Faunal response to benthic and hyporheic sedimentation varies with direction of vertical hydrological exchange.

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Abstract

1. Sedimentation and clogging of benthic and hyporheic zone substrates is increasingly being recognised as one of the greatest threats to the ecological integrity of riverine ecosystems globally. This *ex-situ* study examined the influence of sedimentation (benthic and hyporheic) and pattern of hydrological exchange on the vertical distribution of the freshwater shrimp *Gammarus pulex* within the experimental substrates of running water mesocosms.
2. Six sediment treatments representing a continuum from a clean gravel substratum through to heavy sediment loading of both benthic and hyporheic substrates were used to examine the distribution of *G. pulex* in relation to the direction of hydrological exchange (downwelling, upwelling and no exchange).
3. The vertical distribution of fauna varied significantly for both sediment treatment and pattern of hydrological exchange. There was a significant interaction between the two effects indicating that the effect of sedimentation varied depending on the pattern of vertical hydrological exchange.
4. Sedimentation of benthic sediments resulted in significant modification to the distribution of *G. pulex* when there was no hydrological exchange (no flow) within the column, although there were only limited changes with downwelling flow and no statistical differences with upwelling flow.
5. Sedimentation of multiple layers of the column (benthic and hyporheic) significantly reduced the ability of individuals to utilise the lower layers of the substratum (i.e. the hyporheic zone). This was most marked for upwelling conditions, where it resulted in a complete reversal of the vertical distribution pattern recorded.
6. This study demonstrates that faunal movement, and use of benthic and hyporheic substrates, may be influenced by sedimentation and modified by the pattern of vertical hydrological exchange. Severe sedimentation (colmation) has the potential to prevent benthic fauna from accessing the hyporheic zone and it resources.

Keywords: surface water and groundwater exchange, upwelling and downwelling, fine sediment, colmation, *Gammarus pulex*, mesocosm experiment.

Introduction

Fine sediment deposition (sedimentation) is widely implicated as a major contributor to ecosystem impairment across the globe (Walling, 2009; Collins et al., 2011). Changes in agricultural practices and land use (Stundinski et al., 2012), urbanisation (Taylor & Owens, 2009; Wang et al., 2012) and channel management / habitat modification (Dunbar et al., 2010) have increased the erosion and delivery of fine sediments (typically referred to as particles <2 mm in diameter) to aquatic ecosystems. The effects of excessive sedimentation have been demonstrated at all trophic levels from fish (Walters et al., 2003; Kemp et al., 2011) and benthic invertebrates (Larson & Ormerod, 2010; Jones et al. 2012a), through to macrophytes and periphyton (Izagirre et al., 2009; Jones et al., 2012b), although the potential effects on biota within the hyporheic zone are less well defined (Boulton et al., 2010; Richards & Bacon, 1994).

The hyporheic zone is a dynamic ecotone situated below the river bed which is composed of saturated sediments that exchange water between the surface stream and underlying groundwater (White, 1993). The hyporheic zone represents the interface between the river channel and groundwater and plays a key role in many hydrological and biogeochemical processes in river systems (Boulton & Hancock, 2006; Robertson & Wood, 2010). Consequently, the hyporheic zone is increasingly being recognised as an integral component of lotic ecosystems (Krause et al., 2011) with vertical hydrological connectivity now widely recognised as being a strong determinant of the patterns observed (Malard et al., 2002; Boulton, 2007; Heppell et al., 2009).

Hydrological exchange between surface water and groundwater occurs at a variety of spatial and temporal scales, resulting in a mosaic of habitat patches which are characterised by differing connectivity, permeability and physio-chemical conditions (Dole-Oliver & Marmonier, 1992; Krause et al., 2011). Surface water enters the river bed and hyporheic zone when the hydraulic head is greater than that of the groundwater (downwelling water). This water may be subject to further exchanges, either passing deeper into the groundwater zone or travelling through the sediments until the water emerges from the interstices (upwelling water) (Brunke & Gonser, 1997; Krause et al., 2011). Alternatively, in some rivers there may be limited or no vertical hydraulic exchange due to limited connectivity between surface and groundwater or the presence of layers of impermeable bedrock (Ryan & Boufadel, 2006; Malcolm et al., 2003).

The pattern of vertical hydrological exchange is one of the primary controls of dissolved oxygen concentrations (Olsen and Townsend, 2003), thermal characteristics (Evans & Petts, 1997), nutrient levels (Franken et al., 2001), stream metabolic processes and organic matter breakdown in alluvial rivers (Krause et al., 2011). Patterns of hydrological exchange have also been shown to be associated with distinct benthic (Pepin & Hauer, 2002; Davy-Bowker et al., 2006) and hyporheic invertebrate communities (Plenet et al., 1995; Fowler & Scarsbrook, 2002).

