Body size affects the vertical movement of benthic amphipods through subsurface sediments in response to drying

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Abstract This study aimed to experimentally examine how riverbed drying and different rates of water level reduction influenced the vertical movement of amphipods of various sizes into different subsurface sediment compositions. Using sediment columns (mesocosms) filled with different sized transparent substrates, we explored how varying speeds of drawdown affected vertical movement and stranding of individuals. We hypothesised that: (1) larger individuals would be less able to migrate within subsurface sediments compared to smaller ones; (2) smaller sediment particles would lead to more individuals becoming stranded and; (3) faster rates of water level drawdown would increase the likelihood of individuals becoming stranded above the waterline. Body size significantly influenced the final position of an individual, with smaller individuals accessing deeper sediments more readily. Larger amphipods were more likely to become stranded above the waterline. Amphipods migrated to greater depths during faster water level reduction rates with smaller individuals displaying greater overall movement. Sediment particle size did not influence the ability of amphipods to move vertically into subsurface sediments in response to water level reduction. The results indicate that subsurface sediments may serve as a refuge from surface drying but that both the size of individual invertebrates influences their ability to migrate vertically.

Keywords Stream drying · Sediment particle-size · Macroinvertebrate · Burrowing · Head-width · Water level reduction

Introduction

The dewatering of benthic sediments has increased globally due to natural events and anthropogenic activities (e.g., Pyne & Poff, 2016; Stubbington et al., 2017; Datry et al., 2018). Flow decrease and cessation can occur naturally, either seasonally or during drought (Bogan et al., 2017; Aspin et al., 2019), or anthropogenically, associated with river management activities such as hydroppeaking for power generation.
The loss of surface water can have important effects on the fluxes of organic matter and lead to modified faunal community structure both during and post-drying (e.g., Hill et al., 2018; Pašil et al., 2019). Moreover, the legacies of such events may influence subsequent recolonization and recovery patterns of fauna and flora (Piano et al., 2019). Given the increasing pressures associated with surface and groundwater abstraction and diversion for anthropogenic use (White et al., 2018; Mihalicz et al., 2019), and the predicted increase in the frequency and duration of droughts (Prudhomme et al., 2014; Manning et al., 2019), there is a pressing need to understand how freshwater organisms respond to riverbed drying events.

A key driver of aquatic macroinvertebrate community structure is channel dewatering and drying of benthic sediments (Bogan et al., 2015; Rosset et al., 2017). As drying occurs, waterbodies lose their connectivity with the landscape through the loss of lateral (i.e. riparian zone and floodplain), longitudinal (upstream-downstream) and vertical (surface-subsurface) dimensions (Lake, 2003; Chadd et al., 2017). Channel drying and loss of surface water results in distinct species assemblages (Leigh et al., 2016; Bogan et al., 2017; Mathers et al., 2019a), characterised by fauna exhibiting resistance and resilience traits to surface water drying such as use of atmospheric oxygen (Stanley et al., 1994), desiccation-resistant life stages (Stubbington et al., 2016), or the ability to rapidly recolonize following the rewetting and resumption of favourable conditions (Vander Vorste et al., 2016a; Pašil et al., 2019). Although surface water may not be available, water may persist in subsurface sediments (hyporheic zone) which may provide a potential refuge for macroinvertebrates (Williams & Hynes, 1974; Vadher et al., 2018a). However, the refuge potential may be highly variable depending on water table depth (Vander Vorste et al., 2016b) and the nature of surface-groundwater exchange (Folegot et al., 2018).

The ability of fauna to access the subsurface habitat reflects both sedimentary characteristics (Gayraud & Philippe, 2003; Vadher et al., 2018b) and faunal traits (Wickson et al., 2012; Loskotová et al., 2019). Sediment characteristics such as pore size, ratio of gravel framework to fine sediment matrix, and particle size and heterogeneity have been highlighted as key abiotic factors affecting the ability of invertebrate fauna to access subsurface sediments (Mathers et al., 2014; 2019b; Vadher et al., 2017; Loskotová et al., 2019). A reduction in sediment pore space due to excessive deposition of fine sediments and clogging may limit the ability of macroinvertebrates to move vertically through interstitial pathways and access subsurface habitats (Navel et al., 2010; Vadher et al., 2015; 2017). These abiotic factors operate in conjunction with faunal traits that may facilitate resistance to drying and dewatering including behavioural adaptations (Lytle et al., 2008), vermiform body morphology (Vadher et al., 2017; Loskotová et al., 2019) and physiological traits (Wickson et al., 2012; Stubbington et al., 2016). Recent research has also demonstrated how the vertical movement of macroinvertebrates may be influenced by their relative body size within sediments of varying heterogeneity (Mathers et al., 2019b). However, current knowledge of the relationship between body size and the ability to access subsurface habitats during dewatering of sediments is limited.

