



RESEARCH ARTICLE

Do legacy effects of deposited fine sediment influence the ecological response of drifting invertebrates to a fine sediment pulse?

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Abstract

The deposition of excess fine sediment and clogging of benthic substrates is recognised as a global threat to ecosystem functioning and community dynamics. Legacy effects of previous sedimentation create a habitat template on which subsequent ecological responses occur, and therefore, may have a long-lasting influence on community structure. Our experimental study examined the effects of streambed colmation (representing a legacy effect of fine sediment deposition) and a suspended fine sediment pulse on macroinvertebrate drift and community dynamics. We used 12 outdoor stream mesocosms that were split into two sections of 6.2 m in length (24 mesocosm sections in total). Each mesocosm section contained a coarse bed substrate with clear bed interstices or a fine bed substrate representing a colmated streambed. After 69 days, a fine sediment pulse with three differing fine sediment treatments was applied to the stream mesocosms. Added fine sediment influenced macroinvertebrate movements by lowering benthic density and taxonomic richness and increasing drift density, taxonomic richness, and altering drift assemblages. Our study found the highest dose of sediment addition (an estimated suspended sediment concentration of 1112 mg l⁻¹) caused significant differences in benthic and drift community metrics and drift assemblages compared with the control treatment (30 l of water, no added sediment). Our results indicate a rapid response in drifting macroinvertebrates after stressor application, where ecological impairment varies with the concentration of suspended sediment. Contrary to expectations, bed substrate characteristics had no effect on macroinvertebrate behavioural responses to the fine sediment pulse.

Keywords Stream mesocosms · Colmation · Sedimentation · Bed substrate · Faunal responses

Introduction

At a global scale, many freshwater ecosystems experience increased fine sediment loadings that impact their ecological functioning and biodiversity (Ormerod et al. 2010). Fine sediments (generally defined as inorganic and organic particles < 2 mm in size: Wood and Armitage 1997; Jones et al. 2012) can infiltrate into bed substrates and cause streambed colmation/clogging (Mathers et al. 2017a; Wilkes

et al. 2019; McKenzie et al. 2020), which can alter macroinvertebrate community structure and functioning (Jones et al. 2012; Descloux et al. 2013; Wood et al. 2016; Mathers et al. 2017b). The ecological impacts of fine sediment on macroinvertebrates depends on the magnitude, frequency and duration of fine sediment supply and transport (Evans and Wilcox 2014). In addition, previous abiotic and biotic legacies influence the habitat template on which subsequent ecological responses occur (Parsons et al. 2006). Therefore, colmation may have a long-lasting influence on macroinvertebrate communities and effect their responses to future disturbances. Identifying the legacy effects of colmation and other stresses on river ecosystems is important for water managers and conservation efforts in order to understand the responses of macroinvertebrate communities to future disturbances.

High loads of suspended particles and deposited fine sediment have a complex mix of direct (physical and chemical) and indirect effects on macroinvertebrate communities

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(Sear et al. 2008; Jones et al. 2012; Wharton et al. 2017). Suspended fine sediment and saltating particles can physically dislodge periphyton and macroinvertebrates from the substrate by abrasion (Bilotta and Brazier 2008; Neale et al. 2008), and cause damage to fleshy body parts and gills in macroinvertebrates (Jones et al. 2012; Wharton et al. 2017). Increased turbidity reduces available light for primary producers and visual predators (Rowe and Dean 1998; Parkhill and Gulliver 2002) and alters the feeding efficiency of filter-feeders and grazers (Broekhuizen et al. 2001). Successive pulses of fine particles in gravel-bedded rivers can infill void spaces in bed substrates and modify particle size composition (Evans and Wilcox 2014). Thus, historical fine sediment pulses (i.e. legacy effects) may influence the ecological responses of macroinvertebrates to future sediment disturbances. Previous studies have examined invertebrate community responses to suspended fine sediment additions (e.g. Gibbins et al. 2007a; Larsen and Ormerod 2010; Béjar et al. 2017), but less research has incorporated the legacy effects of previous fine sediment pulses on the response of macroinvertebrates to future sediment disturbances.

Colmated streambeds can cause changes to benthic macroinvertebrate community structure and functioning (Growth et al. 2017; Mathers et al. 2017b, 2019; Beermam et al. 2018; Blöcher et al. 2020). Previous studies have demonstrated declines in benthic diversity and density, and changes in assemblage composition with increased deposited fine sediment (Lenat et al. 1979; Waters 1995). Invertebrates tolerant of low dissolved oxygen concentrations and taxa capable of burrowing into the substrate tend to dominate colmated streambeds (Angradi 1999; Zweig and Rabeni 2001; Rabeni et al. 2005). Furthermore, taxa that are vulnerable to damage of filter-feeding apparatus or gills tend to be absent from colmated streambeds (Wood and Armitage 1997; Larsen et al. 2009). The proportion of Ephemeroptera, Plecoptera and Trichoptera (EPT) typically declines with increases in suspended and deposited fine sediment (Bjornn et al. 1977; Lenat et al. 1979), whilst other taxa, such as Oligochaeta, show the opposite pattern (Angradi 1999; Zweig and Rabeni 2001; Gayraud et al. 2002). These changes in benthic assemblages are partly due to habitat homogenisation, and reductions in porosity and interstitial habitat (Descloux et al. 2013). In colmated sediments, reduced porosity and permeability influence the volume of interstitial space for invertebrates and the size of movement pathways between grains (Stubington 2012). Coarse-grained frameworks allow bidirectional migration of macroinvertebrates between the benthic and the hyporheic zone, but colmation can limit or prohibit vertical movement, leading to changes in the hyporheic community (Jones et al. 2015). Yet, there is an absence of research examining the behavioural response of macroinvertebrates to pulse disturbances when vertical migration pathways are disrupted.

Key invertebrate behavioural responses to suspended and deposited fine sediment, and other stresses include drift (i.e. the active or passive downstream movement of organisms; Bilton et al. 2001), vertical migration to the hyporheic zone (e.g. the hyporheic refuge hypothesis; Palmer et al. 1992), and aerial colonisation (Heino 2013). Less common dispersal mechanisms include upstream migration by some rheophilic taxa (Bruno et al. 2012), and lateral movements to floodplain habitats by crawling, flying or swimming (Turner 1993). Invertebrate drift may reflect an individual's decision to maximise foraging opportunities (Hildebrand 1974; Kohler 1985) and to avoid predators and other unfavourable abiotic conditions (both natural behavioural decisions; Gibbins et al. 2007b; James et al. 2009; Larsen and Ormerod 2010). Periodicity of drift density is typically crepuscular with peaks at dawn/dusk (Neale et al. 2008) and seasonal peaks linked with emergence behaviour (Townsend 1980; Cellot 1989; Sagar and Glova 1992). The density of drifting invertebrates generally increases with high-velocity flow conditions and suspended fine sediment loads (Culp et al. 1986; Doeg and Milledge 1991; Suren et al. 2005; Larsen and Ormerod 2010). Substantial drift can modify benthic community composition, but dispersal abilities and propensity to drift vary between taxa. Bivalves and gastropods are sedentary, less motile and depend on drifting to colonise new habitats, whereas more motile taxa, such as trichopterans and plecopterans also crawl and swim (Mackay 1992). Abundant taxa in the drift include baetid and leptophlebiid mayflies, *Gammarus* (Gammaridae), and simuliid and chironomid fly larvae (Giller and Malmqvist 2003). Caddis fly larvae from the families Hydropsychidae and Polycentropodidae are also common drifters, whereas heptageniid mayflies, planarians, cased caddis, and molluscs are rarer in the drift (Giller and Malmqvist 2003). Nevertheless, the extent to which macroinvertebrates use drift to avoid unfavourable conditions depends on what other avoidance strategies are possible. Few studies have examined how bed substrate characteristics impact the propensity of macroinvertebrates to drift during a suspended fine sediment pulse.

