Influence of bioturbation and fine sediment clogging on hyporheic exchange in streams

Shivansh Shrivastava
ORCID ID: 0000-0002-0389-7701

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Department of Infrastructure Engineering

The University of Melbourne

Parkville, Victoria 3010

Australia

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Abstract

Sediment permeability and its heterogeneity exert strong control on the hyporheic exchange which underpins several hydrological, biogeochemical and ecological services provided by streams. Streambed permeability has been observed to vary over several orders of magnitude, both in space and time. This thesis argues that a definitive explanation for this observed variability has not been provided due to limited fundamental understanding of three critical in-stream processes- bioturbation, fine sediment clogging, and bioclogging. Feedback mechanisms exist between these processes which collectively influence the structure, composition and hydraulic properties of streambeds. This PhD is directed to advance our current understanding of bioturbation and fine sediment clogging on modifying the streambed permeability and consequently the hyporheic flow regime in fluvial ecosystems.

A conceptual model is presented which identifies the causal pathways through which bioturbation process could alter small-scale hyporheic exchange in lotic environments. To support the arguments presented in this model, experiments in re-circulating flumes are conducted to study the effects of bioturbating organisms (*Lumbriculus variegatus*) on dune-induced hyporheic exchange. Results showed that macroinvertebrate bioturbation has complex effects on the hyporheic flow regime which resulted in modification of hyporheic flux, residence time distributions and penetration depth in treatment flumes. The observed variability in these characteristics of hyporheic exchange are attributed to the generation of a heterogeneous & anisotropic permeability field in sediment beds and alteration of bed morphology due to the bioturbation by model organisms. The experimental results also indicated that sediment re-working time and size of bioturbating organisms are dominant controls on the extent to which hyporheic exchange is moderated.

To advance the understanding of fine sediment clogging in streams, experiments were conducted in re-circulating flumes to study distribution of clay-sized sediments in streambeds comprising of different grain sizes. The results suggested that the infiltration pattern of clay-sized particles depends on the relative size of fine particles & bed grains and the initial concentration of fine particles in the surface water. The observed profiles of deposition/infiltration of clay particles also highlighted that fine sediments are preferentially transported with downwelling hyporheic flow paths into the streambed. The clogging by fine sediments is expected to reduce bed permeability and subsequently hamper the hyporheic exchange. Fine sediment deposition in streambeds reduced hyporheic flux, inhibit deeper penetration and increase median residence times. These results also indicated that clogging by clay-sized particles can have a larger influence on the hyporheic flow regime in coarse-bedded streams compared to fine-bedded streams.

Finally, the impact of macroinvertebrate bioturbation on modifying hyporheic exchange in clogged streams was assessed by conducting experiments in re-circulating flumes using a control (clogged flumes) and treatment (clogged flumes + *Lumbriculus variegatus*) design. The observations from treatment flumes provided evidence of mitigation of clogging by the activities of model bioturbating organisms. The invertebrates infiltrated the top layer of deposited fine sediments, mixed them with underlying bed grains and disturbed the clay deposits in interstitial regions within a sediment bed. The bioturbation of the clogging layer improved the vertical connectivity in treatment flumes producing shorter residence times, greater penetration depths and higher hyporheic flux than the control flumes. These experiments illustrated that the extent to which the characteristics of hyporheic exchange are modified depends on the overall streambed composition i.e., the size of both fine sediments and underlying grains, and the size of bioturbating organisms.

Primarily, the findings from this study suggested that the interacting in-stream abiotic and biotic processes could potentially induce spatio-temporal variability in streambed permeability and modify hyporheic exchange in streams. This holds direct implications for modeling strategies that aim to predict hyporheic exchange in stream networks but consider streambed as a homogenous porous medium with non-transient hydraulic properties for simplicity. These critical processes and their mutual interaction could also influence biogeochemistry in hyporheic zones and must not be overlooked in stream management and restoration programs. Thus, it is argued that more interdisciplinary research must be conducted to comprehend the role of these processes in modifying streambed properties and associated ecosystem functions.

Declaration

This is to certify that:

1. this thesis comprises only my original work towards the PhD,

2. due acknowledgment has been made in the text to all other material used,

3. the thesis is less than 100,000 words in length, exclusive of tables, maps, bibliographies, and appendices.

Shivansh Shrivastava

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Preface

This dissertation is the outcome of four years of training and research under supervision of Prof. Michael Stewardson (primary supervisor) and Dr. Meenakshi Arora (co-supervisor) in the Department of Infrastructure Engineering at The University of Melbourne. Fundamentally, it stems from a comprehensive literature review (Chapter 2) that highlights limited understanding of in-stream abiotic & biotic processes and mutual interactions between them that jointly influence the structure and hydraulic properties of streambeds such as permeability. The identified research gaps were addressed by conducting laboratory experiments at the Sexton Ecohydraulics laboratory to advance the current understanding of effects of two riverine processes- bioturbation and fine sediment clogging on modifying streambed properties and subsequently the hyporheic exchange across sediment-water interface. The findings from these experiments are presented in Chapters 3, 4 and 5.

These four Chapters i.e., Chapters 2-5, are intended to be submitted to relevant journals and have been prepared as individual manuscripts. I am the primary author (80% contribution) of all four manuscripts and was responsible for originally drafting each of these. My supervisors, M. Stewardson and M. Arora, have provided their valuable comments and suggestion at different stages, and actively engaged in iterative revisions. Additionally, critical feedback was provided by my supervisors on other Chapters presented in this thesis.

I hope the narrative presented in this dissertation interests the reader and provides useful insights into complex functioning of stream ecosystems.

Acknowledgements

This thesis work is culmination of four years of research, hard work, thinking and introspection. My heartfelt gratitude is due to everyone who has been directly or indirectly associated with my PhD journey.

Firstly, I would like to acknowledge my principal supervisor Prof. Michael Stewardson and co- supervisor Dr. Meenakshi Arora for their unwavering guidance, support and motivation. You have always encouraged me to work independently and made sure I am progressing on the right track. I would also like to thank you for the emotional support and guidance that you have provided over affairs outside the academic arena.

My sincere thanks to Prof. Andrew Western for being an incredible chair of the committee members. I humbly acknowledge the valuable feedback and constructive suggestions he has provided throughout my candidature.

I would like to express my gratitude towards the Melbourne India Postgraduate Program (MIPP) for providing me the opportunity to conduct my doctoral studies at the prestigious University of Melbourne. On this note, I would also like to thank my previous alma mater, Indian Institute of Technology, Kanpur, India and my supervisor back there Dr. Vinod Tare for

his valuable contributions towards introducing me to the world of academia and encouraging me to pursue a PhD post completion of my Master's degree.

I am fortunate to be a part of the Ecohydraulics lab group, led by Dr. Angus Webb. I am indebted to all the wonderful group members with whom I have had several insightful discussions and shared great food in the monthly group meetings. A special mention to Late Dr. Alexander Mccluskey, Dr. Roser Casas-Mulet, Priyaga Fernando, Garima Lakhanpal and Elise King with whom I have worked closely. I deeply appreciate help of Mr. Rodger Young, technical officer at the Department of Infrastructure Engineering, who has always been on toes to help me with the logistics. He has also been an inspiration and has given some serious health goals for rest of my life.

My family back in India deserves a loud applause for standing by me in all what I have endeavoured so far. Finally, a big salute and a thank you to my wife, Sonam, who started her doctoral journey with me, and has been a solid rock battling out all the odds that we faced during our candidatures. It would have been a lot more difficult to withstand the frustrations and hardships on this voyage had you not walked together with me.

Abbreviations and Notations

$C^*(t)$	Normalized dye concentration at any time t
C_0^{fs}	Initial concentrations of fine sediments in the water column (gm/l)
C_0	Initial concentration of the dye after complete mixing of dye in the water column (ppb)
C_{eq}^*	Normalized equilibrium dye concentration in the water column
C_{eq}	Equilibrium dye concentration at end of the experiment in the water column and in pore water (ppb)
d_{clog}^{fs}	Average depth of clogging layer (m)
d_{max}^{fs}	Maximum infiltration depth of fine sediments into the bed (m)
$\bar{d}$	Equivalent penetration depth (m)
$\bar{R}(\tau)$	Flux-weighted average residence function

RT_{mean}	Mean residence times (min)
RT_{med}	Median residence times (min)
V_p	Volume of water in hyporheic zone (m^3)
V_{sw}	Volume of water in flume system excluding the pore water (m^3)
A	Plan area of the bed (m^2)
$C(t)$	Observed dye concentration at any time t in the water column (ppb)
d'	Effective depth, obtained by dividing V_{sw} by A (m)
d_{50}	Diameter than which 50% of infiltrating grains are smaller (mm)
D_{50}	Diameter than which 50% of substrate grains are smaller (mm)
dh/dl	Hydraulic gradient
dp/dl	Pressure gradient
g	Acceleration due to gravity ($m.sec^{-2}$)
K	Hydraulic conductivity ($m.sec^{-1}$)
m	Accumulated mass per unit plan area of bed divided by C_0
q	Average hyporheic flux or volumetric flow rate averaged over the bed surface area obtained from the initial gradient of breakthrough curve ($m.min^{-1}$)
Q	Flow through the medium (m^3)

q'	Average hyporheic flux calculated from penetration depth and mean residence times (m.min^{-1})
SWI	Sediment-water interface
t	Time (sec)
κ	Permeability (m^{2})
μ	Dynamic viscosity of fluid (Pa.sec)
ρ	Density of fluid (gm.cm^{-3})
σss	Geometric standard deviation of substrate sediments (mm)

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Chapter 1

Introduction

1.1 Background and context

The surface and ground water components are connected in a riverine landscape, and they could potentially interact in a region of saturated sediments that extends underneath the streambed and adjacent to the stream banks, known as hyporheic zones (Boano et al., 2014; White, 1993). The term 'hyporheic' (derived from two Greek words; hypo- under and rheic- flows) was first coined in 1955 by a Romanian hydrobiologist, Traian Orghidan (Orghidan, 2010) and the research into hyporheic zones gained momentum in the late 20th century (Findlay et al., 1993; Grimm and Fisher, 1984; Jones Jr et al., 1995; Stanford and Ward, 1993).

Hyporheic zone underpins important biogeochemical and ecological functions of stream ecosystems (Boulton et al., 1998; Dole-Olivier et al., 1997; Pusch, 1996), and therefore, its healthy functioning is crucial for stream restoration and conservation programs (Boulton, 2007; Hester and Gooseff, 2010). For instance, hyporheic zone is regarded as a stream's liver as it is rich in microbial communities that are responsible for processing nitrogen and carbon in stream networks (Fischer et al., 2005). Similarly, the attenuation of contaminants and pollutants largely occur in the hyporheic zones (Gandy et al., 2007; Landmeyer et al., 2010). The ecological role of hyporheic zones in serving as refugium for benthic organisms such as invertebrates during extreme hydrological conditions i.e., floods and drying, has also been demonstrated (Stubbington, 2012).

The hyporheic zones facilitate a two-way exchange of mass and energy across the sediment-water interface (SWI), a process defined as hyporheic exchange (Triska et al., 1993). It is broadly described as the movement of stream water into and adjacent to streambed, which may mix with ground water as it travels within the bed before finally emerging back into the stream. The critical characteristics of hyporheic exchange that influence the biogeochemical and ecological functions of hyporheic zones are hyporheic flux, hydraulic residence time distribution and penetration depth (defined in Chapter 3) (Findlay, 1995; Gomez et al., 2012; Jones Jr et al., 1995).

Hyporheic exchange, particularly at small scale, is partially controlled by streambed permeability (or closely associated hydraulic conductivity) and its heterogeneity (Salehin et al., 2004; Sawyer and Cardenas, 2009; Tonina et al., 2016). Permeability is defined as the ability of porous media to transmit water through it (Freeze and Cherry, 1979). In general, beds comprising of highly permeable sediments (e.g. gravel) exhibit larger hyporheic flux, shorter residence times and greater depths of solute penetration than beds comprising of low permeability sediments (silt or clay). Streambed permeability has been reported to vary over several orders of magnitude, both in space and time (Calver, 2001; Genereux et al., 2008). The literature review conducted in this PhD (Chapter 2) highlights that a comprehensive explanation for the observed variability is lacking due to limited understanding of the fundamental abiotic and biotic riverine processes which could influence structure, composition and hydraulic properties of streambeds. These processes include bioturbation (biotic), fine sediment clogging (abiotic) and bioclogging (biotic). Further, these processes co-occur in natural settings and feedback mechanisms exist between them. By inducing spatio-temporal dynamism in streambed permeability, these interacting environmental processes have consequences for hyporheic exchange across the SWI and associated stream ecosystem functions.

The research in this PhD is directed to advance our current understanding of role of macroinvertebrate bioturbation and fine sediment clogging in stream ecosystems. Aquatic sediments host a plethora of faunal organisms that move, feed & excrete, dig and construct biogenic structures such as burrows within the bed. By doing so, these organisms re-work the bed sediments, a process broadly described as bioturbation (Kristensen et al., 2012), and could potentially alter the structure and hydraulic properties of the bed. While there is abundant evidence of this affect in marine sediments, little is known about influence of bioturbation on modifying streambed properties and subsequently on hyporheic exchange (Solan and Herringshaw, 2008). Fine sediment clogging is a process of deposition of fine sediments on and into streambed which could potentially reduce its permeability (Brunke, 1999; Datry et al., 2015). Although this process is long known, distribution of fine sediments within the structure of roughness features (e.g. dunes) and its subsequent influence on hyporheic exchange has begun to receive interest only recently (Fox et al., 2018; Jin et al., 2019a; Jin et al., 2019b). The bioturbation and fine sediment clogging processes potentially interact with each other in natural environments and could synergistically alter bed permeability, however, these interactions are not well-understood.

1.2 Research questions

Based on the research gaps, the overall objective of this research is to better understand the individual and combined influences of bioturbation and fine sediment clogging processes on modification of sediment permeability and thus on hyporheic exchange in streams. This objective will be achieved by answering the following research questions:

1) How does macroinvertebrate bioturbation influence hyporheic exchange in streams?

2) What are the effects of size of bioturbating organisms and re-working time (contact time of organisms with the sediments) on modification of hyporheic flow?

3) How clay-sized sediments are distributed in fine- and coarse-grained streambeds when present at different concentrations in the surface water? In turn, how this deposition of fine sediments influence dune-induced hyporheic flow regime?

4) Can macroinvertebrate bioturbation mitigate fine sediment clogging and enhance hyporheic exchange in clogged streambeds?

The thesis is divided into seven chapters and the above-mentioned research questions have been addressed in Chapters 3, 4 and 5 as presented in section 1.3.

1.3 Thesis structure

Chapter 1 (this chapter) provides the introduction and background of this thesis. It briefly discusses the research gaps and present the research questions that will be addressed in this work.

Chapter 2 presents a comprehensive review of existing knowledge and research gaps in current understanding of fine sediment clogging, bioturbation and bioclogging, and mutual interactions between them which could influence permeability of streambeds in space and time. It further expands on highlighting need of developing a conceptual model for temporal evolution of streambed and its permeability based on trajectory of responses of these three environmental processes after a high flow event.

Chapter 3 investigates into the role of bioturbation process in modifying hyporheic exchange in stream ecosystems. It presents a conceptual model which underlines the causal pathways through which activities of bioturbating organisms could influence hyporheic flow regime. To test the arguments presented in the model, laboratory experiments in re-circulating flumes were conducted to study alteration in hyporheic flux, penetration depths and residence time distributions due to macroinvertebrate bioturbation for dune-induced hyporheic flow. This chapter also explores the effect of size of bioturbating organisms and their contact time with the sediments on modifying these characteristics of hyporheic exchange.

Chapter 4 is directed to understand the distribution of clay-sized sediments in fine- and coarse-grained model streambeds with dunes as topographical features. It investigates the influence of concentration of fine sediments in the surface water on their infiltration pattern in streambeds. The effect of this clogging on hyporheic flux, penetration depths and residence time distributions of dune-induced hyporheic exchange is further investigated.

Fine sediments and bioturbating organisms co-exist in stream environments, and Chapter 5 focuses on studying the effect of sediment-organism interaction on mixing and mobilisation of fine sediments. Macroinvertebrate bioturbation could potentially mitigate clogging, thus, its influence on enhancing hyporheic exchange across the SWI is also examined.

Chapter 6 presents a comprehensive discussion on the contribution of this PhD to the body of literature. It presents a synthesis of results based on the experimental findings and suggest implications for theoretical strategies that predict hyporheic exchange. It further expands on the importance of bioturbation and fine sediment clogging processes in modulating biogeochemistry of hyporheic zones. It also presents the directions for future research to further advance our understanding of these processes in modifying hyporheic exchange in streams.

The overall summary and conclusions are presented in Chapter 7.

Chapters 2, 3, 4 and 5 have been prepared as manuscripts and this PhD work is intended to be submitted as thesis by publications. The relevant research methodology associated with laboratory investigations is presented in each of the experimental chapters (Chapters 3 to 5).

Chapter 2

Literature review

This Chapter is intended to be submitted as a manuscript with full title as: **'Understanding streambeds as complex systems: Review of multiple interacting environmental processes influencing streambed permeability'**. I am the primary author of this manuscript (80% contribution), and my supervisors, Prof. Michael Stewardson and Dr. Meenakshi Arora are the co-authors. The authors would like to acknowledge Dr. Robert Payn, Associated Editor, Freshwater Science, and two anonymous reviewers for their suggestions on a previous version of this manuscript.

Abstract

The permeability of streambeds (κ) and the closely related hydraulic conductivity (K) affect physical, chemical and biological processes in sub-surface sediments that underpin important ecosystem services provided by rivers. Streambed K has been observed to vary over several orders of magnitude, but the environmental processes influencing this variation have received little attention. This review is a collective synthesis of three processes- a) physical clogging due to fine sediments, b) biological clogging due to microbial biomass and c) bioturbation by in-stream fauna, which can potentially modify streambed permeability. We highlight that there is limited evidence of influence of the biotic processes on altering structure and hydraulic properties of streambeds, and further expand on complex feedback mechanisms between the three environmental processes. We suggest that interdisciplinary research exploring these biotic and abiotic processes including their two-way interactions is necessary to advance our understanding of variation in streambed permeability. To this end, we propose need of developing a conceptual model representing the evolution of streambed and its K after a high flow event and present a possible scenario for the same based on the trajectory of responses of above-mentioned environmental processes.

Keywords: streambed permeability, hydraulic conductivity, fine sediment clogging, bioclogging, bioturbation, hyporheic zones, streambed evolution

2.1 Introduction

With over 20 years of expansive research on surface-subsurface interactions in fluvial ecosystems, the hyporheic zones have been recognized as a unique ecotone supporting diverse hydrological, biogeochemical and ecological processes in streams (Boulton et al., 1998; Findlay et al., 1993; Marmonier et al., 2012; Mulholland et al., 1997). Hyporheic zone can be defined as a zone of saturated sediments lying below and adjacent to the streambed where, surface water seeps into the bed, may mix with ground water and re-emerges to meet the stream (Brunke and Gonser, 1997; Findlay, 1995; Ward, 2016). Hyporheic exchange occurs through a wide range of spatial scale (from individual bed grains to whole catchment), however, most studies have focused on the reach or finer scales (Boano et al., 2014) presumably because conducting field, experimental and modelling studies to elucidate the key ecosystem processes are more feasible at small scales (Hughes et al., 2001).

At small scales, streambed permeability (κ) is a key physical factor affecting hyporheic exchange (Bardini et al., 2012; Boulton et al., 1998; Burkholder et al., 2008; Mauclaire et al., 2006). Permeability is an intrinsic property of a porous media described as its ability to transmit fluid (Freeze and Cherry, 1979). Streambed permeability depends largely on the sediment properties (e.g. grain size, sorting, pore network). Mathematically, it forms a part of proportanility constant in Darcy's law and is represented as,

$$Q = -\frac{\kappa}{\mu} A \frac{dp}{dl} \ldots\ldots\ldots\ldots\ldots\ldots\ldots (\textit{Equation } 2.1)$$

where,

Q = flow through the medium, κ = permeability, A = area of cross-section, μ = dynamic viscosity of the fluid and dp/dl = pressure gradient.

The focus of this paper is on streambed permeability, but we also refer to the closely related hydraulic conductivity (K) which is widely measured and reported in the literature. Like permeability, K also refers to how quickly fluid can move through the pore spaces. However, in addition to properties of sediments, K depends on properties of fluid passing through the medium. K can be mathematically represented as follows,

$$\mathrm{Q} = \mathrm{KA}\frac{\mathrm{dh}}{\mathrm{dl}} \ldots\ldots\ldots\ldots\ldots\ldots\ldots (\textit{Equation } 2.2)$$

where,

K = hydraulic conductivity and dh/dl = hydraulic gradient. Permeability and hydraulic conductivity are related as,

$$\mathrm{K} = (\kappa\rho\mathrm{g})/\mu \ldots\ldots\ldots\ldots\ldots\ldots\ldots (\textit{Equation } 2.3)$$

where,

ρ = density of fluid and g = acceleration due to gravity.

The reported K values for streambeds in the literature range from 10^{-10} to 10^{-2} m/s for point measurements and 10^{-5} to 10^{-3} m/s for reach-average values (Stewardson et al., 2016). This variation has been observed over a range of spatial and temporal scales (Table 2.1). For instance, K varies within a reach, between reaches of the same stream and at different depths for same sites (Calver, 2001; Chen, 2011). Similarly, K has been observed to change in time over a few days during a flow event (Mutiti and Levy, 2010) and between seasons (Wroblicky et al., 1998). The reported dynamism in K values could be site specific and it has been partially attributed to factors such as different bed compositions and morphologies (Sebok et al., 2015; Wu et al., 2015a), flow dynamics (Hatch et al., 2010), temperature (Briggs et al., 2014; Matheswaran et al., 2014), measurement techniques (Landon et al., 2001) and last bed-disturbance (Stewardson et al., 2016). However, a comprehensive explanation for the observed variability in K is lacking due to limited understanding fundamental of in-stream processes that could spatially & temporally modify the structure and hydraulic properties of streambeds.

Table 2.1: Summary of K measurements from previous studies including reported range of K and explaination for observed variability.

References	Site details		Measurement method	Reported K range		Justification given for variability in K by the authors
	Location	River bed		Spatial	Temporal	
Cardenas and Zlotnik, 2003	456 measurements in 50 m long and 20 m wide reach in Prairie Creek	Gravel and Sand	Multi-level constant head injection	0.15-74.7 m/d		Scouring and deposition occurring at the channel bends
Chen, 2011	80 Depth related measurements at 9 sites in Platte River	Mostly Gravel and Sand in top 50 cm	Permeameter	For 0-3 m: 25.6 m/d For 3-9 m: 6.4 m/d For 9-14.5 m: 2.6 m/d		Hyporheic processes in top sediments make the top layer more permeable
Cheng et al. 2011	Around 600 measurements in 300 Km of Platte River	Sand	Permeameter	16.8-48.2 m/d Higher K values in centre of the channel		Confluence of tributaries causing increased sediment load in downstream regions

						Higher velocities in middle of the channel
Genereux et al. 2008	487 measurements in 262.5 m long reach in West Bear Creek	Mostly sand in centre with silt and clay in sides	Permeameter	0.01-66 m/d K value twice in centre than in sides	4-24 m/d in top 36 cm of sediments during a water year	Erosion and deposition due to storm water flow. Higher stream velocity in centre of the channel. Acknowledged role of factors like bioturbation, gas bubbles, microbial clogging etc.
Hatch et al.2010	7 sites over a stretch of 11.2 Km of Pajero River	Sandy streambed	Time series thermal methods	0.1-9 m/d 1 order higher K in right section than in left and centre	1-3 order of change in magnitude of K over a period of 4-5 months	K varies due to change in discharge and seepage rates
Leek et al.2009	2 river reaches 20 m apart in Touchet River (each 50 m long)	Coarse gravel and cobbles	Slug test using piezometers	2-3 order difference in K between sites		Sedimentation environment, deposition occurring under different flow regimes

Levy et al. 2011	Around 60 direct measurements at single site (120 m wide and 3 m deep) in Great Miami River	Visibly from pebbles to cobbles	Seepage meters and slug test	0.017-1.7 m/d in top layer An order higher K for underlying sediments		Deposition of fine sediments and forming a heavily clogged top layer which doesn't erode completely even during high flow events
Ryan and Boufadel, 2006	80 m reach of Indian creek with total of 85 measurements at 2 different depths	Gravel and cobbles	Permeameter	Upper layer (7.5-10 cm):1.4-15.3 m/d Lower layer (10-12.5 cm): 0.09-28.5 m/d Mean K higher in upper layer		Clogging of permeable bed with fine sand, silt and clay
Sebok et al. 2015	Total of 50 measurements on a straight and bent channel on Skjern River	Sand and silt	Permeameter	0.01-8 m/d	Variability of one order of magnitude between 2 months of a water year.	Low values attributed to the presence of thin organic layer in sediments Scouring and Sedimentation processes

Wu et al. 2015	443 measurements in a 8.5 m reach of Dawen River at 5 depths	Largely sand and gravel with traces of silt and clay	Permeameter	Top layer: 112 m/d Bottom layer: 45 m/d		Deposition and erosion, Sedimentation environment
Stewardson et al. 2016	2482 measurements in 119 reaches (reach lengths: 40-840 m)	Largely Gravel	Slug test	0.86-49 m/d		Clogging of coarser streambed with fine sediments
Song et al. 2007	7 sites on 3 different rivers at 2 depths	Largely sand and gravel with traces of silt and clay	Permeameter	K values 1.5-5 times higher in top layer		Hyporheic exchange flow increased pore space in top layer Acknowledged Bioturbation and gas bubbles

Song et al. 2016	100 m reach in Beiluo River with 25 measurements each in 3 sediment layers	Sand in top 30 cm, silt and clay beyond 45 cm and mixture of all three in between 30-45 cm	Permeameter	Top layer- 0.03-9.52 m/d Middle layer- 0.01-1.05 m/d Bottom layer- 0.01-0.80 m/d Higher K in top layer with gradual decline as depth increases	Different K values in different months of a water year	Acknowledged Bioturbation, gas production Flood event causing erosion and then deposition Temperature change
Blaschke et al.2003	2 sites at Danube River	Sandy Gravel	Derived from leakage coefficients and sediment thickness	K values were dependent on the type of clogging ranging from <0.008 – 86 m/d	3-4 order change in magnitude of K over continuous clogging and declogging cycles over period of 3-4 years	Bioturbation, algal growth Low and high flows during successive water years

It is critical to understand this spatio-temporal heterogeneity in K as it is expected to alter stream ecosystem functions (Claret and Boulton, 2009; Irvine et al., 2015; Salehin et al., 2004; Tonina et al., 2016). For instance, Salehin et al. (2004) showed that streambed heterogeneity resulted in greater hyporheic flux and shorter mean residence times. Similarly, Tonina et al. (2016) demonstrated an overall reduction in volume of hyporheic zones and hyporheic exchange flows in the heterogeneous sediment beds. The modification to characteristics of hyporheic flow (e.g. residence times, hyporheic flux) would subsequently affect the biogeochemical transformation of contaminants/nutrients and ecology of hyporheic zones (Boulton, 1993; Zarnetske et al., 2011). This also has implications for stream management and conservation programs that aim to restore stream functions by modifying properties of streambed by either building structures of lower or higher K (depending on the purpose of the program) in shallow sub-surface region (Ward et al., 2011), or by directly changing the streambed composition via deposition or raking sediments (Pander et al., 2015).

Two potential in-stream processes which could induce spatio-temporal variability in hydraulic properties of streambeds are- clogging and bioturbation. Clogging (also referred as colmation) can be understood as a state of streambeds in which the porous volume and subsequently the K reduces (Datry et al., 2015; Descloux et al., 2010) and could occur due to several physical, chemical and biological processes (Table 2.2). For instance, fine sediments could deposit on or infiltrate into the pore matrix (physical clogging) and reduce its permeability. The pore matrix could also get clogged due to growth of bacterial mass, known as bioclogging. Bioturbation is defined as re-working of sediments due to aquatic fauna such as macroinvertebrates and fish (Kristensen et al., 2012; Solan and Herringshaw, 2008). Small invertebrates like tubificid worms can dig up to 2-10 cm deep in sediments (Mermillod-Blondin et al., 2001) while freshwater mussels can go as deep as 20 cm (Richter et al., 2016). As these organisms move, dig and construct burrows, the bed grains are mixed and mobilized which could potentially alter sediment permeability.

Table 2.2: Summary of various physico-chemical and biological processes that can cause clogging in streambeds.

Processes leading to clogging	Causes	References
Deposition and intrusion of fine sediments in coarser streambeds	Presence of fine sediments in stream water	(Ryan et al. 2006, Stewardson et al. 2016)
Development of biofilms on and within streambeds	Microbial growth due to availability of suitable physical, chemical and biological environment	(Baveye et al. 1998, Thullner 2010)
Precipitation of metals like Iron or Manganese in streambeds	Presence of metal containing minerals, appropriate pH range, redox potential of water. It can also be mediated by certain microorganisms	(Bouwer 2002, Jeong et al. 2018)
Swelling of clay particles	Presence of clay in sediment pores	(Baveye et al. 1998)
Formation of gas bubbles in the streambeds	Air entrapment in sediments or due to production of gases by microorganisms such as during fermentation or nitrification	(Orlob et al. 1958, Constantz et al. 1988, Seki et al. 1998)

The evidence of influence of these above-mentioned processes in altering streambed permeability is disproportionate as they have been explored to different extents. Physical clogging is the most dominant form of clogging in streams and has been investigated in several field, laboratory and modelling studies (Blaschke et al., 2003; Brunke, 1999; Cui et al., 2008; Schälchli, 1992). While bioclogging in streambeds has been subject to limited research in the past (Hartwig and Borchardt, 2015; Newcomer et al., 2016; Thullner, 2010), evidences for chemical clogging (e.g. metal precipitation) are sparse (Bouwer, 2002), presumably due to lesser impact relative to other two clogging processes in stream ecosystems. The physical disturbance of sediment beds due to bioturbation has been extensively studied in marine sediments, but the role of in-stream bioturbating organisms in modifying hydraulic properties of their habitat has gained momentum only recently (Marmonier et al., 2012). Further, these abiotic and biotic processes co-exist in natural environment and are expected to mutually interact. However, due to limited fundamental understanding of the individual processes (biotic processes in particular), the feedback mechanisms between them are poorly comprehended.

In this review, we synthesize the state-of-art knowledge and existing gaps in our understanding of physical clogging, bioclogging and bioturbation processes. Whilst we provide a brief overview of the vast literature dealing with physical clogging, we primarily focus on the biotic processes (bioturbation and bioclogging) because this area has received relatively less attention in the past. We highlight that these processes have been studied in isolation based on discipline driven research objectives and perspectives (e.g. ecological, biogeochemical, hydrological), and emphasize that strong feedbacks exist between them which are more complex than they have been conceptualized in earlier studies (Gerbersdorf and Wieprecht, 2015; Richter et al., 2016; Yao et al., 2017). In the end, we highlight need of developing an evolution model of streambed and its permeability and present a possible scenario for the same based on the trajectory of responses of these interacting environmental processes after a high flow event.

