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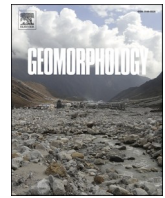
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Vertical reworking of sediment by the cased caddisfly Glossosomatidae (*Agapetus fuscipes*) increases sand exposure and availability in armoured gravel-bed rivers

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ABSTRACT

Landscapes and ecosystems are the result of two-way interactions between hydro-geomorphic and biological processes. Many animals, particularly those that build structures or transport sediment, are important bio-geomorphic agents. Glossosomatidae caddisfly larvae (Insecta, Trichoptera) are globally widespread and abundant inhabitants of gravel-bed rivers. Glossosomatidae build mobile cases from sand that they transport over the river bed. However, there is limited understanding on how Glossosomatidae bioconstructions may influence sand distribution in rivers or how their zoogeomorphic behaviours are influenced by hydraulics or characteristics of the river bed. First, we conducted surveys to quantify the magnitude of sand incorporated into Glossosomatidae (*Agapetus fuscipes*) cases within a UK river. Second, we studied *A. fuscipes* movement behaviour and quantified the direction and magnitude of sediment reworking, in a flume, under differing flow velocity and gravel size treatments. We found that 99 % of *A. fuscipes* larvae transported sediment vertically upwards. This resulted in an average conveyance per larvae of 0.06 g sand upwards by 25 mm (maximum of 50 mm). In gravel beds with a coarse surface layer, this resulted in displacement of sand from sheltered interstices onto the surface of exposed gravel particles. In the flume, this behaviour was maintained even at high flows, sufficient to entrain empty cases from these locations. Whilst the mass of sediment moved by individual larvae is small, dense populations of Glossosomatidae larvae may have important consequences for the vertical distribution of sand in rivers. At our field site, *A. fuscipes* case density averaged 2192 cases m⁻², equivalent to 1.4 t km⁻¹. This finding is important because in gravel-bed rivers frequented by Glossosomatidae larvae, sediment transport is typically limited by the availability of entrainable fine grain sediment at the surface. We discuss the implications of this sediment movement for river bed sedimentary structure, the transport of sand and gravel, and the possible role of Glossosomatidae larvae as ecosystem engineers.

1. Introduction

Animals actively modify landscapes, with consequences for geomorphology (zoogeomorphology; Butler, 1995) and ecology (ecosystem engineering; Jones et al., 1994). Animals have a range of zoogeomorphic effects, dictated by their diverse behaviours, which may lead to either stabilisation or destabilisation of sediments. Many animals rework sediment whilst moving, digging or burrowing. Research on sediment reworking and bioturbation has focussed on fine grained sediment in lakes, marine environments (Shull, 2008) or occasionally sand-bed rivers (e.g., Shrivastava et al., 2021a,b). In contrast, in gravel-bed rivers, studies of bedload transport have traditionally ignored the

activities of animals (Klingeman et al., 1998; Wilcock et al., 2009). However, increasing evidence that a wide range of organisms affect river morphology and sediment distributions is challenging the traditional concept of sediment transport as a purely physical phenomenon (Atkinson et al., 2018; Rice et al., 2012). The higher flow velocity typical of gravel-bed rivers means that reworking of sediment by animals is particularly important if it destabilises water-worked gravels or exposes fine sediment to surface hydraulics (Statzner, 2012).

Larger animals may actively rework coarse sediments. For example, Salmonid fish use powerful tail thrusts during spawning to build nests (redds), lowering gravel incipient entrainment thresholds by 22 % (Buxton et al., 2015) and a broad range of benthivorous fish may have

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similar impacts whilst feeding (Pledger et al., 2016; Rice et al., 2019). Invertebrates have particularly diverse zoogeomorphic behaviours (Mason and Sanders, 2021; Bétard, 2020). Larger invertebrates can also rework gravel substrates. Signal crayfish, for example, can move gravel up to 38 mm (Johnson et al., 2010). Whilst smaller invertebrates cannot rework coarse sediments, they can rework fine sediments when burrowing into river beds (e.g., Worms; Shrivastava et al., 2021a) and banks (e.g., Crayfish; Sanders et al., 2021) or during locomotion (e.g., Shrimp; Pringle et al., 1993). The stonefly larvae *Dinocras cephalotes* hunts for prey in the interstices between gravel particles, disturbing sand grains, which are winnowed from the surface (Statzner et al., 1996; Zanetell and Peckarsky, 1996). Similarly, the crayfish *Orconectes limosus* removed $2.8\text{--}4\text{ kg m}^{-2}\text{ d}^{-1}$ of fine sediment from gravel interstices in riffles (Statzner et al., 2000).

Caddisfly (Trichoptera) are important zoogeomorphic engineers in gravel-bed rivers, exhibiting a range of behaviours with diverse effects on sediment processes (Mason et al., 2019). Filter feeding silk nets built by Hydropsychidae larvae substantially increase the resistance of gravel beds to entrainment (Johnson et al., 2009; Albertson et al., 2014), stabilising gravels up to at least 65 mm diameter (Albertson et al., 2014). Furthermore, many caddisfly species construct cases from mineral and organic materials. Cases allow caddisfly to avoid predation and entrainment by the flow (Ferry et al., 2013).

In a survey of caddisfly sediment use in a UK lowland gravel-bed stream, Mason et al. (2019) found that a single caddisfly species, *Agapetus fuscipes* (Glossosomatidae; Fig. 1A), was responsible for 64 % of

sediment mass incorporated into caddisfly cases. Glossosomatidae larvae are characteristic of gravel surfaces in small, medium velocity, gravel-bed streams and rivers (Houghton and Stewart, 1998; Morris and Hondzo, 2013a; Nijboer, 2004; Wood and Armitage, 1999) with a global distribution (Morse, 2022). In these environments, high densities of Glossosomatidae are common (1000 s m^{-2} ; Hickin, 1967; Mason et al., 2019; Mcneely and Power, 2007).

In gravel-bed rivers, the sediment distribution at the bed surface is a key control on sediment transport (Dietrich et al., 1989) and the habitat provided to organisms (Lancaster and Downes, 2013). Interactions between sediment grains result in vertical sorting with coarser grains overrepresented at the surface compared to the subsurface (Dietrich et al., 1989; Pitlick et al., 2008). A coarse surface layer can result from a combination of processes operating during and between high flows including: (1) fine sediment being more easily entrained and preferentially winnowed from gravel beds; (2) fine sediment infiltrating into interstices between the gravel framework, resulting in a downwards movement of fine particles (Mao et al., 2011); (3) kinematic sorting in which smaller grains preferentially occupy the spaces left by entrained grains during transport (Wilcock, 2001). Furthermore, particles may organise themselves into lines, clusters and nets (Church et al., 1998), further increasing bed stability and sheltering fine grains. As a consequence, sand-sized and finer sediment is predominantly found in the river bed subsurface and when at the surface tends to be hidden in interstices and in the lee of obstacles, where it is sheltered from high flows (Laronne et al., 2001). In the absence of complete breakdown of the

