RESEARCH ARTICLE

Artificial flood reduces fine sediment clogging enhancing hyporheic zone physicochemistry and accessibility for macroinvertebrates

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Abstract

1. River regulation globally has reduced the riverine connectivity (longitudinal, lateral and vertically) with significant consequences for their abiotic and biotic components. To restore the ecological integrity of regulated rivers, artificial floods are increasingly being employed in large-scale flow restoration efforts. Despite considerable recognition regarding the ecological and geomorphological effects of artificial floods on benthic habitats, understanding the implications for the hyporheic zone is essentially absent. This void in our management knowledge base is considerable given that one of the most widely associated consequences of flow regulation is excessive deposition of fine sediment (sedimentation; particles <2 mm) that often disconnects the hyporheic zone from surface waters.

2. In this study, we examined the effects of an artificial flood on the hyporheic zone of the River Spöl in Switzerland. Fine sediment content of shallow benthic substrates (ca. 10 cm) was significantly reduced following the flood. The flushing of fine sediment was also apparent in hyporheic substrates (depths of 0.25 and 0.50 m), resulting in a reconnection of previously clogged interstitial pathways. The opening of interstitial pore space enhanced physicochemical conditions in the hyporheic zone, such as improved dissolved oxygen concentrations, and supported greater taxa richness.

3. Alterations in the composition of shallower hyporheic assemblages (0.25 m) were evident following the flood. These results indicated that benthic pore space became more connected to surface waters following the flood, thereby enhancing accessibility for interstitial organisms.

4. Our results suggest that artificial floods can be an effective management tool to restore spatial heterogeneity in sediment composition and pore space and improve vertical connectivity for macroinvertebrates. We anticipate that artificial floods would be required on a regular basis given the re-accumulation of fine sediment 10 months later in our study system. We encourage river managers and scientists

to consider flow disturbance and restoration in a holistic manner that encompasses the multiple spatial dimensions of connectivity, including the hyporheic ecotone.

1 | INTRODUCTION

Hydrological variability is widely acknowledged to play a pivotal role in the structuring and functioning of aquatic ecosystems (Karaouzas et al., 2019; Palmer & Ruhi, 2019). However, many rivers across the globe have been impounded for the purposes of navigation, irrigation, hydropower and water-diversion schemes, and it is estimated that 2.8 million dams (constituting reservoir areas $>10^3$ m^2) regulate over 500,000 km of rivers and canals (Lehner et al., 2011). Despite these large numbers, recent studies indicate this could be a significant underestimate (Belletti et al., 2020; Jones et al., 2019). River fragmentation disrupts the high levels of spatio-temporal heterogeneity that support healthy river systems by reducing a rivers' connectivity longitudinally, laterally and also vertically – the latter being a component that is often overlooked in the management of rivers (Boulton, 2007; Krause et al., 2011; Ward, 1989).

One widely associated consequence of flow impoundments and residual flows (a minimum discharge rate that is maintained) is the excessive accumulation of fine sediment (sedimentation; typically referred to as particles <2 mm) associated with a loss of flushing flows (Baker et al., 2011; Sear, 1993). Fine sediment, when present in excessive quantities, is known to have negative implications for biodiversity, affecting all trophic levels from algae to macroinvertebrates and fish (see reviews by Jones et al., 2012, 2014; Kemp et al., 2011; Wood & Armitage, 1997). Sedimentation can also lead to clogging of interstitial pore space and habitat homogenization (Larsen & Ormerod, 2010; Mathers, Rice et al., 2017). Loss of pore space can reduce the ability of many macroinvertebrate taxa to access subsurface habitats as large bodied taxa are limited from moving through and into subsurface sediments (Mathers, Hill, et al., 2019; Peralta-Maraver et al., 2019).

In response to the negative ecological effects of residual flows, restoration efforts are being widely advocated globally as a means to balance societal and ecosystem demands, for example by environmental flows (Webb et al., 2018; Yarnell et al., 2020). The term environmental flow is typically used to define the quality, quantity and timing of flows needed to sustain freshwater ecosystems whilst enabling human well-being and livelihoods to be maintained (see review by Acreman, 2016). One method of implementing environmental flows and which is seeing increasing recognition is the artificial release of high flows to restore ecological integrity (Konrad et al., 2011; Olden et al., 2014). By implementing high flows on a regular basis in locations of residual flow, environmental managers can seek to restore flushing flows that are otherwise absent, leading to enhanced habitat quality and subsequent

improvements in ecological integrity over time (Ortlepp & Mürle, 2003; Robinson et al., 2003, 2018). Globally, there are a few long-term flood release schemes; two such examples are the Colorado River below Lake Powell in USA and the River Spöl in Switzerland – the focus of this study. Contemporary objectives of high-flow releases are system dependent (Olden et al., 2014) with artificial floods in the Spöl aimed at stimulating a more natural flow regime to restore habitat conditions for the brown trout fishery (Ortlepp & Mürle, 2003; Scheurer & Molinari, 2003). Here, artificial floods have also resulted in shifting macroinvertebrate assemblages over time (Robinson, 2012; Robinson & Uehlinger, 2008; Robinson et al., 2003, 2018). More recently, artificial floods have been used as a management tool following sediment flushing with the aim of remobilizing deposited fine sediment and accelerating biological recovery (Doretto et al., 2019).

Despite a significant body of research examining the ecological and morphological implications of artificial floods for benthic habitats (e.g., Melis et al., 2012; Robinson, 2012; Robinson & Uehlinger, 2008), our understanding of the effects of such floods for the vertical dimension of lotic ecosystems remains essentially absent (but see Hancock & Boulton, 2005 for impacts on hyporheic water quality). This represents a significant deficit in our knowledge base of how environmental flows can restore habitat quality and thus ecological integrity. Where fine sediment clogging occurs, the transfer of resources and organisms below the clogged layer may become limited with the hyporheic zone effectively becoming disconnected from surface waters and sediments (Descloux et al., 2013; Hartwig & Borchardt, 2015; Mathers et al., 2014). Importantly, a vertically connected and healthy hyporheic zone is vital to maintain wider ecosystem functioning (Stanford & Ward, 1993) and it can sustain fundamental processes such as carbon processing even without surface flows (Burrows et al., 2017).

In many streams, invertebrate production in hyporheic sediments can exceed that of the benthos (Boulton et al., 1998; Dorff & Finn, 2020; Smock et al., 1992). Furthermore, many taxa and early instars use the hyporheic zone as a refuge from intra- and interspecific predation (Mathers, Rice, et al., 2019; Vander Vorste et al., 2017) and the more stable and predictable conditions present in hyporheic substrates are important for eggs, pupae, diapausing stages of invertebrates as well as fish embryos (Geist et al., 2002; Malcolm et al., 2005). A well-connected hyporheic zone can act as a refuge during adverse hydrological conditions and has been the focus of a large body of recent work associated with flow intermittency and droughts (Bruno et al., 2020; Maazouzi et al., 2017; Stubbington et al., 2015). The limited number of studies focussing on the use of the hyporheic zone during natural floods
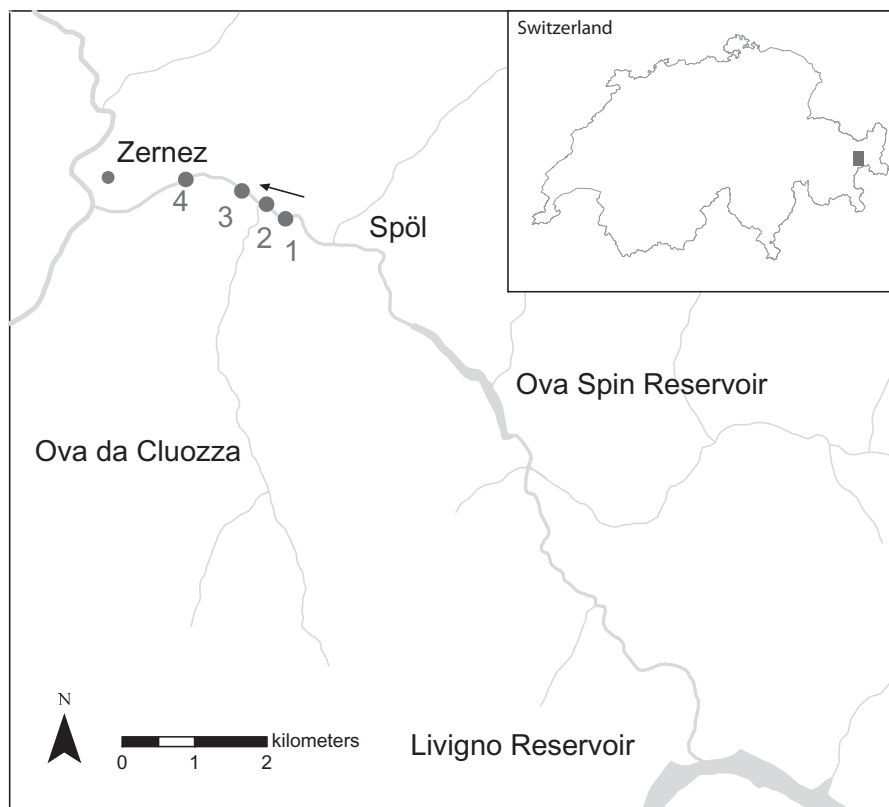
FIGURE 1 Map of the study sites on the River Spöl in the Swiss National Park. The artificial flood was released from the Ova Spin Reservoir in September 2018

have cited its importance as a refuge, although use of the hyporheic zone during flooding remains generally less understood (Dole-Olivier & Marmonier, 1992; Dole-Olivier et al., 1997).