Interstitial sedimentation has the potential to reduce the porosity and permeability of the substratum (Boulton et al., 1998; Bo et al., 2007), thereby limiting the vertical exchange of water and nutrients across the surface and groundwater ecotone (Brunke, 1999; Descloux et al., 2013). The associated reduction of available interstitial habitat may also lower hyporheic metabolism and productivity, and significantly reduce the ability of fauna to exploit the resources of the hyporheic zone (Boulton, 2007; Descloux et al., 2013). The accumulation of fine sediments is not ubiquitous, and patterns of sediment deposition and erosion vary temporally reflecting the flow regime, fine sediment availability and local channel morphology (Boano et al., 2007). As a result, gravel-bed rivers are commonly comprised of a mosaic of substratum patches which are characterised by variable patterns of vertical hydrological exchange, and fine sediment deposition and flushing processes (Dole-Olive and Marmonier, 1992; Boulton & Stanley, 1995).

Fine sediment particles may be deposited on the surface of the river bed (benthic sedimentation) or transported into the river bed where they may be deposited beneath the armour layer or deeper in the hyporheic zone (Huettel et al., 1996; Ren & Packman, 2007; Simpson & Meixner, 2012). This clogging of the interstices directly below the armour layer is typically referred to as colmation, and it may result in the formation of a thin seal (clog) which can disconnect surface water and hyporheic habitats (Brunke, 1999; Packman & Mackay, 2003). Consequently, colmation of hyporheic sediments may be present even in the absence of benthic fine sediment deposits, and surface sedimentation may be poorly correlated with subsurface colmation (Descloux et al., 2010). Ultimately, high levels of fine sediment deposition may lead to the filling of interstitial spaces, particularly in areas of downwelling water (Brunke & Gosner, 1997). In contrast, strongly upwelling water may maintain open pathways of flow by preventing further fine sediment ingress and in some instances flushing fines from the bed (Packman & Salehin, 2003).

The effects of sedimentation on the hyporheic zone are now regarded as a significant ecological threat to many rivers (Boulton, 2007; Boulton et al., 2010). To-date published studies assessing sedimentation effects on hyporheic faunal communities have reported a reduction in the density and/or diversity of fauna with increasing volumes of fine sediment (Bo et al., 2007; Sarriquet et al., 2007; Bruno et al., 2009; Pacioglu et al., 2012; Descloux et al., 2013; 2014). The relatively small number of studies reflects the difficulties associated with replicating and quantifying natural hyporheic fine sediment concentrations prior to the onset of experimental conditions within spatially heterogeneous alluvial river beds (Descloux et al., 2013). As a result, the need for controlled and replicated *ex-situ* experimental approaches is increasingly being recognised in groundwater ecology (Stump & Hose 2013; Navel et al., 2012; Larned, 2012).

In this *ex-situ* study, the vertical distribution of the freshwater amphipod, *Gammarus pulex* (L.) (Amphipoda: Crustacea) was examined in response to different patterns of vertical hydrological exchange and sedimentation (benthic and hyporheic) within experimental running water mesocosms. *G. pulex* is a widespread and abundant model organism that has been extensively studied (Sutcliffe, 1993). It is known to colonize benthic, hyporheic and hypogean habitats within the UK (Gledhill et al., 1993). In many riverine communities *G. pulex* is the dominant macroinvertebrate in terms of biomass (MacNeil et al., 1997). It is moderately sensitive to fine sediment and is capable of burrowing through substrate to find suitable habitat / resources (Sutcliffe, 1993; Extence et al., 2013). Consequently, any alterations to the distribution of this taxa are likely to represent the effect of sedimentation on the wider invertebrate community.

We hypothesised that the vertical distribution of *G. pulex* would be influenced by sedimentation and vertical hydrological exchange. Specifically, we predicted that: i) increasing levels of fine sedimentation would modify the vertical distribution of *G.*

pulex within the experimental columns by limiting and/or preventing movement in to deeper sections; and ii) the influence of sedimentation on the vertical distribution of individuals within the columns would differ for each pattern of hydrological exchange (no exchange downwelling or upwelling).

Methods

Experimental sediment columns

Experiments were undertaken within two identical sediment columns of five interlocking sections / layers (Figure 1 – sections A-E). Each section was 22 cm in diameter and contained 50 mm depth of coarse riverine sediments (gravel particles 20-64 mm in diameter). The sections stacked vertically to provide a total sediment column depth of 250 mm. Ten holes (10 mm diameter) were drilled into the base of four sections (0 - 200 mm depth) to allow water and organisms to pass between sections. The final section (200-250 mm depth) was perforated with smaller holes (2 mm diameter) to permit the vertical exchange of water but prevented 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 (90x40 cm, volume = 100 L). Two external pumps delivered flowing water to the columns (4.5-4.8 L min^{-1}). This flow of water was sufficient to maintain low interstitial flow velocity through the sediments but was not high enough to transport or erode the deposited sediments. Consequently any movement of fine sediments during the experimental period was primarily a function of gravity and bioturbation associated with the movement of *G. pulex.* Three different hydrological flows were simulated; no exchange, downwelling and upwelling.

