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The importance of substrate heterogeneity and vertical hydrological connectivity for ecological diversity

Mathers Kate L.[1], Robinson Christopher T.[2,3], Weber Christine[2], Wood Paul J.[1]
[1] *Loughborough University, UK*
[2] *Swiss Federal Institute of Aquatic Science and Technology Eawag, Switzerland*
[3] *ETH Zurich, Switzerland*

I. Introduction

Natural streams are characterised by high levels of spatial and temporal heterogeneity in substrate conditions, which in turn supports diverse plant and animal communities. High levels of instream substrate heterogeneity typically result in greater resilience of stream communities to disturbance events through the provision of refugia habitats [1]. However, anthropogenic activities, including disruptions to bedload transport, have resulted in the homogenisation of riverbeds and their associated ecological communities. Many rivers across the globe have been impounded [2], modifying connectivity in four dimensions (longitudinally, laterally, vertically and temporally sensu [3]) and thereby disrupting the natural spatio-temporal heterogeneity of riverine processes (e.g. geomorphological, hydrological and ecological). One widely associated consequence of flow impoundments and residual flows (a minimum discharge rate that is maintained) in the absence of flushing flows and bedload transport is the excessive accumulation of fine sediment (sedimentation; typically referred to as particles $<$2 mm [4].

Fine sedimentation and clogging of interstitial pore space is widely considered to be one of the most significant threats to riverine ecosystem integrity and functioning globally. Where substrate clogging occurs, the transfer of resources and movement of organisms below the clogged layer may become prohibited with the hyporheic zone effectively becoming disconnected from surface waters [5]. However, a vertically connected and healthy hyporheic zone is vital to maintain wider ecosystem functioning [6]. Despite several early papers that identified the potential importance of vertical hydraulic connectivity (e.g. [7, 8]), the linkages between surface waters and groundwater (hyporheic flows) remains poorly studied and is typically not considered in riverine management schemes. This remains a significant knowledge gap given it can sustain fundamental processes such as carbon processing even in the absence of surface flows [9]. In many streams, invertebrate production in hyporheic sediments can exceed that of the benthos [10]. Furthermore, many taxa and early life stages of aquatic invertebrates use the hyporheic zone as a refuge from predation and perturbations [11, 12], and the more stable and predictable conditions present in hyporheic substrates are important for the development of eggs, pupae, diapausing stages of invertebrates as well as fish embryos [13].

The processes and conditions that control vertical hydrological exchange vary at different spatial scales, from reach to meso-scale (m-mm). At large scales, hyporheic water exchange may be influenced by landscape features such as valley width, depth of bedrock and aquifer properties, whilst at the reach scale, variability in bed topography, substrate composition and porosity all influence the vertical hydraulic exchange regime [14]. Substratum diversity is therefore an integral characteristic controlling exchange patterns which results in the hydraulic conductivity of most streambeds typically being heterogeneous [15]. As such, the loss of the natural dynamic flow regime via impoundment, resultant reductions in bedload transport and the subsequent accumulation of excessive fine sediment deposits threaten the ecological integrity of riverine systems.

This paper will reflect on: the importance of vertical connectivity and substate diversity in controlling macroinvertebrate community composition at the riffle scale; will demonstrate the influence of vertical hydrological exchange and negative implications of excessive fine sediment deposition for macroinvertebrate utilisation of subsurface sediments using laboratory experiments; will demonstrate the disconnection of the hyporheic zone within residual flow reaches as a consequence of excessive fine sediment deposition; and finally will reflect on the potential for experimental flow regimes to restore vertical substrate connectivity.

II. The Importance Of Vertical Hydrological Exchange At The Riffle Scale For substrate Composition And Macroinvertebrate community Composition

The use of an in-situ field experiment allowed the examination of the ingress and storage of fine sediment in subsurface substrates at the riffle scale [16]. Benthic and hyporheic macroinvertebrate communities from the riffle head and tail were also quantified. The study stream, Blackbrook, is a small UK lowland river regulated via a small reservoir 800 m upstream of the study reaches with discharge values during the study period indicating stable but gradually declining baseflow values (average 6.5 m^3). The river predominantly drains pastoral agricultural land and rises to a height of 250 m. Benthic macroinvertebrate assemblages were found to differ between the head and tail of riffles (Figure 1a), illustrating the presence of clear microdistribution patterns of fauna (sensu [17]). The fine sediment content of hyporheic