In this study, we experimentally examined how the rate of water level reduction for different sediment grain sizes and an individual’s body size influences organismal vertical movement into subsurface sediments using laboratory mesocosms. We used two amphipod species with comparable morphology to provide a body size continuum (ca. 5–30 mm in size), *Gammarus pulex* (Linnaeus, 1758) (Amphipoda: Gammaridae) and *Dikerogammarus villosus* (Sowinsky, 1894) (Amphipoda: Gammaridae), and employed transparent sediments to enable direct observations (sensu Vadher et al., 2017). Specifically, we hypothesised that: (1) larger individuals of both species would be less able to migrate within the subsurface compared to smaller ones; (2) smaller sediment grain sizes and pore space would result in greater potential for individuals to become stranded and; (3) faster water level reduction would enhance the likelihood of organismal stranding above the waterline.

**Materials and methods**

**Experimental set-up**

Ten sediment column mesocosms were constructed using transparent acrylic pipes (60 cm × 4.6 cm
internal diameter), each filled with 50 cm of transparent sediments (adapted from Vadher et al., 2017; Fig. 1) and filled to a depth of 55 cm with pre-treated tap water (AquaSafe® - Tetra®; OxyTabs® - JBL®, Germany). To control water level reduction accurately (0.5 mm accuracy), sediment columns were sealed at the base using a rubber bung with a 5 mm glass tube (3 mm internal diameter) through the centre to act as a drain (Fig. 1). A silicone tube, secured with a Hoffman clip (Fig. 1), was fitted around the glass drain. Sediment columns were mounted side by side onto a horizontal rack using clamps and black cloth was placed over the columns to provide complete darkness analogous to subsurface streambed sediments.

Treatments

Three sediment treatments were employed (large, small and mixed) to cover varying particle and pore sizes (but not pore volume / porosity). The large sediment treatment comprised rounded gravel sized particles of 14–20 mm in diameter with an average interstitial volume of 311 ml (± 1.87 ml—total of 194 particles per column). The small sediment treatment comprised angular particles 10–15 mm in diameter with an average interstitial volume of 303.2 ml (± 1.30 ml—total of 816 particles per column) and the mixed sediment treatment comprised a 50–50% mix of large and small particles creating an interstitial volume of 304.4 ml (± 1.65 ml—total of 408 small particles and 97 large particles). The fine gravel-sized particles used in the study are typical of those recorded in the surface and subsurface substrates of lowland streams in the area where organisms were collected (Mathers & Wood, 2016). Four water level reduction treatments were employed: very slow (3.75 cm/h), slow (7.5 cm/h), fast (15 cm/h) and very fast (30 cm/h). These treatments reflect rapid reductions in water level associated with drying events downstream of small weirs in lowland rivers (Hill et al., 2019), as well the very rapid variability in flow due to hydropoeaking reservoir operations (Lange et al., 2019).

Test Amphipods

Two freshwater amphipod species were employed in the study, G. pulex and D. villosus. Both are predominantly benthic organisms and have comparable body morphology but vary in their maximal sizes, with G. pulex reaching up to 21 mm body length (Pinkster, 1970) and D. villosus reaching 30 mm (Rewicz et al., 2014). Both amphipod species typically dominate macroinvertebrate community biomass in temperate European rivers where they occur and display overlapping habitat preferences (McGrath et al., 2007; De Gelder et al., 2016). Individuals of both G. pulex and D. villosus have been recorded inhabiting gravel (2–64 mm) and cobble (64–256 mm) substrates (Dahl & Greenberg, 1996; Clinton et al., 2018).