2.2 Processes affecting streambed permeability

2.2.1 Physical clogging

The surface water is laden with both inorganic and organic fine particles that tend to deposit on or into the streambed. The accumulation of fine sediments reduces the porosity and permeability of streambed, a process known as fine sediment clogging (Brunke, 1999; Datry et al., 2015). Although clogging is a natural phenomenon in lotic environments, but activities such as deforestation, land use change and alteration of flow regimes has dramatically increased fine sediment delivery in streams (Owens, 2005; Wharton et al., 2017). Several previous studies have demonstrated that fine sediment clogging in streams hampers hydrological connectivity across SWI (Hancock, 2002; Hartwig and Borchardt, 2015), affects sub-surface ecology detrimentally (Bo et al., 2007; Brunke and Gonser, 1997; Wood and Armitage, 1997) and poses high threat of chemical contamination and toxicity (Farkas et al., 2007; Ongley et al., 1992) in streambeds. Consequently, mitigating fine sediment pollution has become a primary focus of several stream conservation and management practices globally (Mathers et al., 2017; Wharton et al., 2017; Wood and Armitage, 1997).

The fate and transport of fine sediments in stream ecosystems has been studied for over 50 years (Einstein, 1968; Lisle, 1989; Schälchli, 1992). The clogging by fine sediments is generally divided into 2 broad categories- internal and external clogging (Blaschke et al., 2003; Schälchli, 1992). When fines deposit on top of the streambed, it is referred as external clogging. Internal clogging refers to the infiltration of fine particles into the pore matrix of a streambed. Penetration of fine particles can occur due to advection with downwelling hyporheic flow or gravitational pull, known as depth infiltration (Brunke, 1999). The particles travelling downwards are ultimately trapped by straining, settling or due to electrochemical properties of fine particles. A reverse process, known as de-clogging, may result in re-suspension of settled or trapped fine particles and cause re-mobilization of sediment bed (Wharton et al., 2017). For instance, during high flows the deposited sediments may get transported longitudinally (Blaschke et al., 2003) or laterally within the streambed (Casas-Mulet et al., 2017; Casas-Mulet et al., 2018). As fine sediments are removed from the pore voids, the local permeability is expected to increase.

Previous literature has demonstrated clogging with different combinations of substrate and fine sediments such as gravel as bed material with silt or fine sand as fine material, and sand as bed material with clay or silt as fine material (Cunningham et al., 1987; Packman et al., 2000a; Schälchli, 1992; Wooster et al., 2008). Pioneering work by Einstein (1968) observed that fines are first delivered to the deep regions of streambeds and clogging commences from bottom of the bed. This implied that upper layer of streambeds would not be clogged if there is a limited input of fine sediments. Since then, numerous studies have shown that accumulation of fine sediments does not necessarily commence from bottom, and the penetration depth of fines is controlled by variables such as the relative size of substrate and fine sediments (Gibson et al., 2009a; b; Wooster et al., 2008) , concentration of fine sediments (Herrero et al., 2015; Khullar et al., 2013; Mathers et al., 2019b), flow velocity (Cunningham et al., 1987), bed shear stress (Parker, 1990; Schälchli, 1992; Wilcock et al., 1996). The rate of clogging and fine particle deposition has also been demonstrated in some experimental studies (Packman and MacKay, 2003; Rehg et al., 2005). For instance, in multiple clay injection experiments, Rehg et al. (2005) observed progressively less deposition with subsequent injections. The deviation in amount of clay deposition between subsequent injections depends on the amount of clay previously accumulated in the bed and the amount of clay added with the current injection. A summary of experimental studies on infiltration of fine particles in coarser bed is documented in Khullar (2007).

Theoretical and modelling approaches were developed following the early laboratory investigations of clogging (Lauck, 1991; Sakthivadivel and Einstein, 1970). For instance, Lauck (1991) developed a model to predict the infiltration of fine sediments in coarser streambed and demonstrated that fine sediments penetrate only to a limited depth, however, it also justified Einstein's result and regarded it as a special case where size of bed particles is substantially greater than infiltrating particles. Over the years, these models have been modified and more realistic theory of fine sediment infiltration has been developed (Cui et al., 2008). Further, modelling approaches based on advective pumping mechanism have been developed to predict colloidal exchange with streambeds by combining flow hydraulics, particle filtration and subsequent settling in coarse sediments (Packman et al., 2000b).

As fine sediments are associated with bed toxicity and negatively affecting streambed ecology, the assessment of their infiltration patterns has been a significant topic of research. Two types of infiltration profiles- unimpeded static percolation and bridging have been reported in literature (Gibson et al., 2009a; b). In order to predict the depositional profiles, threshold ratios, based on relative size of infiltrating particles and bed grains have been developed in the past (Gibson et al., 2009a; Huston and Fox, 2015). However, this criterion for predicting the patterns of fine sediment deposition largely exists for fine sand (infiltrating particles) and gravel (bed grain) sediment system. It is expected that such metrics could significantly differ for other types of sediment systems, particularly for infiltrating particles smaller than fine sand such as silt as shown in a recent study (Fetzer et al., 2017). Further, distribution of fine sediments within the structure of roughness features (e.g. dunes) and its subsequent influence on hyporheic exchange has begun to receive interest only recently (Jin et al., 2019a; Jin et al., 2019b).

2.2.2 Bioturbation

Bioturbation is broadly defined as the disturbance to sediments caused by movement, feeding, excretion and other activities of organisms inhabiting sediment beds. For example, invertebrates like ‘tubificids’ construct galleries (Mermillod-Blondin and Lemoine, 2010) and fish dig nests (Moore et al., 2007). Similarly, some organisms feed on sediments at the surface and egest out faecal pellets in deep sediments while some feed at depth and egest at the surface (Michaud et al., 2005). As a result, bed grains are mixed and mobilized leading to modification of the structure and hydraulic properties of aquatic sediments. The degree to which sediment beds are re-worked is influenced by several variables such as size (Heilskov and Holmer, 2001; Thrush et al., 2006), density (Duport et al., 2006; Marinelli and Williams, 2003) & bioturbation behaviour of the organisms (De Backer et al., 2011; Michaud et al., 2006), re-working time (Davis, 1993; Maire et al., 2008) and bed composition (Mermillod-Blondin and Rosenberg, 2006). For instance, the bed permeability could both increase and decrease based on burrowing behavior of the bioturbating organisms (Meadows and Tait, 1989). Similarly, Navel et al. (2012) demonstrated variable influence of macroinvertebrate bioturbation on modification of structure of fine- and coarse-grained beds.

The process of bioturbation has been shown to reduce sub-surface clogging and increase the K of streambeds. For example, Nogaro et al. (2006) conducted laboratory experiments in infiltration columns (i.e. standing water) and showed that K in columns with invertebrates was significantly greater than those without invertebrates. Correspondingly, Roche et al. (2016) demonstrated through a combined laboratory and modelling experiments that 90% of sediments up to depth of 5 mm were reworked due to bioturbation by worms. The results can be thought to pose direct implications on potential modification of the top layer of clogged streambeds. In another field study, exposed fine sediment patches of streambed were found to have extensive burrows and tubes of invertebrates up to depth of 5 cm with diameter varying from 1 to 6 mm (Song et al., 2010). The average K of sediments in top layer was reported higher (almost double) than lower layers due to presence of the invertebrates.

Besides mobilizing fine particles within the streambed, certain bioturbating organisms could release fine particles (de-clogging) or prevent erosion of fine particles from the bed (Gottesfeld et al., 2008; Hassan et al., 2011; Rice et al., 2016). Sediment movement in downstream regions and alteration in streambed morphology due to salmon bioturbation has been well documented (Gottesfeld et al., 2004; Peterson and Quinn, 1996). Fish can potentially cause sediment movement during both, spawning and post-spawning periods (Crisp and Carling, 1989;

Gottesfeld et al., 2008; Gottesfeld et al., 2004). For instance, during the spawning period, high densities of fish are found in regions which have good supply of food and nutrients. The magnitude of sediment disturbance will be most likely higher in such regions. Similarly, post spawning period is characterized by digging up to 20-30 cm to protect the eggs from predators and physical turbulence. In contrast to salmonid nest digging activities, some organisms (e.g. net spinning caddisflies) can cause consolidation of the sediment bed and reduce its vulnerability to scouring (Cardinale et al., 2004).

The bioturbation process has been also associated with alteration of pore and surface water chemistry (Colombo et al., 2016; Mermillod-Blondin et al., 2001; Xie et al., 2018). For example, Colombo et al. (2016) and Xie et al. (2018) illustrated that bioturbation by invertebrates and polychaetes caused enhanced flux of Zinc (Zn) and Copper (Cu) respectively from pore water to overlying water. Similarly, Mermillod-Blondin et al. (2003) observed enhanced exchange of water and nutrients across the SWI in sediment columns due to activities of invertebrates.

The modification of sediment beds due to activities of bioturbating organisms is spatially and temporally variable. For instance, macroinvertebrate could be non-uniformly distributed along the bed such as in riffles & pools sections (McCulloch, 1986), and modification to these sections would occur to different extents causing spatially heterogeneous permeability fields. The activity of bioturbating organisms is also susceptible to temporal variations based on their life-cycle history, temperature and flow regimes (Bunn and Arthington, 2002; Meysman et al., 2010; Ouellette et al., 2004). For example, some aquatic inhabitants re-work the sediments actively during night (Loperfido et al., 2010; Rice et al., 2016). Similarly, seasonal variation in bioturbation activity including their population density has been also observed in previous studies (Giberson and Hall, 1988; Richardson et al., 2009).

The modification of bed permeability due to bioturbation has been reported in studies related to marine sediments (Meadows and Tait, 1989; Murray et al., 2002) but there is a limited understanding of this process in stream environments (Marmonier et al., 2012; Solan and Herringshaw, 2008). The research related to bioturbation in freshwater sediments has been largely laboratory-based, with experiments mostly conducted in infiltration columns i.e., in standing water (Mermillod-Blondin et al., 2001; Mermillod-Blondin et al., 2003; Nogaro et al., 2006). Although these studies indicate that bioturbation modifies the hydraulic properties and subsequently the exchange across sediment beds, they fail to represent the complex hydrodynamics that exist at the SWI due to flow of water over undulated streambeds. Further, field evidence of effect of bioturbation on streambed permeability are scarce (Song et al., 2010; Song et al., 2016). Additionally, habitat modification by bioturbating organisms is variable in space and time due to dependency on other variables such as presence of predators, hydrological environment (Boulton et al., 1992; Fortino, 2006; Malard et al., 2003; Moldovan and Levei, 2015; Palmer, 1990), which further complicates its understanding in fluvial environments.

2.2.3 Bioclogging

The clogging of pore spaces due to growth and multiplication of microbial organisms such as bacteria or fungi is broadly known as bioclogging. The microorganisms secrete EPS (external polysaccharides), which is a sticky substance that binds microbial cells together to form biofilms (Chen-Charpentier et al. 2009, Vu et al. 2009) and clog the pore matrix. In addition to filling up of pore spaces, microorganisms mediate several biogeochemical reactions which produce gases as products or by-products. For instance, methane (CH_4) is produced due to fermentation and dinitrogen (N_2) or nitrous oxide (N_2O) are formed due to denitrification (Battersby et al. 1985, Reynolds et al. 1992). The gas bubbles could get trapped and potentially clog the porous media.

The multiplication of microorganisms and their development into localized or continuous biofilms depend on conducive environmental conditions and transport processes. Several studies have examined the role of different environmental variables such as oxygen levels, availability of carbon, pH, temperature, ratio of carbon to nitrogen and grain size on EPS production and bioclogging in porous media (Hand et al. 2008, Miqueleto et al. 2010, Xia et al. 2014). The transport of microorganisms is also critical to biofilm growth, which in turn, is controlled by several physical, chemical and biological processes (Taylor et al. 1990, McCaulou et al. 1994, Ginn et al. 2005, Díaz et al. 2010). For example, advection, dispersion and straining are some of the key physical processes which result in movement of microorganisms. Advection can be defined as transport of bacteria with flowing water while dispersion involves movement of microorganisms from region of high to low density in porous media. Straining can be considered as retaining of microorganisms in the pore throats which are smaller than their size and blocking their free movement.

The process of bioclogging has been largely investigated through small-scale laboratory experiments and numerical modelling (Cunningham et al. 1991, Wu et al. 1997, Seki et al. 1998, Seifert et al. 2007, Thullner 2010). Studies conducted in columns (1-dimensional) and sandbox experiments (two dimensional) have indicated decline in K by 1 to 3 orders of magnitude due to bioclogging (Taylor et al. 1990, Kildsgaard et al. 2002, Engesgaard et al. 2006). However, field evidences of bioclogging in modifying hydraulic properties of streambeds are rare (Battin and Sengschmitt, 1999; Hartwig and Borchardt, 2015). Several modelling approaches have been developed to reproduce observed results of reduction in hydraulic properties of porous media from laboratory experiments. These models could be broadly divided into two categories- a) analytical models, which assume the effects of biomass growth in porous media and relate it to reduction in K, and b) pore network models, which take into account the growth of biomass (either as continous films or in microcolonies) at pore scale and study reduction in pore volume of the entire pore network. The models of bioclogging have been comprehensively reviewed in Thullner (2010).

Bioclogging has been relatively less studied in stream ecosystems presumably due to complications involved in studying biological processes. The small-scale studies provide useful insights into the role of microbial communities in modifying streambed K, however, the results could not be extended to natural environment. Further, bioclogging depends on various environmental factors which may cause growth of microorganisms and their activities to vary in space and time, but little is known about this variability.

2.2.4 Interactions between abiotic and biotic processes

The physical clogging, bioclogging and bioturbation processes have been largely studied in isolation, however, these processes co-exist in natural environments and synergistically influence physical structure and hydraulic properties of streambeds. In this section, we report the potential feedback mechanisms between these abiotic and biotic processes (Figure 2.1).

In addition to clogging pore spaces, growth of bacterial mass to form biofilms or mats could prevent mobilization of bed sediments, a process described as biostabilization (Paterson, 1997; Paterson, 1989). Sedimentological processes such as erosion and transport of fine sediments during high flows, and their accumulation within streambeds during low flows can be affected by the presence of biofilms (Droppo et al., 2007; Fang et al., 2016; Roche et al., 2017). The release of fine sediments is less likely to occur in beds covered with microbial biomass compared to beds free of bioclogging (Droppo et al., 2001). Further, Chen et al. (2017) demonstrated that biostabilization due to EPS production is not only restricted to surface but can penetrate deeper and bind the underlying sediments. The experimental results in their study showed that even after erosion of surficial biofilms, the suspension of sediments did not occur to the extent as expected from abiotic sediments highlighting that EPS held the sediments together and reduced the erosion rates.

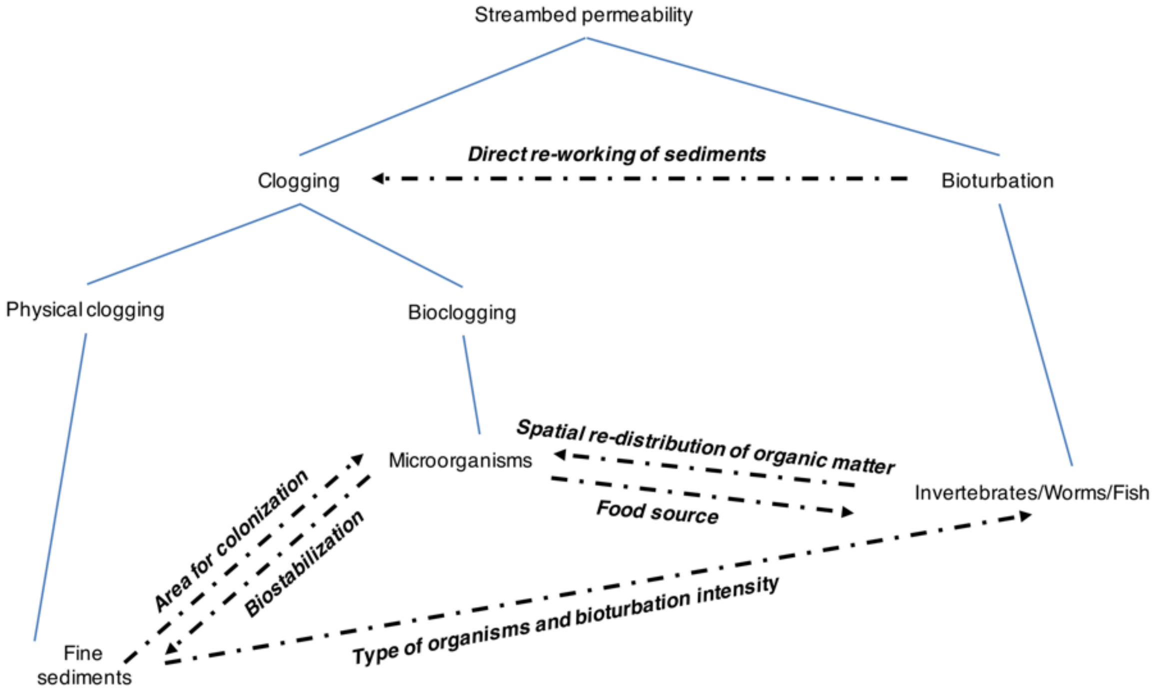


Figure 2.1: Interactions between bioturbation, fine sediment clogging and bioclogging that could potentially influence streambed permeability.

The composition of the bed (coarse or fine grains) influences both the growth of bacterial biomass and the extent to which the bioturbating organisms interact with their physical habitat. The grain size influences microbial communities in two ways- a) determines surface area of the substrate available for microorganisms to attach, and b) determines permeability of sediments and regulate supply of nutrients and organic matter to grow (Mendoza-Lera et al., 2017). Fine grains provide higher surface area for microbial biomass to adhere and grow in comparison to coarser grains, while the latter have higher permeability which allows rapid exchange of nutrients at SWI to promote microbial growth. It has also been demonstrated that fraction of fines in streambeds can modulate the type of bacterial communities (aerobic or anaerobic) colonizing sediments (Nogaro et al., 2010).

The activities of bioturbating organisms and the degree to which sediments are re-worked also partially depends on composition of sediment beds. For instance, restricted vertical movement of freshwater amphipods has been reported in heterogeneous sediment beds with high fraction of fine sediments (Mathers et al., 2019a). Further, excessively clogged sediment beds have been generally associated with reduced diversity and density of faunal organisms (Descloux et al., 2013; Wood and Armitage, 1997), which imply limited sediment-organism interactions. However, certain macroinvertebrates have been observed to thrive in fine sediment deposits and actively re-work top layer of beds to reduce clogging (Nogaro et al., 2006).

The potential of sediment re-working activities by bioturbating organisms to modify microbial communities has been also investigated. For instance, Mermillod-Blondin et al. (2004) showed that burrow building organisms alter the microbial characteristics of sediments to a greater degree compared to bioturbating organisms that mix the sediments. Similarly, Boeker et al. (2016) demonstrated variable influence of bioturbating organisms on structure & composition of microbial communities based on their functional behavior. The authors argued that bioturbating organisms which construct voluminous burrows and not consume oxygen within sediments provide conducive environment for growth and activities of aerobic microorganisms. In contrast, Richter et al. (2016) did not find strong evidences of feedbacks between bioturbation and diversity & abundance of microbial communities.

Further, invertebrates and microbial biomass form two basic and inter-dependent trophic levels in hyporheic food web (Marmonier et al., 2012). For instance, invertebrates feed on biofilms and modify the composition and structure of microbial communities. Barlocher and Murdoch (1989) presented early evidence of dependency of interstitial invertebrates on biofilms for food. This is supported by Franken et al. (2001) who showed that invertebrate abundance and diversity was positively correlated with biofilm growth in the sediment bed. Likewise, mixing & mobilization of bed-grains and bio-deposition (release of fecal pellets) by bioturbating organisms would result in spatial re-distribution of organic matter which can promote spatially heterogeneous biomass growth (Shen et al., 2017). In contrast, Storey and Dudley Williams (2004) observed a weak relationship between invertebrate density & richness and their dependency on microbial communities for food.

Clearly, the feedback mechanisms between the three environmental processes are complex and the understanding of their cumulative influence on inducing spatial and temporal dynamism in K is underdeveloped. The stabilization of aquatic sediments due to biofilms has been more extensively studied in marine environments compared to freshwater environments (Austen et al., 1999; Droppo et al., 2007; Sutherland et al., 1998; Underwood et al., 2004), and, moreover, only limited field evidences of biostabilization have been presented in literature (Droppo, 2009; Piqué et al., 2016). Further, the spatial and temporal heterogeneities in biofilm structure & composition due to its dependency on varying environmental factors make biostabilization process in fluvial settings more challenging to study (Schmidt et al., 2016; Thom et al., 2015). Furthermore, inconsistent findings between the studies focusing on understanding feedbacks between micro- and macro-organisms reflect need for more research to advance our understanding of their roles in inducing dynamism in K of streambeds.

2.3 Discussion

2.3.1 Evolutionary model of streambeds

Like other complex geomorphological settings such as stream channels (Simon, 1989; 1992), valleys (Schumm and Ethridge, 1994), deltas (Galloway, 1975) and floodplains (Aslan and Autin, 1999; Howard, 1996), streambeds and their K can be thought to evolve over relevant time-scales, particularly after a disturbance event (e.g. floods) with rates of evolution dependent on rates of the underpinning abiotic and biotic processes. Channel evolution models have been used to describe the morphological responses and predict the profile or dimensions of the channel after a disturbance (Schumm et al., 1984; Simon, 1989; Simon and Rinaldi, 2006). It would be valuable to develop such models for streambed evolution after streambed sediments are mobilized in a high flood event as they can facilitate better comparison of permeability and its variation among different reaches or streams. They could also aid stream restoration and management programs focussing on modifying structure and hydraulic properties of streambeds to improve ecological or biogeochemical status of stream sediments (Kasahara et al., 2009; Mendoza-Lera and Datry, 2017).

We anticipate that the three environmental processes and their mutual interactions would form a fundamental premise to streambed evolution model. However, given that each stream ecosystem is distinct in context of its physical, chemical and biological characteristcs, encompassing natural diversity and associated complex feedback mechanisms in a single model is truly challenging and goes beyond the scope of this manuscript. Nonetheless, as a way forward, we provide an example of one possible trajectory of streambed evolution post a storm event by incorporating abiotic and biotic responses and making necessary assumptions.

For simplicity, we assume that given sufficient time since a high flow event, a streambed possesses a fully developed state, where there are mutual feedbacks between its physical and biological components. The flood event is assumed to be aseasonal, but not catastrophic, and could be characterized by its magnitude, duration, frequency and shear force exerted at the bottom of the streambed (Fraterrigo and Rusak, 2008; Lake, 2000; Phillips and Van Dyke, 2016; Poff et al., 1997).

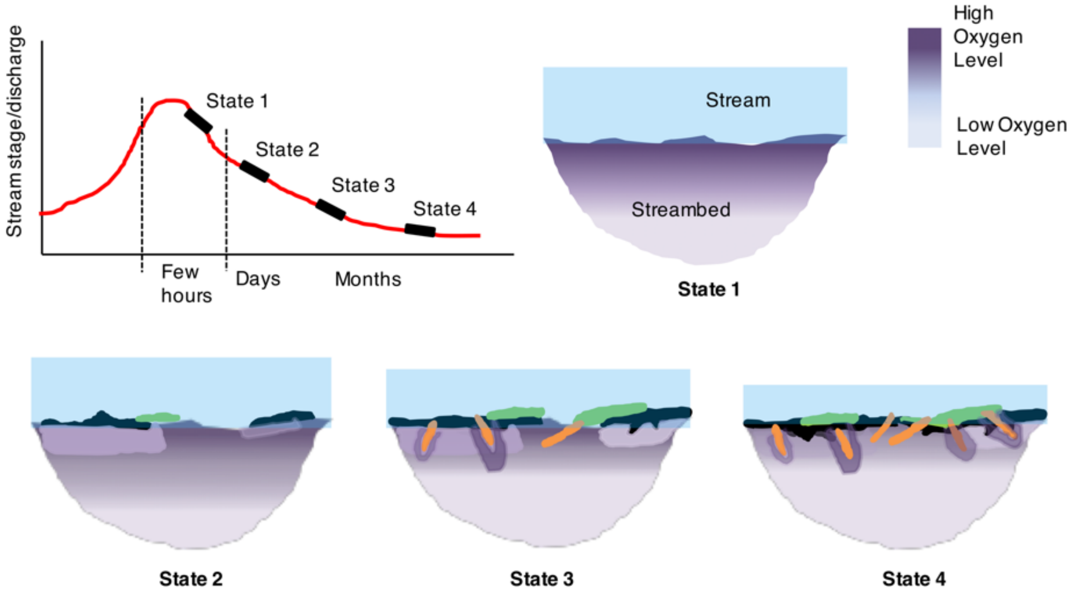


Figure 2.2: Temporal evolution of streambeds after a high flow event based on trajectory of response of fine sediment clogging, bioturbation and bioclogging processes in streams.

Further, flood hydrographs could possess different skewness and exhibit different flow recession behavior. However, we illustrate this example considering a hypothetical flood hydrograph (Figure 2.2). We also assume that no high flow event follows the above-described (assumed) flood event i.e., flow recession/dry period is long. Such a flood event is considered to scour the streambed (i.e., streambed comprises of soft sediments), re-suspend the settled sediments, and displace or kill the biological communities (both microbial and and macroorganisms). The size of hyporheic zone would also alter during such a flow event depending on the dynamics of surface water, local water table and ground water flow (Bhaskar et al., 2012; Dudley-Southern and Binley, 2015; Malzone et al., 2016). Following such an event, the sequential response of reviewed environmental processes, fine sediment clogging, biological clogging and bioturbation, is expected to produce different evolutionary phases of the streambed. We discuss this transition of streambed from one phase to other, including changes in the hydraulics and chemistry (oxygen levels for demonstration purpose) of hyporheic zones for each phase.

Immediate post-flood phase: Bed erosion would occur during the flow event leading to re-suspension of sediments and microbial films leaving the bed with diminished density & diversity of biological organisms. During such a high flow event, the dynamics between rapidly changing stream stage and local water table would result in temporary expansion or contraction in the size of hyporheic zone (Dudley-Southern and Binley, 2015; Zimmer and Lautz, 2014). Due to scouring of the top layer of sediments, it is likely that permeability of streambeds would increase, and subsequently the hyporheic flux and depth of penetration of water and solutes would increase. The enhanced exchange will bring more oxygenated water into the hyporheic zone, thus, dissolved oxygen levels in upper layer of streambeds would be higher (Figure 2.2). As the flood event recedes, settling and infiltration of fine particles would begin and potentially lead to formation of a clogging layer (Coleman, 1969; Simpson and Meixner, 2012). In addition to factors mentioned in section 2.2.1, the motion of the bed would influence the structure and sorting of sediments (Bacchi et al., 2014; Dudill et al., 2017). For instance, it is likely that the deposition of fine sediments would occur to a limited depth if the coarse bed grains are immobile. Compositionally, fine sediments would form the top layer of streambed in such case. When the coarse bed grains are in motion, entrainment of fine sediments would occur. This would cause coarse grains to surface up and fine sediments to percolate deeper in the streambed. There could be some marginal microbial activities occuring in streams at this stage but negligible growth & abundance of microbial cultures and macroorganisms (Dodds et al., 2004). Due to high energy of water and mobilization of sediments, it is the physical processes (e.g. sediment transport, clogging) which would have early influence on physical structure and properties of streambeds.

Early recovery phase: The stream stage would decline and it is assumed that stream would be fed by groundwater resulting in contraction of the hyporheic zone. As the contribution from ground water and the level of local water table reduces in time, the size of hyporheic zone is expected to increase. Based on the amount of sediments mobilized during the flood event, the sediment accumulation in streambed continues to occur resulting in development of morphological features such as bed-forms. The deposition/infiltration of fine sediments would also cause variability in bed permeability which is expected to produce heterogenous physico-chemical characteristics of streambed (Salehin et al., 2004; Zimmer and Lautz, 2014). For instance, hyporheic exchange at clogged sites would reduce which could result in local areas of low oxygen concentration (Figure 2.2).

Biota would take some time to re-colonize streambeds after a distubance as exhibited in numerous studies of ecological succession (Dodds et al., 2004; Dodds et al., 1996; Fisher et al., 1982; Reisinger et al., 2017; Wallace, 1990). The time period may span from few days to months, and in general, microbial communities appear first in the streambeds followed by macroinvertebrates (Dodds et al., 2004). For instance, Fritz and Dodds (2004) demonstrated that for a 50 y flood, invertebrate richness and diversity returned to the pre-floods level in less than 3 months. Similarly, Fisher et al. (1982) reported that invertebrates re-appeared within few days and their numbers recovered the pre-flood state in ~60 days following a high flow event. In the same study, recovery of algal biomass was reported in less than 2 weeks. However, some studies have also demonstrated that in case of a catastrophic flow event, ecological species took from several months to years to re-colonize (Milner et al., 2013; Woodward et al., 2015).

Late recovery phase: The groundwater flow into stream is assumed to recede, and consequently the size of hyporheic zone is expected to increase. With a large proportion of flood-mobilized fine sediments being deposited or infiltrated and substantial growth of biological communities & colonization by macroorganisms, the interactions between these abiotic and biotic compartments continue to grow as the streambed progresses towards a late recovery. The physical structure and hydraulic properties of the streambed would exhibit spatial and temporal variations based on the degree of interaction between these processes, and subsequently influence the pore water chemistry in hyporheic zone. For instance, macroinvertebrate bioturbation could increase permeability in some patches of upper layer of streambeds which could potentially increase the hyporheic flux across SWI and bring more oxygenated stream water in those patches (Figure 2.2).

Quasi-equilibirium phase: It is a fully developed phase where the interactions between physical and biological processes in streambed are well-established (pre-storm state) and the physical properties of streambed sediments including K reach a quasi equilibirium state (Stewardson et al., 2016). The evolved streambed may not necessarily be physically or functionally similar to the pre-flood state. For instance, Wu et al. (2015a) showed that streambed composition differed between pre-flood (mostly sand and gravel) and post-flood conditions (sandy bed with silt and clay). Similarly, the native species may wash off or experience drift during the flood, and a different specie could colonize the bed after the flood event (Arango et al., 2015). The dominant non-native species could be functionally different to the previous macroorganisms, possessing different bioturbation modes, and may influence the physical structure of streambeds differently.