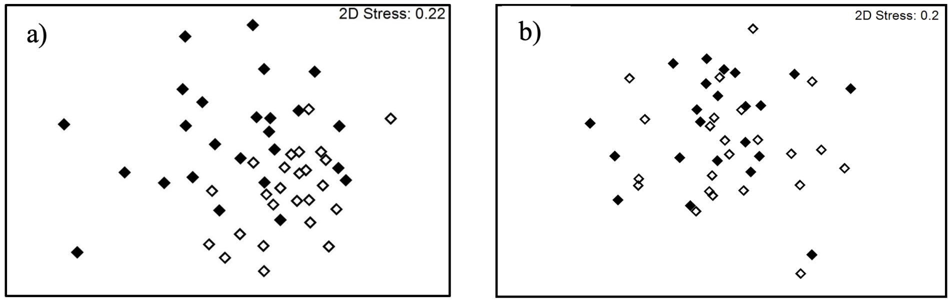

Fig. 1. Non-metric multidimensional scaling (NMDS) of a) benthic macroinvertebrate communities and; b) hyporheic communities from the head and tail of riffles on Blackbrook (UK). Solid symbol = riffle head and open = riffle tail (adapted from [16].

substrates (subsurface sediments) was found to be significantly greater at the riffle heads in this study, reflecting the widely reported characteristics of vertical hydraulic exchange (Figure 2). When present with abundant fine sediment supply conditions, downwelling water is typically associated with the transport of fine sediment into the riverbed at the head of riffles, whilst upwelling water, often at the riffle tail, has the potential to flush fine sediments from interstitial spaces.

In marked contrast to benthic samples, no significant differences in hyporheic communities were evident between head and tail communities (Figure 1b). The lack of differences between hyporheic communities in the two zones in this study may reflect the homogenous nature of the hyporheic zone with clogging of subsurface interstitial spaces (colmation) by fine sediment reducing the available pore spaces between substrates [18] in the absence of high discharge events (Sear, 1993). Other studies have documented that macroinvertebrate diversity is often greatest in downwelling zones [19]. These findings, however, are typically a function of the physiochemical properties of the water (such as dissolved oxygen content) which also influences the macroinvertebrate species found at the micro-scale. Patch scale removal of fine sediment in the same river via the installation of colonisation cylinders to a depth of 20 cm [19] identified significantly different macroinvertebrate communities at the heads and the tails of riffles suggesting that fine sediment content was a limiting factor.

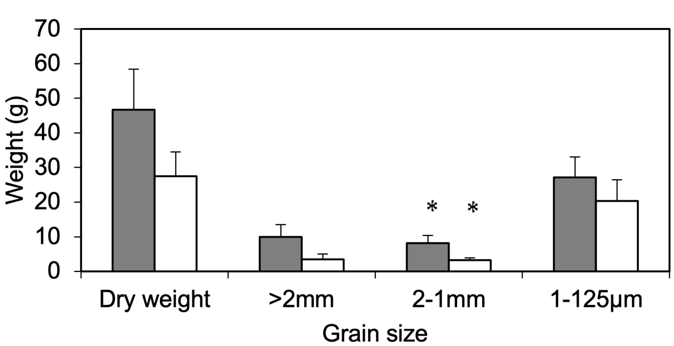

Fig. 2. Mean (±1 Standard Error) fine sediment distribution collected from hyporheic pump samples on Blackbrook (UK). Grey = riffle head and white = riffle tail. Significant differences between the two locations (head and tail) for individual grain sizes are indicated by asterisk ($P<0.05$). Adapted from [16].

III. Macroinvertebrate Response To Benthic And Hyporheic Sedimentation Varies With Direction Of Vertical Hydrological exchange And Particle Size

Utilising an ex-situ laboratory experiment, the vertical distribution of a freshwater amphipod species (*Gammarus pulex*) was examined in response to different patterns of vertical hydrological exchange and sedimentation (benthic – surface and hyporheic – subsurface) within experimental running water mesocosms [5]. The vertical distribution of macroinvertebrates was found to be significantly associated with both the sediment treatment and direction of hydrological exchange, with a significant interaction between the two effects also being evident. Sedimentation of surface sediments (benthic) and one layer of subsurface substratum resulted in amphipods being less abundant within treated than in untreated layers (either above or below the treated layer). Under heavy sedimentation of multiple layers, individuals were typically more abundant in the surficial benthic layer. For all treatments with downwelling water, the abundance of amphipods declined with depth regardless of fine sediment distribution (surface or subsurface) or volume (single or multiple layers of the column). However, under upwelling flow conditions with or without sedimentation of one layer (surface or subsurface), the majority of *G. pulex* migrated to the deepest layer of subsurface substratum.

