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ORIGINAL ARTICLE

The effect of increasing fine sediment load and drying duration on the re-emergence of *Gammarus pulex* (Amphipoda: Gammaridae) from the subsurface following flow resumption

Atish N. Vadher[1] | Sian Watson[1] | Ruth Copeland-Phillips[1] | Louis J. Durrant[2] | Paul J. Wood[3]

[1]Faculty of Arts, Science and Technology, University of Northampton, Northampton, UK

[2]LEMA Research Group, Department of Architecture, Geology, Environment and Constructions, University of Liège, Liège, Belgium

[3]Geography and Environment, Loughborough University, Loughborough, UK

Correspondence
Atish N. Vadher, Faculty of Arts, Science and Technology, University of Northampton, Northampton, NN1 5PH, UK.
Email: AtishVadher306@Gmail.com

Abstract

1. Environmental change and growing anthropogenic pressure on water resources is increasing the duration and intensity of drying events in streams in many geographical locations. Favourable sediment characteristics (e.g. high porosity and low fine sediment load within the substrate matrix) may facilitate benthic macroinvertebrate use of subsurface sediments in response to drying. However, the influence of sedimentary characteristics on the use and subsequent recovery of macroinvertebrates from initial vertical migration into, survival during unfavourable conditions within, and subsequent re-emergence from subsurface sediments have not been directly observed.
2. Transparent mesocosm tanks were used to directly observe the vertical movement and subsequent re-emergence of *Gammarus pulex* from subsurface sediments in response to increasing dry period (1, 7, or 21 days) and fine sediment load (0.5–1 mm particle diameter used for light and heavy sediment treatment) and following rehydration and resumption of flowing conditions.
3. Increasing volumes of fine sediment addition limited the ability of *G. pulex* to access subsurface sediment in response to drying and re-emerge following rehydration. The longest dry period (21 days) reduced the ability of *G. pulex* to re-emerge from the subsurface sediments following rehydration and flow resumption.
4. Increasing fine sediment load negatively affects taxa using subsurface sediments as a refuge. Increased fine sediment deposition has the potential to reduce both access to the sub-surface and re-emergence once surface flow resumes.
5. As many rivers are beginning to dry out, or are showing prolonged drying due to global warming, it is increasingly important that river management reduces the input of fine sediment into rivers and increase sediment porosity of riverbeds to facilitate access into the subsurface refuge by benthic fauna.

KEYWORDS
direct observation, Hyporheic refuge, intermittent flow, recovery, sedimentation

1 | INTRODUCTION

It is increasingly recognised that many stream channels across the globe cease to flow or lose surface water periodically (Leigh et al., 2016; Messager et al., 2021; Stubbington et al., 2017); and that the proportion of stream channel length subject to drying is likely to increase in the future due to climate change and increasing human demands on freshwater resources (Datry et al., 2017, 2018; Pyne & Poff, 2017). Temporary streams occur in every climatic zone from the polar (McKnight et al., 1999) and temperate zones (Stubbington et al., 2017; Vadher et al., 2018a) through to the Mediterranean and arid regions (Bogan et al., 2015; Hose et al., 2005). Although the biotic response to waterbody drying has been increasingly quantified (Sarremejane et al., 2019; Storey, 2016), research considering the mechanisms underpinning the responses that facilitate persistence when exposed to harsh environmental conditions, for example refuge use, behavioural adaptation, or physiological adaptation, remains limited (but see Bogan & Boersma, 2012; Strachan et al., 2015; Vadher et al., 2017).

When stream drying occurs, surface flow ceases and surface water can become fragmented into isolated pools along the channel as a result of reduced discharge and streambed topography (Bogan et al., 2015; Boulton, 2003). Habitat quality within isolated pools may become increasingly unfavourable in the absence of groundwater recharge causing a gradual reduction in water quality in constricting available aquatic habitats (Gómez et al., 2017; Gómez-Gener et al., 2021; Vadher et al., 2018a). Combined with the potential intensification of biotic interactions (e.g. predation, cannibalism, competition for space; Lake, 2003; Vander Vorste et al., 2017) these changes may ultimately result in biota being stranded at the surface as water recedes (Extence, 1981; Vadher et al., 2017). In response to surface drying, individuals may display resistance (ability to withstand) and resilience (ability to recover) traits (Hershkovitz & Gasith, 2013), such as the use of desiccation-resistant life stages (Stubbington et al., 2016), uptake of atmospheric oxygen (Stanley et al., 1994), and active movements into subsurface sediments (Vadher et al., 2017), that may facilitate persistence during adverse hydrological conditions and the recovery period. The filtering effect of gradual drying until the complete loss of surface water occurs leads to major changes in aquatic macroinvertebrate communities that have been widely documented for intermittent lotic systems (e.g., Bogan et al., 2015; Bonada et al., 2007; Clarke et al., 2010; Hill & Milner, 2018; Mathers, Hill, Wood, & Wood, 2019).

