The role of fine sediment characteristics and body size on the vertical movement of a freshwater amphipod

Kate L. Mathers[1*], Matthew J. Hill[2], Connor D. Wood[3] and Paul J. Wood[1]

1. *Department of Geography, Centre for Hydrological and Ecosystem Science, Loughborough University, Loughborough, Leicestershire, LE11 3TU, United Kingdom*
2. *School of Applied Sciences University of Huddersfield, Queensgate, Huddersfield, HD1 3DH, UK*
3. *Woodbrook Vale, Grasmere Road, Loughborough, Leicestershire, LE11 2ST*

** Present address; Eawag, Department of Surface Waters Research and Management, 6047 Kastanienbaum, Switzerland.*

Author for Correspondence

Paul Wood
Department of Geography,
Centre for Hydrological and Ecosystem Science,
Loughborough University,
Loughborough,
Leicestershire,
LE11 3TU,
United Kingdom
Email – p.j.wood@lboro.ac.uk

Running title: Sediment deposition and hyporheic body size

The role of fine sediment characteristics and body size on the vertical movement of a freshwater amphipod

Kate L. Mathers, Matthew J. Hill, Connor D. Wood and Paul J. Wood

Abstract

1. Sedimentation and clogging (colmation) of interstitial pore spaces with fine sediment particles is widely considered to be one of the most significant threats to lotic ecosystem functioning. This paper presents the results of a running water mesocosm study examining the effect of benthic and hyporheic fine sediment loading and particle size on the vertical movement and distribution of the freshwater amphipod *Gammarus pulex*.
2. A gradient of fine sediment loading and different particle sizes were used to examine the ability of *G. pulex* from two body size classes to access and migrate vertically within subsurface sediments.
3. We tested three hypotheses: i) sediment loading would modify the distribution of *G. pulex* by limiting vertical movement; ii) the deposition of large particles and heterogenous sediments would limit the vertical movement of individuals more than homogeneous fine grained sediments; and iii) large bodied individuals would be prevented from migrating vertically with increasing sediment loading and particle size / heterogeneity.
4. Sediment loading, particle size and heterogeneity of deposited sediment had a significant effect on the vertical movement of individuals, with heterogeneous sand (0.125 - 4 mm) acting as the strongest barrier to the vertical movement of individuals through the infilling and clogging of interstitial spaces followed by coarse (1 - 4mm) and fine sand (0.125 - 4 mm).
5. Fine sediment loading and particle size acted as a filter on body size and limited the ability of large bodied individuals to migrate vertically to a greater extent than small bodied individuals.
6. This study demonstrates that the effects of fine sediment on habitat availability and faunal movement is dependent on both sedimentological characteristics and an individual's body size. The results illustrate the importance of both abiotic and biotic factors when evaluating the ecological effects of fine sediment deposition.

Keywords: colmation, particle size, substrate composition, hyporheic zone, invertebrate.

Introduction

Fine sediment transport and deposition is a natural component of healthy river systems, but in many regions across the globe fine sediment inputs have been increasing and are now far in excess of historic background levels (Foster et al., 2011; Collins and Zhang, 2016). In excessive quantities, fine sediment (defined here as particles ≤ 4mm; Sear 1993) is widely recognised to be a major contributor of ecosystem degradation, modifying biological, geomorphological and hydrological processes (Wood and Armitage, 1997; Church, 2002; Stewardson et al., 2016). Substrates comprising high fine sediment content typically have reduced porosity and hydraulic permeability, limiting the exchange of nutrients and oxygen between the surface and subsurface sediments (Bo et al., 2007; Datry et al., 2015; Hartwig and Borchardt, 2015). The infiltration of fine sediments into the river bed, commonly referred to as 'clogging' (Blaschke et al., 2003) or 'colmation' (Wharton et al., 2017), can also lead to a disconnection of surface substrates from the subsurface hyporheic zone, reducing the availability of interstitial habitat (Brunke, 1999; Descloux et al., 2013; Mathers et al., 2014).

The sediments immediately below the active riverbed and the hyporheic zone are widely recognised as integral to lotic ecosystem functioning (Stanford and Ward, 1988; Bo et al., 2007; Krause et al., 2011), serving as the ecotone between surface and groundwater ecosystems (Hancock, 2002) and frequently acting as a refugium for benthic fauna during adverse conditions in surface water habitats (Dole-Olivier, Marmonier and Buffy, 1997; Wood et al., 2010; Maazouzi et al., 2017). Typically, the hyporheic zone is limited in spatial extent to around a metre vertically below the riverbed (Williams and Hynes, 1974), although some lotic fauna have been recorded up to 10m below the riverbed and several kilometres laterally (Stanford and Ward, 1988).

Fine sediment deposition and infiltration into riverbeds can lead to habitat homogenisation, altering both the structure and function of instream communities (Kaller and Hartman, 2004; Descloux et al., 2013; Jones et al., 2015; Doretto et al., 2017). Substrates dominated by fine sediment typically support a greater proportion of taxa tolerant of low dissolved oxygen concentrations and that are capable of burrowing into the substrate (Rabeni et al., 2005; Cover et al., 2008). Moreover, the reduction of interstitial space may preclude large bodied organisms from accessing subsurface hyporheic sediments (Boulton, 2007). There have been a limited number of field-based studies which have investigated the role of body size on the distribution of macroinvertebrates. Those which have considered body size have reported a reduction in the maximum body size of organisms within substrates dominated by fine sediment (Buendia et al., 2013; Descloux et al., 2014; Mathers, Rice & Wood, 2017). However, direct evidence demonstrating and quantifying the role of body size on the ability of taxa to access subsurface substrates under varying fine sediment loads is lacking.

The extent of fine sediment clogging is dependent on a number of hydraulic and sedimentological parameters (Dudill et al., 2017). The direction and strength of hydrological exchange exerts a strong control over sediment ingress, with upwelling water limiting the infiltration of fine sediments and where sufficiently strong it can flush and clear interstitial pore spaces of fine sediment (Huettel et al., 1996; Ren and Packman, 2007). In contrast, downwelling water typically transports fine sediment and associated nutrients into the hyporheic zone, facilitating the process of clogging (Boulton, 1993; Mathers, Hill and Wood, 2017). Lateral hydraulic exchange may also be an important pathway for fine sediment transport within subsurface sediments of gravel-bed rivers (Pettricrew et al., 2007; Mathers and Wood, 2016; Harper et al., 2017; Casas-Mulet et al., 2017).

The sedimentological characteristics of both the coarse grained structural framework (Frostick et al., 1984) and the fine sediment matrix (Franssen et al., 2014) of a gravel deposit strongly influences the availability of pore spaces and the potential for fine sediment infiltration. The ratio between the diameter of coarse particles (forming the framework) and the infiltrating fine sediment (termed the grain size ratio) has been the focus of experimental work, in an effort to understand and quantify infiltration processes (e.g., Frings et al., 2008; Gibson et al., 2009a, 2009b; Herrero and Berni, 2016). In riverbeds where interstitial space permits, fine sediment typically infiltrates unhindered with pore spaces being filled from the base of the deposit upwards (Diplas and Parker, 1992), termed unimpeded static percolation. In gravel beds where this infiltration process dominates, interstitial space may be maintained in the presence of flushing flows. Larger grains in contrast, may be too large to infiltrate or pass through interstitial spaces and may become lodged in the gravel pore opening, impeding subsequent infiltration of fine sediment in a process termed bridging (Beschta and Jackson, 1979). This process can be ecologically significant as it may prohibit the transfer of resources below the clog and reduce the movement of organisms within and between interstitial spaces. Despite the potential ecological significance of characterising the dominant infiltration process occurring during sediment loading, relatively few studies to date have considered the distribution of infiltrating sediments when evaluating the effect of sedimentation in the field due to the inability to make direct observations. Consequently, a mechanistic understanding of the implications of fine sediment deposition as a function of the particle grain size for biota is limited.

In this paper, we examine the response of the freshwater amphipod, *Gammarus pulex* (L.) (Amphipoda: Crustcea) to different fine sediment loadings and particle sizes using *ex-situ* running water mesocosms specifically designed to allow the vertical location and distribution of individuals to be determined. The influence of body size on the ability of amphipods to access subsurface sediments was also examined. Amphipod crustacea occur widely in benthic, hyporheic and subterranean aquifers and caves, often dominating the biomass where they occur (MacNeil et al., 1997; Wood et al., 2010; Johns et al., 2015). *G. pulex* is rheophilic with a fully aquatic life history resulting in both adult and juveniles of different sizes being present within waterbodies throughout the year (Gledhill et al., 1993). *G. pulex* is moderately sensitive to sedimentation but is capable of burrowing through fine sediment deposits (Mathers et al., 2014), therefore making it an ideal model organism to examine the effect of fine sediment loading on its vertical movement patterns. We hypothesised that increasing sediment loading, particle size and body size of *G. pulex*, would influence the vertical distribution of individuals within the mesocosms. Specifically, we predicted that: 1) increasing levels of sediment loading would modify the vertical distribution of *G. pulex* within the experimental columns by limiting and / or preventing their movement to greater depths; 2) increasing particle size and heterogeneity of fine sediment would enhance the process of interstitial clogging and limit movement to greater depths and; 3) greater body size would limit an individual's ability to access deeper substrate layers under increasing sediment loading and particle size / heterogeneity.