Building on this work, the particle size of the fine sediment also plays an influential role in controlling the vertical distribution of macroinvertebrates (Figure 4; [21]). Increasing the particle size and heterogeneity of fine sediment exerts a strong influence on the propensity for clog formation and the ability of individuals to access deeper layers of the column. Coarse sand (1-4 mm) treatments resulted in the formation of surface clogs with particles unable to percolate into the subsurface and the bridging of pore spaces [22] even at the lowest sediment loadings. This effect was most marked for heterogeneous sand (0.125–4 mm) which had the strongest filtering effect on macroinvertebrate use of subsurface substrates.

IV. The potential role of artificial floods in reducing fine sediment clogs and restoring hyporheic accessibility for macroinvertebrates

Using an artificial flood associated with the release of water from an impoundment in September 2018, the biotic and

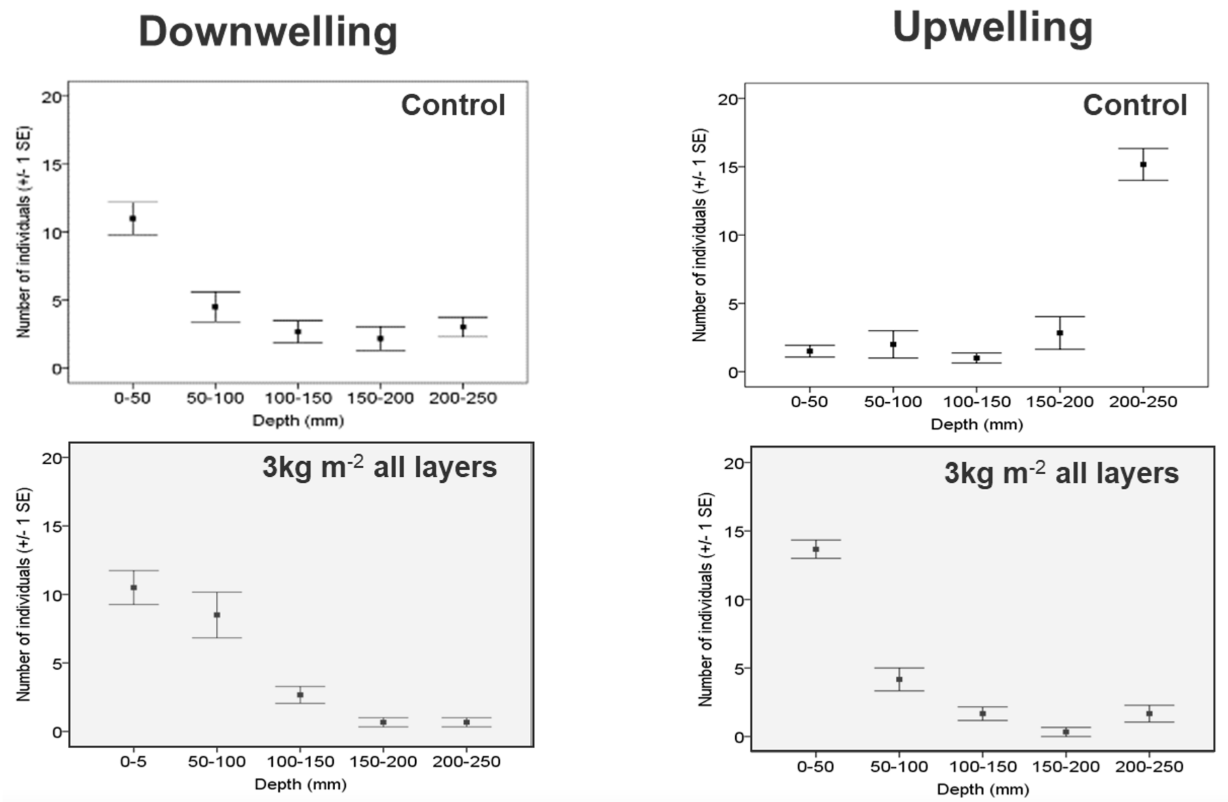

Fig. 3. Mean number of *Gammarus pulex* (±1SE) recorded within each section of the sediment column (0–50 mm; 50–100 mm; 100–150 mm; 150–200 mm and 200–250 mm) during downwelling and upwelling flow under control (no sedimentation) and heavy sedimentation of all sediment layers of the experimental column. Adapted from [5].

