Sediment reworking in streambeds with fine sediment deposits and its influence on hyporheic flow regime

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Key Points:

- Effect of sediment-organism interaction on hyporheic flow in streambeds with fine sediment deposits is studied in re-circulating flumes
- Sediment reworking by model organisms caused enhanced hyporheic exchange flux, shorter residence times, and deeper solute penetration
- The extent of modification of hyporheic flow regime depends on interaction of organisms with both substrate and deposited fine sediments

Abstract

The mobilization and mixing of sediments by the activities of in-stream fauna, referred to as sediment reworking, constantly modifies the hydro-physical properties of streambeds. This sediment-organism interaction has been increasingly recognized to influence the hyporheic exchange flows in stream ecosystems, particularly in low flow environments (e.g. during base flow). In this work, we advance the knowledge of sediment reworking process by studying its impact on hyporheic exchange flows in streambeds with fine sediment deposits. Laboratory experiments are conducted in re-circulating flumes following a control (only fine sediments) and treatment- (fine sediments + organisms) based design. The experiments involve studying the interaction of model organisms (*Lumbriculus variegatus*) with fine sediment (clay) deposits, and its subsequent influence on hyporheic flow regime in homogenous streambeds with fine sand, coarse sand, and gravel as substrate sediments. We observe that model organisms burrowed extensively into the fine sediment layer, mixed the clay particles with underlying grains, and eventually exposed the substrate sediments in the treatment flumes. Consequently, the treatment flumes exhibited greater solute penetration depth, shorter residence times, and higher hyporheic exchange flux compared to their respective control flumes. The results also suggest that the modification of hyporheic exchange flows depends on the overall reworking of the beds i.e., the interaction of organisms with both substrate material and deposited fine sediments. It is critical to comprehend the influence of streambed inhabitants on mass and energy exchange across the sediment-water interface as it has implications on the overall quality of both stream and groundwater.

Plain Language Summary

The exchange of water and solutes between the surface and groundwater in a stream landscape facilitates important ecosystem services such as the natural processing of nutrients/contaminants. This two-way exchange could be hampered due to the presence of fine sediments on/into the streambed. Besides fine sediments, several faunal organisms such as macroinvertebrates are present in the streambeds. These organisms could move and construct burrows within the fine sediment deposits and potentially enhance the exchange process across streambeds. We explore this idea by performing laboratory experiments in Perspex built long channels to simulate a streamflow environment. These channels were filled with sediments to mimic streambeds which were clogged with clay particles (fine sediment). It was observed that the sample organisms could penetrate and disintegrate the clay deposits. This enhances the rate of transfer of water/solute molecules across the streambeds, reduces the time they reside in the bed, and increases the exchange depth. The degree to which exchange characteristics are influenced depends on the interaction of animals with both deposited fine sediments and bed grains. Further research must be conducted to understand how faunal organisms modify exchange processes across streambeds as it has a direct influence on overall stream ecosystem functioning.

1 Introduction

The two-way exchange of mass and energy across the sediment-water interface (SWI) in streams, referred to as hyporheic exchange, underpins several ecosystem functions such as natural processing of nutrients/pollutants [*Bardini et al.*, 2012; *Gandy et al.*, 2007] and supporting sub-surface ecology [*Brunke and Gonser*, 1997]. Among the major drivers of hyporheic exchange, particularly at small scales, are the pressure gradients at the bed surface (arise due to interaction between surface water and morphological features like bedforms) and the bed permeability (a hydraulic property of sediments) [*Bardini et al.*, 2012; *Packman and Salehin*, 2003; *Storey et al.*, 2003]. Two critical processes that can modify the morphology and permeability of streambeds, and consequently the hyporheic exchange flows are – fine sediment clogging and sediment reworking by in-stream faunal organisms [*Shrivastava et al.*, 2020a]. While the influence of fine sediment clogging on hyporheic exchange has garnered a lot of attention in the past [*Fox et al.*, 2018; *Karwan and Saiers*, 2012; *Packman and Brooks*, 2001; *Packman and MacKay*, 2003; *Rehg et al.*, 2005], the research on the influence of faunal activity on bed properties and hyporheic flow regime has gained momentum only recently. Importantly, fine sediments are often present on/into the streambeds and the organisms could likely rework the deposited fines along with the substrate sediments. This work focuses on studying the sediment reworking process in streambeds with fine sediment deposits and its impact on hyporheic exchange.

Streambeds host a wide range of organisms that perform activities such as burrowing and feeding to constantly mix and mobilize bed sediments, a process described as sediment reworking. For example, mobilization and downstream transport of sediments due to sediment reworking by fish (e.g. salmon) and crustacean (e.g. crayfish) species have been documented in the literature [*Gottesfeld et al.*, 2004; *Johnson et al.*, 2011]. Similarly, invertebrates have been observed to construct burrows of depth up to 5cm and diameter ranging from 1-6 mm in streambeds [*Song et al.*, 2010]. This sediment-organism interaction could influence the exchange of mass and solutes across the SWI in stream ecosystems, but there is limited understanding in this area [*Marmonier et al.*, 2012]. Most of the previous experimental work related to sediment reworking in freshwater sediments has been conducted in small mesocosms [*Anschutz et al.*, 2012; *Morad et al.*, 2010] or infiltration columns [*Mermillod-Blondin et al.*, 2001; *Mermillod-Blondin et al.*, 2003; *Nogaro et al.*, 2006]. The results from these experiments may have limited applicability to flowing water (or lotic) environments where complex hydrodynamic conditions can be produced at the SWI due to the flow of water over undulated beds. In our recent work [*Shrivastava et al.*, 2021], we studied the sediment reworking process in long re-circulating hydraulic flumes to better represent the flow conditions in streams. We reported that burrowing, feeding, and excretion by model organisms (*Lumbriculus variegatus*) resulted in mixing and mobilization of bed grains leading to a significant alteration in the hyporheic flow regime, particularly in low flow environments (e.g. during dry season or in regulated streams that experience less frequent floods).

In natural settings, fine sediment deposits have been often observed on the surface or within pore spaces of streambeds, a process referred to as fine sediment clogging [*Brunke*, 1999; *Schälchli*, 1992]. Fine sediment clogging has been demonstrated to negatively impact the stream biodiversity [*Wood and Armitage*, 1997], however, certain organisms such as chironomids and oligochaetes have been reported as tolerant to excessive fine sediment input [*Datry et al.*, 2003; *Lenat et al.*, 1981; *Zweig and Rabeni*, 2001]. Particularly, oligochaetes have been observed to maintain high densities in heavily clogged streambeds [*Descloux et al.*, 2013]. Previous work has reported that excessive accumulation of fine sediments in streambeds could hamper the exchange processes across SWI [*Rehg et al.*, 2005; *Shrivastava et al.*, 2020b]. Based on the findings from *Shrivastava et al.* [2021], it can be expected that organisms could rework the accumulated fine sediments as well as the substrate sediments to modify the hydro-physical properties of streambeds and subsequently enhance the hyporheic exchange flows.

In the current work, we aim to advance the understanding of sediment reworking process in stream ecosystems by investigating the influence of the activities of macroinvertebrates on hyporheic exchange in streambeds having fine sediment deposits. The objectives of the work are two-fold: i) study the reworking of streambeds comprising fine (clay particles) and substrate (homogenous beds with sediments of different sizes) sediments by model organisms (*Lumbriculus variegatus*) in long re-circulating flumes following a control and treatment-based experimental design, and ii) conduct dye tracer test to evaluate and compare the hyporheic flow characteristics (hyporheic exchange flux, residence times, and exchange depths) in control and treatment flumes.