Specimens were collected by gently disturbing benthic sediments and catching individuals downstream in a standard kick net (1 mm mesh, 230 mm × 255 mm frame, 275 mm bag depth) before being placed in 5 l buckets of stream water at least 12 h prior to experimental runs commencing. Specimens were returned to the laboratory, placed in aerated holding tanks containing stream water and allowed to acclimate to water temperatures of 18–20 °C (reflecting the ambient air temperatures when experiments were conducted during May-July in England). A surplus of food was provided in the form of raw carrot and aquarium crayfish food pellets. G. pulex were collected from Burleigh Brook, Loughborough (52°45’05.0”N, 1°14’02.6”W) and D. villosus from Pitsford Reservoir, Northamptonshire (52°32’36.2” N, – 0°88’30.2501” W). Juvenile individuals less than 5 mm total body length in size were
not used in experimental trials (as determine by allowing juveniles with smaller heads to pass through a 2 mm sieve at the field site).

Experimental procedure

One individual was left to acclimate for 20 min in the pre-prepared sediment column before the start of each experiment (time = 0; sensu Vadher et al., 2015; 2017). Only one individual was used in each column so that vertical distance moved could be accurately recorded throughout the experimental period. Prior to the reduction of water every 20 min, the depth position of each individual relative to the sediment surface was recorded using a small LED light. LED was used to minimise light disturbance during observations and eliminate photophobic behaviour often observed in gammarids (Lagru et al., 2011). An individual’s depth position from the sediment surface (depth = 0) was recorded to 5 mm accuracy and individuals observed on the sediment surface or in the water column were recorded to have a depth position of 0 mm. Water levels were reduced every 20 min until a 15 cm water refuge was retained (35 cm below the sediment surface; Fig. 1). It should be noted that the duration of water level reduction (time) varied due to the differing water level reduction rates (very slow, 3.75 cm/h; slow, 7.5 cm/h; fast, 15 cm/h; very fast, 30 cm/h), ranging from 10 h 40 min (3.75 cm/h) to 1 h 20 min (30 cm/h). Each experimental trial was replicated 10 times for each of the three sediment mixtures, four water level reduction rates and two amphipod species providing a total \( n \) of 240 experiments (\( G.\ pulex\ n =120 \) and \( D.\ villosus\ n = 120 \)).

Once a 15 cm refuge was retained, the column was left for 24 h (from the start of the experiment) to allow for any individuals stranded above, but close to the water line, to migrate into the water. Individuals above the water line at the end of experiments were classified as stranded organisms. After 24 h, the mesocosms were deconstructed to remove amphipods and sediments washed thoroughly to remove biological waste. Individual amphipods were preserved using 70% industrial methylated spirit (IMS) to enable an individual’s head size to be measured. Head size was employed as a standardised proxy for the body size of individuals (Kokkotis & McLaughlin 2002) as body size may vary depending on body posture even when preserved. Standardized measurements of head size for both \( G.\ pulex\) and \( D.\ villosus\) were taken from the base of the antenna to the posterior margin of the head carapace using a light microscope fitted with a calibrated eye-piece graticule.

Data analysis

Data analysis was conducted in R version 3.6.0 (R Development Core Team, 2019). Three metrics were extracted from the experimental data for statistical analysis; final vertical position after 24 h, mean distance moved between each 20 min observation period and stranding of an individual above the waterline at the end of the experimental period. As vertical positions were calculated to a 5 mm accuracy (i.e. 5–10 mm, 10–15 mm), the midpoint was taken and used in subsequent analyses. Preliminary analyses were conducted to confirm that head sizes differed statistically between species. A Kruskal–Wallis non-parametric test confirmed that the head sizes differed statistically between the two species and that \( D.\ villosus\) individuals (mean head size: 1.36 mm ± 0.02 mm, range 0.70–1.98 mm) were significantly larger than \( G.\ pulex\) individuals (mean head size—0.92 mm ± 0.03 mm—range 0.4–1.33 mm) (\( x^2 =105.25, P \leq 0.001 \)).

To test whether an individual’s final position or the mean distance moved per 20-min observation period differed, a Generalised Linear Model (GLM) was fitted using a Gaussian error distribution and identity link using the \( \text{glm} \) function in the ‘\text{stats}’ package. The model was fitted with the terms water level reduction rate, sediment treatment, head size and all interactions of these factors. To test the likelihood of individuals being stranded above the water line at the end of the 24-hour experiment a binary response characterising stranded and not stranded as “1” or “0” respectively was employed. A GLM was subsequently fitted using a binomial error distribution and logit link and fitted with the terms water level reduction rate, sediment treatment, head size and the interaction of these factors.