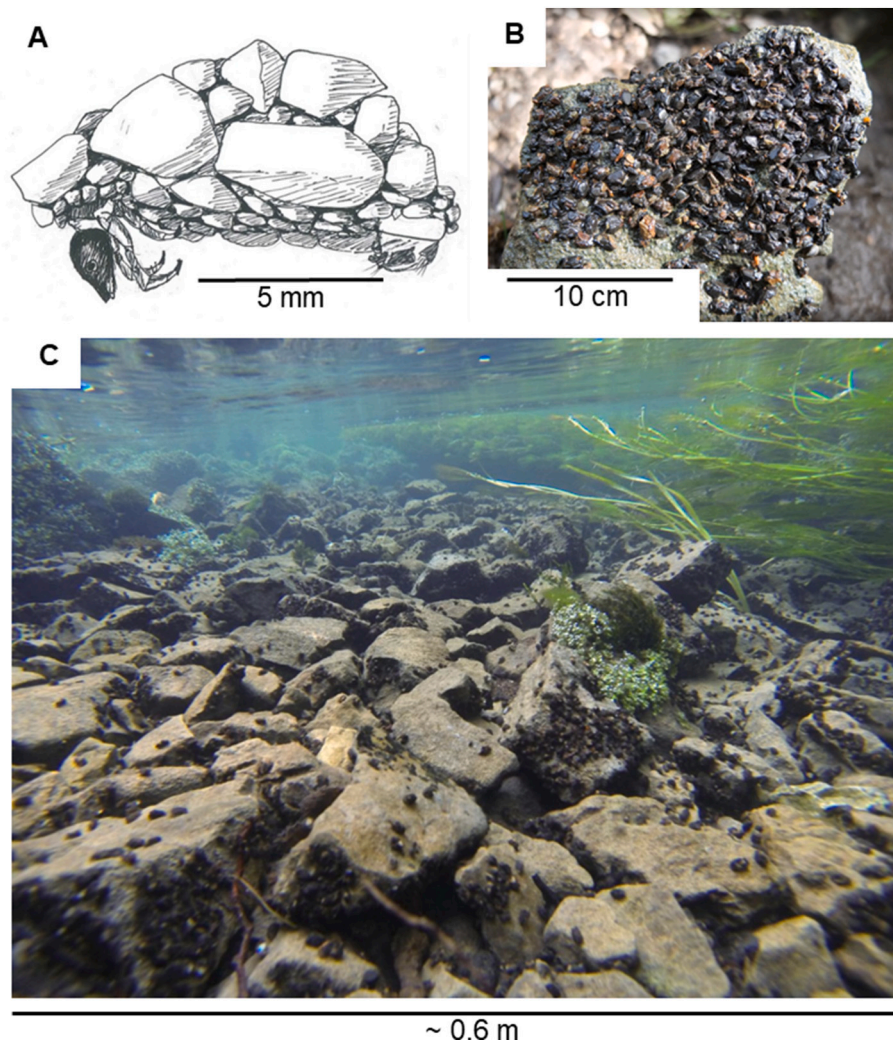


Fig. 1. Glossosomatidae caddisfly larvae construct cases from sand and occupy exposed locations on river-bed surfaces that would otherwise have scarce fine sediment (adapted from Mason et al., 2019). (A) Sketch of Glossosomatidae *Agapetus fuscipes* case design. Note the use of a relatively broad range of sand sizes, often with larger particles on the case sides. (B) Dense aggregations on the exposed face of a cobble. (C) Cases visible on the upper surface of gravel particles on the river bed. B and C both from the River Dove, Derbyshire, UK.

coarse armour layer, the transport of sands is dependent upon the availability of particles at the surface (Parker and Sutherland, 1990). Small changes in the amount of sand at the surface can substantially alter exposure to flow and subsequently sand sediment transport (Kirchner et al., 1990; Garcia et al., 1999; Powell, 1998).

Glossosomatidae larvae prefer to locate themselves on the exposed upper faces of gravel-bed particles where they can access oxygenated water and algal food that they graze from within their cases (Fig. 1B & C; Kovalak, 1976; Olden et al., 2004). Consequently, the sand-sized sediment that Glossosomatidae prefer to use for case construction is not present in the zones of high flow exposure sought by larvae. This suggests that Glossosomatidae larvae construct cases from sands available in sheltered areas (e.g., grain interstices), and then move with their case onto the gravel surface. Consequently, reworking of sediment by Glossosomatidae larvae occurs at the sediment water interface, where their zoogeomorphic effects are likely to have the most impact by removing sands from interstices and increasing the exposure of fine sediment to entraining flows.

We investigated the role of the Glossosomatidae species *A. fuscipes* larvae as zoogeomorphic agents. We combined a field survey to quantify the scale of sediment use by *A. fuscipes* larvae with a flume experiment to understand how *A. fuscipes* larvae redistribute sediment within river gravel beds. In the field, we measured the magnitude of sediment incorporated into *A. fuscipes* cases on the surface of gravel beds. In the flume, we considered whether *A. fuscipes* larvae modified the vertical

distribution of sediment and whether this behaviour was affected by gravel size and water flow velocity. We considered three research objectives;

1. To estimate the magnitude of sediment used by Glossosomatidae *A. fuscipes* larvae on the bed surface of a section of a UK river.
2. To determine if *A. fuscipes* larvae alter the vertical and horizontal distribution and flow exposure of sediment incorporated into their cases, and to quantify any sediment displacement.
3. To quantify the influence of flow velocity and gravel size on *A. fuscipes* behaviour, case construction and sediment displacement.

2. Methods

2.1. River Dove survey

We measured the quantity of sediment incorporated into *A. fuscipes* cases in the River Dove, Derbyshire, UK (Fig. 2; downstream site located at Dovedale car park 53.05631 N, -1.78178 E). The Dove is a gravel-bed river (bed material $D_{50} = 64$ mm), approximately 9 m wide in the study reach, primarily groundwater fed, draining a catchment of Carboniferous limestone with a mixture of pasture and deciduous woodland in the riparian zone. A flow gauge located at the lower end of the reach (Fig. 2B) drains a catchment area of 83 km² and the Q50 discharge was 1.35 m s⁻³ (mean of annual Q50 between 2010 and 2018, data source:

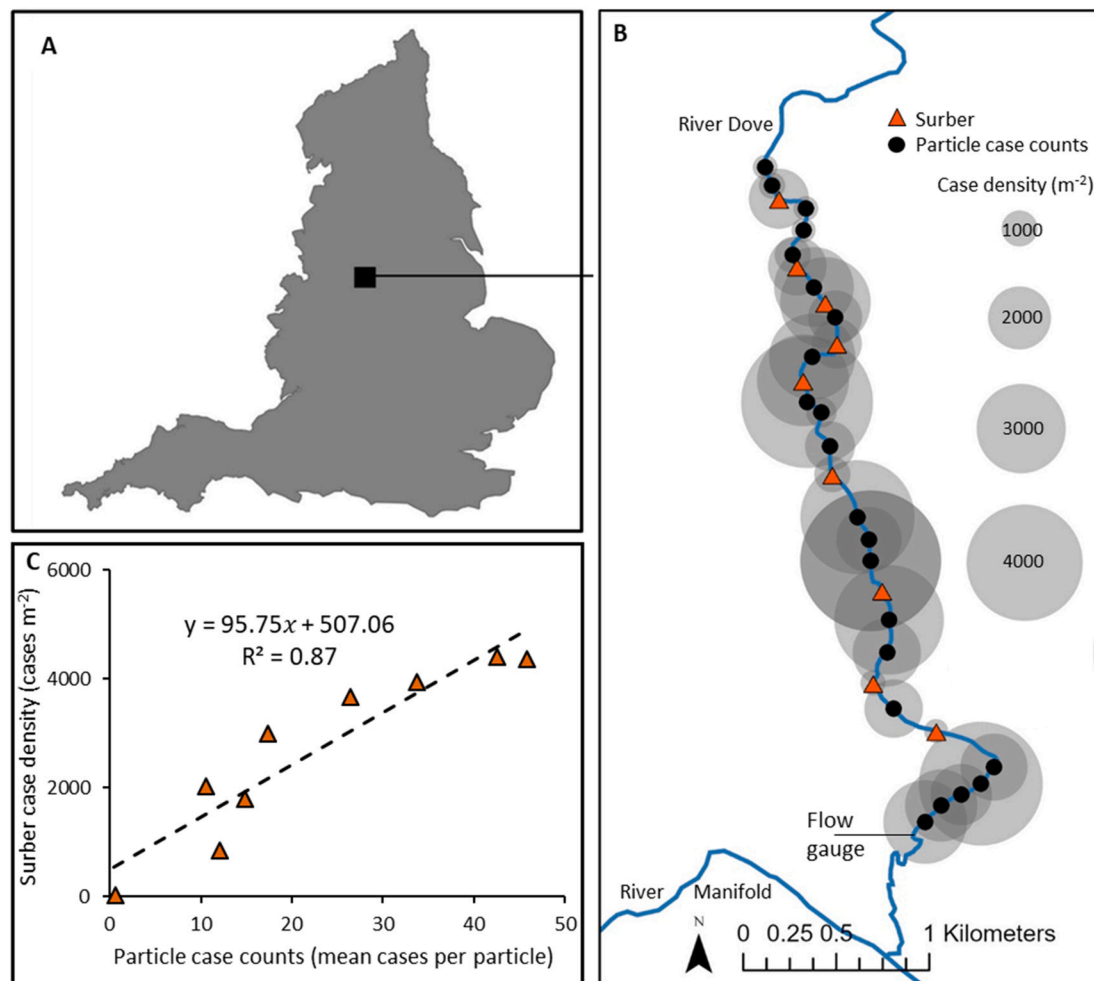


Fig. 2. Survey of Glossosomatidae *A. fuscipes* sediment used in case construction. (A) The River Dove is located in the UK Peak District, Derbyshire. (B) 31 sites were sampled along 5.4 km of the River Dove. Size of marker buffer denotes estimated density of cases according to panel C. A flow gauge located at the downstream end of the section was used for calculation of discharge parameters and catchment size. (C) Association between Surber density measurements and particle case counts.

NRFA, 2021).

Surveys of *A. fuscipes* cases on the bed surface were conducted over 5.4 km of river in July 2014 within the Dovedale section (Fig. 2B). Case densities were measured using a Surber sampler (Surber, 1937). Within the Surber (area = 0.1 m^2) the size of surface grains was measured and the number of Glossosomatidae cases on each rock counted (this included abandoned or empty cases) with a 1 mm diameter net fixed downstream to catch any entrained Glossosomatidae cases, providing a fully quantitative measure of case density. Subsequently, we searched the Surber area and net for *A. fuscipes* cases not attached to surface grains. Surber samples were collected at nine sites distributed along the study section (Fig. 2B). At each site, six replicate Surber samples were taken (total Surbers = 54). At each Surber location, 30 cases were taken back to the laboratory for analysis of mass and grain size distribution. In the laboratory, we dried the cases and weighed them. We used image analysis in ImageJ (Abramoff et al., 2004) to determine case size from photos taken against a white background (following Statzner et al., 2009).