At present, vertical connectivity is often neglected in river restoration efforts and evaluations of management schemes despite historical calls (e.g., Boulton et al., 2010), but is essential to fully restore the health of lotic ecosystems and enhance resilience to future climatic change (Lewandowski et al., 2019; Magliozzi et al., 2019). Consequently, it is important to consider the fine sediment content of surface substrates and connectivity of surface–subsurface substrates when evaluating the success of artificial floods – knowledge that is currently absent. To better understand the integrative relationship between artificial floods and the hyporheic zone, we studied the response of a number of abiotic and biotic ecosystem properties to an artificial flow release on the River Spöl in Switzerland. We hypothesized that:

1. The artificial flow pulse would flush fine sediment (particles <2 mm) from the surface, interstitial pore spaces and the hyporheic zone of the gravel-bed river.
2. Removal of fine sediment throughout the vertical profile of the riverbed would subsequently enhance the connectivity of surface and hyporheic habitats, leading to improved physicochemical conditions following the artificial flood.

3. Improvements in vertical pathways and physiochemical conditions following the flood would lead to increased use of the hyporheic zone by macroinvertebrates.
4. Macroinvertebrates would use the hyporheic zone as a refuge during the artificial flood.

2 | MATERIALS AND METHODS

2.1 | Study location

The River Spöl flows in the central Alps across the Switzerland–Italian border and is regulated by two hydroelectric dams. Flow regulation in the form of residual flows commences downstream of Livigno reservoir (Punt dal Gall dam) where the Spöl flows ~5.7 km through a canyon-confined valley in the Swiss National Park and into the lower Ova Spin reservoir. From this lower reservoir, the Spöl flows a further 5.5 km to its confluence with the Inn River, a major tributary of the Danube, at the town of Zernez, Switzerland. Study sites were located in this lower flow-regulated stretch of the Spöl ~2.7 km downstream of the Ova Spin outlet, where the Spöl opens up from a canyon-confined valley to an open floodplain. The only tributary of hydrological importance, the river Cluozza, joins the Spöl ~3.2 km downstream of the Ova Spin outlet (Figure 1).

Prior to regulation in 1970, the Spöl exhibited a natural snowmelt/glacial meltwater flow regime, with high flows in summer and low flows in winter. Periodic floods from heavy rainfall occurred during summer/early autumn with peak discharges between 20 and 60 m^3 s^{-1} (Robinson et al., 2018). Average annual flow of the Spöl at the Livigno reservoir fluctuated between 12.5 and 6.6 m^3 s^{-1}, but post completion of the dam the residual flow was set to an average flow of 1 m^3 s^{-1}. In the lower flow-regulated section from Ova Spin to Zernez, the location of the present study, the flow is reduced further, being permanently set to 1 m^3 s^{-1} in summer and 0.3 m^3 s^{-1} in winter (Scheurer & Molinari, 2003).

Land use within the 295 km^2 catchment (BAFU, 2020) is predominately coniferous forest (*Picea excelsa* and *Pinus mugo*) with some grassland and sedges present in the lower floodplain. Climate in the region is continental with high seasonal variation in temperature, but with low precipitation values (Barry, 1992). River sediments originate primarily from dolomitic and calcareous scree from rocky, high gradient valley slopes and locally from remnant glacial moraines (Trümpy et al., 1997). Bedrock is present in many areas of the riverbed.

2.2 | Artificial flood and study reaches

The most notable feature of the flow regime of the regulated Spöl was the absence of peak flow events. As a result, the Engadine power company, Swiss National Park and state authorities began to implement artificial floods, predominately in the upper regulated part of the Spöl in 2000. However, 13 artificial floods have been undertaken in the lower flow-regulated section, the most recent in August 2017 with a peak discharge of 35 m^3 s^{-1} (2000–2017; Kevic et al., 2018). In September 2018 (the focus of this study), an artificial flood was released from the outlet of the Ova Spin reservoir over an 8-hour period. Peak discharge of 25 m^3 s^{-1} (equivalent to low-magnitude snow pulse flows pre-regulation) was attained 4 hours into the flood event and lasted around 2 hours, with rising and falling limbs being incremental. Previous studies showed this high flow is sufficient to mobilize bed sediments and reduce algae levels with minimal fish mortality (Mürle et al., 2003; Ortlepp & Mürle, 2003; Uehlinger et al., 2003). To note, the dam is a deep release reservoir and therefore the thermal regime remains relatively constant (Jakob et al., 2003).

The effects of the 2018 artificial flood were monitored at four locations downstream of Ova Spin reservoir over a 1.5-km section of river. Sites 1 and 2 were located upstream of the unregulated Cluozza tributary, with site 1 located ~2.7 km downstream of the Ova Spin outlet (Figure 1). Sites 3 and 4 were located downstream of the tributary where the channel takes on a braided form. All sampling was conducted over a 2-week period with pre-flood samples being collected the week before the flood. Two immediate time periods were employed after the flood for hyporheic sampling to understand the immediate flood implications for the community (1 day after flood – resistance) and then to assess if hyporheic accessibility for macroinvertebrates was enhanced following the flood (7 days post-flood). Benthic substrate sampling was conducted immediately following the flood as changes here would be instantaneous and was conducted again 10 months later to assess the temporal longevity of flood effects. There were no changes in hydrological conditions during the 10-month period following the flood, with flow during this period being residual flow. More details for each method can be found below.

2.3 | Sampling methods

2.3.1 | Surface and total benthic fine sediment content

To quantify the fine sediment content (particles <2 mm) of surface and shallow interstitial (ca. 10 cm) substrates, a resuspension technique using a stilling well was employed (Collins & Walling, 2007; Lambert & Walling, 1988). Sample patches were approached from downstream and an open-ended stainless-steel cylinder (height 55 cm, diameter 34 cm) was carefully pushed manually into the riverbed until a seal with the substrate was achieved (i.e., there was no flow of surface water through the cylinder). Care was taken to introduce minimal disturbance and prevent the winnowing of fine material. The water depth within the cylinder was measured prior to sampling. To take each surface fine sediment sample, the water within the cylinder was vigorously agitated using a small metal trowel for 60 s to suspend fine sediment on the riverbed surface into the water column. Following this period, a 50-ml vial was inverted in the water column and then turned upright and brought to the surface (sensu Duerdoth et al., 2015). Subsequently, a further 60 s of agitation was undertaken with the spade, including 30 s of digging/mixing the top 10 cm of the bed substrate, with a 50-ml sample again being taken at the end of this period.

This technique provided a sample of both the surface and total benthic fine sediment content from an individual patch. To ensure that spatial variability in fine sediment deposition was accounted for at each site, samples were taken from two visually distinct erosional and three depositional areas (sensu Duerdoth et al., 2015), providing five replicates per site before (1 week) and after the flood (2 days). The fine sediment content was sampled again in June 2019 approximately 10 months following the flood, thus providing three time periods of sampling. Three background water samples were taken from each site for pre- and post-flood samples to account for natural turbidity in the water column; background samples were not taken for June 2019 due to negligible suspended sediment in the water column.

All resuspension samples were returned to the laboratory and refrigerated in the dark till processing took place. Samples were filtered using pre-washed 0.45-μm Whatman glass microfiber filters and routinely analysed for mineral content through oven drying at 105°C overnight followed by Loss-On-Ignition (LOI) at 550°C (2 h; Dean, 1974). Finally, water depths within the stilling well were subsequently used to convert laboratory weights to a mass of fine sediment per square metre of riverbed, with values representing the surface and the total benthic fine sediment content.

2.3.2 | Hyporheic macroinvertebrates, physico-chemistry and fine sediment samples

Hyporheic samples (see below for pumping details) were collected by driving a 1.2-m-long stainless steel Bou–Rouch standpipe into riverbed sediments using a sledgehammer to two sampling depths: 0.25 and 0.50 m (following Davy-Bowker et al., 2006). Samples were taken only from riffles and therefore did not follow the same criteria as the resuspension samples. A minimum of five randomly distributed replicates (six at site 1 and for two time periods at site 2 due to large spatial variability in flow and substrate conditions) were taken from each sampling depth per site (Boulton et al., 2003), and each standpipe was located at least >1 m apart to minimize any influence from adjacent wells (O'Sullivan et al., 2019). Study sites were sampled on three occasions; before the artificial flood (hereafter called pre-flood ~7 days before the flood), ~1 day after the flood (1 day post-flood) and ~7 days after the flood (7 days post-flood) providing a total of 113 samples (36 at site 1, 32 at site 2, 30 at site 3 and 15 at site 4). Only 0.25 m samples were taken at site 4 due to highly compacted substrate making sampling to deeper depths difficult.

