

# Influence of Bioturbation on Hyporheic Exchange in Streams: Conceptual Model and Insights from Laboratory Experiments

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## Key Points:

- Causal pathways through which sediment reworking and burrow ventilation processes could modify hyporheic exchange are presented
- Effect of sediment-biota interaction on hyporheic exchange is investigated by conducting experiments in re-circulating flumes
- Sediment reworking by model organisms significantly altered the hyporheic flux, residence times, and penetration depth of solutes

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## Abstract

Bioturbation occurs in streambeds by the action of a range of faunal species, but little is known about how it could modify the hyporheic exchange in streams. Previous experimental work investigating the effects of sediment-biota interaction on exchange across the sediment-water interface has been largely conducted in small mesocosms or infiltration columns that do not represent the lotic environment adequately. Therefore, the experimental findings from these studies may not be transferable to flowing water environments (e.g., streams). In this work, we first present a conceptual model demonstrating the causal pathways through which the sediment reworking and burrow ventilation processes (together referred to as bioturbation) could potentially modify the hyporheic flow regime. Next, to study the role of activities of faunal organisms in lotic environments and test some of the arguments presented in the model, laboratory experiments are conducted in re-circulating flumes. The experiments involved investigating the modification of dune-induced hyporheic flow due to the activities of a model bioturbating organism, *Lumbriculus variegatus*, following a control (without organisms) and treatment (with organisms) based experimental design. The sediment reworking activities such as surficial deposition of fecal pellets and burrowing by *L. variegatus* caused significantly higher hyporheic flux, longer mean residence times, and deeper solute penetration in the treatment flumes relative to the control flumes. We advocate that more intensive laboratory experiments and field investigations must be conducted to test the propositions put forward in the conceptual model and advance our understanding of the role of bioturbation process in fluvial ecosystems.

## Plain Language Summary

The exchange between surface and groundwater underpins several stream ecosystem services such as biochemical cycling of nutrients and attenuation of contaminants. In this regard, a comprehensive understanding of the in-stream processes influencing the exchange across sediment-water interface is essential for holistic stream management. Detailed research has been undertaken in the past to investigate the effects of physical variables such as flow velocity or flow depth on surface and groundwater exchange. However, little is known about how the activities of faunal organisms such as macroinvertebrates that inhabit streambeds affect the surface and sub-surface exchange. In this work, we advance the conceptual understanding of how activities such as feeding and excretion, locomotion, and construction of galleries by macroinvertebrates could alter the two-way exchange across sediment-water interface. We also conduct laboratory experiments by forming streambeds in Perspex built long channels to perform preliminary testing of the propositions presented in the conceptual model. The results reveal that activities of sample macroinvertebrates significantly modified the rate of transfer of water across the sediment-water interface, the time it resides in the bed, and to what depth it is exchanged. This modification in the exchange characteristics has direct consequences for the overall functioning of stream ecosystems.

## 1 Introduction

The exchange of mass and energy across the sediment-water interface (SWI), regarded as hyporheic exchange [Boano *et al.*, 2014], underpins several stream ecosystem functions such as processing of organic matter [Findlay *et al.*, 1993; Pusch, 1996], cycling of nutrients [Bardini *et al.*, 2012], and attenuation of pollutants or contaminants [Gandy *et al.*, 2007]. These stream functions are largely controlled by the hyporheic flux, hydraulic residence times, and penetration depth of solutes in the hyporheic zones [Findlay, 1995; Gomez *et al.*, 2012; Jones Jr *et al.*,

1995]. The hyporheic flux is the rate at which water/solutes enter and exit the hyporheic zone. The residence time can be regarded as a period for which a parcel of water/solute remains in contact with biologically active sediments within the hyporheic zone. The penetration depth relates to the size or volume of the hyporheic zone in the sub-surface sediments and determines the spatial extent to which surface water could mix with pore water in hyporheic interstices. The influence of the physical variables (e.g. flow rate, temperature, morphology) on hyporheic flow is well known [Cardenas *et al.*, 2004; Wondzell, 2006], however, the impact of biotic variables on hyporheic exchange is not investigated in detail [Shrivastava *et al.*, 2020b]. The latter could significantly influence the exchange across SWI in streams, particularly in low flow environments such as during the dry season or in streams that experience less frequent flood disturbances. The focus of this work is to improve the current understanding of the effect of the activities of faunal organisms on hyporheic flow in streams.

Early evidence of the ability of faunal organisms to modify their physical habitat is illustrated in Darwin's work where he observed that earthworms mixed the soil particles in a garden significantly [Darwin, 1892]. This phenomenon of particle reworking was later studied in aquatic ecosystems, and it was regarded as one of the important processes that modify the structure and composition of marine sediments [Cullen, 1973; J Grant, 1983; Rhoads, 1967]. Besides mobilizing bed sediments, some faunal organisms are capable of transporting the overlying water and suspended sediments into their burrows, a process described as burrow ventilation [Aller, 1984; Marinelli, 1994; Meysman *et al.*, 2006; Shull *et al.*, 2009]. Taken together, the sediment reworking and burrow ventilation processes by faunal organisms are referred to as bioturbation [Erik Kristensen *et al.*, 2012]. Bioturbation has been studied extensively in marine environments. For example, 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 bed sediments [Cullen, 1973].

Similar to marine environments, stream ecosystems also host a wide range of bioturbating organisms that modify their physical habitat [Clarke *et al.*, 2008; Datry *et al.*, 2010; De Figueroa *et al.*, 2013; Gottesfeld *et al.*, 2004; Song *et al.*, 2010]. For instance, salmon and crayfish, found commonly in streams, have been associated with a significant streambed erosion [Gottesfeld *et al.*, 2004; Usio and Townsend, 2004]. Similarly, invertebrates such as tubificid worms have been observed at a density as high as  $10^6$  ind.m<sup>-2</sup> in riverine sediments [Brinkhurst and Kennedy, 1965]. These invertebrates could construct a dense network of galleries, for instance, burrows of depth up to 5 cm and diameter ranging from 1-6 mm have been observed in field settings [Song *et al.*, 2010].