This study addresses the individual and interactive effects of a suspended fine sediment pulse and streambed colmation on macroinvertebrate community response using outdoor stream mesocosms. Outdoor flow-through channels or stream mesocosms that are naturally fed by river water and colonised by invertebrates are useful to reproduce natural conditions and examine the effects of stressors on macroinvertebrate communities (Connolly and Pearson 2007), whilst allowing users to reduce confounding factors present in field settings (O'Hop and Wallace 1983). This study aimed to identify the effect of differing doses of suspended fine sediment on the propensity of invertebrates to drift whilst accounting for the legacy effects of previous streambed colmation. The following hypotheses were tested:

1. Suspended fine sediment additions will lower benthic and increase drift density, taxonomic richness, and modify benthic and drift assemblages.
2. Differences in bed substrate (i.e. coarse and fine) will influence benthic and drift invertebrate structure (i.e. densities, taxonomic richness and assemblages) before and during the fine sediment pulse. We predict a higher density of invertebrates drifting from the fine compared with the coarse bed substrate, but with differing drift responses between taxa.

Colmated streambeds are characterised by fine particles and small pores restrict large individuals and limit vertical migration into the hyporheic zone (Gayraud and Philippe 2001; Descloux et al. 2013; Vadher et al. 2015; Mathers et al. 2019). If individuals are unable to access subsurface sediments, there may be increased invertebrate drift from a colmated streambed in response to suspended fine sediment pulses due to limited interstitial space.

Materials and methods

Study site

Twelve outdoor flow-through stream mesocosms were used for the experiment at the River Laboratory in Dorset, in the UK (Fig. 1). The stream mesocosms are fed by the Mill Stream, which is a branch of the River Frome. The River Frome is a lowland meandering river (8.1–264.6 mAOD) and is dominated by pool-riffle-glide morphology (National River Flow Archive [NRFA] 2020). The catchment area is 414 km² and the land-use is predominantly agriculture/horticulture (47.3%) and grassland (37.5%), with other minor land-uses of woodland (9.4%), urban sites (3.6%) and heathland/bog (1.3%; NFRA 2020). The Frome flows through Jurassic limestones, mudstones and cretaceous upper greensand in the headwaters, cretaceous chalk bedrock in the upper and middle reaches, and mixed tertiary geology including sands, gravels and clays in the lower reaches (Collins and Walling 2007; Environment Agency 2012). Mean annual discharge was 6.662 m³ s⁻¹ and the baseflow index was 0.86 during 1965–2018 at East Stoke gauging station, which is located at the study site (NRFA 2020).