2 Experimental methods

2.1 Model sediment reworking organisms

Lumbriculus variegatus (commonly known as California blackworms), were used as model organisms (Figure 1a). *L. variegatus* (hereafter referred to as worms) are freshwater oligochaetes (found throughout Europe and North America) that prefer to dwell in shallow sub-surface regions of lakes or marshes feeding on organic material and microorganisms [*Govedich et al.*, 2010]. However, these worms have been also observed in alluvial and lowland river environments [*Datry et al.*, 2010; *Verdonschot*, 2001]. The typical behavior of these burrowing organisms is to keep their head down into the sediment bed to forage and tail up in the water to facilitate gas exchange [*Work et al.*, 2002]. This behavior is similar to other sediment reworking invertebrates such as tubificids, which are found readily in streams of several continents including Asia, Europe, and North America [*Anlauf and Moffitt*, 2008; *Brinkhurst and Kennedy*, 1965; *Lin and Yo*, 2008; *Postolache et al.*, 2006]. Previous experimental work has reported that model organisms generally rework the upper 2-3 cm of bed sediments [*Roche et al.*, 2016; *Shrivastava et al.*, 2021]. These worms could tolerate harsh environments and have been extensively used in several toxicological studies related to freshwater sediments [*Blankson and Klerks*, 2016; *Leppänen and Kukkonen*, 1998]. The tendency of these worms to dwell close to the SWI and their ability to survive in a range of environmental conditions make them an appropriate model organism for this study.

2.2 Flume set up and bed materials

The experiments were performed in the Sexton Ecohydraulics laboratory at The University of Melbourne using six Perspex recirculating flumes, each having dimensions 3 m (L) x 0.2 m (W) x 0.4 m (D) (Figure 1b, additional details related to the flume set up can be found in *Shrivastava et al.* [2020b]). The flow rates in the flumes were controlled by a pump controller and measured using GPI-TM series flowmeters. The slopes could be adjusted using scissor-jacks at the upstream end. The flow rates (1.6 L s^{-1}) and slopes (1:300, dz:dx) were fine-tuned to attain uniform flow in the flumes to achieve an average flow depth of 9 cm. The flow velocity (~8.7 cm s^{-1}) was obtained by dividing the flow rate by cross-sectional area (flume width x flow depth). These hydraulic variables were kept constant during the experiments and were similar across all the flumes. The experiments were conducted using tap water (pH = 6.7, salinity = 220 μS cm^{-1}). The evaporative loss of water over time was covered by adding tap water into the flumes (on alternate days, ~125 ml in each flume) to maintain constant flow depth and water volume throughout the experimentation period.

Fine sand (indexed as FS, D_{50} = 0.28 mm, porosity = 0.45), coarse sand (indexed as CS, D_{50} = 1.7 mm, porosity = 0.37), and gravel (indexed as G, D_{50} = 5.5 mm, porosity = 0.38) grains were washed to remove any foreign material (e.g. dirt) before filling into the flumes to form compositionally homogenous streambeds. Each grain type was filled into two flumes (one control- without organisms and another treatment- with organisms) and dune-shaped model streambeds with an average depth of 30 cm (based on 20 measurements performed from the base of the flume to the bed surface) were obtained. As the hyporheic flow is sensitive to bed morphology [*Chen et al.*, 2018], the dunes were shaped by hand to ensure that the dune height (3 cm) and the distance between two consecutive dunes' troughs or crests (24 cm) are uniform across all the experimental flumes at the start of experiments (Figure 1b). In each of the flumes, a known mass of ball clay (d_{50} = 0.006 mm) was introduced as fine sediments to achieve desired suspended sediment concentration in the overlying water (400 g in flumes with fine and coarse sand grains and 800 g in flumes with gravel grains). The obtained initial suspended sediment concentrations in the flumes are representative of stream environments that receive high fine sediment input, for example in forested catchments [*Sadeghi and Saeidi*, 2010]. A detailed procedure of clay addition into the experimental flumes is presented in [*Shrivastava et al.*, 2020b]. It took approximately 5, 3, and 2 days in flumes with fine sand, coarse sand and gravel grains respectively for clay particles to settle on/into the streambeds. The depositional profiles of fine sediments i.e., the thickness of the fine sediment layer at the bed surface and depth of infiltration of fine sediments were assessed manually from the flume walls (based on 20 measurements between crests and troughs). No re-suspension of clay particles was observed visually after their settlement on/into the bed.

After the clay had deposited on/into the bed, pumps were turned off in all the treatment flumes and worms were introduced to achieve a density of ~9000 individuals m^{-2} (~4500 worms in each flume) which is within the range these organisms have been reported in freshwater sediments [*Cook*, 1969]. The worms were fed (only once throughout the experimentation period) with fish food after their introduction and the flow in treatment flumes was reinstated after ~2 days. The flow velocity in the flumes was low enough to not erode both fine particles and worms. Burrow density was estimated based on visual observations of the bed surface (20 patches on the reworked bed each having area ~25 cm^2 were randomly chosen and burrows/holes were manually counted). The worms were recovered from the flumes at the end of the experiments by manually digging the top surface of the bed. The spatial distribution and depths traversed by worms in the sediment beds were assessed through direct observations from the flume walls and during worm recovery.

2.3 Tracer test to characterize hyporheic flow regime

In this work, the characteristics of hyporheic flow were assessed by injecting a fluorescent dye tracer (Rhodamine WT) into the water column at downstream end of the experimental flumes after the worms reworked the sediments for 15 days. The dye was added slowly over one re-circulation cycle of water (~90 sec) to ensure rapid and homogenous dye mixing, and its concentration in the water column was measured (every two minutes) using Turner Designs Cyclops 7 sensors. The initial dye concentration obtained in the surface water of the experimental flumes was ~300 ppb. The dye concentration in the water column decreases over time due to exchange with the pore water until an equilibrium (rate of change of dye concentration in the water column is close to 0) is reached leading to uniform dye concentrations in the water column and hyporheic zone. The experiments were ceased after this equilibrium condition was attained. The dye behaved inertly as also observed in our previous works [*Shrivastava et al.*, 2020b; 2021]. The experiments were done in a closed room avoiding any direct contact of the dye with the sunlight to prevent its photochemical decay.

The methodology to estimate the characteristics of hyporheic flow (i.e., the hyporheic exchange flux, residence time distributions, and exchange depths) are only briefly discussed here, a detailed description is presented in [*Shrivastava et al.*, 2021]. The hyporheic exchange flux (q, m min^{-1}) was estimated from the initial gradient of the temperature-corrected time-series concentration of dye in the water column. An exponential equation is fitted (using principles of least squares) to the temperature-corrected time series of dye concentration and the mathematical function for the observed concentration profile is obtained. The observed and fitted concentration profiles match closely as indicated by the root mean square errors (less than 0.0065 for all curves). Using the mathematical function for the observed dye concentration and the approach presented in *Elliott and Brooks* [1997], the residence time distribution function (denotes the fraction of solutes that entered the bed at time t = 0 and still remain in bed at a time t = τ) and subsequently the median (RT_{med}, min) and mean (RT_{mean}, min) residence times were obtained. A mass balance of dye at beginning and end of the experiment was established to obtain the volume of water in hyporheic zone (V_p, m^3) that mixes with the surface water. The equivalent dye penetration depth ($\bar{d}$) or the depth of exchange was obtained as the ratio of V_p to bed plan area (A, m^2). Further, the average hyporheic exchange flux is dependent on both the depth of exchange and mean residence times (RT_{mean}). Thus, another estimate, q' (m min^{-1}), was calculated from the ratio of $\bar{d}$ to RT_{mean} to re-assure our findings of modification in hyporheic exchange flux.

3 Results

3.1 Depositional profiles of fine sediment in control and treatment (before worms' addition) flumes

Both control and treatment flumes for each sediment type exhibited similar depositional profiles of clay particles. In beds with fine sand, a superficial fine sediment layer of average depth ~4 mm was deposited on the top and no infiltration of fine sediment was visible through flume walls (Figure 2a). In coarse sand beds, fine sediments largely deposited on top of the beds to form a layer of average depth ~3 mm (shallow infiltration of ~0.2 mm was observed at some locations) (Figure 3a). In gravelly substrate, both infiltration of fine sediments into the bed (average depth ~4.8 cm) and deposition on the surface (~2.4 mm) were observed (Figure 4a).

