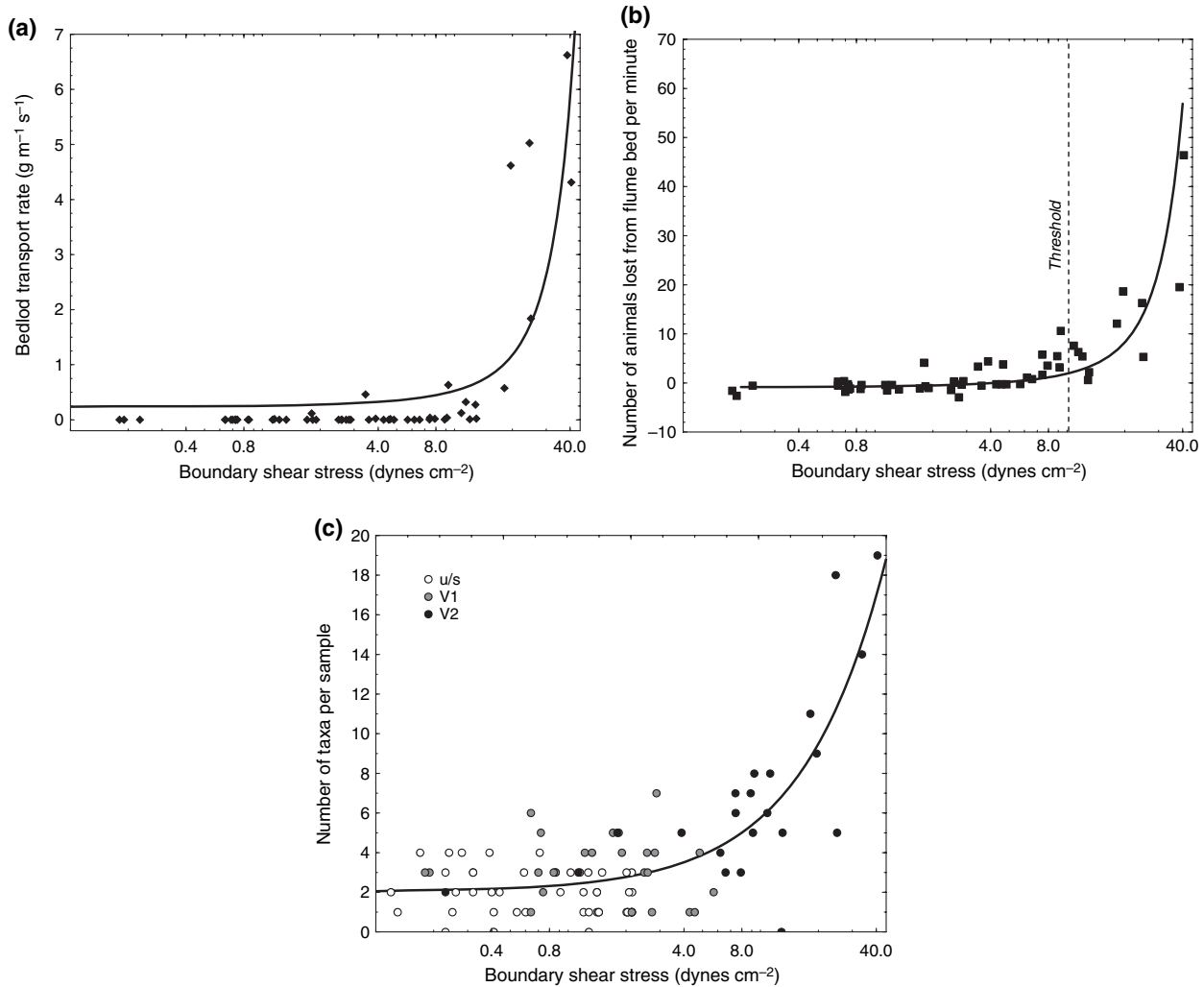


Fig. 5 Relations between the shear stress and (a) bedload transport rate, (b) number of animals lost from the streambed and (c) the number and taxon richness of the drift. In each case, exponentials proved to be the best fit to the data. For shear stress versus bedload transport, the equation is: bedload transport rate = $0.235 \times e^{0.08 \times \text{shear}}$; r^2 0.67; $P < 0.0001$. The equation for the line fitted to the relation between shear stress and loss of animals from the bed is: number lost from the bed = $(2.12 \times e^{0.08 \times \text{shear}}) - 3$; $r^2 = 0.51$; $P < 0.0001$; note that the -3 relates to the constant of 3 added to the dependent variable to remove negative values (see Methods for further explanation). The vertical line shown on (b) is the threshold identified using spline analysis. The equation for the line fitted to the shear stress versus taxon richness data is: number of taxa = $2.021 + (0.373 \times \text{shear})$; $r^2 = 0.39$; $P < 0.0001$.