It is well-established that bioturbation alters the exchange of water and solutes across the SWI in marine environments, which in turn, influences other physico-chemical and biological processes [Bertics *et al.*, 2010; Cable *et al.*, 2006; Guimond *et al.*, 2020; Kostka *et al.*, 2002; Erik Kristensen, 1988; E Kristensen and Blackburn, 1987; Volkenborn *et al.*, 2007]. In comparison to marine sediments, bioturbation in freshwater sediments has received less attention and only limited evidence of the effect of bioturbating organisms on overall functioning of freshwater ecosystems is available in the literature. For example, Mermillod-Blondin *et al.* [2003] demonstrated that deposition of fecal pellets and construction of tubes or galleries by invertebrates modified the bed porosity, which in turn, altered the aerobic and anaerobic

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microbial processes in the hyporheic sediments. In another study, tubificid worms were observed to increase the hydraulic conductivity of clogged sediments by constructing deep galleries which eventually increased the exchange between the surface and sub-surface sediments [Nogaro *et al.*, 2006]. Although the previous work provides invaluable information on the role of bioturbating organisms in freshwater sediments, the results may not be transferable directly to running water systems such as streams. Previous experimental investigations have been conducted largely in 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]. These experimental setups do not mimic the flow conditions in a lotic environment where complex hydrodynamics exists at the SWI due to the flow of surface water over undulated streambeds.

In this work, we first propose a conceptual model describing various causal pathways through which bioturbation can potentially affect small-scale hyporheic exchange in streams. Next, laboratory experiments in re-circulating flumes are conducted to study the influence of activities of faunal organisms on the exchange across SWI and test some of the arguments presented in the conceptual model. Specifically, the experiments involve investigating the modification of hyporheic flux, penetration depth, and residence time of water/solutes for dune-induced hyporheic flow due to bioturbation by model organisms.

## 2 Conceptual model

The exchange of water and solutes across the SWI occurs through a series of hyporheic flow paths. Sediment reworking and burrow ventilation processes are anticipated to alter the geometry of these flow paths and subsequently modify the hyporheic flow regime. In the following paragraphs, we present a conceptual model illustrating causal pathways through which bioturbation could potentially alter the small-scale hyporheic exchange in lotic environments (Figure 1).

One of the primary drivers of hyporheic exchange is the generation of pressure gradients at the SWI as the surface water flows over a bed with irregular topography [Boano *et al.*, 2014]. Pressure gradients may develop due to the presence of morphological features ranging from a few millimeters (e.g., individual grains, dunes) to several kilometers (e.g., meanders) [Käser *et al.*, 2013; Stonedahl *et al.*, 2013]. The formation of flow-induced topographical features and their influence on water circulation in porous media has received a lot of attention [Buffington and Tonina, 2009; Packman and Salehin, 2003], however, little is known about how the activities of faunal organisms could influence the pressure distribution at the SWI. Burrow openings and deposition of fecal pellets by faunal organisms at the bed surface result in the development of biogenic micro-topography, also termed as bioroughness, which has been shown to influence pressure gradients at the SWI [Han *et al.*, 2019; Huettel and Gust, 1992]. For example, Huettel and Gust [1992] demonstrated that formation of topographical features (as small as 700  $\mu\text{m}$ ) associated with the activity of faunal organisms resulted in generation of local pressure gradients leading to advective flow in the porous media. Modeling studies have revealed that salmon spawning creates both low- and high-pressure regions across the structure of the redd (nest) at streambed surface [Buxton *et al.*, 2015; Tonina and Buffington, 2009]. Further, sediment reworking has been associated with the erosion of bed grains, which would eventually deposit at some other downstream location and modify the bed morphology. For example, it has been observed in a field study that the spawning activity of salmon is a dominant control on sub-reach scale topographical changes to the bed surface [Hassan *et al.*, 2008].

Hydraulic properties of sediments (e.g., permeability and hydraulic conductivity) are also a dominant control on hyporheic exchange [Sawyer and Cardenas, 2009], and they can be modified by the activities of faunal organisms. For instance, Buxton *et al.* [2015] reported that fine sediments are winnowed from the bed due to fish spawning, and as a consequence, the hydraulic conductivity of spawned bed regions was observed to be higher by two orders of magnitude in comparison to unspawned regions. They also demonstrated that the mean residence time decreases and the hyporheic flux increases as a greater proportion of the bed is subject to spawning. Similarly, a mosaic of macro-pores in the sediment bed could develop due to burrow construction by invertebrates leading to preferential transport of water/solutes [Mermillod-Blondin *et al.*, 2003]. Feeding and excretion by faunal organisms could also modify the permeability [Erik Kristensen *et al.*, 2012]. For example, vertically oriented head-up organisms (known as downward conveyors) feed on sediments at the surface and egest out fecal pellets in the interstitial regions. This behavior could alter the size and packing of bed sediments and consequently modify the bed permeability. Further, as the organisms generally move to a limited depth in the bed, it can be expected that sediment permeability in the lower layer may remain largely unaffected by their activities. In other words, a vertical permeability gradient could be generated in the sediment bed due to the faunal activities. The hyporheic flow in such streambeds could be considered similar to the flow in layered or stratified beds and the modification in exchange characteristics for such beds has been demonstrated in previous studies [Gomez-Velez *et al.*, 2014; Marion *et al.*, 2008]. Furthermore, anisotropic permeability fields could develop in the bioturbated layer based on organism activities, which could also re-direct the flow paths and modify the hyporheic flow regime [S Liu and Chui, 2018; Zlotnik *et al.*, 2011].

The characteristics of hyporheic flow could also get modified by the process of burrow ventilation [Erik Kristensen *et al.*, 2012; Y Liu *et al.*, 2019]. Some burrow dwelling invertebrates are capable of pumping the surface water into the sediment using mechanisms such as peristaltic body movements and ciliary actions and result in pressure variations within the sediments [Brand *et al.*, 2013; Erik Kristensen *et al.*, 2012]. As a consequence, the surface and pore water exchange and the pore water transport (advective and diffusive) in the regions surrounded by burrows could be influenced [Roskosch *et al.*, 2010b; Shull *et al.*, 2009]. Quantitative or qualitative evidence of the effects of burrow ventilation on exchange across SWI in stream environments has not yet been reported, however, studies in marine and lake environments have demonstrated that a significant volume of surface water could be pumped by burrow ventilating organisms [Christensen *et al.*, 2000; Roskosch *et al.*, 2010a]. For example, Roskosch *et al.* [2010b] estimated that a burrow ventilating invertebrate, *Chironomus plumosus*, could pump water equal to the volume of the surface water of the lake ( $\sim 3.7 \times 10^7 \text{ m}^3$ ) in approximately 5 days at a density of 745 ind.m<sup>-2</sup>. Similarly, Cable *et al.* [2006] estimated an average pumping of  $\sim 5 \text{ cm.d}^{-1}$  by the bioturbating organisms in Indian River Lagoon and reported that bioturbation can significantly influence the seepage meter measurements in marine sediments. It should be noted that suspended sediments in the overlying water could infiltrate into the porous streambed as an organism pumps water into its burrow, thus bed permeability could be also modified.