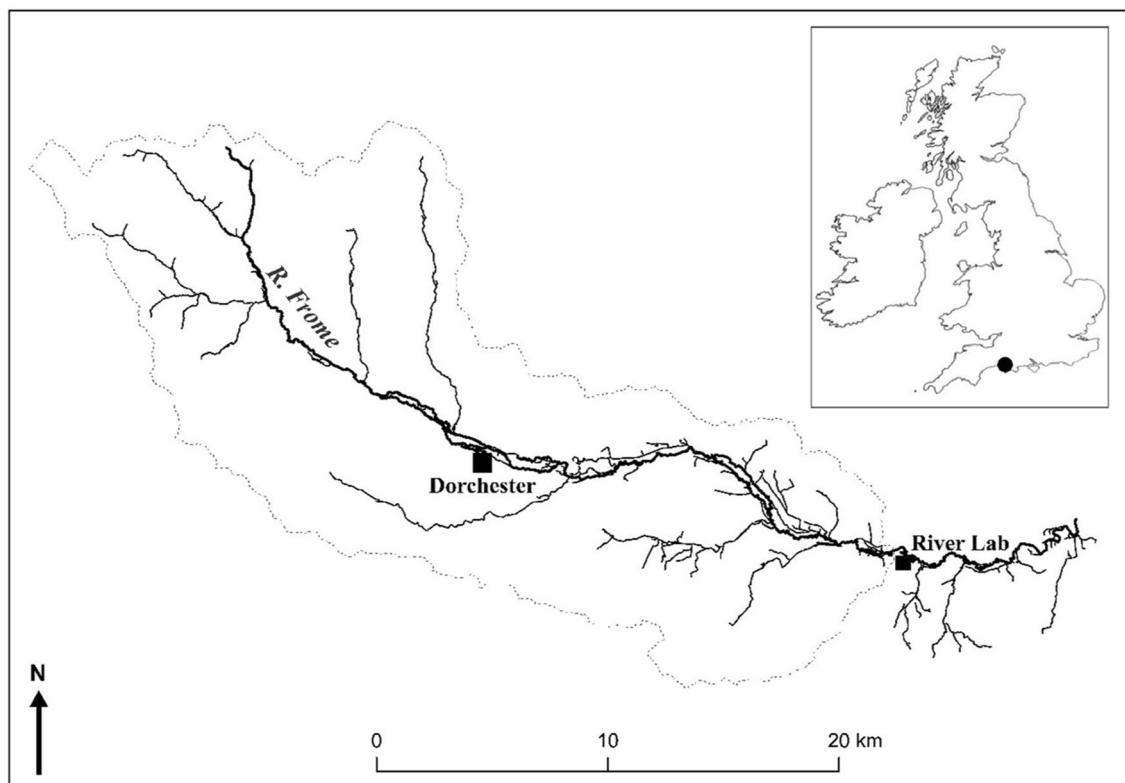


Fig. 1 Position of the stream mesocosms at the River Laboratory in Dorset, UK

Experimental design and procedure

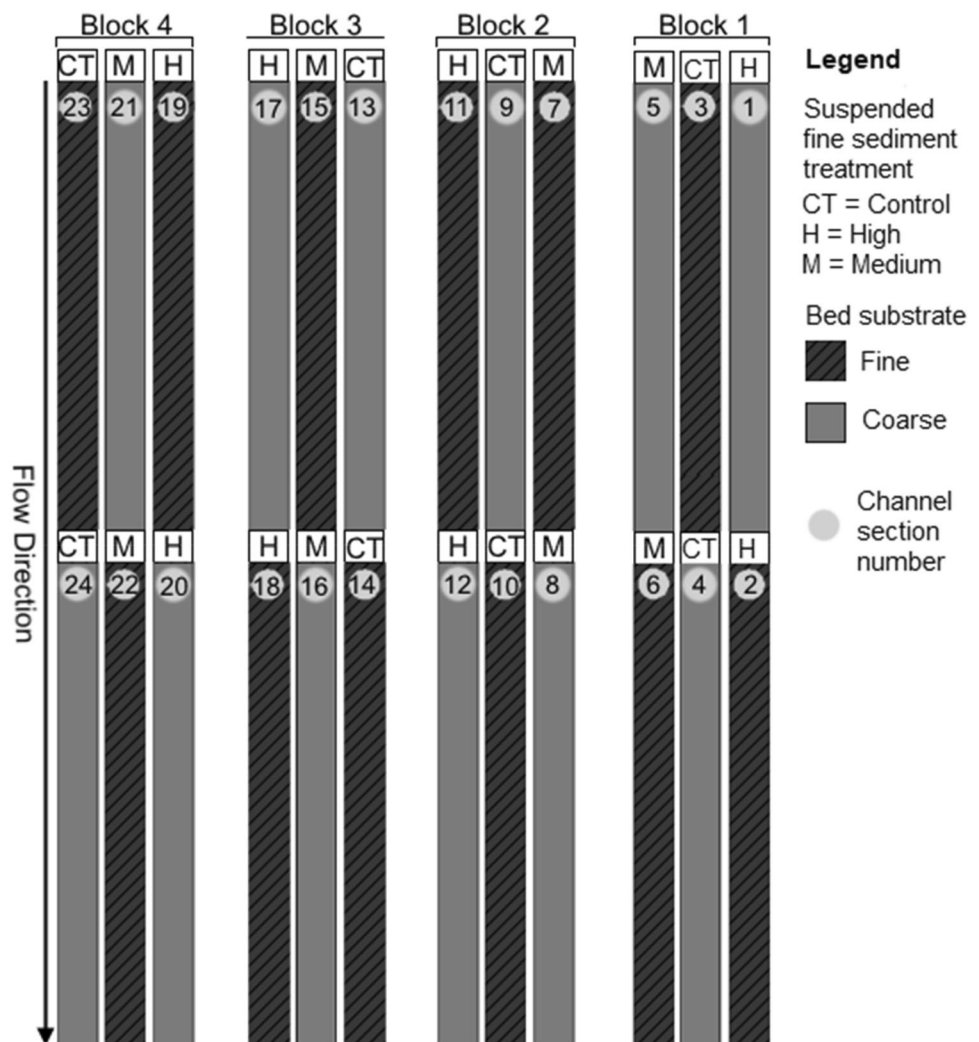
The experiment ran between June and September 2015 using 12 flow-through stream mesocosms. The mesocosms were arranged in four blocks containing three steel linear stream mesocosms, situated at $\sim 140^\circ$ to the Mill Stream. Each mesocosm was 0.33 m in width, 12.4 m in length and 0.30 m in depth, and the distance between each block was 2.5 m. We split each stream mesocosm into two 6.2 m sections to provide 24 mesocosm sections.

Sediment for the coarse and the fine bed substrate was obtained from a local quarry who sourced the sediment from a gravel pit on the River Frome floodplain. The coarse bed substrate comprised sand (<2 mm, 6.6%), gravel (10 mm, 13.3%), pebble (20 mm, 66.6%) and cobbles (>64 mm, 13.3%), whereas the fine bed substrate contained sand (25%), gravel (37.5%) and pebble (37.5%). The sediment proportions were selected to reflect the particle range found in chalk streams (Armitage 1995; Ledger et al. 2009). The coarse bed substrate had clear bed interstices and represented

a reach with relatively little fine sediment deposition. The fine bed substrate was used to represent a colmated streambed that had experienced high fine sediment deposition and lacked interstitial space. We filled each mesocosm section to a depth of 20 cm with either coarse or fine dry substrate, which provided 12 coarse and 12 fine mesocosm sections (Fig. 2).

Water from the Mill Stream was diverted through each block of mesocosms on 9 June 2015 (day 1). Average current velocity in the mesocosms was $0.11 \text{ ms}^{-1} \pm 0.01$ (mean \pm SE; $n=24$) and average water depth was 5.16 ± 0.18 cm ($n=24$; measured once on day 99). Mesocosms were left for 69 days for natural colonization by drifting invertebrates and algae from the Mill Stream (Jones et al. 2015). Natural colonization in each mesocosm was supplemented by adding invertebrates from four 3 min kick samples collected from the Mill Stream. Benthic macroinvertebrates were sampled from four riffles that possessed a coarse-grained structure with no fine sediment infiltration. Equal aliquots were added directly to the head of each mesocosm. During the colonization phase,

Fig. 2 Experimental setup of bed substrate and suspended fine sediment treatments in the stream mesocosms



shade cloths covered the mesocosms to reduce the development of diatom mats that may have encouraged fine sediment deposition (Jones et al. 2014).

Sediment for the suspended fine sediment treatments was obtained from deposited material in nearby reaches of the River Frome. The sediment was frozen for 48 h to eliminate any invertebrates and sieved using a 2 mm mesh to remove any coarse particles. This sediment was mixed with water from the Mill Stream to produce three suspended fine sediment treatments: (1) no sediment (30 l of water), (2) a moderate suspended fine sediment input (a suspension of 15 kg sediment in 30 l of water = 0.5 kg l^{-1}), and (3) a concentrated slurry of fine suspended (i.e. a high treatment of 30 kg sediment in 30 l of water = 1 kg l^{-1}). Over a 4-h period, we calculate the medium and high suspended fine sediment treatment would give suspended sediment concentrations of 556 mg l^{-1} and 1112 mg l^{-1} (based on average velocity and depth values). The suspended fine sediment treatments were added at the head of each of the 24 mesocosm section in a crossed design with the bed substrate types (Fig. 2).

Prior to the addition of the suspended fine sediment treatments, a 5-l sample of substrate was taken randomly from the coarse and the fine bed substrate to ensure consistency within the bed sediment types between the mesocosm sections, and to confirm differences between the coarse and the fine bed sediment upon installation. The substrate in each sample was oven dried at $60 \text{ }^\circ\text{C}$ and sieved into the following size fractions: <0.125 , 0.25 , 0.5 , 1 , 2 , 4 , 8 , 16 , 31.5 , 45 and 63 mm or greater. Each size fraction was weighed to determine the particle size distribution within each substrate sample.