To extrapolate these results across a wider area, a particle size count (modified from the widely used method of Wolman (1954) & Leopold (1970)) was used to estimate the spatial extent of *A. fuscipes* cases on

surface grains (hereafter *particle case count*). Particle case counts were conducted at the nine Surber sites and a further 22 sites, spaced at approximately equal distances along the river section (Fig. 2B).

Particle case counts were conducted over an area of river equal in width and length to the width of the river at that site. At each site, 30 surface particles were selected using a random walk (Leopold, 1970) and the number of *A. fuscipes* cases on each particle was recorded. A strong correlation exists between *A. fuscipes* density measurements from Surber samples and particle case counts (Fig. 2C). The linear equation describing the association between Surber and particle case counts was used to estimate the density of Glossosomatidae cases at all 31 particle case count sites (Fig. 2B & C).

2.2. Flume experiments

The case building behaviour and movement of sediment by *A. fuscipes* larvae was measured in a recirculating hydraulic flume to simulate riverine conditions. Before each flume run, caddisfly larvae were removed from their cases and introduced into a small section of the flume, which contained fine sediment for case construction and algae coated gravels, positioned to simulate an armoured gravel bed. After 21

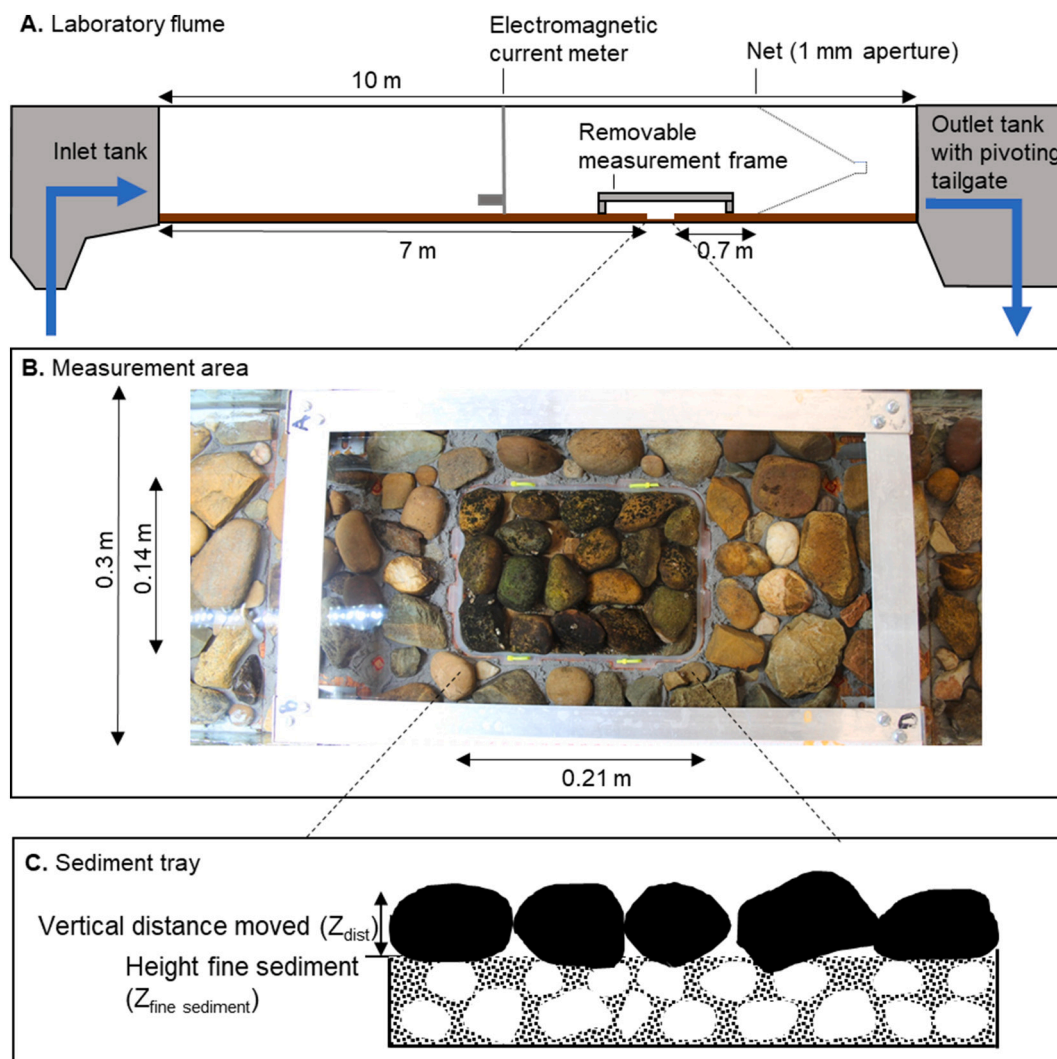


Fig. 3. The laboratory flume setup. (A) Experiments were conducted in a 10 m long flume within a sediment tray (0.03 m^2). Mean flow velocity was measured using an electromagnetic current meter located 1 m upstream of the sediment tray at 0.05 m elevation from the bed. (B) A tray of loose sediment was added to the flume, flush with the bed. An aluminium frame could be placed over the tray area facilitating accurate measurement of *A. fuscipes* locations, but was removed during the flume runs. (C) Side profile of the sediment tray, containing a framework of gravel particles infilled with fine sediment. Fresh, algae coated gravel particles were placed on the surface to simulate a coarse gravel surface layer.

h, the position of *A. fuscipes* larvae and the hydraulics they were exposed to were measured. Upstream and downstream movement was measured and, by measuring the elevation of the fine sediment before the flume experiment, and the eventual elevation and mass of caddisfly cases after the experiment, the vertical flux in sand grains caused by caddisfly larvae activity was determined. Caddisfly larvae positioning and sediment displacement were compared between four treatments; low and high flow velocity and small and large gravel particles.

2.2.1. Flume setup

The flume had a working section 10 m long and 0.3 m wide (Fig. 3A). Throughout the flume, a bed of fixed gravel (16–64 mm diameter, $D_{50} = 38$ mm) was raised from the flume base by 0.08 m. Measurements and observations were taken within a tray of loose sediment (hereafter *sediment tray*) located 7 m from the flume inflow (Fig. 3B). The sediment tray measured 0.21 m length and 0.15 m width, large enough to accommodate sufficient *A. fuscipes* larvae at densities representative of the field, whilst small enough to allow the locations of larvae to be observed and measured. The sediment tray was narrower than the flume to reduce the influence of hydraulic disturbances introduced by the flume side walls.

The sediment tray was filled with gravel and sand, collected from local streams and designed to replicate a water-worked gravel bed. The tray was first filled with gravel and sand until level with the tray rim (Fig. 3C). Sand was between 0.355 and 2.8 mm to include the D_{50} – D_{95} range used by *A. fuscipes* larvae locally (Mason et al., 2019). Gravels collected the previous day from the surface of a local stream were added to the tray surface to simulate a coarser bed surface layer (Fig. 3C). This gravel was placed in the sediment tray with algae covered faces upmost (as they were positioned in the river). A net (1 mm aperture) was placed across the full width of the flume 0.7 m downstream of the sediment tray to catch drifting larvae.

An aluminium measurement frame was designed which could be placed inside the flume to facilitate accurate determination of the X, Y and Z location of any point within the sediment tray (where X is the streamwise, Y cross-stream and Z vertical position; Fig. 3A & B). X and Y location were determined using rulers on the frame, whilst Z locations were measured using a digital calliper. Comparing the mean of measurements of six known locations before and after each experimental run gave a measurement error for Z of mean 0.3 mm (maximum = 1.25 mm, $n = 204$). This accounts for error in the placement of the measurement frame, the precision of the digital callipers and operator error. Oxygen availability was measured at the start and end of each run and remained above 99 % saturation. Water temperature was kept between 13 and 15.6 °C and light was provided to mimic the natural daylight cycle.

2.2.2. Gravel size and flow velocity treatments

Two levels of flow velocity, two gravel sizes and the interactions between flow and gravel size were considered, resulting in four treatments (Table 1). The two flow velocity treatments represent a low flow velocity (0.14 m s^{-1}) and high flow velocity (0.6 m s^{-1}) at the upper limit achievable in the flume whilst maintaining stable flow conditions. For the sediment treatments, large gravel had a b axis between 45 and 65 mm and small gravel, 32 and 45 mm.