The example presented above is a simplified representation of various phases through which a streambed evolves after a flood disturbance. The assumptions related to surface and ground water dynamics during and after the flood event overlook various other possible hydrological responses of a catchment. Further, the example is limited to just one kind of stream type and flood magnitude. The trajectory of response of stream communities could differ among streams based on extremity of the flood event, its timing (seasonal or aseasonal), stream type (intermittent, perennial), streambed composition, pre-flood dwelling communities, life history of organisms and availability of refugium (Dole-Olivier et al., 1997; Lytle, 2002; McEwan and Joy, 2013; Palmer et al., 1992). For instance, following a mild storm event, the biotic processes may influence phases of evolution to a greater degree than abiotic processes. The re-suspension and transport of fine sediments may get restricted due to biostabilization. The microbial life and macroinvertebrates may quickly recover to the pre-storm state or remain unaffected. This example can be considered as one of the many possible scenarios that could occur in streams after being disturbed due to a flood event. Several other scenarios can be formulated by incorporating various responses of local surface-ground water hydrology and ecology in a stream ecosystem. We suggest that such different scenarios corresponding to different stream ecosystems must be taken into account to develop a robust and widely applicable streambed evolution model.

2.3.2 Future research directions

This review focuses on the interacting biotic and abiotic processes that control streambed permeability. We focus on permeability because of its dominance in regulating many hyporheic processes through its strong influence on the transport of mass and energy within the hyporheic zone and exchange with overlying water. Whilst permeability is an important characteristic of streambed sediments, we recognise this is a part of the broader challenge of understanding the close interactions between abiotic and biotic processes in streambeds. For example, the study of nitrogen transformations in streams must consider the same interacting abiotic and biotic processes because they regulate the supply of nitrogen and reaction rates within streambeds.

As a result of the coupled nature of these processes and other complexities associated with natural environment, controlled laboratory experiments are ideal to advance the fundamental understanding of these in-stream processes. Recall that small-scale studies focussing on impact of fine sediment dynamics on influencing K of streambeds are immense, but there is limited exploration of this effect by bioclogging and bioturbation processes. For instance, the previous research on studying bioturbation in fresh water sediments has been largely carried out in vertical columns with standing water which do not mimic actual stream environment (running water). Although these experiments have provided valuable insights on potential role of sediment mixing and burrowing activities in modifying bed permeability, the results cannot be extended to lotic ecosystems. Similarly, the experimental research related to bioclogging has been also largely limited to 1-D column experiments which ignore the complex hydrodynamics associated with streamflow over sediment beds. Therefore, the future experiments studying role of bioturbation and bioclogging in influencing structure and hydraulic properties of streambeds should be conducted in running waters. A potential approach is to perform experimentation in long hydraulic flumes which adequately represent the stream flow environment. The controlled laboratory conditions facilitate examining the influence of these individual processes and help in tracking response of biological organisms to a wide range of environmental conditions such as altered availability of nutrients or presence of predators. In addition to developing thorough understanding of individual processes on streambeds, future research should seek to determine their combined influence on permeability of streambeds and associated ecosystem functions.

Given that the streambed permeability is dependent on the nested response of these complex environmental processes, developing predictive methodologies to understand role of individual processes and their interactions in governing permeability of streambeds is crucial. The applicability of models of bioturbation and bioclogging developed to study modification in bed permeability must be tested in stream environments. Further, with increasing understanding of biotic processes, more realistic models of fate and transport of fine sediments in fluvial networks must be developed considering grains as biological sediments (Fang et al., 2017; Vignaga et al., 2013). More robust and widely applicable models to study interactions between these processes could be formulated with a better conceptual framework. In this regard, the proposition of developing a streambed evolution model based on responses of physical and biological components of stream ecosystems after a disturbance must be advanced further by incorporating more complexities which were simplified for illustration purpose in this manuscript.

It is critical to understand the spatio-temporal heterogeneity in K and incorporate it in theoretical and modelling approaches focussing on investigating exchange of mass and energy between surface and sub-surface water. The traditional representation of streambeds in most of the modelling studies is a homogenous porous media and non-transient, meaning that the permeability or K of streambeds are considered constant in space and time (Boano et al., 2006; Gooseff et al., 2006b; Hester and Doyle, 2006; Packman and Bencala, 2000; Partington et al., 2017). Modelling studies generally adopt K based on published values in literature derived from well-sorted sediments (Hester and Doyle, 2006; Ward et al., 2011) or estimate hydraulic properties using some empirical equations based on grain size distributions (Kiel and Cardenas, 2014). It is important to note that some numerical modelling studies have accounted for spatially variable K by incorporating heterogeneous K fields (Cardenas et al., 2004; Kasahara and Wondzell, 2003), but temporal variations have been rarely considered. The exchange models based on the assumption of homogenous and isotropic sediment beds could fail to mimic exchange across natural streambeds where localized areas of higher or lower permeability could exist (Elliott and Brooks, 1997; Tonina and Buffington, 2007), potentially due to range of physical and biological processes occurring simultaneously in streams. A better prediction of exchange at natural sites is directly related to our likelihood of estimating streambed permeability, which in turn, depends on accuracy and robustness of models of bioturbation, bioclogging and fate & transport of suspended sediments.

There are limited number of studies that have investigated role of bioturbation and bioclogging processes in modifying streambed K at larger scale. Moreover, the existing field investigations have studied these processes in isolation and with discipline driven focus. We suggest that the future field studies must adopt a holistic approach with inputs from various disciplines such as hydrology, ecology, hydrogeology, sedimentology and chemistry. The interdisciplinary endeavors will lead the community of stream scientists to delineate relative importance of each of the process and develop comprehensive explanations for the observed spatio-temporal variability in streambed permeability. These field studies will not only aid in validating the results from various predictive methodologies but also encourage and assist the scientists to set up experiments with close-to-natural settings.

2.4 Conclusion

The permeability and closely associated hydraulic conductivity are critical hydraulic properties of streambeds exerting a strong control on several important stream ecosystem services. These hydraulic properties have been reported to vary over a wide range in both space and time, but a comprehensive and process-based understanding of this variability is lacking. In this review, we underline clogging due to fine sediments, and relatively less explored, bioclogging by microbial growth and bioturbation by in-stream faunal organisms as potential processes that induce spatio-temporal heterogeneity in permeability of streambeds. This review also emphasizes that feedback mechanisms between the three environmental processes must be comprehensively understood as they co-exist in stream environments and collectively influence the physical structure and hydraulic properties of streambeds. We propose that streambeds must be considered as complex systems and highlight the need for developing a conceptual model for evolution of streambed and its K. Finally, a possible scenario of transition of streambed through different phases based on trajectory of responses of these environmental processes after a high flood event (disturbance) is presented.

Chapter 3

Influence of bioturbation on hyporheic exchange in lotic environments

This Chapter is intended to be submitted as a manuscript with full title as: **'Influence of bioturbation on hyporheic exchange in streams: Insights from laboratory experiments in lotic environments'**. I am the primary author of this manuscript (80% contribution), and my supervisors, Prof. Michael Stewardson and Dr. Meenakshi Arora are the co-authors.

Abstract

Bioturbation occurs in streambed by the action of a range of faunal species, but its consequences for hydraulic properties of streambeds and subsequently for hyporheic exchange in streams has not been investigated comprehensively. In this work, we first propose a conceptual model identifying various causal pathways through which macroinvertebrate bioturbation can potentially influence hyporheic exchange. The arguments presented in the model are then tested by studying modification of dune-induced hyporheic flow in re-circulating flumes due to activities of a model bioturbating organism, *Lumbriculus variegatus*, following a control (without organisms) and treatment (with organisms) based experimental design. The results suggest that feeding, egestion, digging and burrowing activities alter the bed permeability and its morphology, which in turn, modifies the hyporheic exchange across SWI. All three treatment flumes exhibit higher mean and median residence times compared to the control flume. The penetration depth and hyporheic flux in treatment flumes were observed to be both higher and lower relative to the control flume based on the experimental conditions. These experiments also provide useful insights on influence of re-working time and size of bioturbating organisms on hyporheic exchange. We advocate that more intensive laboratory experiments and field investigations must be conducted to validate the conceptual model and advance our understanding of role of bioturbation in fluvial ecosystems.

3.1 Introduction

The hyporheic zone is a unique ecotone located between the surface and sub-surface regions of a stream ecosystem (Boulton et al., 2010; Stanford and Ward, 1993). The water and solutes (e.g. nutrients or contaminants) are driven into the hyporheic zone where they travel in porous media and may mix with ground water before emerging back into the stream. This results in exchange of mass and energy across the sediment-water interface (SWI), a process known as hyporheic exchange (Boulton et al., 1998; Findlay, 1995). It 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/contaminants (Gandy et al., 2007; Peralta-Maraver et al., 2018), which influences the overall quality of both the surface and pore water.

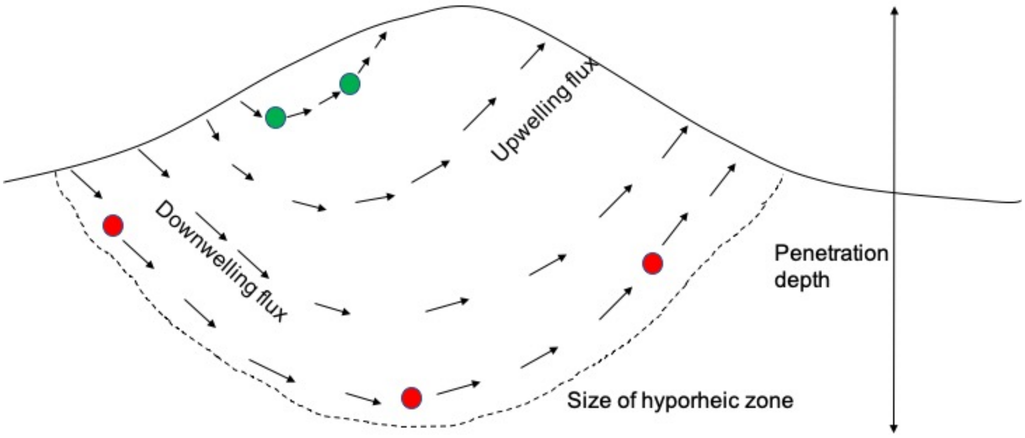


Figure 3.1: Schematic representation of downwelling and upwelling flow with water/solutes exchange occurring through a series of sample flow paths (arrows). The green circles denote molecules travelling along shorter flow paths (short residence times) while red circles denote molecules getting transported along longer flow paths (longer residence times).

The critical features of hyporheic flow influencing stream biogeochemistry and ecology are the hyporheic flux, hydraulic residence times and penetration depth of solutes in the hyporheic zones (Figure 3.1) (Findlay, 1995; Gomez et al., 2012; Jones Jr et al., 1995). The hyporheic flux is the rate at which water or solutes are transported across the SWI and represents the amount of solute entering/exiting the hyporheic zone. The residence time can be understood as a time 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 hyporheic zone in the sub-surface sediments, and determines the spatial extent to which surface water could mix with pore water in hyporheic interstices.

These characteristics of hyporheic flow, particularly at small scales, are influenced by streambed permeability (or closely associated hydraulic conductivity) and its heterogeneity (Bardini et al., 2012; Boano et al., 2014; Packman and Salehin, 2003; Sawyer and Cardenas, 2009). Permeability is defined as the ability of porous media to transmit water through it (Freeze and Cherry, 1979). In general, beds comprising of highly permeable sediments (e.g. gravel) exhibit larger hyporheic flux, shorter residence times and greater depths of solute penetration than beds comprising of low permeability sediments (silt or clay). Natural streambed generally comprises of range of grain sizes and its hydraulic properties vary both spatially and temporally. For instance, reach-average hydraulic conductivity values (based on averaging point measures) vary over three orders of magnitude (Chen, 2011; Cheng et al., 2011; Genereux et al., 2008; Min et al., 2013; Taylor et al., 2013) and point measures vary over eight orders (Calver, 2001). This heterogeneity has direct implications on hyporheic flux, residence times, penetration depths and geometry of flow paths (Cardenas et al., 2004; Gomez-Velez et al., 2014; Pryshlak et al., 2015; Salehin et al., 2004; Tonina et al., 2016; Zhou et al., 2014). For example, Tonina et al. (2016) demonstrated an overall reduction in the volume of hyporheic zone and the mean hyporheic flow in heterogeneous sediments. They also showed that due to compression of hyporheic zone in heterogeneous media, the residence time for longer hyporheic flow paths decreased while residence time for shorter hyporheic flow paths increased due to an increased tortuosity.

One of the potential processes that could cause heterogeneity in sediment permeability is bioturbation by streambed inhabitants such as macroinvertebrates (Blaschke et al., 2003; Marmonier et al., 2012). These organisms continuously mix the sediments and modify the bed structure by performing activities such as food foraging, egestion of faecal pellets, digging and burrowing (Kristensen et al., 2012; Solan and Herringshaw, 2008). The modification of bed permeability due to bioturbation has been reported in studies related to marine sediments (Meadows and Tait, 1989; Murray et al., 2002), but there is a limited understanding of this process in stream environment (Song et al., 2010; Song et al., 2016). The research related to bioturbation in freshwater sediments has been largely laboratory-based, with experiments mostly conducted in infiltration columns i.e., in standing water (Mermillod-Blondin et al., 2001; Mermillod-Blondin et al., 2003; Nogaro et al., 2006). Although these studies indicate that bioturbation modifies the hydraulic properties of bed sediments, they fail to represent the complex hydrodynamics due to flow of water over undulated streambeds, known to drive the exchange across SWI (Boano et al., 2014). Thus, the experimental research in standing water may not be transferrable to flowing water environments.

In this work, we first propose a conceptual model describing various causal pathways through which macroinvertebrate bioturbation can potentially affect small-scale hyporheic exchange in stream ecosystems. Next, we conduct experiments in re-circulating flumes to study impact of bioturbation on hyporheic flux, residence times and penetration depth induced by dune-shaped bedforms perform preliminary model testing. In these experiments, we also investigate how these exchange characteristics vary with sediment-organism contact time (or re-working time) and size of organisms.

3.2 Conceptual model

Fundamentally, small-scale hyporheic exchange is driven by pressure gradients over the bed surface and its permeability (Boano et al., 2014; Sawyer and Cardenas, 2009). The pressure gradients at the SWI are partially affected by the bed morphology i.e., shape and size of bedforms (Gooseff et al., 2006a; Marion et al., 2002), whereas, the size of grains and their sorting & packing are major controls on bed permeability (Chen et al., 2009; Zetsche et al., 2011). In the subsequent paragraphs, we discuss how macroinvertebrate bioturbation could potentially influence both these variables and alter the hyporheic flow across SWI (Figure 3.2).

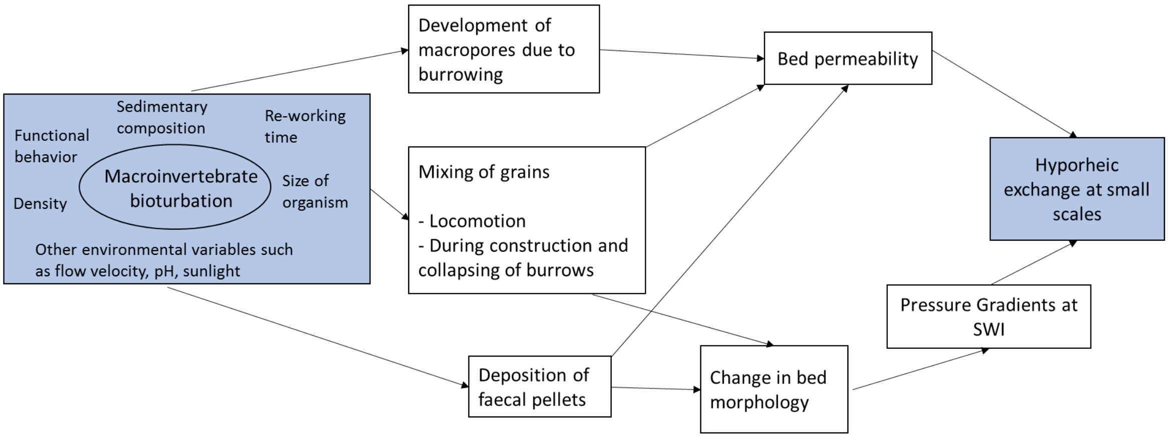


Figure 3.2: Conceptual model illustrating various pathways through which macroinvertebrate bioturbation influences dune-induced hyporheic exchange.

The activities of faunal organisms result in biogenic micro-topography, also termed as bioroughness, which has been shown to influence pressure gradients at the SWI (Huettel and Gust, 1992). Further, bioturbation by certain organisms has been associated with erosion of bed grains (Cooper et al., 2016; Statzner et al., 1996), which would eventually deposit at some other downstream location. This aggradation and degradation due to bioturbation could occur at a wide spatial scale ranging from a few centimeters to several meters and result in pressure variations over the bed surface.

Macroinvertebrate bioturbation has been observed to modify permeability in the upper layer of sediment beds due to mixing and re-mobilization of grains. For instance, vertically oriented head-up organisms (known as downward conveyors) feed on sediments at the surface and eject in the interstitial regions which could block the pores (Kristensen et al., 2012). Similarly, mosaics of macro-pores could develop in the bioturbated zone (upper layer) of the bed due to construction and destruction of burrows (Mermillod-Blondin et al., 2003). As the organisms could move to a limited depth in the bed, the permeability of the sediments in lower layer remains largely unaffected by their activities. This implies that bioturbation could generate a vertical permeability gradient resulting in spatially heterogeneous permeability fields. Further, in the bioturbated layer, anisotropic permeability fields could develop based on organism activities. For instance, if the burrows are oriented vertically, the permeability in vertical direction would be greater than in horizontal direction.

The degree to which sediment beds are re-worked is influenced by several variables such as size (Heilskov and Holmer, 2001; Thrush et al., 2006), density (Duport et al., 2006; Marinelli and Williams, 2003), bioturbation behaviour of the organisms (De Backer et al., 2011; Michaud et al., 2006), re-working time (Davis, 1993; Maire et al., 2008) and bed composition (Mermillod-Blondin and Rosenberg, 2006). The bed permeability has been shown to both increase and decrease based on burrowing behavior of the bioturbating organisms (Meadows and Tait, 1989). Navel et al. (2012) demonstrated modification of structure and hydraulic properties of fine- and coarse-grained beds to different extents due to macroinvertebrate bioturbation. 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. We anticipate that the locomotion and burrowing by bioturbating organisms could develop new pore spaces or enlarge existing pores if their size is larger than the pore size. In contrast, worms could use the existing pores to move without affecting the sediment structure if their size is much smaller than the pore size.

The sediment-organism interaction could be variable in space and time, which adds another layer of complexity to understand influence of this biotic process in stream ecosystems. Macroinvertebrates could be non-uniformly distributed along the bed such as in riffles and pools (McCulloch, 1986), and modification to these sections would occur to different extents causing spatially heterogeneous permeability fields. The colonization of a substrate would further depend on in-stream abiotic (e.g. flow velocity, water quality) and biotic variables (e.g. presence of predators) (Rader and Belish, 1999; Usio and Townsend, 2004; Verspoor et al., 2011). The activity of bioturbating organisms is also susceptible to temporal variations based on their life-cycle history, temperature and flow regimes (Bunn and Arthington, 2002; Meysman et al., 2010; Ouellette et al., 2004). For example, some aquatic inhabitants tend to actively re-work the sediments during night compared to day time (Loperfido et al., 2010; Rice et al., 2016). Similarly, seasonal variation in bioturbation activity including their population density has been also observed in previous studies (Giberson and Hall, 1988; Richardson et al., 2009). The heterogeneous modification to streambed physical structure and its hydraulic properties implies spatially and temporally variable influence on hyporheic exchange.

The modifications of a streambed's permeability and morphology due to bioturbation is expected to alter the system of nested flow paths through which hyporheic exchange across the SWI. In a dune-induced hyporheic flow, for instance, reduction in height of dune would decrease the pressure gradients over the bed surface and reduce hyporheic exchange (Ren et al., 2019). Similarly, presence of vertical burrows could direct the flow paths in the upper sediment layer to deeper regions in the bed and increase the average residence times of solutes in the bed. However, if the permeability in upper sediment layer is low due to fine sediment deposition in upper layer (clogged streambeds) then bioturbation activities could potentially increase the vertical connectivity, promote faster exchange and eventually reduce the average residence times. Flow paths in the bioturbated zone of sediment beds could also be re-directed due to obstruction by organisms. The overall penetration depth of solutes or extent of hyporheic exchange would also depend on the thickness of bioturbated sediments as evidenced from previous studied related to hyporheic exchange in layered or stratified beds (Gomez-Velez et al., 2014; Marion et al., 2008; Packman et al., 2006). For instance, Gomez-Velez et al. (2014)

showed that presence of low permeability layer in the underlying bed regions could compress the flow paths and limit penetration depth of solutes.

3.3 Experimental methods

To test the propositions presented in the above-described conceptual model, modification in dune-induced hyporheic flow due to macroinvertebrate activities was studied in re-circulating flumes. The experiments follow a control and treatment design. The control flume (A) was free of worms and represents the exchange characteristics of dune-induced hyporheic flow. The exchange characteristics determined for treatment flumes (B, C and D) demonstrate the effect of bioturbation on dune-induced hyporheic flow based on their experimental conditions (Table 3.1). Note that no duplications were performed for the control and treatment flumes.

3.3.1 Flume set up and bed material

All experiments were performed in 3m (L) x 0.2m (W) x 0.4m (D) Perspex recirculating flumes (Figure 3.3) in the Sexton Ecohydraulics Laboratory at The University of Melbourne. The experiments were performed with tap water and the flow rates were measured using a GPI-TM series flowmeter. The flow rate (~0.0016 m^3/sec) and slope (1:300, V:H) were adjusted to attain uniform flow with an average flow depth of 9 cm. The flow velocity was chosen such that no erosion of bed grains or worms was observed. These hydraulic variables were similar across all 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 dunes at the top. The dunes were formed manually to obtain a similar morphology across all flumes at the start of experiments (Figure 3.3). Additional tap water was added into the flumes to compensate for evaporative loss over time and maintain constant flow depth and water volume throughout the experimentation period.

3.3.2 Model bioturbating organisms

Lumbriculus variegatus (commonly known as California blackworms), were used as model organisms to study macroinvertebrate bioturbation. *L.variegatus* (hereafter referred as worms) are freshwater oligochaetes which prefer to dwell in shallow sub-surface regions of lakes or marshes feeding on organic material and microorganisms (Brinkhurst and Gelder, 1991), and have been extensively used in several toxicological studies related to freshwater sediments (Blankson and Klerks, 2016; Leppänen and Kukkonen, 1998). A typical behaviour of these worms 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).

Average depth of sand bed: 30 cm
Height of bedforms: 3 cm
Wavelength of bedforms: 24 cm
Flow velocity: 8.5-8.8 cm/sec
Average flow depth: 9 cm

Figure 3.3: Flume set up with dune-shaped bedforms (left) and hydraulic conditions in all the experiments (right).

Two sizes of worms were used in this study; the small worms were cultured in our laboratory whereas, the big worms were obtained from a local farm. The worms available from the farm were both longer and thicker (almost double in diameter) as compared to the worms cultured in our laboratory (Figure 3.4). Visual comparison of the locomotion of large and small worms on the bed also indicates that the former were much larger than the pore sizes in comparison to the small worms (Figure 3.5).

Figure 3.4: Visual comparison between the size of worms used in the experiment. Small worms (on left) were cultured in the lab while the large worms (on right) were cultured in a farm.

The pumps in treatment flumes were temporarily switched off before introducing the worms. The worms were added into the flumes to achieve a density of ~8000-10000 individuals/m^2 as observed in natural environments (Cook, 1969; Mason, 1994). 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 worms were recovered from the flumes by manually digging the bed at the end of experiments (~85-90% 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.

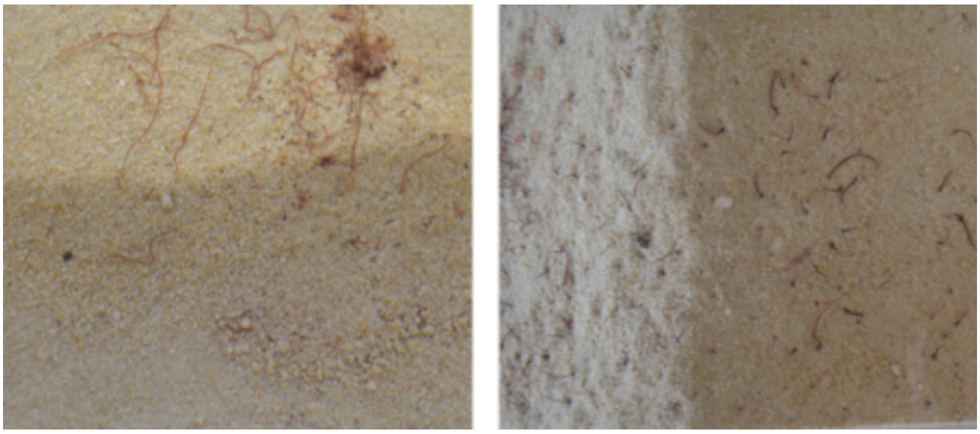


Figure 3.5: Top view in flumes C (left) and D (right) after 2 days of worms' introduction.

3.3.3 Tracer test to measure hyporheic exchange

Tracer injection into the water column and sediments has been extensively used to assess hyporheic exchange in recirculating flumes (Grant et al., 2012). In this study, hyporheic flux, residence times and penetration depths were investigated by injecting a fluorescent dye tracer (rhodamine WT) into the water column. The dye was added slowly over one re-circulation cycle of water (~90 sec) to ensure rapid & homogenous dye mixing, and its concentration in water column was monitored using Turner Designs Cyclops 7 sensors. The dye concentration decreased over time due to exchange with the pore water until an equilibrium is reached leading to uniform dye concentrations in the water column and hyporheic zone. It took ~10 days after dye injection to reach this equilibrium condition in the flumes and the experiments were ceased at this stage. Temperature correction was applied to the observed dye concentration in the water column as fluorescence intensity of the dye tracers varies with temperature (Blaen et al., 2017). The conservative behaviour of tracer grade rhodamine WT used in the experiments was confirmed by investigating its isomeric composition (Vasudevan et al., 2001) through Nuclear magnetic resonance spectroscopy (NMR) and conducting batch experiments (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.

3.3.3.1 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 and was estimated from the slope of the breakthrough curves (rate of decline of dye concentration in the water column) at the beginning of the experiment (t close to 0).

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 still remain in bed at a time t = τ.

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

$$m(t) = \bar{q} \int_{\tau=0}^{t} C^*(t-\tau)\bar{R}(\tau)d\tau \ldots\ldots\ldots\ldots\ldots\ldots \textit{(Equation 3.1)}$$

$$C^*(t) = 1 - \frac{m(t)}{d\prime} \ldots\ldots\ldots\ldots\ldots\ldots\ldots \textit{(Equation 3.2)}$$

where,

$C^*(t)$ is the normalized dye concentration obtained by dividing observed dye concentration at any time *t* (temperature corrected in our experiments), ($C(t)$, 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 depth of penetration of solutes into the bed, and d' (m) is the ratio of total volume of water in flume system (excluding the pore water) (V_{sw}, m^3) and the plan area of the bed (A, m^2).

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

$$d'(1 - C^*(t)) = q\ [\bar{R} * C^*] \ldots\ldots\ldots\ldots\ldots\ldots \textit{(Equation 3.3)}$$

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

$$\mathcal{L}\{[\bar{R} * C^*]\} = \frac{d'}{q}\mathcal{L}\{1\text{-}\ C^*(t)\} \ldots\ldots\ldots\ldots\ldots\ldots\ldots \textit{(Equation 3.4)}$$

$$\mathcal{L}\{\bar{R}\}.\mathcal{L}\{C^*(t)\} = \frac{d'}{q}\mathcal{L}\{1\text{-}\ C^*(t)\} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \textit{(Equation 3.5)}$$

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

$$= \mathcal{L}^{-1}\,\frac{\frac{d'}{q}\,\mathcal{L}\{1 - C^*(t)\}}{\mathcal{L}\{C^*(t)\}} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{(Equation 3.6)}$$

An exponential equation is fitted to the $C^*(t)$ using the principles of least square method to obtain the mathematical functions for the observed dye concentrations. The median (RT_{med}) and mean (RT_{mean}) residence times were obtained from the average residence time distribution function.

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^3) which mixes with the surface water was obtained (Equation 7). In general, the mixing between surface and pore water due to 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 defined such that if the dye were to homogenously 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 ratio of V_p to A.

$$V_p = V_{sw} \times \left(\frac{1}{C_{eq}^*} - 1\right) \ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{(Equation 3.7)}$$

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}.

3.4 Results

3.4.1 Bioturbation activity

For all the treatments, the activities of worms began soon after their introduction into the flumes and considerable digging was observed within a few hours (Figure 3.6b). Deposition of faecal pellets in form of coarse grains was observed at the dune troughs for all the treatment flumes (Figure 3.7 and Figure 3.5). The worms travelled 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 in all the treatment flumes. Reduction in height of some of the dunes which were densely colonized by worms was observed in flumes C and D (Figure 3.6d).

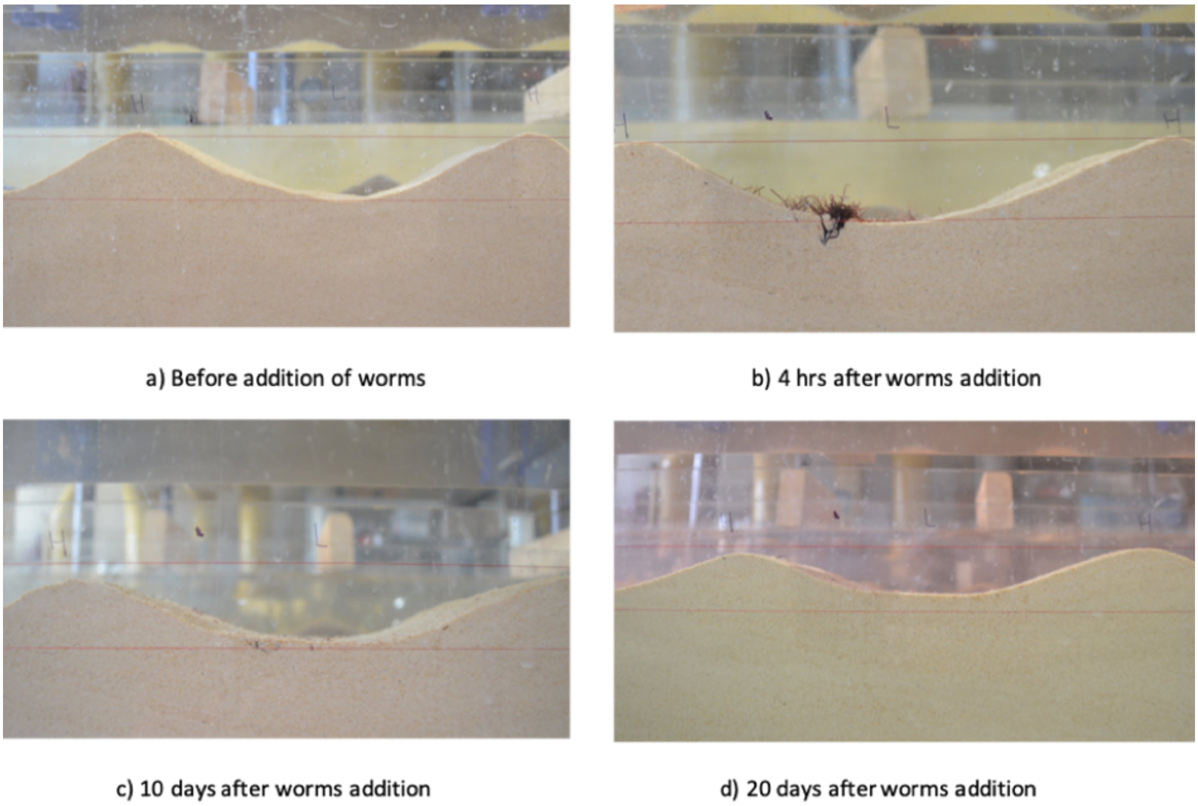
Table 3.1: Experimental details and hyporheic exchange characteristics in all the experimental flumes.