3.2 Observation of worm activity and disturbance to clay deposits

In treatment flume with fine sand (FS-T), the worms were found concentrated in the top 2-3 cm and the holes or burrows dug by them were readily visible at the bed surface (Figure 2b and 2d). On contrary, in coarse-bedded treatment flumes (coarse sand and gravel grains), worms navigated to deeper bed regions as observed from the flume walls. Worms were observed across the depth of the bed in treatment flume with coarse sand (CS-T) (Figure 3b) whereas, a significant proportion of worms almost reached the bottom of the flume with gravel bed (G-T) leaving only a few worms reworking the top layer. The average number of burrows per m^2 of bed surface estimated on the 15th day after worms' introduction were ~5 x 10^4, ~2 x 10^4, and ~6 x 10^3

in FS-T, CS-T, and G-T respectively. Nearly 85-90% of worms were recovered at the end of experiments.

The visual observations through the flume walls in treatment flumes indicate that clay particles were transported to deeper bed regions and mixed with underlying sediments in all the treatment flumes. In FS-T, the interface between the fine sand and clay layer progressively dissolved due to the mixing of sediments by worms (Figure 2b and 2c) exposing the top surface of the sand bed at some locations (Figure 2d). The clay particles were observed to be mixed with the sand grains up to a depth of ~2 cm. In CS-T, clay particles were transported up to a depth of ~3 cm (Figure 3c) and disintegration of surficial clay layer was also observed (Figure 3d). For the gravel substratum, the clay layer on the top disappeared and the infiltrated clay particles were re-worked to unclog the pores in the top 5 cm of the bed (Figure 4b-d).

3.3 Hyporheic exchange characteristics

The q (estimated from the slope of curves presented in Figure 5a-c) was highest in flumes with gravel and lowest in flumes with fine sand. For all three sediment types, treatment flumes exhibited higher q than their respective control flumes (Table 1). The q in treatment flumes with fine sand, coarse sand, and gravel grains were higher by approximately 25%, 60%, and 50% respectively than their respective control flumes. The estimates of q' (derived as the ratio of depth of exchange to mean residence time) followed a similar trend as q i.e., treatment flumes exhibited higher hyporheic exchange flux compared to their respective control flumes. Note that the q' estimates were consistently lower and within 70% of the q.

Table 1: Calculated exchange characteristics in control (C) and treatment (T) flumes with fine sand (FS), coarse sand (CS), and gravel (G) grains. RT_{med} and RT_{mean} represents the median and mean residence times respectively, $\bar{d}$ represent the equivalent dye penetration depth, and q and q' represent the hyporheic exchange fluxes estimated from the initial gradient of the tracer concentration decay curves and as the ratio of $\bar{d}$ to RT_{mean} respectively.

Flume index	RT_{med} (min)	RT_{mean} (min)	$\bar{d}$ (m)	q x10^{-5} (m min^{-1})	q' x10^{-5} (m min^{-1})
FS-C	2426	3781	0.035	1.23	0.95
FS-T	864	3596	0.050	1.53	1.39
CS-C	804	1769	0.219	17	12
CS-T	346	1069	0.238	27	22
G-C	110	223	0.165	92	74
G-T	56	139	0.173	140	125

The residence time distributions for all the experimental flumes are presented in Figure 5d. For each sediment type, the RT_{med} and RT_{mean} were shorter in treatment flumes compared to their respective control flumes (Table 1). The calculated $\bar{d}$ was greatest in coarse sand and smallest in fine sand beds. For each sediment type, the treatment flume exhibited higher $\bar{d}$ compared to the respective control flume. The $\bar{d}$ in FS-T, CS-T, and G-T was higher by ~42%, ~10% and, ~5% respectively than their respective control flumes. Note that the beds in experimental flumes were not completely mixed with surface water.

4 Discussions

4.1 Sediment-organism interaction and bed disturbance

The model organisms reworked the fine sediments that were deposited on/into the bed in the treatment flumes. As a consequence, the deposited clay particles were either transported from the surface to underlying bed regions or potentially re-suspended into the water column. The transport of clay particles into the bed and their subsequent mixing with the underlying grains occurred due to activities such as burrowing, feeding, and excretion. These activities may have also loosened up the deposited clay layer leading to erosion of the fine particles at the interface followed by re-suspension in the surface water. It is also a possibility that after the surficial clay deposits were reworked by the worms, the downwelling and upwelling hyporheic flow may have contributed to the mobilization of fines, particularly in coarse-bedded treatment flumes.

In a conceptual model presented in *Shrivastava et al.* [2021], it was proposed that the modification to structure and hydraulic properties of streambed due to sediment reworking depends on the size of organism relative to the size of grains and pore spaces. The experimental findings from the current work strengthen the ideas presented in the conceptual model. In all the treatment flumes, the clay layer deposited at the bed surface was disturbed readily as the relative size of clay particles and interstitial pores are likely to be much smaller than the model organisms. However, the interaction of worms with the underlying sediments differed amongst the treatment flumes. In FS-T, the pore sizes are expected to be smaller than the size of worms which could have potentially resulted in re-mobilization of sand grains (along with the clay particles) and development of macro-pores due to worms' activities (e.g. burrowing). On contrary, in CS-T and G-T, the visual observations suggest that worms easily moved within the large pores after penetrating the deposited clay layer leaving the sediment structure in the bed layers largely undisturbed. Further, mobilization of coarse grains was limited due to their much larger size compared to fine sand.

4.2 Influence of sediment reworking on hyporheic flow regime

The accumulated clay particles formed a seal of low permeability clogging layer which potentially inhibited dye transport in the control flumes. The digging of beds and construction of burrows destroyed the fine sediment layer and exposed the underlying coarser bed grains. Consequently, the vertical transport of dye in the treatment flumes was enhanced leading to greater $\bar{d}$ compared to the control flume of each sediment type. The bed permeability at the SWI in treatment flumes is expected to be higher than the control flume due to reworking of the deposited clay layer. As a result, the dye is exchanged rapidly across the SWI which potentially caused shorter RT_{med} and RT_{mean} in the former. For the same reasons, q in treatment flumes for each sediment type was higher than its respective control flume. The enhancement of hyporheic exchange flux due to sediment reworking is further confirmed by higher q' in treatment flumes compared to their respective control flumes which could be attributed to greater $\bar{d}$ and shorter RT_{mean}.

The modification of hyporheic flow across the treatments of different grain sizes was dependent on the overall degree of bed disturbance due to the interaction of worms with the fine sediment layer and underlying bed grains. For instance, in coarse-bedded treatment flumes, the destruction of fine sediment layer at the top supported rapid vertical exchange leading to shorter RT_{mean} and higher hyporheic exchange fluxes compared to their respective control flumes.

However, the flow in underlying sediment layers of these flumes is expected to not alter to a great extent as the reworking activities could only marginally influence the structure and hydraulic properties of coarse-grained beds (as described in section 4.1). Consequently, the exchange depths in CS-T and G-T were only slightly greater than their respective control flumes. Contrastingly, in treatment flumes with fine sand, worms were able to mix and mobilize the sand grains and built extensive burrows in the top layer of bed sediments leading to deeper dye transport in FS-T compared to FS-C. It should be also noted that downward transport of clay particles due to sediment reworking and their subsequent accumulation within the pore spaces of sand grains may have reduced the permeability of lower layers in the bed. It could be a possible reason for the observation of slower dye exchange across the SWI in FS-T compared to FS-C at a later stage of the experiment. With reduction in the exchange rate, the dye particles resided in the bed for longer times which resulted in only marginally shorter mean residence times in FS-T compared to FS-C (whereas the median residence time in FS-T was ~3 times shorter than FS-C).