Macroinvertebrate sampling

Drifting invertebrates were collected using drifts nets ($0.4 \times 0.25 \text{ m}$; 1 mm mesh size) that were positioned at the end of each mesocosm section (at 6.2 m and at 12.4 m) to intercept all the flow and thus, to reduce any influence of spatial variation (Neale et al. 2008). The drift nets spanned the width of the mesocosms (i.e. 0.33 m). Each mesocosm section was treated as a separate, independent experimental unit. Drift samples were collected before, during, immediately after (24 h after suspended fine sediment input) and 30 days after the suspended fine sediment pulse. On each sampling occasion, drift nets were deployed for 24 h and invertebrates were collected every 6 h (i.e. providing four 6-h drift samples for each sampling period) to accommodate the crepuscular nature of macroinvertebrate drift. The experimental set-up comprised 24 mesocosm sections \times four 6-h drift samples \times 4 sampling occasions, which provided 384 drift samples.

Benthic invertebrates were sampled from each mesocosm section on the day before, immediately after (24 h after

suspended sediment input) and 30 days after suspended fine sediment addition. A benthic sample was taken at a random upstream and downstream location within each mesocosm section using a Surber sampler (0.2 m^2 , 250 μm mesh net) where the bed substrate was disturbed using a metal rod for two minutes. In total, 144 benthic samples were collected (i.e. 2 benthic invertebrate samples \times 24 mesocosms \times 3 sampling occasions). All benthic and drift invertebrate samples were sieved through a 250 μm mesh and were preserved in the field using 99% industrial methylated spirits. Invertebrates were identified to the lowest taxonomic level possible, in many cases to species, although, *Oligochaeta* and *Hydracarina* were identified at the class level.

Statistical analysis

Variation in bed sediment particle size and the percentage of fine particles between the colmated and the clean bed at the start of the experiment were examined using a one-way Analysis of Similarity (ANOSIM) and visualised using a cumulative frequency graph. A square root transformation was applied to the particle size data to decrease any effects of skewed distributions before the ANOSIM analyses and Euclidean distance was used as a dissimilarity measure (Clarke and Gorley 2006).

Before statistical analysis, macroinvertebrate data was $\log_{10}(x+1)$ transformed to normalise residuals. Differences in benthic and drift density (the number of drifting invertebrates per 100 m^{-3}) and taxonomic richness to suspended fine sediment additions and bed substrate conditions were tested by linear mixed effects models (LMMs) using the *lme* function from the package *nlme* (Pinheiro et al. 2018). Bed substrate type, time, and suspended fine sediment treatment were included as fixed interacting factors and block was specified as a random factor to account for any potential positional effect caused by the mesocosms. All LMMs were fitted using the restricted maximum likelihood (REML) estimation function. Tukey's honestly significant difference (HSD) tests were used for all pairwise differences (i.e., for bed substrate, time and suspended fine sediment treatments) to decrease the probability of a Type I error. These tests were undertaken using the *glht* function in the *multcomp* package (Hothorn et al. 2008).

First, LMMs identified any effect of bed substrate on benthic and drift community metrics before suspended fine sediment was added. Bed substrate was fitted as a fixed interacting factor and block as a random effect. This LMM aimed to examine the effect of bed substrate on the four-community metrics before stressor application. Further LMMs identified the individual and interactive effects of suspended fine sediment treatment, bed substrate and time (all fixed factors with block as a random factor) on benthic and drift community structure (i.e. the four-community metrics). Lastly,

LMMs determined any differences in drift community structure with varying suspended fine sediment treatments during and after the fine sediment pulse. This analysis aimed to test if the fine sediment pulse caused an immediate or a delayed response in drift. All univariate analyses were carried out using R, version 3.6.3 (R Development Core Team 2015).

Permutational Multivariate Analysis of Variance (PERMANOVA) models were used to determine any differences in benthic and drift assemblages caused by the main factors and their interactions. Similar to the univariate analysis, a PERMANOVA model examined the influence of bed substrate on benthic and drift assemblages before the fine sediment pulse. A further PERMANOVA determined the effect of time and suspended fine sediment treatments on drift assemblage. Bed substrate, time, and suspended fine sediment treatments were fitted as fixed factors and block was a random factor in both PERMANOVA models. Similarity percentage analysis (SIMPER) was conducted to determine which species were driving differences in assemblages between the main factors, and Non-metric Multidimensional Scaling (NMDS) ordination plots were used to visualise compositional patterns. Bray–Curtis similarity coefficients were used for all multivariate analyses (i.e., all PERMANOVA models, SIMPERs and NMDS ordination plots) on the invertebrate data set. All multivariate analyses, including the particle size data were performed using PRIMER V7 and the PERMANOVA + add-on (PRIMER-E Ltd, Plymouth, UK; Clarke and Gorley 2006; Anderson et al. 2008).

Results

Bed sediments

Before the suspended fine sediment pulse, there was a significant difference in the size of bed sediment particles between the coarse and the fine bed substrate (ANOSIM; $r=0.907$, $p<0.001$; Fig. 3). The colmated bed contained a higher percentage of fine particles (18%) compared with the coarse bed (3.89%; ANOSIM; $r=0.655$, $p=0.001$). D_{50} was 8.79 mm in the colmated bed and 16.51 mm in the clean bed. The ANOSIM analysis was visually supported by a cumulative frequency plot that shows distinct particle size distributions between the fine and the coarse bed (Fig. 3).

Influence of colmation on benthic and drift metrics and invertebrate assemblages

Tanypodinae and Tanytarsini (both dipterans: Chironomidae) dominated the benthic community, accounting for 27.7 and 27.4% of the total benthic invertebrate abundance. Ten other taxa comprised 1–9% of the benthic community: Oligochaeta (8.8%), *Asellus aquaticus* (Asellidae; 7.8%), Baetidae (5.1%), *Gammarus pulex* (Gammaridae; 4.4%), *Hydropsyche pellucidula* (Hydropsychidae; 4.2%), *Hydroptila* spp. (Hydroptilidae; 2.2%), *Radix balthica* (Lymnaeidae; 2.1%), Chironomini (1.9%), Ostracoda (1.2%), and *Ephemerella danica* (Ephemeraeidae; 1.1%). These 12 taxa accounted