It is important to note that the influence of bioturbation on the hyporheic exchange would partially depend on the streamflow characteristics such as discharge, flow velocity, and magnitude and frequency of floods [Moore, 2006]. For instance, very high flow velocities or more frequent and intense flooding could destroy biogenic structures built by organisms and transport organisms to downstream regions or even kill them. In such streams, the effects of

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bioturbation on physical and hydraulic properties of streambeds and subsequently on the exchange across SWI are unlikely to be significant. In contrast, bioturbation could significantly modify the processes at SWI in regulated streams where the flow conditions are not variable or in streams that experience less frequent flooding. Similarly, bioturbating organisms could perform their activities effectively during base flow periods in a stream. This argument is supported by field evidence where bioturbation by crayfish has been reported to influence suspended sediment fluxes and causing diel turbidity cycles during the base flow period [Rice *et al.*, 2016]. Thus, tiny bioturbating organisms could produce proportionally large effects on the functioning of fluvial ecosystems including the exchange of water/solutes across the SWI during low flow periods or under stable flow conditions.

Provided the conducive hydrological environment, several physico-chemical and biological variables determine the degree to which the exchange across SWI is altered due to bioturbation. Sediment reworking could be affected by variables such as size [de Nadai-Monoury *et al.*, 2013; Heilskov and Holmer, 2001; Thrush *et al.*, 2006], density [Duport *et al.*, 2006; Marinelli and Williams, 2003] and bioturbation behavior of the organisms [De Backer *et al.*, 2011; Michaud *et al.*, 2006], reworking time [Davis, 1993; Maire *et al.*, 2008], and bed composition [Mermillod-Blondin and Rosenberg, 2006]. For example, a range of surface sediment reworking rates was observed for four taxonomically different in-stream faunal organisms – *Gammarus fossarum* (invertebrate, body size: up to 2 cm long), *Sericostoma* (invertebrate, body size: 1-2 cm long), *Cordulegaster boltonii* (invertebrate, body size: up to 4 cm long), and *Barbatula barbatula* (fish, body size: ~10 cm long) in an experimental study [de Nadai-Monoury *et al.*, 2013]. The per capita sediment reworking rates for *G. fossarum*, *Sericostoma*, *C. boltonii*, and *B. barbatula* were  $6.25 \times 10^{-3} \text{ cm}^2 \cdot \text{d}^{-1}$ ,  $3.93 \text{ cm}^2 \cdot \text{d}^{-1}$ ,  $3.42 \text{ cm}^2 \cdot \text{d}^{-1}$ , and  $63.5 \text{ cm}^2 \cdot \text{d}^{-1}$  respectively. Similarly, Meadows and Tait [1989] reported that U-shaped burrow building invertebrates (*Corophium volutator*, burrow length: 3-4 cm) could decrease the bed permeability while the invertebrates that construct deep burrows (*Nereis diversicolor*, burrow length: 8-10 cm) could have an opposite effect. Their experiments were conducted at different densities of *C. volutator* (2500, 7500, and 22,500 ind. $\cdot\text{m}^{-2}$ ) and *N. diversicolor* (1000, 3000, and 9000 ind./ $\text{m}^2$ ), and a greater degree of influence on the permeability was observed at higher densities of invertebrates. Mermillod-Blondin and Rosenberg [2006] proposed that the physical characteristics of benthic systems are important controls on the bioturbation activity. Bioturbating organisms could significantly influence the sediment properties and directly produce water/solute flux in diffusion-dominated systems (fine-grained sediment bed, low pore water flow rate). In advection-dominated systems (coarse-grained sediment bed, strong advective pore water flow), the organisms may not considerably influence the sediment properties and could only modulate the flux of water/solutes. In another work [Navel *et al.*, 2012], a six-fold increase in bed permeability was observed in sedimentary columns filled with fine sand due to burrow construction by *Tubifex tubifex* (invertebrate, density: 12,800 ind. $\cdot\text{m}^{-2}$ ). However, these invertebrates could not considerably alter the permeability of columns filled with coarse sand. Though not explicitly stated in their study, the relative size of worms and pores could be considered as an important control on the extent of bed disturbance. It can be anticipated that the locomotion and burrowing by faunal organisms could develop new pore spaces or enlarge existing pores if their size is larger than the pore size. Alike sediment reworking, variables such as mechanism and purpose of burrow flushing [Erik Kristensen *et al.*, 2014], burrow morphology [Erik Kristensen *et al.*, 2012], burrow density [Shull *et al.*, 2009], and sediment permeability [Meysman *et al.*, 2005] have been shown to affect the magnitude of burrow ventilation.

The effect of the sediment-organism interaction on the exchange across SWI could exhibit a spatio-temporal variability as the activities of bioturbating organisms are influenced by several environmental variables. For instance, based on nutrient availability and sedimentary composition, macroinvertebrates could be non-uniformly distributed along the riffles and pools sections in the streams [McCulloch, 1986], and thus, the physical reworking of sediments and burrow ventilation in these sections would be spatially heterogeneous. The activities of bioturbating organisms are also susceptible to temporal variations depending on variables such as life-cycle history and bioturbation behavior of the organism and temperature [Bunn and Arthington, 2002; Meysman et al., 2010; Ouellette et al., 2004; Roskosch et al., 2012]. For example, some aquatic inhabitants tend to actively re-work sediments during the night compared to the daytime [Loperfido et al., 2010; Rice et al., 2016]. In Rice et al. [2016], the seasonal variability in crayfish bioturbation in a headwater tributary of the River Nene (United Kingdom) was also reflected. They reported that the winter months were characterized by lower bioturbation activity which could be attributed to lower temperatures and higher flows. In contrast, a significantly higher disturbance to bed sediments occurred during the summer months (base flow periods). Further, Ouellette et al. [2004] conducted experiments at four different temperatures – 1°C (winter), 6°C (fall/spring), 13°C (summer), and 18°C (summer tide pool) to study the seasonal difference in sediment reworking by *Neanthes virens* (polychaete). They found that the sediment mobilization by sample organism was higher at 13°C and 18°C compared to the cold regime (1°C and 6°C). Similarly, a higher rate of ventilation activity has been observed at a higher temperature (20°C in comparison to 10°C) in an experimental study [Roskosch et al., 2012]. This spatio-temporal heterogeneity in the bioturbation activity adds another layer of complexity in understanding the influence of this biotic process on stream ecosystem functioning.

