ORIGINAL PAPER

Short-term responses of macroinvertebrate drift following experimental sediment flushing in a Japanese headwater channel

Takashi Gomi · Sohei Kobayashi · Junjiro N. Negishi · Fumitoshi Imaizumi

Abstract We examined short-term responses of macroinvertebrate drift associated with experimental sediment flushing in a headwater. Increases in the drifting abundances of Ephemeroptera and Plecoptera coincided with increases in bed load yield rather than peaks in discharge or suspended sediment concentrations. The approach and arrival of a sediment wave may provide a physical cue that initiates the escape of benthic macroinvertebrates. Because fine bed load sediments, with diameters <4 mm, tended to accumulate on and in the substrate matrix, such sedimentation affected the benthic macroinvertebrates residing on and in the substrate, increasing the number of macroinvertebrates in the drift. Therefore, the decreases observed in the densities of most macroinvertebrate taxa following sediment flushing were probably associated with sediment deposition and the resulting escape of macroinvertebrates from benthic habitats. The magnitudes of the decreases in macroinvertebrate density were lower at sites located 200 m downstream from the sediment sources than at sites located 20 m downstream. The results from this experimental flushing study suggest that bed load movement and resulting sediment accumulation alter macroinvertebrate drift patterns and cause decreases in the abundances of benthic macroinvertebrates in headwater streams.

Keywords Sediment flushing · Macroinvertebrate drift · Bed load sediment · Suspended sediment · Sediment accumulation · Headwater channel

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Introduction

Channel morphology and benthic communities are affected by episodic sediment supply. Episodic sediment releases to channels in mountain watersheds are typically associated with sediment flushing at dams, dam removal, mining, and forestry activities (Cline et al. 1982; Lamberti et al. 1991; Water 1995). Mass movements and bank failures are natural episodic sediment events, and such sediments directly enter stream channels (Gomi et al. 2002; Imaizumi and Sidle 2007). When sediment supply overwhelms transport capacity, sediment particles tend to be deposited on the channel bed (Montgomery and Buffington 1997; Imaizumi et al. 2009). Excess sediment supply can fill in pools in pool-riffle and step-pool channels (Lisle 1982; Lisle and Hilton 1992). Surface and subsurface conditions, such as the particle size distribution and channel roughness (e.g., smoothness), can also be altered by sediment events

(Nuttall 1972; Water 1995). The deposition of fine sediments on streambeds can reduce pore water flux and the overall rate of surface and subsurface exchanges (Packman and MacKay 2003).

Changes in suspended and bed load sediment yields associated with increases in sediment supply are among the most pervasive factors structuring benthic communities. High sediment deposition due to high suspended and bed load concentration reduce habitat availability for benthic macroinvertebrates (Nuttall 1972; Wood and Armitage 1997; Angradi 1999; Bond and Downes 2003; Rabeni et al. 2005; Matthaei et al. 2006; Molinos and Donohie 2009). Moving sediment particles can destroy the surface layer of stream bed (Culp et al. 1986; Ciesielka and Bailey 2001; Schofield et al. 2004). Accumulation of bed load and suspended sediment in hyporheic zones can reduce current velocity and dissolved oxygen levels, which are essential for stream benthos (Richards and Bacon 1994; Brunke 1999).

Macroinvertebrate drift is one of the important responses by which aquatic invertebrates persist through disturbances such as high flow conditions and sediment transport (Allan 1994; Kobayashi et al. 2010). Both laboratory experiments and field monitoring have shown increases in macroinvertebrate drift in response to changes in flow conditions, the concentration of suspended sediments, and the bed load transport rate (Rosenberg and Wiens 1978; Culp et al. 1986; Imbert and Perry 2000; Suren and Jowett 2001; Gibbins et al. 2007; Molinos and Donohie 2009). Responses of stream biota, such as the abundance of macroinvertebrate drift, to changes in specific physical conditions can be sensitive to the timing of sediment movement (Lancaster 1999; Shaw and Richardson 2001). However, observations of macroinvertebrate drift after sediment additions have generally been conducted with hourly to daily increments at the finest scale, particularly during field investigations (e.g., Culp et al. 1986; Schofield et al. 2004). Because pulses in sediment movement and processes related to catastrophic sediment accumulation occur at the scale of seconds to minutes (Thomas 1988; Ergenzinger et al. 1994), the typical observation time intervals cannot capture the potential responses of macroinvertebrate drift following sediment pulses. Sediment transport regimes after sediment input can vary temporally, depending on the specific size class (Lisle et al. 2001).
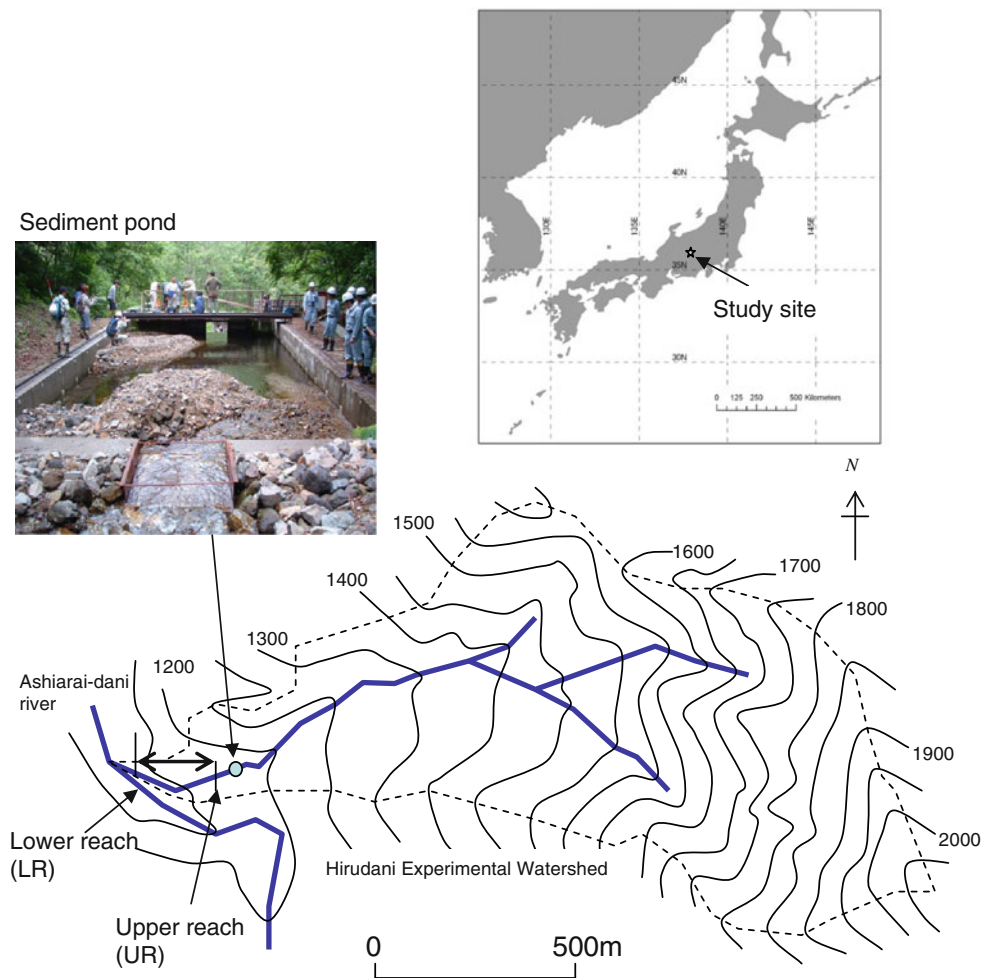
To identify the mechanisms by which specific sediment movements affect benthic communities and habitats, it is essential that we understand the processes, and the timing of those processes, that lead invertebrates to enter the water column in response to sediment movement. We conducted experimental sediment releases from a check dam, flushing water and sediments in a mountainous watershed in Japan. We examined short-term responses of flow conditions,