Flume	Details	Bioturbation time before dye addition	RT_{med} / RT_{mean} (min)	$\bar{d}$ (m)	q/q' x10^{-5} (m/min)
A	No worms (control)	0	1138/3756	0.044	1.32/1.17
B	Small worms	5	2962/5919	0.032	0.66/0.54
C	Small worms	10	4172/7120	0.062	0.96/0.87
D	Large worms	10	1842/4936	0.060	1.36/1.2

3.4.2 Exchange characteristics

In comparison to the control flume, the estimated $\bar{d}$ was smaller in flume B and greater in flumes C & D (Table 3.1). The $\bar{d}$ values were similar in flumes C and D. Note that the $\bar{d}$

observed in flumes A and B is ~height of dunes (3 cm). The $\bar{d}$ in flumes C and D was nearly twice the height of dunes.


a) Before addition of worms

b) 4 hrs after worms addition

c) 10 days after worms addition

d) 20 days after worms addition

Figure 3.6: State of sand bed in flume D at various stages of the experiments.

The effect of bioturbation on residence times of the dye is illustrated by the average residence time function, $\bar{R}$ (Figure 3.9). All the treatment flumes exhibited longer RT_{med} and RT_{mean} than the control flume (Table 3.1). Amongst the treatments, the RT_{med} and RT_{mean} were longest in flume C and shortest in flume D.

Figure 3.7: Faecal pellets deposited by the worms on top of the sand bed in flume D. Faecal pellets were observed largely in trough of the dunes.

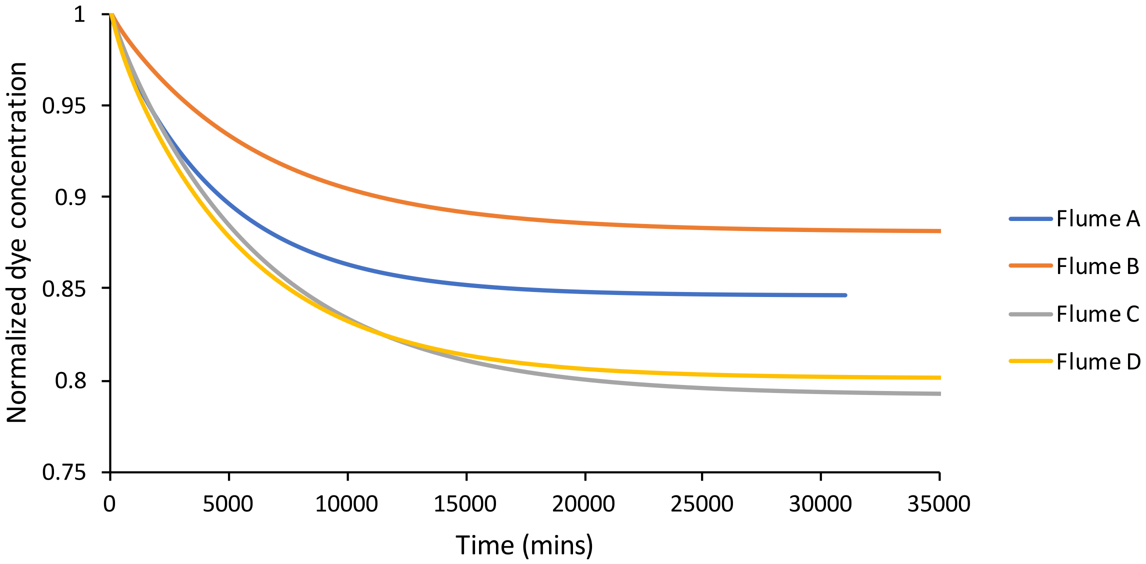


Figure 3.8: Breakthrough curves derived from fitting the time-series of normalized dye concentration in water column for control (flume A) and treatment flumes (flumes B, C and D). The root mean square error (RMSE) values for all the fits are less than 0.006.

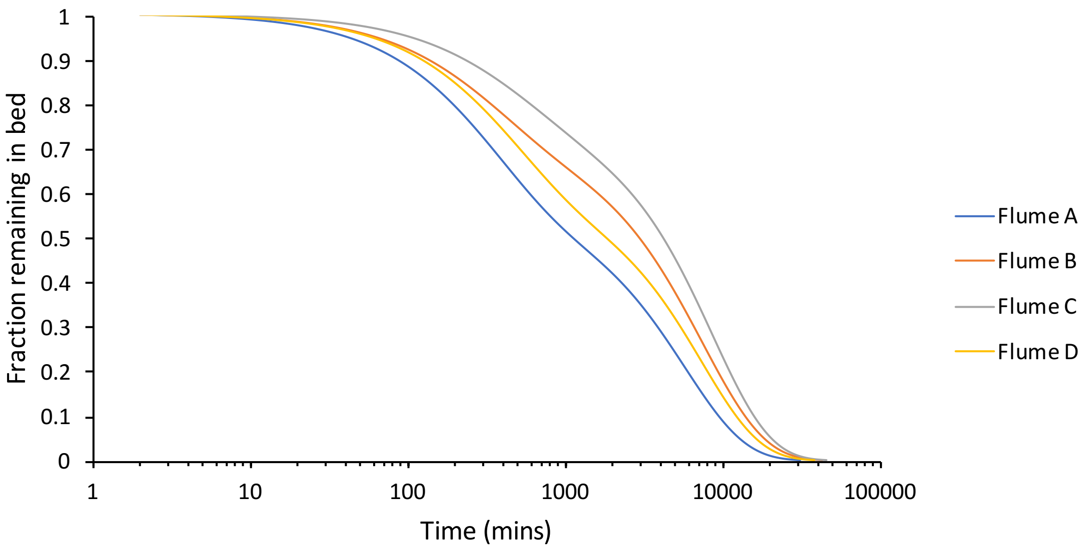


Figure 3.9: Flux-weighted cumulative residence time distribution for the dye tracer in all the experimental flumes.

In comparison to the control flume, the *q* (estimated from breakthrough curves presented in Figure 3.8) in flume D was slightly higher but lower in flumes B and C. The estimates of *q'* for control and treatment flumes exhibited similar trend as *q*. The *q'* values were within 80% of the *q*, but consistently lower than the latter (Figure 3.10).

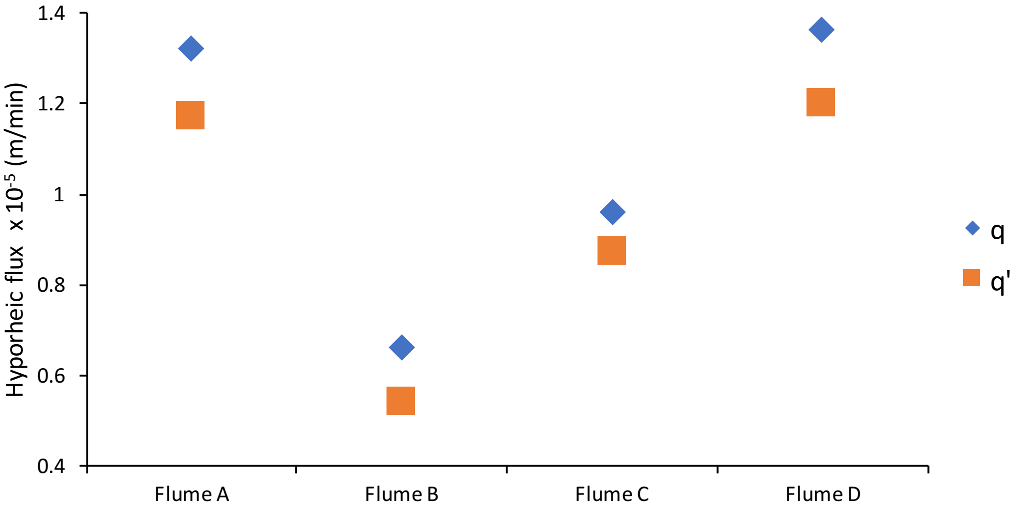


Figure 3.10: Plot of average hyporheic flux estimated from the initial gradient of the breakthrough curve (q), and calculated from the equivalent dye penetration depth and mean residence times (q').

Compared to the control flume, there was a reduced hyporheic flux (proportion of q) in short residence time range (<404 minutes) for all the treatment flumes (Figure 3.11). The hyporheic flux in this residence time range was maximum in flume D amongst the treatment flumes. Further, flume D exhibited greater hyporheic flux in the intermediate residence time range (404-8103 minutes) than both the control and other two treatment flumes. At longer residence time range (>8103 minutes), the hyporheic flux was similar in flumes C and D, and greater than in flume B. These ranges are chosen based on the mean and median residence times observed in the experimental flumes (the numbers are derived from powers of natural exponential function, e^n , where n = 0,1,2,3…).

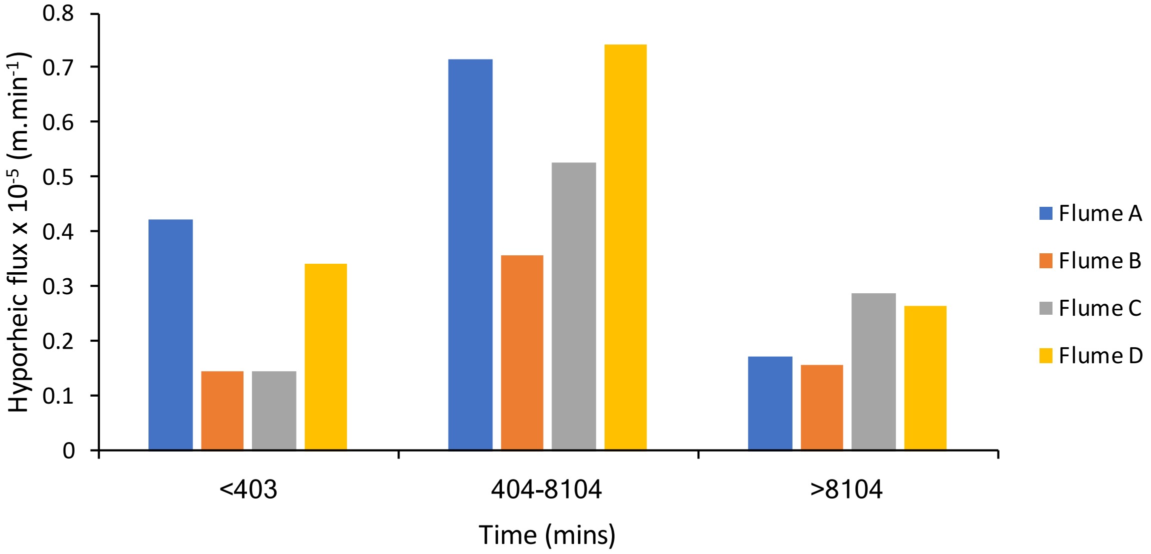


Figure 3.11: Hyporheic residence time distribution shown as flux for short, intermediate and long residence time ranges.

3.5 Discussions

3.5.1 Modification of hyporheic exchange

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 flumes produced due to hydraulic gradient down the flumes (Cardenas and Wilson, 2007a; Qian et al., 2008). If the underflow is fast, it may compress the hyporheic flow field and limit the vertical depth of exchange in the sediment bed (Cardenas and Wilson, 2007b).

For given physical and hydraulic variables (flow velocity, height of dunes, bed permeability), the dye was exchanged with the bed in the control through a series of short, intermediate and long flow paths (Figure 3.12A). The worms re-worked the beds in treatment flumes which is expected to alter the hyporheic flow field. Additionally, a primary result of this study is evidence of complex effects of bioturbation with dependencies on time of sediment re-working and size of bioturbating organisms on hyporheic exchange. These effects are large with mean residence times, equivalent dye penetration depths and average hyporheic flux (q') varying between 4936-7120 minutes, 0.032-0.062 m and 0.54-1.22 x 10-5 m.min^{-1} respectively in different treatment flumes. The potential causes of these modifications in light of the conceptual model (section 3.2) is presented in this section, however, further experimental research is needed to test these explanations and understand the complex influences of bioturbators on hyporheic flow.

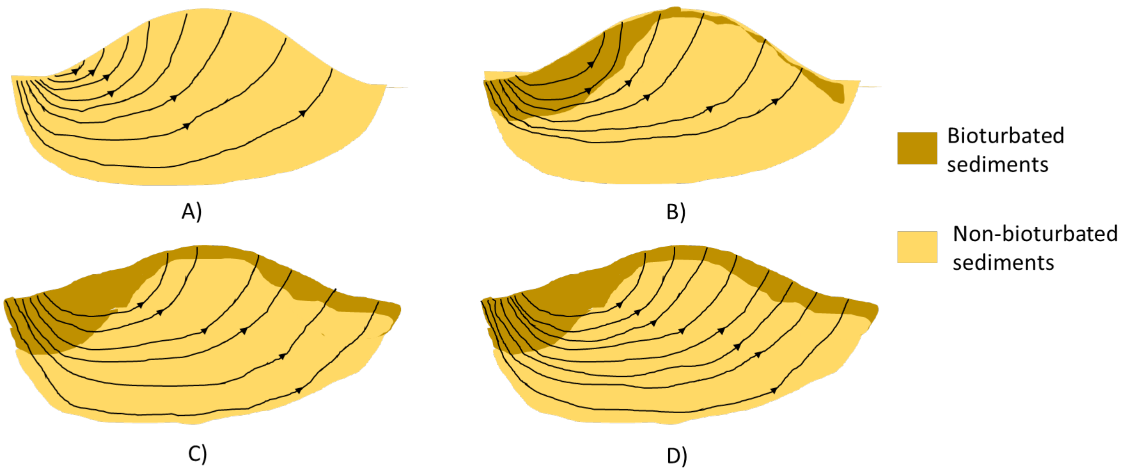


Figure 3.12: Proposed modification to hyporheic flow paths in treatment flumes (B,C and D) compared to the control flume (A).

The worm activities could induce both heterogeneity and anisotropy in the bed permeability and modify hyporheic flow paths. The sample bioturbators, Lumbriculus variegatus, dug burrows in vertical direction and could have potentially directed shorter flow paths in the upper layer (bioturbated sediments) deeper into the bed. This would decrease the proportion of flux exhibiting shorter residence times and eventually increase the RT_{med} & RT_{mean} in treatment flumes compared to the control flume. The permeability in the upper sediment layer is expected to be higher than the lower layer (undisturbed sediments) due to digging, burrowing and deposition of coarse faecal pellets at the interface. The sub-surface flow field developed in the model bed due to this permeability gradient in the vertical direction can be considered similar to flow fields that develops in stratified beds. Layered beds in which upper sediment layer possesses greater permeability, the flow paths extending to deeper regions tend to compress and limit the extent of exchange across SWI (Figure 3.12B). This is a likely explanation for lower $\bar{d}$ in flume B than the control flume. The hyporheic flux is related to both residence times and dye penetration depth, thus the higher RT_{mean} and lower $\bar{d}$ together resulted in lower q' in flume B than the control flume.

Flume C was bioturbated for double the number of days than flume B, and therefore, both the thickness of the bioturbated sediments and the permeability in vertical direction is expected to be higher in former than in latter. This could have directed the flow paths in upper sediment layer in flume C deeper compared to flume B (Figure 3.12C). Moreover, with a greater depth of re-worked sediments, the interface between the two sediment layers is pushed deeper into the bed potentially leading to extension of flow paths. This could have caused longer RT_{med} & RT_{mean} and greater $\bar{d}$ in flume C compared to both flume B and control flume. Although the $\bar{d}$ was greater in flume C than control flume, much longer RT_{mean} resulted in lower q' in former. In addition, longer bioturbation time in flume C caused alteration in morphology of some dunes (reduction in their height). As the amplitude of dunes reduces, the pressure gradients over their surface are expected to decrease, which in turn reduces the advective pore water velocity and lowers hyporheic exchange.

The length and width of worms in flume D was greater than worms in flume C. Although the burrows built by worms are not characterized in our experiments, we anticipate them to be both thicker and longer in flume D than in flume C. This is supported by the visual observations from the two flumes as the holes dug by worms in flume D were readily visible compared to flume C (Figure 3.5). It also indicates that the size of worms in flume D was much larger than the pore sizes in the bed. Due to presence of dense-network of macro-pores and voluminous burrows, the water and solutes could get pumped across the bed at faster rate and resulted in lower RT_{med} & RT_{mean} in flume D than flume C. The thickness of bioturbated sediments could be considered similar for both the flumes (Figure 3.12D) as the sediment-worm contact time and the depth traversed by worms were similar. This could have potentially resulted in similar $\bar{d}$ values for both the flumes. The higher q' in flume D than both flume C and the control flume could be attributed to rapid dye exchange occurring over a greater depth in the bed.

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 creation of burrows and deposition of faecal pellets increased the porosity of sediments which in turn increased the height of sediment layer in the columns and subsequently resulted in longer residence times. Our study further advances the understanding of influence of bioturbation in fluvial ecosystems by accounting for hydrodynamics associated with flow of surface water over topographical features (e.g. bed-forms). We observed similar modes of disturbances to physical structure of experimental beds by model bioturbators which potentially modified the flow field in hyporheic zones and caused alteration in residence times, penetration depths and hyporheic flux.

The observation of worms being concentrated near troughs towards the stoss side of the dunes in treatment flumes (although introduced uniformly along the flume length) provides evidence of spatially heterogeneous distribution of worms. These regions correspond to downwelling zones for dune-induced hyporheic flow and are generally well-oxygenated due to regular supply of oxygen from the overlying water. This could be a possible explanation for dense population of worms in these regions. The preference of spatial alignment of worms suggests that their activities were concentrated near troughs and the crests were only minimally disturbed. Although the influence of this site-selective sediment re-working on modification of hyporheic flow was not investigated in this study, it is anticipated that bioturbation could affect the flow paths in downwelling and upwelling regions to different extents.

3.5.2 Implication of results

A large variation in sediment permeability and closely-related hydraulic conductivity has been observed in the literature (Calver, 2001). Blaschke et al. (2003) and Stewardson et al. (2016) identified bioturbation as one of the potential processes that could influence sediment permeability. The conceptual model presented in this paper and the results from experiments in re-circulatory flumes support this argument and provide evidence of spatio-temporal modification of bed permeability due to bioturbation process. It has implications on modelling strategies of surface and sub-surface exchange that assume homogenous and non-transient bed properties (Boano et al., 2006; Hester and Doyle, 2006). This simple representation of streambeds would cause uncertainties in estimating exchange characteristics, particularly at sites with high faunal densities. Furthermore, bioturbation in streams is crucial to predicting sediment transport in streams. For instance, Hassan et al. (2011) reported significant bed load transport as a result of salmon bioturbation (mass spawning). Similarly, release of fine sediments from the streambeds could occur due to bioturbation of small invertebrates and aquatic insects (Wilkes et al., 2019). Thus, the models of hyporheic exchange and traditional sediment transport theories must integrate the influence of bioturbation to develop robust predictive methodologies for fluvial processes.

The potential of macroinvertebrate bioturbation to modify exchange characteristics across SWI has direct relevance to the biogeochemistry in hyporheic zones, and thus on the overall quality of surface and sub-surface water. For instance, findings from this study suggest that hyporheic flux could both increase or decrease due to the activities of worms, and the hyporheic flux has been demonstrated to be a dominant control on concentration of dissolved oxygen and several other biochemical activities in hyporheic zones (Reeder et al., 2018). Similarly, alteration in residence times will influence the contact time of solutes with the biochemically active hyporheic sediments. In addition to influencing streambed chemistry by re-configuring 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). Although we do not focus on the concept of ecosystem engineering in this manuscript, it is worth noting that bioturbation by model organism could have altered the community of microorganisms by redistributing organic matter by ejecting faecal pellets. Similarly, oxygen and other solutes could get transported to anoxic zones in deeper sediments through the worm burrows which may support aerobic organisms. The change in community structure of microorganisms would eventually cause variability in cycling and attenuation of nutrients or pollutants.

3.5.3 Limitations and future directions

The current literature of bioturbation in freshwater sediments consists of limited laboratory experiments conducted in lotic environments (Work et al., 2002). Our work, performed in re-circulating flumes, provide valuable insights on effect of macroinvertebrate activities on hyporheic exchange characteristics in stream environment. However, these experiments do not validate all propositions presented in the conceptual model, and do not represent full-range of complexities that exist in natural environment due to limited scope. The experiments were performed in a controlled set-up (simpler representation of fluvial environments) and were restricted to just one faunal specie exhibiting a specific bioturbation behaviour. In natural environments, wide-range of species co-exist and the degree of sediment re-working depends on several environmental variables such as presence of predators, vertical connectivity, sunlight, temperature and pH (Boulton et al., 1992; Fortino, 2006; Moldovan and Levei, 2015; Palmer, 1990). Further, the model streambeds were homogenous comprising of just sand grains and were static. We anticipate that *Lumbriculus variegatus* could have caused minimal disturbance in coarse-grained beds (e.g. gravel). On contrary, 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. Furthermore, all the experiments were conducted at a single flow rate such that bed grains or model bioturbating organisms were not washed away. It is likely that the interaction of bioturbating organisms with their physical habitat would have been different if the experiments were conducted at different flow rates (or velocities) within the safe range for organisms and grains. This will also have influence on other biogeochical and ecological functions.

The conceptual model that we present in this study can serve as a basis for further investigations which could be directed to explore the complex pathways through which macroinvertebrates can influence their habitat in natural settings. The imminent research must focus on conducting experiments with different types and mix of species, in beds with different compositions & geomorphologies, different flow and environmental conditions. Field observations of bioturbation are scarce so more qualitative and quantitative evidence for bioturbation at larger scales should be also obtained.

3.6 Conclusions

In this work, we present a conceptual model describing potential pathways through which macroinvertebrate bioturbation could alter hyporheic flow in streams. To support the arguments presented in the conceptual model, laboratory experiments in re-circulating flumes were conducted and effects of bioturbation process on dunes-induced hyporheic exchange was studied. The activities of model bioturbators modified the bed morphology and permeability of sediment beds which subsequently altered the hyporheic flow paths. Consequently, the treatment flumes exhibited both higher and lower solute penetration depths and mean hyporheic flux than the control flume. The mean residence times were higher in all the treatment flumes. The experiments provide early evidence for the role of size of bioturbating organisms and sediment-organism contact time on determining the extent to which these characteristics of hyporheic exchange are modified. Additional work is required to support and strengthen the ideas presented here and advance our understanding of role of sediment-organism interactions in fluvial ecosystems.

Chapter 4

Distribution of fine sediments in streambeds and influence on hyporheic exchange

This Chapter is intended to be submitted as a manuscript with full title as: **'Distribution of clay-sized sediments in streambeds and influence of fine sediment clogging on hyporheic exchange'**. I am the primary author of this manuscript (80% contribution), and my supervisors, Prof. Michael Stewardson and Dr. Meenakshi Arora are the co-authors.

Abstract

Laboratory experiments in re-circulating flumes are conducted to investigate the distribution of clay-sized fine particles in streambeds and its influence on dune-induced hyporheic exchange. Fine sand, coarse sand and gravel grains were used to form homogenous model streambeds (one control and two treatment flumes for each grain). The treatment flumes were subject to different initial concentrations of fine sediments (clay particles) in the water column, while control flumes had no fine sediments. The assessment of clogging profiles in coarse-grained beds reveals that fine particles preferentially infiltrate with the downwelling hyporheic flow. The experimental results also suggest that the depositional pattern of clay particles depends on both the relative size of the fine sediments & substrate sediments and the initial concentration of fine sediments in the surface water. The effect of this fine sediment accumulation on hyporheic exchange was studied by conducting dye tracer tests which indicate that clogging hampers hyporheic flow across sediment-water interface. The treatment flumes for each grain size exhibit lower hyporheic flux and higher median residence times compared to their respective control flumes. The dye penetration depths were lower in treatment flumes with fine and coarse sand compared to their respective control flumes. Interestingly, higher penetration depths were observed in treatment flumes with gravel compared to the control flumes. Further, assessment of alteration in exchange characteristics between the fine- and coarse-grained streambeds shows that clogging by clay-sized particles has a greater influence on the latter. Primarily, this study highlights that the interplay between fine sediments and hyporheic exchange is complex and calls for further research at both small and large scales to advance our understanding of fine sediment dynamics in fluvial environments.

4.1 Introduction

Hyporheic exchange is generally described as the movement of stream water into & adjacent to the streambed and its subsequent travel within the bed where it may mix with ground water before finally emerging back into the stream. It facilitates exchange of mass (solutes) and energy (heat) across the sediment-water interface (SWI). The zone in which this exchange occurs is defined as hyporheic zone and is regarded as a unique ecotone that underpins several stream ecosystem services such cycling of nutrients (Triska et al., 1993), processing of organic matter (Pusch, 1996), regulating temperature regime in surface and interstitial waters (Arrigoni et al., 2008b) and providing refuge to invertebrates (Dole-Olivier et al., 1997). These stream ecosystem functions are dependent on gradients in physico-chemical and biological properties of the hyporheic zones (Boulton et al., 1998; Brunke and Gonser, 1997), which in turn, are modulated by hyporheic flux, hydraulic residence times and penetration depth of solute-laden surface water (described in detail in Chapter 3). The hyporheic flux represents the rate at which water enter or exit the hyporheic zone. The time for which solute molecules remains within hyporheic interstices before emerging out of the streambed is regarded as residence time. The penetration depth relates to the size or volume of hyporheic zone in the sub-surface sediments. It determines the spatial extent to which solutes could travel into the bed along hyporheic flow paths.

These critical characteristics of hyporheic flow are partially controlled by bed permeability and its heterogeneity, particularly at small scales (Laube et al., 2018; Salehin et al., 2004; Sawyer and Cardenas, 2009; Tonina et al., 2016). For instance, Salehin et al. (2004) showed that streambed heterogeneity resulted in greater hyporheic flux and shorter mean residence times. In contrast, Tonina et al. (2016) demonstrated an overall reduction in volume of the hyporheic zone and consequently reduced hyporheic flow in heterogeneous sediments. They also showed that due to compression of the hyporheic zone in heterogeneous media, the residence time for longer hyporheic flow paths decreased while residence time for shorter hyporheic flow paths increased possibly due to an increased tortuosity of flow paths. The modification in these exchange characteristics has direct implications on stream functions (Harvey et al., 2013; Marzadri et al., 2016), which ultimately affects the overall quality of surface and sub-surface water.

Natural streambeds are characterized by heterogeneous permeability (or closely related hydraulic conductivity) (Calver, 2001; Genereux et al., 2008), and field investigations report that this variability is largely regulated by fine sediment fraction in streambeds (Stewardson et al., 2016). Fine particles tend to occupy the porous volume in streambeds and reduce their permeability, a process widely known as physical clogging (Brunke, 1999). The deposition of fine sediments on and into streambeds has been studied for over 50 years (Einstein, 1968; Lisle, 1989; Schälchli, 1992). The pioneering work by Einstein (1968) demonstrated that fine sediments infiltrate to the deepest regions and clog the bed from the bottom upward. Later, numerous studies showed that clogging does not necessarily commence from the bottom of the bed (Beschta and Jackson, 1979; Carling, 1984; Cui et al., 2008), and even a small concentration of fine sediments can potentially initiate clogging in the top layer of streambeds (Packman and MacKay, 2003). The observed clogging profiles have been broadly divided into two types- a) internal and b) external (Blaschke et al., 2003; Brunke, 1999). A streambed is referred as internally clogged if fine sediments infiltrate the bed armor layer and deposit within the substrate material. A streambed is externally clogged when an additional fine sediment layer deposit on top of the bed.

The key variables controlling the distribution of fine sediments in coarser sediment beds such as the relative size of bed sediments to fine sediments (Gibson et al., 2009a; b; Wooster et al., 2008), flow velocity (Cunningham et al., 1987), bed shear stress (Parker, 1990; Schälchli, 1992; Wilcock et al., 1996) have been highlighted previously. For instance, based on relative grain sizes of bed and infiltrating material, two kinds of fine sediment infiltration mechanisms have generally been discussed in literature- a) unimpeded static percolation, and b) bridging (Gibson et al., 2009a; b; Wharton et al., 2017). The unimpeded static percolation occurs when fine sediments fill up the voids in bed framework from bottom upwards as observed in laboratory investigations by Einstein (1968). When the size of infiltrating grains is larger relative to pore throats, their penetration is restricted to shallow depths which impedes the subsequent deposition and ultimately results in formation of a seal of fine sediments known as bridge layer (Gibson et al., 2009a). Transport of fine sediments driven by hyporheic flow and their retention in hyporheic interstices have been also demonstrated in experimental (Packman et al., 2000a; Rehg et al., 2005) and theoretical studies (Karwan and Saiers, 2012; Packman et al., 2000b; Ren and Packman, 2007). The fine sediments could infiltrate into the regions of stream water inflow into the beds (downwelling regions) and subsequently deposit in the substrate material (Packman and MacKay, 2003). An upward movement of fine sediments along upwelling hyporheic flow is also possible which could eventually release them back into the stream (Wharton et al., 2017).

Given that fine sediment input to streams is rising alarmingly (Owens, 2005; Wharton et al., 2017) and it influences the physical, chemical and biological environment of streambeds (Jones et al., 2012; Petts et al., 1989; Weigelhofer and Waringer, 2003), studying and predicting depositional pattern of fine sediments is critical to stream management programs. For instance, profiling of fine sediments is crucial to assess vertical profiles of bed toxicity (Ongley et al., 1992; Rice, 1999) as fines are associated with elevated concentrations of nutrients/contaminants due to their high adsorptive capacity (McDowell and Sharpley, 2001; Ren and Packman, 2004). Likewise, fine sediment infiltration is imperative to hyporheic and benthic ecology as fines can potentially ingress up to a depth pertinent to macroinvertebrate migration (Vadher et al., 2015) or fish spawning (Kemp et al., 2011). The distribution of fine sediments within a bed also partly controls the likelihood of their mobilization on/within the bed due to declogging or decolmation (Schälchli, 1992; Wharton et al., 2017) and bioturbation (Gottesfeld et al., 2004), and therefore, relates to a catchment's fine sediment budgets and mitigation strategies.