Although the process of streambed drying results in the loss of surface water, subsurface sediments and the hyporheic zone (ecotone between the groundwater and surface water) often remain saturated and may provide a potential refuge for lotic fauna (Maazouzi et al., 2017; Vadher et al., 2018a; Williams & Hynes, 1974). Recent field studies have indicated that macroinvertebrates may rapidly recolonise benthic habitats following drying events by using the deeper subsurface sediments as a refuge (e.g., Pařil et al., 2019; Vander Vorste, Malard, & Datry, 2016). However, due to the inherent difficulty of making observations within subsurface habitats and tracing organisms within it, only a limited number of experimental studies have been able to directly observe or quantify the movement of fauna from the surface/benthic zone into the subsurface when surface water declines (Vadher et al., 2017; Vadher et al., 2018b; Vander Vorste, Mermillod-Blondin, Hervant, Mons, Forcellini, & Datry, 2016). Furthermore, no studies have directly observed the subsequent return of individual fauna into the benthic zone when surface water returns.

Excessive fine sediment (particles <2 mm diameter) deposition in rivers is widely recognised as an increasing pressure on surface waterbodies (e.g., Jones et al., 2012; Wilkes et al., 2018) and especially the healthy functioning of hyporheic systems across the globe (Jones et al., 2015; Mathers et al., 2014). Sediment characteristics such as grain-size distribution, porosity, heterogeneity, and fine sediment content have been widely recognised as key factors affecting macroinvertebrate ability to access subsurface sediments, and their resultant resistance to surface water drying (Loskotová et al., 2019; Patel et al., 2021; Vadher et al., 2015, 2017). The presence of deposited fine sediment may impede macroinvertebrate access and ability to migrate through subsurface sediments by reducing the size of sediment pore spaces, as well as bridging and closing interstitial pathways (Navel et al., 2010; Vadher et al., 2015: Vadher, Millett, & Wood, 2018; Loskotová et al., 2019).

Gammarus pulex (Linnaeus, 1758; Amphipoda: Gammaridae) is a predominantly benthic organism widespread throughout northwestern Europe (Crane, 1994; MacNeil et al., 1997). *G. pulex* is an ecologically important macroinvertebrate due to its role as prey for fish, potential predator of other invertebrate species, and shredder of organic matter in lotic ecosystems (Kelly et al., 2002; MacNeil et al., 1997). *G. pulex* has been widely recorded in benthic sediments and the hyporheic zone of perennial and temporary streams (Dole-Olivier et al., 1997; Stubbington et al., 2011) and is known to move into subsurface sediments in response to biotic competition (McGrath et al., 2007) and water level reduction (Stubbington et al., 2015; Vander Vorste, Mermillod-Blondin, et al., 2016). As a result of these characteristics and its wider use as a model organism in laboratory studies (e.g. Folegot et al., 2018; Vadher et al., 2015, 2017), *G. pulex* is an ideal test organism for experiments examining subsurface sediment use.

This study specifically aimed to quantify the re-emergence and recolonisation potential of *G. pulex* from subsurface sediments subject to increasing fine sediment load and periods of surface drying. *G. pulex* was selected as a model organism to study re-emergence as previous experiments have demonstrated that it actively moves into subsurface sediments in response to water level reduction (Vadher et al., 2015; Vadher et al., 2018b). We hypothesised that under direct observation through transparent mesocosm tanks: (1) increasing fine sediment load would limit the ability of *G. pulex* to access subsurface sediments in response to surface drying; (2) reduced subsurface porosity (increased fine sediment load) would reduce the recolonisation potential of *G. pulex* by impeding subsequent re-emergence from subsurface sediments when surface flow returned; and (3) an increase in the duration of the dry period would reduce

the recovery/recolonisation potential of *G. pulex* from subsurface sediments when surface flow returned.

2 | METHODS

2.1 | Test organism and collection

Gammarus pulex individuals were collected from Wood Brook (52°46,007.5″N 1°12,034.6″W) in Loughborough (Leicestershire, U.K.) using a kick-sampling technique with a standard kick-net (900-μm mesh, 23-cm × 25.5-cm frame, 27.5 cm bag depth). *G. pulex* individuals were carefully transferred onto a 1-mm aperture sieve to ensure only individuals >5 mm body length were used in experiments (see Mathers, Stubbington, Leeming, Westwood, & England, 2019; Patel et al., 2021) and placed into a 5-L container of stream water, prior to transportation to the laboratory within 12 hr.