The conceptual model presented above highlights the potential ways through which the faunal organisms could alter the small-scale hyporheic exchange. It can be recalled that experimental research on investigating the role of faunal organisms in modifying the exchange across SWI in lotic environments is very limited. Therefore, to support some of the arguments presented in the conceptual model, we conducted experiments in re-circulating flumes and investigated the influence of bioturbation activity on the hyporheic flow regime. Note that not all propositions put forward in the conceptual model could be tested as the experiments have a limited scope.

### 3 Experimental methods

The experiments were conducted in re-circulating flumes to investigate the modification in the hyporheic flow regime due to the activities of a model bioturbating organism. The experiments follow a control and treatment design (three control and as many treatment flumes). The control flumes (C1, C2, and C3) were free of bioturbation activity and they represent the exchange characteristics for a dune-induced hyporheic flow. The exchange characteristics determined for treatment flumes (T1, T2, and T3) demonstrate the effect of activities of bioturbating organisms on the dune-induced hyporheic flow regime. The statistical significance of the observed differences in the exchange characteristics between control and treatment flumes was evaluated using Student's t-test.

### 3.1 Model bioturbating organisms

*Lumbriculus variegatus* (commonly known as California blackworms), were used as model bioturbating organisms (Figure 2a). *L. variegatus* (hereafter referred to as worms) are freshwater oligochaetes which prefer to dwell in shallow sub-surface regions of lakes or marshes feeding on organic material and microorganisms [Sun and Ghosh, 2007]. However, these worms have been also observed in the river environments [Datry *et al.*, 2010]. These worms are known to construct burrows, and they 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 bioturbation activities carried out by several other invertebrates such as tubificid worms, which are found readily in streams [Brinkhurst and Kennedy, 1965]. Also, these worms are tolerant to a wide range of environmental conditions and have been extensively used in several toxicological studies related to freshwater sediments [Blankson and Klerks, 2016; Leppänen and Kukkonen, 1998b]. These worms do not ventilate their burrows and therefore, only the effect of sediment reworking activities on the hyporheic exchange could be demonstrated.

### 3.2 Flume set up and bed material

The experiments were performed in six Perspex re-circulating flumes (Figure 2b) in the Sexton Ecohydraulics Laboratory at The University of Melbourne. The dimensions of the flumes were 3m (L) x 0.2m (W) x 0.4m (D) (additional details related to the experimental setup can be found in Shrivastava *et al.* [2020a]). The flow rate was measured using a GPI-TM series flowmeter and the flume slope was adjusted using scissor jacks at the upstream section of the flumes. Both flow rate (1.6 L/s) and flume slope (1:300, V:H) were adjusted to attain uniform flow in the flumes with an average flow depth of 9 cm. The flow velocity ( $\sim 8.7 \text{ cm.s}^{-1}$ ) was obtained by dividing the flow rate by cross-sectional area (flume width x flow depth) and it was such that no erosion of bed grains or worms was observed. These hydraulic variables were kept constant during the experiments and were similar across all the flumes. Fine sand ( $D_{10}$ : 0.165 mm,  $D_{90}$ : 0.315 mm, and porosity: 0.45) was washed to remove any foreign material (e.g., dirt) before filling into the flumes to form 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). 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 2b). The experiments were conducted using tap water (pH = 6.7, salinity =  $220 \mu\text{S.cm}^{-1}$ ). 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.

The pumps in treatment flumes were temporarily switched off before introducing the worms. The worms were added into these flumes to achieve a density of  $\sim 9000 \text{ ind.m}^{-2}$  as observed 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  $\sim 2$  days. These flumes were bioturbated for 10 days before the dye tracer test was performed to measure hyporheic exchange characteristics (section 3.3). The worms were recovered from the flumes by manually digging the bed at the end of experiments ( $\sim 85\text{-}90\%$  of worms were recovered). The spatial distribution and depths traversed by worms in the sediment bed were assessed through direct observations from the flume walls and during worm recovery.

### 3.3 Tracer test to measure hyporheic exchange

Tracer injection into the water column or sediments has been extensively used to assess hyporheic exchange in recirculating flumes [S B Grant *et al.*, 2012]. In this study, hyporheic exchange was investigated by injecting a fluorescent dye tracer (rhodamine WT) into the water column at the downstream end of the flume. 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 monitored (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. It took ~9-10 days after dye injection to reach this stage in the flumes after which the experiments were ceased. Temperature correction was applied to the observed dye concentration in the water column as the fluorescence intensity of dye tracers varies with temperature [Blaen *et al.*, 2017]. The dye behaved inertly as also observed in our previous work (Shrivastava *et al.* [2020a], also see Aubeneau *et al.* [2016]). The experiments were done in a closed room avoiding any direct contact of the dye with the sunlight to prevent its photochemical decay.

#### 3.3.1 Definition and determination of exchange characteristics

##### *Hyporheic flux*

The hyporheic flux ( $q$ ) is defined as the volumetric flow rate averaged over the bed surface area. It was estimated from the initial gradient of the tracer concentration decay curve (Figure 3a) as also presented in several previous studies [Fox *et al.*, 2016; Shrivastava *et al.*, 2020a].

##### *Residence time distributions*

Elliott and Brooks [1997] presented an approach for estimating the flux-weighted average residence function ( $\bar{R}(\tau)$ ) of solutes in streambeds constituted of regular dunes. In their approach,  $\bar{R}(\tau)$  denotes the fraction of solutes that entered the bed at time  $t = 0$  and remains in bed at a time  $t = \tau$ .

The Elliot and Brooks (1997) method involves solving a set of coupled equations;

$$m(t) = q \int_{\tau=0}^t C^*(t - \tau) \bar{R}(\tau) d\tau \dots \dots \dots (Equation 1)$$

$$C^*(t) = 1 - \frac{m(t)}{d'} \dots \dots \dots (Equation 2)$$

where,

$C^*(t)$  is the normalized dye concentration obtained by dividing observed dye concentration at any time  $t$ , ( $C(t)$ , ppb), with initial concentration after complete mixing of dye in the water column ( $C_0$ ),  $q$  (m/min) is the hyporheic flux into the bed surface,  $m$  (m) denotes the accumulated mass per unit plan area of bed divided by  $C_0$  and is related to the depth of penetration of solutes into the bed, and  $d'$  (m) is the ratio of the total volume of water in the flume system (excluding the pore water) ( $V_{sw}$ , m<sup>3</sup>) to the plan area of the bed ( $A$ , m<sup>2</sup>).