Downwelling conditions were simulated by pumping water directly into the top experimental section and allowing water to pass through the column under gravity. To mimic upwelling conditions, water was pumped through a large funnel / diffuser (200 mm diameter) placed at the base of the column. Water rose through the column and was allowed to overflow. The top of the column was covered with a 0.25mm mesh to prevent *Gammarus* escaping. Both standing water (no exchange) and downwelling experiments were conducted with 10 cm depth of water over the substratum to mimic overlying surface water. The experimental containers were aerated through the use of an aquaria aeration pump and held at a constant temperature (15^{o}C +/- 0.4^{o}C) via an external water-cooler (Aqua medic, Titan 150).

Fine sediments used in the experiment comprised of pre-washed riverine sands (0.125 µm - 1 mm in diameter). Silt and clay fractions (<0.125µm) were removed through wet sieving to ensure that turbidity did not vary between experiments. Prior to each experiment, fines were applied evenly to the surface of each wet gravel section using a 1 mm sieve. Preliminary tests indicated that the application of an equivalent of 5 kg m^{-2} filled all interstices (100% of interstitial volume) of each section and covered the surface of all gravel particles. Six fine sediment treatments were examined (Figure 1) and for all treatments 50 mm of gravel was placed in each section prior to fine sediment treatment:

1. An open gravel framework: 50 mm depth of gravel in all sections of the column (control);

2. Benthic sedimentation: the equivalent of 3 kg m^{-2} fine sediment applied to the top section resulting in the clogging of 55-60% interstitial volume (0-50 mm – section A);

3. Heavy benthic sedimentation: the equivalent of 5 kg m^{-2} fine sediment applied to the top section (section A);

4. Hyporheic sedimentation of one section: the equivalent of 3 kg m^{-2} fine sediment applied to section C (100-150 mm depth);

5. 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); and

6. Benthic and hyporheic-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).

The sediment treatments (*n*=6) and patterns of hydrological exchange (*n*=3) were combined in a full-factorial design giving 18 treatment combinations. Each combination was replicated 6 times to give a total of 108 individual experiments. Treatments were randomly allocated to a run.

All *G. pulex* specimens were collected from a local stream where the taxon occurs at high abundances (>100 individual per m^{-2}). Twenty–five individuals of mixed sizes (5-16 mm length) 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 sediment columns. A single pre-conditioned horse chestnut leaf (*Aesculus hippocastanum*) was placed in each section for food (Joyce et al., 2009). At the end of each experiment, individuals were collected from each section by washing the contents of each section through 0.25 mm sieves. All fine sediments were removed from the column and retained for use in subsequent experimental runs.

Statistical Analysis

Differences in the abundance of *G. pulex* in each section of the column relative to the impact of sedimentation and pattern of vertical hydrological exchange were tested using a Linear Mixed Model (LMM) in IBM SPSS Statistics 20.0 (IBM Corp. 2011). 'Section' was specified as a fixed within-subject (repeated) effect and the pattern of hydrological exchange and sedimentation treatments were specified as fixed between-subject effects. Covariance between sections of the columns was modelled using a compound symmetry (CS) covariance structure. The model was tested using an AR(1) covariance structure, but assessment of Akaike’s information Criterion (AIC) indicated that the CS covariance structure was more appropriate. The model was fitted using Residual / Restricted Maximum Likelihood (REML) estimation. Differences between sections within each treatment combination were tested using a Fisher’s LSD post-hoc test.

Results

Faunal response to the pattern of sedimentation and vertical hydrological exchange

Overall recapture rates for all experiments were 91%, with downwelling and upwelling treatments having the highest and lowest rates respectively (96% and 88%). When all experiments were considered *G. pulex* abundance was greatest in the top column section (A) (mean ± SE = 8.04 ± 0.237), followed by the second (5.33 ± 0.237) and the bottom (200-250 mm) layer (5.31 ± 0.237). The fewest *G. pulex* were recovered from the third (section C) and fourth (section D) layers of the columns (2.31 ± 0.237 and 1.82 ± 0.237 respectively). However, the extent and pattern of these differences was significantly affected by both the sedimentation treatment ($F_{20,360}$ = 13.05, P = <0.001) and the pattern of vertical hydrological exchange ($F_{2,90}$ = 7.43, P = <0.001). There was a significant interaction between the effect of these two treatments on the abundance of *G. pulex* in all sections ($F_{40,360}$ = 6.27, P = <0.001). As such, the effect of sedimentation on the distribution of abundance within the sections of the columns differed depending on the pattern of vertical hydrological exchange.

