Architects under the streams: influence of macroinvertebrate sediment reworking on hyporheic exchange in clogged streambeds

Shivansh Shrivastava[1], Michael J Stewardson[1], and Meenakshi Arora[1]

[1]University of Melbourne

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Abstract

The mobilization and mixing of sediments by the activities of streambed inhabitants, referred to as sediment reworking, constantly modify the physical and hydraulic properties of streambeds. However, limited progress has been made to explore the influence of this sediment-organism interaction on hyporheic exchange. In this work, we advance the understanding of the role of macroinvertebrate sediment reworking in altering the hyporheic exchange flows in clogged streambeds. Laboratory experiments are conducted in re-circulating flumes following a control (clogging) and treatment (clogging + sediment reworking) 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 model streambeds comprising fine sand, coarse sand, and gravel sediments. We observe that model organisms burrowed extensively into the clogging layer, mixed the clay particles with underlying grains, and eventually eroded or disintegrated the clogging layer at the bed surface in the treatment flumes. As a consequence, the treatment flumes exhibited greater solute penetration depth, shorter median and mean residence times, and higher hyporheic 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 including both fine and substrate sediments. The alteration of hydro-physical properties of streambeds and subsequently the hyporheic flow regime due to sediment reworking has direct implications for the biogeochemistry of hyporheic zones and may impact the overall quality of surface and sub-surface waters, particularly in low flow environments.

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S. Shrivastava, M. J. Stewardson, and M. Arora

Affiliation for authors: Environmental Hydrology and Water Resources Group, Department of Infrastructure Engineering, The University of Melbourne, Parkville, Victoria Australia 3010.

Corresponding author: Shivansh Shrivastava (sshrivastava653@gmail.com)

Key Points:

- Sediment reworking by in-stream faunal organisms is studied in long re-circulating flumes.
- The activities of macroinvertebrates can improve hydrological connectivity in clogged streambeds.
- Hyporheic flow regime could be modified due to macroinvertebrate sediment reworking.

Abstract

The mobilization and mixing of sediments by the activities of streambed inhabitants, referred to as sediment reworking, constantly modify the physical and hydraulic properties of streambeds. However, limited progress has been made to explore the influence of this sediment-organism interaction on hyporheic exchange. In this work, we advance the understanding of the role of macroinvertebrate sediment reworking in altering the hyporheic exchange flows in clogged streambeds. Laboratory experiments are conducted in re-circulating flumes following a control (clogging) and treatment (clogging + sediment reworking) 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 model streambeds comprising fine sand, coarse sand, and gravel sediments. We observe that model organisms burrowed extensively into the clogging layer, mixed the clay particles with underlying grains, and eventually eroded or disintegrated the clogging layer at the bed surface in the treatment flumes. As a consequence, the treatment flumes exhibited greater solute penetration depth, shorter median and mean residence times, and higher hyporheic 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 including both fine and substrate sediments. The alteration of hydro-physical properties of streambeds and subsequently the hyporheic flow regime due to sediment reworking has direct implications for the biogeochemistry of hyporheic zones and may impact the overall quality of surface and sub-surface waters, particularly in low flow environments.

Plain Language Summary

The stream-groundwater exchange underpins several critical ecosystem services such as natural processing of nutrients/contaminants and any modification to the exchange flows will directly influence the overall quality of both surface and sub-surface waters. It is well known that the accumulation of fine sediments could clog the streambeds and hamper the exchange of water and energy across the sediment-water interface. In addition to the presence of fine sediments, streambeds host a range of faunal organisms such as macroinvertebrates that burrow, feed, and excrete in the sediments, however, little is known how these activities could modify the hydro-physical properties of clogged streambeds and consequently the exchange flows. In this work, we conduct 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). The results reveal that the activities of sample macroinvertebrates could penetrate and disintegrate the clay deposits. This enhances the rate of transfer of water molecules across the streambeds, reduces the time they reside in the bed, and increases the exchange depth. The modification of the exchange characteristics has direct consequences for the overall functioning of stream ecosystems.