On substituting  $m(t)$  from Equation 2 in Equation 1 we get,

$$d'(1 - C^*(t)) = q [\bar{R} * C^*] \dots \dots \dots (Equation 3)$$

We apply Laplace transform to Equation 3 and rearrange it to get,

$$\mathcal{L}\{\bar{R} * C^*\} = \frac{d'}{q} \mathcal{L}\{1 - C^*(t)\} \dots \dots \dots (\text{Equation 4})$$

$$\mathcal{L}\{\bar{R}\} \cdot \mathcal{L}\{C^*(t)\} = \frac{d'}{q} \mathcal{L}\{1 - C^*(t)\} \dots \dots \dots (\text{Equation 5})$$

Further rearranging and taking inverse Laplace transform to obtain  $\bar{R}$ ,

$$= \mathcal{L}^{-1} \frac{\frac{d'}{q} \mathcal{L}\{1 - C^*(t)\}}{\mathcal{L}\{C^*(t)\}} \dots \dots \dots (\text{Equation 6})$$

An exponential equation (Equation 7) is fitted to the  $C^*(t)$  (temperature corrected) curve using the principles of least square method to obtain the mathematical function of observed concentration (Figure 3a). The fitted curves match closely with their corresponding observed concentration profiles as indicated by the root mean square errors (Table 1).

$$a_1 + (1 - a_1)(a_2 e^{-a_3 t} + (1 - a_2) e^{-a_4 t}) \dots \dots \dots (\text{Equation 7})$$

where,  $a_1, a_2, a_3, a_4$  are the parameters used to fit the  $C^*(t)$  curves.

The mathematical function of  $C^*(t)$  for each flume was input to Equation 6 to obtain their corresponding residence time distribution (Figure 3b). The median ( $RT_{med}$ ) and mean ( $RT_{mean}$ ) residence times were subsequently estimated from this distribution (Table 1).

Table 1: Experimental details and hyporheic exchange characteristics observed in the control and treatment flumes.

#	Flume index	Bioturbation time	RMSE <sup>a</sup>	$RT_{med}$ <sup>b</sup> (min)	$RT_{mean}$ <sup>c</sup> (min)	$\bar{d}$ <sup>d</sup> (m)	$q^e \times 10^{-5}$ (m/min)	$q^f \times 10^{-5}$ (m/min)
Control	C1		0.0031	1522	3730	0.043	1.31	1.15
	C2	-	0.0029	1290	3840	0.042	1.24	1.10
	C3		0.0050	1732	3782	0.042	1.28	1.11
Treatment	T1		0.0027	1355	4298	0.055	1.43	1.33
	T2	10	0.0047	1812	4917	0.06	1.40	1.22
	T3		0.0041	2132	4521	0.054	1.39	1.20

<sup>a</sup>root mean square error values for the observed and fitted time series of dye concentration in the water column.

<sup>b</sup>median residence time. <sup>c</sup>mean residence time. <sup>d</sup>average dye penetration depth in the bed. <sup>e</sup>hyporheic flux estimated from the initial gradient of the tracer concentration decay curves. <sup>f</sup>hyporheic flux estimated from the  $RT_{mean}$  and  $\bar{d}$ .

#### Dye penetration depth

The normalized equilibrium dye concentration,  $C_{eq}^*$ , was used to establish the mass balance of dye at beginning and end of the experiment, and the volume of water in hyporheic zone ( $V_p$ , m<sup>3</sup>) which mixes with the surface water was obtained (Equation 8). In general, the mixing between surface and pore water due to the exchange of dye across SWI results in non-uniform dye concentration in the bed [Elliott and Brooks, 1997]. For this work, a physical quantity ‘equivalent penetration depth’ ( $\bar{d}$ , m) is determined, as also demonstrated in previous work [Elliott and Brooks, 1997], such that if the dye were to homogeneously mix and produce uniform dye concentration in the bed up to this depth (and unmixed below), the net dye exchanged across the SWI equals the actual exchange occurring due to non-homogenous dye mixing. Mathematically, it can be expressed as the ratio of  $V_p$  to  $A$  (Table 1). For dune-shaped

sandy beds, the advective flow across the SWI is expected to cause rapid transport of dye particles whereas the diffusive transport may occur at a later time. Dye transport via these two mechanisms may get enhanced with the activities of bioturbating organisms.

$$V_p = V_{sw} \times \left( \frac{1}{C_{eq}^*} - 1 \right) \dots \dots \dots (\text{Equation 8})$$

Further, the average hyporheic flux is dependent on the depth of exchange and  $RT_{mean}$ . In addition to  $q$ , another estimate of average hyporheic flux ( $q'$ ) was calculated as the ratio of  $\bar{d}$  to  $RT_{mean}$  (Table 1).

## 4 Results

### 4.1 Bioturbation activity

The activities of worms in treatment flumes began soon after their introduction into the flumes and digging of bed was observed within a few hours (Figure 4a and 4b). The worms traveled no more than 2-3 cm into the bed and were concentrated around the trough region of the dunes as seen from the flume walls and during worm recovery. Small-scale aggradation and degradation of sand grains around some of the dunes which were densely colonized by worms were also observed in the treatment flumes (Figure 4c). The heads of the worms were buried in the bed and their tails were observed at the bed surface (Figure 4d) indicating their feeding and excretion behavior (upward conveyors). The deposition of fecal pellets was observed on the bed surface for all the treatment flumes (Figure 4d).

### 4.2 Exchange characteristics

The hyporheic flux,  $q$ , in treatment flumes was observed to be significantly higher than the control flumes (Figure 5a,  $p = 0.005$ ). The other estimate of hyporheic flux,  $q'$ , was also significantly higher in the treatment flumes compared to the control flumes (Figure 5a,  $p = 0.021$ ). The  $q'$  was consistently lower and within 85% of the  $q$  (Table 1). In comparison to the control flumes, treatment flumes exhibited significantly larger dye penetration depths,  $\bar{d}$  (Figure 5b,  $p = 0.001$ ). The difference in median residence times,  $RT_{med}$ , between the treatment and control flumes was not significant (Figure 5c,  $p = 0.387$ ), however, the mean residence times,  $RT_{mean}$ , in the former was significantly longer than the latter (Figure 5c,  $p = 0.012$ ).

In the short residence time range (<404 minutes), the treatment flumes exhibited smaller hyporheic flux (proportion of  $q$ ) than the control flumes but the difference was non-significant (Figure 5d,  $p = 0.062$ ). The difference in the hyporheic flux between the control and treatment flumes in the intermediate residence time range (404-8103 minutes) was also not significant ( $p = 0.98$ ). A significantly higher hyporheic flux was observed in the treatment flumes compared to the control flumes in the longer residence time range (>8103 minutes). Note that these ranges are chosen based on the mean and median residence times observed in the experimental flumes (the

numbers are derived from powers of the natural exponential function,  $e^n$ , where  $n = 0, 1, 2, 3, \dots$  for instance,  $e^6 = 403$ ,  $e^9 = 8103$ ).