Faunal response to sedimentation under no exchange conditions.

There were marked differences in the distribution of *G. pulex* when subjected to varying levels of sedimentation under no-exchange conditions (Figure 2). In the open gravel experiments, the greatest number of individuals was recorded in the top (section A) and bottom (section E) layers of the column (Figure 2a). In the benthic sedimentation treatments, a significantly higher number of individuals were recorded in the second (section B) and bottom section (E) of the column for the moderate (3 kg m^{-2}) sedimentation treatment (Figure 2b), and in the second section for the heavy (5 kg m^{-2}) sedimentation treatment (Figure 2c). Hyporheic sedimentation of the third layer (section C) resulted in a similar pattern to that recorded for the heavy (5 kg m^{-2}) benthic sedimentation treatment (Figure 2d). Hyporheic sedimentation of 3 layers (sections B, C and D) and all layers of the sediment column resulted in significantly higher numbers of individuals in the top and second layers (section A and B) (Figure 2e and Figure 2f).

Faunal response to sedimentation under downwelling conditions.

The distribution of *G. pulex* in all downwelling hydrological exchange experiments was characterised by a reduction in the number of individuals with increasing depth in the column (Figure 3). The majority of individuals were recorded in the top layer of the column (section A) for the open gravel treatment, with <5 individuals typically recorded in the lower sections (Figure 3a). When sedimentation of the benthic layer occurred a significantly higher number of individuals were recorded in the top and second layers (section A and B) for the moderate treatments (3 kg m^{-2}) and in the top, second and third layers (section A-C) for heavy sedimentation (5 kg m^{-2}) treatments (Figure 3b and Figure 3c). Hyporheic sedimentation of one layer (section C) resulted in a less marked gradient (Figure 3d). Hyporheic sedimentation of 3 layers (sections B, C and D) and all layers of the sediment column resulted in similar gradients with the majority of individuals being recorded in the top three layers (sections A, B and C) and upper two layers (sections A and B) of the sediment column respectively (Figure 3e and Figure 3f).

Faunal response to sedimentation under upwelling conditions.

In upwelling experiments, *G. pulex* distribution was characterised by a significantly greater number of individuals in the bottom section (section E) for control (Figure 4a), moderate benthic sedimentation (Figure 4b), heavy benthic sedimentation (Figure 4c), and hyporheic sedimentation of one layer (section C) treatments (Figure 4d). However, sedimentation of 3 hyporheic layers (sections B, C and D) resulted in no statistical difference in the number of individuals among any sections of the column (Figure 4e). Sedimentation of all layers of the column resulted in a complete reversal the distribution of individuals compared to control conditions with a significantly greater numbers being recorded in the top layer (section A) of the column (Figure 4f).

Discussion

The results of the experiments presented in this study provide evidence to support our first hypothesis (increasing levels of sedimentation will modify the vertical distribution of *G. pulex* within the experimental columns). Sedimentation of the benthic layer (0-50 mm depth) did not affect the distribution of individuals when flowing water (upwelling or downwelling) occurred. Only in the absence of flow was there a significant effect; although benthic sedimentation did not appear to impede vertical movement as more individuals were recorded below the treated layer than above it. In marked contrast, sedimentation of multiple layers (3 layers – 50-200 mm depth and 5 layers – 0-250 mm depth) resulted in a significant reduction in the abundance of individuals with increasing depth with the majority of individuals confined to the top 100 mm of the substratum under the highest sediment loads; although this did not modify the vertical distribution pattern of individuals during the downwelling flow experiments. The deposition of fine sediments within riverine substrates potentially reduces porosity and permeability (Ren & Packman, 2007; Simpson & Meixner, 2012) leading to significant modification of interstitial habitat characteristics. Sedimentation is widely reported to reduce benthic and hyporheic interstitial habitat availability (Richards & Bacon, 1994; Gayraud & Philippe, 2003).

The results of the experiments also provide evidence to support our second hypothesis (the vertical distribution of individuals would differ for each of the patterns of hydrological exchange - upwelling, downwelling and no exchange). There were significant differences in the vertical distribution of taxa recorded for each of the patterns of hydrological exchange when no fine sediment was present in the columns. These differences persisted until fine sediment had been applied to multiple layers of the substratum. When all benthic and subsurface layers were treated with fine sediment the majority of individuals were recorded in the top and second layers of the substratum under all hydrological conditions. For upwelling flow conditions this represented a complete reversal in the pattern of vertical distribution compared to control conditions and suggests that individuals were unable to migrate through the column due to clogging of interstitial spaces. For the less severe fine sediment treatments, pore space connectivity appears to have been maintained; most clearly for the upwelling flow experiments.