The findings from our experiments corroborate the previous work that investigated the interaction of sediment reworking organisms with fine sediment layers in streambeds [*Nogaro et al.*, 2006; *Song et al.*, 2010]. For example, in a field study [*Song et al.*, 2010], it was observed that burrows and tubes constructed by *Neoheterocerus* sp. (invertebrate, burrow depth: 50 mm, burrow diameter = 1-6 mm, maximum density: 2 x 10^4 burrows per m^2) caused destruction of the fine sediment deposits at the bed surface. This caused higher vertical hydraulic conductivity in the upper streambed layer leading to improved surface-groundwater exchange. *Nogaro et al.* [2006] conducted laboratory experiments in slow infiltration columns and demonstrated that certain macroinvertebrates (e.g. tubificids) could potentially reduce fine sediment clogging and maintain high hydraulic conductivity in the bed sediments. However, the effects of modification of hydraulic properties on exchange across SWI in vertical columns could not be translated to lotic environments where water and solutes are driven in and out of the bed due to stream flow over undulated bed surface. The re-circulating flume setup is a better representation of the stream environment and has been extensively used to study hyporheic exchange flows in the past [*Packman and MacKay*, 2003; *Rehg et al.*, 2005; *Salehin et al.*, 2004]. Thus, our experimental observations of alteration in dune-induced hyporheic flow due to the activities of macroinvertebrates in streambeds having fine sediment deposits are more relevant than previous laboratory investigations.

4.3 Implications of the work on real stream systems

The permeabilities in natural streambeds have been reported to vary over several orders of magnitude [*Calver*, 2001] and the justification for this variability has been largely based on the deposition or erosion of fine sediments with the streamflow [*Cardenas and Zlotnik*, 2003; *Leek et al.*, 2009; *Levy et al.*, 2011; *Wu et al.*, 2015]. Our previous theoretical and experimental work has provided evidence of the modification of bed permeability due to the burrowing, feeding, and excretion behavior of the in-stream fauna. The findings from current experiments further advance our understanding of the sediment-organism interactions and suggest that sediment reworking organisms could potentially mobilize fine sediments within the bed or re-suspend them into the surface water. By doing so, these organisms are capable of altering the permeability of clogged streambeds. Moreover, both longitudinal transport [*Gottesfeld et al.*, 2004; *Statzner et al.*, 1996] or consolidation of fine particles [*Cardinale et al.*, 2004] could occur based on the reworking behavior of the organisms which might influence the bed morphodynamics. This ability of streambed inhabitants to influence fine sediment dynamics in streams has implications on existing sediment transport theories that largely ignore biotic influences on the fate and transport of fine sediments.

With the ability to modify streambed properties and subsequently the hyporheic flow regime, sediment reworking organisms could also potentially influence the biogeochemistry of hyporheic zones. The rates of processing of nutrients and pollutants would get affected by the modification in hyporheic exchange flux and residence times of solutes in the biologically reworked zones of streambeds. Additionally, macroinvertebrates are regarded as ecosystem engineers [*Jones et al.*, 1994], and can potentially modify the structure and composition of microbial communities in hyporheic zones by regulating the availability of resources. For instance, clogged streambeds are generally characterized by an impeded supply of oxygen to the sub-surface sediments that could result in the development of anoxic environments in deeper bed regions supporting the activities of anaerobic organisms. However, mitigation of clogging due to sediment reworking could potentially improve the vertical connectivity and supply oxygen from surface water to deeper regions and stimulate activities of aerobic organisms. The modulation in biologically mediated chemical transformations of solutes would potentially influence the overall quality of surface and sub-surface waters and thus has implications for stream management and conservation programs that aim to restore biogeochemical functions in streams.

4.4 Limitations and future directions

These experiments provide valuable insights into the interaction of sediment reworking organisms with the accumulated fine sediments in a streambed. However, the experimental flumes and flow conditions are yet a simplistic representation of the stream environment. For instance, the beds were homogenous and the flow regime (e.g. flow velocity and depth) was such that no erosion of fine/bed sediments or model organisms occurred during the experiments. The degree of sediment reworking and its influence on hyporheic exchange flows would be expectedly different if the sediments or organisms were transported to downstream regions due to higher flow rates. Another limitation of this study is the lack of replication. The validity of our findings would have been improved if more control and treatment flumes for each sediment type were accommodated in the experimental design. Moreover, the experiments were conducted in a controlled environment and did not incorporate the impact of environmental variables such as availability of nutrients and conducive temperature regime [*Fortino*, 2006; *Malard et al.*, 2003; *Mermillod-Blondin et al.*, 2004; *Palmer*, 1990; *Shelton et al.*, 2016] on the biological reworking of sediment beds.

Further, the experiments were performed with just one species of reworking organisms, whereas, organisms in natural settings exhibit different reworking behaviors which may influence the bed properties and hyporheic flow regime differently. For instance, based on the feeding behavior of model organisms, they are regarded as upward conveyors i.e. they move sediments towards the bed surface by feeding at depth and depositing fecal pellets at the SWI [*Kristensen et al.*, 2012]. Some sediment reworking organisms exhibit an opposite feeding strategy i.e., they feed on sediments at the surface and deposit fecal pellets within the bed (referred to as downward conveyors). It can be expected that modification of hydro-physical properties of the beds due to sediment reworking by downward conveyors would be different than the model organisms used in our study. Similarly, it has been observed that organisms that build U-shaped burrows (*Corophium volutator*, burrow length: 3–4 cm may decrease bed permeability while the organisms that build deep burrows (*Nereis diversicolor*, burrow length: 8–10 cm) may have an opposite effect [*Meadows and Tait*, 1989]. The extent to which sediment beds are reworked may also depend on the body size of the organisms. Large-size organisms may construct thicker burrows and re-mobilize bed grains more vigorously compared to organisms of smaller size. For example, an experimental study [*Nadaï-Monoury et al.*, 2013] reported that *Barbatula barbatula* (fish, body size: ~10 cm long) reworked the surface sediments to a greater degree (~20 times greater) compared to *Cordulegaster boltonii* (invertebrate, up to 4 cm long). Furthermore, as several organisms co-exist in stream environments, their prey-predator relationship may play a critical role in determining how the streambed properties would be influenced due to sediment reworking.

Clearly, comprehending the influence of sediment reworking organisms on streambed processes is complicated and we call for performing more intensive laboratory experiments under variable physico-chemical and biological environments. Also, field evidence of the modification of hydro-physical properties of streambeds due to feedback mechanisms between the fine sediment clogging and sediment reworking processes are rare, thus future research must be also directed to study impacts of sediment-organism interactions at large scales.

5 Conclusions

Laboratory experiments in re-circulating flumes were conducted to investigate the effects of sediment reworking by macroinvertebrates on hyporheic flow regime in compositionally different streambeds having deposits of clay-sized fine sediments. The model organisms, *Lumbriculus variegatus*, re-worked the deposited clay layer leading to enhanced vertical hydrological connectivity in treatment flumes compared to control flumes. For all the treatment flumes, the penetration depths were greater, mean and median residence times were shorter, and hyporheic exchange fluxes were higher than the respective control flumes. Our experiments reveal that the modification to hyporheic flow characteristics in the treatment flumes was dependent on the interaction of organisms with both fine sediments and underlying bed grains. The results highlight that the size of organisms relative to the size of bed grains and pores is a dominant control on the extent to which model streambeds were disturbed. We suggest that more intensive laboratory experiments along with field evidence of sediment-organism interactions should be the focus of imminent studies to advance our understanding of the role of in-stream fauna in stream ecosystems.

Acknowledgments and Data

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The authors declare no conflicts of interest.