from the bed data overall (Fig. 5b). Spline analysis indicated that the breakpoint in this relation occurred at a value between 8.88 and 9.13 dynes cm^{-2} ; greater precision is not possible because of the lack of sample observations between these values. Thus, data indicate that invertebrate drift began to increase at a greater rate once shear stress reached a value of approximately 9 dynes cm^{-2} . This is coincident with the point above which bedload was consistently recorded (bedload was recorded in all manipulations where shear stress exceeded 9 dynes cm^{-2} but only seven (16%) of those where shear stress was < 9

dynes cm^{-2}). At shear stresses < 9 dynes cm^{-2} in the Ribera Salada, the average loss of animals from the bed was equivalent to a drift rate of 16 individuals $\text{m}^{-2} \text{min}^{-1}$. Above 9 dynes cm^{-2} rates increased to an average of 139 $\text{m}^{-2} \text{min}^{-1}$ and reached a maximum of 575 $\text{m}^{-2} \text{min}^{-1}$. Drift densities below the threshold averaged 0.2 m^{-3} , while above the threshold the average was 1.3 and the maximum 3.5 m^{-3} .

Between shear stress values of 0.18 (the lowest recorded in the flume) and the 9 dynes cm^{-2} threshold, the line fitted to the invertebrate loss data is almost horizontal and close to zero. Seven data points

within this low shear stress range sit above the fitted line, indicating drift losses higher than represented the general trend. In each of these cases there was also a small amount of bedload transport. The presence of bedload probably reflects the small size of the material in these particular patches, relative to that in the patches overall; these finer materials would be entrained at low shear stress values relative to the general trend represented by the fitted line.

As shear stress increased and bedload transport was initiated, the number of taxa present in the drift increased (Fig. 5c). The discrimination of the u/s, V1 and V2 samples indicates that the hydraulic manipulations produced the highest shear and taxon richness values. In the absence of bedload, on average 11% of the taxa found in the benthic samples from the reach were present in the drift samples. In those manipulations where bedload transport occurred, on average 37% of the taxa present in the benthos were found in the drift.

Drift and benthic samples formed distinct groups across the NMDS ordination (Fig. 6). Four *a priori*

groups of samples [(i) benthos; (ii) u/s and V1; (iii) V2 where shear stress < 9 dynes cm^{-2} and (iv) V2 where shear stress > 9 dynes cm^{-2}] proved to be significantly differentiated across the ordination space (MRPP test statistic = -34.3 ; observed $\delta = 0.62$; expected $\delta = 0.77$; $P < 0.0001$). The composition and relative abundance of the drift in samples from the u/s and V1 manipulations differed most from benthos (groups at opposite ends of axis 1). The V2 samples occupied an intermediate position with respect to axis 1, but these subdivided [groups (iii) and (iv)] in a way that reflected shear stress and the presence of bedload. The polygon representing the high shear stress drift samples was closest to (and overlapped with) that of the benthic samples, indicating that during these manipulations the composition of the drift was very similar to that of the benthos. The apparent outlier positions of a number of the samples can be explained by their taxonomic composition. Samples labelled A, B and C are unusual in that they contained no *Baetis*, while the position of the sample coded D can be