Table 1

Four treatments were conducted with low or high flow velocity (U) (LV or HV) and small or large gravel size (SG or LG). Physiochemical conditions remained similar across all treatments. Numbers of larvae remaining within the sediment tray are the sum of all runs for each treatment. Percent remaining is shown in brackets. Only those larvae which remained in the sediment tray had their vertical (Z) movement measured. Treatments with LV had significantly lower near bed flow velocities to those with HV, whilst SG had significantly smaller gravel particles (c axis) to LG (Tukey HSD, $p < 0.05$).

| Treatment (runs) | Gravel (mm) | U (m s^{-1}) | Temp (°C) | O ₂ (mg L^{-1}) | N larvae remaining (% remaining) | Near bed velocity (m s^{-1}) (SD) | Gravel c axis (mm) (SD) |
|------------------|-------------|-------------------------|-----------|---------------------------------------|----------------------------------|--|-------------------------|
| LV-SG (4) | 32–45 | 0.14 | 13.80 | 10.71 | 121 (69 %) | 0.05 (0.01) | 28.82 (2.90) |
| LV-LG (2) | 45–65 | 0.14 | 13.88 | 10.63 | 67 (71 %) | 0.08 (0.03) | 38.95 (2.03) |
| HV-SG (3) | 32–45 | 0.6 | 15.25 | 10.22 | 96 (70 %) | 0.40 (0.11) | 28.57 (1.94) |
| HV-LG (4) | 45–65 | 0.6 | 14.60 | 10.78 | 68 (53 %) | 0.32 (0.09) | 44.18 (1.52) |
| All (13) | | | | | 352 (66 %) | | |

Analysis of variance (ANOVA) followed by post-hoc Tukey Honest Significant Difference (HSD) tests conducted in R using the *stats* package (version 3.5.1, R Core Team, 2018), demonstrated significant differences ($p < 0.05$) in particle c axis between small and large gravel treatments, but not between runs of the same gravel treatment (Table 1). C axis was chosen because particles were placed with this vertically and therefore this provides a measure of bed elevation. Similarly for near bed velocity, collected with a Nixon Streamflow velocity probe with 11.6 mm diameter rotor, ANOVA and HSD tests found a significant difference ($p < 0.05$) between low and high flow treatments but not treatments at the same flow level.

2.2.3. Experimental procedure

Prior to each experiment, the sediment tray was installed and the measurement frame was used to measure the height of fine sediment ($Z_{\text{fine sediment}}$; Fig. 3C) within the tray at 10 locations spaced across the tray surface. The measurement frame was then removed during the experiment so that it did not affect flow conditions.

A. fuscipes larvae were collected from a local stream (Black Brook; 52.775944 N, –1.299333 W) the evening before experiments and then acclimatised overnight in aerated aquaria. The mean head width of *A. fuscipes* in each run ranged between 0.47 and 0.51 mm, indicating that all larvae were final instar (Wallace et al., 2003). Fifty *A. fuscipes* larvae were added in each flume run to reproduce a population density in the sediment tray comparable to that in the River Dove (Fig. 2B) and local streams (Mason et al., 2019). *A. fuscipes* larvae were gently removed from their cases using blunt forceps. Larvae were added to the sediment tray under low flow velocity conditions (velocity = 0.11 m s^{-1} , depth = 82 mm), which were maintained for 2 h, with larvae contained within the sediment tray by a plastic surround. This two-hour acclimation period was identified in preliminary trials to allow larvae sufficient time to settle and begin case construction (sensu. Houghton and Stewart, 1998). Subsequently, the plastic surround was removed, discharge was gradually increased, and the tail gate lowered until the desired velocity was reached. A constant depth of 100 mm was maintained, representative of that in the River Dove. This velocity was maintained until the following morning (11 am); a total of 21 h (with 2 h acclimatisation, the total experiment duration was 23 h). At this point, the flow velocity adjacent to each visible *A. fuscipes* case was measured using the Nixon velocity probe. Subsequently, discharge was reduced and a series of measurements were taken:

1. Larvae X,Y,Z locations were obtained using the measurement frame and callipers. For larvae that had migrated outside of the sediment tray, only X and Y were recorded using a tape measure.
2. The position of each larvae on the gravel particle was recorded, allowing flow exposure to be inferred (i.e., top and stoss = exposed; side, lee and bottom = sheltered; sensu. Kovalak, 1976).
3. Following the measurement of the visible larvae, the sediment tray and measuring frame were removed from the flume. Each gravel particle was lifted to check for larvae on the fine sediment surface or within the substrate, the locations of which were also recorded.

2.2.4. Caddisfly and case analysis

Following the flume runs, caddisfly and cases were stored in 70 % Industrial Methylated Spirit. Larvae were removed from their cases, identified (all larvae were confirmed as *A. fuscipes*) and their length and head width measured using a microscope eyepiece graticule calibrated using a stage micrometer. The length and width of cases was measured as for larvae. Cases were thoroughly rinsed in deionised water and then dried at 105 °C overnight. All cases from each flume run were amalgamated to determine their mass and grain size characteristics. Case sediment was sieved through 38 mm diameter sieves at half phi intervals down to 0.063 mm.

2.2.5. Flume experiment data analysis

The X, Y and Z of each larvae location were used to ascertain longitudinal and vertical migration of larvae within the flume. Distance travelled in a vertical direction was calculated by comparing measured height of each larvae at the end of the flume run to the mean level of fine sediment in the tray measured prior to the flume run (Fig. 3C), according to Eq. (1):

$$Z_{\text{dist}} = Z_{\text{case}} - Z_{\text{fine sediment}} \quad (1)$$

where Z_{dist} was the vertical distance moved, Z_{case} the height of larvae/case at the end of the run and $Z_{\text{fine sediment}}$ was the height of the fine sediment surface prior to the flume run, from which larvae had constructed their cases. For longitudinal movement, distance travelled upstream or downstream was calculated relative to the upstream and downstream edges of the sediment tray.

Thirteen flume runs were conducted, incorporating a total of 650 individual *A. fuscipes* larvae. Initially three replicates were intended for each treatment (1–4), however, an extra replicate of treatment 4 was added because of low numbers of larvae remaining to be measured, and one run of treatment 2 had to be discounted because of accidental disturbance to flow conditions during the run (Table 1). Linear mixed effects models allowed the best statistical use of this data, considering the full number of larvae in each treatment whilst controlling for any variability resulting from the specific run. Linear mixed effects models were used to investigate the association between velocity and gravel size (as fixed effects) on vertical distance travelled by *A. fuscipes* larvae (response variable), using the lme4 package in R Studio (Bates et al., 2014). Run number was controlled for as a random effect. This was repeated for larvae longitudinal movements. For all larvae that moved upstream or downstream from the measurement tray (those to the side of the measurement tray were ignored), the influence of flow velocity and gravel size (fixed effects) on longitudinal position (response variable) was assessed, again controlling for run number (random effect). Visual inspection of the residual plots showed little deviation from homoscedasticity or normality. Significance was determined using likelihood ratio tests (using analysis of variance) between the full model and models with the fixed effect in question removed (with restricted maximum likelihood true only for the final model).

Analysis of variance followed by post hoc Tukey HSD tests were used to assess differences in mean values between treatments for case mass, case D_{50} and the percent of larvae occupying exposed locations.

3. Results

3.1. River Dove survey

In the River Dove, Glossosomatidae were found at high density throughout most of the 5.4 km stretch (Fig. 2B). *A. fuscipes* case density was estimated to vary from 545 to 4918 cases m^{-2} (Mean = 2192 cases m^{-2} ; Fig. 2B). Average case mass was 0.06 g (± 0.02 SD). Using this average, a mean of 131.95 g m^{-2} of fine sediment was incorporated in *A. fuscipes* cases (minimum = 32.84, maximum = 296.11 g m^{-2} ; Research question 1). By extrapolating mean sediment use by mean river

width we determined that an average of 1.4 t km^{-1} of sediment was used by *A. fuscipes* in the River Dove.

Glossosomatidae larvae were observed to reside primarily on the upper surfaces of gravel and cobble particles (Fig. 1). We found an average of 17.8 cases per bed surface particle with up to 383 cases on a single rock. The number of cases per particle was extremely variable but on average increased with particle size up to 90 mm and then plateaued (Fig. 4).

3.2. Flume experiment

Once added to the sediment tray, *A. fuscipes* larvae crawled over the bed surface before beginning case construction. Several abandoned “emergency” cases were found; built from finer sediment than the final cases and with little structural integrity. Final cases were morphologically similar to those built in the field.

From the 650 larvae added to the flume (Table 1), 352 remained in the sediment tray and had vertical as well as horizontal positions measured. In all treatments larvae moved both upstream and downstream (Fig. 5). The number of larvae remaining in the sediment tray (from the original 50 in each run), ranged between 13 and 39, averaging 66 % although this figure was lower in treatment 4 (Table 1). Velocity affected longitudinal migration ($p \leq 0.001$, $\text{Chi}^2 = 16.41$) with larvae that left the experimental tray positioned on average 405 mm farther upstream in low flow treatments. Gravel size did not significantly affect longitudinal movement ($p > 0.05$).