The data related to the laboratory experiments can be accessed at

http://www.hydroshare.org/resource/3e2de290b3344443b751aa6a199c065c

References

Anlauf, K. J., and Moffitt, C. M. (2008), Models of stream habitat characteristics associated with tubificid populations in an intermountain watershed. *Hydrobiologia*, *603*(1), 147-158.

Anschutz, P., Ciutat, A., Lecroart, P., Gérino, M., and Boudou, A. (2012), Effects of tubificid worm bioturbation on freshwater sediment biogeochemistry. *Aquatic Geochemistry*, *18*(6), 475-497.

Bardini, L., Boano, F., Cardenas, M. B., Revelli, R., and Ridolfi, L. (2012), Nutrient cycling in bedform induced hyporheic zones. *Geochimica et Cosmochimica Acta*, *84*, 47-61.

Blankson, E. R., and Klerks, P. L. (2016), The effect of lead from sediment bioturbation by Lumbriculus variegatus on Daphnia magna in the water column. *Ecotoxicology*, *25*(10), 1712-1719.

Brinkhurst, R. O., and Kennedy, C. R. (1965), Studies on the biology of the Tubificidae (Annelida, Oligochaeta) in a polluted stream. *The Journal of Animal Ecology*, *34*(2), 429-443.

Brunke, M. (1999), Colmation and depth filtration within streambeds: retention of particles in hyporheic interstices. *International Review of Hydrobiology*, *84*(2), 99-117.

Brunke, M., and Gonser, T. (1997), The ecological significance of exchange processes between rivers and groundwater. *Freshwater biology*, *37*(1), 1-33.

Calver, A. (2001), Riverbed permeabilities: information from pooled data. *Ground Water*, *39*(4), 546-553.

Cardenas, M. B., and Zlotnik, V. A. (2003), Three-dimensional model of modern channel bend deposits. *Water Resources Research*, *39*(6), 1141.

Cardinale, B. J., Gelmann, E. R., and Palmer, M. A. (2004), Net spinning caddisflies as stream ecosystem engineers: the influence of Hydropsyche on benthic substrate stability. *Functional Ecology*, *18*(3), 381-387.

Chen, X., Cardenas, M. B., and Chen, L. (2018), Hyporheic exchange driven by three-dimensional sandy bed forms: Sensitivity to and prediction from bed form geometry. *Water Resources Research*, *54*(6), 4131-4149.

Cook, D. G. (1969), Observations on the life history and ecology of some Lumbriculidae (Annelida, Oligochaeta). *Hydrobiologia*, *34*(3-4), 561-574.

Datry, T., Lafont, M., and Larned, S. (2010), Hyporheic annelid distribution along a flow permanence gradient in an alluvial river. *Aquatic Sciences*, *72*(3), 335-346.

Datry, T., Hervant, F., Malard, F., Vitry, L., and Gibert, J. (2003), Dynamics and adaptive responses of invertebrates to suboxia in contaminated sediments of a stormwater infiltration basin. *Archiv für Hydrobiologie*, *156*(3), 339-359.

Descloux, S., Datry, T., and Marmonier, P. (2013), Benthic and hyporheic invertebrate assemblages along a gradient of increasing streambed colmation by fine sediment. *Aquatic Sciences*, *75*(4), 493-507.

Elliott, A. H., and Brooks, N. H. (1997), Transfer of nonsorbing solutes to a streambed with bed forms: Theory. *Water Resources Research*, *33*(1), 123-136.

Fortino, K. (2006), Effect of season on the impact of ecosystem engineers in the New River, NC. *Hydrobiologia*, *559*(1), 463-466.

Fox, A., Packman, A. I., Boano, F., Phillips, C. B., and Arnon, S. (2018), Interactions between suspended kaolinite deposition and hyporheic exchange flux under losing and gaining flow conditions. *Geophysical Research Letters*, *45*(9), 4077-4085.

Gandy, C. J., Smith, J. W., and Jarvis, A. P. (2007), Attenuation of mining-derived pollutants in the hyporheic zone: a review. *Science of The Total Environment*, *373*(2-3), 435-446.

Gottesfeld, A. S., Hassan, M. A., Tunnicliffe, J. F., and Poirier, R. W. (2004), Sediment dispersion in salmon spawning streams: the influence of floods and salmon redd construction. *Journal of the American Water Resources Association*, *40*(4), 1071-1086.

Govedich, F. R., Bain, B. A., Moser, W. E., Gelder, S. R., Davies, R. W., and Brinkhurst, R. O. (2010), Annelida (Clitellata): Oligochaeta, Branchiobdellida, Hirudinida, and Acanthobdellida, in *Ecology and classification of North American freshwater invertebrates*, edited by J. H. Thorp and A. P. Covich, pp. 385-436, Elsevier.

Johnson, M. F., Rice, S. P., and Reid, I. (2011), Increase in coarse sediment transport associated with disturbance of gravel river beds by signal crayfish (Pacifastacus leniusculus). *Earth Surface Processes and Landforms*, *36*(12), 1680-1692.

Jones, C. G., Lawton, J. H., and Shachak, M. (1994), Organisms as ecosystem engineers, in *Ecosystem Management*, edited, pp. 130-147, Springer, New York.

Karwan, D. L., and Saiers, J. E. (2012), Hyporheic exchange and streambed filtration of suspended particles. *Water Resources Research*, *48*(1).

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C. O., and Banta, G. T. (2012), What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*, *446*, 285-302.

Leek, R., Wu, J. Q., Wang, L., Hanrahan, T. P., Barber, M. E., and Qiu, H. (2009), Heterogeneous characteristics of streambed saturated hydraulic conductivity of the Touchet River, south eastern Washington, USA. *Hydrological Processes*, *23*(8), 1236-1246.

Lenat, D. R., Penrose, D. L., and Eagleson, K. W. (1981), Variable effects of sediment addition on stream benthos. *Hydrobiologia*, *79*(2), 187-194.

Leppänen, M. T., and Kukkonen, J. V. (1998), Relationship between reproduction, sediment type, and feeding activity of Lumbriculus variegatus (Müller): implications for sediment toxicity testing. *Environmental Toxicology and Chemistry: An International Journal*, *17*(11), 2196-2202.

Levy, J., Birck, M. D., Mutiti, S., Kilroy, K. C., Windeler, B., Idris, O., and Allen, L. N. (2011), The impact of storm events on a riverbed system and its hydraulic conductivity at a site of induced infiltration. *Journal of Environmental Management*, *92*(8), 1960-1971.

Lin, K.-J., and Yo, S.-P. (2008), The effect of organic pollution on the abundance and distribution of aquatic oligochaetes in an urban water basin, Taiwan. *Hydrobiologia*, *596*(1), 213-223.

Malard, F., Ferreira, D., Dolédec, S., and Ward, J. (2003), Influence of groundwater upwelling on the distribution of the hyporheos in a headwater river flood plain. *Archiv für Hydrobiologie*, *157*(1), 89-116.

Marmonier, P., Archambaud, G., Belaidi, N., Bougon, N., Breil, P., Chauvet, E., Claret, C., Cornut, J., Datry, T., and Dole-Olivier, M.-J. (2012), The role of organisms in hyporheic processes: gaps in current knowledge, needs for future research and applications, paper presented at Annales de Limnologie-International Journal of Limnology, EDP Sciences.

Meadows, P., and Tait, J. (1989), Modification of sediment permeability and shear strength by two burrowing invertebrates. *Marine Biology*, *101*(1), 75-82.

Mermillod-Blondin, F., Gérino, M., Degrange, V., Lensi, R., Chassé, J.-L., Rard, M., and Châtelliers, M. C. d. (2001), Testing the functional redundancy of Limnodrilus and Tubifex (Oligochaeta, Tubificidae) in hyporheic sediments: an experimental study in microcosms. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(9), 1747-1759.