Methods

Experimental sediment columns

Experiments were undertaken within two identical sediment columns comprising five interlocking sections as outlined in Mathers et al., (2014) (Figure 1 – sections A-E). Sections were 22 cm in diameter and contained 50 mm depth of coarse riverine sediments (gravel particles 20-64 mm in diameter). Each section was stacked vertically to provide a total sediment column depth of 250 mm. Ten holes (10 mm diameter) in the base of the top four sections (0 - 200 mm depth) permitted the transfer of water and organisms between sections. The final section (200-250 mm depth) was perforated with smaller holes (2 mm diameter) to allow the vertical exchange of water but prevent the movement of individuals outside of the experimental column. In addition, 0.25 mm mesh sieves were placed over the base and the top of the sediment columns for the duration of each experiment, and a 5 mm rubber seal was created around the base of each section to prevent the migration of individuals outside the column.

The sediment columns were placed inside separate large cylindrical black plastic water containers (90 x 40 cm, volume = 100 L). Two external pumps delivered flowing water to the columns (4.5-4.8 L min^{-1}) at a rate which was sufficient to maintain interstitial exchange through the sediments but which did not initiate sediment transport and consequently, any vertical movement of fine sediment during the experimental period was primarily a function of gravity or the direct activity of *G. pulex* movement. Experiments were conducted under upwelling hydraulic exchange conditions. Previous experiments have demonstrated the affinity of *G. pulex* for subsurface substrates under upwelling hydrological exchange and for surface substrates under downwelling conditions (Mathers et al., 2014), reflecting their rheophilic nature. The use of upwelling flow conditions in the absence of any fine sediment therefore provided a baseline distribution pattern of *G. pulex* for the experiments and allowed the effect of fine sediment clogging to be detected as a reduction in the number of individuals located beneath fine sediment treatments.

To simulate upwelling hydraulic conditions, water was pumped through a 200 mm funnel / diffuser on which the base of the experimental column was placed. Water rose through the column and overflowed from the top section of the column. Each experiment was conducted with a minimum of 10 cm water depth over the substrate and experimental containers were aerated via an aquaria pump and held at a constant water temperature (15^{o}C +/- 0.4^{o}C) by an external water-cooler (Aqua medic, Titan 150).

Three particle size treatments of pre-washed fine sediment were used in the experiments; i) fine sand (0.125 - 1 mm in diameter), ii) coarse sand (1 - 4 mm) and iii) heterogeneous sand which consisted of a 50 / 50 mixture of the coarse and fine sands (0.125 – 4 mm). The two size fractions were selected to include grains with a low propensity to clog interstitial spaces (0.125 – 1 mm) and grains with a high propensity to bridge between framework clasts thereby preventing further infiltration (1 – 4 mm). These particular grain sizes were determined using calculations based on studies by Gibson et al., (2009b) and Frings et al., (2008) who provide ratios to discriminate between pore filling loads and bed structure loads. Silt and clay fractions (<0.125 mm) were removed via wet sieving to ensure that turbidity did not vary between experiments. Prior to each experiment, dry fine sediment was applied evenly to the surface of each wet gravel section using a 4 mm sieve to enable fines to infiltrate under gravity. The same clean gravel framework was retained within each mesocosm layer throughout the experimental period for consistency.

Preliminary tests indicated that the application of an equivalent of 5 kg m^{-2} of the fine sand fraction (0.125 - 4 mm) filled all available interstices (100% of interstitial volume) of each section and covered the surface of all gravel particles. In addition to this heavy sediment loading which filled all interstitial spaces and covered all particles in the section of the column, a moderate sediment loading of 3 kg m^{-2} was applied in other treatments. This treatment filled the interstitial spaces of the lower half of the treated layer (when the 0.125 - 1 mm fraction was applied) but gravel particles remained visible at the surface, thereby representing conditions comparable to those observed in the field. Five sediment treatments were examined which were adapted from Mathers et al., (2014): 1. Heavy surface (benthic) sedimentation: the equivalent of 5 kg m^{-2} fine sediment applied to the top section (section A); 2. Subsurface (hyporheic) sedimentation of one section: the equivalent of 3 kg m^{-2} fine sediment applied to section C (100-150 mm depth); 3. Hyporheic sedimentation of three sub-surface sections (simulating hyporheic clogging): the equivalent of 3 kg m^{-2} applied to sections B, C and D (50-100 mm, 100-150 mm and 150-200 mm); 4. Benthic and subsurface-sedimentation (simulating benthic and hyporheic clogging) – the equivalent of 3 kg m^{-2} applied to all five layers (sections A, B, C, D and E); and 5. Control experiments (O – Figure 1) in which no fine sediment was applied and which consisted of an open gravel framework: 50 mm depth of gravel in all sections of the column. For all treatments, 50 mm gravel was retained in each section prior to the fine sediment treatment (Figure 1).

The sediment treatments (4 applications and 1 control, n = 5) and sediment grain sizes (n = 3) were combined in a full-factorial design giving 15 treatment combinations and one set of control experiments. Each combination was replicated six times to give a total of 90 individual experiments. Treatments were randomly allocated to an experimental trial. All *G. pulex* specimens were collected from a local stream (Burleigh Brook, Loughborough; 52°76’20”N., -1°24’18”W.) where they occurred in high abundances. To assess the influence of body size on the ability of an organism to utilize subsurface sediments, two body sizes classes were distinguished i) < 2mm head width and ii) > 2mm head width. Individuals were placed onto a 2 mm sieve allowing those small enough to pass through freely and thereby separating the two size classes. Fifteen individuals from the two sizes classes (total = 30 individuals) were released onto the top section of the prepared column (0-50 mm) and left for 24-hours to allow individuals to redistribute within the column. A single pre-conditioned horse chestnut leaf (*Aesculus hippocastanum*) was placed in each section for food (Joyce et al., 2007). At the end of each experiment (24-hours), individuals were collected from each section by washing the contents of each section through a nest of sieve sizes 4 – 0.125 mm. All fine sediments were removed from the column and retained for use in subsequent experimental trials.

Statistical analysis

Abundance

Differences in the abundance of *G. pulex* in each section as a function of sediment grain size and sediment loading were tested via a linear mixed effects model (LME) using the *lme* function from the package nlme (Pinheiro et al., 2018). Section (n = 5), sediment loading (n = 5) and sediment grain size (n = 3) were specified as fixed effects and section was nested within the experimental replicate (column) as a random factor (reflecting the fact that sections within individual columns were not independent from each other). Models were fitted using the restricted maximum likelihood (REML) estimation. Differences between sections within each sediment combination were tested using a Tukey *post hoc* test using the *glht* function in the multcomp package (Hothorn et al., 2008). *Post hoc* tests between the same section for each sediment grain size and sediment loading are provided in supplementary material (Tables S1-S3).

Body size

To assess the influence of body size on the ability of individuals to migrate vertically, data was coded so that the abundance of large and small bodied individuals above and below the section(s) in columns where the sediment treatment was applied could be analysed separately. This allowed us to examine the effect of both sediment grain size and sediment loading on the distribution of the two body size classes. For example, for sediment loading in the third layer, location above the sediment clog was calculated as the total abundance of individuals in sections 1-3 (0 – 150 mm), and sections 4-5 (150 - 250 mm) for below the sediment treatment. Differences were statistically tested using a linear mixed effects model with a similar structure to that employed in the abundance tests with location in column (n = 2), sediment loading (n = 4), sediment grain size (n = 3) and body size (n = 2) specified as fixed effects, and location nested within the experimental replicate (column) as a random factor. To assess the influence of body size on the vertical distribution of individuals as a function of sediment loading and sediment grain size, abundances were converted to the proportion of individuals above and below the sediment treatment for the respective size classes (small and large). An arcsine square root transformation was applied to the data, and differences in the proportion of individuals above the clog by sediment loading and sediment grain size were tested using a Tukey *post hoc* test using the *glht* function in the multcomp package. These tests were conducted for small and large bodied organisms separately and are presented as supplementary material (Tables S3 & S4). All statistical analyses were undertaken in the R environment (R Development Core Team, 2017).