1 Introduction

Hyporheic zone is regarded as a unique ecotone facilitating the exchange of mass and energy between the groundwater and stream. The two-way exchange 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]. The physical (e.g. bed morphology) and hydraulic (e.g. bed permeability or closely related hydraulic conductivity) properties of streambeds are among the major drivers of hyporheic exchange, particularly at small scales [*Bardini et al.*, 2012; *Aaron I Packman and Salehin*, 2003; *Storey et al.*, 2003]. These hydro-physical properties of streambeds and consequently the hyporheic exchange flows could be modified due to several in-stream processes among which fine sediment clogging (abiotic) and sediment reworking by streambed inhabitants (biotic) are the critical ones [*Shrivastava et al.*, 2020b]. It is important to comprehend the alteration in hyporheic flow regime (e.g. flux, residence times, and depth of exchange) as it has direct implications on the overall quality of surface and sub-surface waters. While the influence of fine sediment clogging on hyporheic exchange has been subject to extensive research in the past, little is known about how the activities of faunal organisms could modify the exchange across SWI in stream ecosystems. The focus of this work is to advance the understanding of the impact of the in-stream faunal organisms on their physical habitat and subsequently on the hyporheic flow regime.

Sediment reworking is described as the mobilization and mixing of sediments due to the activities such as locomotion, burrowing, feeding, and excretion performed by the aquatic organisms inhabiting sediment beds [*Kristensen et al.*, 2012]. For instance, polychaetes' activities such as ingestion of sediments, deposition of fecal pellets, and construction of tubes have been observed to rework the tidal sediments up to a depth of 30 cm [*Rhoads*, 1967]. Similarly, ostracods (also known as seed shrimp) of average size ~0.5 mm were observed to construct burrows up to a depth of 4 mm leading to re-mobilization of marine sediments [*Cullen*, 1973]. In freshwater environments, the influence of sediment reworking by fish (e.g. salmon) and crustacean (e.g. crayfish) species on sediment mobilization and transport has been documented [*Gottesfeld et al.*, 2004; *Johnson et al.*, 2011]. Streambeds also host a wide range of oligochaetes with some of the organisms observed at a density as high as 10^6 individuals.m^{-2} (e.g. *Tubifex tubifex*) [*Brinkhurst and Kennedy*, 1965]. These invertebrates could construct a dense network of galleries, for instance, burrows of depth up to 5 cm and a diameter ranging from 1-6 mm have been observed in streambeds [*Song et al.*, 2010].

Compared to marine ecosystems, there is limited understanding of the influence of sediment reworking organisms on modifying the properties of their habitat and subsequently the exchange of mass and solutes across the SWI in stream ecosystems [*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; *Geraldine 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 by the interaction of flow and channel boundary. To better represent the flow conditions in streams, in our recent work [*Shrivastava et al.*, 2021], we conducted experiments in long re-circulating hydraulic flumes and demonstrated that sediment reworking by macroinvertebrates could significantly alter the hyporheic flow regime, particularly in low flow environments (e.g. during dry season or in regulated streams that experience less frequent floods).

Stream water is generally laden with fine sediments that deposit on/into the streambeds, a process described as fine sediment clogging [*Brunke*, 1999; *Schälchli*, 1992]. Accumulation of fine materials in a coarser streambed alters its composition and structure [*Beschta and Jackson*, 1979; *Ryan and Packman*, 2006] and subsequently impacts the overall stream ecosystem functioning [*Brunke and Gonser*, 1997; *Hartwig et al.*, 2012; *Géraldine Nogaro et al.*, 2010; *Ongley et al.*, 1992]. Particularly, clogging of the streambeds has a negative influence on sub-surface ecology and has been associated with the reduction in stream biodiversity [*J I Jones et al.*, 2012; *Wood and Armitage*, 1997]. However, certain species such as Chironomid and Oligochaetes have been reported as tolerant of excessive fine sediment input to streams [*Datry et al.*, 2003; *Lenat et al.*, 1981; *Zweig and Rabeni*, 2001]. It can be expected that these organisms could rework the fine sediment deposits and modify the hydro-physical properties of streambeds leading to alteration of the hyporheic flow regime.

In the current work, we focus on assessing the interactions of sediment reworking organisms with fine sediment deposits on/into the streambeds and the subsequent influence on hyporheic exchange flows in stream ecosystems. More specifically, we conduct experiments in re-circulating flumes following control and treatment-based design to study the role of model organisms (*Lumbriculus variegatus*) in re-mobilizing the accumulated fine sediments (clay) in homogenous streambeds of different sedimentary composition (fine sand, coarse sand, and gravel). Dye tracer tests are performed to evaluate the hyporheic flux, residence times, and exchange depths in the control and treatment flumes.