## 5 Discussions

### 5.1 Modification of hyporheic exchange

For given physical and hydraulic variables (flow velocity, height of dunes, bed permeability), the dye was exchanged with the bed in the control flumes through a series of short, intermediate, and long flow paths. The sediment beds in the treatment flumes were reworked by the bioturbating organisms, which in turn, altered the system of nested flow paths in the sand beds. As a result, a significant modification to the mean residence times, equivalent dye penetration depths, and average hyporheic flux were observed in the treatment flumes. The potential causes of these modifications considering the conceptual model (section 2) are presented in this section, however, further experimental research is needed to test these explanations and understand the complex influences of bioturbating organisms on hyporheic flow.

The smaller  $\bar{d}$  values in control and treatment flumes relative to the average bed depth (30 cm) indicate that the sediment beds were not fully mixed with the surface water. We speculate that it could be attributed to the underflow in the bed produced due to the hydraulic gradient in the flumes [Cardenas and Wilson, 2007b]. It has been observed in previous investigations that the presence of underflow may compress the hyporheic flow field and limit the vertical depth of exchange in the sediment bed [Cardenas and Wilson, 2007a].

Based on the visual observations from this study and results from previous research [Colombo et al., 2016; Lick, 2006], it is evident that sediment reworking by sample organisms could alter the surface topography and hydraulic properties of bed sediments. Deposition of fecal pellets in form of coarse particles generated microtopography and also enhanced bed permeability at the SWI. The holes/burrows dug by these organisms were readily visible in the treatment flumes (Figure 4d) indicating that the size of worms was larger than the size of pores in the sand bed. Thus, burrowing by the worms could have caused the development of dense-network of macro-pores. Such modification to the bed properties in treatment flumes potentially resulted in the pumping of dye across the SWI at a faster rate compared to the control flumes, and therefore, the  $q$  and  $q'$  were observed to be significantly higher in the former compared to the latter. Further, *L. variegatus* have been observed to burrow in vertical direction [Lick, 2006] which could have resulted in the preferential flow of dye to the deeper bed regions leading to significantly larger  $\bar{d}$  in treatment flumes compared to the control flumes. As the flow paths are directed to deeper bed regions, a significantly higher hyporheic flux was observed in the long residence time range in the treatment flumes compared to the control flumes. This also explains the observation of lower hyporheic flux (although not significant) in the treatment flumes in short residence time ranges compared to the control flume as the presence of burrows in the upper layers of the bed could have potentially directed the shorter flow paths deeper into the bed.

Due to the extension of flow paths into deeper regions, the dye resided for a longer time in the bed before emerging back to the surface water. Consequently, the mean residence times in the treatment flumes were significantly longer than the control flumes. The observation of higher residence times of solutes in treatment flumes is consistent with findings of Mermillod-Blondin et al. [2003] in which experiments were performed using infiltration columns. The authors

reported that the creation of burrows and deposition of fecal pellets increased the porosity of sediments which in turn increased the height of the sediment layer in the columns and subsequently resulted in longer residence times. Our study further advances the understanding of the influence of bioturbation in fluvial ecosystems by taking into account the hydrodynamics associated with the flow of surface water over topographical features such as dunes. Note that local sediment transport due to sediment reworking activities resulted in the alteration of the structure of a few dunes (Figure 4c). However, the morphology of a large section of the flume (> 80%) remains unchanged, and therefore, the modification in hyporheic flow regime due to alteration in dune morphology may be considered insignificant.

The observations from the treatment flumes provide evidence of the spatially heterogeneous distribution of worms in the sediment bed. Although the worms were initially introduced uniformly along the flume length, they relocated themselves predominantly at the troughs of the dunes as the experiments progressed (Figure 4b and 4c). The worms were observed at both the lee and stoss side of the dunes near the trough regions. The downstream side of the dune (lee side) where the worms were observed correspond to the flow recirculation region which exhibits a relatively low flow environment. The surface water is directed into the sediments at the stoss side of the dunes; this region is expected to be well-oxygenated due to the regular supply of oxygen from the overlying water (however, the sample organisms can tolerate low oxygen levels). Thus, more conducive dwelling conditions were available in the regions close to the dunes' troughs compared to other bed regions which supported a dense population of worms near the troughs. The preferential spatial alignment of worms could have potentially resulted in a greater degree of sediment reworking near troughs compared to the crests. The influence of this site-selective sediment reworking on modification of hyporheic flow was not investigated in this study, however, it is anticipated that the modification of hyporheic flow paths due to bioturbation could be spatially heterogeneous.

The pore water dye concentrations could also be influenced by the uptake of dye particles into the bodies of *L. variegatus*, a process described as bioaccumulation [Ingersoll *et al.*, 1995; Leppänen and Kukkonen, 1998a; Van der Oost *et al.*, 2003]. The potential routes of this accumulation are – a) ingestion of sediment having solute particles adsorbed on its surface, and b) pumping of solute particles dissolved in the pore water. The previous research in this area has largely focused on bioaccumulation of hydrophobic organic chemicals and heavy metals on/into the bodies of aquatic organisms [Goodyear and McNeill, 1999; Mäenpää and Kukkonen, 2006; Rainbow and Luoma, 2011]. It has been observed that the solutes dissolved in pore water are more readily available to *L. variegatus* and several studies have estimated the uptake rate of different chemical compounds by these worms [Khan *et al.*, 2015; Leppänen and Kukkonen, 1998a; Wang *et al.*, 2020]. For example, the uptake rate of fipronil (an insecticide) by *L. variegatus* from pore water has been estimated to be  $\sim 5 \times 10^{-3}$  L.g lipid<sup>-1</sup>.min<sup>-1</sup> [Wang *et al.*, 2020]. Similarly, [Khan *et al.*, 2015] observed that the influx rate of silver (Ag) particles from pore water into the bodies of *L. variegatus* was  $\sim 0.9 \times 10^{-3}$  L.dry weight<sup>-1</sup>.min<sup>-1</sup>. We anticipate that although dye particles could get exchanged between the worms' bodies and pore water, this exchange would be insignificant in comparison to the advective exchange between the surface water and pore water.