sediment transport, and macroinvertebrate drift to episodic experimental sediment flushes from a dam pond in a headwater stream. Our experimental flushing provided sediment at relatively large scales compared to previous sediment additions (Lanet et al. 1981; Culp et al. 1986; Bond and Downes 2003; Matthaei et al. 2006). Therefore, the channel reach of a segment downstream of the dam was appropriate for observing changes in sediment accumulation, substrate condition, and habitat use by benthic invertebrates. We also examined changes in substrate condition and the pre- and post-flushing benthic macroinvertebrate community. We hypothesized that: (1) bed load sediment movement would have a more detectable impact on benthic invertebrates and drift compared to flow conditions (e.g., flow peak) and suspended sediment yield; and (2) impacts on benthic invertebrates would differ with distance from the sediment source, depending on the propagation of the sediment wave.

Study area

This study was conducted in the Hirudani Experimental Watershed (137°35′E; 36°16′N; 0.85 km²) located in the Zintsu river system, central Japan (Fig. 1). The elevation of the experimental watershed ranges from 1165 m above sea level (a.s.l.) at the junction of the Ashiarai Valley, a tributary of the Zintsu River at the western portion of the watershed, to 2085 m a.s.l. at the southeast end of the watershed (Fig. 1). The upper half of the watershed (the area higher than 1600 m a.s.l.) is comprised of Carboniferous and Permian slate, while the lower half is underlain by Mesozoic granite porphyry and quartz porphyry. Small landslides and exposed mineral soils at the northern end are the major sediment sources in the watershed. Freeze–thaw dynamics and subsequent dry gravel occur in early winter and late spring. Average annual rainfall at the Hirudani Experimental Watershed is approximately 2300 mm, and snow accounts for 20% of the annual precipitation. The entire watershed is covered by snow (mean snow depth >50 cm) from December to March. Snowmelt from April to the beginning of June causes high flows.

The check dam for measuring sediment transport and runoff was constructed in 1966 and is located approximately 200 m upstream from the junction of the Hirudani Watershed and the Ashiarai River. Investigations of bed load transport and suspended sediment concentrations have been conducted using this facility (Ashida et al. 1975). Significant amounts of bed load sediment yield typically occur during peak discharges that exceed $0.15 \ m^3 \ s^{-1}$ (Ashida et al. 1975). All bed load sediments are captured in the pond behind the dam. Sediment that accumulates in the pond is released once a year to maintain the sediment

Sediment pond

Study site

N

1500
1600
1700
1400
1800
1300
1200
Ashiarai-dani
river

1900

2000

Lower reach
(LR)

Hirudani Experimental Watershed

Upper reach
(UR)

0   500m

storage capacity of the dam. By opening the gate of the
dam, both water and sediment are simultaneously flushed
out downstream (Imaizumi et al. 2009). The first flooding
pulse appears at a given point downstream, followed by the
pulse of suspended sediment. The pulse of bed load sedi-
ment occurs later, after the flood and suspended sediment
pulses, because of lower mobility. Several hours after the
first flush (typically 3 h after the gate is opened), the gate is
closed for a second flush. In this study, we focused on
biotic and abiotic responses within the stream ecosystem
during the first flush.

The channel gradient for the stretch from downstream of
the culvert to the river junction is approximately 9.0°,
which is within the gradient range that step-pool sequences
typically form (Fig. 2; Montgomery and Buffington 1997).
A small paved road is located 20 m from the dam; a culvert
(1 m in diameter) crosses under the road and drains into the
upstream water. We set the upstream end of the study
section at a point 10 m downstream of the culvert outlet to
avoid the effects of the culvert on sediment transport pro-
cesses. The first 30 m of the study section were designated
the upper reach (UR). Three steps and three pools were

identified in the UR by field surveys (Fig. 2). Riffles were
the dominant bed form within the UR. The second 30-m
monitoring reach was located at the downstream end of the
section (approximately 200 m downstream of the culvert),
and was referred to as the lower reach (LR).

Methodology

Experimental flushing and field measurements

Sediment flushing was conducted on 17 June 2005. Flow
discharge remained stable (base flow conditions) before the
experiment; the last heavy rainfall (total rainfall >10 mm)
in the Hirudani Watershed had occurred on 5 June 2005.
The gate of the dam was opened at 11:02, and sediment
was evacuated by impounded water flowing out of the
gate. We manually shoveled out sediment soon after
opening the gate to accelerate the evacuation of sediment
from the dam. The gate was closed at 11:55 to reserve
water for the next sediment flushing. Water height was
measured within the UR using a capacitive water level
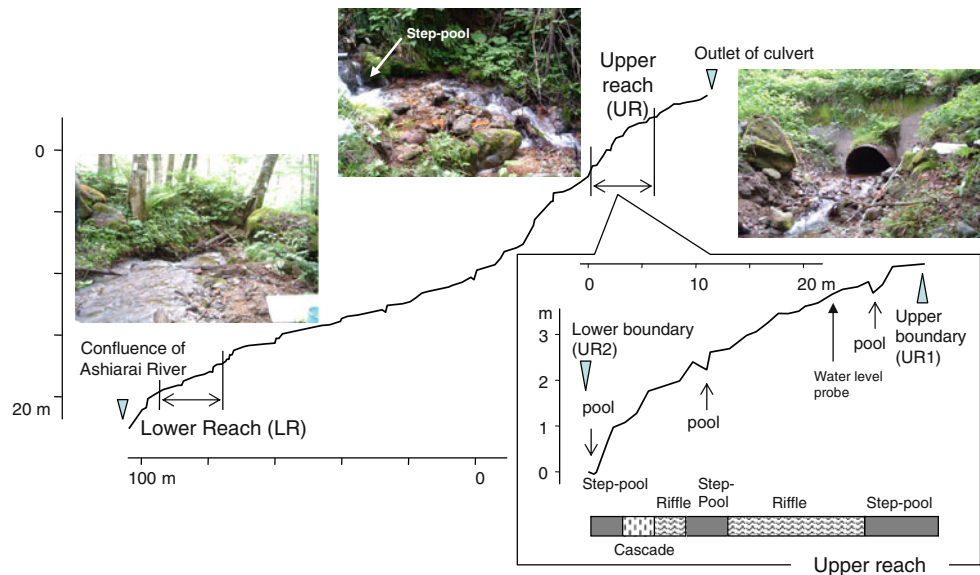
probe (Trutrack, WT-HR) with a measurement range of 0.5 m (accurate to within 5 mm) at intervals of 30 s. Detailed information for discharge estimation from the stage gauge was provided by Imaizumi et al. (2009).