The results of field observations and experiments (Olsen & Townsend, 2003), and theoretical insights (Krause et al., 2011) suggest that the effects of sedimentation on macroinvertebrates may be modified by the nature of hydrological exchange. *Gammarus pulex* is widely reported to be rheopolic, demonstrating a preference for flowing water conditions (Gledhill et al., 1993). It was therefore not unexpected that under control conditions (open gravel framework), the greatest number of individuals were recorded in areas where the highest flow velocities occurred (in the benthic zone for downwelling condition and at the base of the column for upwelling water). Under no flow / hydrological exchange conditions and sedimentation of one section of the substratum, the majority of individuals were recovered from the surface layers (0-100 mm) or within the final section (200-250 mm). However, sedimentation of multiple layers appeared to limit movement into the lower layers of the column (100-250 mm).

Fine sediment deposition (clogging / colmation) and the pattern of surface water – groundwater exchange have been implicated as major factors in the structuring of benthic and hyporheic faunal communities (Maridet et al., 1992; Richards & Bacon, 1994; Olsen & Townsend, 2003; Descloux et al., 2013). The ability of fauna to move and migrate from the surface stream (benthic zone) into the underlying groundwater environment (hyporheic zone and groundwater) may be impeded in the presence of heavy fine sediment loading (Boulton, 2007). Contrary to published reviews that address the effects of benthic sedimentation on macroinvertebrates (see Wood & Armitage, 1997; Jones et al., 2012a), heavy fine sediment loading of surface sediment in the experiments resulted in limited changes to the distribution of individuals in the presence of flow. The large, homogenous gravel matrix used in the experiments most likely helped maintain open interstitial spaces despite sedimentation of the benthic layer (0-50mm). In addition, it is likely that some movement of sediment from the surface into lower sections of the experimental column occurred during the experiments due to the effect of gravity and the activity of individuals. This effectively maintained the interstitial spaces and porosity (Xu et al., 2012) thus allowing faunal movement when only one layer of the column was treated. Substratum composition and particle size have been widely acknowledged as playing a pivotal role in the influence of fine sediment on invertebrate communities, with heterogeneous river beds cited as having the greatest clogging potential (Weigelhofer & Waringer, 2003). Consequently, the coarse grained sedimentary characteristics of the substrates which are subject to sedimentation may determine the effects experienced by the ecosystem.

Reductions of interstitial pore space have been reported to limit the ability of fauna to migrate within the hyporheic zone, most notably larger bodied invertebrates (Williams and Hynes, 1974; Gayraud & Phillipe, 2001). However, in this study the effect of body size was not considered as the varying pattern of hydrological exchange would have confounded the results (with the maximum number of individuals being recorded at opposing ends of the columns for upwelling and downwelling conditions in most of the experimental runs). Further experimental studies focussed on specific patterns of hydrological exchange would be required to enable the effect of body size or other morphological traits on the ability of fauna to utilize interstitial spaces to be examined (see Descloux et al., 2014).

The results from this study suggest that sedimentation / colmation of the hyporheic zone has the potential to effectively disconnect it from benthic sediments and macrofaunal use. This disconnecting off effect may prevent the hyporheic zone acting as a refugium during adverse conditions in the surface stream (Wood et al., 2010) potentially limiting stream productivity and reducing ecosystem resilience (Boulton, 2007; 2010). These results provide insights that support *in-situ* observational studies regarding the deleterious effects of sedimentation on macroinvertebrates, with reductions in the abundance and diversity of invertebrates with increasing depth recorded (Richards & Bacon, 1994; Bo et al., 2007; Descloux et al., 2013).

The approach applied in this study represents a novel experimental design which can be easily replicated and adapted to enable the the effects of sedimentation and / or patterns of hydrological exchange on other specific taxa or combinations of taxa forming the macroinvertebrate community to be examined. However, care is required when applying the results to other aquatic invertebrate taxa and the wider community. This study examined a single taxon, however the findings from a number of *in-situ* studies do suggest a similar response to hyporheic sedimentation for other mobile taxa. Only tube building Chironomidae and burrowing Oligochaeta have been widely reported to thrive on the presence of high volumes of fine sediment within the hyporheic zone (Zweig & Rabeni, 2001; Weigelhofer & Waringer, 2003; Sarriquet et al., 2007). In addition, the current experiments were undertaken under highly controlled conditions. In the natural environment, physical conditions and water quality will probably differ significantly between upwelling and downwelling flow (Olsen & Townsend, 2003; Krause et al., 2011). This strong physio-chemical gradient may exert a strong influence on the distribution of both benthic and hyporheic invertebrate communities and thus may influence invertebrate response (Pepin & Hauer, 2002; Davy-Bowker et al., 2006). There is clearly a need for additional experimental studies to gain a better understanding of the factors controlling the use of the hyporheic habitats by benthic fauna and to quantify the influence of sedimentation on macroinvertebrate communities.