Through an extensive literature review on the process of fine sediment clogging, we identified some of the knowledge gaps in current understanding of fine sediment dynamics in lotic environments. Most of the previous laboratory investigations have investigated accumulation profile of fines in the gravelly substrata with flat topography (Beschta and Jackson, 1979; Gibson et al., 2009b; Herrero et al., 2015; Kuhnle et al., 2012; Wooster et al., 2008), whereas, coupling between fine sediment dynamics and hyporheic flow has been largely studied in sandy substrates (Fox et al., 2018; Packman et al., 2000a; Rehg et al., 2005). Further, the metric based on relative size of fine and substrate sediments which is conventionally used to predict clogging profiles has been developed for fine sand (fine) and gravel (substrate) sediment system. The threshold ratios developed for this sediment system may not be applicable for other type of sediment systems as evidenced from a recent study (Fetzer et al., 2017). Moreover, studies focusing on the distribution of fine sediments in the hyporheic zones, the induced heterogeneity in the hydraulic properties of topographical bed features such as dunes, and the subsequent influence on hyporheic exchange have gained momentum only recently (Fox et al., 2018; Jin et al., 2019a; Jin et al., 2019b).

To address these gaps, we investigate the distribution of clay-sized sediments in homogenous streambeds comprising of fine sand, coarse sand and gravel with dune-shaped morphology. These model streambeds were subjected to different initial concentrations of fine sediments (clay particles) in the surface water and the depositional profiles of clay particles was assessed. Further, the clogging by fine sediments is expected to modify dune-induced hyporheic flow, and therefore, its influence on hyporheic flux, residence times and penetration depths is studied by performing dye tracer tests.

4.2 Experimental methods

The above-mentioned research questions were addressed by conducting laboratory experiments following a control and treatment design. The experiments were conducted in Perspex built 3 m (L) x 0.2 m (W) x 0.4 m (D) re-circulating flumes in Sexton Ecohydraulics laboratory at The University of Melbourne (Figure 4.1). The experiments were conducted with tap water and the flow rate (~0.0016 m^3/sec) in flumes were measured by GPI-TM series flow meters. The slope (1:300, V:H) was adjusted using scissor jacks attached at upstream section of the flumes. Both flow rates and slopes were fine-tuned to attain uniform flow in the flumes with an average flow depth of 9 cm. The flow velocity was chosen such that no erosion of bed grains or worms was observed. These hydraulic variables were similar across all flumes.

Average depth of model beds: 30 cm
Height of bedforms: 3 cm
Wavelength of bedforms: 24 cm
Flow velocity: 8.5-8.8 cm/sec
Average flow depth: 9 cm

Figure 4.1: One of the experimental flumes (left) and hydraulic variables for all the experiments (right).

These flumes were filled with 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) to form homogenous beds. One control (C) and two treatment (T1 and T2) flumes for each sediment type was prepared (see Table 4.1 for details). The flumes were filled with pre-washed sediments and were washed again in the flumes to get rid of any foreign material (e.g. dirt) before forming dunes of desired configurations (Figure 4.1).

Table 4.1: Details of clogging and characteristics of hyporheic exchange in control (C) and treatment (T) flumes comprising of fine sand (FS), coarse sand (CS) and gravel (G) grains.

Sediment type	Flume index	C_0^{fs} (gm/l)	Clogging type	d_{clog}^{fs} x 10^{-3} (m)	d_{max}^{fs} x 10^{-3} (m)	RT_{med} / RT_{mean} (min)	đ(m)	*q/q'* x10^{-5} (m/min)
Fine sand	FS-C	0	-	-	-	1138/3758	0.044	1.32/1.17
	FS-T1	1.6	External	2	0	1875/3208	0.035	1.29/1.11
	FS-T2	3.2	External	4	0	2426/3783	0.034	1.23/0.90
Coarse sand	CS-C	0	-	-	-	155/528	0.267	55/50
	CS-T1	1.6	Internal	0	32	257/767	0.221	32/29
	CS-T2	3.2	External	3	0	804/1770	0.219	17/12
Gravel	G-C	0	-	-	-	25/85	0.132	178/153
	G-T1	3.2	Internal	0	66	79/163	0.145	102/89
	G-T2	6.4	Internal and	2.5	68	110/223	0.165	92/74

Once the desired bed topography and flow conditions were attained, a solution with known mass of box clay (d_{50} = 0.006 mm) was injected into the water column of treatment flumes to obtain required initial concentrations of fine sediments (C_0^{fs}, gm/l) (Table 4.1). The settlement/infiltration of fines was photographed from the side of flumes at regular intervals to observe clogging profiles. Average depth of clogging layer (d_{clog}^{fs}, m) formed due to deposition of clay particles on top of the bed and their maximum infiltration depth into the bed (d_{max}^{fs}, m) was measured manually through the flume walls. Flow velocities were low and no re-suspension of fine sediments was observed throughout the experiments.

A detailed description of dye tracer tests and methodology adopted to measure characteristics of hyporheic exchange is presented in Chapter 3. The following paragraphs will only briefly cover the experimental procedure. After deposition of fines, Rhodamine WT (fluorescent dye tracer) was added slowly into the water column over one re-circulation cycle (~90 sec) to ensure rapid & homogenous dye mixing. The dye concentration in surface water decreased due to mixing with pore water and it was monitored using Turner Designs Cyclops 7 sensors. The experiments were ceased when an equilibrium dye concentration (C_{eq}, ppb) i.e., change of dye concentration over time is minimal (~10 days for fine sand, ~6 days for coarse sand and ~15 hrs for gravel). The temperature corrected time series of normalized dye concentration (ratio of C_{eq} to initial dye concentration upon homogenous mixing) was fitted to an exponential equation and presented as break through curve. Tap water was manually added into the flumes to compensate for evaporative water loss and to ensure that the experiments were conducted with a constant water volume.

The hyporheic flux (q) was estimated from the initial gradient of the breakthrough curve and represents the volumetric flow rate averaged over the bed surface area (A, m^2). The residence time distribution function, denoting the fraction of solutes that entered the bed at time t = 0 and still remain in bed at a time t = τ, was calculated based on approach presented in Chapter 3, and the median (RT_{med}) and mean (RT_{mean}) residence times were obtained. The normalized equilibrium dye concentration was used to establish the mass balance of dye at beginning and the end of experiment to estimate the volume of water in hyporheic zone (V_p, m^3) which mixes with the surface water. In general, the mixing between surface and pore water due to 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 defined such that if the dye were to homogenously 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 ratio of V_p to A. As the average hyporheic flux is related to the depth of exchange (volume of water exchanged) and mean residence times, another estimate of average hyporheic flux (q') was calculated as the ratio of $\bar{d}$ to RT_{mean}.

4.3 Results

4.3.1 Observation of clogging

The model streambeds exhibited both internal and external clogging as observed from the flume walls (Table 4.1). Whilst the clay particles deposited on top of the beds in FS-T1, FS-T2 and CS-T2, infiltration of fines was observed in CS-T1, G-T1 and G-T2 (Figure 4.2-Figure 4.4). The d_{clog}^{fs} was higher in FS-T2 than FS-T1. The treatment flumes with gravel exhibited higher d_{max}^{fs} compared to CS-T1. The infiltration of fines to deeper regions occurred largely in the downwelling regions (stoss side of the dune) in CS-T1. In G-T1, fine sediment ingress was observed all along the flume length, but preferential accumulation of fines occurred at stoss side of the dunes near the troughs. In addition to pattern in G-T1, patchy deposition of fine sediments on top of the bed was observed in G-T2.

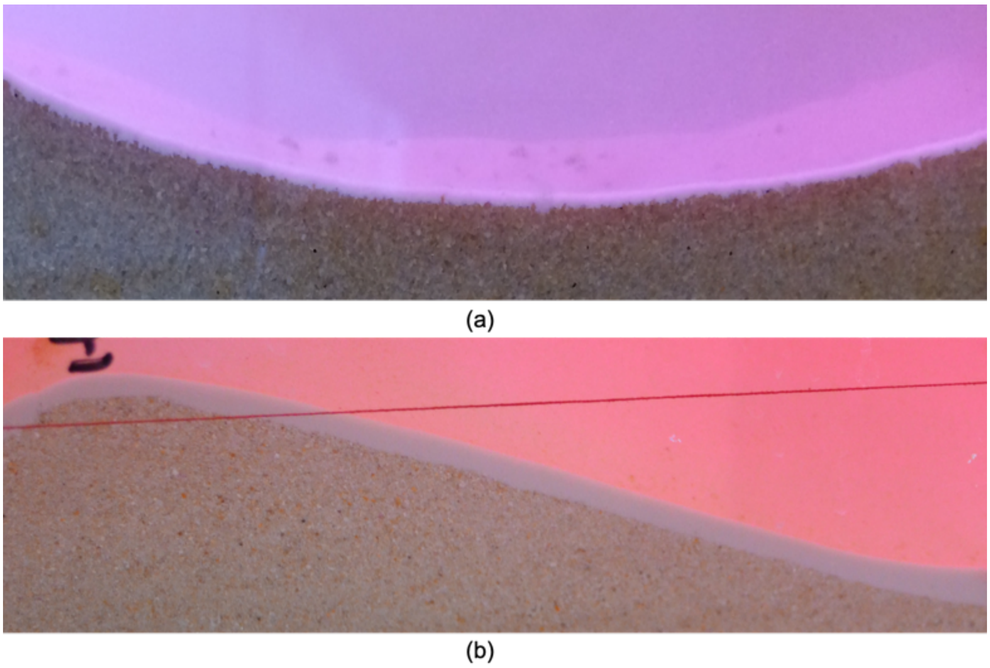


Figure 4.2: Fine sediment profile in treatment flumes with fine sand (FS) subject to initial concentrations a) 1.6 gm/l (FS-T1) and b) 3.2 gm/l (FS-T2) of fine sediments in the water column.

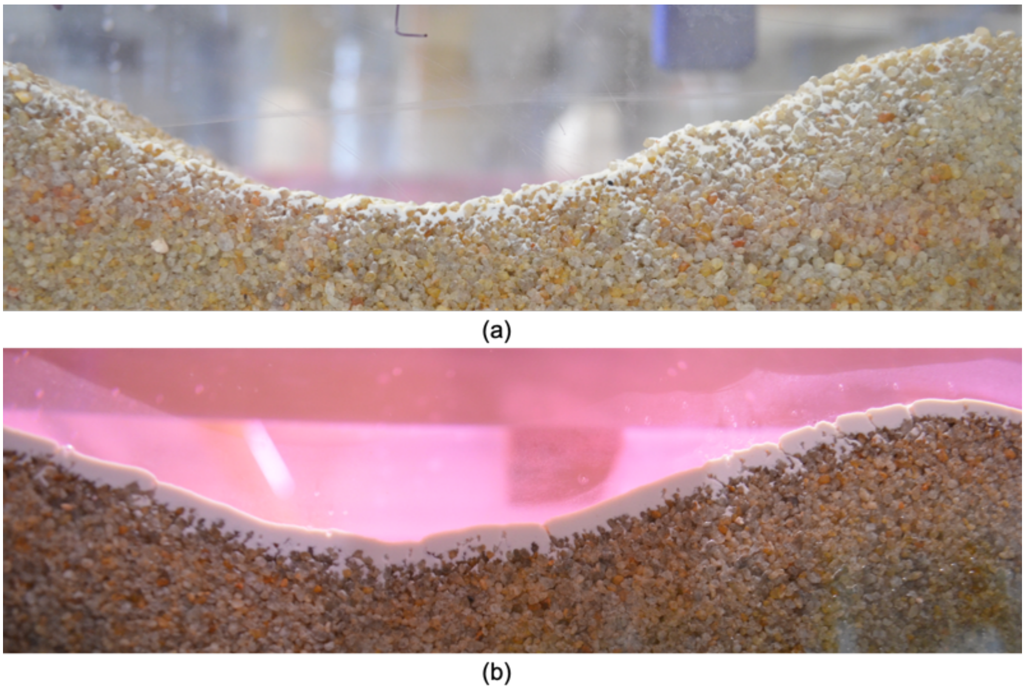
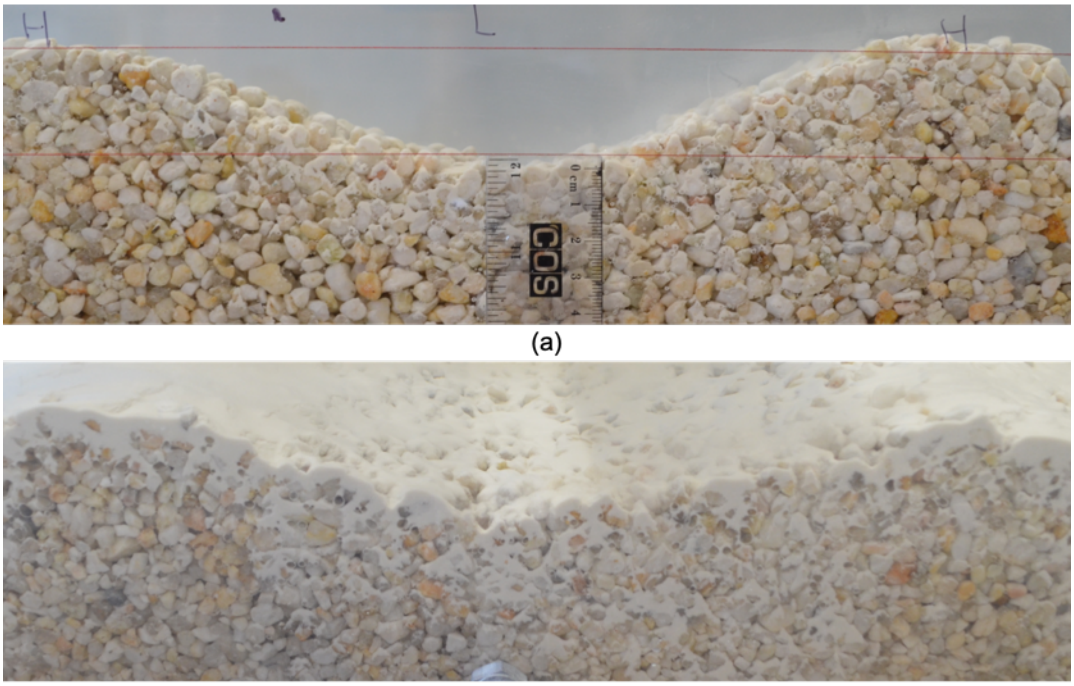


Figure 4.3: Fine sediment profile in treatment flumes with coarse sand (CS) subject to initial concentrations a) 1.6 gm/l (CS-T1) and b) 3.2 gm/l (CS-T2) of fine sediments in the water column.



(a)

(b)

Figure 4.4: Fine sediment profile in treatment flumes with gravel (G) subject to initial concentrations a) 3.2 gm/l (G-T1) and b) 6.4 gm/l (G-T2) of fine sediments in the water column.

4.3.2 Hyporheic exchange characteristics

For all three sediment types, treatment flumes exhibited lower q (estimated from breakthrough curves presented in Figure 4.5) than their respective control flumes (Table 4.1). The q in both FS-T1 and FS-T2 were lower by <10% than FS-C. The q in CS-T1 and CS-T2 were lower than CS-C by ~24% and 69% respectively. The q in G-T1 and G-T2 were lower than G-C by ~43% and ~93% respectively. The calculated q' was consistently lower than q and within 70% of the latter for all the flumes (Figure 4.6)

For fine and coarse sand, the $\bar{d}$ were lower in the treatment flumes compared to their respective control flumes (Table 4.1). The treatment flumes subjected to highest C_0^{fs} (i.e., FS-T2 and CS-T2) exhibited lowest $\bar{d}$ for both the sediment types. Contrastingly, G-T1 and G-T2 exhibited greater $\bar{d}$ than the G-C (greatest in G-T2).

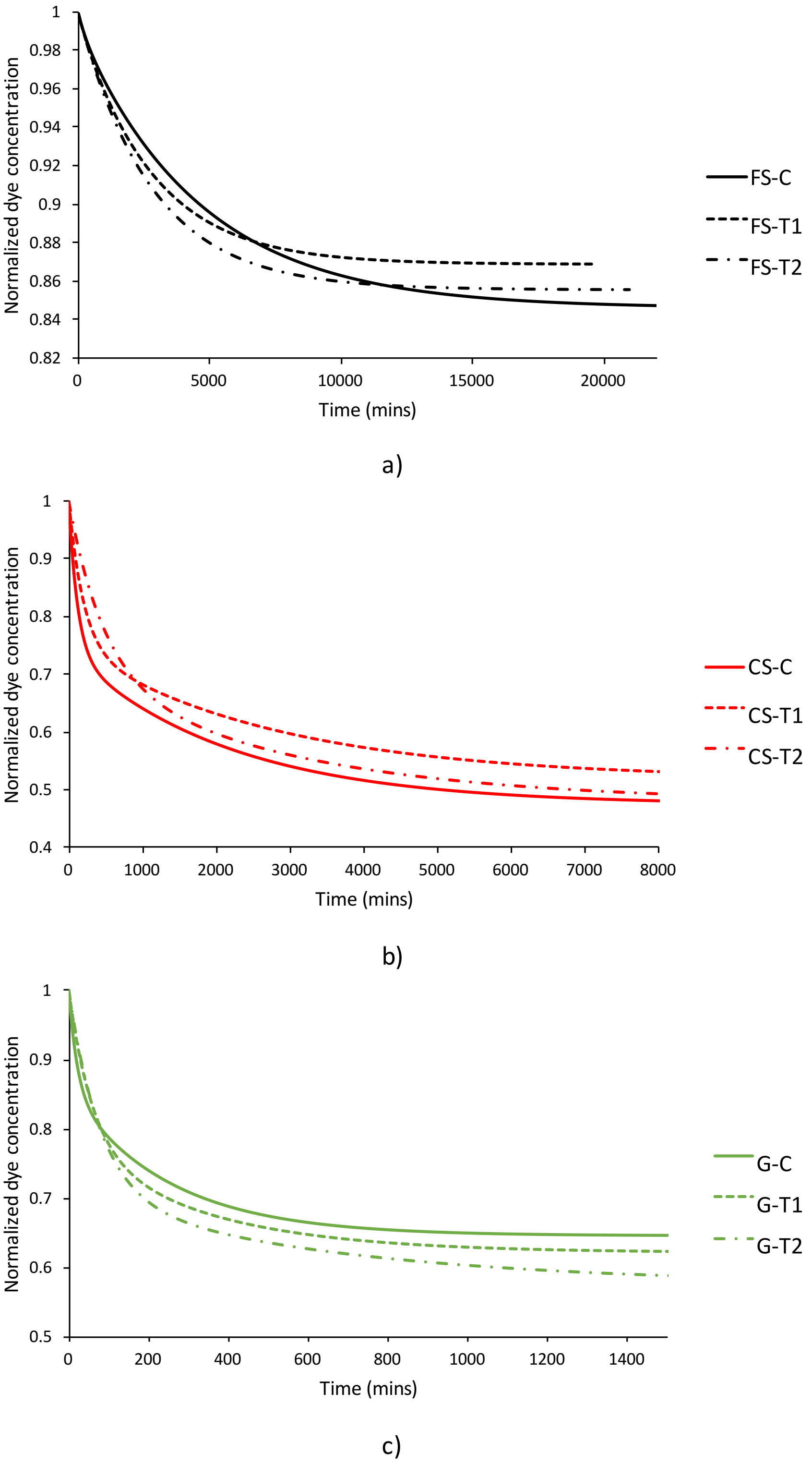


Figure 4.5: Breakthrough curves for control and treatment flumes with a) fine sand b) coarse sand and c) gravel beds obtained by fitting the time series of normalized dye concentration (temperature-corrected) in the water column. The root mean square error (RMSE) values for all the fits are less than 0.006.

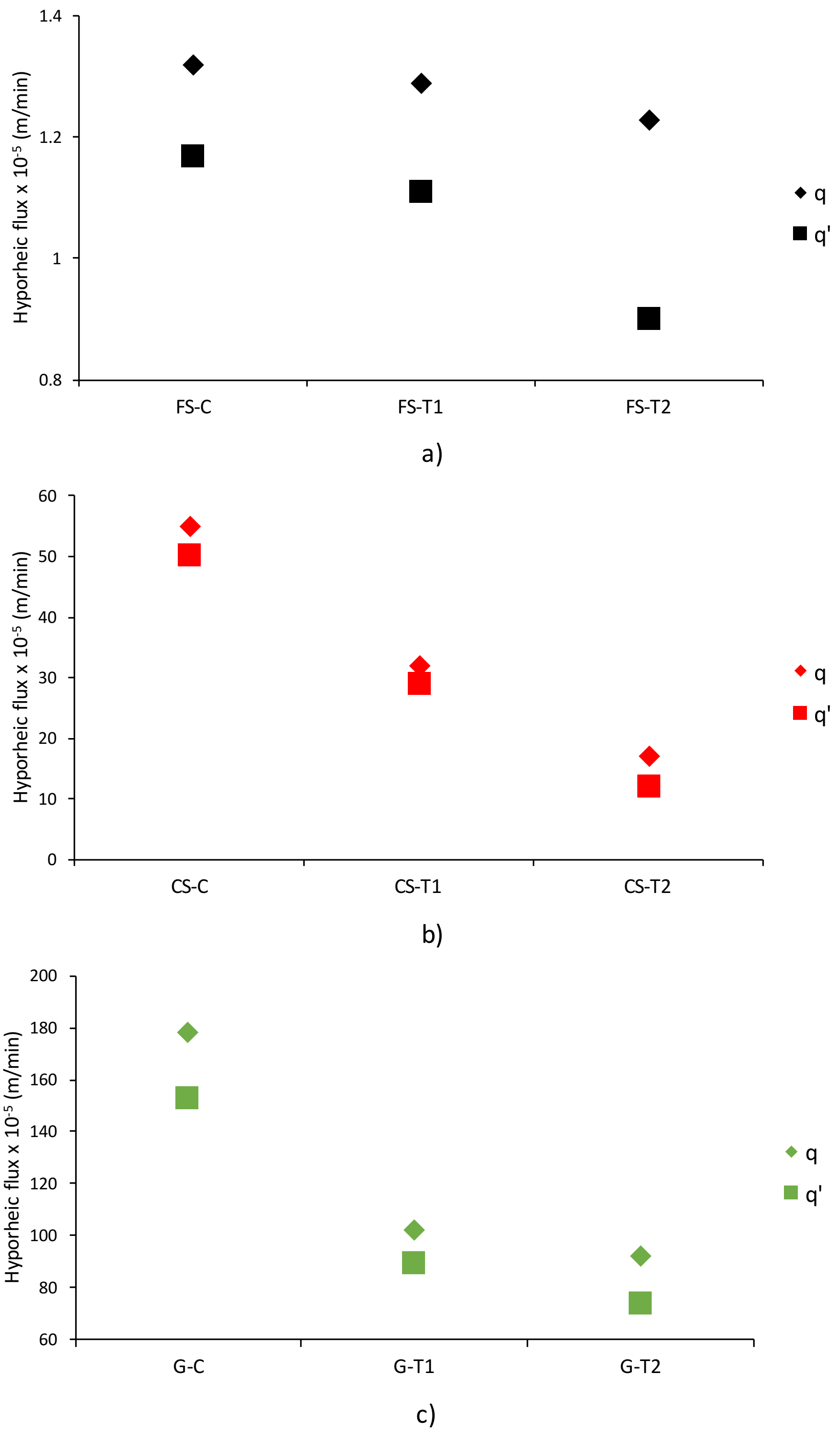


Figure 4.6: Comparison between hyporheic fluxes estimated from initial gradient of break through curve (q), and from depth of penetration and mean residence times (q') in control and treatment flumes with a) fine sand b) coarse sand and c) gravel.

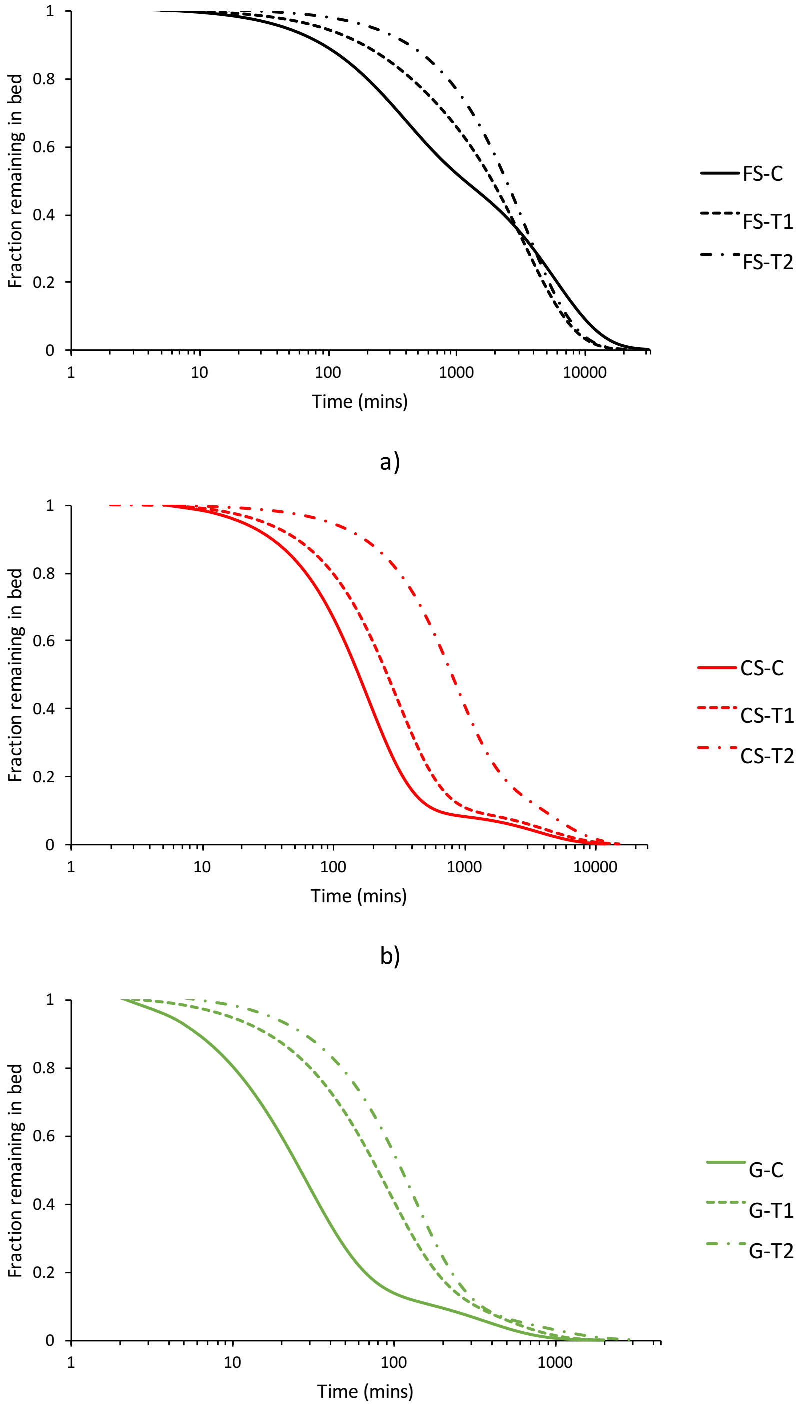
The flumes with gravel beds exhibited lower RT_{med} and RT_{mean} than flumes with fine and coarse sand (Figure 4.7). For each sediment type, the RT_{med} and RT_{mean} were longest in treatment flumes subjected to higher C_0^{fs} (FS-T2, CS-T2, G-T2). The RT_{mean} were longer in CS-T1 and G-T1 but shorter in FS-T1 than their respective control flumes.

The hyporheic flux (proportions of q) in short residence time ranges; shorter than 404 mins, 148 mins and 55 mins for fine sand, coarse sand and gravel respectively, were consistently lower in treatment flumes than their respective control flumes (Figure 4.8). The hyporheic flux in long residence time ranges; longer than 8103 mins, 2981 mins and 403 mins for fine sand, coarse sand and gravel respectively, were largely unchanged in treatment flumes with coarse sand and gravel but lower in treatment flumes with fine sand compared to their respective control flumes. In the intermediate residence time range; 404-8103 mins, 148-2981 mins and 55-403 mins for fine sand, coarse sand and gravel respectively, the hyporheic flux were higher for treatment flumes with fine sand and gravel but lower for coarse sand than their respective control flumes. Note that the short, intermediate and long residence time ranges for each sediment type were chosen based on their median and mean residence times (the numbers for these ranges are derived from the powers of natural exponential function, e^n, where n = 0,1,2,3… For instance, the long residence time ranges are determined as $e^6 = 403$, $e^8 = 2981$, $e^9 = 8103$).

4.4 Discussion

4.4.1 Fine sediment infiltration profiles

The infiltration profiles of clay particles in treatment flumes could be attributed to different sediment transport mechanisms. In coarse sand, the infiltration of fine particles (>3 cm) occurred largely at the stoss-side of the dunes near troughs indicating transport of fines along downwelling hyporheic flow paths as also observed in some previous investigations (Chen et al., 2010; Jin et al., 2019b). The fine sediments were transported to depths <1.5 cm at other locations in the bed. This transport of fines to shallow depths beneath the surface layer occurred potentially due to gravitational settling.



a)

b)

c)

Figure 4.7: Flux-weighted cumulative residence time distribution for the dye tracer in control and treatment flumes with a) fine sand b) coarse sand and c) gravel beds.