Results

Head size was significantly associated with an individual’s final position, with smaller \( G.\ pulex\) individuals accessing deeper sediments more readily (Fig. 2;
Table 1). There were no significant effects of sediment treatment, water level reduction rate or the interaction of these factors on the final position recorded (Table 1). Head size and water level reduction rate were significantly associated with the mean distance moved during each 20-min observation period and amphipod species. Note amphipod species are presented to allow visual comparison with *G. pulex* being smaller than *D. villosus*.

**Fig. 2** Mean (± 1 SE) final vertical position (mm) of amphipod individuals within subsurface sediments at the end of experiment (24 h) as a function of water level reduction rate and amphipod species. Note amphipod species are presented to allow visual comparison with *G. pulex* being smaller than *D. villosus*.

**Table 1** Summary of general linear model testing the influence of water level reduction rate, sediment treatment, head size and the interaction of these factors on the final vertical position of individuals at the end of the experiment (24-h). Significant terms are emboldened.

| Factor                              | $\chi^2$ | df | $P$    |
|-------------------------------------|----------|----|--------|
| Drawdown rate                       | 2.50     | 3  | 0.48   |
| Sediment type                       | 0.29     | 2  | 0.87   |
| Head size                           | 137.23   | 1  | < 0.001|
| Drawdown rate × sediment type       | 5.78     | 6  | 0.45   |
| Drawdown rate × head size           | 0.30     | 3  | 0.96   |
| Sediment type × head size           | 2.62     | 2  | 0.27   |
| Drawdown rate × sediment type × head size | 3.65 | 6  | 0.61   |

$P \leq 0.05$
More amphipods of both species migrated into deeper sediments during the faster water level reduction treatments (very fast and fast) than the slower water level reductions (slow and very slow), and smaller *G. pulex* individuals displayed greater overall vertical movement (Figs. 3, 4). Larger head sizes were significantly associated with an individual’s likelihood of stranding for both *D. villosus* (not stranded mean head size 1.18 mm ± 0.03 mm vs stranded mean head size 1.50 mm ± 0.03 mm) and *G. pulex* (not stranded mean head size 0.91 mm ± 0.02 mm vs stranded mean head size 1.03 mm ± 0.04 mm; Fig. 4). In particular, larger *D. villosus* individuals became stranded above the water line more readily (Table 3; Fig. 5). Across all experimental trials, 55% of *D. villosus* and 12.5% of *G. pulex* individuals became stranded (see Table 4 for a breakdown of stranding by experiment). However, there were no other significant effects of water level reduction rate, sediment treatment or the interaction of factors on the likelihood of individuals stranding.

**Discussion**

Our findings support our first hypothesis that the vertical movement of *G. pulex* and *D. villosus* would vary as a function of their relative body size, with larger individuals being less able to move through subsurface sediments compared to smaller individuals. *G. pulex* and *D. villosus* have a comparable body morphology but differ in their overall body size, with adult *D. villosus* being larger than *G. pulex* (Pinkster, 1970; Rewicz et al., 2014). Our results demonstrate that larger amphipod individuals have a reduced ability to access and move through subsurface sediments. In agreement with previous studies (Gayraud & Philippe, 2001; Loskotová et al., 2019; Mathers et al., 2019b), these results indicate that body size is a key factor influencing an individual’s ability to access subsurface sediment. Furthermore, we found clear evidence that larger individuals of both amphipod species were more susceptible to stranding during water level reduction, whereas smaller individuals readily accessed deeper subsurface sediments. We hypothesise that individuals smaller than interstitial pore size openings may be able to move more freely.
through the sediment, whereas individuals of a similar size or larger than the sediment pore size are more likely to become stranded during water level reduction (Vadher et al., 2017; Loskotová et al., 2019); although direct measurement of pore size openings would be required to verify this.

The experimental results did not support our second hypothesis that vertical movement of amphipods...
would vary as a function of sediment size, given that the migration of amphipods through the three sediment treatments followed comparable trends. This finding may reflect the open sediment framework and relatively large number of interstitial spaces available for all sediment treatments (i.e. total pore volume was comparable among the three treatments). Previous studies have shown that in the presence of increased fine sediment deposition (< 2 mm in size), macroinvertebrates are less able to access and move through subsurface sediments (e.g. Bo et al., 2007; Vadher et al., 2015; Korbel et al., 2019; Mathers et al., 2019b). The absence of interstitial fine sediment in our experiments suggests that maintaining an open framework will facilitate the downward migration to subsurface sediments during drying for macroinvertebrates with similar or smaller body sizes to that of the interstitial openings.