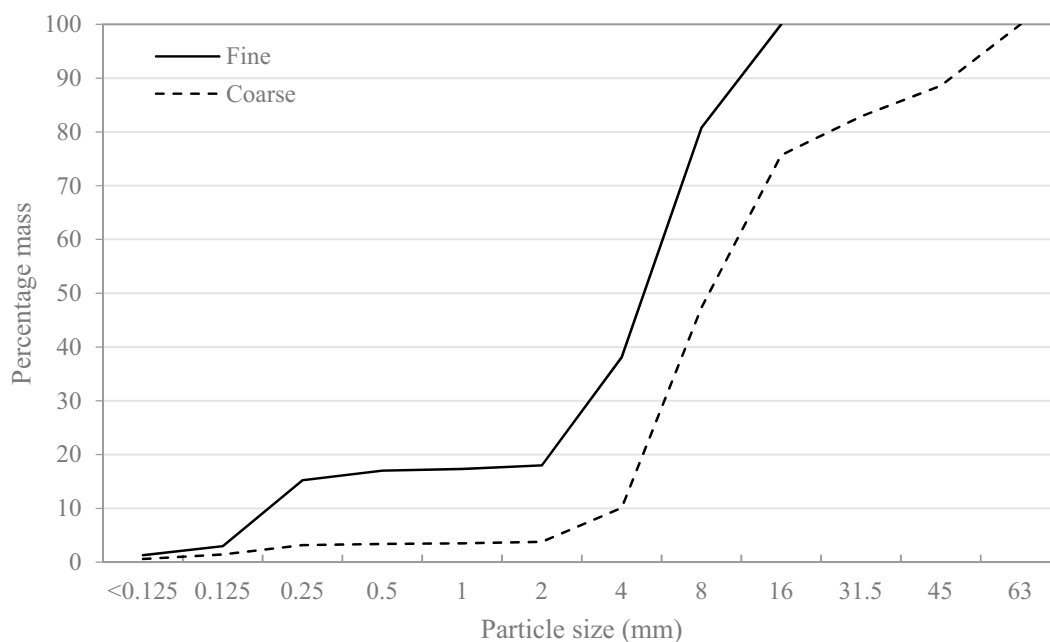


Fig. 3 A comparison of particle size distributions between bed substrates prior to suspended fine sediment inputs

for 93.9% of the benthic community with another 38 taxa constituting the remaining benthic invertebrate abundance.

The drift assemblage was characterised by *R. balthica* (19% of total abundance), *G. pulex* (15.4%) and baetids (11%). A total of 14 other taxa comprised 1–7% of the drift assemblage: *Limnius volckmari* (Elmidae; 6.4%), *Brachycentrus subnubilus* (Brachycentridae; 6.1%), *H. pellucidula* (5.3%), Tanytarsini (5.2%), *Hydroptila* spp. (3.8%), Tanypodinae (3.5%), *A. aquaticus* (3.4%), *Crangonyx pseudogracilis* (Crangonyctidae; 3%), Hydrophilidae (1.6%), *Hydropsyche contubernalis* (Hydropsychidae 1.4%), Corixidae (1.2%), Psychodidae (1.1%), Simuliidae (1.1%) and *Elmis aenea* (Elmidae; 1%). These 17 taxa contributed 89.7% of the drift assemblage whilst a further 45 taxa accounted for <1%.

Before the suspended fine sediment additions, LMMs showed no difference in benthic density and taxonomic richness between the fine and the coarse bed (Table 1). Similarly, there were no difference in drift density and taxonomic richness between bed substrates (Table 1). *Baetis rhodani*, *B. subnubilus* and *G. pulex* were the most abundant taxa drifting from the coarse bed. Similarly, *B. subnubilus*, *B. rhodani* and *R. balthica* occurred in high densities from the colmated bed. Streambed colmation had no effect on the benthic (PERMANOVA; F value = 2.33, $p > 0.05$) or the drift assemblage (PERMANOVA; F value = 1.21, $p > 0.05$) prior to the suspended fine sediment pulse (Fig. 4).

Effect of suspended fine sediment additions and substrate on benthic and drift structure

Benthic density and taxonomic richness differed with time but did not vary with suspended fine sediment treatment or bed substrate (Table 2). Both benthic community metrics indicated a significant difference before and immediately after the suspended fine sediment pulse (LMMs; both p values < 0.001). Benthic densities increased from immediately after to 30 days post the fine sediment pulse (LMM; F value – 2.59, p value < 0.05). None of the two-way or three-way

interactions were significant for any of the benthic community metrics (Table 2).

Drift density and drift varied with time and suspended fine sediment treatment (Table 2). Post-hoc tests revealed drift density and drift taxonomic richness significantly differed between sampling occasions. Both drift community metrics differed before and 30 days after suspended fine sediment addition, during and 30 days after suspended fine sediment addition, and between 1 and 30 days after suspended fine sediment addition (Supporting Information Table S1). Differences in both community metrics also existed between suspended fine sediment treatments. Post-hoc tests showed significantly higher drift density and higher drift taxonomic richness from the high suspended fine sediment treatment compared with the control, but no significant difference in community metrics were detected between the moderate and the high suspended fine sediment treatments (Table 1 and Supporting Information Table S2). Furthermore, no differences in drift density or drift taxonomic richness existed between bed substrates, indicating no effect of the colmated bed. LMMs also indicated no interactive effects between any of the main factors (all p values > 0.05; Table 1).

Drift assemblage (PERMANOVA; $F = 6.52$, $p < 0.001$) differed significantly with time (Table 3 and Fig. 5a). Planned contrasts revealed drift assemblages differed significantly between all time periods (Table 3). The drift assemblages of the different time periods were widely dispersed and overlapping, indicating high community heterogeneity within groups, but were still significantly different from one another (Fig. 5a). The top five taxa characterising the time period before suspended fine sediment addition were *B. rhodani* (26.3% contribution to the dissimilarity), *R. balthica* (17.9%), *B. subnubilus* (14%), *G. pulex* (12.6%) and Tanypodinae (6.2%). These five taxa accounted for 77% of the drift assemblage. During the fine sediment pulse, *L. volckmari* (27.6%), *G. pulex* (23.1%), *B. rhodani* (13.1%), *R. balthica* (8.1%) and *H. pellucidula* (5.8%) dominated the drift assemblage (accounting for 77.6% of the composition). 24 h after the suspended fine sediment pulse, three of the five taxa continued to characterise the assemblage: *R. balthica* (34.2%), *G. pulex* (24.4%), and Baetidae (9.5%) with *C. pseudogracilis* and Tanypodinae contributing smaller abundances (5.8% and 4.9% respectively). These five taxa cumulatively accounted for 78.7% of the assemblage. Post 30 days, the drift assemblage continued to comprise high abundances of *R. balthica* (25%) and *G. pulex* (18%). *H. pellucidula* (8.4%), *B. rhodani* (7.3%) and *Hydroptila* spp. (6.2%) contributed smaller abundances (cumulatively the five taxa accounted for 64.8% of the drift assemblage). Although many taxa occurred in most time periods, variation in abundances of these taxa contributed to significant differences in drift assemblage between sampling occasions.