After opening the gate, we began collecting bed load sediment (>1 mm in diameter), suspended sediment (<1 mm in diameter), drift macroinvertebrates, and transported organic matter. Bed load sediment was sampled using two Helley–Smith samplers (7.8 cm opening width, 0.5 mm sampling bag mesh) at the upper (UR1) and lower (UR2) boundaries of the UR (Fig. 2). Bed load samplers were located in the middle of the flow at UR1 and UR2. The sampling interval was approximately 1–2 min, starting shortly after the dam was opened; the interval was increased to 5 min after 11:30 when the discharge volume tapered to a steady-state condition. Sampling was paused at 13:10, prior to the second flush. We assumed that the bed load sediment consisted of particles larger than sand (>1 mm in diameter), because particles smaller than 1 mm are likely to be carried in suspension during rough and turbulent flow conditions in steep channels (Gomi and Sidle 2003). The bed load transport rate of the Helley–Smith samplers was calculated from the dry weight of the sampled sediment by dividing by the duration of the sampling event (30 s on average) (Imaizumi et al. 2009). Bed load transport values were multiplied by the ratio between the channel cross-sectional width (which changed over time) and the width of the sampler (7.8 cm) to estimate the amount of bed load across the entire channel width. Although the sampling efficiency of the Helley-Smith samplers was biased towards large sediment particles (Vericat et al. 2006), we assumed that bed load sediments with diameters smaller than 39 mm (half the size of the sampler intake) were accurately collected,

especially during low flow conditions with high sediment concentrations.

Macroinvertebrate drift captured by the Helley–Smith sampler was separated by hand from the bed load samples at site UR2 1 day after sampling. We did not use drift nets, which are typically used to sample macroinvertebrate drift, because drift nets were considered ineffective for sampling drift individuals during the period of high bed load yield. Individual macroinvertebrates were preserved in 5% formalin, and only individuals with body sizes >1 mm were examined in this study. The number of macroinvertebrates in the drift was multiplied by the ratio between channel cross-sectional width, which changed over time, and the width of the sampler (7.8 cm) in order to estimate the number of macroinvertebrates that drifted across the entire channel width.

Suspended sediment was collected using grab water sampling with 1000 mL bottles at a site 3 m upstream from UR2. The sampling interval was determined arbitrarily based on changes in flow discharge and concentration, and typically ranged between 1 and 5 min. Grab samples contained only sediments finer than 1 mm, based on field and laboratory observations. Total suspended solids (TSS) were determined by passing a known volume of stream water through a glass fiber filter with an effective retention of 1.2 μm; filters were oven-dried at 100°C, and the residual sediment was weighed. Suspended sediment (SS), the mineral portion of the sample, was weighed after the TSS sample had been burned at 550°C for approximately 2 h.

At the same location where the suspended sediment sampling was performed, organic matter was measured based on 80 L of surface water (sampled twice using a 40 L bucket) and a 0.25 mm mesh Nytex screen. The sampling

interval for organic matter ranged from 1 to 5 min. A known volume of water was sampled using a bucket during the experiment. All organic matter retained on the screen was brought back to the laboratory. The samples were further filtered through nested 0.25, 1, 8, and 16 mm sieves to classify the size of the organic matter. Inorganic material and macroinvertebrates found on the sieves were hand-picked and removed from the samples. The organic matter was dried for 48 h at 60°C to a constant mass, and then each size class was weighed.

Pre- and post-sediment flushing

Bed surface materials (depth <10 cm) in the UR and LR were sampled 1 day before and 1 day after the sediment flushing on 17 June 2005 to clarify any changes in the grain-size distribution. Large cobble and boulder components of >0.2 m (framework particles of the channel steps and cascades; after Grant et al. 1990 and Gomi and Sidle 2003) were excluded because of their relative immobility except during landslide and debris flow events. Four sediment samples were collected at various depths in the sediment pond. The grain size distribution in the sediment deposited in the pond was analyzed using sieves with mesh sizes of 1, 2, 4, 8, 16, and 32 mm. A detailed longitudinal profile of the channel reach downstream from the culvert was surveyed using an engineering level before the first flush.

Sediment accumulation and filling on the channel bed matrix was examined based on bed surface materials collected at the UR and LR. To estimate excess sediment deposits after sediment flushing, we used the particle size distribution of the stream substrate sampled before and after flushing. Firstly, based on bed load data from the Helley–Smith sampler, we identified the diameter class of the maximum mobile sediment (d_n) during the experiment. Maximum mobile sediment referred to the maximum diameter class of bed load sediment. The bed sediment size class greater than d_n remained the same before and after sediment flushing. Thus, we could assume that the proportion of substrate particles greater than d_n (nth class of sediment) was identical in the pre- ($^{pre}d_n$) and post- ($^{post}d_n$) flush samples. Second, we estimated the standardized sediment mass of the post-flush samples for the ith size class ($^{post}d_i^*$) based on the following equation:

$$^{post}d_i^* = {}^{post}d_i \times \frac{^{pre}d_n}{^{post}d_n}. \tag{1}$$

For each ith size class, we also estimated the rate of change of the percentile of the particle size distribution by dividing the standardized sediment mass post-flush by the pre-flush percentile of the particle size. Estimated ratios of greater than 100% indicated the percentage of the substrate

matrix on which sediment had accumulated after sediment flushing.

Benthic macroinvertebrates within the UR and LR were sampled both the day before and the day after sediment flushing. Four replicated samples were collected at randomly selected riffle locations within each study reach. A Surber sampler with a 900 cm^2 frame and a 0.25 mm mesh net was used for sampling. We disturbed the substrate to approximately 10 cm in depth to ensure we were sampling both the surface and the subsurface of the channel bed. Samples were preserved in 5% formalin in the field. In the laboratory, the samples were rinsed on a 1 mm sieve, and any macroinvertebrates retained on the sieve were sorted, enumerated, and identified to genus level.

Two-way analysis of variance (ANOVA) was conducted to examine changes in the number of benthic invertebrates because of the experimental flushing, using periods (pre- and post-flush) and reaches (UR and LR) as the main factors. Invertebrate counts were log-transformed before analysis to improve normality and homogeneity of variances.

Results

Flushing water and sediment

The discharge level in the UR increased shortly after the dam gate was opened at 11:00 and decreased gradually, with occasional surges, after peaking at 11:04 (0.15 m^3 s^{-1}). By 11:30, the discharge had subsided to a level similar to that recorded prior to the experiment and it then remained at the pre-flush condition (Fig. 3). We could not record the discharge level after 12:04 because sediment aggradations prevented the water level probe from functioning properly. Based on our field observations, after the cessation of discharge recording, the discharge level attained a steady state. The peak suspended sediment concentration occurred 15 min after the peak stream flow, whereas the peak level of particulate organic matter (POM) transport occurred 45 min after the dam gate was opened, after which the level of the bed load yield peaked (Fig. 3). POM ranging from 0.25 to 8 mm was present at a greater concentration than coarser POM.