Mermillod-Blondin, F., Gaudet, J. P., Gérino, M., Desrosiers, G., and Creuzé des Châtelliers, M. (2003), Influence of macroinvertebrates on physico-chemical and microbial processes in hyporheic sediments. *Hydrological Processes 17*(4), 779-794.

Mermillod-Blondin, F., Gaudet, J. P., Gerino, M., Desrosiers, G., Jose, J., and Châtelliers, M. C. d. (2004), Relative influence of bioturbation and predation on organic matter processing in river sediments: a microcosm experiment. *Freshwater Biology*, *49*(7), 895-912.

Morad, M., Khalili, A., Roskosch, A., and Lewandowski, J. (2010), Quantification of pumping rate of Chironomus plumosus larvae in natural burrows. *Aquatic Ecology*, *44*(1), 143-153.

Nadaï-Monoury, D., Lecerf, A., Canal, J., Buisson, L., Laffaille, P., and Gilbert, F. (2013), A cost-effective method to quantify biological surface sediment reworking. *Hydrobiologia*, *713*(1), 115-125.

Nogaro, G., Mermillod-Blondin, F., Francois-Carcaillet, F., Gaudet, J.-P., Lafont, M., and Gibert, J. (2006), Invertebrate bioturbation can reduce the clogging of sediment: an experimental study using infiltration sediment columns. *Freshwater Biology*, *51*(8), 1458-1473.

Packman, A. I., and Brooks, N. H. (2001), Hyporheic exchange of solutes and colloids with moving bed forms. *Water Resources Research*, *37*(10), 2591-2605.

Packman, A. I., and Salehin, M. (2003), Relative roles of stream flow and sedimentary conditions in controlling hyporheic exchange. *Hydrobiologia*, *494*(1-3), 291-297.

Packman, A. I., and MacKay, J. S. (2003), Interplay of stream-subsurface exchange, clay particle deposition, and streambed evolution. *Water Resources Research*, *39*(4), 1097.

Palmer, M. A. (1990), Temporal and spatial dynamics of meiofauna within the hyporheic zone of Goose Creek, Virginia. *Journal of the North American Benthological Society*, *9*(1), 17-25.

Postolache, C., Rîşnoveanu, G., and Vădineanu, A. (2006), Nitrogen and phosphorous excretion rates by tubificids from the Prahova River (Romania). *Hydrobiologia*, *553*(1), 121-127.

Rehg, K. J., Packman, A. I., and Ren, J. (2005), Effects of suspended sediment characteristics and bed sediment transport on streambed clogging. *Hydrological Processes*, *19*(2), 413-427.

Roche, K. R., Aubeneau, A. F., Xie, M., Aquino, T., Bolster, D., and Packman, A. I. (2016), An Integrated Experimental and Modeling Approach to Predict Sediment Mixing from Benthic Burrowing Behavior. *Environmental Science and Technology*, *50*(18), 10047-10054.

Sadeghi, S. H., and Saeidi, P. (2010), Reliability of sediment rating curves for a deciduous forest watershed in Iran. *Hydrological sciences journal*, *55*(5), 821-831.

Salehin, M., Packman, A. I., and Paradis, M. (2004), Hyporheic exchange with heterogeneous streambeds: Laboratory experiments and modeling. *Water Resources Research*, *40*(11), W11504.

Schälchli, U. (1992), The clogging of coarse gravel river beds by fine sediment, in *Sediment/Water Interactions*, edited by H. B.T. and S. P.G., pp. 189-197, Springer, Dordrecht.

Shelton, J. M., Samways, M. J., Day, J. A., and Woodford, D. J. (2016), Are native cyprinids or introduced salmonids stronger regulators of benthic invertebrates in South African headwater streams? *Austral Ecology*, *41*(6), 633-643.

Shrivastava, S., Stewardson, M. J., and Arora, M. (2020a), Understanding streambeds as complex systems: review of multiple interacting environmental processes influencing streambed permeability. *Aquatic Sciences*, *82*(4), 1-18.

Shrivastava, S., Stewardson, M. J., and Arora, M. (2020b), Distribution of clay-sized sediments in streambeds and influence of fine sediment clogging on hyporheic exchange. *Hydrological Processes*, *34*(26), 5674-5685.

Shrivastava, S., Stewardson, M. J., and Arora, M. (2021), Influence of Bioturbation on Hyporheic Exchange in Streams: Conceptual Model and Insights from Laboratory Experiments. *Water Resources Research*, *57*(2), e2020WR028468.

Song, J., Chen, X., and Cheng, C. (2010), Observation of bioturbation and hyporheic flux in streambeds. *Frontiers of Environmental Science & Engineering in China*, *4*(3), 340-348.

Statzner, B., Fuchs, U., and Higler, L. W. (1996), Sand erosion by mobile predaceous stream insects: implications for ecology and hydrology. *Water Resources Research*, *32*(7), 2279-2287.

Storey, R. G., Howard, K. W., and Williams, D. D. (2003), Factors controlling riffle-scale hyporheic exchange flows and their seasonal changes in a gaining stream: A three-dimensional groundwater flow model. *Water Resources Research*, *39*(2), 1034.

Verdonschot, P. F. (2001), Hydrology and substrates: determinants of oligochaete distribution in lowland streams (The Netherlands). *Hydrobiologia*, *463*(1), 249-262.

Wood, P. J., and Armitage, P. D. (1997), Biological effects of fine sediment in the lotic environment. *Environmental Management*, *21*(2), 203-217.

Work, P. A., Moore, P. R., and Reible, D. D. (2002), Bioturbation, advection, and diffusion of a conserved tracer in a laboratory flume. *Water Resources Research*, *38*(6), 24-21-24-29.

Wu, G., Shu, L., Lu, C., Chen, X., Zhang, X., Appiah-Adjei, E. K., and Zhu, J. (2015), Variations of streambed vertical hydraulic conductivity before and after a flood season. *Hydrogeology Journal*, *23*(7), 1603-1615.

Zweig, L. D., and Rabeni, C. F. (2001), Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. *Journal of the North American Benthological Society*, *20*(4), 643-657.

Figure Captions

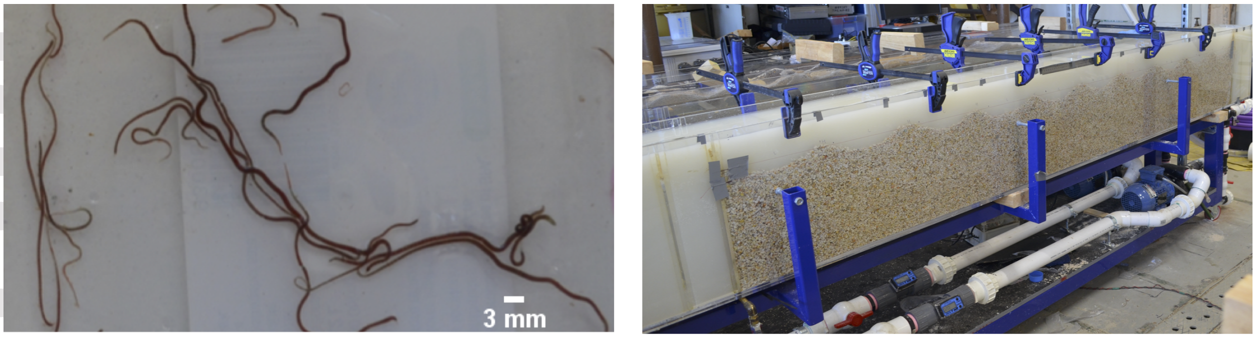
Figure 1: *Lumbriculus variegatus* used as model sediment reworking organisms in the experiments, and b) one of the re-circulating flumes with dune-shaped gravel streambeds.