Table 1 Effect of bed substrate on benthic and drift invertebrate structure before the suspended fine sediment pulse

Metric	F value	p value
Benthic structure		
Density	3.47	0.069
Taxonomic richness	3.92	0.054
Drift structure		
Density	1.71	0.104
Taxonomic richness	–0.15	0.883

Significant values ($p < 0.05$) are presented in bold

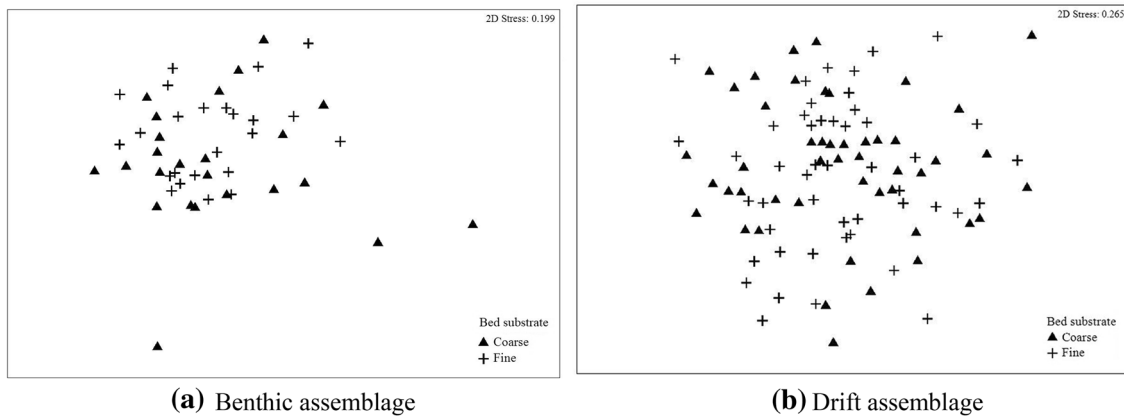


Fig. 4 NMDS ordinations of bed substrate on **a** benthic and **b** drift assemblages

The different concentrations of suspended fine sediment added also impacted macroinvertebrate drift assemblages (PERMANOVA; $F=1.65$, $p<0.05$). A significant difference was evident between the drift assemblages that experienced no added fine sediment (i.e. the control) and the high suspended fine sediment treatment (Table 2; Fig. 5b). Macroinvertebrate taxa causing compositional differences between sediment treatments were *G. pulex* (contributing 8.8% to the dissimilarity), *B. rhodani* (8.4%), *R. balthica* (7.8%), *L. volckmari* (6%) and *B. subnubilus* (5.5%), which all occurred in higher abundances in the high suspended fine sediment treatment. Bed substrate did not influence drift assemblages

Table 2 Influence of time, fine sediment treatment and bed substrate on benthic and drift univariate community metrics

Source of variance	df	Benthic structure		Drift structure	
		F value	p value	F value	p value
Density					
Time (T)	3	6.40	0.002	14.37	<0.001
FS treatment (FST)	2	1.27	0.285	6.07	0.004
Substrate (S)	1	1.72	0.192	1.23	0.271
T × FST	6	0.19	0.941	0.94	0.475
T × S	3	0.83	0.440	0.18	0.911
FST × S	2	0.32	0.729	0.57	0.568
T × FST × S	6	0.17	0.953	0.25	0.959
Taxonomic richness					
T	3	8.29	<0.001	10.47	<0.001
FST	2	1.69	0.189	3.7	0.03
S	1	3.32	0.071	0.19	0.666
T × FST	6	0.47	0.759	1.01	0.427
T × S	3	1.08	0.343	0.378	0.769
FST × S	2	0.73	0.485	0.13	0.879
T × FST × S	6	0.51	0.730	0.34	0.913

Significant values ($p<0.05$) for the LMMs are presented in bold

and none of the interactions between the main factors were significant (Table 3; Fig. 5c).

Influence of suspended fine sediment treatment on drift structure during and immediately after the fine sediment pulse

Drift macroinvertebrate density and drift taxonomic richness were greater in the high suspended fine sediment treatment than the control during the suspended fine

Table 3 Summary of PERMANOVA outputs for differences in drift assemblages associated with time, bed substrate and fine sediment treatments

Variable	df	Assemblage composition	
		F value	p value
Time (T)	3	6.52	<0.001
Substrate (S)	2	0.40	0.937
Fine sediment treatment (FST)	3	1.65	0.036
T × S	3	1.06	0.399
T × FST	6	0.75	0.917
S × FST	2	0.65	0.874
T × S × FST	6	0.78	0.889
Planned contrasts			
Time			
Before vs during	1	2.63	0.005
Before vs 1 day after	1	5.15	0.002
Before vs 30 days after	1	5.92	0.002
During vs 1 day after	1	3.55	0.004
During vs 30 days after	1	6.18	<0.001
After vs 30 days after	1	4.43	0.009
Suspended fine sediment treatment			
Control vs high FST		2.70	0.019

Significant values ($p<0.05$) are presented in bold

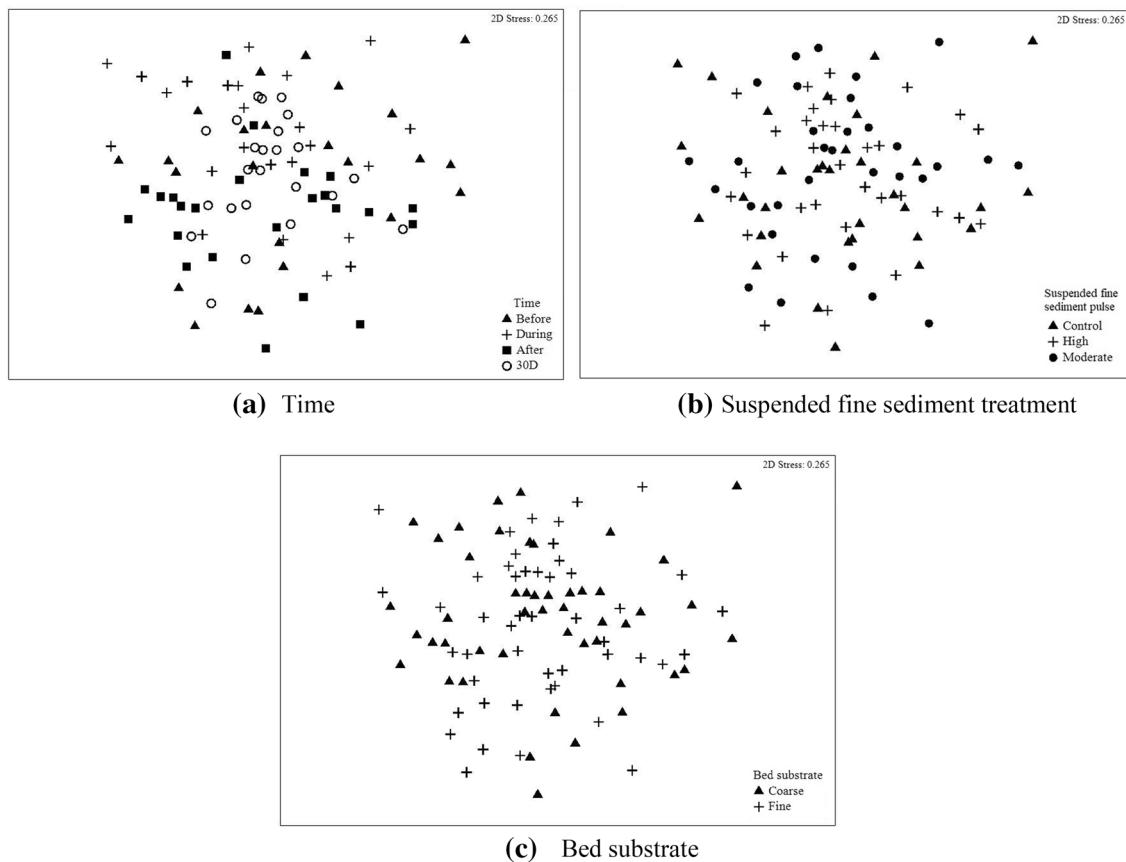


Fig. 5 NMDS ordinations of the drift assemblage grouped by a time, b suspended fine sediment treatment and c bed substrate