Most of the released sediment was deposited immediately below the dam to 0.5 m in depth. Some sediment was transported farther downstream, passing through the culvert and reaching the UR. The propagation of sediment to the LR was lower than to the UR. Sediment particles in the sediment pond ranged from silt to gravel. The maximum particle size class in the pond was 31.5–63.0 mm. The 50th percentile of particle size (D_{50}) was 8.0 mm. The maximum size class for bed load sediments captured at the
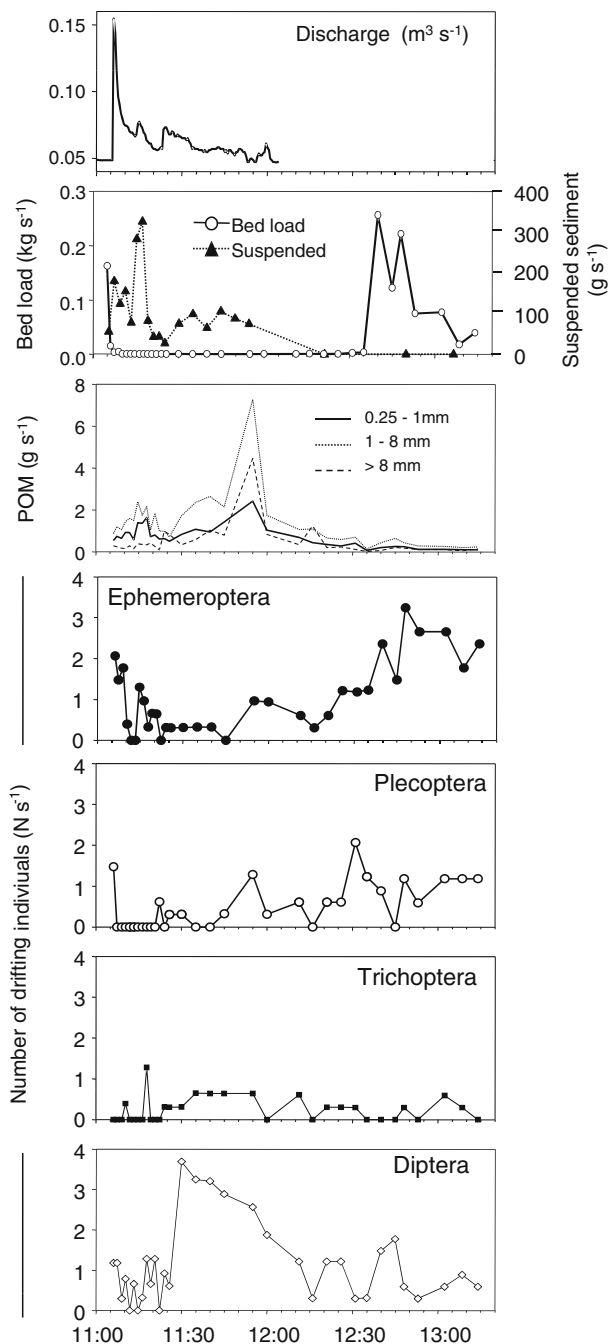
Fig. 3 Changes in discharge, sediment transport, organic matter, and macroinvertebrate drift throughout the sediment flushing experiment. Bedload sediment was defined as particles >1 mm. Responses of macroinvertebrate drift are shown using order level classification. The bed load sediment transport shown in the figure was estimated at site UR2

upper boundary of the UR (UR1) was 16.0–31.5 mm. Sediment particles transported to the UR were smaller than 31.5 mm; presumably, the size classes of >31.5 mm were deposited between the downstream end of the dam and upstream of the culvert.

Responses of sediment transport and macroinvertebrate drift

A small bed load peak was observed within 10 min after the dam was opened, corresponding to the discharge peak (Fig. 3). The bed load transport rate recorded at UR2 decreased rapidly after the peak discharge. The bed load transport rates at 11:06 were less than 0.16 kg s^{-1}. At UR2, no clear change in bed load transport rate occurred until 12:35. The peak bed load transport rate was observed at 12:40, reaching 0.232 kg s^{-1} for all grain sizes (Fig. 3). This bed load peak was associated with the migration of the sediment wave.

Comparing the bed load sediments captured at UR1 and UR2, the total bed load transport rate was lower at UR2 than at UR1, indicating that sediments of all grain size fractions were deposited in the 30 m channel section between these sites (Fig. 6; also see Imaizumi et al. 2009). The ratio of deposition was greatest for the 1–2 mm size class (80%) followed by the 2–4 mm size class. The 16–32 mm size class made up only a small portion of the combined bed load samples; it is possible that all of this material was deposited within the study section.

Numerically dominant drift macroinvertebrate taxonomic groups included Ephemeroptera (36.7%), Plecoptera (16.9%), Trichoptera (8.0%), and Diptera (38.3%; Fig. 3). We did not identify specific genera within the taxonomic groups because only small numbers of individuals were captured for each genus or family. Based on our field observations, *Drunella*, *Baetis*, *Baetiella*, and *Epeorus* were dominant among the Ephemeroptera. Dominant Plecoptera included *Protonemura*, Chloroperlidae, and *Calineuria*. *Lepidostoma* and *Rhyacophila* were dominant Trichoptera. The dominant Diptera were Chironominae. The peak abundance of drift Diptera occurred 30 min after the dam gate was opened (Fig. 3). The abundance of Trichoptera was low and consistent throughout the experiment. The numbers of drift Ephemeroptera and Plecoptera increased toward the end of monitoring, with peak abundances occurring approximately 1.5 h after the gate was opened, although the stream flow reached a steady state condition after 12:00 (Fig. 3). High abundances of drift Ephemeroptera and Plecoptera occurred slightly before the bed load transport rate increased (Fig. 3).

Substrate particle size distribution

Pond sediments were finer than the bed surface materials sampled at the UR and LR before the flushing (Fig. 4a). Bed surface materials at both the UR and LR after flushing were finer than those before flushing. The 50th percentile of the pre-flush particle size distribution (D_{50}) from the UR and LR was approximately 30–40 mm, whereas D_{50} in the

post-flush samples was 10–20 mm. The UR was directly affected by the sediment wave, whereas the sediment wave did not completely reach the LR.

Substrate fining was more pronounced at the UR, which was reached by the sediment wave, than the LR. Because the bed load sediment consisted of particles smaller than 31.5 mm, we assumed that the proportion of the substrate particles with sizes ranging from 31.5 to 63 mm was consistent between pre- and post-flush samples. Based on Eq. 1, the total standardized sediment from post-flush substrate samples became 269 and 164% at the UR and LR, respectively (Fig. 4b). This implies that additional sedimentation occurred over 269 and 164% of the bed substrate matrix during post-flush conditions at the UR and LR, respectively. According to Eq. 1, the amounts of substrate sediment for sizes ranging from 1 to 8 mm became 5.0- to 7.0-fold greater than the pre-flush distribution at the UR (Fig. 4). The standardized particle size distribution at the LR increased 3.6- to 5.0-fold for sizes ranging from 1 to 8 mm. This comparison shows that fine particles were likely deposited on the substrate surface or filled in the

subsurface matrix as the sediment wave propagated downstream: the effect of the sediment wave on substrate fining was more pronounced at the UR than the LR.