Figure 2: State of the treatment flume with fine sand grains (FS-T) as observed from the flume walls during the experiments – a) before addition of worms, b) on Day 7 after worms' addition, and c) on Day 15 after worms' addition. The top view of the flume on Day 10 (d) illustrates the holes/burrows, tails of the worms, and the disappearance of deposited clay layer at the bed surface as a result of sediment reworking. The insets in sub-figures 'b' and 'c' (top left corner) are the zoomed-in bed regions demonstrating the worms' burrows and mixing of clay particles with the underlying sand grains respectively. The red lines visible in sub-figures 'a-c' are the threads placed at the outside of the flume wall to assist in shaping bedforms with consistent height and wavelength along the flume at the beginning of the experiments.

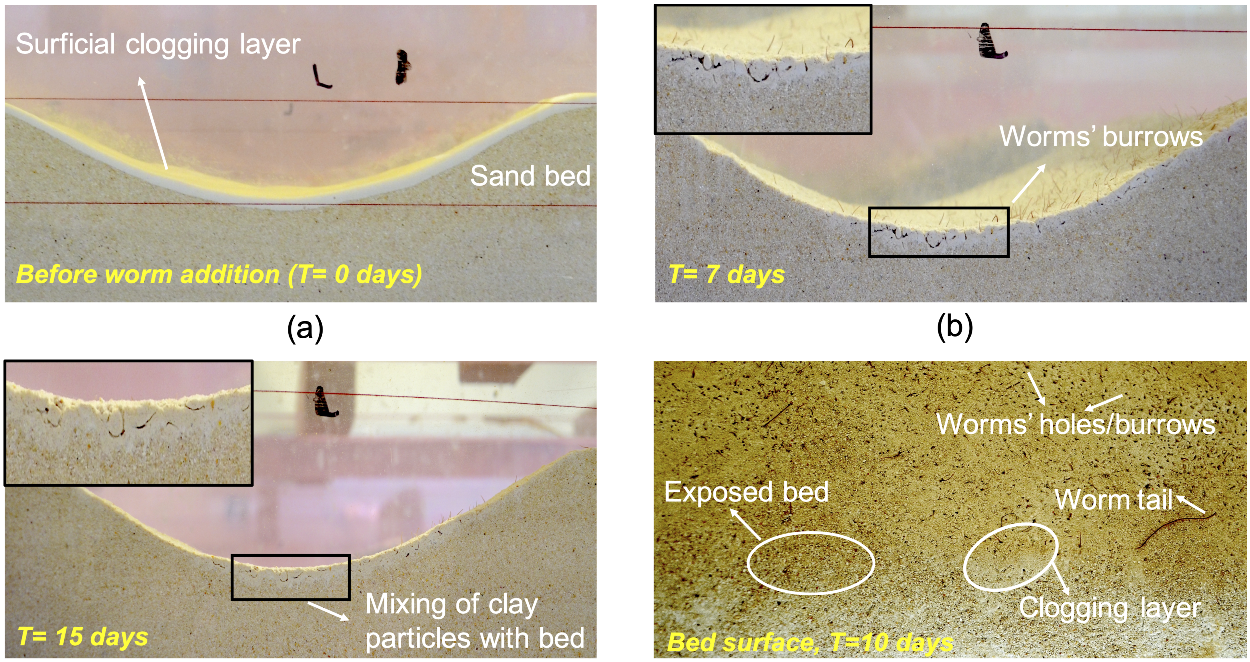
Figure 3: State of the treatment flume with coarse sand grains (CS-T) as observed from the flume wall during the experiments – a) before addition of worms, b) on Day 7 after worms' addition, and c) on Day 15 after worms' addition. The top view of the flume on Day 10 (d) illustrates the holes/burrows and disintegration of the deposited clay layer due to the activities of model sediment reworking organisms. The insets in sub-figures 'b' and 'd' (top left corner) are the zoomed-in bed regions demonstrating the worms moving within the bed and worms' burrows at the bed surface respectively. The red lines visible in sub-figures 'a-c' are the threads placed at the outside of the flume wall to assist in shaping bedforms with consistent height and wavelength along the flume at the beginning of the experiments.

Figure 4: State of the treatment flume with gravel grains (G-T) as observed from the flume wall during the experiments – a) before addition of worms, b) on Day 7 after worms' addition, and c) on Day 15 after worms' addition. The top view of the flume on Day 10 (d) illustrates the disappearance of fine sediment (clay) layer from the bed surface as a result of sediment reworking by model organisms.

Figure 5: The observed (markers, presented as Obs in the legend) and fitted (lines, presented as Fit in the legend) temperature-corrected normalized dye concentration in the water column of control (C) and treatment (T) flumes - a) fine sand (FS), b) coarse sand (CS), and c) gravel (G). The flux weighted cumulative residence time distributions for all the experimental flumes are presented in sub-figure 'd'.