2 Experimental methods

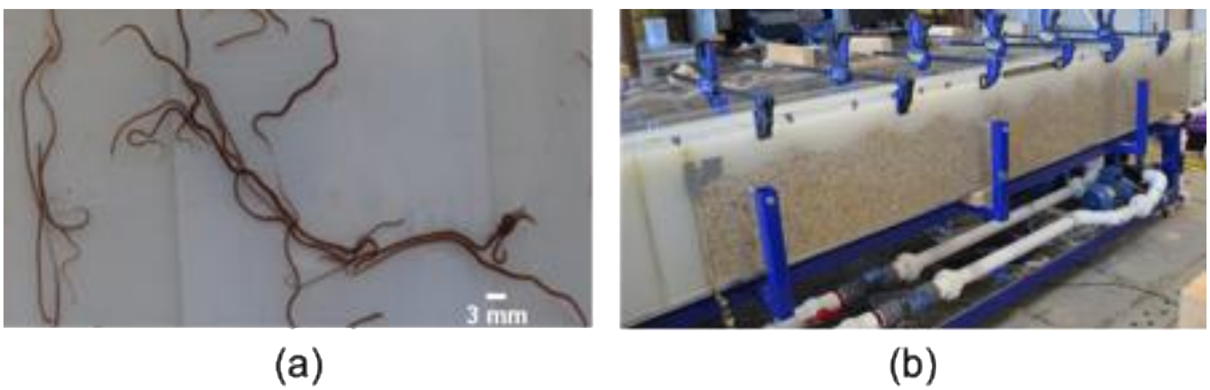

Figure 1: *Lumbriculus variegatus* used as model sediment reworking organisms in the experiments, and b) one of the re-circulating flumes with dune-shaped gravel streambeds.

2.1 Model bioturbating 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 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 the river environments [*Datry et al.*, 2010]. 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 several other sediment reworking invertebrates such as tubificid worms, which are found readily in streams [*Brinkhurst and Kennedy*, 1965]. These worms could tolerate harsh environmental conditions and have been extensively used in several toxicological studies related to freshwater sediments [*Blankson and Klerks*, 2016; *Leppänen and Kukkonen*, 1998].

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.* [2020a]). 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. Both flow rates (1.6 $L.s^{-1}$) and slopes (1:300, V:H) 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 $\mu S.cm^{-1}$). The evaporative loss over time was checked (on alternate days) by adding tap water into the flumes 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 top of sand bed) were obtained. As the hyporheic exchange 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 clog the beds (400 gm in flumes with fine and coarse sand grains and 800 gm in flumes with gravel grains). A detailed procedure of clay addition into the experimental flumes is presented in [*Shrivastava et al.*, 2020a]. 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 clogging profiles were assessed manually from the flume walls (based on 20 measurements between crests and troughs) and no re-suspension was observed visually throughout the experiments.

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 $individuals.m^{-2}$ which is commonly found in natural environments [*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. 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 measure hyporheic exchange

In this work, the hyporheic exchange was assessed by injecting a fluorescent dye tracer (Rhodamine WT) into the water column at downstream end of the experimental flumes after 15 days of worms' addition. 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 (two-minute interval) using Turner Designs Cyclops 7 sensors. 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.*, 2020a; 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 exchange (i.e., the hyporheic flux, residence time distributions, and exchange depths) are only briefly discussed here, a detailed description is presented in [*Shrivastava et al.*, 2021]. The hyporheic 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 based on the equilibrium dye concentration and the volume of water in hyporheic zone (V_p, m^3) which mixes with the surface water was obtained. The equivalent dye penetration depth ($\bar{d}$) or the depth of exchange was obtained as the ratio V_p to bed plan area (A, m^2). Further, the average hyporheic flux is dependent on both the depth of exchange and mean residence times (RT_{mean}). Thus, another estimate of average hyporheic flux (q', m.min^{-1}) was calculated from the ratio of $\bar{d}$ to RT_{mean}.