Comparison of benthic macroinvertebrates between pre- and post-flushing

In total, 39 benthic macroinvertebrate taxa were identified in the Hirudani stream. The numbers of taxa found in the pre-flush samples were 33 and 30 in the UR and LR, respectively. In contrast, 20 and 30 taxa were found in the post-flush samples from the UR and LR, respectively. Mean total densities (±standard errors) from four replicated samples in the UR and LR were 4008 (±2004) and 3056 (±3033) individuals m^{-2}, respectively. In the post-flush samples, the mean total macroinvertebrate densities (±standard errors) in the UR and LR were reduced to 296 (±134) and 761 (±381) individuals m^{-2}, respectively, i.e., they decreased to 6.7 and 25.1% of the pre-flush means. The numerically dominant taxa in the pre-flush samples were *Protonemura* (19.3%), *Drunella* (13.0%), *Baetiella*

Fig. 4 Particle size distributions in the upper (*UR*) and lower (*LR*) reaches (**a**) and estimated rates of change of the percentiles of particle size in the UR and LR after sediment flushing (**b**). Equation 1 was applied to estimate the ratio of sediment accumulation

a Particle size distribution

b Estimated rate of changes in substrate sediment distribution
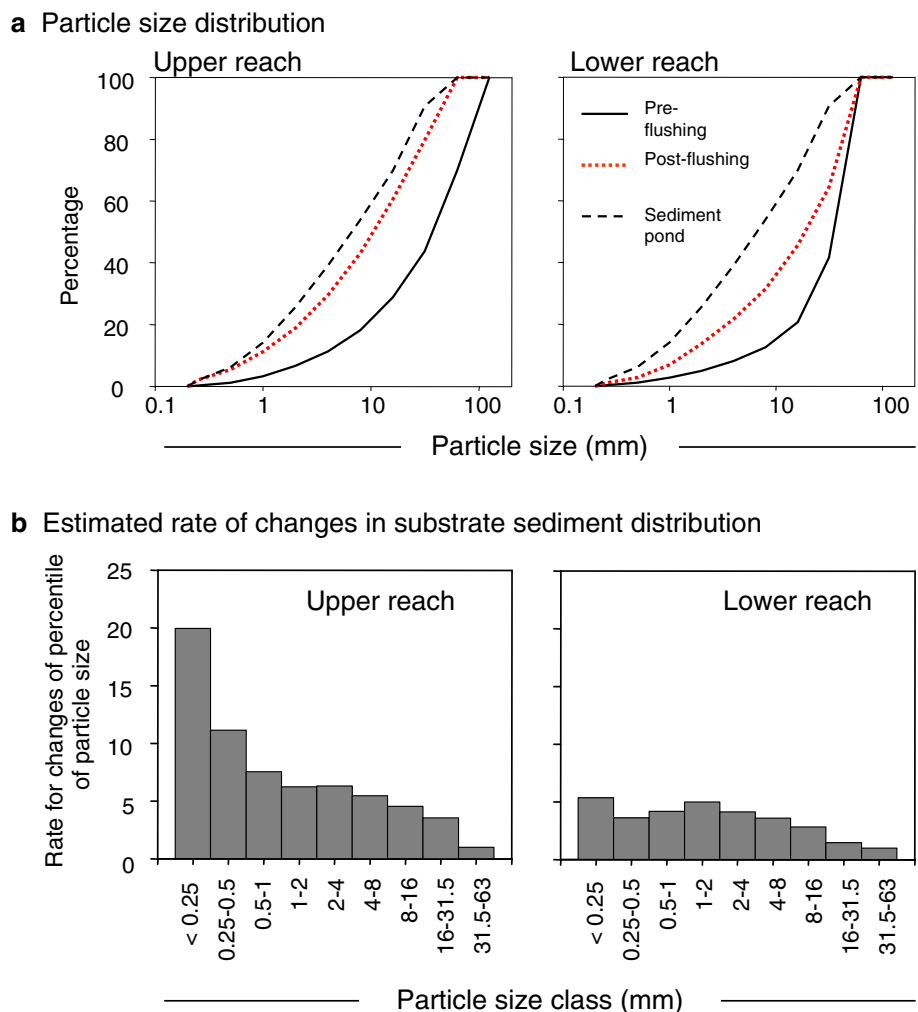
(10.1%), *Epeorus* (6.7%), and Chloroperlidae (8.1%; Fig. 5). Most of the taxa were substantially decreased after flushing ($P < 0.05$ for all dominant taxa). In the post-flush samples, the numerically dominant taxa were *Protonemura* (23.7%), *Drunella* (12.1%), *Baetiella* (11.3%), Chloroperlidae (6.5%), and *Epeorus* (4.0%; Fig. 5). Chironominae represented 4.3% of the individuals observed in the post-flush benthic samples (Fig. 5 and the "Appendix").

The decrease in benthic invertebrates was more pronounced in the UR than the LR, although macroinvertebrate densities decreased in both reaches (Table 1). Interaction effects in the two-way ANOVAs were significant for *Baetiella*, *Kogotus*, Orthocladiinae, and total invertebrates, suggesting that changes in population densities after sediment flushing differed between the UR and LR. For example, the mean density of *Baetiella* in the post-flush samples from the LR was reduced to 36.9% of the pre-flush mean density (113.9 N m^{-2}), whereas the mean density at the UR dropped to 1.8% of the pre-flush mean (8.3 N m^{-2}). Similarly, the order of magnitude of the

decreases in mean densities for *Drunella* and Chloroperidae in the post-flush samples in the LR tended to be smaller than those for the UR samples. The post-flush mean density of *Protonemura* at the UR was reduced to 26.5% of the pre-flush mean density, while the post-flush mean density of *Protonemura* at the LR was 8.5% of the pre-flush mean. On the other hand, the decreases in the densities of *Epeorus*, *Cinygmula*, and *Calineuria* were of a similar magnitude for both reaches (Fig. 5).