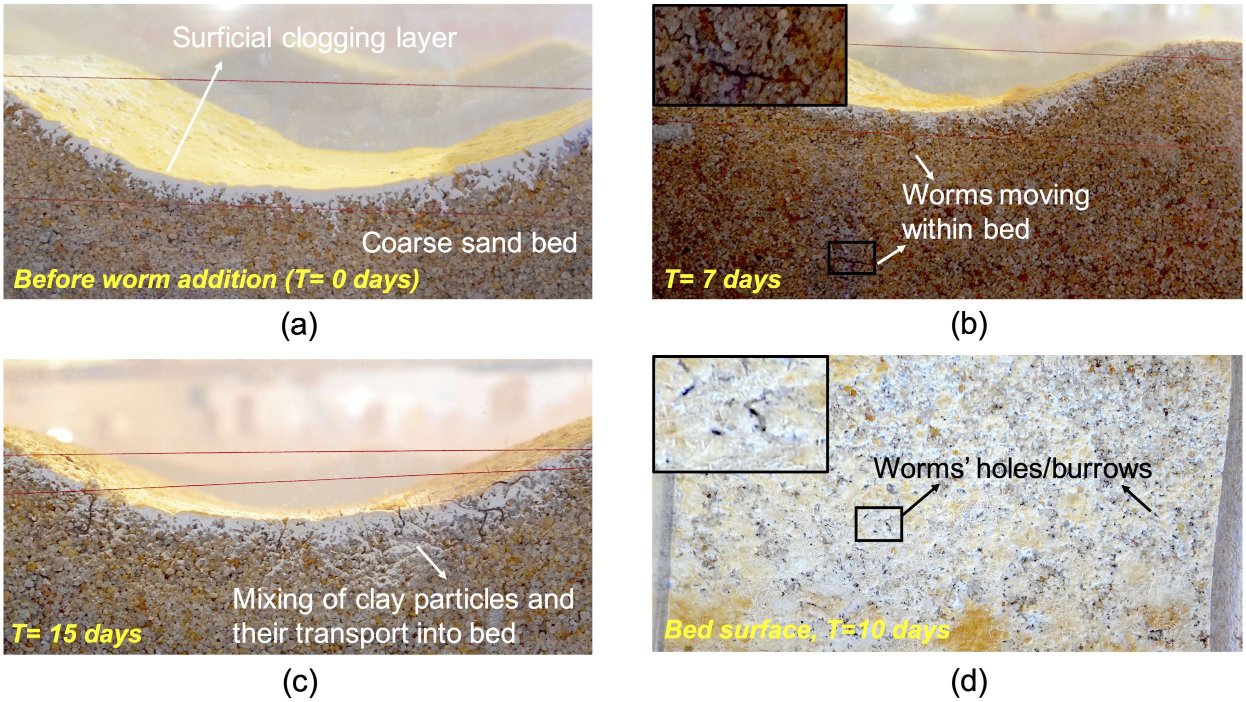


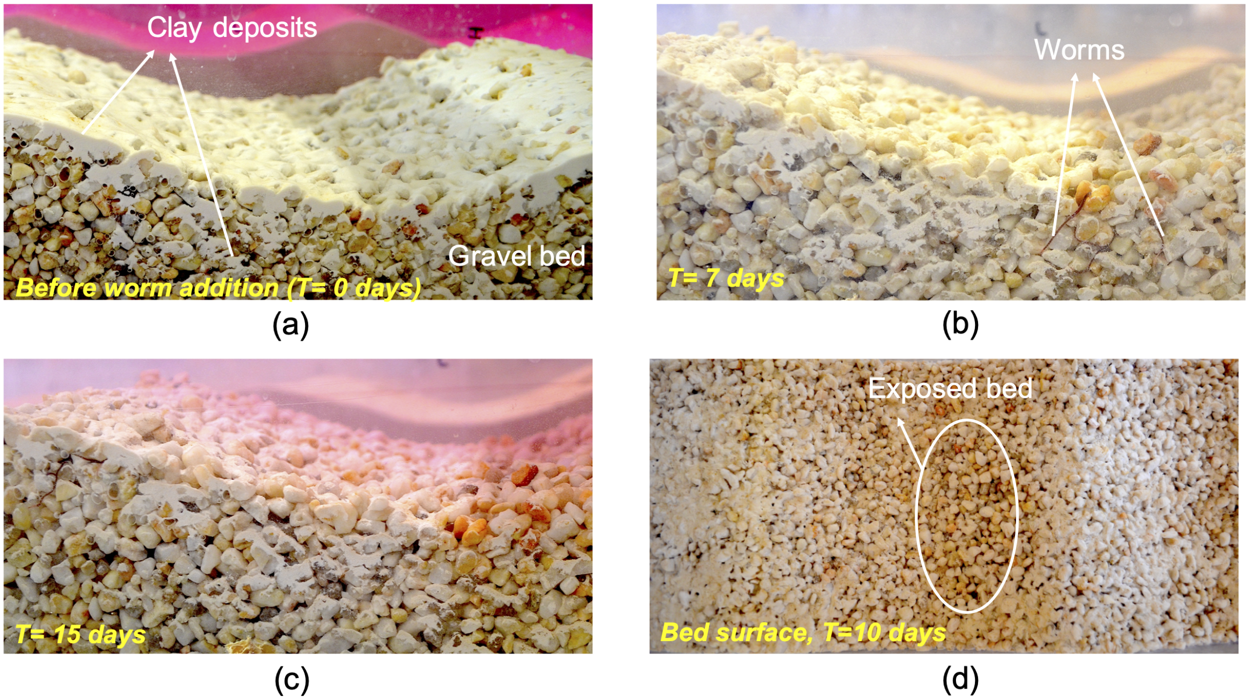
(a) (b)

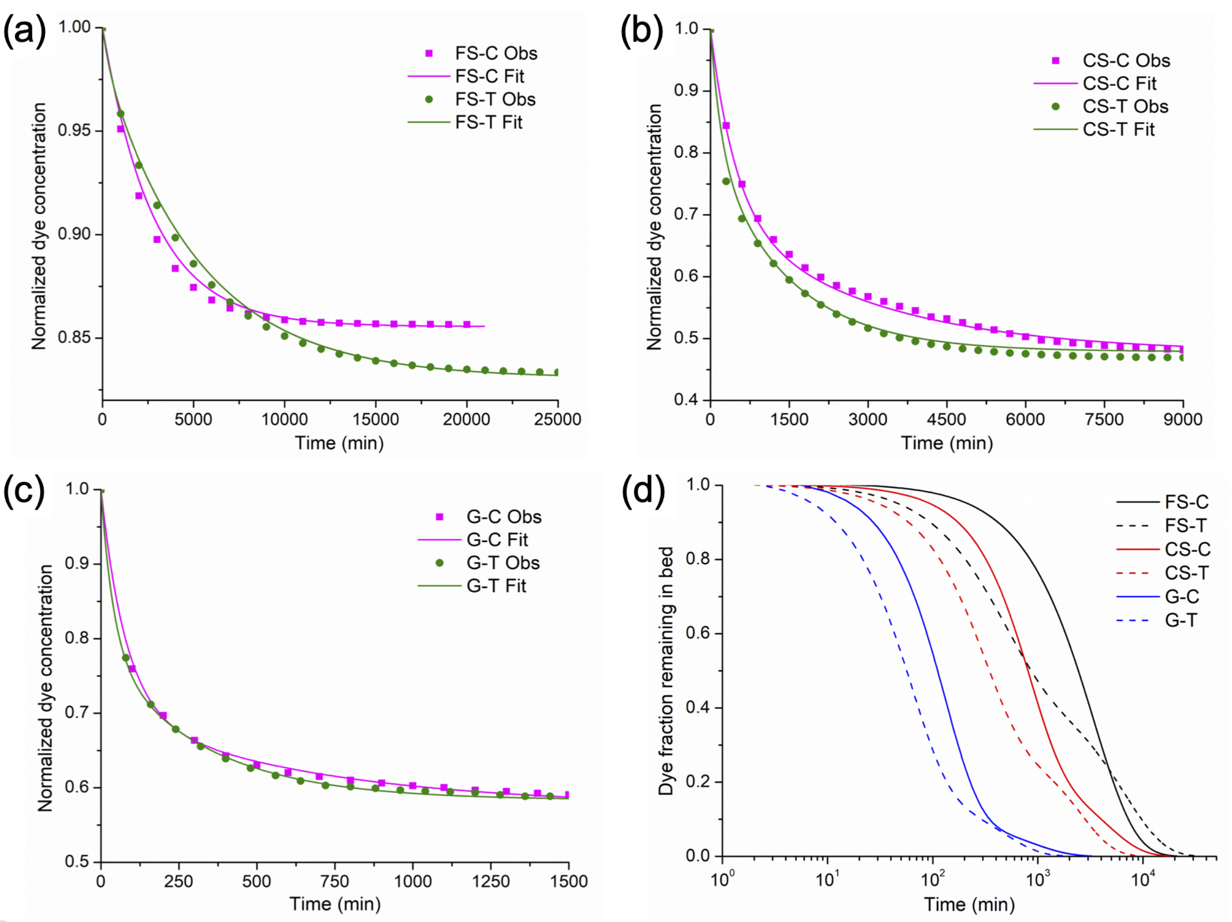

Surficial clogging layer
Sand bed
Before worm addition (T= 0 days)
Worms' burrows
T= 7 days
T= 15 days
Mixing of clay particles with bed
Worms' holes/burrows
Exposed bed
Worm tail
Clogging layer
Bed surface, T=10 days

(a) (b)

(c) (d)


Surficial clogging layer
Coarse sand bed
Before worm addition (T= 0 days)
(a)
Worms moving within bed
T= 7 days
(b)
Mixing of clay particles and their transport into bed
T= 15 days
(c)
Worms' holes/burrows
Bed surface, T=10 days
(d)


Clay deposits
Gravel bed
Before worm addition (T= 0 days)
(a)
Worms
T= 7 days
(b)
T= 15 days
(c)
Exposed bed
Bed surface, T=10 days
(d)


(a)
Normalized dye concentration
1.00
0.95
0.90
0.85
0
5000
10000
15000
20000
25000
Time (min)
FS-C Obs
FS-C Fit
FS-T Obs
FS-T Fit
(b)
Normalized dye concentration
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0
1500
3000
4500
6000
7500
9000
Time (min)
CS-C Obs
CS-C Fit
CS-T Obs
CS-T Fit
(c)
Normalized dye concentration
1.0
0.9
0.8
0.7
0.6
0.5
0
250
500
750
1000
1250
1500
Time (min)
G-C Obs
G-C Fit
G-T Obs
G-T Fit
(d)
Dye fraction remaining in bed
1.0
0.8
0.6
0.4
0.2
0.0
10^0
10^1
10^2
10^3
10^4
Time (min)
FS-C
FS-T
CS-C
CS-T
G-C
G-T