Table 4 Effects of fine sediment treatment on drift structure during and immediately after the suspended fine sediment pulse

Fine sediment treatment	During		After	
	F value	p value	F value	p value
Drift density				
Control vs moderate	4.29	0.063	0.24	0.633
Control vs high	19.51	0.001	3.48	0.089
Moderate vs high	18.24	0.001	0.99	0.340
Drift taxonomic richness				
Control vs moderate	0.76	0.403	0.11	0.747
Control vs high	7.87	0.017	0.30	0.597
Moderate vs high	18.24	0.001	1.13	0.311

Significant values ($p < 0.05$) are presented in bold

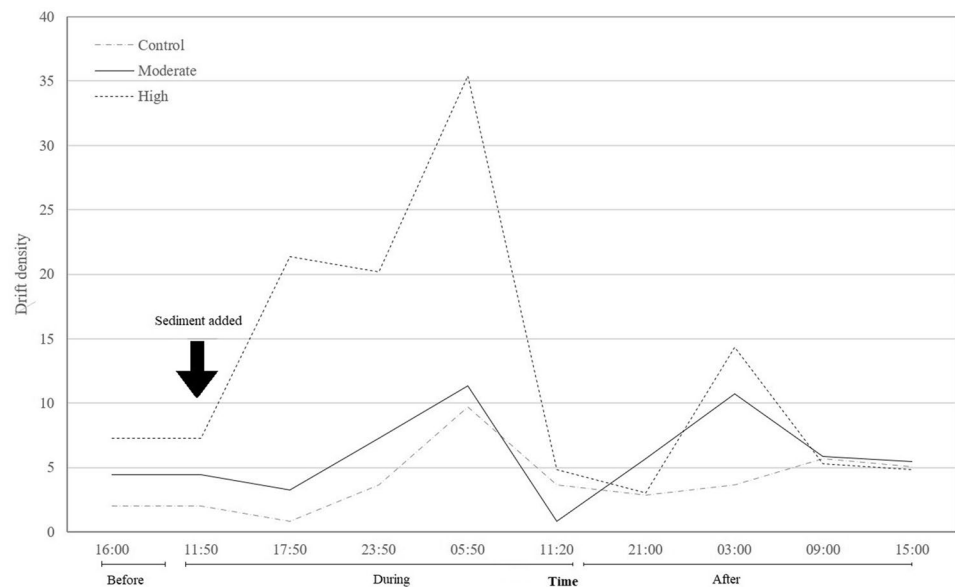
sediment pulse (Table 4). Drift densities and taxonomic richness were also greater in the high compared to the moderate suspended fine sediment treatment. Differences in both drift community metrics changed rapidly with time after the fine sediment pulse. No differences

occurred in any of the drift community metrics 24 h after the disturbance event (Table 4).

Crepuscular drift

An increase in drift density occurred immediately after the high suspended fine sediment treatment was added, but drift density from the control and moderate suspended fine sediment treatment initially remained comparable to pre-disturbance densities (Fig. 6). In all three suspended fine sediment treatments, drift densities increased significantly during the first evening and night after the fine sediment pulse (sampling period 17:50–23:50 and 23:50–5:50 h). A second, smaller peak in invertebrate drift occurred the second night after sediment input in mesocosms that experienced the moderate and high suspended fine sediment treatment (sampling period 21:00–3:00 and 3:00–9:00 h). However, drift densities from the control were noticeably lower compared with the other sediment treatments and exhibited no distinct second night peak.

Fig. 6 Diel invertebrate drift density ($N/100\text{ m}^3$) before, during and immediately post suspended fine sediment input. Time shown on the x axis represents the time of sampling in 6-h intervals



Discussion

Effects of increased suspended fine sediment

Our first hypothesis that increases in suspended fine sediment will lower the density and taxonomic richness of the benthos, cause greater drift rates, and alter the composition of the drift assemblage was supported. Invertebrates typically leave the bed in increasing numbers as suspended fine sediment increases (e.g. Ciborowski et al. 1977). Key mechanisms suggested for increased drift include abrasion and clogging of gills and filter-feeding apparatus (Allan 2004; Jones et al. 2012). Abrasion by fine material can dislodge invertebrates from the bed (i.e. passive drift), but individuals may also actively release from the bed as a behavioural response to escape higher suspended sediment loads (i.e. active drift; Jones et al. 2012). Active drift may also occur in response to changes in bed composition caused by increased suspended sediment loads, i.e. an increase in fine sediment in the surface drape. Although many invertebrate species benefit from inputs of organic (food) particles associated with high fine sediment inputs, problems occur when sediment accretion exceeds the ability of invertebrates to excavate themselves (Wood et al. 2005). Increases in drift density may also be a behavioural response to the threat of burial (Béjar et al. 2017). Invertebrates may also enter the drift to avoid altered habitat conditions and decreased food quality and availability (Hildebrand 1974; Buendia et al. 2013a,b), a knock-on effect of bed composition changes. Our study demonstrated an initial increase in drift densities under the high fine sediment treatment, indicating either dislodgement or immediate avoidance behaviour to the fine sediment addition. However, most of the increase in invertebrate drift was

delayed until after sunset (c. 21:00 h in summer) coinciding with a peak in drift in the control and moderate suspended fine sediment treatment (Fig. 6). This delayed response may reflect a behavioural reaction to changed benthic conditions after the suspended fine sediment pulse had passed or be a consequence of the crepuscular pattern of drifting (Tanaka 1960; Waters 1962; Muller 1963; Neale et al. 2008). Invertebrates actively drifting at night may also be deliberate to reduce predation risk from visually foraging, drift-feeding fishes (Allan 1978; Flecker 1992).