The standpipe had an internal diameter of 5 cm and was perforated with 0.5 cm-diameter holes along the distal 5 cm of the pipe. At each sampling point, a total of 5 L (following Boulton et al., 2003) was extracted using a manual bilge pump into a bucket at the fastest consistent rate to ensure sample comparability (Hunt & Stanley, 2000). Water temperature (°C), pH, conductivity (μS cm^{-1}) and total dissolved solids (TDS, ppm) were measured from each hyporheic water sample using a Hanna Hi 9813–6 multiprobe. Dissolved oxygen content (DO, mg L^{-1}) was measured using a WTW Oxi 3310 probe. Following water chemistry measurements, water was passed through a 500-μm sieve to retain macroinvertebrates and fine sediment and preserved in the field in 70% ethanol. For each well, the strength and direction of local hydrological exchange was obtained by measuring the distance from the top of the piezometer to the water level in the piezometer using an electronic dipstick – groundwater level (A), the distance from top of piezometer to the river water level (B) and the distance from top of piezometer to sediment (C). The direction of vertical exchange (delta) was obtained via Equation (1) and the vertical hydraulic gradient (VHG) by Equation (2).

$$\text{delta} = B - A \text{ (where if delta positive}$$
$$= \text{upwelling, if negative} = \text{downwelling} \tag{1}$$

$$\text{VHG} = \frac{\text{delta}}{\text{SD}} \text{ where SD} = \text{length of pipe} - C. \tag{2}$$

In the laboratory, hyporheic samples were fully enumerated for macroinvertebrates. Further, all fine sediments were retained, oven-dried at 105°C, gently disaggregated using a pestle and mortar and then passed through a series of sieves. Each fraction was weighed to determine the following grain size fractions: total mass <2000, 1000–2000 and 500–1000 μm (sensu Mathers, Hill et al., 2017). All hyporheic invertebrates were identified to the lowest possible taxonomic level, most to species or genus with the exception of some Diptera families (Ceratopogonidae, Chironomidae, Simuliidae, Empididae and some Limoniidae) and Oligochaeta, which were recorded as such.

2.4 | Statistical analyses

2.4.1 | Surface and total benthic fine sediment content

All resuspension samples were considered independently in statistical analyses to enable site variability to be visualized via standard error plots. Differences in fine sediment content over time associated with the artificial flood were statistically tested via a linear mixed-effects model (LMM) via the *lmer* function in the 'lme4' package in the R environment (R v3.6.0; Bates et al., 2015; R Development Core Team, 2019). Two models were constructed, the first testing the response of surface fine sediment content and the second testing total benthic content. Time (pre-flood, post-flood and post-flood 2019) was fitted as a fixed factor and site was fitted as a random effect to reflect that sediment composition through time will be correlated at individual sites. Where significant differences occurred by time, post hoc pairwise comparisons were performed using estimated marginal means and *p*-values were adjusted for multiple comparisons via Tukey tests within the 'emmeans' package (Lenth et al., 2020).

2.4.2 | Hyporheic physicochemistry and fine sediment content

Differences in the hyporheic physicochemical conditions between pre-flood, 1 day post-flood and 7 days post-flood were examined via Principal Component Analyses (PCA) for the two depths independently (0.25 and 0.50 m) using the '*prcomp*' function in the 'stats' package. Highly correlated variables, with Pearson's *r* values > 0.75, were considered redundant (TDS and VHG) and removed to minimize collinearity. As delta and pH exhibited low loadings on the first two principal components (PC), these two metrics were not taken any further. Linear models were constructed using the following five variables: conductivity, temperature, DO, mass of fine sediment 1000–2000 μm and mass of fine sediment 500–1000 μm. To assess the independent statistical significance of the changing hyporheic environmental parameters associated with the flood, LMMs were subsequently fitted to each environmental parameter. Conductivity and sediment masses were log transformed to satisfy LMM model assumptions. All models were fitted with the fixed effects of time (pre-flood, 1 day post-flood and 7 days post-flood), depth (0.25 and 0.50 m) and their interaction. Site was fitted as a random effect to account for potential spatial and temporal autocorrelation. Post-hoc pairwise comparisons of groups were performed using estimated marginal means as outlined in the above section.

2.4.3 | Hyporheic macroinvertebrate communities

Statistical differences in community composition associated with the interactive explanatory factors of site and time (pre-flood, 1 day

post-flood and 7 days post-flood) were assessed via a permutational multivariate analysis of variance (PERMANOVA) using the '*adonis*' function. Where significant differences occurred by time, pairwise comparisons of differences were performed using the '*pairwise.adonis*' function (Arbizu, 2019). To assess if beta diversity varied over time associated with the artificial flood, homogeneity of multivariate dispersions among assemblages was examined using the '*betadisper*' function using a Bray–Curtis distance matrix and tested for statistical differences via Tukey post hoc tests. Where significant differences in community composition occurred associated with the artificial flood, taxa driving these differences were identified via the Similarity Percentage (SIMPER) using the '*simper*' function. Differences in total abundance, taxa richness and the abundance of the top three taxa identified through SIMPER analyses were statistically tested via GLMMs with a Poisson error distribution and log link using the *glm* function in the '*stats*' package. All models were fitted with the fixed effects of time (pre-flood, 1 day post-flood and 7 days post-flood), depth (0.25 and 0.50 m) and their interaction. Site was fitted as a random effect to account for potential spatial and temporal autocorrelation. Post-hoc pairwise comparisons of groups were performed using estimated marginal means as outlined in a previous section.

2.4.4 | Hyporheic macroinvertebrate community associations with physicochemical and fine sediment content variables

To assess relationships between hyporheic macroinvertebrate composition and the physicochemical parameters, redundancy analysis (RDA) was performed using the '*ordistep*' function in '*vegan*' (Oksanen et al., 2019). Specifically, pH, conductivity, temperature, DO, delta, mass of fine sediment 1000–2000 μm and mass of fine sediment 500–1000 μm were employed as the physicochemical parameters. Prior to analysis, a Hellinger transformation (Legendre & Gallagher, 2001) was applied to the species-abundance data. A stepwise (forward and backward) selection procedure using permutational-based significance tests (999 permutations) was used to identify factors that influenced assemblages, with only significant variables included in the final model. Final variables were checked for collinearity using the *vif* function in the '*car*' package to ensure that all 'variance inflation factors' were <3 (Zuur et al., 2010).

3 | RESULTS

3.1 | Surface and total benthic fine sediment content

Total benthic fine sediment content varied significantly by time ($\chi^2_{2,58} = 6.90$, $p = 0.032$), whilst surface fine sediment content was marginally insignificant ($\chi^2_{2,58} = 5.79$, $p = 0.060$). Pairwise comparisons of benthic fine sediment content indicated that immediately following the flood, fine sediment content was significantly reduced

($t = 2.63$, $p = 0.0113$). However, there was no significant difference in benthic fine sediment content 10 months post-flood compared to pre-flood levels ($t = -1.23$, $p = 0.224$). Notably following the artificial flood (post-flood), fine sediment content of surface and benthic substrates demonstrated little to no variation compared to pre-flood conditions (Figure 2).

3.2 | Hyporheic physicochemistry and fine sediment content

PCA indicated differences in the physicochemistry of both 0.25 and 0.50 m hyporheic sediments associated with the artificial flood sample time on PC1 (accounting for 33.6% and 24.9% of total variance, respectively; Figure 3). Physicochemistry of pre-flood samples was distinct to that after the flood, but there was little separation between 1- and 7-day post-flood samples. The PCA models indicated that temperature, conductivity and DO were the primary drivers of variation between pre- and post-flood samples. Temperature and pre-flood samples plotted negatively on PC1, whilst post-flood samples (1 and 7 day), conductivity and DO plotted positively. Both fine sediment grain size fractions had a negative loading on PC1 for 0.50 m samples. VHG (and the correlated value of delta) demonstrated similar values over time (pre-flood −0.13, 1 day after −0.10 and 7 days −0.13), although variability was much greater following the flood (standard deviation values of 0.20, 0.41 and 0.30).

When the five environmental parameters were tested independently for statistical differences, all parameters statistically differed with sample time with only DO displaying a significant depth × time interaction (Figure 4; Table 1). Water temperatures displayed reduced values after the artificial flood with a stepwise decline being evident most likely associated with ambient weather changes with all pairwise time comparisons being significant (Table S1; Figure S1). DO concentrations varied as a function of time and depth (Table 1; Figure 4a) with deeper substrates of 0.50 m displaying lower values. Post hoc tests indicated that both 1- and 7-day post-flood samples had significantly higher DO concentrations than pre-flood (Table S1). Conductivity values of 7-day post-flood samples were significantly higher than pre and 1-day post-flood samples but there was no difference in pre-flood versus 1 day post-flood (Figure 4b; Table S1). Grains in the fractions 1000–2000 μm varied significantly associated with sample time and depth with lower mass values at 0.50 m (Table 1; Figure 4c). The mass of fine sediment in the fraction 1000–2000 μm was found to be significantly lower in 7-day post-flood samples than pre-flood samples (Table S1; Figure 4c), whilst grains in the fraction 500–1000 μm were significantly reduced in both 1- and 7-day post-flood samples (Figure 4d; Table S1).