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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: 1. Open gravel framework at all layers (control conditions); 2. Benthic sedimentation with the equivalent of 3 kg m^2; 3. Benthic sedimentation with the equivalent of 5 kg m^2; 4. Hyporheic sedimentation of one layer (100-150 mm) with the equivalent of 3 kg m^2; 5. Hyporheic sedimentation of three layers (50-200mm) with the equivalent of 3 kg m^2 applied to each layer; and 6. Benthic and hyporheic sedimentation (all layers) with the equivalent of 3 kg m^2.

Figure 2. Mean number of *Gammarus pulex* (+/- 1SE) recorded within each section of the sediment column (0-50 mm; 50-100 mm; 100-150 mm; 150-200 mm and 200-250 mm) under no hydrological exchange (no flow) conditions: a. Open gravel framework at all layers (control conditions); b. Benthic sedimentation with the equivalent of 3 kg m^2; c. Benthic sedimentation with the equivalent of 5 kg m^2; d. Hyporheic sedimentation of one layer (100-150 mm) with the equivalent of 3 kg m^2; e. Hyporheic sedimentation of three layers (50-200mm) with the equivalent of 3 kg m^2 applied to each layer; and f. Benthic and hyporheic sedimentation (all layers) with the equivalent of 3 kg m^2. Sections within the column where the number of individuals were not significantly different are indicated with the same letter (Fisher's LSD, P <0.05).

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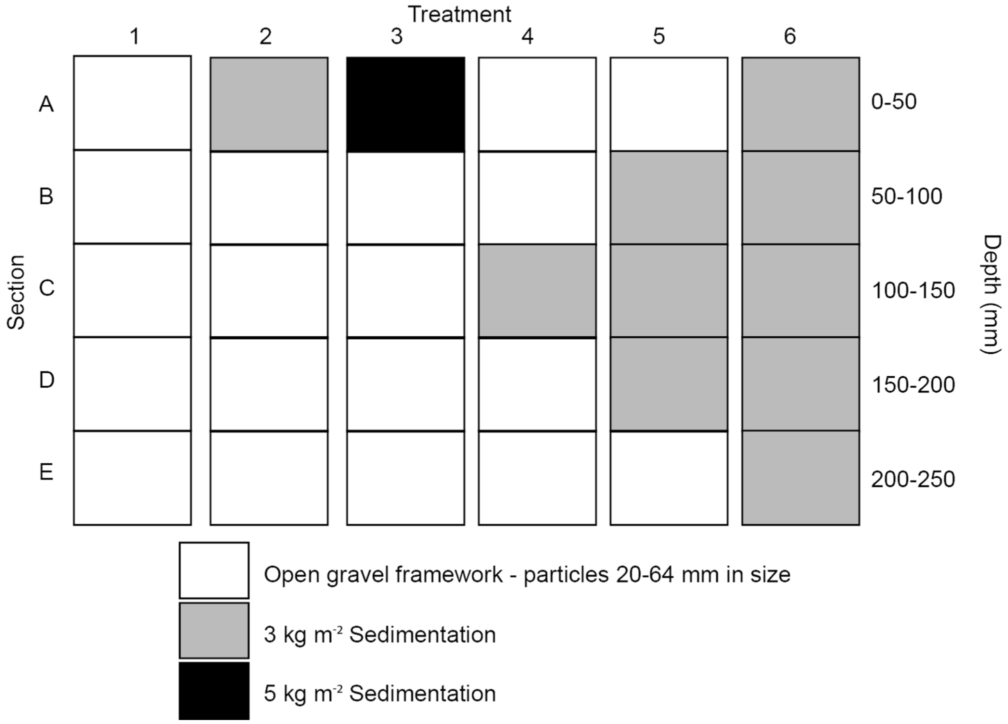