3 Results

3.1 Clogging profiles in control and treatment (prior to worms' addition) flumes

Both control and treatment flumes for each sediment type exhibited similar clogging profiles. In beds with fine sand, a superficial clogging 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 clogging layer of average depth ~3 mm (shallow infiltration of ~0.2 mm were 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). These depositional patterns match closely to clogging profiles observed in our previous work [*Shrivastava et al.*, 2020a].

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 as noted in previous experimental studies [*Roche et al.*, 2016; *Shrivastava et al.*, 2021] and the holes or burrows dug by them were 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 distributed randomly across the depth of the bed in treatment flume with coarse sand (CS-T) (Figure 3b) whereas, a significant proportion of worms almost reached to the bottom of the flume with gravel bed (G-T) leaving only a few worms reworking the top layer. Nearly 85-90% of worms were recovered at the end of experiments.

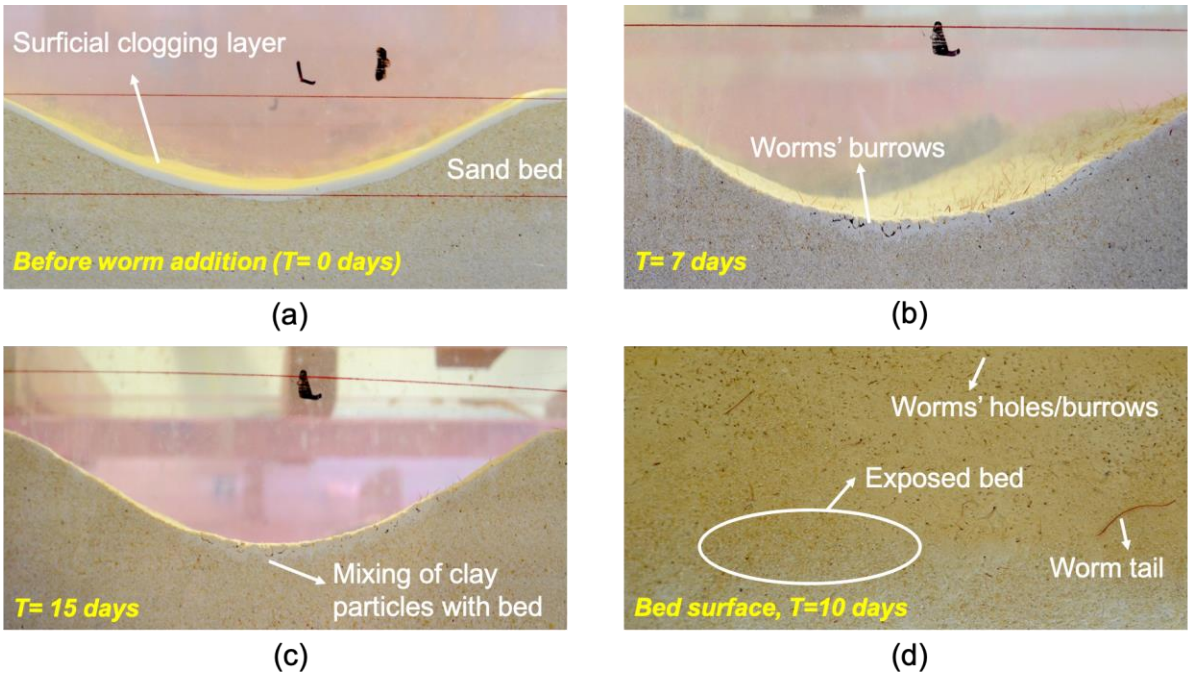

Figure 2: State of the treatment flume with fine sand grains (FS-T) as observed from the flume walls during the experiments – a) before addition of worms, b) on Day 7 after worms' addition, and c) on Day 15 after worms' addition. The top view of the flume on Day 10 (d) illustrates the holes/burrows and tails of the worms and the disappearance of clogging layer from the bed surface as a result of sediment reworking.

The visual observations through 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 mixing of sediments by the 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 clogging 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 un-clog 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) were 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 coarse grains (CS-T and G-T) and fine sand (FS-T) were higher by over ~50% and

~25% respectively than their respective control flumes. The estimates of q' were consistently lower and within 70% of the q.