Of larvae in the sediment tray, the mean vertical migration was 25.40 mm upwards from the level of fine sediment (Table 1; Fig. 6A) and only six larvae travelled <5 mm vertically upwards. Therefore, 99 % of larvae whose vertical elevation was measured moved upwards, up to a maximum of 50 mm (Fig. 6A). Consequently, *A. fuscipes* transport sediment vertically by incorporating it into their cases and crawling upwards (Research question 2).

The experiment studied *A. fuscipes* larvae positions under four treatments, differing in gravel size and flow velocity (Table 1; Research question 3). Mixed effects models indicated that gravel size affected the vertical distance travelled by *A. fuscipes* larvae ($p = 0.01$, $\text{Chi}^2 = 6.56$), with larvae moving to locations on average 5.49 ± 2.14 mm (standard error, SE) higher when larger gravel particles were present (Fig. 6A). During the small gravel treatments, the mean elevation of *A. fuscipes* larvae was 22 and 24 mm, compared to a mean particle c axis (equivalent to maximum bed elevation) of 29 mm (compare Fig. 6A and c axis

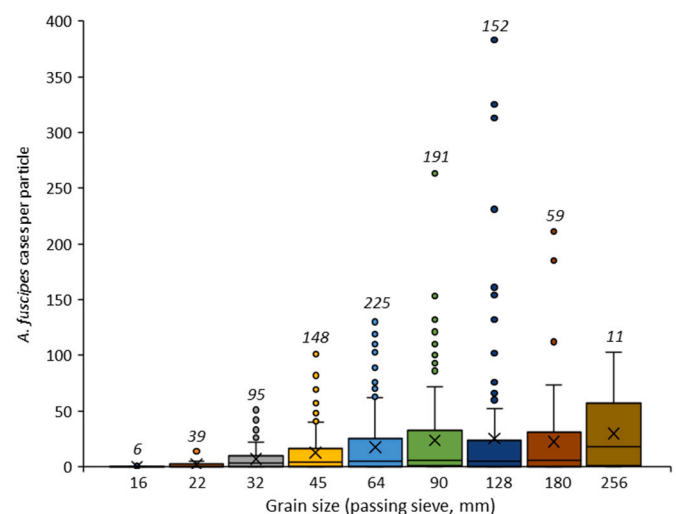


Fig. 4. The number of *A. fuscipes* larvae inhabiting each surface grain size. The numbers above the error bars refer to the total number of particles of this size fraction sampled in the particle case counts.

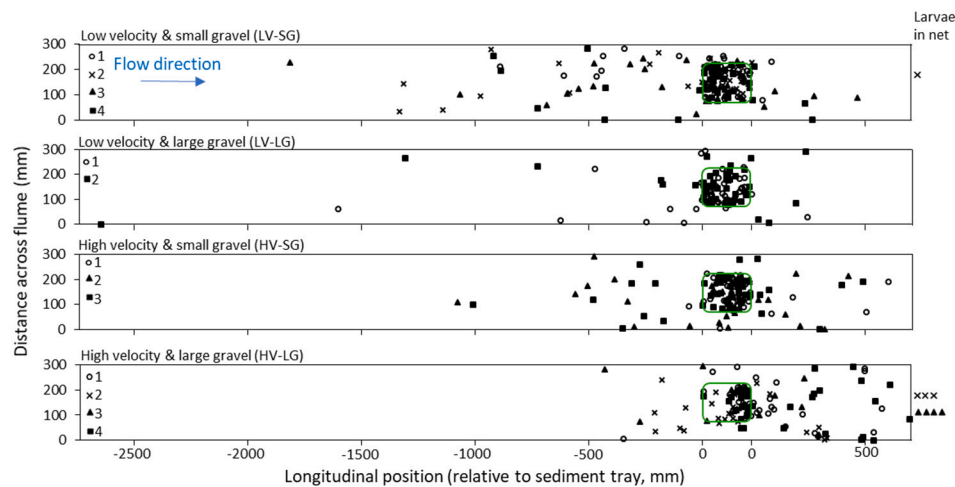


Fig. 5. Horizontal positions of *A. fuscipes* larvae in the flume. Longitudinal distance moved was measured relative to the sediment tray where larvae started. Positive x-axis values indicate downstream movement. Replicate runs of each treatment denoted by different shapes. A net prevented larvae moving more than 700 mm downstream.

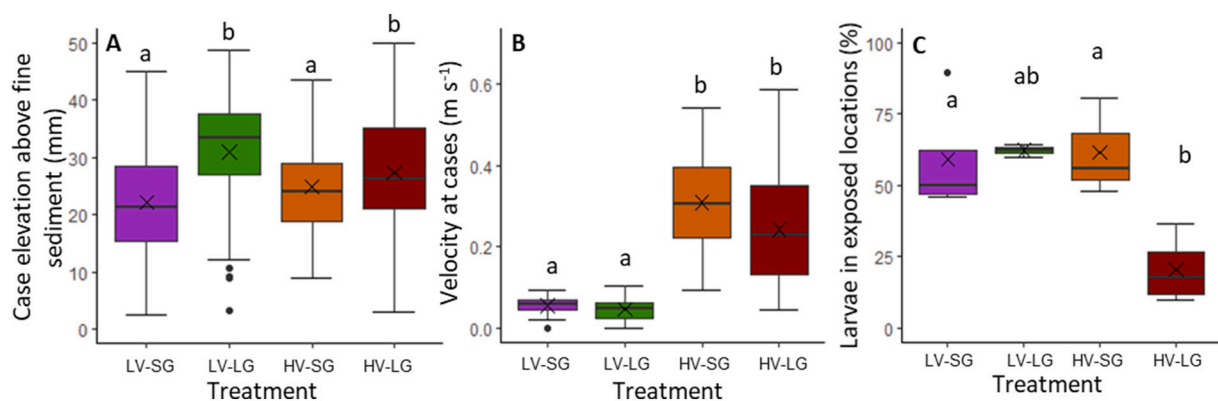


Fig. 6. Glossosomatidae case exposure. (A) *A. fuscipes* larvae transport sediment upwards, from interstices onto the surfaces of gravel particles. This was true for all treatments and larvae elevation increased with gravel size but not flow velocity (treatments labelled with the same letter did not differ significantly from one another). (B) Flow velocities experienced by larvae (i.e., measured beside cases) were significantly higher in high velocity treatments but did not differ between gravel treatments. (C) The percentage of larvae occupying exposed microhabitats within the gravel bed was lower when high flow and large gravel size interacted. Treatment codes: HV = high velocity, LV = low velocity, SG = small gravel, LG = large gravel.

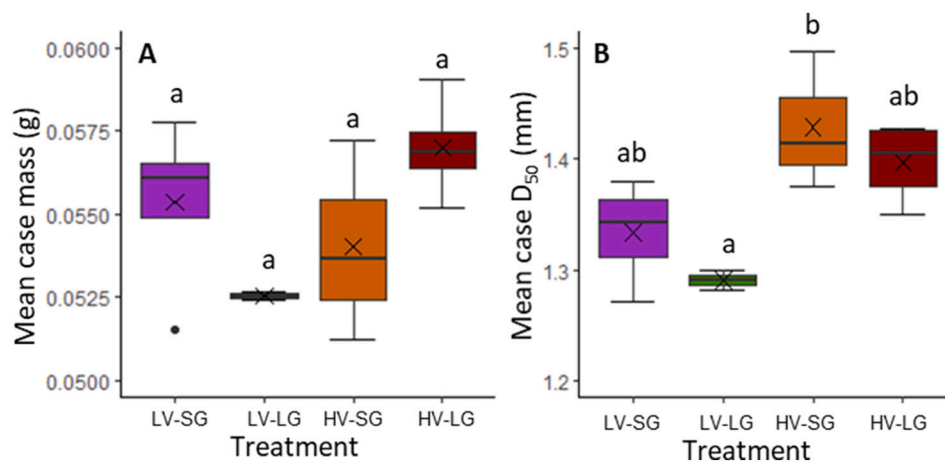


Fig. 7. Characteristics of *A. fuscipes* cases built during each treatment (A) Case mass (B) Case median particle size, D_{50} . Treatments labelled with the same letter did not differ significantly from one another according to ANOVA and post-hoc Tukey HSD ($p < 0.05$) (there were no significant differences between treatments for mean case mass). Treatment codes: HV = high velocity, LV = low velocity, SG = small gravel, LG = large gravel.

in Table 1). Mean larvae elevations during the large gravel treatments were 31 and 27 mm compared to a mean gravel c axis of 40 and 44 mm, respectively. Therefore, at larger gravel sizes, larvae moved higher up particles but were not restricted to the highest surfaces and occupied a wide range of elevations in both treatments (Fig. 6A). Flow velocity did not significantly affect vertical distance travelled ($p = 0.93$). The interaction between gravel size and flow velocity also did not have a significant effect on vertical movement.