Results

Recapture rates of amphipods for all experiments were high (average = 95.6%, range = 90 – 100%) and did not differ significantly between experiments. The distribution of *G. pulex* between the sediment layers was dependent on the sediment loading, fine sediment particle size and the interaction of these factors (all $p < 0.001$; Table 1). When amphipod body size was considered, the distribution of *G. pulex* above and below the sediment clog was dependent on sediment loading, fine sediment particle size, amphipod body size and the interaction of these factors (Table 2). Consequently, patterns in the vertical distribution of *G. pulex* vary in relation to sediment loading and sediment particle size (Tables S1 – S4).

Control conditions

Under upwelling conditions, the distribution of *G. pulex* was characterised by the greatest number of individuals being recorded in the bottom section (Section E, average 17 individuals, range = 19 - 16) and on average two individuals being recorded in the surface section (range = 4 – 0; Figure 2).

Faunal response to sedimentation under fine sand sediment conditions

In fine sand experimental trials, the greatest number of individuals were recorded in the bottom section (Section E; 200 – 250 mm) for the heavy surface sedimentation (Figure 3a; average = 19, range = 22 - 16). Subsurface (hyporheic) sedimentation of one layer (Section C; 150 – 200 mm) resulted in a less marked gradient of increasing abundance by depth (Figure 3b) and subsurface sedimentation of three layers (Sections B, C and D; 50 – 200 mm) resulted in no apparent differences in the abundance of individuals amongst the sections of the column (Figure 3c). Sedimentation of all layers resulted in a reversal of the distribution of individuals (Figure 3d) compared to the open gravel framework (no sediment addition; Figure 2) with greater numbers being recorded in the top layer (Section A; average = 15 individuals, range = 18 – 12).

Faunal response to sedimentation under coarse sand sediment conditions

Heavy surface sedimentation (Section A) under coarse sand conditions resulted in a reversal of the distribution of individuals compared to the open gravel framework with significantly greater numbers of *G. pulex* being recorded in the surface layer (Section A, average = 21 individuals, range = 24 – 18; Figure 3a). Subsurface (hyporheic) sedimentation of one layer (Section C) resulted in no statistical difference in the abundance of *G. pulex* between the sections (Figure 3b). Subsurface sedimentation of three layers (Sections B, C and D) also resulted in little variation in the distribution of amphipods between the sections with the greatest number of *G. pulex* recorded directly above the sediment treatment (Section B; average = 12 individuals, range = 14- 8; Figure 3c). Sedimentation of all sections resulted in the greatest number of amphipods in the surface layer, with relatively few individuals being recorded in any of the other four sections (Sections B – E; 7% of total abundance; Figure 3d).

Faunal response to sedimentation under heterogeneous sand sediment conditions (mixed of fine and coarse sand)

Under heterogeneous sand conditions, the distribution of *G. pulex* was characterised by greater numbers of individuals being recorded within the surface layer under all sediment treatments (Figure 3). The gradient of amphipod distribution by depth was however highly variable as a function of the sediment loading. Heavy surface sedimentation (Section A) and sedimentation of all sections resulted in significantly greater numbers of *G. pulex* being recorded in the surface layer (Figure 3a, d) with only 4.6% and 7% of total amphipod abundance being recorded in the bottom four layers for the two treatments respectively (Sections B – E). Subsurface (hyporheic) sedimentation of one (Section C) and three layers (Sections B, C and D) resulted in a decline in abundance with depth and was most marked under the three section sedimentation treatment (Figure 3b, c).

The influence of amphipod body size on the vertical distribution of G. pulex

Increasing sediment loading and particle size / heterogeneity resulted in an increasing proportion of amphipods being recorded above the deposited fine sediment (Figure 4). This pattern was most marked for large bodied individuals with a greater proportion of smaller individuals being able to migrate through the sediment treatment in all instances. The homogeneous fine sand treatment resulted in the greatest proportion of individuals migrating through the sediment treatment whilst the heterogeneous mixed fraction had the lowest (Figure 4a). With the exception of the fine sand treatment (0.125 – 1 mm) >90 % of large bodied individuals were unable to migrate through the sediment treatment. In contrast, the majority of small bodied individuals (> 50%) were able to migrate through the homogeneous fine sand (0.125 – 1 mm) and coarse sand treatments (1 - 4 mm), with the exception of the coarse sand treatment of all column layers (Sections A-E). Heterogeneous fine sediment (0.125 – 4 mm) resulted in the greatest proportion of large and small bodied individuals being recorded above the sediment treatment; although a greater proportion of small bodied individuals were able to migrate through the fine sediment treatment (Figure 4b). The number of large bodied individuals recorded below the sediment clog, as a function of sediment loading, demonstrated the largest variation for the fine sand treatment and was lowest for the heterogeneous mixed fraction. For small bodied individuals, coarse sand deposition conditions resulted in the greatest variation.

Discussion

Fine sediment deposition and clogging (colmation) of subsurface interstitial habitats potentially plays a significant role in determining the distribution of benthic and hyporheic invertebrates (Weigelhofer and Waringer, 2003; Mermillod-Blondin et al., 2014), although empirical evidence has been limited thus far. This study specifically sought to examine how varying particle size and sediment loading influenced the vertical distribution of *G. pulex* under upwelling hydraulic exchange conditions. Due to their widespread occurrence in benthic and subsurface habitats *G. pulex*, and other amphipod crustacea, are model organisms to examine the influence of particle size variations, fine sediment deposition and vertical movement patterns within alluvial sediments. Within our experiment we also considered how the vertical movement of individuals from different body size classes was affected by the application of different particle sizes and loading.

During control experiments, with no fine sediment applied, the majority of *G. pulex* individuals migrated to the deepest section of the column. This reflects the strong rheophilic preferences of *G. pulex* (Gledhill et al., 1993; Mathers et al., 2014) and the open gravel framework, which allowed the unimpeded flow of water and movement of individuals within the subsurface under upwelling conditions. Hydrological exchange exerts a strong influence over the distribution of macroinvertebrates (Pepin and Hauer, 2002; Olsen and Townsend, 2003; Mathers, Hill and Wood, 2017), and the deposition of fine sediment (Boulton, 1993; Mathers and Wood, 2016). This was the focus of a previous investigation (Mathers et al., 2014) and so is not considered further here.

Results from the current experiments provide evidence to support our first hypothesis; that increasing fine sediment loading would limit the ability of individuals to access deeper layers of the substrate. The most marked effect of increased loading was recorded for the fine sediment treatments. The application of homogeneous fine sand (0.125-1 mm) to a single section of the column (Section A or C, 0 – 50 mm or 100 – 150 mm) had a relatively limited effect on the movement of individuals due to the large interstitial spaces being maintained and the absence of clog formation (Brunke, 1999; Xu et al., 2012). However, at greater fine sand loadings, pore spaces gradually filled from the base of the column via unimpeded percolation (Diplas and Parker, 1992), limiting faunal access to the deeper sections of the substrate (column). The filling of all available pore space under the greatest sediment loading (3 kg or section A-E) resulted in a reversal in the distribution of *G. pulex* compared to control conditions and demonstrates the potential effect that chronic fine sedimentation loading may have on the ability of organisms to utilise subsurface substrates. As a result of increasing sediment loading the majority of individuals were restricted to the layers of the column above the sediment treatment, leading to a disconnection of surface and subsurface sediments. Sedimentation by homogeneous coarse sand (1 – 4 mm) restricted the ability of individuals to access subsurface sediments more than homogeneous fine sand (0.125 – 1 mm). This effect was enhanced through the addition of greater sediment loadings for homogeneous fine and coarse sand but was less marked with the addition of heterogeneous sand (0.125 – 4 mm) because even at the lower loadings the vertical movement of almost all individuals was prevented.

In support of our second hypothesis, the results also indicate that increasing particle size and heterogeneity of fine sediment exerts a strong influence on the propensity for clog formation and the ability of individuals to access deeper layers of the column. Coarse sand resulted in the formation of surface clogs associated with particles being unable to percolate into the subsurface and the bridging of pore spaces (Beschta and Jackson, 1979) even at the lowest sediment loadings. This effect was most marked for heterogeneous sand (0.125 – 4 mm) which had the strongest filtering effect and resulted in up to 25 individuals being recorded in the surface (benthic) layer of the column (0 – 50 mm).