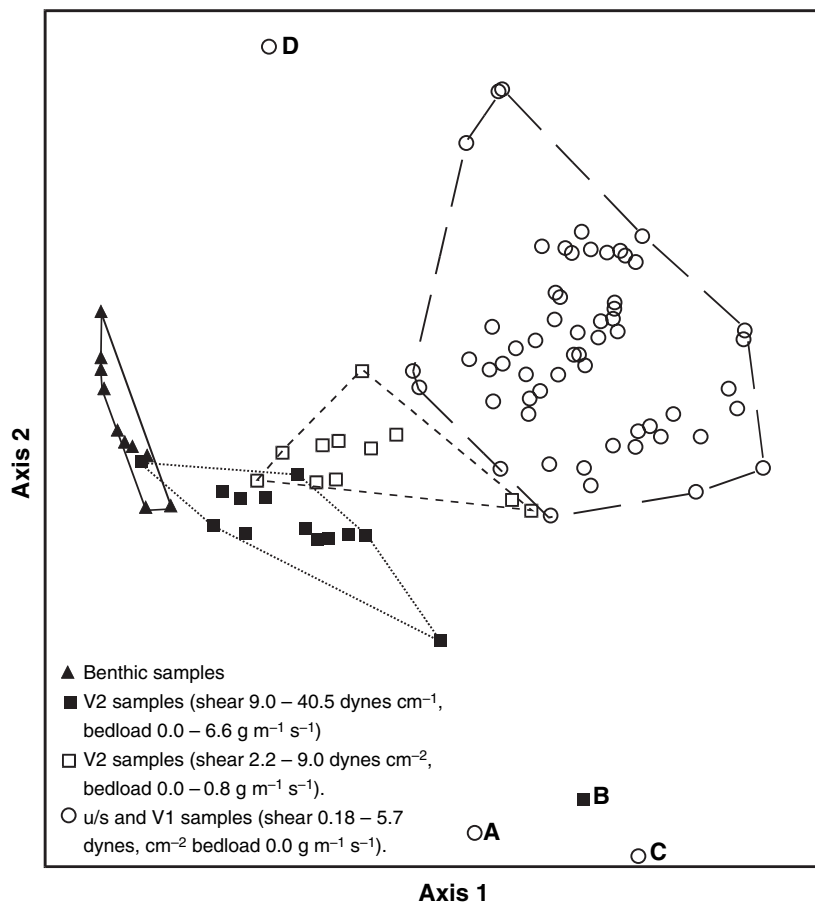


Fig. 6 Non-metric multidimensional scaling (NMDS) ordination of drift and benthic samples. Final stress value for the 2-D solution is 0.19. Samples are coded according to pre-defined groups: V1 and u/s samples are from unmanipulated conditions, while V2 samples are those in which hydraulics were manipulated. V2 samples are subdivided according to shear stress, with associated ranges of bedload shown. Samples labelled A–D are considered outliers; see text for discussion of these.

explained by the presence of only two animals, one of which was the rarely encountered beetle *Dupophilis* (Elmidae).

Discussion

Drift rates and densities

Floods have the potential to act as ecological disturbance events. It is now generally accepted that disturbances should be defined not by their magnitude but on the basis of whether they have a measurable impact on, or elicit a response by, the ecosystem (Resh *et al.*, 1988). An increase in invertebrate drift is one such response. The term catastrophic drift is used routinely to distinguish between the normal daily and seasonal rhythms in drift and the large-scale loss of animals observed during floods; thus, it is synonymous with disturbance. However, the processes that trigger mass entry of invertebrates into the water column remain poorly understood (Faulkner & Copp, 2001). Ours is one of the first published studies to describe the relations between shear stress, sediment transport and the loss of animals from specific patches of bed in a natural river channel. As detailed in Methods, our values of drift loss from the patches of stream bed inside the flume are estimates based on drift-in and drift-out data and so are subject to a degree of error. However, estimating loss in this way does not weaken our two main conclusions: (i) that drift increases markedly above the background rate once bedload transport begins and (ii) when bedload transport is occurring, the taxonomic composition and relative abundance of taxa in the drift are most similar to the benthic community.

Because of geographical and methodological differences, it is prudent to make only general comparisons between drift densities calculated from our flume data and those reported in other studies. In a similar sized upland river to the Ribera Salada (channel width 5–10 m), Gibbins *et al.* (2004) reported daytime drift densities of 0.1–0.8 individuals m^{-3} during stable, low-flow conditions. Drift densities in our V1 manipulations ($<0.5 \text{ m}^{-3}$) therefore fall within the lower range reported in this and other studies (see Table 7.1 in Giller & Malmqvist, 1998). This suggests that without manipulation of hydraulic conditions, drift densities in the flume equate to natural, daytime

(background) drift. This conclusion is supported by the curve fitted to the shear stress versus drift loss data, where the loss of animals from the stream bed was close to zero at all shear stress values $<9 \text{ dynes cm}^{-2}$. The spline analysis indicated that the slope of the drift loss curve increased once shear stress exceeded 9 dynes cm^{-2} and sediment was mobilized. Moreover, NMDS ordination and MRPP analysis indicated that drift samples collected under conditions of bedload movement were significantly different to those collected when sediment in patches remained stable. Data therefore allow us to discuss changes in quantitative (rates) and qualitative (taxonomic composition and relative abundance) characteristics of the drift associated with changes in bed stability, changes which have previously been used to define catastrophic drift (Brittain & Eikeland, 1988).