2.2 | Tank mesocosms

Re-circulating transparent tanks (50 cm length × 35 cm height × 5 cm width) were constructed using 1 cm thick clear acrylic sheets (Figure 1; adapted from Vadher et al., 2018b). The tanks were designed to contain substrate made of transparent glass and acrylic particles to a height of 25 cm and water to a height of 30 cm (i.e. 5 cm surface water). To create re-circulating flow across the tanks, silicone tubes (0.5 cm internal diameter × 40 cm length) were fitted to opposite ends of a tank to create an inlet pipe where water could enter the tank (32 cm above the base of the tank) and an outlet pipe where water could drain out from (30 cm above the base of the tank). The position of these pipes allowed the water level to be held constant at 30 cm when flow ceased (Figure 1). The end of the inlet pipe of each tank was attached to a submersible water pump (150 L/hr pump rate) at the bottom of a 750-ml reservoir beaker to generate flow within the tanks. The outlet pipe drained water from the tank into the reservoir beaker through a 0.25-mm sieve to retain any individuals drifting or actively attempting to migrate downstream. A 0.7 cm wide silicone drainage pipe (0.5 cm internal diameter × 40 cm length) was also fitted centrally to the base of each tank for drainage and to allow precise water level reduction (1 mm accuracy) using a Hoffman clip. The tanks were filled to a height of 25 cm with transparent sediments to retain space for 5 cm of surface water above the sediment surface (Figure 1) and held upright on wooden mounts. Experiments were conducted in a dark room to provide lighting conditions analogous to that within subsurface streambed sediments.

2.3 | Sediment treatments

Three types of sediment: (1) large rounded transparent glass particles (large; 14–20 mm diameter); (2) small angular transparent acrylic particles (small; 10–15 mm diameter); and (3) fine sediment particles (fine; 0.5–1 mm diameter riverine sand), were used to create four sediment treatments (very porous, porous, light sedimentation, and heavy sedimentation). The very porous sediment treatment comprised 100% large transparent particles, the porous sediment treatment comprised a mix of 50% large and 50% small transparent particles, the light sedimentation treatment comprised a mix of 50% large and 50% small transparent particles with 167 ml (272.2 g) of fine sediment deposited at the surface, and the heavy sedimentation treatment comprised a mix of 50% large and 50% small transparent particles with 334 ml (544.3 g) of fine sediment deposited at the surface (Figure 2). These treatments are analogous to an *open gravel framework* with no fine sediment content (Bridge & Lunt, 2006) and the same frameworks compromised by fine sediment deposition at two levels. The size range of gravel particles and fine sediment (riverine sand 0.5–1 mm in diameter) used are comparable to those studied in both field and laboratory flume investigations examining sediment deposition processes (Bridge & Lunt, 2006; Gibson et al., 2009, 2010). Prior to determining the sediment load to be added, the minimum quantity of fine sediment required to totally fill the surface layer (i.e. total interstitial volume of the top 5 cm of the porous sediment treatment) was calculated to be 544.3 ± 2.5 g (heavy sedimentation), and 50% of this mass was used for the light sedimentation treatment (272.2 ± 1.2 g). This approach allowed both surface clogging via bridging processes and filling of the substrate from greater depth by unimpeded percolation as demonstrated by

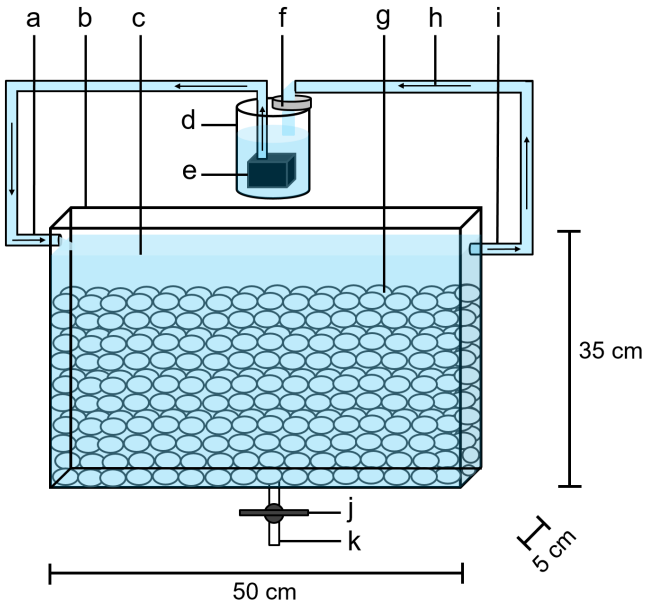


FIGURE 1 Schematic diagram of a tank mesocosm. (a) Water inlet pipe 32 cm above the base of the tank; (b) acrylic tank (50 cm × 35 cm × 5 cm); (c) water level at experiment start (5 cm above sediment surface); (d) 750-ml reservoir beaker; (e) submersible water pump (150 L/hr pump rate); (f) 0.2-mm sieve to catch drifting individuals; (g) 25 cm height of transparent sediment particles; (h) arrows to indicate direction of re-circulating flow; (i) water outlet pipe 30 cm above the base of the tank; (j) Hoffman clip; (k) drainage pipe (0.5 mm internal diameter). Modified from Vadher et al., 2018b. Not to scale