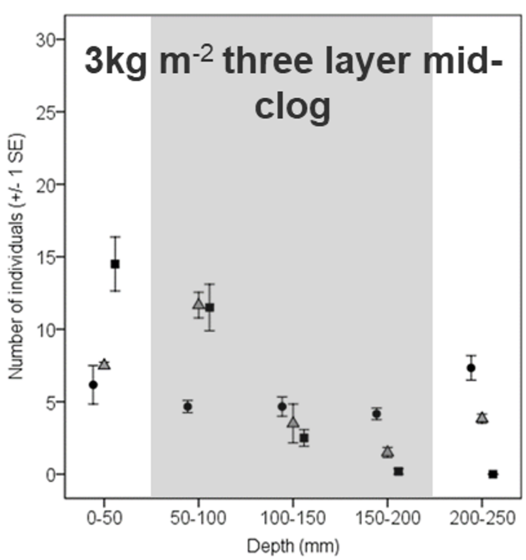

Fig. 4. Mean number of *Gammarus pulex* (±1 standard error) recorded within each section of the sediment column (0–50 mm; 50–100 mm; 100–150 mm; 150–200 mm and 200–250 mm) during downwelling flow sedimentation of three sediment layers of the experimental column. Solid circles = fine sand (0.125–1 mm); grey circles = coarse sand (1–4 mm) and; solid squares = heterogeneous sand (0.125–4 mm). Adapted from [21].

abiotic effects of fine sediment content and hyporheic zone accessibility were examined on the River Spöl in Switzerland [23]. The River Spöl flows in the central Alps and is regulated by two hydroelectric dams. The focus of this study was on the lower section regulated by the Ova Spin reservoir (ca. 1’600 m a.s.l.) with residual flows set to 1 m^3s^{-1} in summer and 0.3 m^3s^{-1} in winter [24]. To restore some semblance of flow integrity, an artificial flood programme was established in 2000 with 13 artificial floods being undertaken in the lower regulated section; the most recent in August 2017. Prior to the artificial flood, residual flows had resulted in excessive fine sediment accumulations within the riverbed from a number of unregulated rivers within the study reach. Following the flood, the fine sediment content of shallow benthic substrates (ca. 10 cm) was significantly reduced. The flushing of fine sediment was also apparent in hyporheic substrates (depths of 0.25 and 0.50 m), resulting in the reconnection of previously clogged interstitial pathways. The opening of interstitial pore space enhanced physicochemical conditions in the hyporheic zone, improving dissolved oxygen concentrations (Figure 5) and resulting in greater taxa richness. Alterations in the composition of shallower hyporheic assemblages (0.25 m) were evident following the flood with three species being recorded in hyporheic substrates that were previously absent. These results indicated that benthic and subsurface interstitial pore space became more connected to surface waters following the flood, thereby facilitating access of the hyporheic zone by