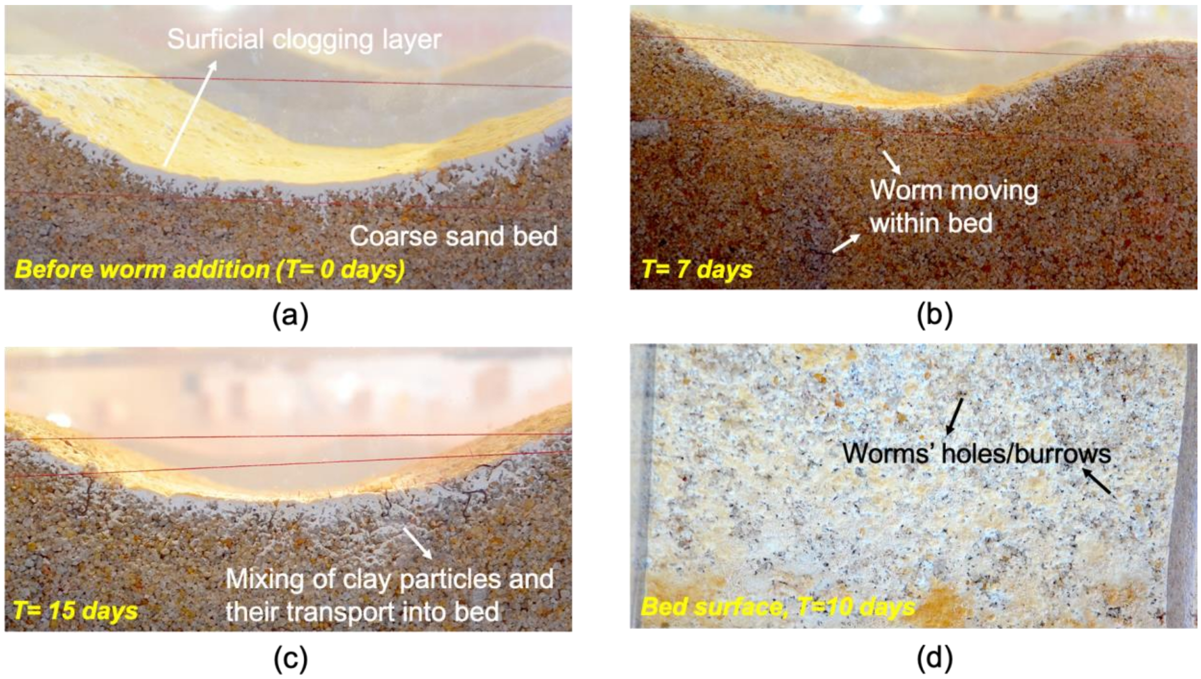

Figure 3: State of the treatment flume with coarse sand grains (CS-T) as observed from the flume wall during the experiments – a) before addition of worms, b) on Day 7 after worms' addition, and c) on Day 15 after worms' addition. The top view of the flume on Day 10 (d) illustrates the holes/burrows and disintegration of the deposited clay layer due to the activities of model sediment reworking organisms.

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 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.