Our findings partially support the third hypothesis that the vertical movement of amphipods would vary as a function of the rate of water level reduction. In fact, the rate of water level reduction influenced the speed and ability of amphipod individuals to migrate vertically but did not influence the final vertical position or likelihood of being stranded above the waterline. G. pulex displayed greater movement in all water level reduction treatments compared to D. villosus which probably reflects average differences in body size and therefore the ability to freely move within interstitial spaces of saturated sediments. Vertical migration into deeper interstitial sediments by G. pulex and D. villosus in response to faster water level reduction rates indicates the ability of amphipods to respond to rapid water level reductions and to actively migrate vertically into the subsurface sediment to avoid surface drying and stranding; although the movement of other faunal groups, such as Gastropoda, may be highly variable (e.g. Poznańska et al., 2015a; 2015b). The use of transparent sediments in laboratory mesocosms has facilitated the direct observation of the vertical migration of organisms of varying sizes in subsurface sediments in response to

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**Table 4** Stranding of individuals (%) associated with water level reduction rate, sediment treatment and species

| Drawdown rate | Sediment | Stranded (%) |
|---------------|----------|--------------|
| **Gammarus pulex** | | |
| Very fast | Large | 10 |
| Fast | Large | 0 |
| Slow | Large | 0 |
| Very slow | Large | 0 |
| Very fast | Small | 20 |
| Fast | Small | 30 |
| Slow | Small | 10 |
| Very slow | Small | 10 |
| Very fast | Mixed | 10 |
| Fast | Mixed | 0 |
| Slow | Mixed | 30 |
| Very slow | Mixed | 30 |
| **Dikerogammarus villosus** | | |
| Very fast | Large | 40 |
| Fast | Large | 30 |
| Slow | Large | 40 |
| Very slow | Large | 60 |
| Very Fast | Small | 60 |
| Fast | Small | 90 |
| Slow | Small | 80 |
| Very slow | Small | 60 |
| Very fast | Mixed | 40 |
| Fast | Mixed | 40 |
| Slow | Mixed | 50 |
| Very slow | Mixed | 70 |
Drying events, whether seasonal (Pinna et al., 2016; Bogan et al., 2017), supra-seasonal (Bogan et al., 2015; Hill et al., 2019) or anthropogenically driven such as dynamic fluctuations during hydropeaking events (Lange et al., 2019; Mihalicz et al., 2019), typically leads to shifts in macroinvertebrate community compositions. The findings of this study provide further evidence that subsurface sediments can act as a refuge during drying events if taxa are not limited by body size and if an open sediment framework exists (i.e. free of fine sediment particles). The ability of macroinvertebrates to access the subsurface habitat when sediment is comprised of more heterogeneous particles or where enhanced sedimentation occurs has been shown to be greatly reduced (Vadher et al., 2015, 2018b). It is widely recognised that disturbance/bioturbation activities of small bodied vermiform (long and thin) invertebrates within benthic and subsurface sediments help maintain open subsurface pore spaces and pathways that in turn can facilitate biogeochemical processing of nutrients and potential pollutants (e.g., Nogaro et al., 2006; Mermillod-Blondin, 2011). There is also growing evidence that larger macrofauna, including amphipod shrimps, can maintain subsurface sediment pathways, pore spaces and hydraulic properties within the subsurface sediments (Hose & Stump, 2019). Future laboratory and field-based research should consider the interactions between channel drying, benthic and subsurface sedimentary characteristics (e.g., grain size distribution, porosity and fine sediment content) and the faunal communities present in aquatic ecosystems subject to regular or irregular drying. This is essential to help predict and manage the effects of anthropogenically enhanced drying and determine the ability of ecosystems to recover following such events. Our findings also demonstrate the value of mesocosm and laboratory-based experiments in answering broader ecological questions. Future research should therefore use a combination of laboratory mesocosm approaches to validate field observations to facilitate a greater understanding of macroinvertebrate responses to drying.

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