Finally, we found evidence to support our third hypothesis, that increasing body size would limit an individual's ability to access deeper substrates. We found that both sediment load and particle size acted as a filter on the ability of an individual to migrate vertically, with only smaller bodied individuals being recorded in the deeper layers of the column for the greatest sediment loadings and for increasing heterogeneity. While the ability of an individual to access subsurface interstitial habitat has been reported to be heavily dependent on body size (Gayraud and Philippe, 2001; Descloux et al., 2014; Vadher et al., 2017), this experimental study provides direct evidence for the filtering effect of fine sediment loading and particle size compared to open frameworks as a result of the ability to quantify the number and size of individuals at different depths within the column. The filtering effect was most marked for large bodied amphipods, with a greater proportion being recorded above the sediment clog for all but two of the 12 sediment applications. For fine sand, sediment loading resulted in marked variability in the number of individuals being recorded above the sediment treatment. In contrast, coarse and heterogeneous sand treatments demonstrated less variability associated with sediment loading, due to the bridging of pore space even under surface sediment applications and the confinement of organisms to substrates above the sediment treatment.

Small bodied individuals demonstrated a similar, but less marked effect, with more individuals recorded below the sediment application for six of the 12 sediment applications. Homogeneous fine sand (0.125 – 1 mm) had little effect on the ability of small individuals to migrate to deeper substrates even for the greatest loading. In contrast to large bodied individuals, around 50% of small bodied individuals were located below the sediment treatment for the homogeneous coarse sand (1 – 4 mm) for three of the applications (5 kg surface – Section A; 3 kg middle – Section C and 3 kg application on three sections B-D). Only with the treatment of all sections of the column (A-E) was the movement of small bodies restricted to the surface layer of the mesocosm. Heterogeneous sand (0.125 – 4 mm) acted as the strongest filter for both size classes; although some small bodied individuals were able to migrate below the sediment treatment in almost every instance. In contrast to large bodied individuals, the effect of different sediment loadings were most marked for the coarse sand treatments. Heterogeneous sand had a consistent effect for small and large bodied individuals regardless of the loading applied. However, it should be noted that the distribution of small bodied individuals may be in part influenced by their reproductory behaviour and the establishment of pre-copulatory pairs (Ward, 1983). Although no pre-copulatory pairs were placed into the mesocosm at the start of experiments, a number were observed at the termination, 24-hours later. As a result, the distribution of some small bodied individuals may be influenced by larger individuals; some in pre-copulatory pairs in the surface layer of the column.

The experiments presented here were conducted under controlled laboratory conditions, with sediment deposition being the only factor which was manipulated. Within the natural environment, clogging of interstitial pore space has the potential to modify interstitial flow and the transport of dissolved solutes and resources, resulting in reduced dissolved oxygen concentrations and water quality (Greig, Sear & Carling, 2005, Sear et al., 2017). Consequently, the effects on an organism's ability to utilise the subsurface sediments following fine sediment loading at levels reported in this study may represent an upper estimate. Although individuals may still be able to access subsurface sediments, the associated changes in the physiochemical conditions may make the abiotic environment unfavourable for most taxa / individuals.

Study implications

Deposition of fine sediment, which results in the clogging of substrates and prevents access to subsurface habitats, may have far reaching consequences for benthic and hyporheic communities. Refugium use reduces the predation risk of benthic invertebrates (Gee, 1982). In the case of *G. pulex*, predator avoidance behaviour and refuge seeking behaviour has been widely documented (e.g., Dahl and Greenberg, 1996; Sih, 1997) and the loss of subsurface habitat due to clogging may increase the risk of predation. However, most research examining the role of habitat availability on predator-prey interactions has focussed on the role of hydrological disturbances (Lancaster et al., 1990; Lancaster, 1996) while the effects of sediment deposition are less well documented (see Jones et al., 2012 for review). Given the well-established substrate size selectivity reported for *G. pulex* (e.g., Thompson and Moule, 1982), sedimentation and clogging of the surface of the substrate may lead to a concentration of biotic interactions in the benthic zone and enhanced predation of large bodied individuals (Strommer and Smock, 1989; Covich et al., 2003). Moreover, a reduction of interstitial space may also affect the growth of *G. pulex* over longer time scales, with interstitial pore space availability being reported to reduce the energy requirements and enhance the growth potential of individuals (Franken et al., 2006). Reductions in growth can have cascading effects on populations associated with reduced egg numbers for smaller females (Glazier, 2000).

This research highlights the importance of characterising both the particle size and heterogeneity of deposited fine sediment when considering the effects on instream invertebrates. To date, only a limited number of studies have specifically considered the grain size distribution of either the gravel-bed matrix or the infiltrating material on instream communities and populations (but see Gayraud and Philippe, 2003; Weigelhofer and Waringer, 2003; Mathers and Wood, 2016; Vadher et al., 2017). However, the current investigation demonstrates that the effect of sedimentation and clogging on faunal distribution of benthic and hyporheic invertebrates is more complex than the gross fine sediment cover. We found that the resultant pattern of faunal distribution is dependent on both the characteristics of the deposited fine sediment (particle size, heterogeneity and loading) and the process of deposition that subsequently takes place (unimpeded percolation or bridging; Dudill et al., 2017). As a result, we recommend that future studies concerned with examining the effects of fine sediment for biota should quantify the grain size distribution of the fine sediment (and the gravel-bed matrix) so that the mechanistic controls of fine sediment on instream ecology can be more clearly understood. Better characterisation of the deposited fine sediments will allow river managers to direct resources more efficiently towards identifying and managing sediment sources within the catchment (Laceby et al., 2017) and where restoration activities are likely to be feasible (Wohl et al., 2015).

There have been recent calls for an improved mechanistic understanding of the effects of fine sediment on macroinvertebrates (Wilkes et al., 2017), with some studies documenting variable responses of benthic invertebrates to sedimentation (Descloux et al., 2014; Mathers, Rice & Wood, 2017; Murphy et al., 2017). The results from these experiments provide the first direct evidence that the effects of sedimentation vary as a function of sediment characteristics (particle size, heterogeneity and loading) and the body size of fauna. Fine sand demonstrated the greatest variability in effects associated with loading for large bodied individuals whilst the effects for small bodied individuals were most variable under coarse sand loading. As a result, broad-scale generalisations regarding an individual species' response to sedimentation are unlikely to reflect the subtle effects of intra-specific variations within the morphological characteristics of a population (such as body size which is typically represented as an average value) or fitness. For example, Orlofske and Baird (2010) reported that 55% of measured body sizes of specific taxa were considerably smaller or larger than those documented in existing trait databases. As a result, there is a need for researchers examining the effect of sedimentation to report the body size of the taxa studied (model organism), such as amphipod crustacea which often comprise populations of varying life-stages and body sizes throughout the year. This will enable potential differences in the mean body size of populations to be more readily compared between studies. This is potentially a vital controlling factor given that the effects of fine sediment deposition for many taxa, especially aquatic insects, will vary at different life stages associated with increasing body size. Enhancing this knowledge base will provide mechanistic evidence for studies which have observed the effects of fine sediment loading on benthic communities to vary temporally under field conditions (e.g., Mathers, Rice and Wood, 2017). The implications of fine sediment deposition are therefore complex and reflect a combination of different factors including loading, particle size and an individual's body size.

Acknowledgements

The authors thank Stuart Ashby and Richard Harland for providing technical and laboratory support whilst undertaking the experiments. PJW acknowledges the support of a Cave Science and Technology Research Fund grant from the British Cave Research Association for support to develop the experimental facility. We would like to thank the three reviewers and the Associate Editor whose helpful comments enhanced the clarity and interpretation of the study outcomes.

Conflict of Interest

The authors declare no conflict of interest.

References

Beschta, R.L., & Jackson, W.L. (1979). The intrusion of fine sediments into a stable gravel bed. *Journal of the Fisheries Board of Canada*, 36, 204-210. 10.1139/f79-030

Blaschke, A.P., Steiner, K.H., Schmalfuss, R., Gutknecht, D., & Sengschmitt, D. (2003). Clogging processes in hyporheic interstices of an impounded river, the Danube at Vienna, Austria. *International Review of Hydrobiology*, 88, 397-413. 10.1002/iroh.200390034

Bo, T., Fenoglio, S., Malacarne, G., Pessino, M., & Sgariboldi, F. (2007). Effects of clogging on stream macroinvertebrates: an experimental approach. *Limnologica-Ecology and Management of Inland Waters*, 37, 186-192. 10.1016/j.limno.2007.01.002

Boulton, A.J. (1993). Stream ecology and surface-hyporheic hydrologic exchange: implications, techniques and limitations. *Marine and Freshwater Research*, 44, 553-564. 10.1071/MF9930553

Boulton, A.J. (2007). Hyporheic rehabilitation in rivers: restoring vertical connectivity. *Freshwater Biology*, 52, 632-650.