3.3 | Hyporheic macroinvertebrate communities

A total of 1198 individuals comprising 17 taxa were recorded in the 113 hyporheic samples. Only one taxon was unique to pre-flood communities (Simuliidae) and three taxa to 7-day post-flood communities
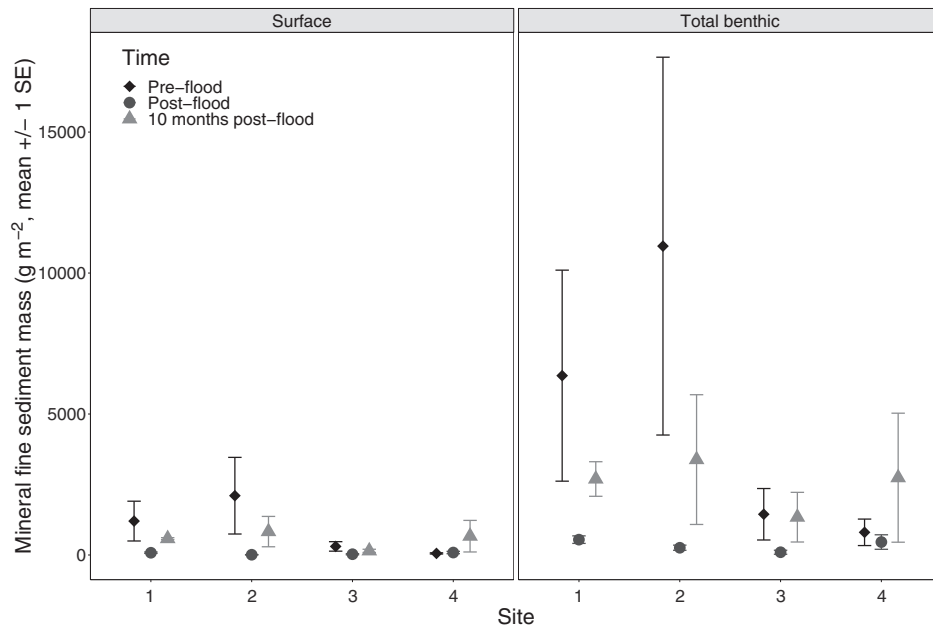
FIGURE 2 Mean (±1 SE) total mass of mineral fine sediment (g m^{-2}) in surface and total benthic substrates (ca. 10 cm deep) associated with site and sample time relative to the artificial flood released. Post-flood is immediately after the artificial flood (2 days after)
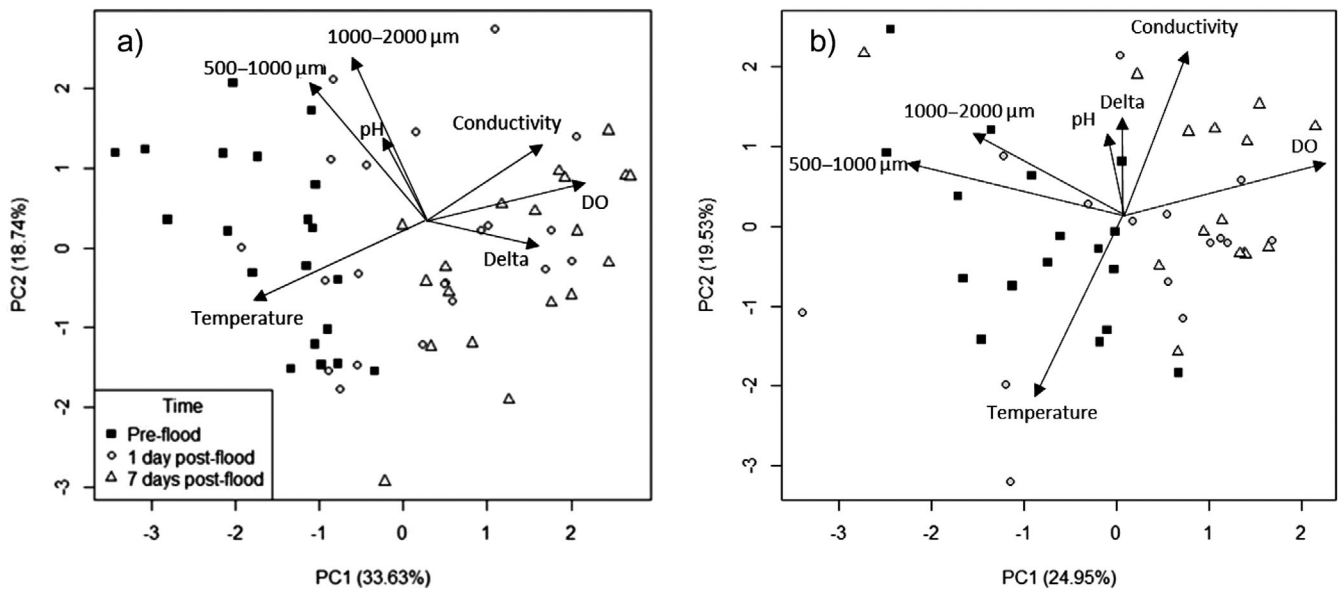

FIGURE 3 Principal component analysis plots of hyporheic physicochemical data of (a) 0.25 m hyporheic sediments and (b) 0.50 m sediments in the Spöl associated with an artificial flood in September 2018

(Limoniidae, *Isoperla rivulorum* and *Rhithrogena* sp.). The most abundant taxon overall was *Gammarus fossarum* (42% of total hyporheic abundance) followed by *Leuctra* sp. (38.5%), Chironomidae (9.3%) and Oligochaeta (6.3%). All other taxa accounted for <1% of total hyporheic abundance with communities being highly patchy in nature.

PERMANOVA highlighted differences in 0.25 m hyporheic macroinvertebrate community composition associated only with flood sample time ($F = 3.43$, $R^2 = 0.07$, $p = 0.006$), whilst the interaction of sample time and site was significant for 0.50 m hyporheic commu-

nities ($F = 2.34$, $R^2 = 0.05$, $p = 0.030$). Pairwise PERMANOVA indicated that the composition of 0.25 m pre-flood communities differed relative to 1- and 7-day post-flood communities ($F = 3.12$, $R^2 = 0.09$, $p = 0.017$ and $F = 3.52$, $R^2 = 0.10$, $p = 0.006$, respectively). There were no significant differences in multivariate dispersion over time for either 0.25 or 0.50 m hyporheic communities ($p > 0.05$). SIMPER for 0.25 m communities indicated that reductions in *G. fossarum* were the primary driver of differences between pre- and post-flood assemblages (Table 2). This pattern was driven primarily by a loss of
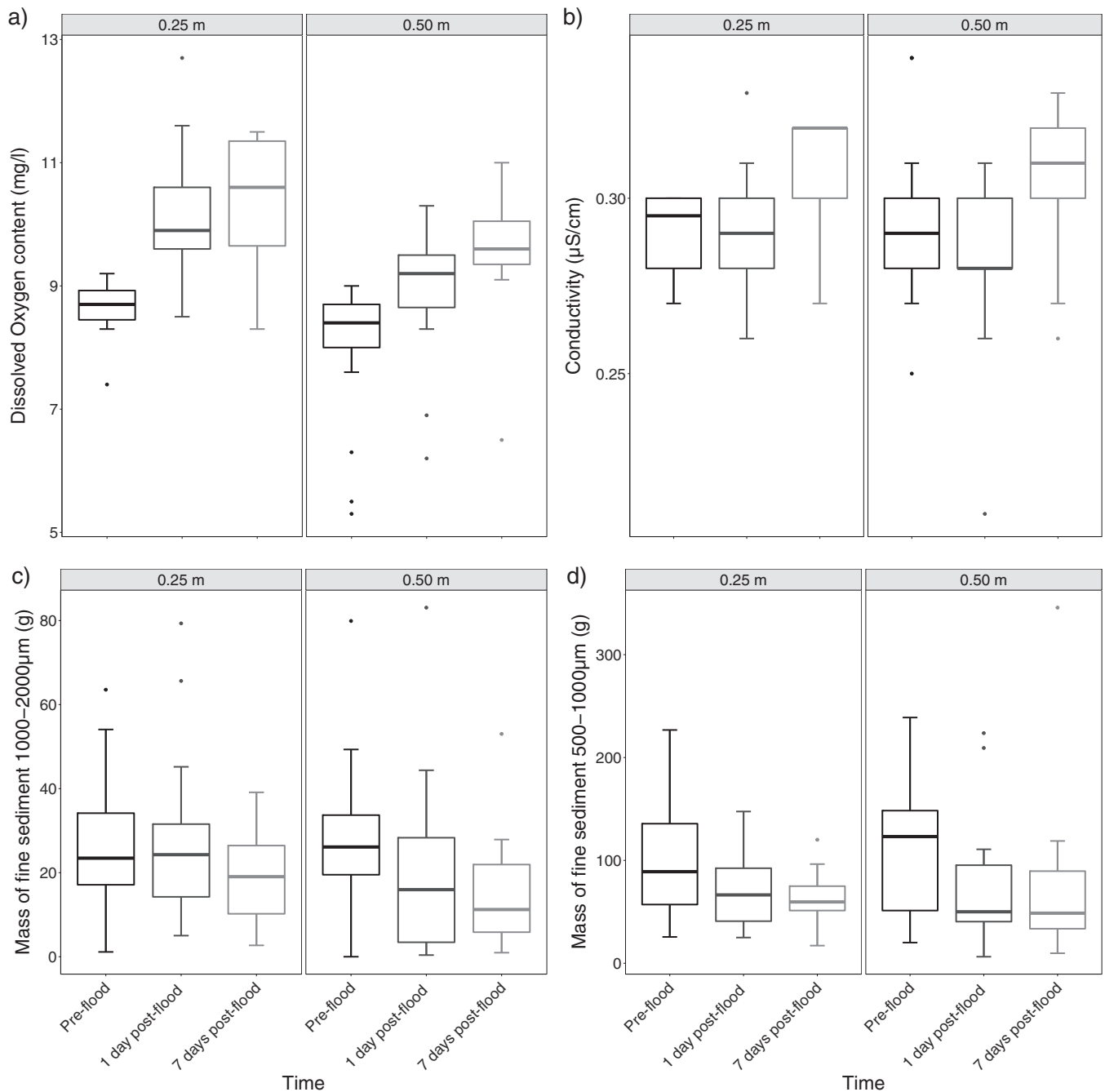
FIGURE 4 Boxplots of (a) dissolved oxygen content; (b) conductivity; (c) mass of fine sediment 1000–2000 μm and (d) mass of fine sediment 500–1000 μm of hyporheic substrates as a function of depth (0.25 or 0.50 m) and sample time (pre-flood, 1 day post-flood and 7 days post-flood)