Larvae experienced much higher velocities in the higher flow treatments (Fig. 6B). The percentage of larvae occupying the upper and upstream-facing surfaces of particles (exposed locations) was broadly similar between treatments 1–3, with slightly more larvae in exposed locations than sheltered in each treatment (Fig. 6C). However, during the treatment with high flow and large gravel particles the number of larvae in sheltered locations remained similar but there were far fewer in exposed locations (Fig. 6C).

Whilst *A. fuscipes* case mass showed no difference between treatments (Fig. 7A) larvae built their cases from marginally larger particles during high flow velocity treatments but this was not significant for most treatments (Fig. 7B).

4. Discussion

The interaction between insects, sediment and hydraulics in rivers has received considerable research, but rarely from a biogeomorphic perspective. Invertebrate zoogeomorphology is recognised as an important process in terrestrial and marine ecosystems (Cadée, 2001; Wilkinson et al., 2009) but research in rivers has focussed on larger taxa (Rice et al., 2012). Nevertheless, the diverse behaviours of invertebrates facilitate zoogeomorphic affects larger than expected from their body size (Albertson and Allen, 2015). Most biogenic structures are stationary and typically expected to stabilise sediment (Fei et al., 2014; Naylor et al., 2002), for example beaver dams (Brazier et al., 2021) and ant and termite mounds (Wilkinson et al., 2009; Viles et al., 2021). In contrast, Glossosomatidae caddisfly larvae create cases from sand, which they move over river bed surfaces. We found that this resulted in an upward conveyance of sand. This behaviour is counter to the geophysical forces that result in disproportionately coarser particles on the upper surface of river beds. Sediment reworking by Glossosomatidae larvae therefore has potential consequences for sediment transport and ecosystem engineering.

4.1. Positioning behaviour of Glossosomatidae larvae relative to flow velocity and benthic substrate characteristics

In the River Dove, Glossosomatidae cases were found on the surfaces of a wide range of particle sizes (from 16 mm up to 256 mm; Fig. 4). In the flume, Glossosomatidae larvae occupied a wide range of elevations in all treatments but on average moved higher in treatments with larger gravel sizes (Fig. 6A). *A. fuscipes* larvae may move to the surface of gravel particles for several reasons, including to improve respiration efficiency and food availability (Wellnitz et al., 2001). Kovalak (1976) recorded that *Glossosoma nigrior* occupied more exposed locations as temperature increased (and therefore dissolved oxygen content decreased). The use of field conditioned gravels means that food availability was comparable to the field. An initial trial for the flume experiment, using gravels without algae coated surfaces, found that most *A. fuscipes* larvae migrated out of the sediment tray. Using fresh algae coated gravels greatly increased larvae retention, suggesting that food availability is also an important control on *A. fuscipes* movement. A second trial run was conducted with gravel particles placed upside down (with most algae now on the base). This run resulted in substantially reduced vertical movement of *A. fuscipes*. Therefore, although this experiment did not explicitly consider food availability, this finding does support Katano and Doi (2014) and Mcneely and Power (2007) who found algal communities to be important for Glossosomatidae larvae

distributions. In river beds, algae predominately grows on the upper surfaces of particles, as in our flume experiment, and therefore we expect Glossosomatidae to migrate to upper surfaces when not restricted by other controls such as hydraulic stress.

In contrast, flow velocity did not appear to affect the vertical elevation of *A. fuscipes* in the flume; larvae moved upwards regardless of flow velocity (Fig. 6A). Glossosomatidae larvae are adapted to maintain their positions in areas of high hydraulic stress by virtue of their case design (Mason et al., 2022) and often attach themselves directly to gravel surfaces with silk (Olden et al., 2004). However, previous research has also documented Glossosomatidae larvae occupying less exposed locations as flow velocity increases (Brooks, 1998 in Lake, 2000; Kovalak, 1976; Houghton, 1997). For example, flume experiments conducted by Lake (2000) found that high flow velocity or turbidity prompted *A. kimminsi* to migrate from the exposed tops to the sides of stable particles, presumably seeking flow refugia. Consequently, it is probable that the high flow treatment used in this experiment (0.6 m s^{-1} ; Table 1) was not enough to restrict larvae movements. Kovalak (1976) found that Glossosomatidae larvae sought less exposed locations at mean velocities over 0.7 m s^{-1} . Therefore, it is expected that *A. fuscipes* move sediment vertically upwards across a broad range of flow velocities (at least $0.1\text{--}0.6 \text{ m s}^{-1}$) and gravel particle sizes (16 mm–256 mm; Fig. 4), with larger particles increasing upwards movement (Fig. 6A).

Interestingly, in our flume treatment with high flow and large gravel, vertical movement of larvae was not less than in other treatments, but larvae did occupy less exposed locations on the gravel particles (i.e., sheltering on the sides and in the lee of the particle; Fig. 6C). It is possible that larger gravel particles forced flow to accelerate over the bed surface, increasing near bed flow velocity in large gravel treatments (Table 1), whilst depth-averaged flow velocity was the same as the small gravel treatment. This suggests that as Glossosomatidae larvae approach the limit of their hydraulic tolerance they adapt at a very local scale to the flow differences across individual particles by seeking out more sheltered microhabitats that still serve their grazing and oxygen requirements.

Flow velocity also appeared to have a strong control on longitudinal movement with larvae moving less far upstream and more larvae moving downstream under high flow treatments (Fig. 5). Poff and Ward (1992) found that as flow velocity increased (up to 0.5 m s^{-1} near the bed, relative to our near bed velocities of $0.3\text{--}0.4 \text{ m s}^{-1}$) the rate of *Agapetus boulderensis* horizontal movement decreased. Gravel size was only manipulated within the sediment area thus had little influence on larvae movement outside of this area (Fig. 5). Furthermore, because of the unnatural environment presented by clean fixed gravel beds, larvae may migrate shorter distances horizontally in real rivers than in the flume as they are more likely to find preferable conditions locally. In all treatments, few larvae were caught in the net (Fig. 5) suggesting that larvae were rarely entrained long distances.

4.2. Influence on fine sediment exposure and mobility

Our flume experiment discovered that Glossosomatidae larvae moved sand upstream, downstream and, of particular interest zoogeomorphically, they conveyed sand vertically upwards from gravel interstices onto the surfaces of gravel particles. This behaviour was not isolated, rather undertaken by 99 % of individuals across differing gravel sizes and flow velocities. Furthermore, in the field, *A. fuscipes* cases were abundant on surface grains (Fig. 1) and therefore, we are confident that the vertical sediment movement observed in the flume also applies to rivers. Redistribution of sand over the surfaces of river beds has potential geomorphic and ecological consequences, particularly when fine sediment is transported upwards into areas of higher flow exposure.

In gravel-bed rivers, fine sediment is typically located in sheltered locations; filling interstices, voids and sheltered patches in the lee of

larger particles (Dietrich et al., 1989; Parker and Sutherland, 1990). This results in a coarse river bed surface, where transport of finer sediment is limited by its availability on this surface prior to breakdown of the surface armour (Church, 2010). Glossosomatidae larvae may transport previously sheltered sand particles out of voids and onto the surface of the gravel bed, thereby increasing its flow exposure and potential for transport (Fig. 8). Furthermore, Glossosomatidae larvae may move fine sediments during base flow, conditioning the bed and increasing the transport of this sediment during subsequent high flows. Therefore, these caddisfly larvae may facilitate transport of sand under early phase transport when gravel remains immobile (Wilcock and Kenworthy, 2002). However, whilst Glossosomatidae larvae increase the flow exposure of fine sediment, the subsequent mobility of this sediment is dependent on its stability in its new exposed location.

The stability of Glossosomatidae sediment in these exposed locations is controlled by (1) the hydraulic and sedimentological conditions in the river, (2) the exposure of the case and (3) the passive and active resistance of the case and larvae to entrainment. *A. fuscipes* larvae can actively resist entrainment by clinging on, by fixing their case to larger particles with silk (Olden et al., 2004), or by moving to a less exposed location (Brooks, 1998 in Lake, 2000). Glossosomatidae may fix their cases under hydraulic stress (Olden et al., 2004) and for pupation.

Fixed Glossosomatidae cases will require considerably greater hydraulic force to entrain. Consequently, sand reworked by Glossosomatidae for pupation may be resistant to entrainment and downstream transport, despite the increase in hydraulic exposure. The stability of the sand displaced by Glossosomatidae larvae is therefore dependent on the behaviour and life stage of the larvae (Fig. 9). Other processes, such as travertine deposition, may further stabilise cases for much longer time periods, potentially extending their ecological and geomorphological implications.