Discussion

Responses of sediment transport and macroinvertebrate drift to sediment flushing

Macroinvertebrate drift responded to bed load movement and resulting sediment deposition rather than high flow or high suspended sediment concentrations. Effects of stream flow on benthic macroinvertebrates were considerably
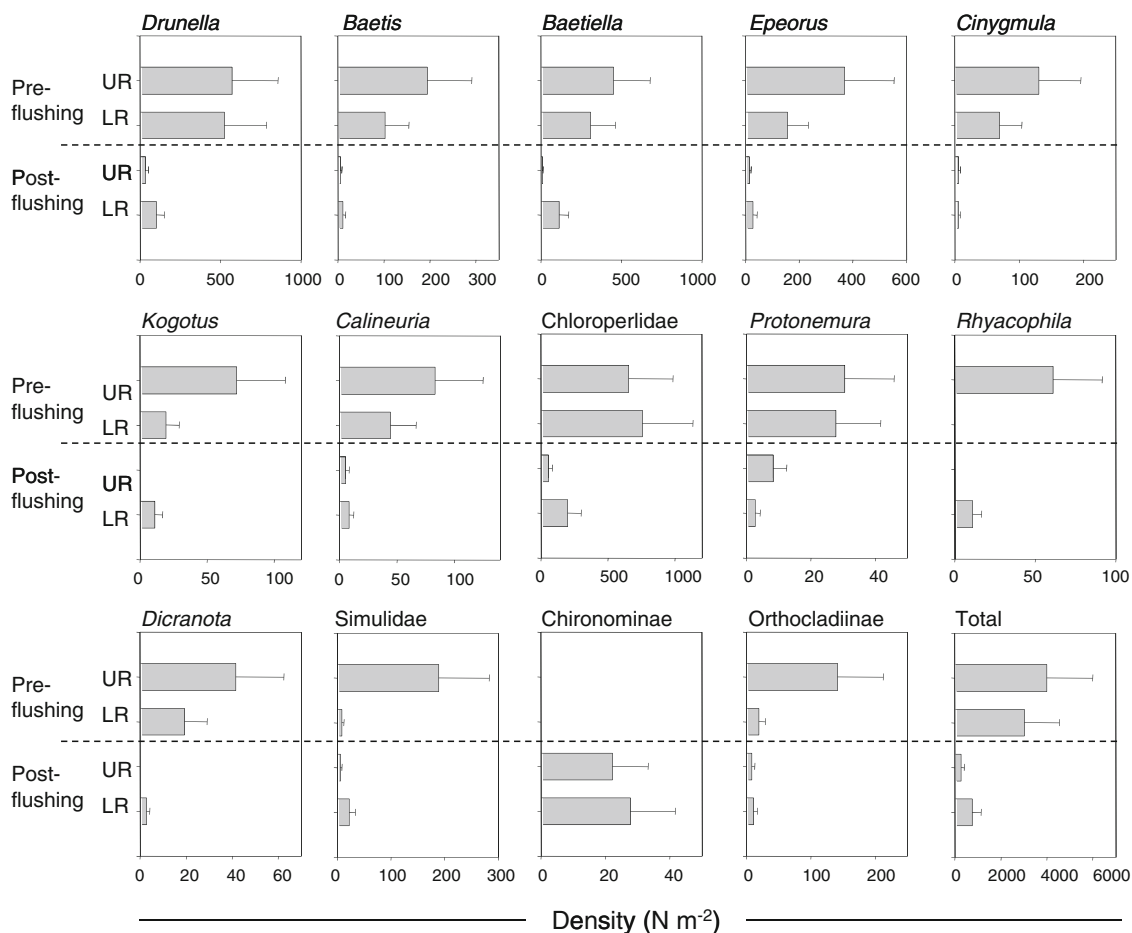

Fig. 5 Densities of macroinvertebrates in riffles (N m^{-2}) for numerically dominant taxa, and total numbers in the upper (*UR*) and lower (*LR*) reaches from pre- and post-flush samples

Table 1 Summary of two-way ANOVAs comparing benthic invertebrates between periods (pre- and post-flush) and reaches (UR and LR)

	Period effects		Reach effects		Period and reach interaction	
	F	P value	F	P value	F	P value
Drunella	**57.0**	**<0.001**	3.17	0.100	3.68	0.079
Baetis	**68.7**	**<0.001**	0.19	0.670	2.459	0.143
Baetiella	**23.8**	**<0.001**	4.377	0.058	**11.066**	**0.006**
Epeorus	**32.4**	**<0.001**	0.505	0.491	3.617	0.081
Cinygmula	**72.7**	**<0.001**	1.343	0.269	0.716	0.414
Kogotus	**10.7**	**0.007**	0.122	0.733	**5.994**	**0.031**
Calineuria	**10.0**	**0.008**	0.51	0.825	0.248	0.628
Chloroperlidae	**37.9**	**<0.001**	0.17	0.687	0.17	0.687
Protonemura	**25.0**	**<0.001**	**5.267**	**0.041**	2.2024	0.180
Rhyacophila	**8.3**	**0.014**	0.434	0.522	0.009	0.927
Dicranota	**13.0**	**0.004**	0.223	0.645	1.155	0.304
Simulidae	1.10	0.315	0.699	0.419	4.482	0.056
Chironominae	**69.3**	**<0.001**	0.148	0.708	0.148	0.708
Orthocladiinae	**9.4**	**0.010**	**5.032**	**0.045**	**7.612**	**0.017**
Total	**67.7**	**<0.001**	3.42	0.089	**7.361**	**0.019**

Significant effects at the 95% confidence level are given in bold font

smaller than sediment accumulation and did not sustain. Our results support the view that sediment accumulation from sediment wave migration induced the escape of benthic invertebrates from surface and interstitial habitats. Our monitoring showed that invertebrate drift, especially of Ephemeroptera and Plecoptera, started to increase prior to peak bed load transport (Fig. 3). These phases may be associated with the arrival of the leading edge of the sediment wave (Lisle et al. 2001; Imaizumi et al. 2009) upstream of our study point (UR2). Therefore, the drift responses were strongly associated with the movement and accumulation of sediment.

The following question still remains: why do increases in macroinvertebrates correspond to increases in bed load transport? If macroinvertebrate drift is simply associated with sediment accumulation, it is possible that increases in drift may occur during much earlier phases after sediment flushing, when sediment accumulation starts at the upper reach. The responses of macroinvertebrates to sediment movement suggested that the drifting macrovertebrates migrated only a few meters from the substrate in which they had originally resided. Thus, when the sediment wave moves downstream, the macroinvertebrates may sequentially drift downstream over relatively short distances.

Catastrophic drifting of Ephemeroptera and Plecoptera occurred in response to bed load sediment movement and accumulation rather than changes in flow conditions (Figs. 3, 7). Previous studies have reported that high flow conditions and resulting bed instability can trigger mass drifts of invertebrates (Imbert and Perry 2000; Gibbins

et al. 2005, 2007). In our experiment, the discharges created by the flushing were smaller than the discharges that are theoretically required to destroy the armor layer (Ashida et al. 1975). Thus, fine bed load movement and sediment deposition could alter the behavior of benthic invertebrates and increase the number of macroinvertebrate drifts (Molinos and Donohie 2009). Because Ephemeroptera and Plecoptera are not likely to excavate themselves from burial, as shown by Wood et al. (2005), they tend to be more responsive to increases in sediment concentration (arrival of sediment wave). On the other hand, Trichoptera such as filter feeders are more likely to be susceptible to sediment accumulation (Wood et al. 2001, 2005). Our study showed that drifting Trichoptera tended to be consistent throughout the monitoring period.

Effect of sediment accumulation on benthic macroinvertebrates

The addition of large amounts of sediment reduced the abundance and the taxonomic richness of benthic macroinvertebrates in riffles. Specifically, the abundances of species that prefer fast-flowing waters, such as *Epeorus*, Chloroperlidae, *Drunella*, and *Baetiella*, decreased significantly after the sediment wave had passed. It is likely that the responses of benthic invertebrates to sedimentation resulted from structural changes in the bed surface materials (substrate). One of the most plausible explanations for structural changes in the substrate is that interstitial spaces were buried by sedimentation that resulted from the

sediment flushing. Habitat structures are potentially buried by fine sediments because fine particles can enter the substrate matrix more easily than coarse particles can (Fig. 6). Some invertebrate taxa, such as *Drunella* and *Baetiella*, often inhabit the surfaces of stones and occupy interstitial spaces formed between or beneath large substrate particles such as pebbles and cobbles (personal observations); these taxa probably experienced habitat loss as sedimentation occurred. Reductions in channel flow velocity within the substrate matrix can reduce macroinvertebrate abundance in the hyporheic zone (Packman and MacKay 2003). The habitats of *Cinygmula* and *Epeorus*, which prefer to cling to the upper surfaces of cobble and boulders (Merritt et al. 2008), can be directly damaged by the passage of a sediment wave and sediment accumulation.