G. fossarum following the flood at site 2 (Figure S2). Notably, *Leuctra* sp. demonstrated increases in abundance post-flood in both time periods, whilst *Protonemura* sp. (1 day after) and Limoniidae (7 days after) were both recorded in hyporheic substrates despite being absent prior to the flood (Table 2). Oligochaeta demonstrated reductions post-flood but demonstrated some recovery 7 days later, whilst Chironomidae demonstrated reduced abundances 1 day post-flood but had recovered and displayed higher abundances than pre-flood 7 days after the flood (Table 2). See Table S2 for SIMPER summary for 0.50 m communities.

In general, total abundance demonstrated no change or a reduction immediately following the flood with the exception of site 4 at 0.25 m and site 1 at 0.50 m that showed increases in abundance 1 day after the flood (Figure 5). The 7-day post-flood abundances displayed comparable (e.g. site 1 at 0.25 m) or values greater than (e.g. site 3 at 0.50 m) preflood abundances. Site 2 was particularly affected by the artificial flood with reductions in total abundance evident in both 0.25 and 0.50 m substrates with some recovery evident in 0.50 m-depth communities 7 days after the flood (Tables 1 and S1). Taxa richness demonstrated

TABLE 1 Summary of LMMs (physicochemistry) and GLMMs (ecological) testing the influence of sample time (pre-flood, 1 day post-flood and 7 days post-flood), depth (0.25 and 0.50 m) and their interaction on a number of hyporheic physicochemical parameters, taxa richness, total abundance and abundance of selected individual taxa. Significant terms are emboldened

Factor	Time		Depth		Time × Depth	
	Chisq	p	Chisq	p	Chisq	P
Temperature (°C)	56.95	**<0.001**	0.25	0.617	11.21	**0.004**
Conductivity ($\mu S\,cm^{-1}$)	21.94	**<0.001**	0.08	0.782	3.31	0.191
DO ($mg\,L^{-1}$)	65.47	**<0.001**	20.47	**<0.001**	2.24	0.327
1000–2000 μm	7.50	**0.024**	6.94	**0.008**	1.44	0.490
500–1000 μm	10.19	**0.006**	0.23	0.633	0.40	0.819
Taxa richness	1.88	0.391	1.47	0.225	0.94	0.624
Total abundance	88.72	**<0.001**	28.45	**<0.001**	77.44	**<0.001**
Gammarus fossarum	150.83	**<0.001**	0.096	0.757	28.68	**<0.001**
Leuctra sp.	70.42	**<0.001**	51.15	**<0.001**	49.28	**<0.001**
Oligochaeta	8.75	**0.013**	0.02	0.882	7.69	**<0.001**

TABLE 2 Summary of top five taxa driving differences in 0.25 m hyporheic communities pre-flood versus 1 day and 7 days post-flood as determined by SIMPER. Total change in abundance following artificial flood indicated in parentheses (±)

0.25 m pre-flood and 1 day post-flood			0.25 m pre-flood and 7 days post-flood		
Taxa	Average abundance pre-flood	Average abundance 1 day after	Taxa	Average abundance pre-flood	Average abundance 7 days after
Gammarus fossarum (−)	9.71	3.00	G. fossarum (−)	9.71	1.88
Leuctra sp. (+)	1.47	4.63	Leuctra sp. (+)	1.47	3.00
Oligochaeta (−)	1.47	0.31	Oligochaeta (−)	1.47	1.06
Chironomidae (−)	0.53	0.13	Chironomidae (+)	0.53	0.94
Protonemura sp. (+)	0.00	0.12	Limoniidae (+)	0.00	0.18

patchy responses to the artificial flood with some communities demonstrating no change (e.g. site 1 at 0.25 m), whilst others demonstrated an increase in richness following the flood (e.g. site 1 at 0.50 m; Figure 5). Leuctra sp. in contrast demonstrated significant increases over time following the flood, particularly at sites 1 and 3, and notably in 0.50 m substrates (Figure 5; Tables 1 and S1). Further, Leuctra sp. demonstrated an increase in abundance at 0.25 m 1 day post-flood at site 2 and then reduced to pre-flood levels 7 days later.

3.4 | Hyporheic macroinvertebrate community associations with physicochemical and fine sediment content variables

When hyporheic macroinvertebrate community composition was tested against physicochemical parameters, the 0.25 m community model was significant ($F = 1.50, p = 0.043$) and accounted for 15.6% of variance on the first two axes. The pH was found to significantly influence 0.25 m hyporheic community composition ($F = 2.53, p = 0.03$), whilst fine sediment in the fraction 1000–2000 μm was significant

at the 90% confidence level ($F = 1.88, p = 0.065$). Neither of these parameters, however, were associated with loadings responsible for the separation of pre- and post-flood communities on RDA axis 2 (Figure 6). Only three taxa showed clear relationships with pre- or post-flood communities. Leuctra sp. displayed loadings comparable to post-flood communities, whilst G. fossarum and Oligochaeta plotted within pre-flood communities (Figure 6). In marked contrast, there was no significant association with measured physicochemical parameters for 0.50 m communities (RDA model $F = 0.77, p = 0.799$) with no separation of pre- and post-flood communities being evident.

4 | DISCUSSION

This study examined the effect of an artificially released flood on a number of abiotic and biotic properties to elucidate the effectiveness of such discharge events on restoring ecological and physicochemical health in interstitial pore spaces and the hyporheic zone. We observed that immediately following the artificial flood, the mass of fine sediment was significantly reduced in benthic substrates providing
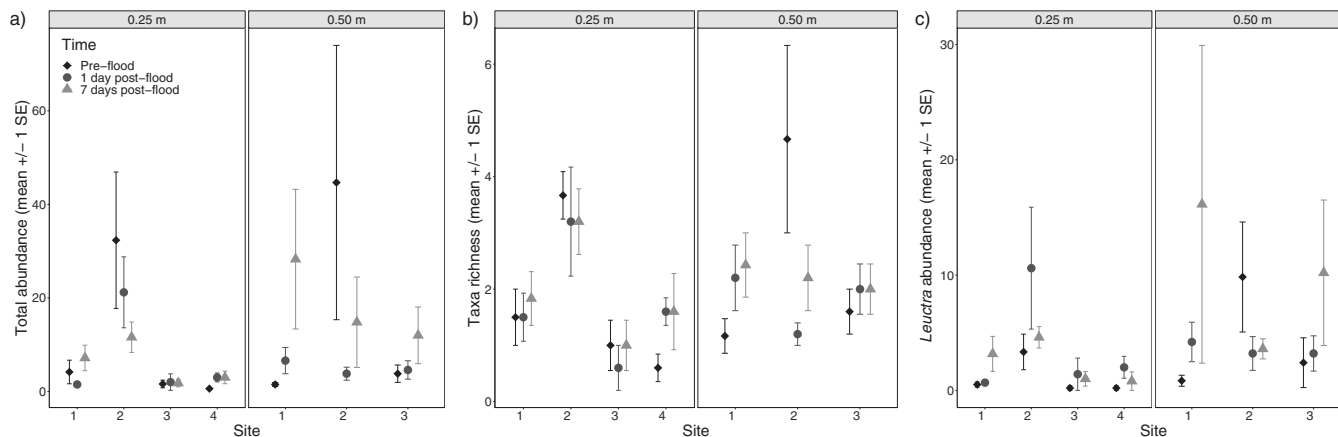
FIGURE 5 Mean (±1 SE) (a) total abundance; (b) taxa richness and (c) *Leuctra* abundance within hyporheic macroinvertebrate communities as a function of site, depth (0.25 or 0.50 m) and sample time (pre-flood, 1 day post-flood and 7 days post-flood)
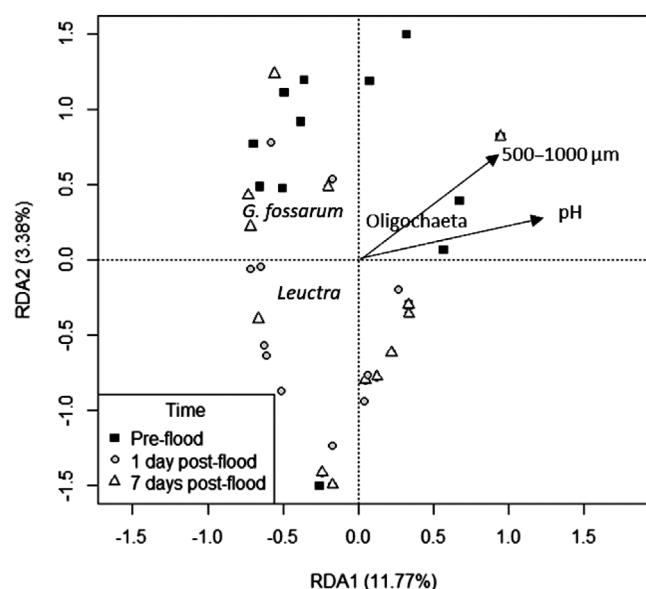