Even if the behaviour of Glossosomatidae larvae means that cases are

stable in their exposed locations, this caddisfly family are unusual among caddisfly because they build a new case at each instar (growth stage; typically 7 instars for *A. fuscipes*; Becker, 2005; Fig. 9B). Furthermore, under adverse conditions, including low oxygen availability (Morris and Hondzo, 2013b) and fine sediment deposition (Wagner, 1987), Glossosomatidae larvae have been observed to abandon their case to drift (more readily than most other caddisfly species; Merrill, 1969; Wagner, 1987). Abandoned Glossosomatidae cases are likely to be more susceptible to entrainment because the larvae may actively prevent entrainment by clinging on or fixing the case to bed sediment with silk. Therefore, although Glossosomatidae larvae transport sediment into zones of higher hydraulic exposure, more research is required to understand how this influences fine sediment transport.

The spatial density of Glossosomatidae is often high, perhaps because they can exploit areas of high shear stress to access high food value because of their cases, which reduce entrainment (Mason et al., 2022) and provide protection from predators (Kohler and McPeck, 1989). In the River Dove abundance was 2191 m⁻² (maximum = 4918 m⁻²; Fig. 2C). These densities only consider larvae on the river bed surface and are slightly higher than a previous survey of caddisfly cases in a small lowland stream (mean = 1804 larvae m⁻², maximum = 4870; Mason et al., 2019). The mass of sediment used by Glossosomatidae was much higher in this study (Mean = 131.95 g m⁻²) than Mason et al. (2019; Mean = 26 g m⁻²) because of the individual case mass being much lower in the latter (0.02 g). Consequently, although the magnitude varies between sites, Glossosomatidae larvae rework substantial quantities of sand in locations where they are abundant.

4.3. Influence on gravel mobility

In gravel-bed rivers, transport of fine sediment constitutes a substantial proportion of bedload (Lisle, 1995) but channel morphology is

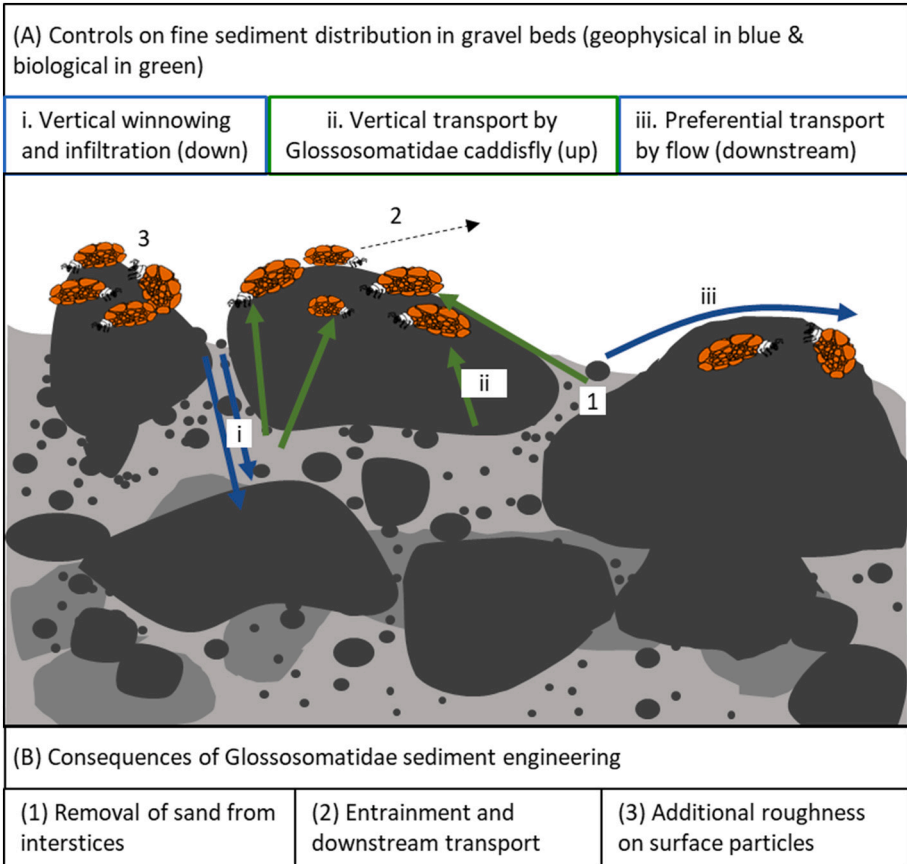


Fig. 8. Physical & biological sediment sorting at gravel-bed surfaces (A) Physical bed armouring processes (blue) and Glossosomatidae movement of sediment (green). (B) Potential zoogeomorphic consequences of upwards transport of sand by Glossosomatidae larvae. Movement of sediment, even small distances by Glossosomatidae can substantially alter the exposure of this sediment to entraining flows and may affect downstream sediment flux in rivers. Glossosomatidae sediment transport opposes vertical winnowing and increases the hydraulic exposure of case sediment.

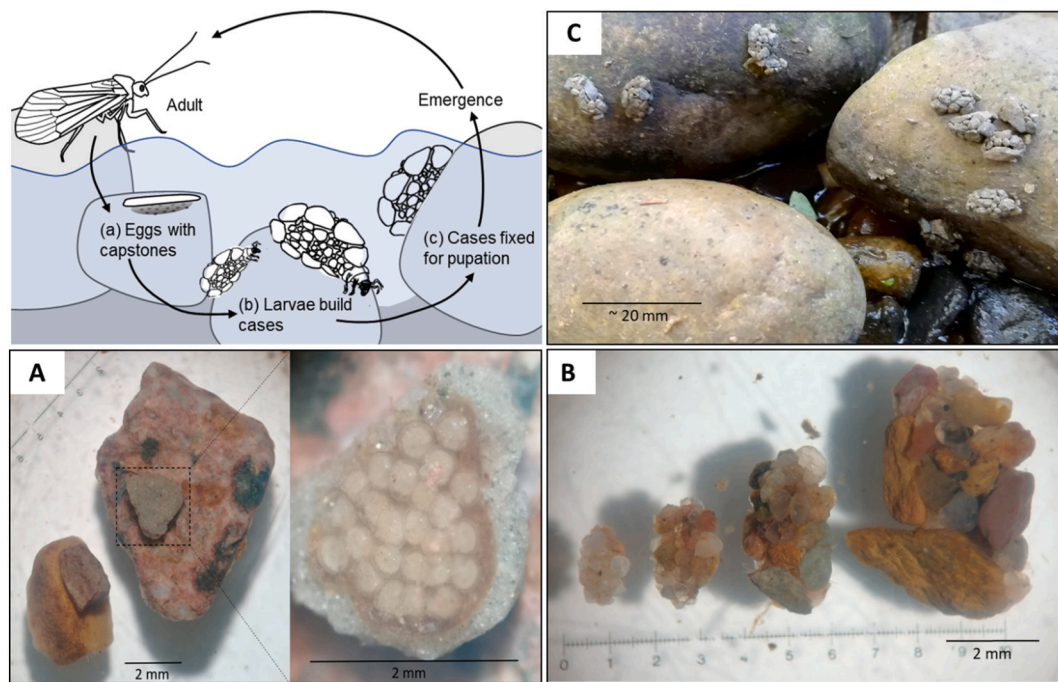


Fig. 9. Zoogeomorphic lifecycle of a Glossosomatidae *A. fuscipes* caddisfly. (A) Eggs are oviposited by the adults beneath a sand capstone. (B) Glossosomatidae larvae build cases, which increase in size and the size of sediment used, with each instar. (C) For pupation, cases are built which are attached with silk to the river bed surface, typically in hydraulically exposed locations (shown here after water levels dropped). All photographs from Black Brook (source of larvae for flume experiments).

dependent on the transport of coarser grains (Church, 2010). Glossosomatidae movement of sand may influence transport of gravel via several mechanisms, including modifications to the size and mass of gravel particles and the fine sediment distribution of the surrounding river bed.

Taking the mass of a spherical particle with diameter equal to measured *b* axis, density as 2650 kg m^{-3} and adding the mass of the maximum number of *A. fuscipes* found on this size particle in the River Dove (Fig. 4), results in a maximum increase in particle mass of 7 % original grain mass, peaking at 22 mm diameter particles. Similarly, *A. fuscipes* cases increase the protrusion of surface grains relative to the mean bed elevation, both by reducing interstitial fine sediment and by fixing cases to the top of gravel particles with silk (Fig. 8). This may be geomorphologically important because small changes in bed protrusion can have significant impacts on transport (Masteller and Finnegan, 2017). A single case would add about 28 % to the *b* axis of a grain with an original *b* axis of 16 mm. Many cases will increase roughness across the exposed surface of these particles. This could be important both by reducing resistance of this gravel particles to entrainment and by modifying near bed hydraulics, probably increasing the height of the boundary layer with consequences for sediment transport and other organisms.