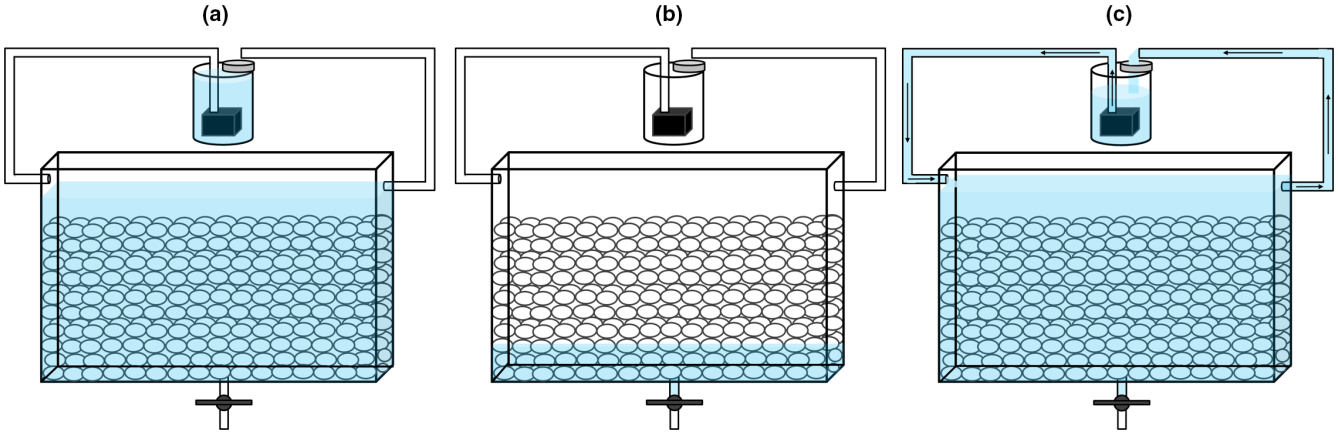
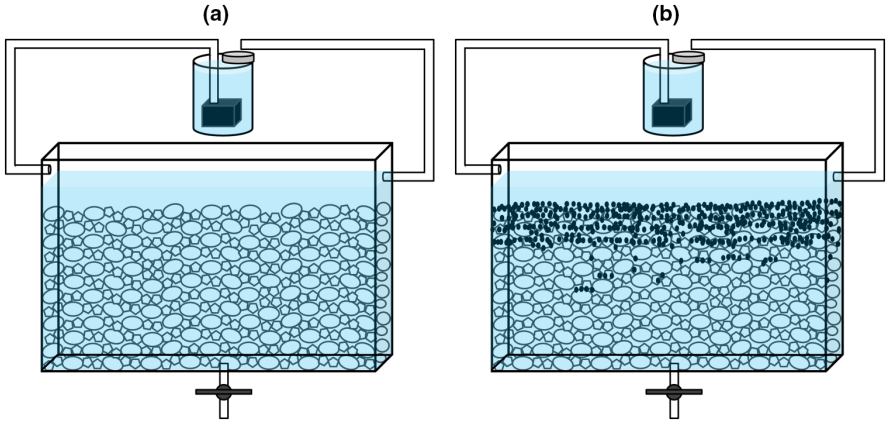


FIGURE 2 Schematic diagram of tank mesocosms at the start of experiments before (a) and after (b) fine sediment addition. Not to scale

FIGURE 3 Schematic diagram of tank mesocosms at experiment start (a), following water level reduction (b) and rehydration and flow resumption (c). Not to scale



Gibson et al. (2009, 2010) to potentially take place. The large and small transparent particles created an open gravel framework (substrate) onto which the two fine sediment treatments were deposited. The interstitial volume in the tanks were 1,503 ± 16 ml for the very porous treatment and 1,407 ± 17 ml for the porous treatment with fine sediment added to the substrate surface during fine sediment treatment.

2.4 | Experiment procedure

Mesocosms were filled with transparent sediment to a height of 25 cm and water to a height of 30 cm, allowing for 5 cm surface water. Sediment treatments with a substrate matrix containing both types of transparent particles were mixed thoroughly prior to use or the addition of fine sediment. The reservoir beaker was filled to 750 ml with tap water and the submersible pump was activated to create re-circulating flow (Figure 1). The water in the tanks were left to circulate for 12 hr prior to experiments commencing, to dechlorinate and stabilise temperature to ambient thermal conditions. Prior to the introduction of *G. pulex*, flow was terminated, and water level was held at 30 cm (Figure 3a). Fine sediments used in treatments were thoroughly washed and distributed evenly over the substrate surface prior to experiments commencing. A small LED light was used to inspect the tanks within the dark room during the experimental procedure to minimise disturbance during the trials.