## 5.2 Implication of results

The role of bioturbation in modifying the ecological and physico-chemical processes of benthic systems is studied to a greater degree in marine environments compared to stream environments. This could be attributed to the fact that marine ecosystems generally comprise of fine-grained sediments (e.g., muddy sand) and the transport of mass and energy in such sediments is expected to be diffusion-dominated [Mermillod-Blondin and Rosenberg, 2006]. For such conditions, sediment reworking and burrow ventilation could significantly alter the physical characteristics of sediments in marine environments. As the stream environments are generally characterized by coarse sediments with advective flows within and across the beds, faunal bioturbation may have been considered inconsequential in lotic environments which could be a likely reason for the limited research on bioturbation in stream ecosystems. However, now it has been increasingly recognized that faunal organisms could modify streambed processes, particularly in streams with low hydrologic energy (e.g. during base flow period) [Moore, 2006; Rice *et al.*, 2016]. The results from our work provide more evidence of the importance of bioturbation in lotic environments and demonstrate that macroinvertebrate bioturbation could significantly alter the small-scale hyporheic exchange. This also implies that the activities of faunal organisms could directly influence the biogeochemistry in hyporheic zones, and thus could modify the overall quality of surface and sub-surface waters. For instance, our findings suggest that sediment reworking could increase the hyporheic flux, which in turn, is a dominant control on the concentration of dissolved oxygen and several other biochemical activities in hyporheic zones [Reeder *et al.*, 2018]. In addition to influencing streambed chemistry by reconfiguring the physical structure, macroinvertebrate bioturbation can potentially manipulate the community of microorganisms including their activities and abundance in porous media [Boeker *et al.*, 2016; Mermillod-Blondin *et al.*, 2004]. Due to their ability to modify the availability of resources for other organisms, macroinvertebrates are recognized as ecosystem engineers [Jones *et al.*, 1994]. We do not focus on the concept of ecosystem engineering in this manuscript, but it is worth noting that model organisms could have altered the community of microorganisms by redistributing organic matter as a result of sediment reworking activities such as excretion of fecal pellets. The change in community structure of microorganisms would eventually cause variability in the cycling and attenuation of nutrients or pollutants.

The permeability and closely-related hydraulic conductivity in streambeds have been observed to vary in space and time [Calver, 2001; Genereux *et al.*, 2008], however, a comprehensive explanation of this variability is not yet achieved. Blaschke *et al.* [2003] and Stewardson *et al.* [2016] identified the reworking of sediments as one of the potential processes that could influence streambed permeability, and our work support this argument. Although not measured in-situ in our experiments, the permeability of bed sediments is expected to be modified due to sediment reworking activities such as burrow construction and deposition of fecal pellets at the bed surface. This also has implications on modeling strategies of surface and sub-surface exchange that assume homogenous and non-transient bed properties [Boano *et al.*, 2006]. This simplistic representation of streambeds could cause uncertainties in estimating exchange characteristics, particularly at sites with high faunal densities.

## 5.3 Limitations and future directions

The current literature of bioturbation in freshwater sediments consists of limited laboratory experiments conducted in lotic environments [Shrivastava *et al.*, 2020b]. Our work,

performed in re-circulating flumes, provides valuable insights on the effect of sediment reworking by macroinvertebrates on hyporheic exchange in streams. However, controlled flume setups in the laboratory are yet a simplistic representation of the fluvial environment. For example, all the experiments were conducted at a single flow rate. The interaction of bioturbating organisms with their physical habitat would likely have been different if the experiments were conducted at different flow rates (or velocities) within the safe range for organisms and grains. Similarly, the experimental beds were homogenous and static. We anticipate that the model organisms could have caused a minimal disturbance in coarse-grained beds (e.g., gravel). On the contrary, the effects of their activities could have been proportionally larger in beds composed of silt or clay (soft sediments). The bioturbation activity by macroinvertebrates may get suppressed if the bed grains are mobile. Our experiments do not incorporate a full range of complexities that exist in natural environments. For instance, the degree of sediment reworking may vary based on several environmental variables such as the presence of predators, vertical connectivity, sunlight, temperature, and pH [Boulton *et al.*, 1992; Fortino, 2006; Moldovan and Levei, 2015; Palmer, 1990].

Further, several propositions presented in the conceptual model concerning the living organisms are not validated due to limited scope of our work. The experiments were conducted at a pre-determined density of a single species, *L. variegatus*, which exhibited a specific size and bioturbation behavior. For instance, considering a scenario where the model organisms were double the size (in length and width) of organisms used in this study, it can be anticipated that the burrows constructed by such worms would have been much larger than the burrows developed in the sand beds in our study. Thus, the rate of transport of water/solutes across the SWI can be expected to be higher than observed in our experiments. In case the sizes of pores and worms were relatively similar, the worms could potentially use the pore spaces to move within the bed. It can be expected that the mixing and mobilization of sediment would have occurred to a lesser degree and fewer macropores would develop in the bed. As a consequence, the flux across SWI may not enhance significantly. Similarly, a greater degree of sediment reworking could have occurred in sand beds if the density of worms was higher than the density used in our experiments. Additionally, the model organisms do not perform burrow ventilation, therefore, our experiments do not provide evidence of how the burrow ventilation process could influence the hyporheic flow regime.

The conceptual model that we present in this study can serve as a basis for further investigations that could be directed to explore the complex pathways through which macroinvertebrates can influence the surface-groundwater exchanges in fluvial settings. The imminent research must focus on conducting experiments with different types and mix of species, in beds with different compositions and geomorphologies, and under different environmental conditions. More intensive research focussing on the above-mentioned aspects is part of our ongoing research. Field observations of bioturbation are scarce so more qualitative and quantitative evidence for bioturbation at larger scales should be also obtained.

## 6 Conclusions

In this work, we present a conceptual model describing potential pathways through which macroinvertebrate bioturbation could alter hyporheic flow in streams. To support some of the arguments presented in the conceptual model, laboratory experiments in re-circulating flumes were conducted and the effects of activities of the model bioturbating organism, *Lumbriculus*

*variegatus*, on the dune-induced hyporheic exchange was studied. As a result of sediment reworking activities such as burrow construction and deposition of fecal pellets at the bed surface, the model bioturbators potentially modified the bed morphology and permeability of sediment beds. Consequently, the treatment flumes exhibited significantly higher mean hyporheic flux, deeper solute penetration depths, and longer mean residence times than the control flumes. The modification to the hyporheic flow regime due to sediment reworking activities can have direct implications on the biogeochemical cycling of nutrients and pollutants in the hyporheic zones which will ultimately influence the overall quality of surface and groundwater in the stream ecosystem. Finally, we provide directions for the imminent studies to support and strengthen the ideas presented in our work and advance the understanding of the role of sediment-organism interactions in fluvial ecosystems.