Floods, bed stability and benthic invertebrate assemblages

Floods are fundamental for the maintenance and periodic restructuring of river channel form, and hence are important in the basic geomorphic functioning of fluvial systems. Matthaei, Peacock & Townsend (1999) found that high flows resulted in a complex mosaic pattern of sediment movement within their study reaches, with some locations experiencing scour, some experiencing fill and others remaining undisturbed by floods. This is consistent with the results of other studies which have reported patch-specific geomorphic impacts of floods (Hassan, 1990; Laronne *et al.*, 1994). Effenberger *et al.* (2006) found that the stability or instability of individual patches of stream bed had an important long-term effect on invertebrates and that flood disturbance history was more important than local habitat parameters in driving patch invertebrate density. Stable clusters of relatively large sediment clasts (so-called microform bed clusters) have been argued to be important refugia for invertebrates, as well as offering a more diverse habitat for colonization and better food resources than less stable individual stones (Biggs *et al.*, 1997). These factors are thought to contribute to the increased invertebrate density which has been reported around stable bed clusters (Scarsbrook, Kelly & Francoeur, 1996). The lower density of invertebrates associated with less stable areas of stream bed may be further reduced during periods of high flow which

mobilize sediment and result in a loss of animals through drift (though of course recolonization by invertebrates may mean that these reductions are transient). Thus, the reach-scale impacts of a flood will depend on the relative availability of stable and unstable areas of stream bed, as well as refugia provided by the hyporheic zone (Dole-Olivier, Marmorier & Befly, 1997) and hydraulic dead zones (Robertson, Lancaster & Hildrew, 1995).

The armour layer is a geomorphic feature that exists in most gravel-bed rivers and contributes to bed stability. The armour is made up of coarse surface material which protects the finer material below. In the study reach, the 49 mm D_{50} of the surface material is twice as large as the subsurface D_{50} , giving an armour ratio of 2. Armoured surfaces are stable and may persist during small floods (Wilcock & DeTemple, 2005). Hence, in addition to the availability of stable bed clusters, the reach-scale impacts of a flood depend on the spatial extent of the armour layer. Exposed patches of fine material comprised around 20% of the surface area of the Ribera Salada study reach, with the remainder protected by the coarse armour layer.

At bankfull discharge ($10 \text{ m}^3 \text{ s}^{-1}$) the armour layer in the study reach completely breaks up (Batalla *et al.*, 2005). Events of this magnitude are infrequent, being equalled or exceeded <1% of the time (Q_1). Once the armoured layer breaks up, the river bed becomes unstable at the reach scale, with bedload transport rates and sizes of mobilized material much greater than created by the flume manipulations (Batalla *et al.*, 2005). However, our data indicate that relatively large numbers of individuals and taxa can be lost from the bed at shear stresses that are only capable of mobilizing fine material from the patches.

When bedload transport occurs at low rates ($<10 \text{ g m}^{-1} \text{ s}^{-1}$) in gravel bed rivers it is known as partial bedload transport (e.g. Wilcock & McArdell, 1993; Church & Hassan, 2005). Thus, even the maximum bedload rate we recorded during the hydraulic manipulations ($6.6 \text{ g m}^{-1} \text{ s}^{-1}$) equates only to partial bedload transport. Moreover, almost half of the bedload rates measured during our manipulations fall below the reference transport rate adopted by Parker, Klingeman & McLean (1982) to signify the practical threshold of motion. We conclude from this that high rates of invertebrate drift can occur from patches of stream bed experiencing little absolute

bedload movement, and certainly insufficient to represent the reach scale geomorphic disturbance associated with the break up of the armour layer.

Bedload transport has been recorded in the Ribera Salada at discharges $<3 \text{ m}^3 \text{ s}^{-1}$ (Batalla *et al.*, 2005). The velocities and rates of bedload transport created by the manipulations approximate those which occur during floods of around $5 \text{ m}^3 \text{ s}^{-1}$ in the study reach (e.g. that of January 2006). Events of this magnitude occur frequently (discharge exceeded *c.* 10% of the time) indicating that the patches of fine sediment regularly (on average, 30 days each year) become unstable and experience some sediment loss. In turn, this suggests that rather than being a rare occurrence associated only with the most extreme floods, episodes of mass drift from patches of fine sediment are probably occurring regularly.