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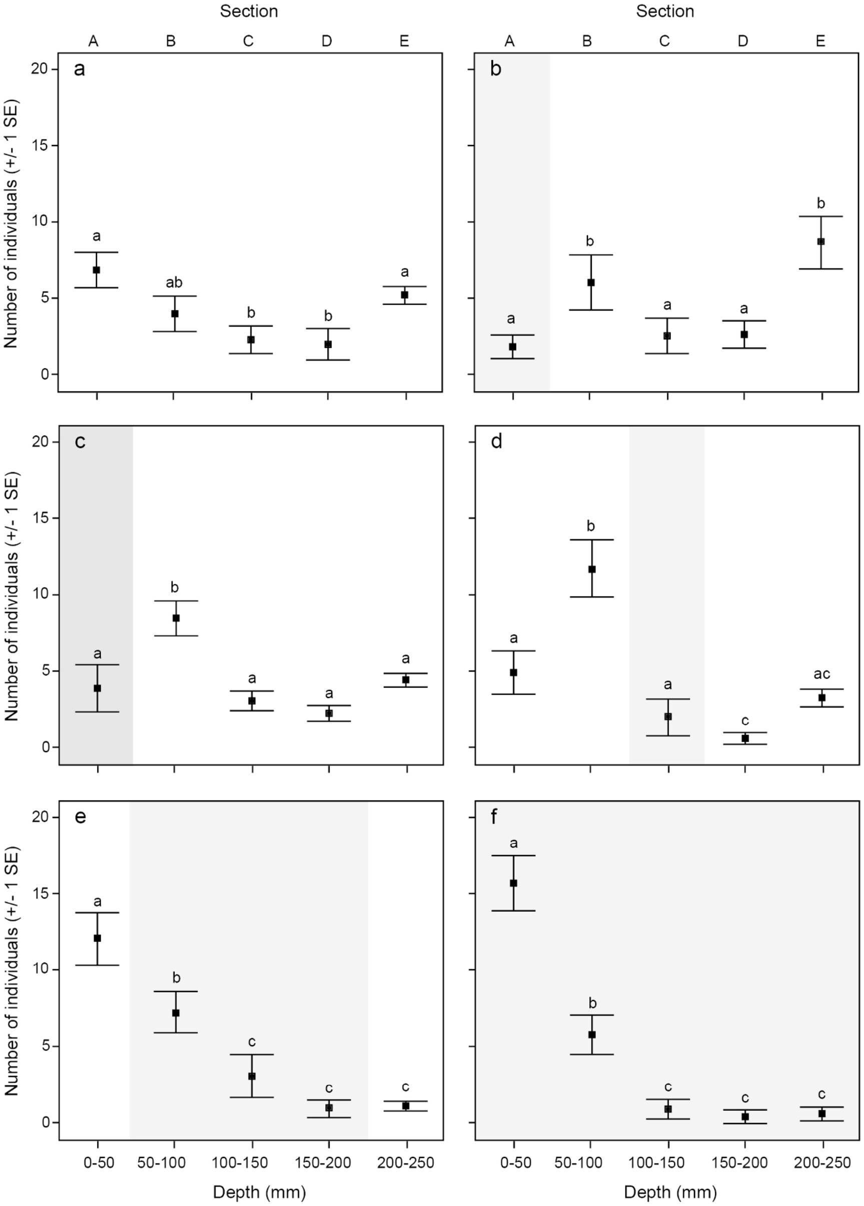

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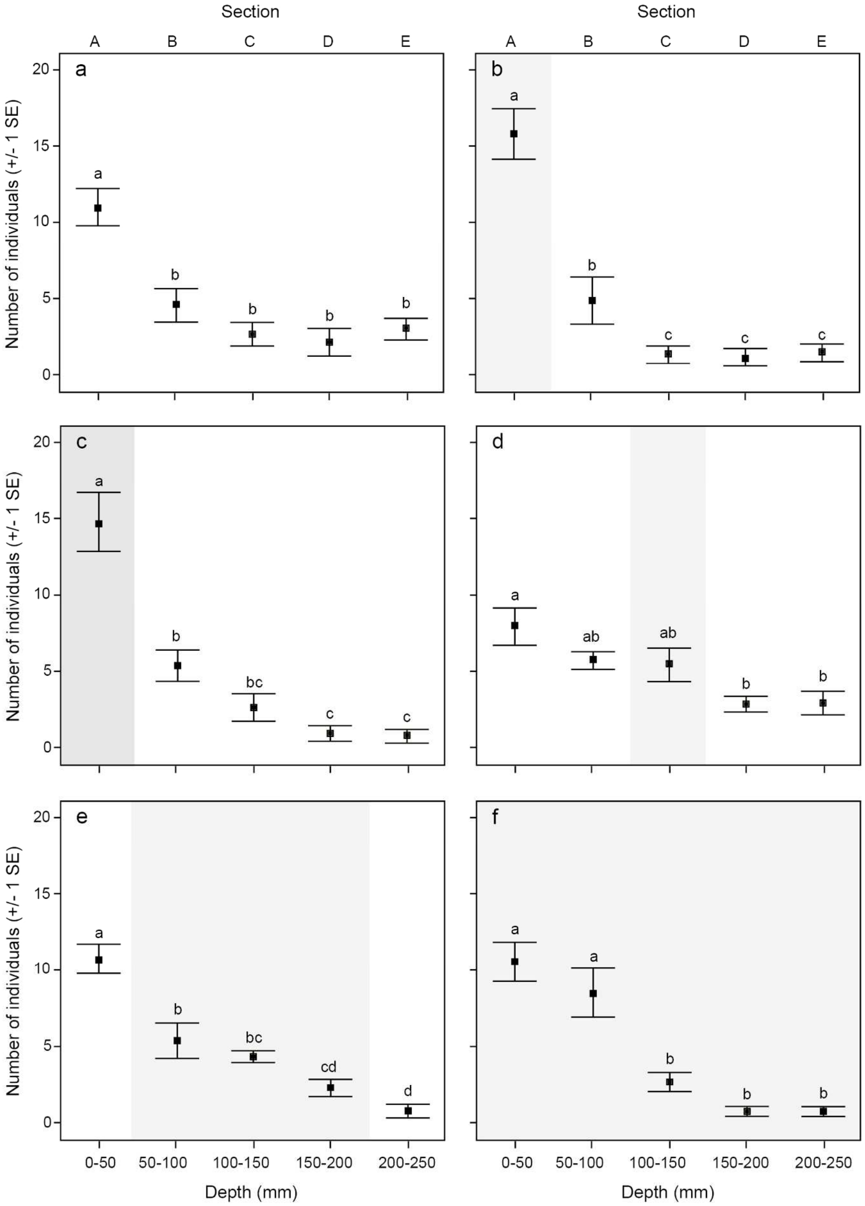