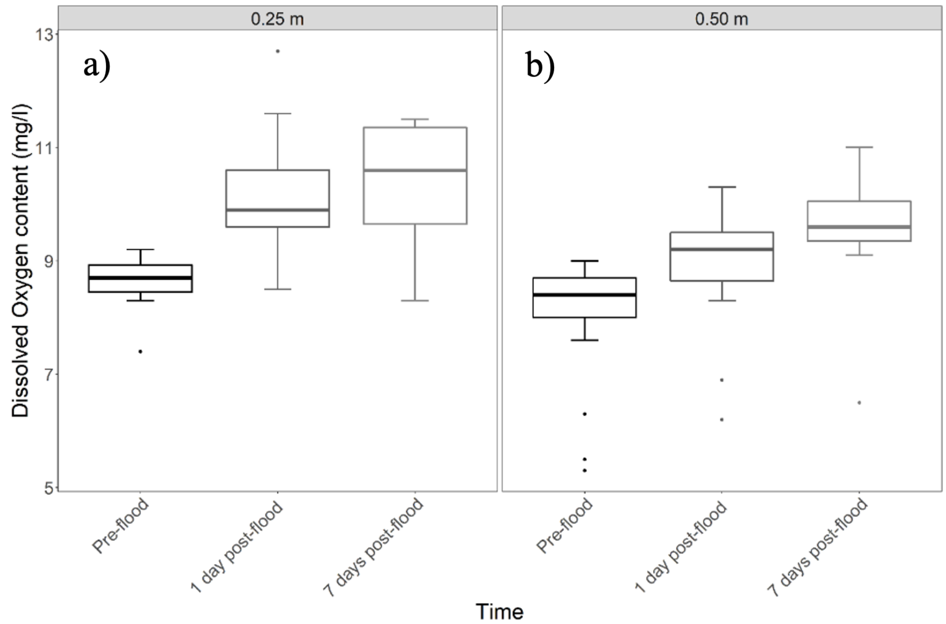

Fig. 5. Boxplots of dissolved oxygen content of hyporheic substrates a) 0.25 m and b) 0.50 m below the riverbed before, 1 day after and 7 days after an artificial flood in the River Spöl in Switzerland. Adapted from [23].

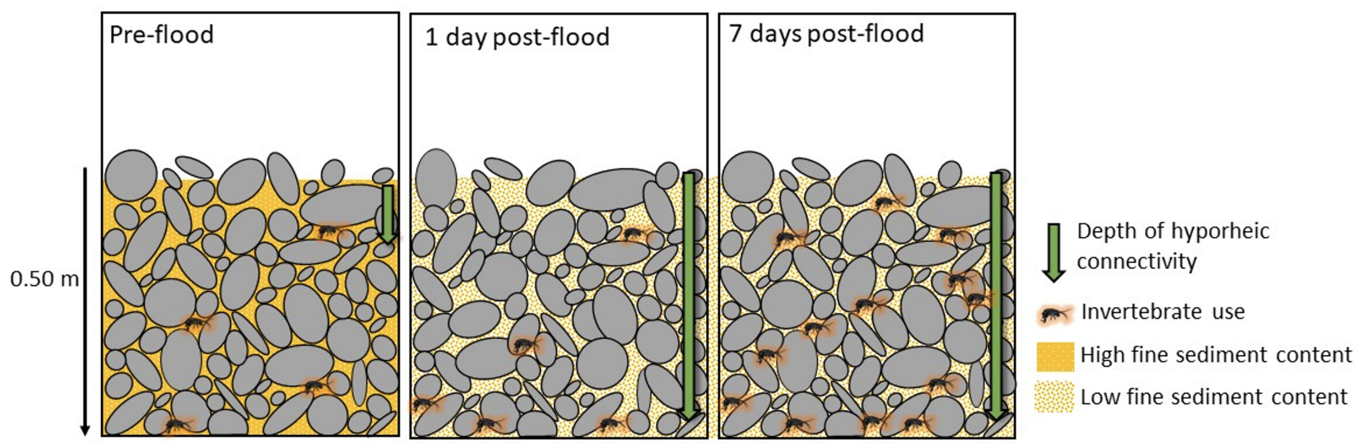

Fig. 6. Conceptualisation of interstitial pore space and hyporheic zone connectivity to 0.50 m depths below the riverbed, before and following the artificial flood in the River Spöl (Switzerland). Adapted from [23].

macroinvertebrate fauna (Figure 6). It is however anticipated that artificial floods would be required on a regular basis given the relatively rapid re-accumulation of fine sediment from the unregulated tributaries.

V. Conclusion

Flow regulation remains an ongoing threat to the integrity of river ecosystems globally [25]. By limiting longitudinal connectivity through the construction of dams, riverbeds are likely to become clogged with fine sediment due to an absence of hydrological events that initiate bedload transport, thereby reducing substrate heterogeneity and subsequently degrading vertical connectivity. Maintaining a healthy and dynamic river system including bedload transport and hydrological events that disturb the armour layer are important for flushing fine sediments from the riverbed. Such events will ensure a spatially and temporally heterogeneous river system that supports diverse benthic and hyporheic macroinvertebrate populations and wider ecosystem functioning.

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