Under normal flow conditions, when drift can be considered as being at the background rate, only a proportion of the taxa present in the benthos are found in the drift. Thus, the drift is qualitatively different to the benthos. Once the bed is destabilized and bedload transport begins, greater numbers of taxa and individuals will be entrained involuntarily and we might expect the drift to more closely resemble the benthos. This is supported by the NMDS and MRPP analyses of the flume data (Fig. 6). Why this marked change in drift occurred in the absence of mass bedload movement is puzzling. One possible explanation relates to the way that, as shear stress approaches the sediment entrainment threshold, sediments become unstable and begin to shake. Thus, once the entrainment threshold for small material in a patch is reached, any larger material present, while not experiencing downstream motion, is being agitated. We observed this phenomenon in the flume and it is well known from previous studies (Schumm & Stevens, 1973; Carling, Kelsey & Glaister, 1993; Garcia *et al.*, 2007). This agitation may result in invertebrates losing their hold and being thrown into the water column. In these circumstances, drift from a patch may result from a combination of sediment transport (finer material) and agitation (larger material).

Catastrophic drift

The spline analysis did not support the idea of two inflections in the drift curve, as predicted by the generalized model of Statzner *et al.* (1984). Rather,

we found a single change in the relation between shear stress and the loss of animals from the bed, coincident with the onset of bedload transport. This breakpoint represents the second inflection predicted by Statzner *et al.* (1984). In our data, the absence of a breakpoint prior to the sediment entrainment threshold probably indicates that the critical threshold for the sediment in the patches was reached before the critical threshold of the animals. The velocities required to shear individual invertebrates from stone surfaces have been determined for a number of taxa (e.g. Table 21 in Statzner, Gore & Resh, 1988) and in many cases these are appreciably higher than those required to mobilize the sands and fine gravels present in our experimental patches. In circumstances where the shear threshold of the sediment is lower than that of the animals, the inflection in drift should only occur once sediment is mobilized. This pattern occurred in the Ribera Salada. The single breakpoint model is compared schematically to that of Statzner *et al.* (1984) in Fig. 7. The comparison illustrates how the pattern of drift entry with respect to shear stress reflects sediment size characteristics.

Our manipulations lend empirical support to the hypothesis that bed instability triggers mass drift of invertebrates. Despite the quantitative and qualitative changes in flume drift once the bed became

unstable, it seems inconsistent to classify this as catastrophic, given that it is probably occurring frequently (i.e. in response to Q_{10} -sized events) and in the absence of reach-scale geomorphic disturbance. Moreover, these drift losses are probably restricted to the limited (20% of reach) patches of exposed fine material that are mobilized by small flood events. Without information on the survival or fecundity of animals entrained and carried downstream, it is not possible to say whether a given episode of drift is actually catastrophic for invertebrate populations. Thus, defining catastrophic drift simply as a marked change from the background rate, triggered by bed instability, does not deal with the ecological consequences of displacement. Until the population consequences of drift are fully understood, we suggest the term 'mass drift' is best used to describe the large increases in drift associated with periods of increased discharge.

While there is little doubt that flood events which give rise to reach-scale geomorphic change result in wholesale loss of animals (Bond & Downes, 2003), there is now much evidence that intermediate levels of hydrological disturbance can influence patchiness in benthic invertebrate density, because of their patch-specific effects (Palmer *et al.*, 1996; Effenberger *et al.*, 2006). Matthaei *et al.* (1999) monitored a number of natural flood events and found that,