Ten *G. pulex* individuals were introduced to each tank and left for 20 min to acclimatise. This time period has been established as a sufficient period for macroinvertebrate acclimation to laboratory experiments and dark room conditions in previous experiments (Vadher et al., 2017; Vadher, Millett, et al., 2018). The water level was controlled and reduced from a height of 30 cm (5 cm surface water) to 5 cm (20 cm below the sediment surface) over 5 hr at a rate of 5 cm/hr using a Hoffman clip on the drainage pipe and direct observation through the transparent mesocosms (Figure 3b). Following water level reduction, tanks were left for a period of either 1, 7, or 21 days to simulate the varying dry period durations.

Following the initial drawdown of water, the number of individuals stranded at the sediment surface (i.e. unable to move into the subsurface sediments) were recorded (H_1). Following the drying treatments (1-, 7-, or 21- day dry period), tanks were rehydrated with dechlorinated water at a rate of 5 cm/hr over 5 hr until 5 cm of surface water (above the sediment surface) was achieved and re-circulating flow was obtained (Figure 3c). Following rehydration, the tanks were left to re-circulate for 3 days allowing individuals emerging from subsurface sediments into the surface water to migrate out

of the tank through the outlet pipe and onto a 0.25-mm sieve (H_2; H_3). Living organisms that did not emerge from the subsurface sediments within 3 days were also recorded.

Water quality parameters (water temperature, pH, dissolved oxygen, and conductivity) were measured prior to and immediately after each dry period using an Aquaread® AP-800 probe (Aquaread Ltd). Water quality before each experiment was measured by immersing the probe into the reservoir beaker; after each dry period water quality was measured by draining a sample of water from the tank immediately prior to rehydration to monitor the changes in water quality following each dry period. Experiments were replicated six times for each sediment treatment and dry period ($n = 72$), using 720 *G. pulex* individuals.

2.5 | Data analysis

We tested our first hypothesis, that reduced sediment porosity and increasing fine sediment load would impede the ability of *G. pulex* to access subsurface sediments in response to water level reduction, using a general linear model (GLM) to compare the percentage of individuals stranded on the substrate surface among sediment treatments, duration of dry period, and their interaction. The percentage of individuals stranded on the sediment surface was the dependent variable, and sediment treatment and dry period were defined as fixed factors. Where their interaction was not significant, the main effects of each were considered. The model was fitted using maximum likelihood estimates (see Vadher et al., 2017). Tukey's post hoc tests were used to identify where significant effects of sediment treatment and dry period occurred between the treatments.

We tested our second and third hypotheses, that reduced sediment porosity (increased fine sediment load; H_2) and increasing dry period (H_3) would impede the ability of *G. pulex* to re-emerge following the resumption of surface flow using GLMs. These GLMs compared the percentage of *G. pulex* that re-emerged and the percentage of *G. pulex* alive in the sediment but did not re-emerge between sediment treatments, duration of dry period and their interaction. Re-emergence and the percentage of individuals alive in the sediment were defined as dependent variables and both sediment treatment and dry period were defined as fixed factors. Where their interaction was not significant, the main effects of each were considered. The model was fitted using maximum likelihood estimates. Tukey's HSD post hoc tests were used where significant effects of sediment treatment and dry period were detected. All GLMs displayed good model fits with an adjusted r^2 of 0.934 (percentage of individuals stranded), 0.975 (re-emergence), and 0.717 (percentage alive in sediment).

Water quality parameters within experiments were compared before water level reduction and immediately prior to rehydration using a paired sample *t* test to characterise changes that occurred during the experimental period. All analyses were conducted using IBM SPSS Statistics (version 26; IBM Corporation).

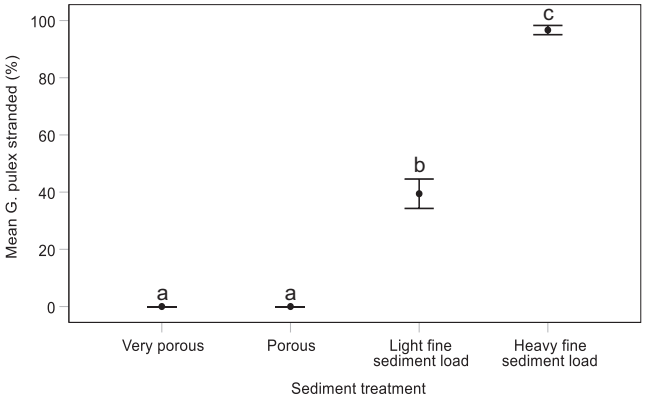


FIGURE 4 Mean percentage (±1 *SE*) of *Gammarus pulex* individuals stranded at the surface during water level reduction. Letters a–c indicate statistically different values (Tukey's HSD, $p < 0.05$)

3 | RESULTS

Sediment treatment had a significant effect on the percentage of individuals stranded at the sediment surface in response to water level reduction (GLM, $F_{3, 60} = 281.51$, $p < 0.001$). The percentage of stranded *G. pulex* was higher in sediment treatments with fine sediment loads (Tukey's HSD, $p < 0.001$) compared to sediment treatments with an open framework (very porous and porous; Tukey's HSD, $p > 0.05$; Figure 4). The percentage of *G. pulex* re-emerging following rehydration reduced in sediment treatments with fine sediment addition but decreased to a greater extent with increasing dry period; there was a significant interaction between sediment treatment and dry period (GLM, $F_{6, 60} = 3.49$, $p < 0.005$; Figure 5).