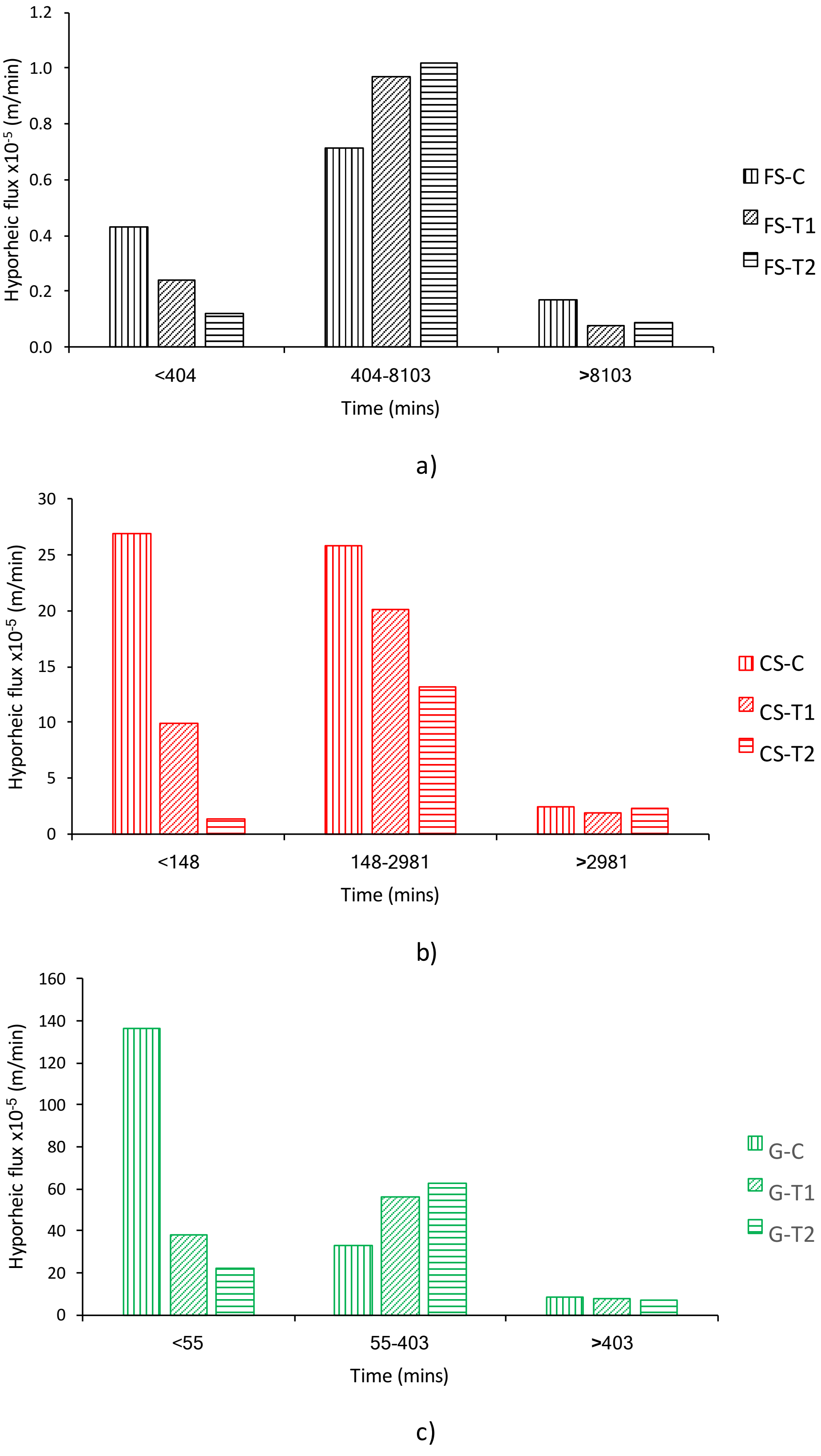


Figure 4.8: Residence time distributions showed as hyporheic flux in short, intermediate and long residence time ranges for control and treatment flumes with a) fine sand b) coarse sand and c) gravel beds.

In gravelly substratum, these two transport mechanisms were further assisted by generation of turbulent pulses (Carling, 1984; Roche et al., 2018) leading to fine sediment infiltration up to a depth of ~3 cm and as deep as ~6.8 cm at dune crests and troughs respectively.

The trapping of infiltrating particles within the pore matrix would have occurred by mechanism of filtration via- physicochemical interaction with bed sediments and physical straining (Bradford et al., 2002; Karwan and Saiers, 2009). Upon settling within the pore throats, the clay particles got attached to the surface of bed grains due to attractive forces between the sediments. The retention of clay particles due to straining occurred when the size of pore throats was narrower than the size of infiltrating particles. Amongst the coarser grains, the clay particles were more susceptible to trapping by these mechanisms in coarse sand compared to gravel due to smaller size of pore throats in the former. Consequently, vertical transport of clay particles occurred only up to shallow depths in the beds comprising of coarse sand compared to beds with gravel. The pore sizes were smallest in fine sand due to which the clay particles were trapped at the surface layer and no infiltration was observed.

A commonly used metric to determine the clogging profile is the relative size of substrate sediments and fine sediments. The ratio, D_{50}/d_{50} or D_{15}/d_{85} (D_x and d_y denotes the diameter than which x% and y% of particles in substrate and fine sediments respectively are finer) have been proposed as threshold value for bridging and unimpeded static percolation infiltration mechanisms (Gibson et al., 2009a; Sakthivadivel and Einstein, 1970). The metrics based on relative sizes of substrate and infiltrating sediments to predict profiles of clogging have been largely derived using gravel (substrate) and fine sand (infiltrating) sediment system. For instance, based on macroanalysis of 10 previous studies, Huston and Fox (2015) proposed an adjusted ratio, $D_{50}/d_{50}\sigma_{ss}$,where σ_{ss} is geometric standard deviation of substrate sediments such that the unimpeded static percolation would occur if this ratio is >27 and bridging would be observed otherwise. In our experiments, this adjusted ratio for gravel-clay sediment system was ~20 times higher than the threshold ratio proposed for unimpeded static percolation in gravel-fine sand sediment system, yet we observed infiltration to finite depth and formation of a bridge layer. Similar clogging patterns were also observed for coarse sand-clay sediment system (adjusted ratio ~100). Thus, our results demonstrate that the threshold ratio for occurrence of unimpeded static percolation in beds subject to cohesive infiltrating particles such as clay could be significantly higher than non-cohesive fine particles such as fine sand. This is consistent with recent findings by Fetzer et al. (2017), in which silt-sized particles formed a bridging layer in substrate comprising of sand even when the adjusted ratio was ~37.

Given that hydraulic variables and physical properties of substrata in treatment flumes of each sediment type were similar, the variation in depositional pattern of clay in coarse grained substrates (Table 4.1) could be attributed to different initial concentration of fine sediments in the water column. For example, infiltration of fine sediments along hyporheic flow paths was observed in CS-T1. However, no infiltration of fine sediments was observed in CS-T2 due to formation of a bridging layer just below the surface sediments which eventually led to all the subsequent clay deposition on the top of bed surface. Similarly, bridging by clay particles occurred both at the interface as well as in interstitial regions in G-T2. We anticipate that at high fine sediment concentration, a large proportion of fine sediments tend to infiltrate the pore throats resulting in clogging of voids at a faster rate and eventually formation a bridging layer which impedes further infiltration of fine sediments into the bed. In coarse sand, the pore throats were small, thus, bridging occurred close to the interface and impeded subsequent vertical transport of fines. In case of gravelly substrata, the surface voids were large to accommodate greater amount of fine sediments, and consequently, both infiltration and a spatially patchy & thin bridging layer was observed.

The transport and retention of cohesive sediments are also influenced by the surface properties of the sediments (Grabowski et al., 2011). As the specific surface area for such sediments is higher, the electro-chemical interactions between the particles control their dynamics in porous media in addition to physical forces (Brunke, 1999; Packman et al., 2000b). For instance, Rehg et al. (2005) demonstrated that colloids subject to different chemical treatments exhibit different mobility. It has been also recognized that attractive forces between the colloidal particles cause formation of flocs due to aggregation (Areepitak and Ren, 2011; Krishnappan, 2007). In our experiments, the clay particles could have potentially aggregated due to cohesive interactions between them and the likelihood of coalescence is expected to be higher at larger colloidal concentrations. The aggregated particles were strained in the upper layers due to relatively smaller size of smaller pore throats leading up to intensive clogging with bridge formation.

4.4.2 Influence of clogging on hyporheic exchange

The assessment of depth of hyporheic exchange ($\bar{d}$) in all the control flumes sediment suggests that the sediment beds were not completely mixed. Further, amongst the three sediment types, the $\bar{d}$ was greatest in coarse sand. However, one would expect mixing up to greater depth in G-C given that the permeability of gravel would be higher than that of coarse sand. Furthermore, the $\bar{d}$ in FS-C was only slightly greater than the height of bedforms (consistent with findings in Chapter 3, Table 3.1). We speculate that these observations could be attributed to the underflow in the flumes produced due to stream slope or hydraulic gradient down the flumes (Cardenas and Wilson, 2007a; Qian et al., 2008). If the underflow is fast, it may compress the hyporheic flow field and limit the vertical depth of exchange in the sediment bed (Cardenas and Wilson, 2007b).

The alteration of hyporheic flow characteristics in treatment flumes could be attributed to deposition of fine sediments on and into the model streambeds. Fine sediment clogging reduced the bed permeability at the SWI via- a) formation of a seal of fine sediments layer on the top and/or, b) infiltration of fine sediments into the pore throats. In both the cases, the exchange across SWI is obstructed and consequently the treatment flumes for each sediment type exhibited lower q and longer RT_{med} compared to their respective control flumes. For the same reason, the $\bar{d}$ were smaller in treatment flumes with fine and coarse sand than their respective control flumes. However, $\bar{d}$ in treatment flumes with gravel beds were greater than G-C which could be potentially attributed to preferential flow through clogged beds or reduction in effect of underflow (or both). The gravel beds have high porosity and greater number of macropores. As the deposition of clay particles in gravel beds was spatially patchy, it may have generated preferential flow paths through which the dye was transported into deeper regions (Chen et al., 2010). The other likely reason could be the reduction in influence of underflow on sub-surface flow field due to fine sediment clogging. This could have resulted in extension of hyporheic flow paths into the deeper regions of the bed causing greater dye penetration.

The modification in residence time distributions (Figure 4.7) could be attributed to alteration in hyporheic flow field due to fine sediment clogging. For all the sediment types, the treatment flumes exhibit significantly lower hyporheic flux when compared to their respective control flumes in corresponding short residence time ranges. The lower hyporheic flux in treatment flumes indicates that the exchange in the upper bed layer (through shorter flow paths) was significantly reduced due to deposition of clay particles on and into the streambeds. In their respective long residence time ranges, the hyporheic flux was lower in FS-T1 and FS-T2 compared to FS-C whereas, both treatment and control flumes with coarse sand and gravel exhibited similar hyporheic flux. This could be attributed to larger effect of clogging in treatment flumes with fine sand compared to treatments flumes with coarse grains. In general, flumes with fine sand exhibited small $\bar{d}$ (~ bedform height), thus, the longer flow paths are expected to be closer to the bed surface. These flow paths in the treatment flumes could get further compressed (as indicated by lower $\bar{d}$ than the control flume) due to presence of a low permeability clogging layer at the SWI (Gomez-Velez et al., 2014). Although compression of flow paths could have also occurred in treatment flumes with coarse sand, the $\bar{d}$ was significantly higher than that of treatment flumes with fine sand (~5 times). Thus, as the exchange in flumes with fine sand was limited to shallow depths, the effect of formation of clogging layer on the hyporheic exchange at longer times was larger in fine sand compared to other grains.

The effects of clogging on hyporheic exchange in model streambeds in their corresponding intermediate residence time ranges was variable. The higher hyporheic flux for G-T1 and G-T2 than G-C in intermediate residence time range (55-403 mins) could be explained by observed increase in $\bar{d}$ due to preferential flow or reduction in underflow (or combination of both) with increase in fine sediment clogging. For coarse sand, lower hyporheic flux in intermediate residence time range (148-2981 mins) could be attributed to reduction in $\bar{d}$. The compression of hyporheic flow field due to fine sediment clogging could have been such that the exchange through intermediate flow paths was impeded. In treatment flumes with fine sand, it can be noted that RT_{mean} was lower (FS-T1) and only slightly higher (FS-T2) than the control flume. However, the RT_{mean} in treatment flumes for other two sediments was consistently higher than their respective control flumes. As the average hyporheic flux is a function of both penetration depth and mean residence times, the higher hyporheic flux in intermediate residence time range in treatment flumes with fine sand could be attributed to influence of clogging on RT_{mean}.

The degree to which hyporheic exchange characteristics were modified due to clogging by fine sediments differed between fine- and coarse-bedded model streambeds. For instance, both FS-T2 and CS-T2 exhibited external clogging with similar depths of clay layer on the top, however, the q in latter was lower by ~70% than CS-C but only marginally lower in the former compared to FS-C. Similarly, RT_{med} and RT_{mean} in treatment flumes with coarse grains were affected to a greater extent than fine sand compared to their respective control flumes. This variable influence of fine sediment clogging on hyporheic flow in model streambeds could be attributed to the difference in intrinsic permeability of the parent bed materials. The dune-induced advective pumping of water and solutes is expected to be more dominant in coarse grains due to their higher permeability compared to fine sand. Consequently, the hindrance to rate of dye transfer across SWI was proportionally larger in the former after deposition of low permeability clogging layer. This suggests that clogging by clay-sized particles at higher concentrations could potentially have greater impact on hyporheic flux and residence times in coarse-bedded streams.

4.4.3 Limitations and future work

Laboratory investigations in re-circulating channels have been long used to study fluvial processes including fine sediment dynamics, however, they are yet a simplistic representation of a stream environment. The infiltration profiles were studied only for one type of fine sediments, ball clay, having specific grain size distribution and chemical properties. However, natural streambeds are exposed to fine material of a wide range of sizes and chemical constituents that may potentially interact with the bed differently. The model streambeds used to study deposition and accumulation profile of fine material were homogenous whereas, streambeds in natural settings are mostly heterogeneous, composed of sediments of different sizes and hydraulic properties. Further, these experiments explored the interplay between fine sediment deposition and hyporheic flow induced by only dunes. Furthermore, all the experiments were conducted at a constant and low flow velocity, thus, do not mimic the wide range of flow conditions in streams which may potentially result in different clogging patterns at a given fine sediment concentration.

Therefore, future work must focus on studying clogging profiles of different types of fine sediments in streambeds with heterogeneous sedimentary and hydraulic properties. Although subject to little research, variety of deposition profile has been observed in laboratory studies with mobile streambeds. We suggest that imminent studies should also explore the accumulation profile of fine sediments in a mobile bed framework (Dudill et al., 2017). Additionally, our results demonstrate that the interplay between fine sediments and hyporheic flow fields generated due to the dunes is complex, thus, fine sediments deposition on and within streambeds of different topographies should be investigated. Moreover, field evidences for distribution of fine sediments and its influence on hyporheic exchange must also be gathered to advance our understanding of fine sediment dynamics in stream ecosystems.

4.5 Conclusions

Laboratory experiments were conducted in re-circulatory flumes to investigate distribution of fine sediments in homogenous streambeds comprising of three different grain sizes (fine sand, coarse sand and gravel). The experimental observations provide evidence of influence of dune-induced hyporheic flow on transport of fine sediments. Further, the results suggest that clogging profiles cannot be determined solely from relative grain sizes of infiltrating and streambed sediments, but are also dependent on initial concentration of fine sediments in the surface water. The clay particles deposited on top of the model streambeds comprising of fine sand as the relative size difference between two sediment types was less. The infiltration of clay particles was observed in coarse sand and gravel beds when subject to low initial concentration of clay particles in the water column. The clay particles deposited on top of the surface layer of both coarse-grained sediments at high initial concentration in the water column. Furthermore, we also investigate the effects of this fine sediment deposition on hyporheic exchange. The flow in treatment flumes was impeded due to presence of clay deposits on or within the streambeds which resulted in lower hyporheic flux and higher median residence times compared to the control flumes. The penetration depths of solutes were smaller in treatment flumes with fine and coarse sand but larger for gravel beds compared to their respective control flumes. Finally, the experimental results highlight that clogging by clay-sized particles has greater influence on exchange characteristics in coarse-grained beds than in beds comprising of fine grains. We suggest that more research should be conducted to further advance our understanding of fine sediment dynamics in streams as it has direct implications on hydrological, biogeochemical and ecological functions in these ecosystems.

Chapter 5

Effect of interplay between bioturbation and fine sediment clogging on hyporheic exchange

This Chapter is intended to be submitted as a manuscript with full title as: **‘Interaction of bioturbating organisms with fine sediments and its influence on hyporheic exchange in clogged streambeds’**. I am the primary author of this manuscript (80% contribution), and my supervisors, Prof. Michael Stewardson and Dr. Meenakshi Arora are the co-authors.

Abstract

Streambed inhabitants constantly interact with their habitat to modify its hydraulic properties such as permeability. However, limited progress has been made to explore the influence of this sediment-organism interactions on hyporheic exchange which underpins several stream ecosystem functions. In this work, we advance the understanding of the role of macroinvertebrate bioturbation in altering hyporheic exchange across sediment-water interface in clogged streambeds. We conduct laboratory experiments in re-circulating flumes to study the interaction of sample bioturbating organisms (*Lumbriculus variegatus*) with fine sediment (clay) layer, and its subsequent influence on hyporheic exchange in homogenous model streambeds comprising of fine sand, coarse sand and gravel. We observe that macroinvertebrate activities re-worked the clay particles, mixed them with underlying grains and eventually eroded or disintegrated the clogging layer at the top in all sediment types. The mitigation of low permeability clay layer resulted in greater solute penetration depth, shorter median and mean residence times and higher hyporheic flux in bioturbated sediments. This modification to characteristics of hyporheic flow has direct implications for biogeochemical reactions that occur in hyporheic zones and regulate overall quality of surface and sub-surface water. Primarily, this study manifests the potential of bioturbation in alleviating clogging and maintaining permeability in the streambeds, and call for more research to advance our understanding of interactions between the fine sediments and bioturbating organisms in stream ecosystems.

Keywords: Bioturbation, clogging, permeability, hyporheic exchange, hyporheic zone

5.1 Introduction

Hyporheic zone is a zone of saturated sediments present below and adjacent to the streambeds, where surface and ground water interacts (Boulton et al., 1998; Triska et al., 1993; White, 1993). It is regarded as a unique and an important ecotone which facilitates exchange of mass and energy across sediment water interface (SWI), a process known as hyporheic exchange. Decades of hyporheic research have demonstrated that hyporheic exchange is central to several stream ecosystem functions such as transformation of nutrients and pollutants (Bardini et al., 2012; Gandy et al., 2007; Mulholland et al., 1997), processing of organic matter (Findlay et al., 1993; Pusch, 1996), modification of surface and sub-surface thermal regime (Arrigoni et al., 2008a; Hester et al., 2009) and fluvial ecology (Boulton et al., 1992; Boulton et al., 2010; Brunke and Gonser, 1997).

The hyporheic flux, residence times and penetration depth of solutes are critical characteristics of hyporheic exchange that control the biogeochemistry and ecology in hyporheic zones (Boulton et al., 2010; Harvey et al., 2013; Zarnetske et al., 2011). The hyporheic flux determines the rate at which solutes enter or exit the hyporheic zone. The time for which water and solutes travel in hyporheic zones and interact with microbial communities is known as residence time. The penetration depth relates to the size or volume of hyporheic zone in the sub-surface sediments and determines the spatial range to which solutes could travel along hyporheic flow paths within the bed. These three characteristics of hyporheic zones cause gradients in physico-chemical and biological properties of hyporheic zones (Boulton et al., 1998; Brunke and Gonser, 1997) and support several hyporheic functions. For example, oxygen availability in the pore water partially depends on the downwelling flux of oxygenated surface water and residence times in hyporheic zones. If the residence times are long, oxygen could get used up by the streambed inhabitants or as preferential electron acceptor by bacterial organisms leading to development of anaerobic conditions, which would potentially support activities of anaerobic microorganisms.

Streambed permeability (or closely related hydraulic conductivity) and its heterogeneity are dominant controls on hyporheic flow characteristics, particularly at small scales (Bardini et al., 2012; Packman and Salehin, 2003; Storey et al., 2003). Permeability is defined as the ability of a porous media to transmit fluid through it (Freeze and Cherry, 1979). Generally, highly permeable sediments (e.g. gravel) exhibit higher hyporheic flux and lower residence times whereas, converse is true for sediments with lower permeability (e.g. silt or clay). Several previous studies have demonstrated modification in exchange characteristics due to heterogeneous bed permeabilities (Salehin et al., 2004; Sawyer and Cardenas, 2009; Tonina et al., 2016). For instance, Tonina et al. (2016) demonstrated an overall reduction in the volume of hyporheic zone and consequently reduced hyporheic exchange flows in heterogeneous sediments. They also showed that due to compression of hyporheic zone in heterogeneous media, the residence time for longer hyporheic flow paths decreased while residence time for shorter hyporheic flow paths increased due to increase in tortuosity of flow paths. This alteration in hyporheic flux, residence times, geometry of flow paths and size of hyporheic zone is expected to alter aforementioned stream ecosystem services and subsequently influence the overall quality of both surface and pore water.

The deposition of fine sediments on or within the streambeds, a process described as physical clogging, is one of the processes which directly influence the hydraulic properties of streambeds (Brunke, 1999; Schälchli, 1992). Accumulation of fine materials in porous matrix of a coarser streambed alters its composition & structure (Beschta and Jackson, 1979; Ryan and Packman, 2006), reduces the porosity and permeability (Fetzer et al., 2017; Gayraud and Philippe, 2001; Packman and MacKay, 2003) and subsequently affects physicochemical and biological environment in hyporheic zones (Brunke and Gonser, 1997; Hartwig et al., 2012;

Nogaro et al., 2010; Ongley et al., 1992). For instance, deposition of low permeability fine sediment layer on the stream bed would decrease the flux of oxygen from surface water and increase the residence times of solutes (e.g. nitrate) in hyporheic zones. A multifold increase in fine sediment input has occurred over the recent years due to human practices such as deforestation or mining (Owens, 2005; Wilcock et al., 2001), and fine sediment pollution has been increasingly recognized as a threat to stream ecosystems worldwide (Wharton et al., 2017).

Although clogging has detrimental effects on sub-surface ecology (Jones et al., 2012; Wood and Armitage, 1997), 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). These organisms move, feed, defecate and construct biogenic structures (e.g. burrows) in the sediments, a process described as bioturbation (Kristensen et al., 2012; Solan and Herringshaw, 2008). These activities result in mixing & mobilization of fine sediments and modify the hydraulic properties of clogged beds.

Whilst habitat modification due to bioturbation has been explored in marine ecosystem (Jones and Jago, 1993; Meadows and Tait, 1989; Rowden et al., 1998), there has been little progress in understanding interactions of in-stream faunal organisms with their physical environment in fluvial settings (Marmonier et al., 2012). Most of the previous studies related to bioturbation in freshwater sediments have been conducted in standing water (Mermillod-Blondin et al., 2003; Nogaro et al., 2006). The results related to modification in bed permeability and subsequently the exchange across SWI from these laboratory experiments in vertical columns (one-dimensional) may have limited applicability to flowing water (or lotic) environments where complex hydrodynamic conditions can be produced by the interaction of flow and the channel boundary. Further, field evidence of bioturbating organisms reducing the clogging and thus maintaining permeability of clogged streambeds is rare (Song et al., 2010).

We address the above-mentioned gap by investigating interactions between bioturbating organisms & fine sediments in lotic environment and its subsequent influence on hyporheic flow across SWI in clogged streambeds. Specifically, experiments in re-circulating flumes were conducted to study role of model bioturbating organisms (*Lumbriculus variegatus*) in disturbing the fine sediment (clay) layer in fine- and coarse-grained streambeds (fine sand, coarse sand and gravel). We evaluate and compare the solute penetration depth, residence times and hyporheic flux of dune-driven hyporheic flow in bioturbated and non-bioturbated sediments for each sediment type. The results from the experiments highlight that the interplay between these organisms, fine sediments and underlying grains is complex, which modifies the bed permeability and consequently the hyporheic exchange across SWI.

5.2 Experimental methods

To achieve the goals of this study, a control and treatment design was adopted. The control flumes would represent exchange characterisitcs in clogged streambeds while the treatment flumes would represent the influence of bioturbation activity on clogging layer and subsequently on hyporheic flow regime in clogged streambeds. The experimental details are presented in sub-sections below.

5.2.1 Flume set up and bed materials

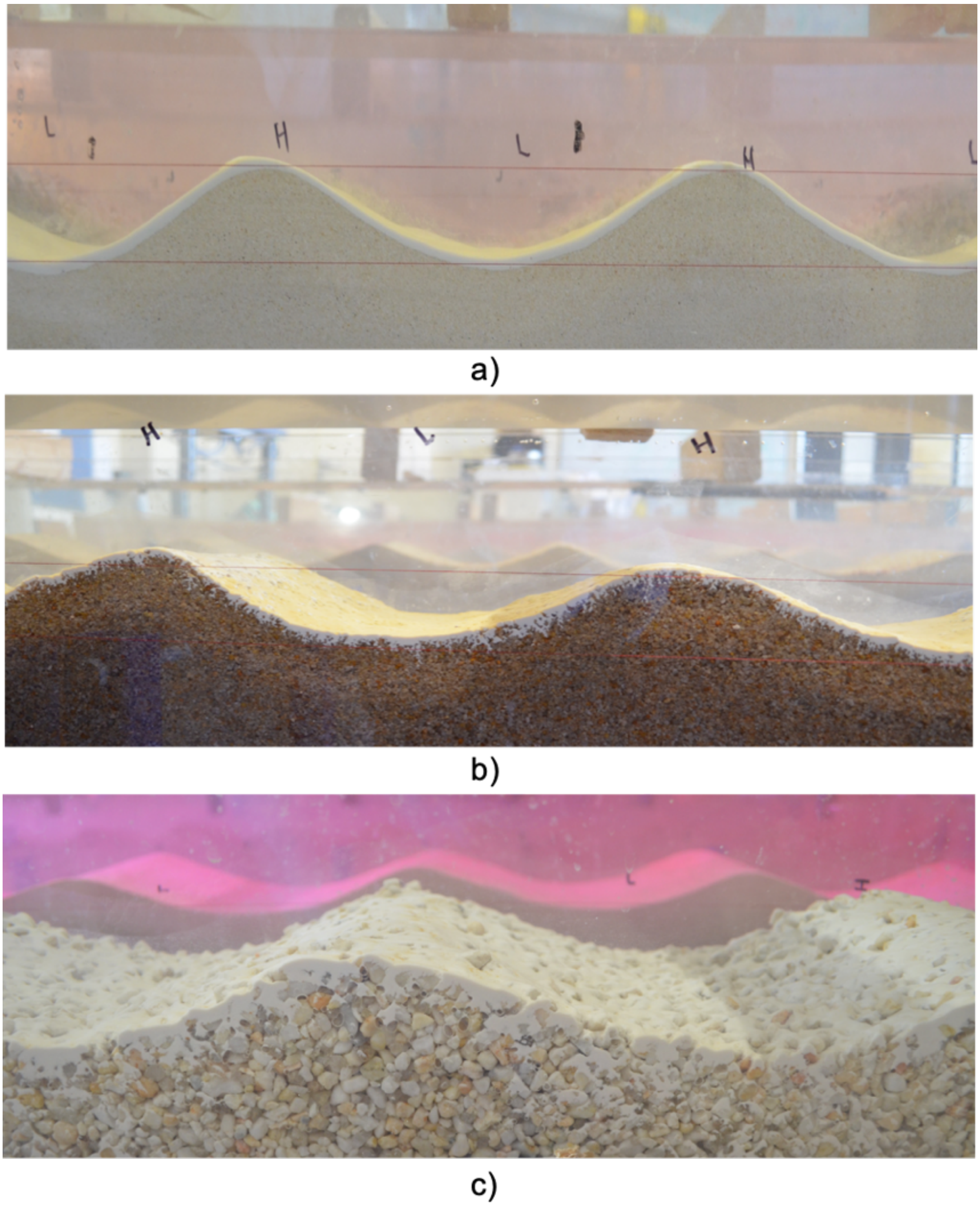
The experiments were performed in the Sexton Ecohydraulics laboratory at The University of Melbourne in six 3 m long, 0.2 m wide and 0.4 m deep Perspex recirculating flumes (Figure 5.1).

Average depth of model beds: 30 cm
Height of bedforms: 3 cm
Wavelength of bedforms: 24 cm
Flow velocity: 8.5-8.8 cm/sec
Average flow depth: 9 cm

Figure 5.1: Re-circulating flume apparatus used for conducting the experiments. The inset on right shows the hydraulic conditions maintained in all the experimental flumes.

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 (0.0016 m^3/sec) 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 hydraulic conditions across all flumes were almost similar. Fine sand (D_{50} = 0.28 mm, porosity = 0.45), coarse sand (D_{50} = 1.7 mm, porosity = 0.37) and gravel (D_{50} = 5.5 mm, porosity = 0.38) were used to form compositionally homogenous model streambeds. All experiments were performed with tap water in the flumes.

Each grain type was filled into two flumes (one control- without organisms and other treatment-with organisms) after thoroughly washing them to remove any foreign material (e.g. dirt) and dunes of desired geometry were artificially formed at the bed surface. For each sediment type, a known mass of ball clay (d_{50} = 0.006 mm) was introduced as fine sediments to clog the beds, and the depositional pattern in both control and treatment flumes was similar. 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 5.2). In coarse sand, fine sediments penetrated to shallow depths (up to 3 mm) at some regions along the length of the beds and then subsequently deposited on top of the beds to form a clogging layer of average depth ~3 mm. In case of gravel substrata, fine sediments both infiltrated (up to 6 cm) and settled on the beds with average depths of clogging layer ~2 mm.



a)

b)

c)

Figure 5.2: Depositional pattern of clay in experimental flumes with a) fine sand b) coarse sand and c) gravel. Both control and treatment flumes for each sediment type exhibited similar clogging profiles

5.2.2 Model bioturbating organisms

Lumbriculus variegatus (commonly known as California blackworms), were used as model bioturbators to study macroinvertebrate bioturbation (Figure 5.3). *L. variegatus* (hereafter referred as worms) are freshwater oligochaetes which prefer to dwell in shallow sub-surface regions of lakes or marshes feeding on organic material and microorganisms (Brinkhurst and Gelder, 1991). A typical behaviour of these worms 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). They have been extensively used in several toxicological studies related to freshwater sediments (Blankson and Klerks, 2016; Leppänen and Kukkonen, 1998).

After all the clay had deposited on or into the bed, pumps were turned off in one of the flumes of each sediment type (referred as treatment flumes) and equal number of worms were introduced to achieve a density of ~8000-1000 individuals/m^2 which is commonly found in natural environments (Cook, 1969; Mason, 1994). The average thickness and length of worms (measured manually and through image processing using ImageJ for 30 worms) were ~0.65 mm and 5 cm respectively. The flow was re-instated after the worms had settled on or penetrated the clogged layer (~2 days). The flow velocities in the flumes were kept 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.

Figure 5.3: Lumbriculus variegatus used as model bioturbating organisms

5.2.3 Tracer test to measure hyporheic exchange

Grant et al. (2012) reported several ways to conduct tracer test to assess hyporheic exchange in recirculating flumes. In this work, we injected a fluorescent dye tracer, Rhodamine WT, into the water column 15 days after introduction of the worms to evaluate hyporheic exchange in control and treatment flumes. The dye was added slowly over one re-circulation cycle of water (~90 sec) to ensure rapid & homogenous dye mixing, and its concentration in water column ($C(t)$, ppb) was monitored using Turner Designs Cyclops 7 sensors. The dye concentration decreases over time due to exchange with the pore water until an equilibrium (C_{eq}, ppb) is reached i.e. dye concentrations in the water column and hyporheic zone are equal. The experiments were ceased after this equilibirium condition was attained. Temperature corrections to the time series data of dye concentration in water column was applied. The conservative behaviour of the dye used in our experiments was confirmed by investigating its isomeric composition (Vasudevan et al., 2001) through Nuclear magnetic resonance spectroscopy (NMR) and conducting batch experiments (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. Evaporation losses from the flume were calculated and additional tap water was manually added into the flumes to compensate for evaporative loss over time and maintain constant flow depth and water volume throughout the experimentation period.