Changes in sediment accumulation along the longitudinal profile from the sediment source induced different responses of benthic invertebrates to the experimental sediment flushing. Sediment accumulation in substrates in the LR was approximately 50% less than in the UR, possibly because the entire sediment pulse had not reached the downstream reach when the benthic samples were collected (Lisle et al. 2001). Additionally, the amount of sediment within the sediment wave was substantially reduced as the wave passed through the UR and LR because of sediment deposition (Fig. 4; also see Imaizumi et al. 2009). The greatest impacts of sediment flushing on invertebrates in the UR were noted in *Baetiella*, *Kogotus* and Orthocladiinae, which showed larger decreases in abundance in the UR than in the LR. On the other hand, species that prefer living on the large surfaces of cobble and boulders, such as *Epeorus*, *Cinygmula* and *Calineuria* (Merritt et al. 2008), showed more pronounced effects and responses to the amount of sediment accumulation in both the UR and LR. This result suggests that, despite the absence of an approaching sediment wave in the LR, the intrusion of excess fine sediment into the substrate and smoothing of the substrate bed caused habitat degradation, reducing habitat availability, even in the downstream portion of our study channel.

Changes in substrate condition and invertebrate drift

Our experiment introduced a concentration of sediment into the channel that was an order of magnitude greater than that provided by natural sediment transport regimes during typical storm events in our watershed. Culp et al. (1986) showed that deposited sediments have little effect on benthic invertebrates, presumably when low quantities accumulate over a short period of time. Lanet et al. (1981) observed that the density and standing stock of benthos could be decreased, although community structure and species richness may not be affected by small sediment additions. Our extreme sediment addition under a low tractive force, a high concentration of sediment movement, and the development of a sediment veneer on the substrate modified the community structure, density, and species richness of benthic invertebrates.

Sediment accumulation in the substrate bed from the passage of the sediment wave buried substrate habitats and smoothed the bed topography. Sediment deposits were >10 cm deep in a pool located approximately 5 m downstream from UR1 (Fig. 2). Veneer deposits of sediment occurred over armored coarse bed surfaces in riffles. The total volumes of sediment that passed through UR1 and to UR2 were 698 and 201 kg, respectively (Fig. 6): 497 kg of sediment were therefore deposited within the channel reach (Fig. 6). Because the distance between UR1 and UR2 was 31.2 m and the average channel width was approximately 1 m, the mean depth of the deposited sediment was 8.6 mm, calculated from the sediment density of 2.65 t m^{-3} and a porosity of 0.7 (Imaizumi et al. 2009). Under these extreme and catastrophic sediment supply conditions with low

Fig. 6 Changes in bed load sediment yield at the upper (*UR1*) and lower (*UR2*) boundaries of the upper reach (*UR*). Sampling locations are shown in Fig. 2. The rate of sediment deposition was estimated by dividing the bed load sediment yield of UR2 by values captured at UR1 for specific particle size classes
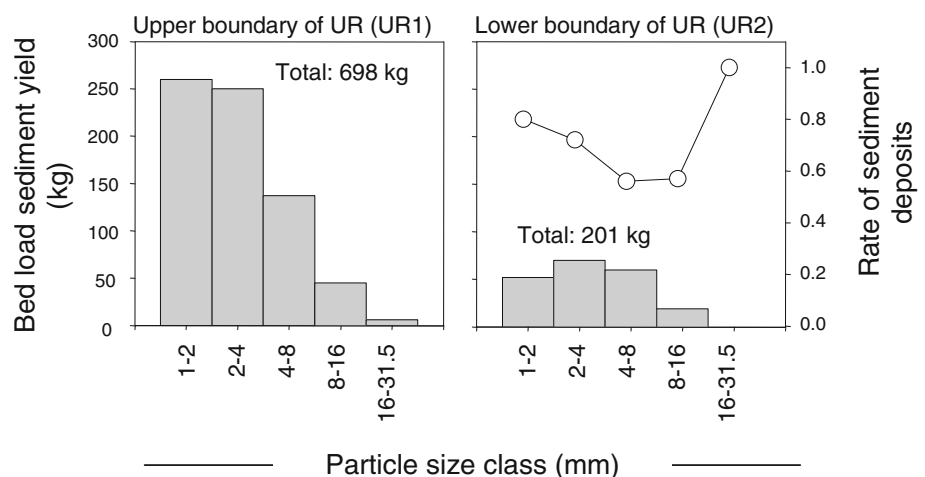
Fig. 7 Schematic illustration of sediment accumulation and short-term responses in invertebrate drift after sediments were flushed by a propagating sediment wave. **a** Sediment wave (pulse with a high bed load sediment concentration) migrates downstream. **b** The approach of the first portion of the sediment wave induces the movement of benthic macroinvertebrates such as Ephemeroptera and Plecoptera. **c** Once the bed sediments have accumulated, most of the benthic invertebrates escape from the reaches or they are buried. **d** A veneer of deposited sediment buries the substrate, and the sediment mobilizes at low hydraulic force (e.g., shear stress)

a Pre-flushing

b Arriving first bed load pulse

c Accumulation of sediment

d Veneer deposition on substrate
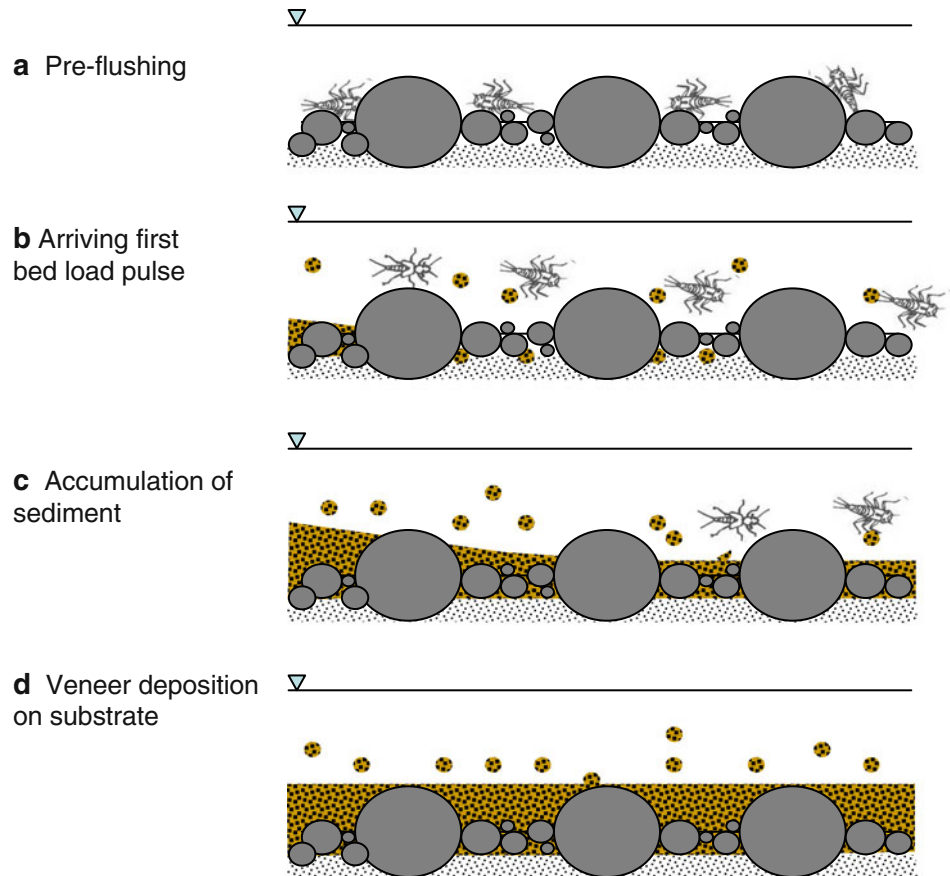
transport capacity, the surface of the channel bed became very smooth, with low roughness (Montgomery et al. 1999), although sediment deposit depth and bed surface roughness could vary spatially with channel topography.