FIGURE 6 Redundancy analysis (RDA) of 0.25 m hyporheic communities from the Spöl associated with an artificial flood in September 2018. Only significant environmental parameters (at 90% confidence level) influencing faunal data are presented. Species shown are those that plot specifically within flood groups

evidence to support our first hypothesis. Surface fine sediment content also demonstrated a reduction but this trend was marginally insignificant ($p = 0.06$). Our results, however, provide further evidence that artificial floods can successfully be employed to flush excessive fine sediment from gravel riverbeds (Doretto et al., 2019).

The implementation of artificial floods should, however, be conducted on a regular basis, as we found evidence to suggest that fine sediment content of surface and shallow benthic substrates (ca. 10 cm) demonstrated some increases in the 10-month period following the artificial flood. Pre-flood concentrations also highlight the importance of natural flushing flows in maintaining interstitial pore space. Greater quantities of fine sediment were present pre-flood at the two sites

located upstream of the unregulated tributary, Cluozza, compared to the two sites downstream that only occasionally experience periodic floods originating from this tributary. Despite being located downstream of a glacial river with high amounts of suspended sediments during natural floods (Mürle et al., 2003; Uehlinger et al., 2003), these two downstream sites (sites 3 and 4) had a lower fine sediment content in both surface and benthic sediments prior to the artificial flood.

In the River Spöl, use of the hyporheic zone by macroinvertebrates prior to the artificial floods was significantly limited and was most likely associated with the large volumes of fine sediment present in interstitial pore spaces as well as subsurface sediments. Fine sediment content was significantly reduced after the floods (1–7 days) in both shallow and deep hyporheic substrates (0.25 or 0.50 m below the riverbed), again supporting our first hypothesis. Reductions in fine sediment content and the flushing of interstitial fine sediment resulted in more favourable physicochemical conditions. DO concentrations and conductivity demonstrated increased values in both shallow and deeper hyporheic substrates 7 days after the artificial flood supporting our second hypothesis. Sarriquet et al. (2007) reported similar findings during the restoration of riverbed sediments with improvements in DO levels and the transfer of resources in substrates 0.15-m deep. However, the reasoning behind the altered physicochemical conditions is not clear as the strength of the vertical hydraulic gradient (VHG) was similar pre- and post-flood. Reductions in fine sediment clogging may have altered microbial processing rates, thereby directly impacting physicochemical conditions, although the relationship between fine sediment and microbial processes is complex (Nogaro et al., 2010). It should be noted that we observed greater variability in the strength of the VHG post-flood, suggesting greater patch scale variation in hyporheic zone connectivity.

Despite alterations in the physicochemical conditions of both shallow and deep hyporheic sediments, alterations to the hyporheic community were heterogeneous in nature. We found that shallow hyporheic communities 0.25 m below the riverbed displayed altered composition after the artificial flood, whilst communities at 0.50 m displayed comparable composition to pre-flood communities (although

some community metrics were altered at 0.50 m depths). Given the differences in depth, it is reasonable to assume that communities at 0.25 m would be the first to react to the changing physicochemical conditions and the restoration of interstitial pathways. Moreover, although individuals from most invertebrate groups and all insect families have been recorded in the hyporheic zone, few of these have been from depths exceeding 0.50 m, suggesting there may be an upper limit on substrate depth use (Boulton, 2000). As we only conducted ecological sampling 7 days post-flood, we are unable to ascertain if community composition shifts were evident in deeper subsurface substrates as length of time since flood increased. We are also unable to directly ascertain the duration of time in which the alterations to hyporheic physicochemical conditions and ecological communities persisted. However, we believe these beneficial effects would have diminished after a few months due to the re-accumulation of fine sediment 10 months following the flood in benthic substrates. This, in addition to the observed pre-flood conditions in both hyporheic physicochemical and ecological health despite an artificial flood being released 13 months prior (peak discharge of 35 m^3 s^{-1}), suggests that regular floods are required to reinitiate/maintain surface–subsurface pathways. This finding is in line with previous research conducted in the Spöl that has documented that regular artificial floods (1–2 year) are required to maintain the benthic ecological benefits of flood pulses (Robinson et al., 2003, 2018). Moreover, Hancock and Boulton (2005) documented no lasting effects on hyporheic water quality 49 days following an artificial flow pulse. Further research is required to understand the temporal longevity of artificial flood effects on the hyporheic zone, including other resources that may be more important in the longer term and which were not monitored here (such as organic matter).

Despite the changes in community composition at a depth of 0.25 m, the implications of the artificial flood for hyporheic communities were highly variable in space, with some sites and depths demonstrating no changes in abundance or taxa richness following the flood, whilst others demonstrated an increase (hypothesis three). Hyporheic communities are widely acknowledged to be highly variable in both space and time associated with vertical hydrological exchange, hydrological conditions, sediment composition and the provision of resources (Dole-Olivier & Marmonier, 1992; Dunscombe et al., 2018). The few studies investigating the response of hyporheic communities to natural floods and spates have similarly found that communities reacted in a patchy fashion with the hyporheic zone representing a variable refuge dependent on the direction of vertical hydrological exchange (upwelling or downwelling), substrate stability and the magnitude of the discharge event (Dole-Olivier & Marmonier, 1992; Dole-Olivier, 1997). However, we did not detect any significant associations between hyporheic communities and the direction of vertical hydrological exchange, conductivity or DO, the latter two being parameters shown to be associated to a change following the flood. We did, however, detect an association with pH and fine sediment in the fraction 500–1000 μm for shallow subsurface communities, but neither of these parameters were related to the changing community composition after the artificial flood. This

result suggests another physicochemical variable not recorded in this study may have influenced the change in 0.25 m hyporheic community composition – that of riverbed instability.

Visual observations indicated that the degree of sediment deposition and erosion in the Spöl was highly variable in space and magnitude, with some locations seeing scour of up to 0.50 m in depth following the artificial flood. Mürle et al. (2003) similarly recorded erosion rates of 0.50–1.50 m from floods of varying magnitudes in the Spöl. The evidence of highly erosive substrates can be seen, in particular, at site 2 where hyporheic abundances and especially the abundance of *G. fossarum* were dramatically reduced. *Gammarus* sp. has been shown to exhibit active vertical migration in response to streambed drying events (Stubbington et al., 2011; Vadher et al., 2018) and as such it was anticipated that this taxon would seek refuge in the hyporheic zone during the flood (hypothesis four). However, it is highly likely that the low substrate stability in the Spöl prevented this activity (Matthaei & Townsend, 2000; Rempel et al., 1999), and they sought alternative refuge in channel margin habitats.

We did see some evidence of hyporheic refuge-seeking behaviour by *Leuctra* sp. 1 day after the flood, a taxon that is widely associated with interstitial and subsurface substrates (Dorff & Finn, 2020). This taxon also demonstrated increased abundances in deeper 0.50 m substrates 7 days following the artificial flood, a pattern also matched by taxa richness, suggesting that pore space had become available for individuals to use following the artificial flood. Importantly, improvements in the physicochemical conditions (including DO) and re-establishment of interstitial pore space show that the hyporheic zone in the Spöl would be accessible by macroinvertebrates to use as a refuge under the increasing prevalence of drying events, thereby potentially enhancing the resilience of the ecosystem (Bruno et al., 2020; Van Looy et al., 2019).

Fragmentation and flow regulation remain an ongoing threat to the integrity of river ecosystems globally (Januchowski-Hartley et al., 2020; Reid et al., 2019). In particular, by limiting longitudinal connectivity and bedload transport through the construction of dams, riverbeds are likely to become clogged with fine sediment that subsequently influences vertical connectivity and effectively disconnects the hyporheic zone. Our work, which focused on this neglected vertical dimension and which significantly advanced our scientific understanding, provides much needed evidence that artificial floods can be an effective means to restore flushing flows, thereby enhancing spatial heterogeneity in sediment composition. This flushing of fine sediment can influence and enhance physicochemical conditions within the hyporheic zone, restore interstitial pathways and ultimately influence the transfer of organisms within the hyporheic zone – even within a river that is taxa poor. The implementation of artificial high flows as a management tool should, however, be conducted on a regular basis, as we found that surface and shallow benthic fine sediment deposits had begun to accumulate again over 10 months following the artificial flood in line with similar findings for benthic taxa requiring regular artificial floods (one or two annually) to maintain the ecological benefits (Robinson et al., 2003, 2018).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology. KLM collected and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data are available via Loughborough Data Repository: https://doi.org/10.17028/rd.lboro.16434759 (Mathers et al., 2021).