Overall, mean re-emergence was similar between sediment treatments for the open gravel framework at 93% ± 2.3% (large particles–very porous) and 90% ± 2.8% (mixed gravel–porous; Tukey's HSD, $p > 0.05$); but was markedly reduced in light sedimentation (21.58% ± 4.9%) and heavy sedimentation (0%) treatments, and were significantly different (Tukey's HSD, $p < 0.001$). Sediment treatment significantly affected the percentage of alive *G. pulex* individuals that did not re-emerge from the subsurface sediments (GLM, $F_{3, 60} = 61.4$, $p < 0.001$). The light sedimentation treatment had a significantly higher percentage of alive *G. pulex* in the subsurface sediments compared to all other sediment treatments (Tukey's HSD, $p < 0.001$; Figure 6).

Overall, duration of the dry period significantly reduced the re-emergence of *G. pulex* (GLM, $F_{2, 60} = 11.19$, $p < 0.001$). Re-emergence following a 21-day dry period was significantly lower (43% ± 7.7%) than re-emergence following a 1 (58% ± 9.2%) and 7-day dry period (53% ± 7.7%; Tukey's HSD, $p < 0.001$; Figure 7). Dry period duration did not have a significant effect on the percentage of individuals alive in the sediments that did not re-emerge (GLM, $F_{2, 60} = 0.64$, $p > 0.05$).

Temperature remained stable during experiments, but pH, dissolved oxygen and conductivity varied significantly (Table 1). The pH and dissolved oxygen declined from the start of the experiment

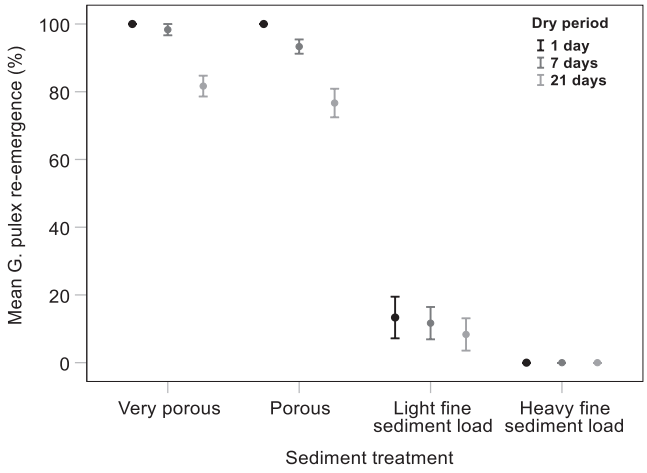


FIGURE 5 Sediment treatment and dry period effect on the mean percentage (±1 *SE*) of *Gammarus pulex* individuals that re-emerged following rehydration and flow resumption

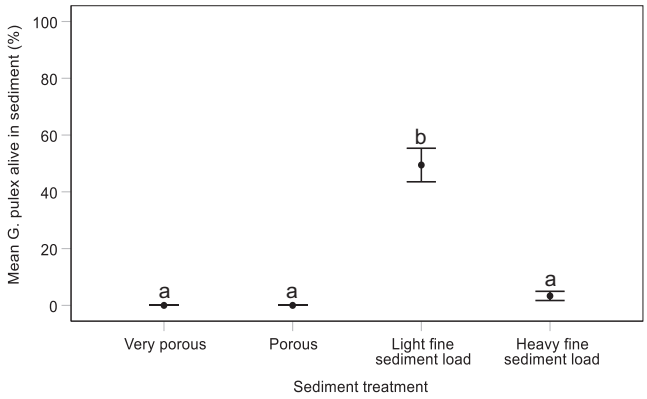


FIGURE 6 Mean percentage (±1 *SE*) of *Gammarus pulex* individuals alive in the sediment but did not re-emerge following rehydration and flow resumption. Letters a and b indicate statistically different values (Tukey's HSD, $p < 0.05$).