Brunke, M. (1999). Colmation and depth filtration within streambeds: retention of particles in hyporheic interstices. *International Review of Hydrobiology*, 84, 99-117. 10.1002/iroh.199900014

Buendia, C., Gibbins, C.N., Vericat, D., Batalla, R.J., & Douglas, A. (2013). Detecting the structural and functional impacts of fine sediment on stream invertebrates. *Ecological Indicators*, 25, 184-196. 10.1016/j.ecolind.2012.09.027

Casas-Mulet, R., Alfredsen, K.T., McCluskey, A.H., & Stewardson, M.J. (2017). Key hydraulic drivers and patterns of fine sediment accumulation in gravel streambeds: A conceptual framework illustrated with a case study from the Kiewa River, Australia. *Geomorphology*, 299, 152-164. 10.1016/j.geomorph.2017.08.032

Church, M. (2002). Geomorphic thresholds in riverine landscapes. *Freshwater Biology*, 47, 541-557. 10.1046/j.1365-2427.2002.00919.x

Collins, A.L., & Zhang, Y. (2016). Exceedance of modern ‘background’ fine-grained sediment delivery to rivers due to current agricultural land use and uptake of water pollution mitigation options across England and Wales. *Environmental Science and Policy,* 61, 61-73. 10.1016/j.envsci.2016.03.017

Cover, M.R., May, C.L., Dietrich, W.E., & Resh, V.H. (2008). Quantitative linkages among sediment supply, streambed fine sediment, and benthic macroinvertebrates in northern California streams. *Journal of the North American Benthological Society*, 27, 135-149. 10.1899/07-032.1

Covich, A.P., Crowl, T.A., & Scatena, F.N. (2003). Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology*, 48, 1199-1206. 10.1046/j.1365-2427.2003.01093.x

Dahl, J., & Greenberg, L. (1996). Effects of habitat structure on habitat use by *Gammarus pulex* in artificial streams. *Freshwater Biology* 36:487–495. 10.1046/j.1365-2427.1996.00096.x

Datry, T., Lamouroux, N., Thivin, G., Descloux, S., & Baudoin, J.M. (2015). Estimation of sediment hydraulic conductivity in river reaches and its potential use to evaluate streambed clogging. *River Research and Applications, 31,* 880-891. 10.1002/rra.2784

Descloux, S., Datry, T., & Marmonier, P. (2013). Benthic and hyporheic invertebrate assemblages along a gradient of increasing streambed colmation by fine sediment. *Aquatic Sciences, 75,* 493-507. 10.1111/j.1365-2427.2011.02725.x

Descloux, S., Datry, T., & Usseglio-Polatera, P. (2014). Trait-based structure of invertebrates along a gradient of sediment colmation: benthos versus hyporheos responses. *Science of the Total Environment*, 466, 265-276. 10.1016/j.scitotenv.2013.06.082

Diplas, P., & Parker, G. (1992). Deposition and removal of fines in gravel-bed streams. In: Dynamics of Gravel-Bed Rivers (Eds P. Billi, R.D. Hey, C.R. Thorne and P. Tacconi), pp. 313–329. John Wiley & Sons Ltd, New York.

Dole‐Olivier, M.J., Marmonier, P. & Beffy, J.L. (1997). Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium? *Freshwater Biology*, *37*, 257-276. 10.1046/j.1365-2427.1997.00140.x

Doretto, A., Bona, F., Piano, E., Zanin, I., Eandi, A.C., & Fenoglio, S. (2017). Trophic availability buffers the detrimental effects of clogging in an alpine stream. *Science of the Total Environmen*t, 592, 503-511. 10.1016/j.scitotenv.2017.03.108

Dudill, A., Frey, P., & Church, M. (2017). Infiltration of fine sediment into a coarse mobile bed: a phenomenological study. *Earth Surface Processes and Landforms*, 42, 1171-1185. 10.1002/esp.4080

Foster, I.D.L., Collins, A.L., Naden, P.S., Sear, D.A., Jones, J.I., & Zhang, Y. (2011). The potential for paleolimnology to determine historic sediment delivery to rivers. *Journal of Palaeolimnology,* 45, 287-306. 10.1007/s10933-011-9498-9

Franken, R.J., Batten, S., Beijer, J.A., Gardeniers, J.J., Scheffer, M., & Peeters, E.T.H.M. (2006). Effects of interstitial refugia and current velocity on growth of the amphipod *Gammarus pulex* Linnaeus. *Journal of the North American Benthological Society, 25,* 656-663. 10.1899/0887-3593(2006)25[656:EOIRAC]2.0.CO;2

Franssen, J., Lapointe, M., & Magnan, P. (2014). Geomorphic controls on fine sediment reinfiltration into salmonid spawning gravels and the implications for spawning habitat rehabilitation. *Geomorphology*, 211, 11-21. 10.1016/j.geomorph.2013.12.019

Frings, R.M., Kleinhans, M.G., & Vollmer, S. (2008). Discriminating between pore‐filling load and bed‐structure load: a new porosity‐based method, exemplified for the river Rhine. *Sedimentology*, 55, 1571-1593. 10.1111/j.1365-3091.2008.00958.x

Frostick, L.E., Lucas, P.M., & Reid, I. (1984). The infiltration of fine matrices into coarse-grained alluvial sediments and its implications for stratigraphical interpretation. *Journal of the Geological Society, 141,* 955-965. 10.1144/gsjgs.141.6.0955

Gayraud, S., & Philippe, M. (2001). Does subsurface interstitial space influence general features and morphological traits of the benthic macroinvertebrate community in streams? *Archiv für Hydrobiologie*, 151, 667-686. 10.1127/archiv-hydrobiol/151/2001/667

Gayraud, S., & Philippe, M. (2003). Influence of Bed-Sediment Features on the Interstitial Habitat Available for Macroinvertebrates in 15 French Streams. *International Review of Hydrobiology, 88,* 77-93. 10.1002/iroh.200390007

Gee, J.H.R. (1982). Resource utilization by Gammarus pulex (Amphipoda) in a Cotswold stream: a microdistribution study. *Journal of Animal Ecology*, 51, 817–832. 10.2307/4007

Gibson, S., Abraham, D., Heath, R., & Schoellhamer, D. (2009a). Bridging process threshold for sediment infiltrating into a coarse substrate. *Journal of Geotechnical and Geoenvironmental Engineering*, 136, 402-406. doi: 10.1061/%28ASCE%29GT.1943-5606.0000219.

Gibson, S., Abraham, D., Heath, R., & Schoellhamer, D. (2009b). Vertical gradational variability of fines deposited in a gravel framework. *Sedimentology*, 56, 661-676. 10.1111/j.1365-3091.2008.00991.x

Glazier, D.S. (2000). Is fatter fitter? Body storage and reproduction in ten populations of the freshwater amphipod *Gammarus minus. Oecolgia*, 122, 335-345. 10.1007/s004420050039

Gledhill T, Sutcliffe D.W., & Williams, W.D. (1993) *British Freshwater Crustacea Malacostraca: A Key with Ecological Notes*. Freshwater Biological Association Publication No.52. 173pp.

Greig S.M., Sear D.A. & Carling P.A. (2005). The impact of fine sediment accumulation on the survival of incubating salmon progeny: Implications for sediment management. Science of the Total Environment, 344, 241–258. 10.1016/j.scitotenv.2005.02.010.

Hancock, P.J. (2002) Human impacts on the stream-groundwater exchange zone. *Environmental Management*. 29, 763-781. 10.1007/s00267-001-0064-5

Harper, S.E., Foster, I.D., Lawler, D.M., Mathers, K.L., McKenzie, M., & Petts, G.E. (2017). The complexities of measuring fine sediment accumulation within gravel-bed rivers. *River Research and Applications,* 33, 1575-1584. 10.1002/rra.3198

Hartwig, M., & Borchardt, D. (2015). Alteration of key hyporheic functions through biological and physical clogging along a nutrient and fine-sediment gradient. *Ecohydrology*, 8, 961-975. 10.1002/eco.1571

Herrero, A., & Berni, C. (2016). Sand infiltration into a gravel bed: A mathematical model. *Water Resources Research*, 52, 8956–8969. 10.1002/2016WR019394

Huettel, M., Ziebis, W., & Forster, S. (1996) Flow-induced uptake of particulate matter in permeable sediments. *Limnology and Oceanography,* 4, 309-322. 10.4319/lo.1996.41.2.0309

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, 50, 346-363.

Johns, T., Jones, J.I., Knight, L., Maurice, L., Wood, P. & Robertson, A. (2015). Regional-scale drivers of groundwater faunal distributions. *Freshwater Sciences*, 34, 316-328.