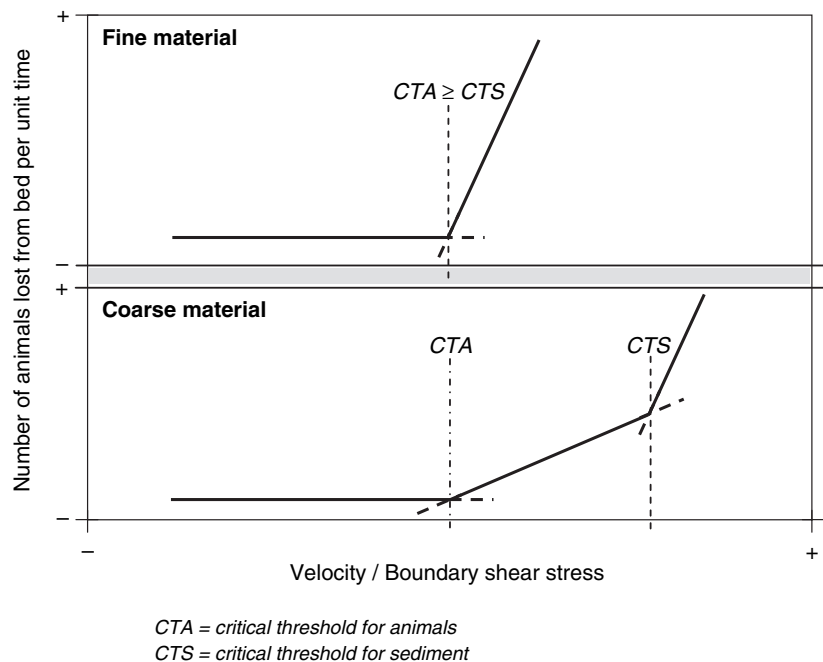


Fig. 7 Conceptual models of drift entry from locations with different sediment size characteristics. The model for coarse material (lower figure) is effectively that given by Statzner *et al.* (1984) except that entry into the water column is expressed as number of animals per unit time instead of probability of entry. The model for fine material (upper figure) represents the pattern observed in the Ribera Salada. Positions of the breakpoints with respect to velocity/shear stress and the rates of change above these breakpoints are schematic only.

even at the highest discharge surveyed ($17 \text{ m}^3 \text{ s}^{-1}$), only around 40% of sample patches experienced bed scour. This discharge resulted in shear stress estimated to be 109 Nm^{-2} (Table 4 in Matthaei *et al.*, 1999). Even allowing for differences in the method used to calculate shear stress, this is markedly higher than the maximum created by our flume manipulations (40 Nm^{-2}). While our data show that small floods which produce such relatively low shear stresses result in bedload transport and drift losses from patches of fine material, we have no empirical evidence of what is happening elsewhere in the reach. There is a need for studies assessing drift from patches of different sized bed material, where stability and scour rates may differ, as well as assessing whether animals in patches which are experiencing sediment deposition actively enter the drift to avoid being smothered.

Portable flumes offer the potential to address these issues as they permit controlled manipulation in natural river channels, free from many of the constraints which affect laboratory flume studies. However, our flume design could be improved upon. The Perspex sheet used to increase shear stress affected the vertical velocity profile such that the standard procedure for calculating point shear stress could not be used. We used a formula which has been tested and shown to be more appropriate for conditions in which nearbed velocities are high relative to those nearer the water surface (Whiting & Dietrich, 1991), as existed in the flume. While overcoming the problem created by the Perspex sheet, this formula relies on constants and bed roughness estimates (Smart, 1999). It should be possible to redesign the flume so that sufficiently high velocities could be created without the need for the Perspex, allowing shear stress to be calculated using the velocity profile. Such an improvement is worthwhile because the flume can be used to provide insights into invertebrate drift-bedload relations as well as the incipient motion of sediment, something which conventional approaches such as Helley-Smith samplers or Birkbeck-type pit traps are unable to do (Batalla *et al.*, 2007).

Acknowledgments

The authors gratefully acknowledge the Leverhulme Trust for funding the work described in this paper. Damia Vericat was employed on this project with grants

from the Catalan Foundation for Research and Innovation and Leverhulme Trust. We thank Dubrovka Pokrajac and Lorna Campbell for suggestions that helped improve the design of the flume and Carlos M. Gomez for his invaluable help with the statistical analysis. Bedload traps are operated within the framework of the SESAM project 'Sediment Export from large, Semi-Arid catchments: Measurements and Modelling' funded by the *Deutsche Forschungsgemeinschaft*. Alan Hildrew and two anonymous referees provided comments and suggestions that greatly improved the paper.

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(Manuscript accepted 13 May 2007)

Appendix

List of notations:

ρ = fluid density in kg m^{-3}

V_z = flow velocity at height d above bed in m s^{-1}

v_m = mean flow velocity at $0.4 \times$ depth in m s^{-1}

v_b = mean flow velocity at $0.2 \times$ depth in m s^{-1}

k = von Karman's constant (= 0.40)

z = height above bed in m

d = water depth in m

D_{84} = size (mm) of the D_{84} sediment

Q_{50} = median discharge in $\text{m}^3 \text{s}^{-1}$

Q_1 = discharge equalled or exceeded 1% of the time ($\text{m}^3 \text{s}^{-1}$)

Q_{10} = discharge equalled or exceeded 10% of the time ($\text{m}^3 \text{s}^{-1}$)

D_{50-s} = median surface material in mm

D_{50-ss} = median subsurface material in mm.