Previous studies examining interactions between suspended fine sediment transport, deposition and invertebrate drift dynamics have often focussed on short temporal scales (i.e. <3 days; e.g. Gibbins et al. 2007b; Larsen and Ormerod 2010). A key feature of our study is the temporal scale as we monitored drift patterns 30 days after stressor application. Drift density was double and taxonomic richness increased 30 days after the suspended fine sediment addition, but there was no lasting effect of the experimental fine sediment pulse (i.e. no difference amongst treatments). Invertebrate drift often exhibits seasonal trends (Keeley and Grant 1997; Jenkins and Keeley 2010), but the direction and magnitude differs among studies (Naman et al. 2016). In temperate river networks, drift densities generally peak in summer and decrease in autumn, partly due to the life history characteristics of the drifting taxa (Fjellheim 1980; Cellot 1996; Giller and Malmqvist 2003), but spring (Hieber et al. 2003; Leeseberg and Keeley 2014) and autumn peaks (Stoneburner and Smock 1979) have also been reported. Neale et al. (2008) found higher densities of drifting invertebrates in summer (June and July) compared with spring (April and May) in a temperate chalk stream in the UK, but the study did not measure autumnal drift. In our study, we suggest increased

drift rates after 30 days were likely due to seasonal and other factors, such as temperature, discharge, food resources, and the life history traits of drifting taxa rather than any legacy effects of increased sediment addition. This finding is important by highlighting the effects of suspended fine sediment inputs are short-lived, transient events, and with time, other abiotic and biotic factors are more influential in determining drift community structure.

Impact of suspended fine sediment treatment

Suspended fine sediment additions influenced drift rates and the taxonomic structure of the drift, which supports our first hypothesis. Drift assemblage structure differed between the control (i.e. no added fine sediment) and the high fine sediment treatment but did not differ between the moderate and the high suspended fine sediment treatments. There are numerous mechanisms that might account for increased drift rates during spates that tend to deliver fine sediments to rivers. Elevated discharges are generally accompanied with increases in near-bed shear stress, turbulence and the entrainment and transport of coarse and fine sediment (Vinson 2001; Bond and Downes 2003; Naman et al. 2017). Saltating particles and fine organic matter scour exposed benthic invertebrates (Gibbins et al. 2007a). If flows are sufficiently high, mobilisation of bed particles can occur and cause entrainment of surface and near-surface invertebrates (Anderson and Lehmkühl 1968). In addition to increased near-bed shear stress and movement of bed particles, pulsed fine suspended sediment events are an additional pressure upon invertebrate communities. In our study, we did not increase flow substantially such that mobilisation of the bed would have occurred. Hence, the differences in drift between the sediment treatments (i.e. the control and the high fine sediment treatment) can be attributed to the effects of the fine sediment alone. This finding is important by revealing different mechanisms governing invertebrate drift, which is useful in developing effective conservation and management strategies.

Influence of substrate characteristics

Our second hypothesis that bed substrate characteristics will cause differences in benthic densities, drift rates and assemblage during increased suspended fine sediment was unsupported. Benthic and drift density, and taxonomic richness were similar from both bed substrates before, during and after the suspended fine sediment pulse. *B. subnubilus* and *B. rhodani* were the most common EPT taxa drifting from the colmated bed. *Brachycentrus* (Trichoptera) are filter feeders and use their forelimbs extended into the water to trap particles (Gallepp 1974), but switch to grazing when suspended sediment loads are high (Voelz

and Ward 1992), possibly due to abrasion from particles or reduced quality of food (Jones et al. 2012). *B. rhodani* is a grazer and is intolerant of sediment deposition (Rabeni et al. 2005; Pollard and Yuan 2010), and drifts quickly as bedload transport rises (Gibbins et al. 2005). The higher drift densities from the colmated bed may reflect increased drift to avoid unfavourable patches or predators, and imply individuals have fewer escape routes in colmated sediments.

Past studies have found the hyporheic zone is an important invertebrate refuge that promotes community resilience during disturbances (Vander Voste et al. 2016). The effectiveness of the hyporheic zone as a refuge may be restricted by fine sediment reducing interstitial space and limiting vertical connectivity on invertebrates accessing lower sedimentary layers (Descloux et al. 2013; Vadher et al. 2015, 2017). We predicted a higher likelihood of invertebrates entering the drift from the fine compared with the coarse bed due to restricted interstitial space within colmated sediments. However, we found no interaction effects between colmation and the suspended fine sediment treatment on drift assemblages. Although physical dislodgement may be responsible for the initial increase in drift, as we detected a delayed response to the effects of the suspended fine sediment pulse in drift density, it is clear that at least part of the increase in drift is driven by an active behavioural response from the macroinvertebrates. Hence, active use of the hyporheos to avoid the negative effects of a fine sediment pulse is possible: the influence of colmation on this avoidance mechanism could be tested by well-planned field, mesocosm and/or laboratory testing.

The advantages of mesocosms and spatial and temporal scales

Identifying the effects of multiple stresses on invertebrate responses to disturbances is complex (Beermann et al. 2018). Outdoor stream mesocosms are highly useful to determine the single and interactive effects of stresses if an appropriate set-up is used. A distinct advantage of using mesocosms that are fed by river water and colonised by invertebrates by drift or aerial oviposition is that the mesocosms have the same light, water temperature and chemistry as the feeder stream (Beerman et al. 2018). Furthermore, specific environmental conditions and stresses, such as bed composition and differing doses of sediment additions can be manipulated. Whilst using stream mesocosms to identify ecological responses to effects of stressors has many benefits, our mesocosms may only represent conditions from small streams. Rivers contain a mosaic of different physical habitats, including erosional and

depositional patches, and a range of refugia that cannot be replicated within stream mesocosms (Larsen and Ormerod 2010). However, our findings are comparable with field surveys of greater spatial scales (e.g. Larsen and Ormerod 2010; Béjar et al. 2017) that have examined the impact of fine sediment on invertebrate communities.

Conclusion

This study shows the impacts of increased suspended fine sediment on benthic and drift structure. Drift structure (i.e. density and taxonomic richness) and assemblage composition were strongly influenced by the suspended fine sediment addition. Both drift structure and assemblage differed significantly between the control and the high fine sediment treatment. This finding demonstrates that the concentration of suspended fine sediment influences invertebrate behaviour. Invertebrates exhibited an immediate increase in drift and delayed avoidance behaviour where they drifted downstream after the fine sediment addition had finished. Despite assumptions that colmation of bed sediments would affect the drift response, as refuge in the hyporheos would be compromised, we found no difference in drift between the colmated and coarse sediments. Future research should evaluate the ecological impact of differing suspended fine sediments on invertebrate behaviour and examine multiple dispersal pathways simultaneously. Understanding the impacts and interactions of deposited and suspended fine sediment on macroinvertebrate behaviour is important for water management strategies to deploy effective conservation measures and address activities which result in increased fine sediment loading to river ecosystems.

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Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article. In addition, the authors have no financial or proprietary interests in any material discussed in this article. Please note that this study was funded by a University of Worcester PhD studentship, which was awarded to Dr George Bunting.

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