Jones, I., Growns, I., Arnold, A., McCall, S., & Bowes, M. (2015). The effects of increased flow and fine sediment on hyporheic invertebrates and nutrients in stream mesocosms. *Freshwater Biology*, 60, 813-826. doi:10.1111/fwb.12536

Jones, J.I., Murphy, J.F., Collins, A.L., Sear, D.A., Naden, P.S., & Armitage, P.D. (2012). The impact of fine sediment on macro‐invertebrates. *River Research and Applications*, 28, 1055-1071. 10.1002/rra.1516

Joyce, P., Warren, L.L., & Wotton, R.S. (2007). Faecal pellets in streams: their binding, breakdown and utilization. *Freshwater Biology*, 52, 1868–1880. 10.1111/j.1365-2427.2007.01828.x

Kaller, M.D., & Hartman, K.J. (2004). Evidence of a threshold level of fine sediment accumulation for altering benthic macroinvertebrate communities. *Hydrobiologia*, 518, 95-104. 10.1023/B:HYDR.0000025059.82197.35

Krause, S., Hannah, D.M., Fleckenstein, J.H., Heppell, C.M., Kaeser, D., Pickup, R., Pinay, G., Robertson, A.L. & Wood, P.J. (2011). Inter-disciplinary perspectives on processes in the hyporheic zone. *Ecohydrology,* 4, 481-499. 10.1002/eco.176

Laceby, J.P., Evrard, O., Smith, H.G., Blake, W.H., Olley, J.M., Minella, J.P., & Owens, P.N. (2017). The challenges and opportunities of addressing particle size effects in sediment source fingerprinting: A review. *Earth-Science Reviews,* 169, 85-103. 10.1016/j.earscirev.2017.04.009

Lancaster, J. (1996). Scaling the effects of predation and disturbance in a patchy environment. O*ecologia*, 107, 321-331. 10.1007/BF00328448

Lancaster J, Hildrew A.G., & Townsend C.R. (1990). Stream flow and predation effects on the spatial dynamics of benthic invertebrates. *Hydrobiologia*. 203, 177-190. 10.1007/BF00005686

Maazouzi, C., Galassi, D., Claret, C., Cellot, B., Fiers, F., Martin, D., Marmonier, P. & Dole-Olivier, M.J. (2017). Do benthic invertebrates use hyporheic refuges during streambed drying? A manipulative field experiment in nested hyporheic flowpaths. *Ecohydrology*, *10*(6). 10.1002/eco.1865

MacNeil C., Dick J.T. & Elwood R.W. (1997) The trophic ecology of freshwater Gammarus spp. (Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group concept. Biological Reviews, 72, 349– 364.

Mathers, K.L., Millett, J., Robertson, A.L., Stubbington, R., & Wood, P.J. (2014). Faunal response to benthic and hyporheic sedimentation varies with direction of vertical hydrological exchange. *Freshwater Biology*, 59, 2278-2289. 10.1111/fwb.12430

Mathers, K.L., & Wood, P.J. (2016). Fine sediment deposition and interstitial flow effects on macroinvertebrate community composition within riffle heads and tails. *Hydrobiologia*, 776*,* 147-160. 10.1007/s10750-016-2748-0

Mathers, K.L., Hill, M.J., & Wood, P.J. (2017). Benthic and hyporheic macroinvertebrate distribution within the heads and tails of riffles during baseflow conditions. *Hydrobiologia, 794,* 17-30. 10.1007/s10750-017-3092-8

Mathers, K.L., Rice, S.P., & Wood, P.J. (2017). Temporal effects of enhanced fine sediment loading on macroinvertebrate community structure and functional traits. *Science of The Total Environment*, 599, 513-522. 10.1016/j.scitotenv.2017.04.096

Mermillod-Blondin, F., Winiarski, T., Foulquier, A., Perrissin, A., & Marmonier, P. (2015) Links between sediment structures and ecological processes in the hyporheic zone: ground-penetrating radar as a non-invasive tool to detect subsurface biologically active zones. *Ecohydrology, 8,* 626-641. 10.1002/eco.1530

Murphy, J.F., Jones, J.I., Arnold, A., Duerdoth, C.P., Pretty, J.L., Naden, P.S., Sear, D.A. & Collins, A.L. (2017). Can macroinvertebrate biological traits indicate fine-grained sediment conditions in streams? *River Research and Applications*, 33, 1606-1617. 10.1002/rra.3194

Olsen D.A. & Townsend C.R. (2003). Hyporheic community composition in a gravel-bed stream: influence of vertical hydrological exchange, sediment structure and physiochemistry. *Freshwater Biology*, 48, 1363-1378. 10.1046/j.1365-2427.2003.01097.x

Orlofske, J.M. & Baird, D.J. (2014). Incorporating continuous trait variation into biomonitoring assessments by measuring and assigning trait values to individuals or taxa. *Freshwater Biology*, *59*, 477-490. 10.1111/fwb.12279.

Petticrew, E.L., Krein, A., & Walling, D.E. (2007). Evaluating fine sediment mobilization and storage in a gravel-bed river using controlled reservoir releases. *Hydrological Processes, 21,* 198-210. 10.1002/hyp.6183

Pepin, D.M. & Hauer, F.R. (2002) Benthic response to groundwater-surface water exchange in 2 alluvial rivers in north-western Montana. *Journal of the North American Benthological Society,* 21, 370-383*.1* 0.2307/1468476

Pinheiro J, Bates D, DebRoy S, Sarkar D & R Core Team (2018). *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-137, https://CRAN.R-project.org/package=nlme.

Rabení, C.F., Doisy, K.E., & Zweig, L.D. (2005). Stream invertebrate community functional responses to deposited sediment. *Aquatic Sciences*, 67, 395-402. 10.1007/s00027-005-0793-2

Ren, J., & Packman, A.I. (2007). Changes in fine sediment size distributions due to interactions with streambed sediments. *Sedimentary Geology,* 3, 529-537. 10.1016/j.sedgeo.2007.03.021

Sear, D.A., Pattison, I., Collins, A.L., Smallman, D.J., Jones, J.I. & Naden, P.S. (2017). The magnitude and significance of sediment oxygen demand in gravel spawning beds for the incubation of salmonid embryos. *River Research and Applications*, *33*, 642-1654. 10.1002/rra.3212

Sear, D. A (1993) Fine sediment infiltration into gravel spawning beds within a regulated river experiencing floods - ecological implications for salmonids. R*egulated Rivers Research and Management,* 8, 373–390. 10.1002/rrr.3450080407

Sih, A. (1997). To hide or not to hide? Refuge use in a fluctuating environment. *Trends in Evolution and Ecology*, 12, 375-376. 10.1016/S0169-5347(97)87376-4

Stanford, J.A. and Ward, J.V. (1988). The hyporheic habitat of river ecosystems. *Nature*, 335, 64-66. 10.1038/335064a0

Stewardson, M.J., Datry, T., Lamouroux, N., Pella, H., Thommeret, N., Valette, L., & Grant, S.B. (2016). Variation in reach-scale hydraulic conductivity of streambeds. *Geomorphology*, 259, 70-80. 10.1016/j.geomorph.2016.02.001

Strommer, J.L., & Smock, L.A. (1989). Vertical distribution and abundance of invertebrates within the sandy substrate of a low-gradient headwater stream. *Freshwater Biology*, *22,* 263-274. 10.1111/j.1365-2427.1989.tb01099.x

Thompson, D.J. & Moule, S.J. (1983). Substrate selection and assortative mating in *Gammarus pulex* L. *Hydrobiologia*. 99, 3-6. 10.1007/BF00013711

Vadher, A.N., Leigh, C., Millett, J., Stubbington, R., & Wood, P.J. (2017). Vertical movements through subsurface stream sediments by benthic macroinvertebrates during experimental drying are influenced by sediment characteristics and species traits. *Freshwater Biology, 62,* 1730-1740. 10.1111/fwb.12983

Xu M., Wang Z., Pan B., & Zhou N. (2012). Distribution and species composition of macroinvertebrates in the hyporheic zone of bed sediment. *International Journal of Sediment Research*, 27, 129-140. 10.1016/S1001-6279(12)60022-5

Ward, P.I. (1983) Advantages and a disadvantage of large size for male *Gammarus pulex* (Crustacea: Amphipoda). *Behavioural Ecology and Sociobiology*. 14, 69-76.