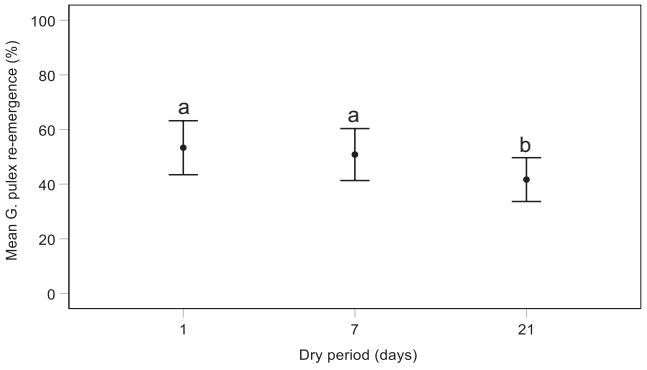


FIGURE 7 Mean percentage (±1 *SE*) of *Gammarus pulex* in all sediment treatments that re-emerged following rehydration and flow resumption of 1-, 7-, and 21-day dry periods. Letters a and b indicate statistically different values (Tukey's HSD, $p < 0.05$)

to immediately prior to rehydration while conductivity increased (Table 1). Temperature, pH, and conductivity varied as the duration dry period increased, and dissolved oxygen showed a decreasing trend with increasing dry period (Table 2). However, the nature and direction of the changes recorded in pH, conductivity, and dissolved oxygen are similar to those reported for naturally drying lotic systems (Day et al., 2019).

4 | DISCUSSION

For over 45 years, aquatic macroinvertebrates have been widely reported as using subsurface sediments as a refuge from adverse hydrological conditions (i.e. flooding and drying; e.g. Fenoglio et al., 2006; Maazouzi et al., 2017; Palmer et al., 1992; Williams & Hynes, 1974). More recent studies have found that invertebrates have the potential to re-colonise surface habitats from subsurface refuges when adverse conditions of drying subside (Loskotová

TABLE 1 Paired sample *t* test analysis between before and after drying (prior to rehydration) for each water quality parameter

Water quality parameter	Mean (±*SE*)		*df*	*t*	*p*
	Before drying	After drying			
Temperature (°C)	16.2 (±0.1)	16.3 (±0.1)	8	−0.588	0.573
pH	7.5 (±0.2)	7.0 (±0.2)	8	3.283	**0.011**
Dissolved oxygen (%)	78.4 (±1.9)	53.0 (±3.8)	8	5.451	**0.001**
Conductivity (μS/cm)	523 (±39)	597 (±39)	8	−4.055	**0.004**

Note: Significant values ($p \leq 0.05$) are emboldened.

TABLE 2 Mean water quality parameters following each dry period

Dry period (days)	Mean (±*SE*) water quality parameter after dry period			
	Temperature (°C)	pH	Dissolved oxygen (%)	Conductivity (μS/cm)
1	16.1 (±0.0)	6.9 (±0.3)	64.6 (±1.7)	453 (±32)
7	16.6 (±0.1)	7.5 (±0.3)	54.4 (±3.2)	680 (±24)
21	16.2 (±0.1)	6.6 (±0.1)	39.9 (±3.1)	658 (±35)

et al., 2021; Pařil et al., 2019; Vander Vorste, Malard, et al., 2016). We present results that support these field observations by directly observing the process of entry into the subsurface by individuals during the drawdown of water through to the re-emergence of the same individuals following flow resumption.

We found evidence to support our first hypothesis, that increasing fine sediment load would limit the ability of *G. pulex* to access subsurface sediments in response to surface drying. Individuals stranded more readily at the sediment surface in treatments with fine sediment added, which supports previous studies that also reported fine sediment deposition reduced macroinvertebrate ability to access and move through subsurface sediments (Bo et al., 2007; Mathers, Stubbington, et al., 2019; Vadher et al., 2015). Previous studies have demonstrated that fine sediment may clog the streambed surface, bridging interstitial pathways through the sediment framework (Gibson et al., 2009, 2010; Harper et al., 2017) and resulting in detrimental effects on hydrological connectivity (Bendaoud et al., 2021; Shrivastava et al., 2020) and ecology (Korbel et al., 2019; Vadher et al., 2018b).

Benthic invertebrates have been reported to demonstrate species-specific responses to drying when migrating vertically into subsurface sediments in response to the loss of surface water (Korbel et al., 2019; Maazouzi et al., 2017; Stubbington et al., 2015; Vadher et al., 2017). Considering that drying events may increase in both frequency and intensity due to climate change and human activity (Datry et al., 2018; Pyne & Poff, 2017), the loss of vertical connectivity through subsurface sediments due to fine sediment deposition is likely to have a negative impact on macroinvertebrate communities (Descloux et al., 2013; Mathers & Wood, 2016) and the refuge capacity of subsurface sediments (Vadher et al., 2015; Vadher et al., 2018b).