The hyporheic flux (q) was estimated from the initial gradient of the breakthrough curve. The residence time distribution function denoting the fraction of solutes that entered the bed at time t = 0 and still remain in bed at a time t = τ, was calculated based on approach presented in Chapter 3, and the median (RT_{med}) and mean (RT_{mean}) residence times were obtained. The normalized equilibrium dye concentration (ratio of C_{eq} and initial dye concentration upon homogenous mixing) was used to establish mass balance of the dye at beginning and end of the experiment, and the volume of water in hyporheic zone (V_p, m^3) which mixes with the surface water was obtained (see Chapter 3). In general, the mixing between surface and pore water due to 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 defined such that if the dye were to homogenously 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 ratio of V_p to A.

Further, the average hyporheic flux is dependent on both the depth of exchange ($\bar{d}$ for these experiments) and mean residence times (RT_{mean}). Thus, another estimate of average hyporheic flux (q') was calculated from the ratio of $\bar{d}$ to RT_{mean}.

5.3 Results

5.3.1 Observation of worm activity

In treatment flume with fine sand (FS-T), the worms were found concentrated in top 2-3 cm as noted in previous experimental studies (Roche et al., 2016) and the holes or burrows dug by them were visible at the bed surface (Figure 5.4). On contrary, in coarse-bedded treatment flumes, 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 5.4) whereas, a significant proportion of worms almost reached to the flume bottom in gravel bed (G-T) leaving only a few worms bioturbating the top layer. Nearly 85-90% of worms were recovered at the end of experiments.

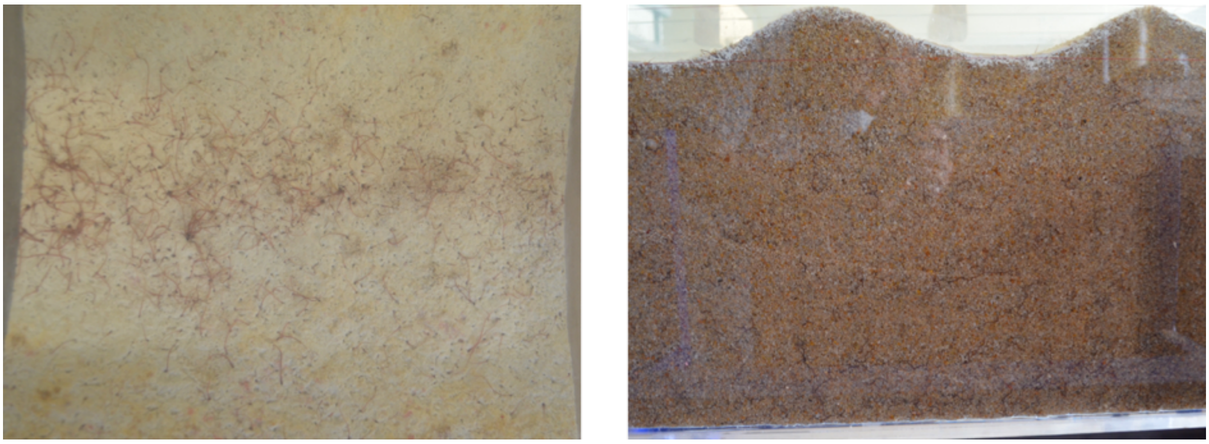
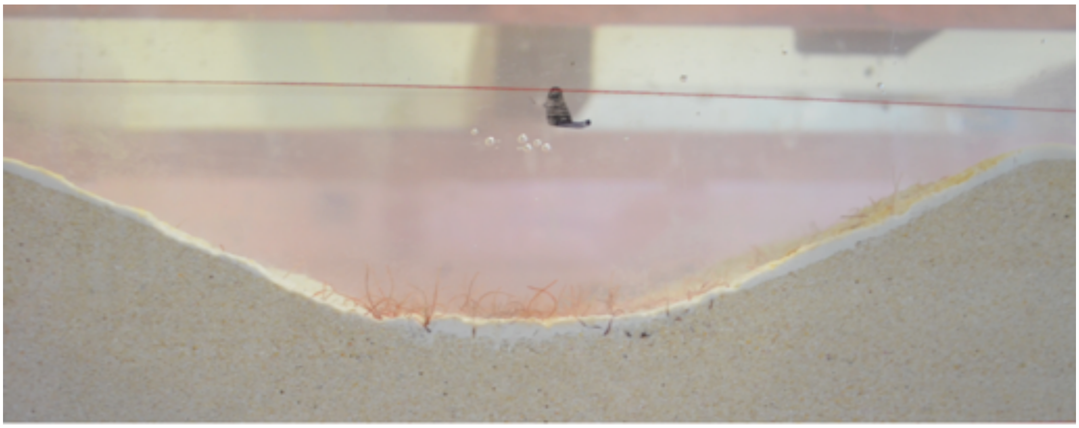


Figure 5.4: Bioturbation activity in fine sand viewed from above (left) and coarse sand viewed from the side (right).

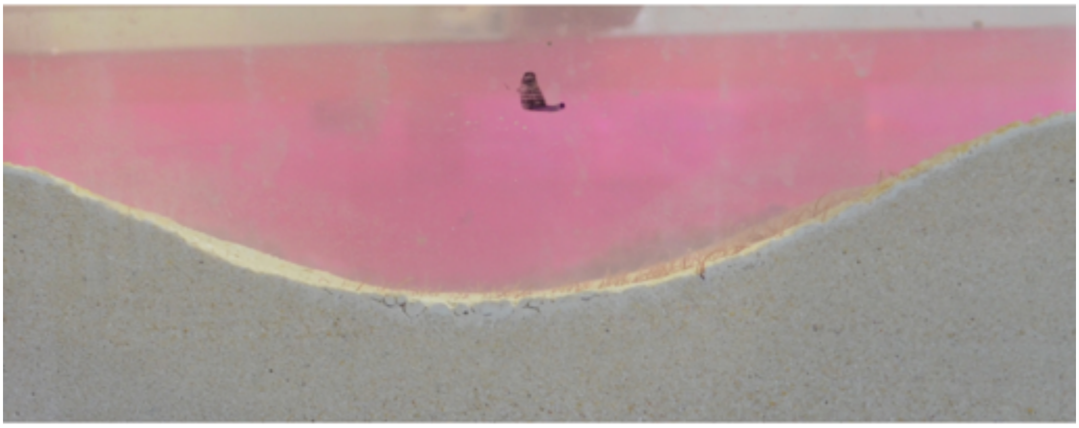
Table 5.1: Experimental details and calculated exchange characteristics in control (C) and treatment (T) flumes with fine sand (FS), coarse sand (CS) and gravel (G).

Sediment type	Mass of clay (gm)	Flume index	RT_{med} / RT_{mean} (min)	$\bar{d}$ (m)	q/q' x10^{-5} (m/min)
Fine Sand	400	FS-C	2426/3781	0.035	1.23/0.95
		FS-T	864/3596	0.050	1.53/1.39
Coarse Sand	400	CS-C	804/1769	0.219	17/12
		CS-T	346/1069	0.238	27/22
Gravel	800	G-C	110/223	0.165	92/74
		G-T	56/139	0.173	140/125

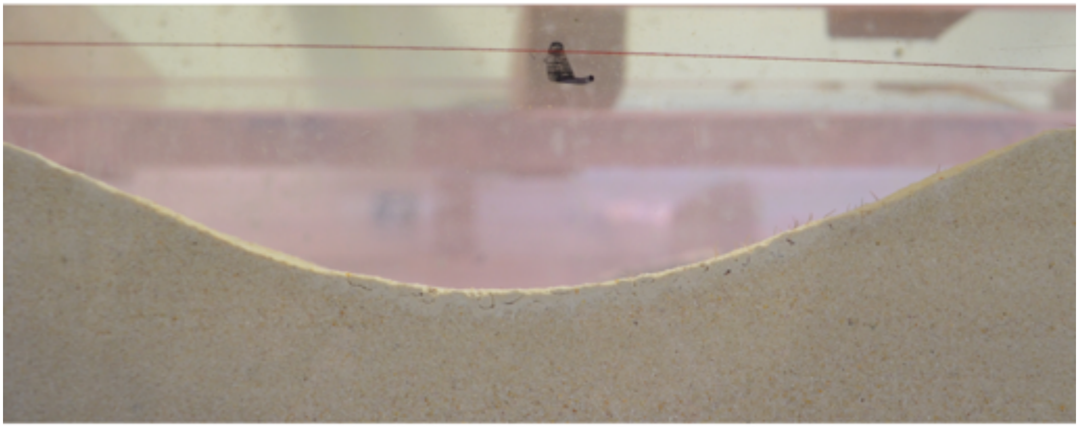
5.3.2 Disturbance to clogging layer and mobilization of fine sediments



Day 2



Day 7



Day 15

Figure 5.5: Temporal change in the clogging layer observed at 2nd, 7th and 15th day after worm addition in FS-T. A significant worm penetration occurred within two days and the clay particles were subsequently mixed with sand grains leading to disappearance of clay layer at the surface by end of the experiment.

The visual observations through flume walls in treatments indicate that clay particles were transported to deeper bed regions and mixed with underlying sediments in the treatments of all grain sizes. For instance, the interface between fine sand and clay layer progressively dissolved as the worms performed their activities in FS-T (Figure 5.5).

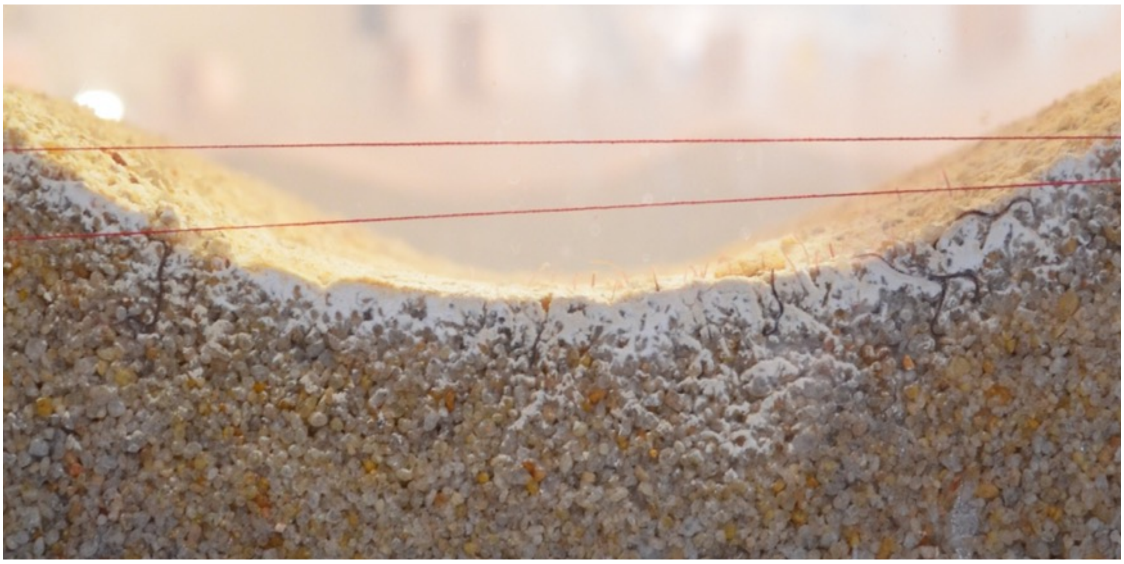


Figure 5.6: The vertical transport of clay particles in coarse sand after the seal of low permeability clay layer at the top was disintegrated by worm bioturbation

By the end of the experiment, the clogged layer was completely eroded exposing the top surface of the bed with clay particles being mixed with the bed-grains up to a depth of 2 cm (Figure 5.6). Similarly, clay particles were transported up to 3 cm in CS-T by the end of the experiment. For the gravel substratum, the clay layer on the top almost completely disappeared and the infiltrated clay particles were re-worked to unclog the pores in top 5 cm of the bed (Figur 5.7).

Figure 5.7: Re-working and mitigation of clay deposits at the surface and in the interstitial regions in G-T at 5th and 15th day after addition of worms

5.3.3 Hyporheic exchange characteristics

The calculated $\bar{d}$ was greatest in coarse sand and smallest in fine sand (Table 5.1). Note that the experimental flumes were not completely mixed with the surface water as also seen in experiments in Chapter 4. This could be attributed to underflow in the flumes. For all the sediment types, treatments exhibited higher $\bar{d}$ compared to their respective control flumes. The $\bar{d}$ in FS-T, CS-T and G-T was higher by ~42%, ~10% and ~5% respectively than their respective control flumes.

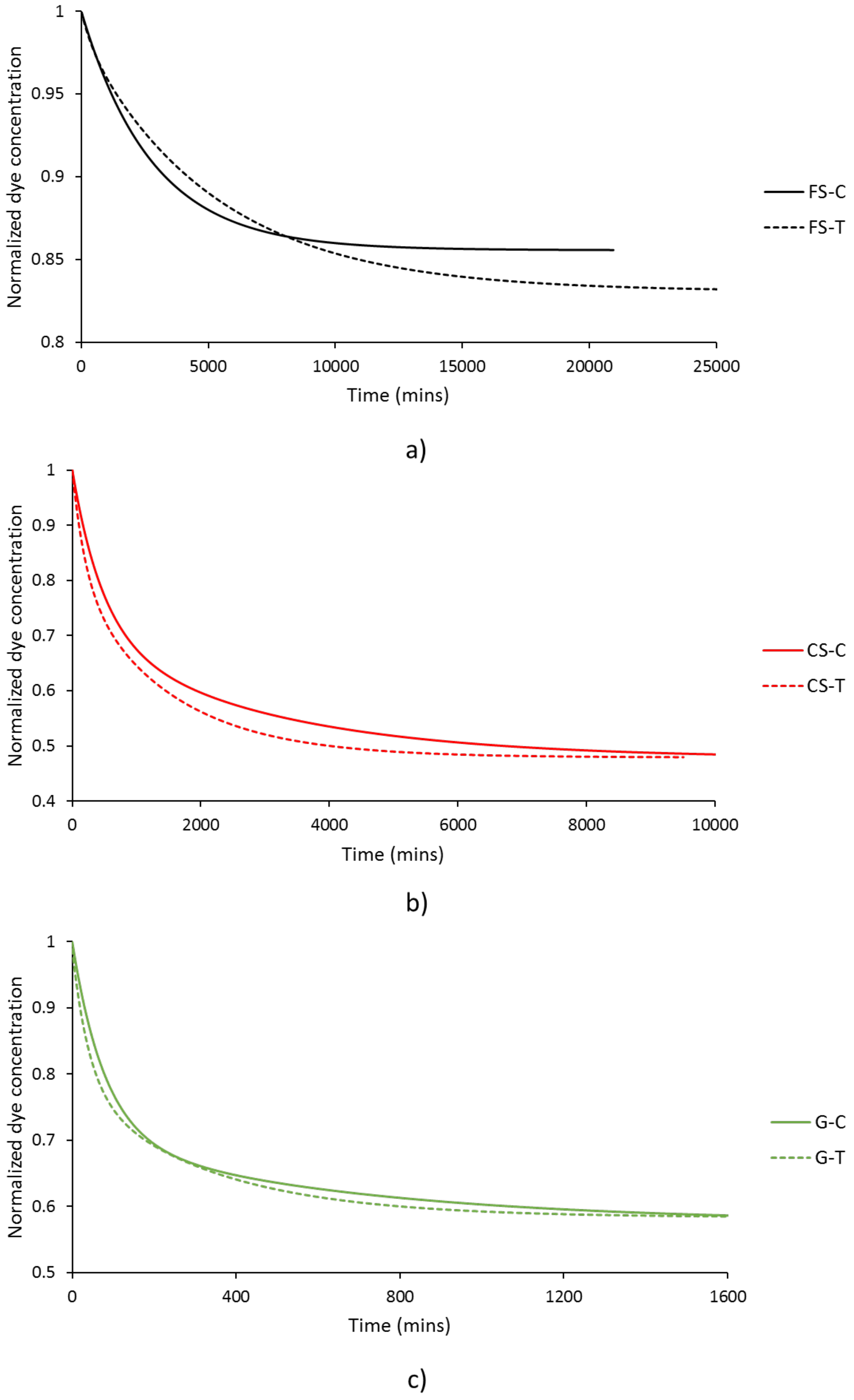


Figure 5.8: Breakthrough curves for control (solid lines) and treatment (dashed lines) flumes with a) fine sand b) coarse sand and c) gravel, obtained from fitting the time-series of dye concentration in water column.The root mean square error (RMSE) values for all the fits are less than 0.006.

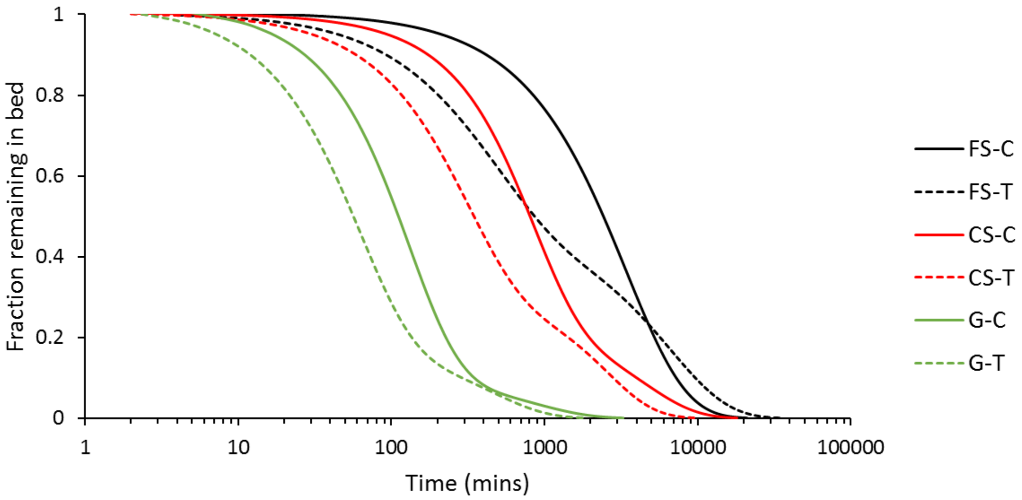


Figure 5.9: Flux-weighted cumulative residence time distribution for the dye tracer in control and treatment flumes of each sediment type.

In general, flumes with gravel beds exhibited lower RT_{med} than flumes with fine sand and coarse sand (Figure 5.9). For each sediment type, the RT_{med} and RT_{mean}were shorter in treatments compared to their respective control flumes (Table 5.1).

The q (estimated from break through curves presented in Figure 5.8) were highest in flumes with gravel and lowest in flumes with fine sand. For all three sediment types, treatments exhibited higher q than their respective control flumes (Table 5.1). The q in treatments 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 q' was consistently lower than q and within 70% of the latter (Figure 5.10) The hyporheic flux (proportions of q) in treatments with short residence time ranges; less than 404 mins, 148 mins and 55 mins for fine sand, coarse sand and gravel respectively, were consistently higher than their control flume for each sediment type (Figure 5.11). The hyporheic flux for long residence time ranges in FS-T (>8103 mins), CS-T (>2981 mins) and G-T (>403 mins) exhibited higher flux than FS-C, CS-C and G-C respectively. In intermediate residence time ranges, hyporheic flux was lower in FS-T, higher in CS-T sand and almost similar in G-T compared to their respective control flumes. Note that these ranges are derived as explained in Chapter 4.

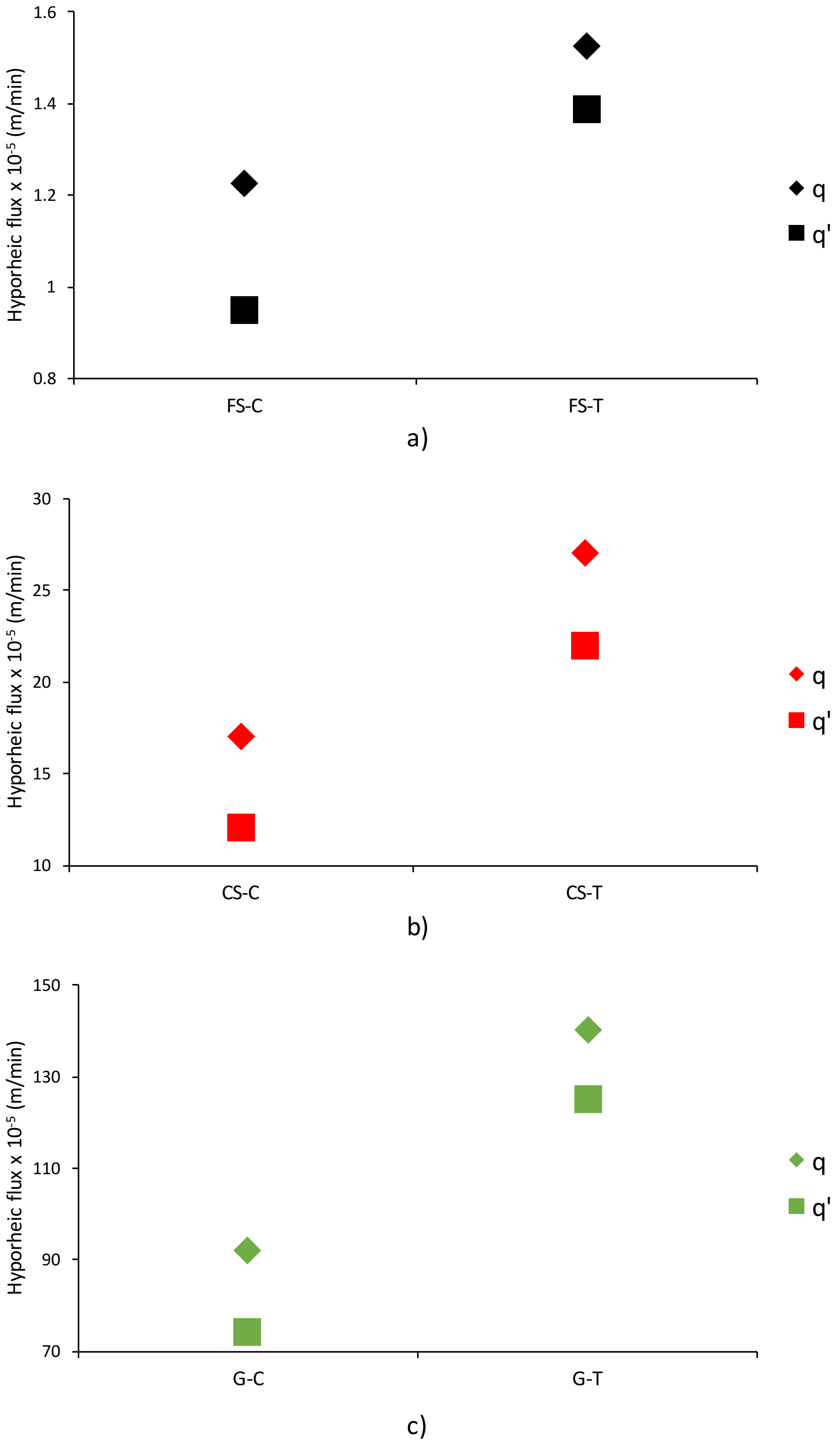
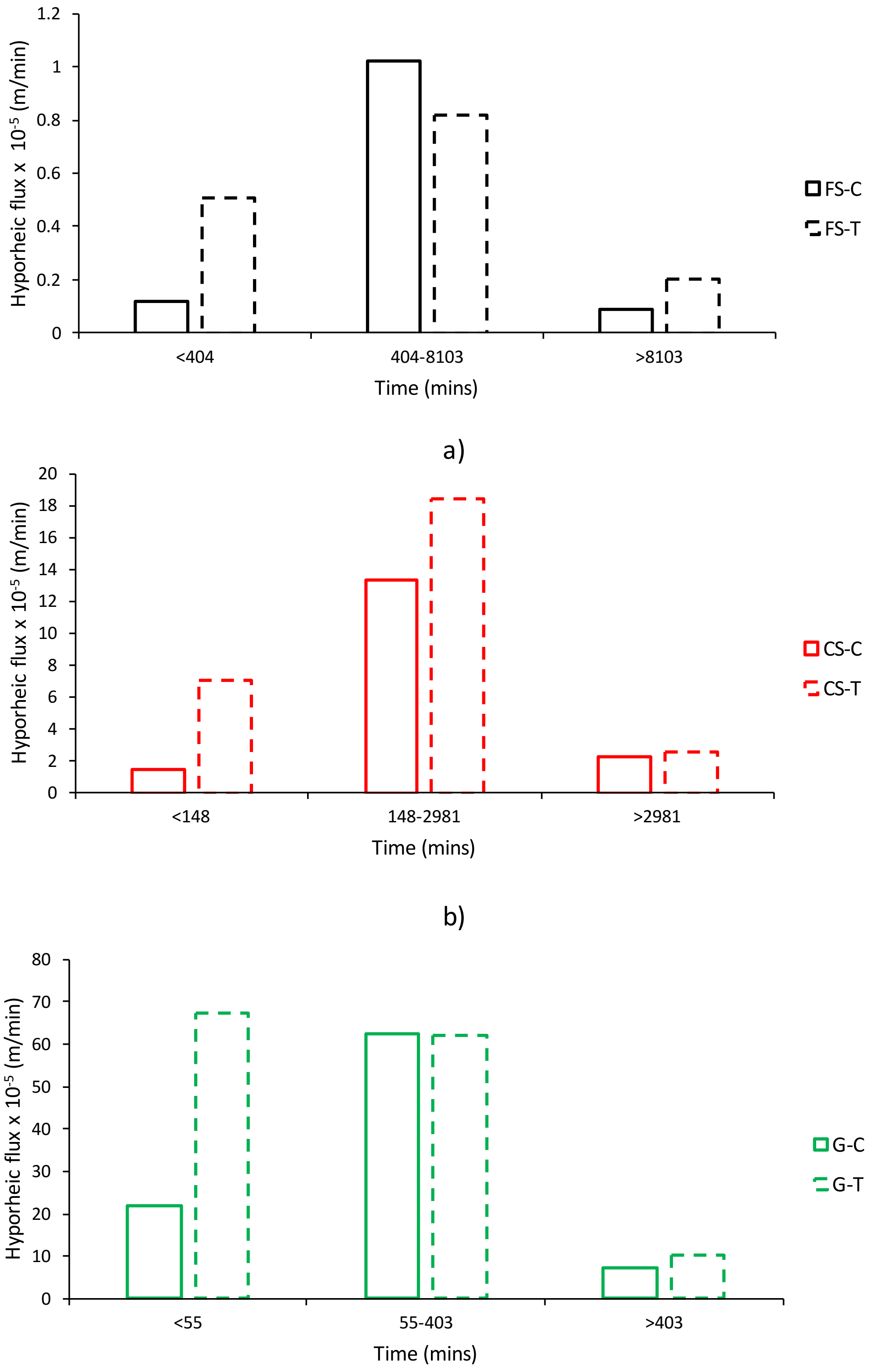


Figure 5.10: Comparison between hyporheic fluxes estimated from initial gradient of break through curve (q), and from depth of penetration and mean residence times (q') in control and treatment flumes with a) fine sand b) coarse sand and c) gravel.



a)

b)

c)

Figure 5.11: Hyporheic residence time distribution shown as flux for short, intermediate and long residence time ranges for control and treatment flumes of each sediment type.

5.4 Discussion

5.4.1 Disturbance to model streambeds

The activities of model bioturbators such as the locomotion, digging or burrowing at the SWI resulted in sequential disappearance of clay layer from the surface. This mitigation of surficial clogging layer could be attributed to transport of clay particles from surface to the underlying bed regions and re-suspension of deposited clay particles into the water column. Vertical transport of clay particles into the bed and their subsequent mixing with the underlying grains occurred due to direct interaction of worms with the deposited fine sediments. Further, worm penetration and locomotion loosened up the densely-packed clogging layer which could have potentially eroded the fine particles at the interface and re-suspended them in surface water. In addition to bioturbation, mobilization of fines would have 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 deposit at the top.

In a conceptual model presented in Chapter 3, it was proposed that modification to structure and hydraulic properties of streambed due to bioturbation depends on the size of an organism and the sub-surface sediment composition (e.g. fine or coarse). In all the treatment flumes, the clay layer deposited at the bed surface was disturbed extensively as the relative size of clay particles & interstitial pores were smaller than size of the model bioturbating organisms. However, interaction of worms with the underlying sediments differed amongst the treatment flumes. In case of FS-T, mobilization and mixing of sand grains (and clay particles), and development of macro-pores due to burrowing occurred readily as sizes of bed-grains and pores were smaller than size of worms (Chapter 3, Figure 3.5). On contrary, after piercing the clogging layer at the top in CS-T, worms could move within the voids leaving the sediment structure in the lower bed layer largely undisturbed. Similarly, the re-working of interstitial clay deposits in G-T (pore size>>worms' size) eventually assimilated into the large pores.

Further, mobilization of bed-grains was limited due to their much larger size rendering bioturbation by smaller organisms ineffective.

5.4.2 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 caused erosion of the fine sediment layer and exposed the underlying coarser bed grains. Consequently, the vertical transport of dye in treatment flumes was enhanced and $\bar{d}$ was greater than the control flume for each sediment type. The bed permeability at the SWI in treatment flumes is expected to be higher than the control flume due to disturbance to the clogging layer. As a result, the dye is exchanged rapidly across the SWI which potentially caused lower 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 $\bar{\mathrm{d}}$ and shorter RT_{mean} in the former.

The re-working of top layer of fine sediments by worms enhanced the hyporheic flux in short residence time ranges for each sediment type (Figure 5.11). It should be also noted from Chapter 4 (Figure 4.8) that the lower hyporheic flux in intermediate residence time range (148-2981 mins) in treatment flumes with coarse sand (clogged flumes, CS-T1 and CS-T2) compared to the control flume was attributed to modification in hyporheic flow field due to clogging by clay particles. The bioturbation by sample organisms mitigated the clogging layer in CS-T which resulted in higher hyporheic flux than in CS-C in intermediate residence time range. The hyporheic flux in corresponding long residence time ranges for coarse sand and gravel were similar between their respective control and treatment flumes. This observation is also consistent with results from Chapter 4 and it could be attributed to underflow in the flumes.