Weigelhofer, G., & Waringer, J. (2003). Vertical distribution of benthic macroinvertebrates in riffles versus deep runs with differing contents of fine sediments (Weidlingbach, Austria). *International Review of Hydrobiology*, 88, 304-313. 10.1002/iroh.200390027

Wharton, G., Mohajeri, S.H., & Righetti, M. (2017). The pernicious problem of streambed colmation: a multi-disciplinary reflection on the mechanisms, causes, impacts, and management challenges. *Wiley Interdisciplinary Reviews: Water*, 4, e1231. 10.1002/wat2.1231

Wilkes, M.A., Mckenzie, M., Murphy, J.F., & Chadd, R.P. (2017). Assessing the mechanistic basis for fine sediment biomonitoring: Inconsistencies among the literature, traits and indices. *River Research and Applications*, 33, 1618-1629. 10.1002/rra.3139

Williams, D. D. & Hynes, H.B.N. (1974). The occurrence of benthos deep in the substratum of a stream. *Freshwater Biology,* 4, 233-256. 10.1111/j.1365-2427.1974.tb00094.x

Wohl, E., Bledsoe, B.P., Jacobson, R.B., Poff, N.L., Rathburn, S.L., Walters, D.M., & Wilcox, A.C. (2015). The natural sediment regime in rivers: broadening the foundation for ecosystem management. *BioScience*, 65: 358-371. 10.1093/biosci/biv002

Wood, P.J., & Armitage, P.D. (1997). Biological effects of fine sediment in the lotic environment. *Environmental management*, 21, 203-217. 10.1007/s002679900019

Wood, P.J., Boulton, A.J., Little, S. & Stubbington, R. (2010) Is the hyporheic zone a refugium for macroinvertebrates during severe low flow conditions?. *Fundamental and Applied Limnology*, 176, 377-390. 10.1127/1863-9135/2010/0176-0377

Tables

Table 1. Univariate linear mixed effects model (LME) analysis for *G. pulex* abundance associated with sediment size (fine, coarse, mixed), sediment loading (n=6), section / depth within the sediment column (n=5) and the interactions between these factors. Significant values (p<0.05) are presented in bold.

Factor	d.f	F	*p*
Section / depth	4, 294	387.10	**<0.001**
Sediment loading	4, 75	0.53	0.718
Sediment size	2, 75	0.33	0.719
Sediment loading x sediment size	8, 75	0.13	0.998
Section / depth x sediment loading	16, 294	201.95	**<0.001**
Section / depth x sediment size	8, 294	132.00	**<0.001**
Section / depth x sediment loading x sediment size	32, 294	29.37	**<0.001**

Table 2. Univariate linear mixed effects model (LME) analysis for *G. pulex* abundance associated with sediment size (fine, coarse, mixed), sediment loading (n=6), location within the sediment column (above or below sediment clog), amphipod body size and the interactions between these factors. Significant values (p<0.05) are presented in bold

Factor	**d.f**	**F**	***p***
Location	1, 120	391.06	**<0.001**
Sediment loading	3, 120	0.79	0.502
Sediment size	2, 120	0.17	0.840
Body size	1, 120	3.16	0.078
Location x sediment loading	3, 120	30.38	**<0.001**
Location x sediment size	2, 120	435.58	**<0.001**
Sediment size x sediment loading	6, 120	0.19	0.979
Location x body size	1, 120	312.85	**<0.001**
Sediment loading x body size	3, 120	0.14	0.935
Sediment size x body size	2, 120	0.67	0.516
Location x sediment loading x sediment size	6, 120	16.75	**<0.001**
Location x sediment loading x body size	3, 120	5.97	**0.001**
Location x sediment size x body size	2, 120	15.99	**<0.001**
Sediment loading x sediment size x body size	6, 120	0.40	0.877
Location x sediment loading x sediment size x body size	6, 120	11.51	**<0.001**

List of Figures

Figure 1. Fine sediment treatments applied to sections / layers of substratum columns (A – 0-50 mm; B – 50-100 mm; C – 100-150 mm; D – 150-200 mm; and E – 200-250 mm) during experiments: O. Open gravel framework for all layers (control conditions); 1. Benthic sedimentation with the equivalent of 5 kg m-2; 2. Hyporheic sedimentation of one layer (100-150 mm) with the equivalent of 3 kg m-2; 3. Hyporheic sedimentation of three layers (50-200mm) with the equivalent of 3 kg m-2 applied to each layer; and 4. Benthic and hyporheic sedimentation (all layers) with the equivalent of 3 kg m-2. Figure adapted from Mathers et al., (2014).

Figure 2. Mean number of Gammarus pulex (± 1SE) recorded within each section of the sediment column (0-50mm; 50-100mm; 100-150mm; 150-200mm; 200-250mm) under open gravel framework conditions (control). For post hoc comparisons between the same section for different sediment loading or grain size see Tables S1 and S2.

Figure 3. Mean number of Gammarus pulex (± 1SE) recorded within each section of the sediment column (0-50mm; 50-100mm; 100-150mm; 150-200mm; 200-250mm) under fine sediment loading a) surface (benthic) sedimentation with the equivalent of 5kg m-2; b) subsurface (hyporheic) sedimentation of one layer (100-150mm) with the equivalent of 3kg m-2; c) subsurface (hyporheic) sedimentation of three layers (50-200mm) with the equivalent of 3kg m-2; d) benthic and subsurface (hyporheic) sedimentation of all layers (0-200mm) with the equivalent of 3kg m-2. Shading on the figure represents where the sediment was applied. Solid circles = fine sand (0.125 – 1mm); grey circles = coarse sand (1-4mm) and; solid squares = heterogeneous sand (0.125 – 4mm). For post hoc comparisons (i.e. between sections for different sediment loading or grain size) see Tables S1 and S2.

Figure 4. Proportion (mean ± 1SE) of a) large bodied and; b) small bodied Gammarus pulex individuals recorded above the sediment clog for each sediment grain size (fine sand, coarse sand and mixed) and sediment loading. Rhombus = surface (benthic) sedimentation with the equivalent of 5kg m-2; circle = subsurface (hyporheic) sedimentation of one layer (100-150mm) with the equivalent of 3kg m-2; square = subsurface (hyporheic) sedimentation of three layers (50-200mm) with the equivalent of 3kg m-2 and; triangle = benthic and subsurface (hyporheic)

sedimentation of all layers (0-200mm) with the equivalent of 3kg m-2. For post hoc comparisons (i.e. between the same section for different sediment loading or grain size) for each body size category see Tables S3 and S4.

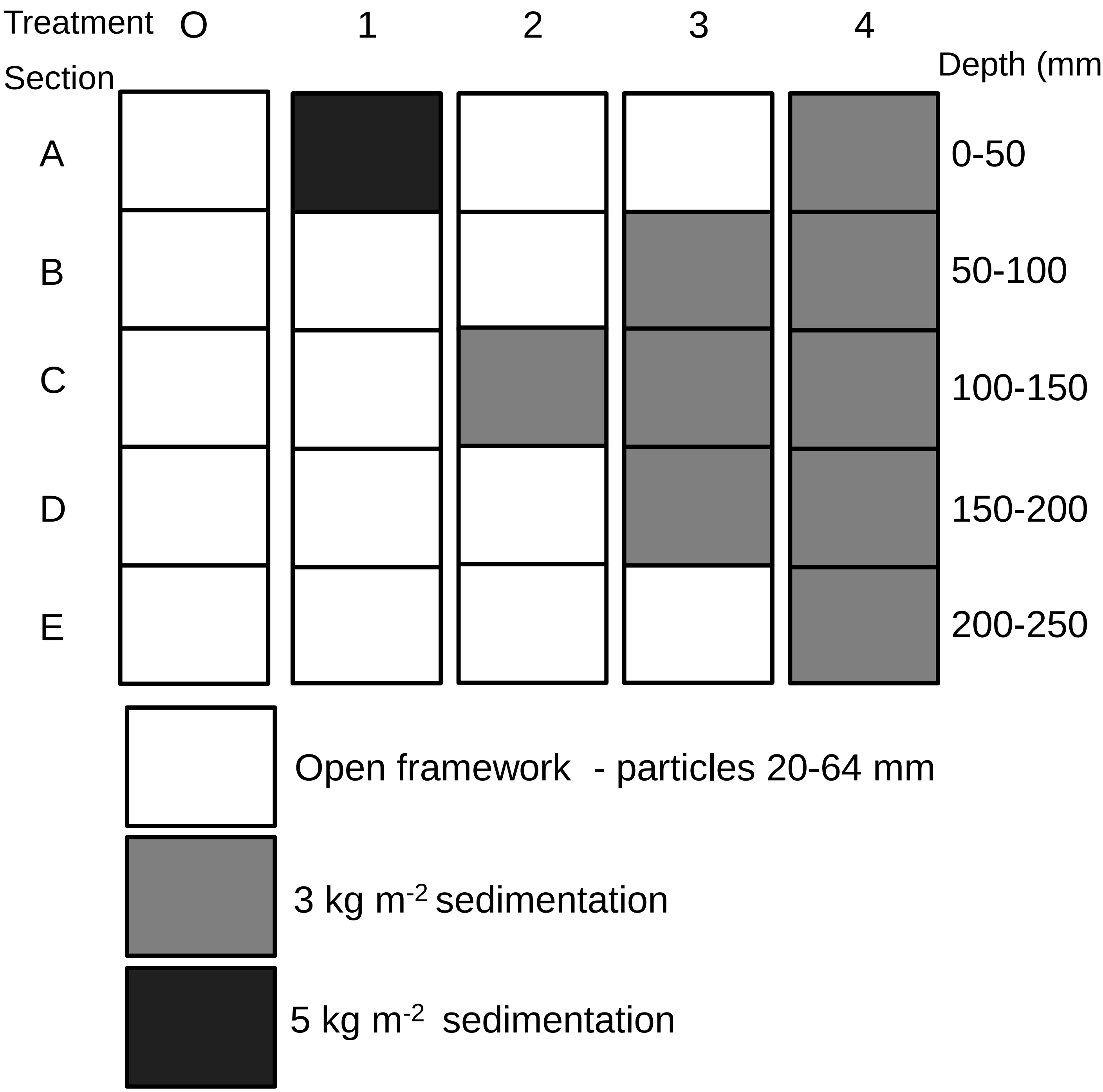

Treatment
O
1
2
3
4
Section
Depth (mm)
A
B
C
D
E
0-50
50-100
100-150
150-200
200-250
Open framework - particles 20-64 mm
3 kg m-2 sedimentation
5 kg m-2 sedimentation

Figure 1.