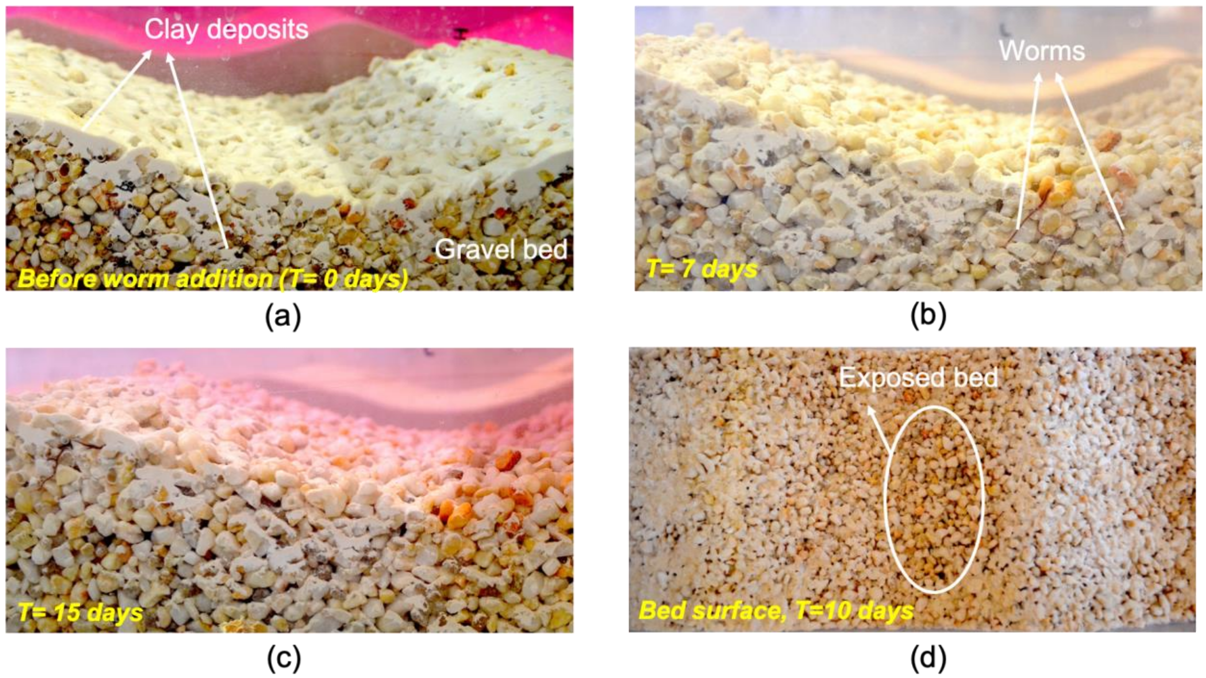

Figure 4: State of the treatment flume with gravel grains (G-T) as observed from the flume wall during the experiments – a) before addition of worms, b) on Day 7 after worms' addition, and c) on Day 15 after worms' addition. The top view of the flume on Day 10 (d) illustrates the disappearance of clogging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

4 Discussions

4.1 Disturbance to model streambeds

The model organisms reworked the fine sediments that were deposited on/into the bed. Sediment reworking either transported the clay particles from the surface to underlying bed regions or potentially re-suspended the deposited particles 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 clogging layer leading to erosion of the fine particles at the interface followed by re-suspension in the surface water. In addition to sediment reworking, mobilization of fines would have partially occurred due to hyporheic flow, particularly in treatments with coarse grains. However, any movement of fine sediments occurred only after the worms disturbed the clay deposits at the top.

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 an organism and the composition of sub-surface sediment (e.g. fine or coarse). 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 clogging 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.