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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/283278963cc6483cb07469af4faa8065>.

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## Figure Captions

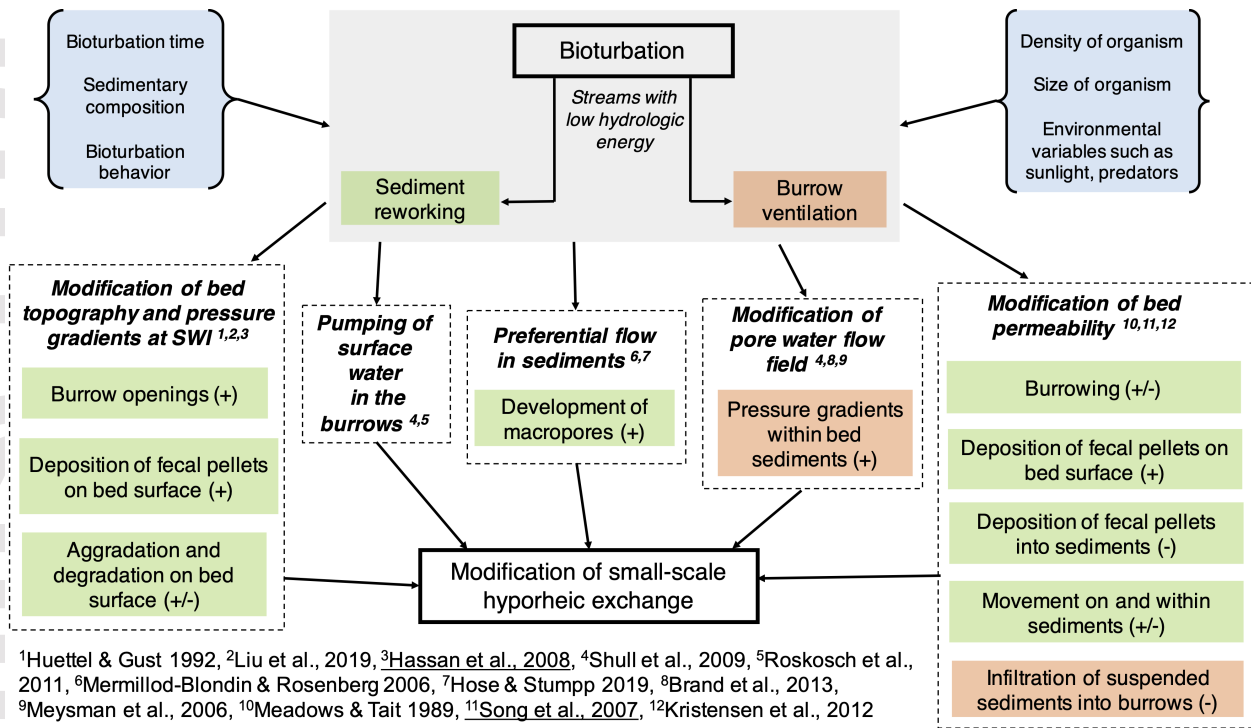
Figure 1: Conceptual model with an arrow diagram presenting the potential pathways through which bioturbation could modify the small-scale hyporheic exchange in lotic environments. Bioturbation is divided into sediment reworking (green box) and burrow ventilation (orange box) processes. The routes through which bioturbation could influence hyporheic flow are presented in bold text within the dotted boxes. The references (superscript numbers) associated with each of these routes are cited at the bottom of the figure (underlined in-figure citations correspond to studies undertaken in lotic environments while the rest are conducted in marine environments). The influence (+/- sign) of a particular faunal activity on a given route is also presented within the dotted boxes. The activities within dotted boxes are classified under sediment reworking or burrow ventilation processes using the above-mentioned color code. The blue boxes (within curly brackets) represent the external variables that could influence the degree to which sediment reworking and burrow ventilation processes occur and may also result in spatio-temporal variability in the bioturbation activity. Note that the influence of bioturbation on the hyporheic flow regime is likely to be significant in streams with low hydrologic energy such as low flow velocity, discharge, and experiencing less frequent high flow events.

Figure 2: *Lumbriculus variegatus* used as model bioturbating organisms in this work, and b) one of the experimental flumes with sand bed having a dune-shaped morphology.

Figure 3: a) The observed (markers) and fitted (lines) temperature-corrected normalized dye concentration in the water column, and b) flux weighted cumulative residence time distributions for the control (C1, C2, and C3) and treatment (T1, T2, and T3) flumes. The root mean square errors for the fits are reported in Table 1.

Figure 4: State of the sand bed in one of the treatment flumes at various stages of the experiment - a) before worms' addition, b) after 4 hrs. of worms' addition, c) after 10 days of worms' addition, and d) top view of the flume (on Day 5) showing fecal pellets, worms' tails and burrow openings at the bed surface.

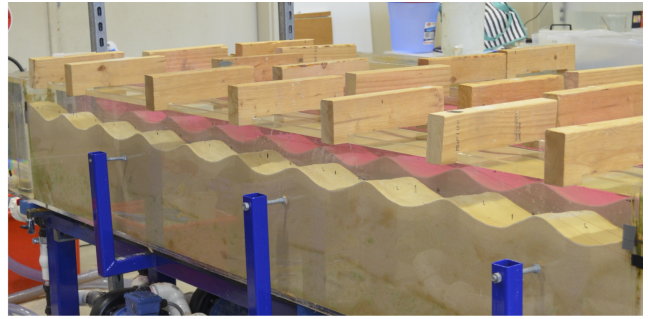
Figure 5: Mean ( $\pm 1$  standard deviation, no. of samples = 3) values for a) average hyporheic fluxes ( $q$  and  $q'$ ), b) depth of dye penetration, c) mean and median residence times, and d) hyporheic residence time distributions shown as flux for short, intermediate, and long residence time ranges in the control and treatment flumes. Asterisk sign (\*) indicates a significant difference between the control and treatment flumes.



<sup>1</sup>Huettel & Gust 1992, <sup>2</sup>Liu et al., 2019, <sup>3</sup>Hassan et al., 2008, <sup>4</sup>Shull et al., 2009, <sup>5</sup>Roskosch et al., 2011, <sup>6</sup>Mermillod-Blondin & Rosenberg 2006, <sup>7</sup>Hose & Stumpp 2019, <sup>8</sup>Brand et al., 2013, <sup>9</sup>Meysman et al., 2006, <sup>10</sup>Meadows & Tait 1989, <sup>11</sup>Song et al., 2007, <sup>12</sup>Kristensen et al., 2012



a)



b)