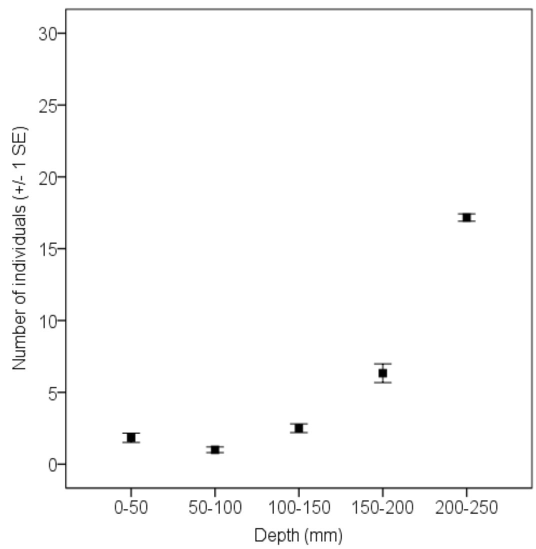

Number of individuals (+/- 1 SE)
30
25
20
15
10
5
0
0-50
50-100
100-150
150-200
200-250
Depth (mm)

Figure 2.

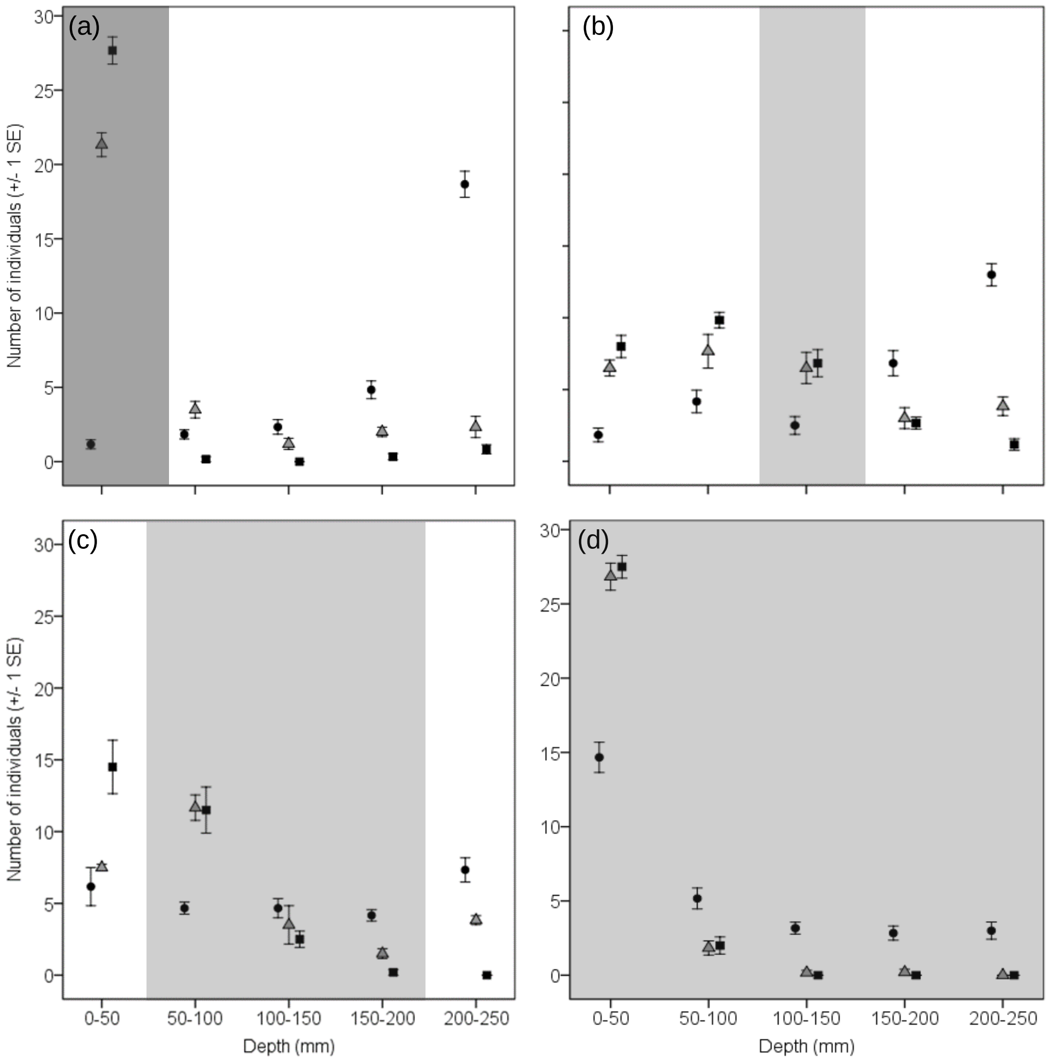
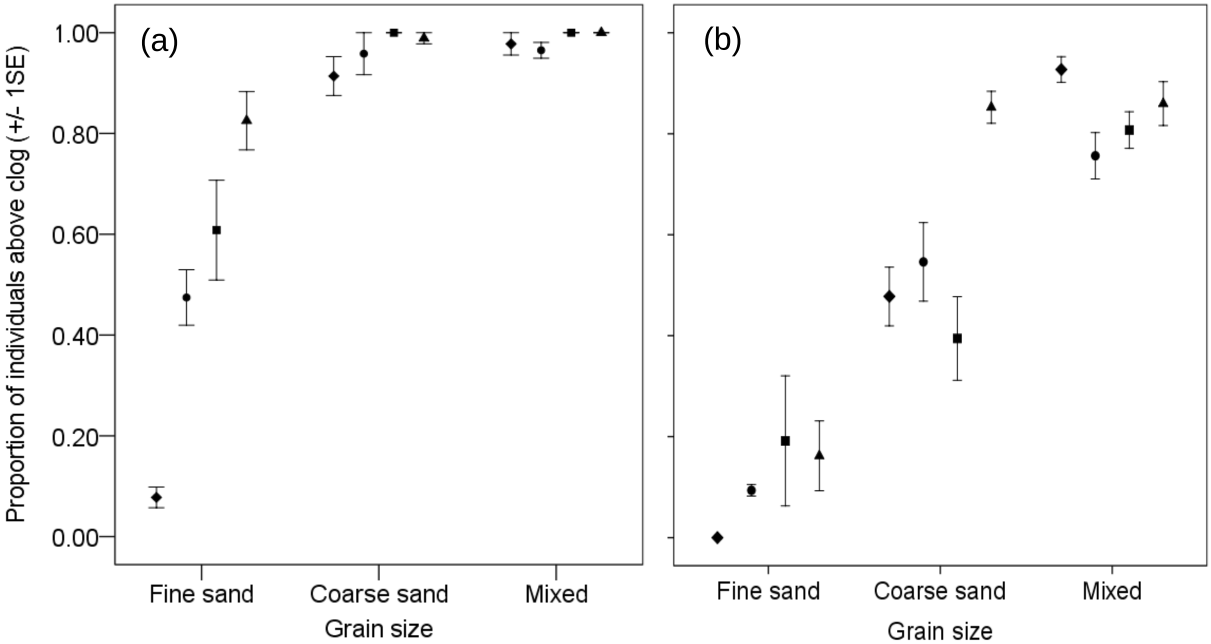

(a)
(b)
(c)
(d)
Number of individuals (+/- 1 SE)
0
5
10
15
20
25
30
0-50
50-100
100-150
150-200
200-250
Depth (mm)

Figure 3.



(a)
(b)
Proportion of individuals above clog (+/- 1SE)
1.00
0.80
0.60
0.40
0.20
0.00
Fine sand
Coarse sand
Mixed
Grain size
Fine sand
Coarse sand
Mixed
Grain size

Figure 4.