Based on our observations of changes in bed load sediment transport, sediment accumulation, and macroinvertebrate drift, we propose the following scenario for changes in substrate conditions and short-term responses of invertebrate drift to sediment flushing (Fig. 7). (1) Once sediment is introduced into the channel, a sediment wave (a pulse with a high bed load sediment concentration) migrates downstream (Fig. 7a). (2) The leading edge of the sediment wave can provide a physical cue, stimulating the movement of benthic macroinvertebrates and benthic invertebrates, which intentionally enter the water column (active drift) to avoid accumulating sediments, as opposed to the accidental dislodging of individuals by sediment or current, especially Ephemeroptera and Plecoptera (passive drift, Fig. 7b; Allan 1994). (3) Once the bed sediment has accumulated, most of the benthic invertebrates escape from the affected reaches and the density of benthic invertebrates decreases substantially (Fig. 7c). (4) After a veneer deposit of sediment buries the substrate, the sediment mobilizes when low hydraulic forces (e.g., shear stress) act on the particles (Fig. 7d; Imaizumi et al. 2009).

While our study allowed the manipulation of a flush flood and sediment flushing, our approach may suffer from problems related to the simplification of responses of benthic invertebrates and drift. The amount of sediment added was extreme in relation to the flow volume compared to most previous studies, which added smaller amounts of sediment than those involved during natural sediment recruitment. Thus, it is difficult to replicate the experiment and validate the potential macroinvertebrate responses under similar sediment flushing conditions (e.g., catastrophic drift). Additional constraints also remain on the interpretation of the response of the macroinvertebrate drift. It is likely that seasonal and diurnal changes in drift affect the number of animals and the timing of drift during flushing experiments (Allan 1994). Investigations performed in both the field and the laboratory can provide insight into the dynamics of sediment movement and macroinvertebrate drift in mountainous gravel bed rivers.

Summary and conclusions

We examined short-term responses of macroinvertebrate drift to experimental sediment flushing in a headwater.

Peak drift abundances of Ephemeroptera and Plecoptera coincided with peak bed load yield rather than peaks in discharge or suspended sediment concentrations. The deposition of finer sediments associated with bed load transport was affected by the grain size distribution of the bed surface sediments. Because fine bed load sediments with diameters <4 mm tended to accumulate on and in the substrate matrix, such sedimentation affected benthic invertebrates and increased the number of macroinvertebrates in the drift. Therefore, the decreased densities observed for most of the macroinvertebrate taxa following sediment flushing were probably associated with sediment deposition and the resulting escape of invertebrates from benthic habitats. However, at the downstream reach that was farthest from the sediment source, the magnitude of the macroinvertebrate density decrease was smaller than that at the upstream reach. The findings of our flushing experiment suggested that bed load movement and the burial of habitats by sediment accumulation alter macroinvertebrate drift and decrease the abundance of benthic macroinvertebrates. In order to get a more comprehensive understanding of the effects of sediment flushing on stream ecosystems, it is important to elucidate the long-term effects of sedimentation and the recovery processes of benthic macroinvertebrate communities.

The conditions associated with our experimental sediment flushing are similar to those caused by excess sediment inputs from natural and anthropogenic events (e.g., reservoir sediment release) in channels (Wohl and Cenderelli 2000; Stanley et al. 2002). Our experimental conditions mimicked excess sedimentation under low tractive force and sediment deposition onto and into streambeds. Our experimental setting was also analogous to rapid sediment recruitment events in headwater catchments, such as mass movements, small bank failures and constructions. Since our study showed that sediment accumulation significantly impacted on the benthic community and drift, it could be necessary to reduce sediment accumulation related to flow conditions in order to minimize its impact and to hasten recovery. There are currently no guidelines for assessing ecological impacts after episodic sediment flushing. Therefore, the findings of this experiment in relation to episodic sediment flushing can be applied to make general predictions about the downstream short-term responses of invertebrate drift to sediment addition and its migration.

Appendix

Taxa that occurred in benthic samples in the upper (UR) and lower (LR) reaches

	Pre-flushing		Post-flushing	
	UR	LR	UR	LR
Oligochaeta	0	+	0	+
Ephemeroptera				
Paraleptophlebia	0	0	0	+
Ephemera japonica	0	0	+	+
Cincticostella nigra	0	+	0	0
Drunella basalis[a]	+	+	0	0
Drunella ishiyamana[a]	+	+	+	+
Drunella trispina[a]	+	+	0	+
Drunella sachalinensis[a]	+	+	0	0
Ameletus	+	+	0	+
Baetis	+	+	+	+
Baetiella	+	+	+	+
Epeorus	+	+	+	+
Cinygmula	+	+	+	+
Plecoptera				
Yoraperla uenoi	+	+	+	0
Stavsolus	+	+	0	0
Kogotus	+	+	0	+
Calineuria	+	+	+	+
Chloroperidae	+	+	+	+
Amphinemura	+	+	+	+
Nemoura	+	+	+	+
Protonemura	+	+	+	+
Trichoptera				
Stenopsyche	0	+	0	0
Glossosoma	+	0	+	+
Rhyacophila impar[b]	+	+	+	+
Rhyacophila towada[b]	+	+	+	0
Rhyacophila[b]	+	+	0	0
Dolophilodes	+	0	0	+
Parapsyche	+	0	0	0
Lepidostoma	+	+	0	+
Coleoptera				
Elmidae	+	0	0	0
Diptera				
Dicranota	+	+	0	+
Hexatoma	+	0	0	+
Tipulidae	0	+	0	0
Simulidae	+	+	+	+
Chironominae	0	0	+	+
Orthocladiinae	+	+	+	+
Atherix	0	0	0	+
Bezzia	0	0	0	+

Appendix continued

	Pre-flushing		Post-flushing	
	UR	LR	UR	LR
Empididae	+	+	0	0

+ Presence, 0 absence

[a] Species in *Drunella* were combined for two-way ANOVA and Fig. 5

[b] Species in *Rhyacophila* were combined for two-way ANOVA and Fig. 5

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