Furthermore, the transport of sediment out of interstices may affect gravel transport. The distribution of the sand fraction in river gravel beds is important for the mobility of gravel particles (Grams and Wilcock, 2007; Venditti et al., 2010; Wilcock, 2001). Gravel transport may be increased or reduced by increased sand content, depending on the relative proportion of sand and gravel fractions (Wilcock and Kenworthy, 2002). Clearance of upper interstitial space by bioturbating stonefly larvae was estimated by Statzner (2012) to increase cobble critical shear stress by 50 % (following Wilcock, 1998; Wilcock and Kenworthy, 2002) but this has not been tested. Therefore, it is likely that by removing sediment from interstices, Glossosomatidae caddisfly affect the interaction between sand and gravel fractions in rivers and the subsequent transport of both sediment size fractions.

4.4. Ecosystem engineering

Caddisfly cases in exposed locations may change microscale hydraulics and facilitate habitation of these environments by other taxa. Glossosomatidae cases increase the roughness of otherwise smooth gravel particles (Fig. 1B). Poff and Ward (1988) found that *Baetis* sp. (Baetidae Mayfly) nymphs occurred in and on occupied *Glossosoma verdoni* cases in greater abundance than on rock surfaces without these cases. Furthermore, McCabe and Gotelli (2003) found that aggregations of other caddisfly taxa; *Brachycentrus* (Brachycentridae) and *Neophylax* (Thremmatidae) pupal cases increased the species richness of macro-invertebrates compared with normal substrate. Personal observation of unoccupied *A. fuscipes* cases fixed to gravel surfaces, found a build-up of fine sediment in the lee, providing evidence for reduced flow velocities in the zone directly affected by the case.

Furthermore, by modifying the vertical distribution of sand, Glossosomatidae may reduce clogging of gravel-bed pore spaces with fine sediment, which is a widespread problem in rivers (Waters, 1995; Wharton et al., 2017). Bioturbation by fish, crayfish and other invertebrates can promote decolmation (Mermillod-Blondin, 2011; Nogaro et al., 2006; Wharton et al., 2017). Therefore, upwards vertical transport of sand by Glossosomatidae larvae may increase water flow and consequently the oxygen content of hyporheic habitats, beneficial for some invertebrate taxa and fish spawning and egg survival (Ferreira et al., 2010).

4.5. Generality of Glossosomatidae zoogeomorphology

The zoogeomorphic effects of Glossosomatidae will vary throughout their lifecycle (Fig. 9). Whilst the case building behaviour studied here is limited to larvae, Glossosomatidae adults also use and cement sediment in rivers, by collecting small capstones that are secured on top of egg masses, presumably to provide protection from predators or flow (Fig. 9a; Anderson, 1973). During the larval stage, *A. fuscipes* typically go through seven instars and build a new and larger case for each instar

(Becker, 2005). Thus, the size and mass of sediment incorporated by each individual will increase with instar (Fig. 9b). Furthermore, the displacement of this sediment is likely to be lessened at earlier instars as they were observed in the River Dove to occupy lower vertical elevations on surface particles and are also less resistant to flow than larger taxa (van Der Lee et al., 2020). During pupation *A. fuscipes* fix their pupal cases on cobbles in flowing water, often on the upstream face (Anderson and Bourne, 1974). These cases are fixed securely with silk and may remain in place for some time after the adult has emerged (Fig. 9c).

The positioning of *A. fuscipes* on the upper surfaces of gravel beds has been widely observed in the field and appears to be consistent across many Glossosomatidae species including *G. nigror* (Kovalak, 1976), *Glossosoma boltoni* (Scott, 1958) and *A. boulderensis* (Olden et al., 2004; Wellnitz et al., 2001). Therefore, this behaviour is not limited to *A. fuscipes*.

Glossosomatidae are characteristic taxa of relatively fast flowing, unimpacted streams (Nijboer, 2004) and have a wide geographic distribution. The Glossosomatidae *Agapetus* genus is found across the Palearctic, Nearctic, Australasian and Oriental biogeographic regions (Morse, 2022) and similar taxa are also reported from the Neotropics (Robertson and Holzenthal, 2006). Therefore, the geomorphic and ecosystem engineering behaviour of Glossosomatidae taxa are potentially a nearly global phenomenon.

Many caddisfly taxa construct cases and transport these over river bed surfaces. However, the case building and movement behaviour of Glossosomatidae larvae cannot be extrapolated to other caddisfly families. Glossosomatidae are especially rheophilic, preferring areas of high flow exposure whilst many other caddisfly taxa prefer to avoid exposed sediment surfaces and may burrow below the surface (e.g., Sericostomatidae; Wagner, 1991), or primarily inhabit interstices (e.g., Limnephilidae; Lancaster et al., 2006). Glossosomatidae also build dome shaped cases whose hydraulic properties differ to the more typical tubular shaped cases of other caddisfly (Mason et al., 2022). These taxa have different zoogeomorphic implications (Mason et al., 2019, 2022).

4.6. Limitations and future research

Understanding how the individual actions of aquatic insect larvae affect processes at larger scales is a challenge because of their small size (Mason and Sanders, 2021). Relative to the size of the study organism, our flume experiment considered a relatively large scale, with 50 larvae introduced in each run (650 total). However, there are a number of limitations to the flume experiment. The flume only represents a short snapshot in time and considered only final instar larvae whilst other life stages may have different zoogeomorphic effects (Fig. 9). Furthermore, the flume does not represent all processes that may influence larvae positioning in the field, such as the presence of predators or fluctuating water levels, which may deter larvae from occupying exposed locations. Last, the findings of the flume experiment are limited to the studied gravel sizes and flow velocity, and expanding to higher velocity in particular would reveal the stability of transported sediment in its new, more exposed, location.

Coupling the flume experiment with a field survey helped to mitigate these limitations and increase the scale of our understanding of sediment movement by *A. fuscipes* larvae. However findings are specific to the River Dove, which is groundwater fed with a stable discharge which may favour high densities of macroinvertebrates (Koetsier et al., 1996). The larger individual case mass found in the River Dove than by Mason et al. (2019) may in part be caused by the high productivity found in the River Dove.

Future research should consider how bioturbation by Glossosomatidae larvae affects the transport of sand incorporated into cases and whether this is more easily transported from its exposed position, or is stabilised by silk (and how this varies through the organisms' life history). The effects of Glossosomatidae sediment reworking on local scale hydraulics are also worthy of further study. In addition to potentially

modifying bed surface roughness caused by the presence of their cases on smooth gravel particles, Glossosomatidae may affect bed permeability and hyporheic conductivity. The role of organisms in modifying hyporheic flow processes are particularly high during low flows (Shrivastava et al., 2021b) and other insects, such as the worm *Lumbriculus variegatus*, increase hyporheic exchange via burrowing (Shrivastava et al., 2021a). The removal of material from interstices and transport to gravel surfaces by Glossosomatidae larvae may have similar affects.

5. Conclusions

The interaction between benthic habitat structure and near bed hydraulics has a strong control on animal movements in rivers (Hoffman et al., 2006). In turn, the activities of animals can influence the distribution of sediments. Glossosomatidae *A. fuscipes* caddisfly transport sediment, incorporated into cases, around the river bed, with larvae moving both upstream, (occasionally by over 2 m in 21 h) and downstream. However, of most interest zoogeomorphically was a vertical upwards movement. Vertical reworking of sediment averaged 25 mm upwards in our flume experiment, increased for larger gravel particles, and was maintained even at flow velocities of 0.6 m s^{-1} , easily sufficient to transport *A. fuscipes* cases from these surfaces (Mason et al., 2022). Whilst the sediment moved by an individual caddisfly is small (0.06 g per case), this sediment movement was repeated by 99 % of Glossosomatidae larvae representing substantial vertical displacement of sand.

In gravel-bed rivers, the transport of fine sediment is typically limited by the supply of this sediment on the surface. The steep gradient in hydraulic exposure between the surface and subsurface of water worked gravel beds means that displacement of fine sediment over small vertical distances could have substantial effects on the exposure of that sediment and its contribution to bedload transport (Powell, 1998). Therefore, animals that disturb or stabilise surface sediments may have disproportionately large zoogeomorphic effects. *A. fuscipes* transport sediment, incorporated into cases, from sheltered interstices between gravel particles, on to the hydraulically exposed surface of gravel beds where it may influence local scale hydraulics, sand transport and ecosystems.

Glossosomatidae are a widespread caddisfly family and, under the appropriate environmental conditions, can reach extremely high abundances (Hickin, 1967; Mcneely and Power, 2007). Consequently, they can transport substantial amounts of fine sediment to the surface of river beds (1.4 t km^{-1} sand in this study). Where present, Glossosomatidae cases are usually conspicuous on the surface of gravel beds (Wiggins, 2004) and are often the only fine sediment visible in these areas of high hydraulic stress (Fig. 1). These results provide further evidence that important zoogeomorphic effects are not restricted to large taxa and are vital to our understanding of the interaction between biology and sediment dynamics in rivers.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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