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REFERENCES

Acreman, M. (2016). Environmental flows—Basics for novices. *Wiley Interdisciplinary Reviews: Water*, *3*, 622–628.

Arbizu, P. M. (2019). *pairwiseAdonis: Pairwise multilevel comparison using adonis*. https://github.com/pmartinezarbizu/pairwiseAdonis

Baker, D. W., Bledsoe, B. P., Albano, C. M., & Poff, N. L. (2011). Downstream effects of diversion dams on sediment and hydraulic conditions of Rocky Mountain streams. *River Research and Applications*, *27*, 388–401.

Barry, R. C. (1992). *Mountain weather and climate*. Routledge.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Belletti, B., de Leaniz, C. G., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., Van de Bund, W., Aarestrup, K., Barry, J., & Belka, K. (2020) More

than one million barriers fragment Europe's rivers. *Nature*, *588*, 436–441.

Boulton, A. J., Findlay, S., Marmonier, P., Stanley, E. H., & Valett, H. M. (1998). The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics*, *29*, 59–81.

Boulton, A. J. (2007). Hyporheic rehabilitation in rivers: Restoring vertical connectivity. *Freshwater Biology*, *52*, 632–650.

Boulton, A. J. (2000). The subsurface macrofauna. In J. Jones & P. J. Mulholland (Eds.), *Streams and ground waters* (pp. 337–361). Academic Press.

Boulton, A. J., Dole-Olivier, M. J., & Marmonier, P. (2003). Optimizing a sampling strategy for assessing hyporheic invertebrate biodiversity using the Bou-Rouch method: Within-site replication and sample volume. *Archiv für Hydrobiologie*, *156*, 431–456.

Boulton, A. J., Datry, T., Kasahara, T., Mutz, M., & Stanford, J. A. (2010). Ecology and management of the hyporheic zone: Stream–groundwater interactions of running waters and their floodplains. *Journal of the North American Benthological Society*, *29*, 26–40.

Bruno, M. C., Doretto, A., Boano, F., Ridolfi, L., & Fenoglio, S. (2020). Role of the hyporheic zone in increasing the resilience of mountain streams facing intermittency. *Water*, *12*, 2034.

Bundesamt für Umwelt (BAFU). (2020). *Hydrologische Daten und Vorhersagen: Spöl – Punt dal Gall 2239*. https://www.hydrodaten.admin.ch/de/2239.html

Burrows, R. M., Rutlidge, H., Bond, N. R., Eberhard, S. M., Auhl, A., Andersen, M. S., Valdez, D. G., & Kennard, M. J. (2017). High rates of organic carbon processing in the hyporheic zone of intermittent streams. *Scientific Reports*, *7*, 1–11.

Collins, A. L., & Walling, D. E. (2007). The storage and provenance of fine sediment on the channel bed of two contrasting lowland permeable catchments, UK. *River Research and Applications*, *23*, 429–450.

Davy-Bowker, J., Sweeting, W., Wright, N., Clarke, R. T., & Arnott, S. (2006). The distribution of benthic and hyporheic macroinvertebrates from the heads and tails of riffles. *Hydrobiologia*, *563*, 109-123.

Dean, W. E. (1974). Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition; comparison with other methods. *Journal of Sedimentary Research*, *44*, 242–248.

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

Dole-Olivier, M. J., & Marmonier, P. (1992). Patch distribution of interstitial communities: Prevailing factors. *Freshwater Biology*, *27*, 177–191.

Dole-Olivier, M. J., Marmonier, P., & Beffy, J. L. (1997). Response of invertebrates to lotic disturbance: Is the hyporheic zone a patchy refugium? *Freshwater Biology*, *37*, 257–276.

Doretto, A., Bo, T., Bona, F., Apostolo, M., Bonetto, D., & Fenoglio, S. (2019). Effectiveness of artificial floods for benthic community recovery after sediment flushing from a dam. *Environmental Monitoring and Assessment*, *191*, 88.

Dorff, N. C., & Finn, D. S. (2020). Hyporheic secondary production and life history of a common Ozark stonefly. *Hydrobiologia*, *847*, 443–456.

Duerdoth, C. P., Arnold, A., Murphy, J. F., Naden, P. S., Scarlett, P., Collins, A. L., Jones, J. I., & Jones, J. I. (2015). Assessment of a rapid method for quantitative reach-scale estimates of deposited fine sediment in rivers. *Geomorphology*, *230*, 37–50.

Dunscombe, M., Robertson, A., Peralta-Maraver, I., & Shaw, P. (2018). Community structure and functioning below the streambed across contrasting geologies. *Science of the Total Environment*, *630*, 1028–1035.

Geist, D. R., Hanrahan, T. P., Arntzen, E. V., McMichael, G. A., Murray, C. J., & Chien, Y. J. (2002). Physicochemical characteristics of the hyporheic zone affect redd site selection by chum salmon and fall Chinook salmon in the Columbia River. *North American Journal of Fisheries Management*, *22*, 1077–1085.

Hartwig, M., & Borchardt, D. (2015). Alteration of key hyporheic functions through biological and physical clogging along a nutrient and fine-sediment gradient. *Ecohydrology*, *8*, 961–975.

Hancock, P. J., & Boulton, A. J. (2005). The effects of an environmental flow release on water quality in the hyporheic zone of the Hunter River, Australia. *Hydrobiologia*, *552*, 75–85.

Hunt, G. W., & Stanley, E. H. (2000). An evaluation of alternative procedures using the Bou-Rouch method for sampling hyporheic invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 1545–1550.

Januchowski-Hartley, S. R., Mantel, S., Celi, J., Hermoso, V., White, J. C., Blankenship, S., & Olden, J. D. (2020). Small instream infrastructure: Comparative methods and evidence of environmental and ecological responses. *Ecological Solutions and Evidence*, *11*, e12026.

Jakob, C., Robinson, C. T., & Uehlinger, U. (2003). Longitudinal effects of experimental floods on stream benthos downstream from a large dam. *Aquatic Sciences*, *65*, 223–231.

Jones, J. I., Murphy, J. F., Collins, A. L., Sear, D. A., Naden, P. S., & Armitage, P. D. (2012). The impact of fine sediment on macroinvertebrates. *River Research and Applications*, *28*, 1055–1071.

Jones, J. I., Duerdoth, C. P., Collins, A. L., Naden, P. S., & Sear, D. A. (2014). Interactions between diatoms and fine sediment. *Hydrological Processes*, *28*, 1226–1237.

Jones, J., Börger, L., Tummers, J., Jones, P., Lucas, M., Kerr, J., Kemp, P., Bizzi, S., Consuegra, S., Marcello, L., & Vowles, A. (2019). A comprehensive assessment of stream fragmentation in Great Britain. *Science of the Total Environment*, *673*, 756–762.

Karaouzas, I., Theodoropoulos, C., Vourka, A., Gritzalis, K., & Skoulikidis, N. T. (2019). Stream invertebrate communities are primarily shaped by hydrological factors and ultimately fine-tuned by local habitat conditions. *Science of the Total Environment*, *665*, 290–299.

Kemp, P., Sear, D., Collins, A., Naden, P., & Jones, I. (2011). The impacts of fine sediment on riverine fish. *Hydrological Processes*, *25*, 1800–1821.

Kevic, M., Ortlepp, J., Mürle, U., & Robinson, C. T. (2018). Effects of experimental floods in two rivers with contrasting valley morphologies. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, *192*, 145–160.

Krause, S., Hannah, D. M., Fleckenstein, J. H., Heppell, C. M., Kaeser, D., Pickup, R., Pinay, G., Robertson, A. L., & Wood, P. J. (2011). Interdisciplinary perspectives on processes in the hyporheic zone. *Ecohydrology*, *4*, 481–499.

Konrad, C. P., Olden, J. D., Lytle, D. A., Melis, T., Schmidt, J. C., Bray, E. N., Freeman, M. C., Gido, K. B., Hemphill, N. P., Kennard, M. J., & McMullen, L. E. (2011). Large-scale flow experiments for managing river systems. *Bioscience*, *61*, 948–959.

Larsen, S., & Ormerod, S. J. (2010). Combined effects of habitat modification on trait composition and species nestedness in river invertebrates. *Biological Conservation*, *143*, 2638–2646.

Lambert, C. P., & Walling, D. E. (1988). Measurement of channel storage of suspended sediment in a gravel-bed river. *Catena*, *15*, 65–80.

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*, 271–280.

Lehner, B., Liermann, C. R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P., Döll, P., Endejan, M., Frenken, K., Magome, J., & Nilsson, C. (2011). High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. *Frontiers in Ecology and the Environment*, *9*, 494–502.

Lenth, R., Buerkner, P., Herve, M., Love, J., Riebl, H., & Singmann, H. (2020). *emmeans*. https://CRAN.Rproject.org/package=emmeans

Lewandowski, J., Arnon, S., Banks, E., Batelaan, O., Betterle, A., Broecker, T., Coll, C., Drummond, J. D., Gaona Garcia, J., Galloway, J., & Gomez-Velez, J. (2019). Is the hyporheic zone relevant beyond the scientific community? *Water*, *11*, 2230.