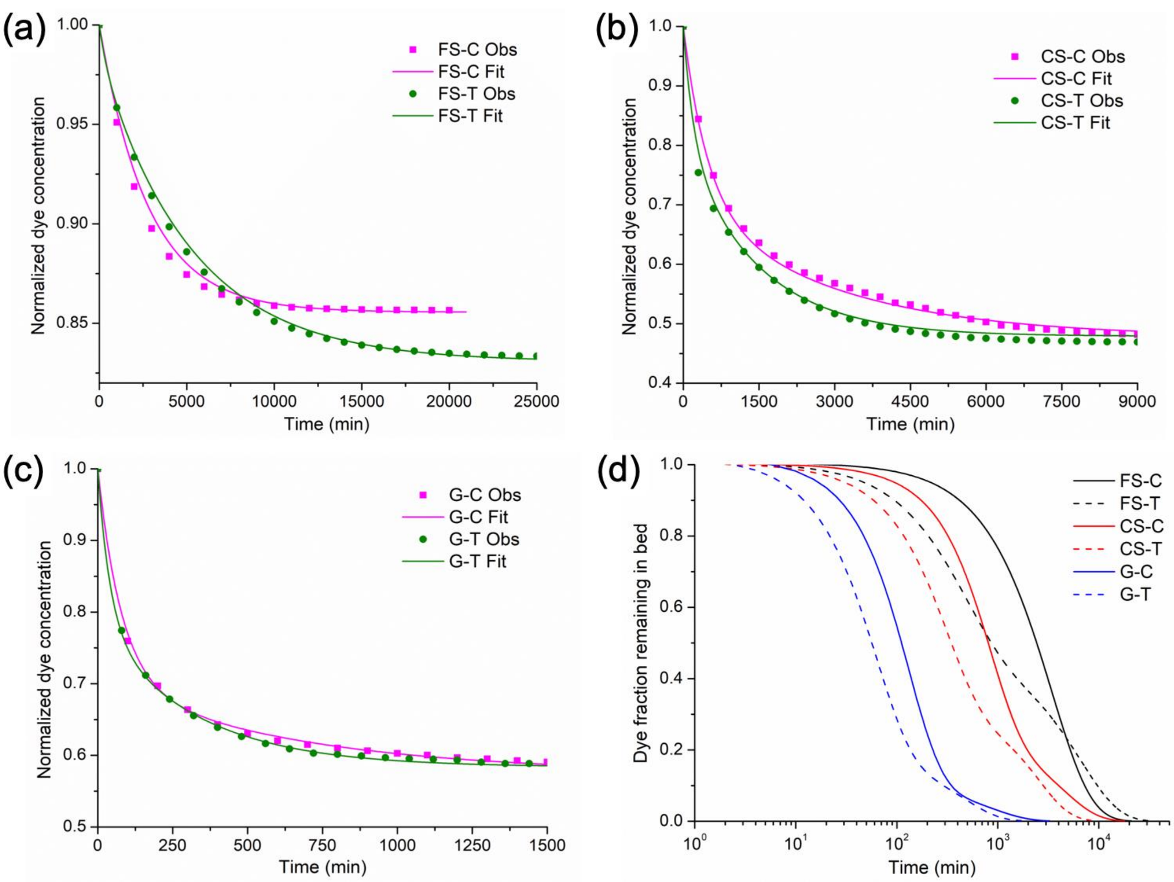

Figure 5: The observed (markers) and fitted (lines) temperature-corrected normalized dye concentration in the water column of experimental flumes with a) fine sand b) coarse sand and c) gravel, and d) flux weighted cumulative residence time distributions for the control and treatment flumes of all sediment types.

4.2 Influence on hyporheic exchange

The accumulated clay particles formed a seal of low permeability clogging layer which potentially inhibited dye transport in the control flumes. The digging of clogged beds and construction of burrows destroyed the fine sediment layer and exposed the underlying coarser bed grains. Consequently, the vertical transport of dye in 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 clogging 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 q' in treatment flumes were higher than their respective control flumes due to greater $\bar{d}$ and shorter RT_{mean} in the former.

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 clogging layer and underlying bed grains. For instance, in coarse-bedded treatment flumes, the destruction of clogging layer at the top supported rapid vertical exchange leading to shorter RT_{mean} and higher hyporheic 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 bed (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.

The results related to sediment bed disturbance from our experiments are consistent with earlier findings from laboratory experiments conducted in slow infiltration columns [*Geraldine Nogaro et al.*, 2006]. The authors reported that certain macroinvertebrates could potentially reduce 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 in the past [*Aaron I. Packman and MacKay*, 2003; *Rehg et al.*, 2005; *Salehin et al.*, 2004]. Thus, our experimental observations of alteration in dune-induced hyporheic flow in clogged streambeds due to the activities of macroinvertebrates are more relevant than previous laboratory investigations.

4.3 Implications of the work

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 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 flux and residence times of solutes in the biologically reworked zones of streambeds. Additionally, macroinvertebrates are regarded as ecosystem engineers [*C G Jones et al.*, 1994], and can potentially modify the structure and composition of microbial communities in the 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 had the bed or organisms were unstable. Further, these experiments demonstrate the interplay of just one species with the fine sediment deposits. However, natural streambeds host a range of organisms exhibiting different sizes and reworking behaviors. The prey-predator relationships between the inhabitants may play a critical role in determining how the streambed properties would be influenced. Additionally, 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. 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 exchange in compositionally different streambeds clogged with clay-sized fine sediments. The model organisms, *Lumbriculus* *variegatus*, re-worked the deposited clogging layer leading to enhanced vertical hydrological connectivity in treatment flumes compared to control flumes. For treatment flume of each sediment size, the penetration depths were greater, mean and median residence times were shorter, and hyporheic fluxes were higher than the respective control flume. Our experiments reveal that the modification to hyporheic flow characteristics in the treatments was dependent on the interaction of organisms with both fine sediments and underlying bed grains. The results also 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

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