The higher hyporheic flux in FS-T compared to FS-C in long residence time range (>8103 mins) could be attributed to greater $\bar{d}$ 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 worms' activities which occurred via mitigation of clogging layer and interaction with underlying bed grains. The clay particles deposited on and accumulated within the bed framework were re-worked in all the treatments as worms moved, fed & egested, dug the surface and constructed burrows. However, these activities modified the structure and hydraulic properties of lower layers in the treatments to different extent. For instance, rapid vertical exchange upon mitigation of clogging layer at the top caused lower RT_{med} and RT_{mean}, and higher q' in treatment flumes with coarse grains. However, the flow in lower layers of the bed is not expected to be altered to the same extent (as discussed in section 5.4.1), and therefore, $\bar{d}$ was only marginally greater than their respective control flumes. In contrast, worms mixed & mobilized the sand grains and built extensive burrows in the top layer of bed sediments. This could have potentially resulted in dye transport to much deeper regions, thus, greater $\bar{d}$ 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 (Nogaro et al., 2006). The authors reported that certain macroinvertebrates could potentially reduce clogging and maintain high hydraulic conductivity. 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 set up is a better representation of stream environment and has been extensively used to study hyporheic exchange in the past (Packman and MacKay, 2003; Rehg et al., 2005; Salehin et al., 2004). Thus, our experimental observations of alteration in dune-induced hyporheic flow in clogged streambeds due to activities of macroinvertebrates are more relevant than previous laboratory investigations.

5.4.3 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 deposition or erosion of fine sediments with the stream flow (Cardenas and Zlotnik, 2003; Leek et al., 2009; Levy et al., 2011; Wu et al., 2015b). In our experiments, the digging and burrowing activities by model organisms resulted in vertical transport of fine sediments into the bed or their re-suspension into surface water. The re-working of fine sediments due to macroinvertebrate bioturbation could potentially increase the permeability of clogged streambeds. Further, distribution of worms and their activities along the flumes were not homogenous suggesting that sediment-organism interactions could be spatially patchy. Thus, variability in permeability due to range of actions of in-stream animals must be also considered when studying heterogeneity in streambed permeability. Further, both longitudinal transport (Gottesfeld et al., 2004; Statzner et al., 1996) or consolidation of fine particles (Cardinale et al., 2004) could occur due to organisms with different bioturbation behavior 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 and could have consequences on fine sediment mitigation and management practices.

The alteration in hydraulic properties of streambeds due to macroinvertebrate bioturbation also influences the biogeochemistry of hyporheic zones. The rates of nutrient cycling or pollutant attenuation would get affected by modification in hyporheic flux and residence times of solutes in zones of streambeds which are re-worked by bioturbating organisms. Additionally, macroinvertebrates are regarded as ecosystem engineers (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 impeded movement of water and solutes and could result in development of anoxic environment in deeper bed regions. Such environment is expected to support activities of anaerobic organisms. However, mitigation of clogging due to worm activities could potentially improve the vertical connectivity and supply oxygen from surface water to deeper regions and stimulate activities of aerobic organisms. This modulation in biologically mediated chemical transformations of solutes would potentially influence the overall quality of surface and sub-surface water and thus has implications for stream management and conservation programs that aim to restore biogeochemical functions in streams.

5.4.4 Limitations and future directions

These experiments demonstrate interaction of just one specie with the clogging layer and its subsequent influence on hyporheic exchange across SWI. However, natural streambeds host organisms of different sizes and exhibiting different bioturbation behaviours which could influence the physico-chemical environment of their habitat differently (Meadows and Tait, 1989; Mermillod-Blondin et al., 2004). Further, controlled environment in our re-circulating flumes does not mimic the natural habitat adequately where the specie richness, density and their activities depend on presence of other organisms, their prey-predator relationships and other 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). Furthermore, all the experiments were conducted at a single flow rate such that bed grains or model bioturbating organisms were not washed away. It is likely that the interaction of bioturbating organisms with the clogging layers would have been different if the experiments were conducted at different flow rates (or velocities) within the safe range for organisms and grains. Clearly, comprehending influence of bioturbating organisms on streambed processes is complicated and more intensive laboratory experiments including a mix of species with different sizes and under variable physico-chemical and biological environment must be performed.

Field evidences of modification of hydraulic properties of streambeds due to interplay between fine sediment layers and bioturbation are rare, thus the future research must be also directed to study impacts of sediment-organism interactions at large scales. The observations from our experiments raise a simple question- can voluntary introduction of benthic invertebrates could be a potential strategy to mitigate fine sediment clogging and alter exchange characteristics in natural streambeds? There are a few studies that involved artificial introduction of certain species into the streams, but those were principally inclined towards evaluating its influence on other in-stream communities (Flecker and Townsend, 1994). However, it can be expected that both foreign and native species would have modified the physico-chemical properties of their habitat. Clearly, further advancements in our understanding of interaction between streambeds and bioturbating organisms would result in more comprehensive and successful stream restoration programs.

5.5 Conclusion

Laboratory experiments in re-circulatory flumes were conducted to investigate effects of macroinvertebrate bioturbation on hyporheic exchange in compositionally different streambeds clogged with fine sediments. The model bioturbators (*Lumbriculus variegatus*) re-worked the fine sediments and subsequently eroded the clogging layer. Due to mitigation of clogging, the permeability at SWI improved which resulted in enhanced vertical connectivity in treatment flumes compared to control flumes. For all the treatment flumes- penetration depths were greater, mean & median residence times were shorter and hyporheic fluxes were higher than the control flumes. Our experiments reveal that the modification to hyporheic flow characteristics in the treatments was dependent on interaction of organisms with both fine sediments and underlying bed grains. The results also highlight that size of bioturbating 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 evidences of sediment-organism interactions should be the focus of imminent studies to advance our understanding of role of macroinvertebrate bioturbation in stream ecosystems.

Chapter 6

Discussions

Streambed permeability (or closely associated hydraulic conductivity) is a crucial hydraulic property of streambed sediments influencing the hydrological, biogeochemical and ecological functions in streams. The literature review identifies that there is a limited understanding of role of fundamental in-stream abiotic and biotic processes (particularly the latter), and the mutual feedback between them which modify streambed permeability. These processes include fine sediment clogging (abiotic), bioclogging (biotic) and bioturbation (biotic).

The clogging due to accumulation of fine sediments and bacterial mass reduces the permeability whereas, bioturbating organisms could potentially increase the permeability by their activities such as movement, food foraging and construction of burrows. Thus, each of these processes could influence the exchange of mass and energy across the SWI and potentially alter stream ecosystem functions. Moreover, these physical and biological components co-occur in natural settings and feedback mechanisms exist between them (Chapter 2, Figure 2.1). For example, microbial film could serve as food source for bioturbating organisms and influence their activities. In turn, the re-distribution of organic matter in form of faecal pellets by invertebrates could cause development of spatially heterogeneous biofilms.

Similarly, while growth of bacterial mass could clog the pore spaces, it may also stabilize bed sediments against erosion during flood disturbances (known as biostabilization). Additionally, both the growth of microbial mass and activities of bioturbating organisms depend on the sedimentary composition of the bed.

6.1 Synthesis of results

The research presented in this work highlights the individual and synergistic influence of macroinvertebrate bioturbation and fine sediment clogging on streambed properties and subsequently on hyporheic exchange in streams. The findings from the experimental work reveals that these processes could influence the two key drivers of hyporheic exchange at small-scales: a) permeability of the bed sediments; and b) pressure gradients over the bed surface. By altering the hyporheic flow regime, these processes can have significant consequences for biogeochemical and ecological services provided by streams.

The literature review (Chapter 2) underlines that the role of bioturbation process in influencing functioning of stream ecosystem has not been studied in detail. The previous work investigating the influence of activities of bioturbating organisms on exchange of mass and energy across SWI have been conducted in vertical columns (Mermillod-Blondin, 2011; Mermillod-Blondin et al., 2003; Nogaro et al., 2006). These studies do not account for complex hydrodynamics that exist at the SWI in lotic environments (flowing water) due to presence of wide range of topographical features at the bed surface (Boano et al., 2014). Therefore, in this work, the experiments were designed in re-circulating flumes to advance the fundamental understanding of bioturbation process in stream environments. The results indicate that activities of bioturbating organisms could generate heterogeneous & anisotropic permeability field in the streambed and alter its morphology. The re-working of sediment beds resulted in modification of hyporheic flux, penetration depths and residence time distributions.

Further, it is well known the permeability of streambeds could get modified due to fine sediment clogging. However, the interplay of fine sediments and hydrodynamics at the SWI has not been subject to a lot of research. In this work, evidence of preferential deposition of clay-sized fine sediments into the streambeds occurring through downwelling hyporheic flow paths is provided. The assessment of clogging profiles indicates that the relative size of fine & substrate sediments and the concentration of fine sediments in surface water influence the depositional patterns. In turn, this deposition would induce heterogeneity in the structure, composition and hydraulic properties of streambeds, and inhibit hyporheic exchange across SWI.

In natural settings, fine sediment clogging and bioturbation processes co-exist and mutually interact to alter streambed properties in space and time. The literature review identified that only a few studies have provided evidence of interplay between these processes in stream environments. The experimental research in this work demonstrated that macroinvertebrate bioturbation could potentially mitigate clogging by mixing the fine sediments with the underlying grains or re-suspending them into the surface water. This could enhance vertical connectivity in stream ecosystems and promote hyporheic exchange. These experiments also reveal that size of bioturbating organisms and composition of bed sediments are important controls on the extent to which organisms modify their habitat. If the grain size and pores are much larger than the body size of bioturbating organisms, the beds would not be actively re-worked as the organisms could easily move between the large pore throats without necessarily digging the bed or constructing burrows. In such cases, the influence of sediment-organism interaction on exchange of mass and energy across SWI would be limited.

Bioturbation and fine sediment clogging processes have an associated spatio-temporal variability. Thus, these processes and their interactions could result in heterogeneous modification of bed permeability and related ecosystem functions. From the experiments in

Chapter 3, it was observed that the model bioturbating organisms were present in large numbers at stoss side of the dunes' troughs. These regions correspond to the downwelling regions for a dune-induced hyporheic flow which are expected to be well-oxygenated and provide conducive environment for the worms to dwell. This suggests that the crest regions were only minimally re-worked by the model bioturbating organisms. The deposition/intrusion of fine sediments also varies in space and time, thus the modification in bed permeability due to fine sediment clogging could be also heterogeneous. For instance, preferential infiltration of clay particles along downwelling hyporheic flow paths in experimental flumes with coarse sand and gravel sediments was observed. (Chapter 4). This local variability in accumulation of clay particles could potentially cause produce a heterogeneous permeability field within the dune structure. Further, Chapter 5 provides evidence of mobilization of fine sediments from the surface layer to deeper regions and their subsequent mixing with underlying grains as a result of bioturbation. Thus, macroinvertebrate bioturbation could potentially re-organize the deposit of fines and modify hydraulic properties of the pore matrix. Besides the experimental work, the evidence of variability in these processes reported in the literature at large scales is presented in Chapter 2.

Overall, the fundamental premise of this PhD is that the streambed properties and subsequently the associated ecosystem functions are influenced by interacting abiotic and biotic processes, therefore, streambeds must be studied as complex systems. The fine sediments, bioturbating organisms and microbial communities are three crucial and coupled components of this system. The experimental research conducted in this work provides valuable insights into modification of structure & hydraulic properties of streambed due to bioturbation, fine sediment clogging and their mutual interaction, which ultimately results in alteration of hyporheic flow regime. It is proposed that a better comprehension of the complexity associated with streambed functioning could be achieved by advancing the fundamental knowledge of each of the processes (particularly biotic processes) and their potential interactions.

In the subsequent sections, a detailed discussion around the overall findings from this PhD in context of advancing current understanding of fluvial ecosystem functioning and implications for stream scientists is presented.

6.2 Implications for modelling strategies of hyporheic exchange

The spatial and temporal variability in permeability induced due to these critical processes and interactions between them holds direct implication for theoretical investigations that predict exchange of mass and energy across SWI but assume homogenous and non-transient hydraulic properties of streambeds for simplicity (Boano et al., 2006; Gooseff et al., 2006a). Modelling studies generally adopt permeability based on published values in literature derived for well-sorted sediments or use empirical equations based on grain size distribution of bed sediments (Hester and Doyle, 2008; Kiel and Cardenas, 2014). Only a limited number of numerical modeling approaches that aim to estimate exchange fluxes have accounted for spatially heterogeneous hydraulic properties of streambed (Kurtz et al., 2013; Tang et al., 2017), while the transient nature of its properties has generally not been incorporated. It is likely that the estimates of exchange fluxes based on models that do not account for spatial and temporal variability in streambed permeability could have systematic bias and may not be reliably used by stream managers focussing on restoring biogeochemical transformations and ecological functions in hyporheic zones.

Given bioturbation and bioclogging processes have been subject to little research, a conceptual framework involving effects of these fundamental biotic processes, and their potential interactions with abiotic processes to study spatio-temporal variability in streambed permeability is lacking. In this regard, Chapter 2 highlights the need for developing a conceptual model for temporal evolution of a streambed and its permeability, and as a way forward, presents a potential scenario based on trajectory of responses of fine sediment clogging, bioturbation and bioclogging after a high flow event. In this scenario, a streambed is shown to transit between four successional stages- immediate post-flood phase, early recovery phase, late recovery phase and quasi-equilibrium phase after a flood disturbance (section 2.3.1). It is argued that as a streambed approaches towards attaining a fully-developed state (transitions between last two phases), its structure and hydraulic properties are increasingly influenced by the mutual interactions between in-stream biotic and abiotic processes. The observations from the experimental flumes (Chapter 5) support the arguments presented in this scenario. The control flumes can be thought as early evolutionary stage where the structure and its permeability of streambed is controlled by the transport and accumulation of fine sediments. After introduction of sample invertebrates in the treatment flumes (i.e., as invertebrates re-colonize the streambed post flood disturbance), the bed permeability was modified as organisms interacted with the fine sediments and underlying grains. The experimental results suggest that macroinvertebrate communities could potentially mitigate clogging and the fine sediments could be re-mobilized within the bed or get released into the surface water. This re-working of sediments was shown to modify hyporheic flux, residence times and penetration depths which could expectedly alter the crucial stream ecosystem services.

Arguably, incorporating a streambed evolution model into existing theoretical strategies could assist in understanding spatio-temporal dynamism in bed permeability and subsequently result in more realistic estimates of hydrological exchange across SWI. This could aid stream managers in assessing the evolutionary phases that a streambed undergoes after a flood disturbance. It would also result in better planning of the restoration activities based on the relative importance of the crucial abiotic/biotic processes at different stages of streambed development in influencing sediment permeability.

6.3 Context dependency: importance of bioturbation in stream ecosystems

6.3.1 Context-dependent relevance of bioturbation

Interaction of in-stream organisms with their habitat and subsequent modifications to stream ecosystem functions partially depends on the magnitude and frequency of disturbance events such as high floods (Moore, 2006). More frequent and intense flooding mobilizes the bed load which could destroy biogenic structures built by organisms, transport organisms to downstream regions or even kill them. In such streams, effects of bioturbation process on streambed structure, composition and hydraulic properties are unlikely to be significant. In the case of our experiments, if the flow rates were sufficiently high to re-suspend fine sediments, bed grains and the bioturbating organisms, it can be expected that modifications in streambed properties would have largely been controlled by hydraulic conditions and sedimentary load.

Bioturbation process and its interaction with other abiotic & biotic processes could significantly modify bed properties in such streams which experience less frequent flooding or in regulated streams where the flow conditions are not variable. Similarly, bioturbating organisms could effectively re-work the bed sediments during base flow periods in a stream. This argument is supported by field evidences where bioturbation by crayfish has been reported to influence suspended sediment fluxes and causing diel turbidity cycles during base flow period (Rice et al., 2016). It should be noted that the flow conditions maintained in the experimental flumes (Chapter 3 and Chapter 5) partially represents the flow environment that is expected to be established in streams during later phases (late recovery and quasi-equilibrium phase) of streambed evolution after a flood disturbance. The model bioturbating organism (*Lumbriculus variegatus*) readily dug the bed, built burrows and mobilized sediments, which subsequently altered the hyporheic flow regime in both unclogged (Chapter 3) and clogged (Chapter 5) streambeds. The field evidences in the literature and results from the experiments, taken together, exhibit the potential of bioturbation process in modifying streambed properties and subsequently associated ecosystem functions, which should not be ignored in streams during low flow periods or under stable flow conditions.

6.3.2 Can tiny organisms produce dramatic effects at large scales?

Amongst the plethora of faunal organisms inhabiting streambeds, organisms such as beavers, fish and burrowing invertebrates are identified as ecosystem engineers (Jones et al., 1994; Moore, 2006; Shirakawa et al., 2013). These organisms could directly or indirectly alter the availability of resources for other organisms by modifying the physical environment of the habitat. By doing so, these organisms have also been shown to influence stream metabolism (Holtgrieve and Schindler, 2011), nutrient cycling (Moore et al., 2007) and sediment transport (Albertson and Daniels, 2018; Creed Jr and Reed, 2004).

Although limited, but there are a few evidences of modification of structure and properties of sediment beds due to bioturbation at large scales (Song et al., 2010; Volkenborn et al., 2007a; Volkenborn et al., 2007b). For instance, a study conducted in marine environment indicates that exclusion of native bioturbating organism (lugworms) from a 400 m^2 area of intertidal fine sand caused enhanced accumulation of fine particles, reduced the permeability (eight-fold reduction) and resulted in limited penetration of oxygen compared to the area which was re-worked by the lug worms (Volkenborn et al., 2007b). The re-working activities created micro-topography (pit-and-mound), maintained sediment permeability and caused enhanced exchange across the SWI. The maintenance of high hydraulic conductivity in upper layer of streambed due to activities of bioturbating organisms has been demonstrated (Song et al., 2010). Further bioturbating organisms have been also associated with sediment-transport in streams, and the bed permeability is expected to modify as the fine sediments are re-suspended or stabilized as a result of bioturbation. For instance, the activities of net-spinning caddisflies (a lotic insect) have been associated with increasing the stability of habitat and making the sediments less susceptible to re-mobilization during floods (Albertson et al., 2019; Cardinale et al., 2004). In contrast, bioturbation by benthic invertebrates such as stoneflies or crayfish causes mobilization of bed sediments and fine sediments, and thus reduces fine sediment accumulation in streambeds (Johnson et al., 2011; Statzner et al., 2000; Zanetell and Peckarsky, 1996). In another study that analysed bedload transport data in streams, the activities of mass spawning salmon mobilized half of the annual bed load yield on an average (Hassan et al., 2008). There is also evidence of influence on nutrient transport and cycling by activities of macroinvertebrates (Covich et al., 1999; Wallace and Webster, 1996), fish (Janetski et al., 2009; McIntyre et al., 2008) and mussels (Vaughn, 2018).

In addition to the field evidences, the experimental findings in this work indicate that bioturbating organisms could readily modify streambed properties and mitigate clogging provided the environmental conditions are appropriate. The observed variation in hyporheic flux, residence time distributions and penetration depths between the control and treatment flumes in Chapter 3 and Chapter 5 is large, which holds implication for biogeochemical transformation of contaminants and nutrients in hyporheic zones. Thus, it can be anticipated that the small-scale re-working activities could have proportionally large effects on functioning of fluvial ecosystems including hydrological exchange across SWI.

6.4 Impact on hyporheic biogeochemistry

One of the primary focus of this research was to assess the influence of bioturbation and fine sediment clogging processes on modifying the bed permeability and subsequently the hyporheic exchange. The modification in hyporheic flux, residence time distributions and penetration depths of solute-laden water has direct consequences for biogeochemistry in the hyporheic zones, which are regarded as a stream’s liver (Fischer et al., 2005). The rate of transformation for chemical species are partially dependent on the availability of reactant and the microbial communities mediating the reactions. Bioturbation and fine sediment clogging could potentially influence both the variables which determine the fate of contaminants and nutrients. In this section, the potential effects of these processes on nitrogenous transformation in hyporheic zones are discussed.

The hyporheic zones support a crucial stream ecosystem function of nitrogen removal from streams. This generally occurs via denitrification (conversion of nitrate into atmospheric nitrogen). Bioturbation and fine sediment clogging processes could modulate the delivery of nitrate into the hyporheic sediments by altering hyporheic flux. The clogging could potentially decrease the flux of nitrate-rich surface water and labile organic carbon into the hyporheic zones, both of which control the rate of denitrification (Harvey et al., 2013). In contrast, bioturbating organisms could construct burrows, mitigate clogging and enhance transfer of nitrate and organic matter into the sediments. It should be also noted that fine sediments have higher adsorption capacity, thus their deposition into the streambeds could potentially increase the nutrient load within the sediments (McDowell and Sharpley, 2001; Ren and Packman, 2004).

In addition to supply of reactants, the rate of transformations is dependent on the time for which solutes reside in the biochemically active hyporheic sediments. For instance, Zarnetske et al. (2011) showed that the residence time distributions control whether a hyporheic zone acts as a sink or source of nitrates. If the residence times are longer than the reaction times, then complete conversion of nitrate into atmospheric nitrogen occurs. In case the residence times are not long enough, by-product such as nitrous oxide (greenhouse gas) is emitted from streams (Marzadri et al., 2014). The experimental findings from this work suggest that clogging could increase the residence times of water and solutes in the hyporheic zones. The observation of higher residence times due to fine sediment accumulation is in agreement with a recent theoretical study (Pescimoro et al., 2019). In their work, it was shown that higher residence times could result in efficient removal of nitrates from the streams. However, as noted earlier, the interaction of bioturbating organisms with their habitat could mitigate clogging and reduce residence times. In this case, if the residence times are shorter than the reaction times, the nitrate would not get converted to atmospheric nitrogen and by-products may form.

The nitrogenous transformations are mediated by nitrifying and denitrifying bacteria. The former supports nitrification (conversion of ammonia into nitrate) and needs oxygenated environment whereas, the latter requires anaerobic environment to support denitrification. The experimental findings from Chapter 4 reveal that fine sediment clogging could inhibit the vertical penetration of solutes. The transport of oxygen to limited depths could result in shallow oxic zones in hyporheic sediments. This could potentially support growth of denitrifying bacteria and promote denitrification. In contrast, the delivery of oxygen in anoxic patches of hyporheic zones by burrow building organisms could shift the metabolism from anaerobic to aerobic and support production of nitrates via nitrification (Krantzberg, 1985). This could also increase rate of reduction of nitrates due to coupled nitrification-denitrification reactions in hyporheic sediments if the nitrate supply is limited (Howe et al., 2004). Besides supplying oxygen to deeper regions through worm burrows, it has also been reported that some freshwater inhabitants consume oxygen from the pore water and potentially create anoxic pockets in sediments (Anschutz et al., 2012). Additionally, deposition of faecal pellets at the interface or within sediments results in re-distribution of organic matter (Wotton and Malmqvist, 2001), which could potentially alter the availability of labile organic carbon for microbial communities and affect their colonization.

Further, the fine sediment clogging and bioturbation processes have an associated spatio-temporal variability, thus, their interactions could generate complex biochemical gradients in the hyporheic zones. For example, the experimental observations from this work suggest that the preferential infiltration of fine sediments and re-working of sediment beds by the model bioturbating organisms occurred at the stoss side of the dune near the trough. As the worms organized themselves largely in these areas, they interacted minimally with the sediments near the crests. The heterogeneous modification of bed structure & hydraulic properties indicates spatial variability in nutrient supply and microbial communities within the streambed which could alter biogeochemical functions in streams.

The discussion above indicates that the bioturbation, fine sediment clogging and their potential interactions have complex effects on the biogeochemistry of hyporheic zones and this raises some important questions. For instance, what is the influence of increased fine sediment delivery into streams on biogeochemistry of hyporheic zones? Can the nitrate loss from regulated streams be tuned by modifying the proportion of fine sediments or voluntary addition of bioturbating organisms? Is it possible to achieve stream restoration targets in context of water quality by modifying hyporheic flow regimes? In the flume experiments, the magnitude of observed variation in hyporheic flow characteristics due to these process is large, and suggest these processes could have significant influence on the overall quality of surface and pore water in the stream ecosystems. However, additional research is required at both small and large scales to understand influence of these processes on biogeochemical functions of hyporheic zones.

6.5 Directions for future work

Not all the causal pathways through which bioturbation could influence morphology & hydraulic properties of streambeds and subsequently the hyporheic exchange (presented in Chapter 3) were studied due to the limited scope of experiments. For example, experiments related to bioturbation (Chapters 3 and 5) were performed with only one type of bioturbating organism, *Lumbriculus variegatus*, which has a specific bioturbation behaviour. There is evidence of modification of hydraulic properties of streambeds to different extents based on functional behaviour of organisms (Meadows and Tait, 1989). Further, streambeds host a wide range of faunal organisms that co-exist and interact with each other depending on their prey-predator relationships which could again alter the activities of bioturbating organisms. Thus, future experimentation could be directed to study influence of mix of species having different body sizes, bioturbation behaviour and subject to different environmental conditions (e.g. flow rates, temperature). Additionally, field evidences of bioturbation are scarce, thus more research at larger scales must be conducted to advance our understanding of role of bioturbation in fluvial ecosystems.

X-ray computed tomography (CT) is a useful imaging technique to obtain 3-D geometries of pore matrix. The re-working of fine sediments and bed grains could be studied by comparing CT scans of cores sampled from the control and treatment flumes. This could also provide information related to density of burrows & their average size and if any sorting of bed grains occurs due to bioturbation. It is an on-going work in collaboration with Department of Earth Sciences at the University of Melbourne.

The flume experiments focussed on studying distribution of fine sediments in model streambeds were carried with ‘box clay’. This fine sediment has a specific chemical composition and grain size distribution. Streams are laden with both organic and inorganic colloidal particles and it is expected that their transport and retention properties could vary based on size and chemical nature of particles. Thus, the imminent experiments could explore infiltration patterns of fines of different sizes & chemical properties, at different concentrations and by varying other variables such as flow velocity and bed-form morphology. In addition, future research must be also directed to study clogging profiles in mobile streambeds as they exhibit different depositional patterns than static beds (Dudill et al., 2017). Further, Chapter 2 points out that limited attention has been given to clogging by microbial organisms in streambeds. Thus, future research must also focus at studying bioclogging at both small and large scales to comprehensively understand mechanisms of reduction in hydraulic properties of streambeds.

While this work points toward physical modification of streambeds due to fine sediment clogging and bioturbation, their subsequent effects on hyporheic biogeochemistry is a subject of future investigation. The modulations in hyporheic flux, residence times and penetration depth of solutes is expected to alter biogeochemical transformation of nutrients and contaminants which ultimately affects overall water quality in surface and sub-surface water.

Chapter 7

Summary and conclusions

Streambed permeability has been observed to vary over several orders of magnitude, however, the understanding of in-stream abiotic and biotic processes, and mutual feedbacks between them which cause this variability is underdeveloped. The heterogeneity induced to these processes is expected to modify hyporheic flow across the sediment-water interface (SWI), which in turn, alters stream ecosystem services such as biogeochemical cycling. The literature review presented in Chapter 2 identifies fine sediment clogging, bioturbation and bioclogging as critical environmental processes that could potentially modify streambed permeability. It highlights that the role of biotic processes and their interactions with abiotic processes in influencing stream functions including hyporheic exchange flows has been understudied. Further, it suggests the need for developing a streambed evolution model based on trajectory of response of these three processes after a flood disturbance. The focus of this PhD work was to advance our current understanding of bioturbation & fine sediment clogging processes and their interactions in stream ecosystems.

The earlier experimentation that investigated the role of bioturbation in affecting the exchange of mass and energy across SWI in freshwater sediments has mostly been conducted in infiltration columns (standing water), and therefore, the results are not transferrable to lotic environments. To advance our understanding of bioturbation process in stream environments, a conceptual model describing the causal pathways through which bioturbating organisms could modify hyporheic exchange in streams is presented in Chapter 3. The model proposes that activities of riverine fauna could alter both the major drivers of small-scale hyporheic flow i.e., the pressure gradients over bed surface and the permeability of bed sediments. To test the arguments presented in the model, experiments were conducted in re-circulating flumes to study the modification of hyporheic flux, residence time distributions and penetration depth of solutes in sandy streambeds due to bioturbation by a freshwater oligochaete, *Lumbriculus variegatus*, with a control (flume without organisms) and treatment (flume with organisms) design. The results indicated that activities of model bioturbators could modify the bed morphology and generate heterogeneous & anisotropic permeability in the zone of re-worked sediments which subsequently alters the hyporheic flow regime. The treatment flumes exhibited both higher and lower solute penetration depths and hyporheic flux than the control. The mean residence times were higher in the former.

These experiments were directed to also explore the effects of size of bioturbating organisms and their contact time with the sediments on the degree to which exchange characteristics are modified. The results from these experiments suggested that if the size of bioturbating organism is larger than the pore size, exchange across SWI could occur at faster rate through the network of voluminous burrows and macro-pores developed due to bioturbation activity. The findings also indicated that a greater volume of bed is re-worked as the contact time of bioturbating organisms with the sediments increases. Thus, the organisms could dig deeper into the bed and construct a dense network of galleries which could potentially increase the penetration depths and hyporheic flux.

Chapter 4 investigated the depositional profiles of fine sediments in compositionally different streambeds comprising of fine sand, coarse sand and gravel sediments with dune morphology, and assessed the subsequent effect of this fine sediment clogging on dune-induced hyporheic exchange. The clogging profiles observed in model streambeds suggest that the distribution of clay-sized sediments in the pore matrix could not be adequately predicted by considering only the relative size of fine sediment and substrate material. The clay-sized sediments exhibited different depositional profiles in streambeds as their concentration in the surface water change. For instance, under similar flow conditions, clay particles infiltrated into the coarse sand bed when present in low concentration in the surface water, but tend to deposit at the top and formed a clogging layer when the bed was subjected to higher fine sediment concentration. The deposition of fine sediments on or into the streambed resulted in reduction of its permeability. Consequently, the hyporheic flux and penetration depths of solutes were lower, while the mean residence times were higher in treatment flumes compared to their respective control flumes. Finally, the comparison of impact of clogging on exchange across SWI in fine- and coarse-grained sediments revealed that clay-sized sediments have greater influence on exchange characteristics in the latter.

The potential of macroinvertebrate bioturbation in mitigating the clogging and enhancing vertical exchange between surface and pore water in stream ecosystems was studied in Chapter 5. The model bioturbating organisms re-worked the deposits of fine sediment (clay particles) both at the SWI and within the pore matrix which resulted in mobilization of fine sediments and their mixing with underlying grains. Worms’ bioturbation eventually reduced the clogging and increased the permeability of model streambeds. Consequently, greater solute penetration depth, shorter median & mean residence times and higher hyporheic flux was observed in treatment flumes compared to their respective control flumes. The experimental observations also support some of the arguments presented in Chapter 2 related to feedback mechanisms between these processes. For instance, the extent of modification of hyporheic flow characteristics due to bioturbation in clogged streambeds was dependent on disturbance caused to both fine and substrate sediments, which in turn, was affected by the relative size of bioturbating organisms and overall bed composition.

Overall, this PhD work contributes to the body of literature by providing valuable insights into bioturbation and fine sediment clogging processes in stream ecosystems. It underlines that these processes could potentially modify sedimentary structure and hydraulic properties such as permeability of streambeds, which ultimately alters hyporheic flow across SWI in streams. Finally, this work advocates that in-stream biotic and abiotic processes co-occur and interact with each other, and it calls for additional research with an interdisciplinary focus to further advance our current understanding of role of these processes in impacting functions of stream ecosystems.

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