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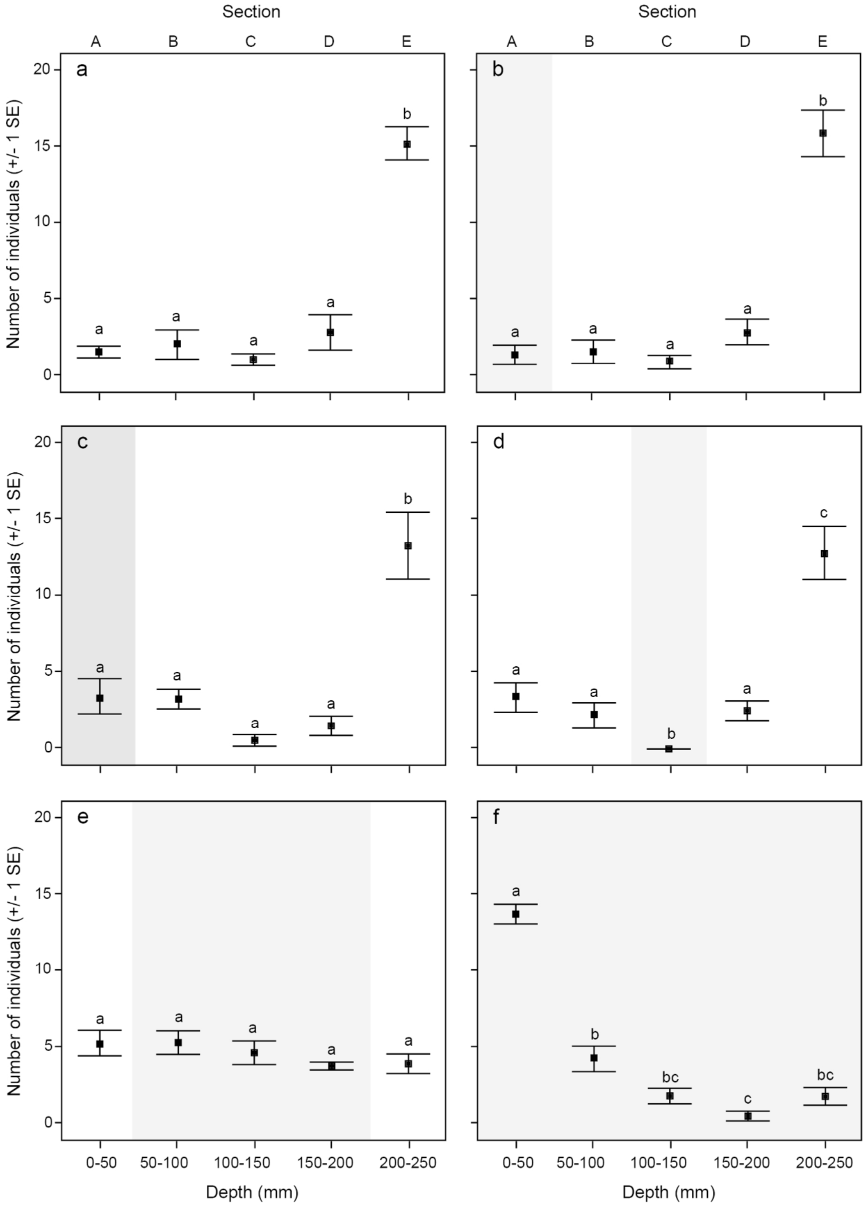

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