Maazouzi, C., Galassi, D., Claret, C., Cellot, B., Fiers, F., Martin, D., Marmonier, P., & Dole-Olivier, M. J. (2017). Do benthic invertebrates use hyporheic refuges during streambed drying? A manipulative field experiment in nested hyporheic flowpaths. *Ecohydrology*, *10*, e1865.

Magliozzi, C., Coro, G., Grabowski, R. C., Packman, A. I., & Krause, S. (2019). A multiscale statistical method to identify potential areas of hyporheic

exchange for river restoration planning. *Environmental Modelling & Software*, *111*, 311–323.

Malcolm, I. A., Soulsby, C., Youngson, A. F., & Hannah, D. M. (2005). Catchment-scale controls on groundwater–surface water interactions in the hyporheic zone: Implications for salmon embryo survival. *River Research and Applications*, *21*, 977–989.

Matthaei, C.D., & Townsend, C. R. (2000). Inundated floodplain gravels in a stream with an unstable bed: temporary shelter or true invertebrate refugium. *New Zealand Journal of Marine and Freshwater Research*, *34*, 147–156.

Mathers, K., Robinson, L., & Weber, C. T. (2021). *Riverine fine sediment content and hyporheic physicochemistry and macroinvertebrate data associated with an artificial flood in Switzerland*. Loughborough University Data Repository. https://doi.org/10.17028/rd.lboro.16434759

Mathers, K. L., Hill, M. J., Wood, C. D., & Wood, P. J. (2019). The role of fine sediment characteristics and body size on the vertical movement of a freshwater amphipod. *Freshwater Biology*, *64*, 152–163.

Mathers, K. L., Hill, M. J., & Wood, P. J. (2017). Benthic and hyporheic macroinvertebrate distribution within the heads and tails of riffles during baseflow conditions. *Hydrobiologia*, *794*, 17–30.

Mathers, K. L., Millett, J., Robertson, A. L., Stubbington, R., & Wood, P. J. (2014). Faunal response to benthic and hyporheic sedimentation varies with direction of vertical hydrological exchange. *Freshwater Biology*, *59*, 2278–2289.

Mathers, K. L., Rice, S. P., & Wood, P. J. (2017). Temporal effects of enhanced fine sediment loading on macroinvertebrate community structure and functional traits. *Science of the Total Environment*, *599*, 513–522.

Mathers, K. L., Rice, S. P., & Wood, P. J. (2019). Predator, prey, and substrate interactions: The role of faunal activity and substrate characteristics. *Ecosphere*, *10*, e02545.

Melis, T. S., Korman, J., & Kennedy, T. A. (2012). Abiotic & biotic responses of the Colorado River to controlled floods at Glen Canyon Dam, Arizona, USA. *River Research and Applications*, *28*, 764–776.

Mürle, U., Ortlepp, J., & Zahner, M. (2003). Effects of experimental flooding on riverine morphology, structure and riparian vegetation: The River Spöl, Swiss National Park. *Aquatic Sciences*, *65*, 191–198.

Nogaro, G., Datry, T., Mermillod-Blondin, F., Descloux, S., & Montuelle, B. (2010). Influence of streambed sediment clogging on microbial processes in the hyporheic zone. *Freshwater Biology*, *55*, 1288–1302.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Wagner, H. (2019). *Vegan: Community ecology package*. R package version 2.5-6.

Olden, J. D., Konrad, C. P., Melis, T. S., Kennard, M. J., Freeman, M. C., Mims, M. C., Bray, E. N., Gido, K. B., Hemphill, N. P., Lytle, D. A., & McMullen, L. E. (2014). Are large-scale flow experiments informing the science and management of freshwater ecosystems? *Frontiers in Ecology and the Environment*, *12*, 176–185.

Ortlepp, J., & Mürle, U. (2003). Effects of experimental flooding on brown trout (*Salmo trutta fario* L.): The River Spöl, Swiss National Park. *Aquatic Sciences*, *65*, 232–238.

O'Sullivan, M., Huallachain, D. O., Antunes, P. O., Jennings, E., & Kelly-Quinn, M. (2019). The impacts of cattle access to headwater streams on hyporheic zones. *Biology and Environment: Proceedings of the Royal Irish Academy*, *119*, 13–27.

Palmer, M., & Ruhi, A. (2019). Linkages between flow regime, biota, and ecosystem processes: Implications for river restoration. *Science*, *365*, eaaw2087.

Peralta-Maraver, I., Robertson, A. L., & Perkins, D. M. (2019). Depth and vertical hydrodynamics constrain the size structure of a lowland streambed community. *Biology Letters*, *15*, 20190317.

R Development Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., & Smol, J.

P. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, *94*, 849–873.

Rempel, L. L., Richardson, J. S., & Healey, M. C. (1999). Flow refugia for benthic macroinvertebrates during flooding of a large river. *Journal of the North American Benthological Society*, *18*, 34–48.

Robinson, C. T. (2012). Long-term changes in community assembly, resistance, and resilience following experimental floods. *Ecological Applications*, *22*, 1949–1961.

Robinson, C., & Uehlinger, U. (2003). Using artificial floods for restoring river integrity. *Aquatic Sciences*, *65*, 181–182.

Robinson, C. T., & Uehlinger, U. (2008). Experimental floods cause ecosystem regime shift in a regulated river. *Ecological Applications*, *18*, 511–526.

Robinson, C. T., Uehlinger, U., & Monaghan, M. T. (2003). Effects of a multiyear experimental flood regime on macroinvertebrates downstream of a reservoir. *Aquatic Sciences*, *65*, 210–222.

Robinson, C. T., Siebers, A. R., & Ortlepp, J. (2018). Long-term ecological responses of the River Spöl to experimental floods. *Freshwater Science*, *37*, 433–447.

Sarriquet, P. E., Bordenave, P., & Marmonier, P. (2007). Effects of bottom sediment restoration on interstitial habitat characteristics and benthic macroinvertebrate assemblages in a headwater stream. *River research and applications*, *23*, 815–828.

Scheurer, T., & Molinari, P. (2003). Experimental floods in the River Spöl, Swiss National Park: Framework, objectives and design. *Aquatic Sciences*, *65*, 183–190.

Sear , D. A. (1993). Fine sediment infiltration into gravel spawning beds within a regulated river experiencing floods: Ecological implications for salmonids. *Regulated Rivers: Research & Management*, *8*, 373–390.

Smock, L. A., Gladden, J. E., Riekenberg, J. L., Smith, L. C., & Black, C. R. (1992). Lotic macroinvertebrate production in three dimensions: Channel surface, hyporheic and floodplain environments. *Ecology*, *73*, 876–886.

Stanford, J. A., & Ward, J. V. (1993). An ecosystem perspective of alluvial rivers: Connectivity and the hyporheic corridor. *Journal of the North American Benthological Society*, *12*, 48–60.

Stubbington, R., Wood, P. J., Reid, I., & Gunn, J. (2011). Benthic and hyporheic invertebrate community responses to seasonal flow recession in a groundwater-dominated stream. *Ecohydrology*, *4*, 500–511.

Stubbington, R., Boulton, A. J., Little, S., & Wood, P. J. (2015). Changes in invertebrate assemblage composition in benthic and hyporheic zones during a severe supraseasonal drought. *Freshwater Science*, *34*, 344–354.

Trümpy, R., Schmid, S. M., Conti, P., & Froitzheim, N. (1997). *Erläuterungen zur Geologischen Karte 1:50 000 des Schweizerischen Nationalparks (Geologische Spezialkarte Nr. 122)*. Nationalpark-Forschung in der Schweiz, Swiss National Park.

Uehlinger, U., Kawecka, B., & Robinson, C. T. (2003). Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (River Spöl). *Aquatic Sciences*, *65*, 199–209.

Vadher, A. N., Millett, J., & Wood, P. J. (2018). Direct observations of the effect of fine sediment deposition on the vertical movement of *Gammarus pulex* (Amphipoda: Gammaridae) during substratum drying. *Hydrobiologia*, *815*, 73–82.

Vander Vorste, R., Mermillod-Blondin, F., Hervant, F., Mons, R., & Datry, T. (2017). Gammarus pulex (Crustacea: Amphipoda) avoids increasing water temperature and intraspecific competition through vertical migration into the hyporheic zone: a mesocosm experiment. *Aquatic Sciences*, *79*, 45–55.

Van Looy, K., Tonkin, J. D., Floury, M., Leigh, C., Soininen, J., Larsen, S., Heino, J., LeRoy Poff, N., Delong, M., Jähnig, S. C., & Datry, T. (2019). The three Rs of river ecosystem resilience: Resources, recruitment, and refugia. *River Research and Applications*, *35*, 107–120.

Ward, J. V. (1989). The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, *8*, 2–8.

Webb, J. A., Watts, R. J., Allan, C., & Conallin, J. C. (2018). Adaptive management of environmental flows. *Environmental Management*, *61*, 339–346.

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

Yarnell, S. M., Stein, E. D., Webb, J. A., Grantham, T., Lusardi, R. A., Zimmerman, J., Peek, R. A., Lane, B. A., Howard, J., & Sandoval-Solis, S. (2020). A functional flows approach to selecting ecologically relevant flow metrics for environmental flow applications. *River Research and Applications*, *36*, 318–324.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3–14.

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