Our findings support our second hypothesis that reduced subsurface porosity (increased fine sediment load) would reduce the recolonisation and recovery potential of *G. pulex* by impeding re-emergence from subsurface sediments when surface flow returned. Sediment characteristics (Gayraud & Philippe, 2003; Vadher et al., 2018b) and biological traits including larger body sizes (Loskotová et al., 2019; Patel et al., 2021; Vadher et al., 2017) affect the ability of macroinvertebrate fauna to move through the subsurface sediments as interstitial pathways through the sediment matrix can become blocked by fine sediment particles deposited on to the surface of the substrate (Harper et al., 2017; Vadher et al., 2018b) and impede movement. The effect of fine sediment impeding access into and through the subsurface sediments has been reported previously (Mathers et al., 2014; Richards & Bacon, 1994; Vadher et al., 2015; Vadher et al., 2018b); however, its effect on re-emergence following flow resumption has not previously been quantified. To our knowledge this is the first experimental study quantifying the impact of deposited fine sediment load on the re-emergence of macroinvertebrate fauna following surface drying.

We found support for our third hypothesis that increasing duration of the dry period would reduce the recovery potential of *G. pulex* from subsurface sediments when surface flow resumed. Based on the individuals that migrated into the subsurface sediments in response to drying, increasing the duration of the dry period reduced the percentage of *G. pulex* that re-emerged from the sediments. Previous studies have reported the negative effect of increasing flow intermittence and dry period on benthic and hyporheic invertebrate abundance and richness (Boersma et al., 2014; Datry, 2012; Leigh & Datry, 2016). Furthermore, experimental studies have found that an increasing dry period reduces the resistance of *G. pulex* within subsurface sediments, with survival decreasing over time (Vadher et al., 2018b; Vadher et al., 2018c). Our findings extend this research and demonstrate the impact of increasing dry period duration on reducing *G. pulex* resilience and their ability to re-emerge and recover when surface conditions become favourable. However, when considering recovery, the individuals that re-emerged as well as the individuals alive in the subsurface all at the end of our experiment all had the potential to promote recolonisation of benthic habitats with the resumption of surface flow. In addition to the duration of the surface drying, the reduction in *G. pulex* resilience may also reflect changes in water chemistry over time as dissolved oxygen declined consistently with increasing dry period (Table 2). Typically, during drying events, temperature and conductivity increase, while dissolved oxygen decreases in remaining waterbodies, often causing a negative impact on most stream macroinvertebrates (Bond et al., 2008; Lake, 2003; Leigh, 2013). The experimental approach employed in the current experiments provided relatively favourable physicochemical conditions to promote a viable subsurface refuge that could facilitate recovery. The relatively stable physicochemical parameters resulted in temperatures well within the thermal tolerance range of the model organism and, although significantly different before and after dry periods, relatively low overall variability in dissolved solutes (conductivity; Table 1) were observed when compared with those recorded in the natural environment (Bogan et al., 2013; Vadher et al., 2018a). However, the reduction in dissolved oxygen observed with increasing dry period is consistent with field observations during drying events (Del Rosario & Resh, 2000; Gómez et al., 2017; Wood et al., 2010) and may have affected the survivorship and the potential for individuals to re-emerge from the subsurface sediment refuge.

The viability of subsurface sediments as a refuge for macroinvertebrates is growing in importance as the frequency and severity of drying events is increasing globally as a result of climate change and anthropogenic activities (Datry et al., 2017; Pyne & Poff, 2017). However, anthropogenic activities including agriculture (Pulley & Collins, 2019), development construction (Ma et al., 2018), and industrial activities such as mineral extraction (Byrne et al., 2012) are increasing fine sediment loads and reducing the refuge potential of subsurface sediments, and therefore macroinvertebrate community resilience in the face of stressors such as stream drying. Our study clearly demonstrates that the effects of increasing fine sediment load on individuals use of the subsurface sediment refuge as fine sediment has the potential to reduce both access to this refuge and re-emergence from it once surface flow resumes.

The use of transparent mesocosms allowed direct observation into subsurface sediments to quantify the impact of increasing fine sediment load and dry period on the resilience of *G. pulex*. This laboratory mesocosm based approach employed in this investigation allowed the effects of specific abiotic factors to be studies with greater control than would be possible under natural field conditions. However, the heterogeneous and dynamic conditions experienced naturally in the field, and especially as intermittent streams dry, clearly demonstrate that the experiments reflect a small range of the possible variability. Further research is therefore required to quantify the effects of fine sediment on the resistance and resilience of macroinvertebrate communities using a combination of insights from field investigations or natural conditions, field experiments, and tightly controlled laboratory experiments. This multidisciplinary and multiscale approach will lead to a greater understanding of the mechanistic processes associated with sedimentation that lead to changes in individual populations and communities within lotic ecosystems.

AUTHOR CONTRIBUTION

Conceptualisation: A.N.V., S.W., R.C.P., P.J.W. Developing methods: A.N.V., S.W., R.C.P., P.J.W. Data analysis: A.N.V. Preparation of figures and tables: A.N.V., P.J.W. Conducting the research, data interpretation, writing: A.V., S.W., L.J.D., R.C.P., P.J.W.

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Atish N. Vadher https://orcid.org/0000-0002-6778-3260
Paul J. Wood https://orcid.org/0000-0003-4629-3163

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