

The zoogeomorphology of case-building caddisfly: Quantifying sediment use

Richard J. Mason,^{1*}  Stephen P. Rice,¹  Paul J. Wood¹  and Matthew F. Johnson² 

¹ Department of Geography and Environment, Loughborough University, Loughborough, Leicestershire LE11 3TU, UK

² School of Geography, University of Nottingham, Nottingham NG7 2RD, UK

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*Correspondence to: Richard J. Mason, Department of Geography and Environment, Loughborough University, Loughborough, Leicestershire LE11 3TU, UK.

E-mail: r.j.mason@lboro.ac.uk

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ABSTRACT: Caddisfly (Trichoptera) larvae are an abundant and widespread aquatic insect group characterized by the construction of silk structures, including nets and cases. Case-building caddisfly have the potential to modify the sorting and mobility of sand and fine gravel via: (1) case construction, resulting in altered sediment properties; (2) transporting sediment incorporated into cases over the river bed; and (3) changing the structure of river beds via burrowing activity. To investigate these mechanisms, it is necessary to understand the mass, size distribution and spatial variability of sediment use by case-building caddisfly larvae.

We quantified the mineral sediment used by individuals and communities of case-building caddisfly in 27 samples, from three sites on a gravel-bed stream. The mass and size distribution of sediment in individual cases varied between taxa (mass = 0.001–0.83 g, D_{50} = 0.17–4 mm). The mean mass of sediment used by the caddisfly community was 38 g m^{-2} and varied locally. Sediment use was predominantly coarse sand (D_{50} = 1 mm). 64% of sediment use was attributable to *Agapetus fuscipes* (Glossosomatidae).

Due to within-species variability in case mass, the abundance of most taxa, including *A. fuscipes*, was only weakly associated with the mass of sediment used by this species, at the river scale. Whilst the caddisfly community used a small percentage of the total sediment available (average 2.99% of the 1–1.4 mm size fraction), *A. fuscipes* used more fine sediment in their cases at sites where it was more available. Despite variability in local habitat, all sites supported diverse case-building caddisfly communities utilizing mineral sediment. Consequently, geomorphological effects of case-building caddisfly are potentially widespread. The results provide novel insights into the specific grain sizes and quantities of fine sediment used by caddisfly larvae, which represents an important step towards understanding their zoogeomorphic activities. © 2019 The Authors. Earth Surface Processes and Landforms Published by John Wiley & Sons Ltd

KEYWORDS: biogeomorphology; zoogeomorphology; macroinvertebrate; fine sediment; Trichoptera; bed armouring; ecology

Introduction

While sediment dynamics in rivers have traditionally been considered a largely physical phenomenon (Reinhardt *et al.*, 2010), it is increasingly recognized that plants and animals can have substantial effects on hydraulics, bed sediment sorting and sediment transport processes (Rice *et al.*, 2012; Statzner, 2012; Wilkes *et al.*, 2018). A growing body of research has demonstrated the importance of biogeomorphology (Viles, 1988) in rivers, particularly for plants and larger animals, such as fish and mammals (Statzner, 2012). For example, both living plants and dead wood effect instream hydraulics and sediment stability (e.g. Cotton *et al.*, 2006), to the extent that they often have large-scale effects on channel planform and longitudinal profiles (for reviews see Montgomery and Piégay, 2003; Corenblit *et al.*, 2007; Wohl, 2013; Gurnell, 2014). Several reviews have highlighted the geomorphic effects of animals in rivers (Moore, 2006; Rice *et al.*, 2012; Statzner, 2012). For example, the construction of beaver dams alters the hydrology, geomorphology

and ecology of smaller rivers and riparian zones (Naimen *et al.*, 1988; Gurnell, 1998; Butler and Malanson, 2005). Salmonid spawning disturbs gravel substrates, reducing their stability (e.g. Gottesfeld *et al.*, 2004; Hassan *et al.*, 2008; Buxton *et al.*, 2015; Fremier *et al.*, 2017). In addition, foraging by benthic-feeding fish can increase sediment mixing and fine sediment suspension (Pledger *et al.*, 2014; Huser *et al.*, 2016), affecting both gravel and sand substrates (Statzner *et al.*, 2003; Pledger *et al.*, 2017).

Zoogeomorphology of riverine invertebrates

Invertebrates have also been shown to have considerable effects on geomorphology, making up for their smaller size (and lower per-capita geomorphic effects) with high abundances and a diverse range of behaviours (Wallace *et al.*, 1993; Albertson and Allen, 2015). In terrestrial ecosystems, some ants are major bioturbators of soils and have been found

to excavate >1 tonne of soil per hectare (Seal and Tschinkel, 2006); similar processes exist in lakes (Krantzberg, 1985) and marine environments (Cadée, 2001). In rivers, invertebrates have been shown to both erode and stabilize sediment (Statzner, 2012). Predatory stonefly larvae can transport substantial quantities of sand from gravel interstices ($200\text{--}400\text{ kg m}^{-2}\text{ year}^{-1}$; Statzner *et al.*, 1996), with reduced prey availability increasing foraging activity, and therefore erosion potential (Statzner *et al.*, 1996; Zanetell and Peckarsky, 1996). Similarly, increased erosion of sand-sized sediments is associated with the foraging activity of freshwater shrimps (Pringle *et al.*, 1993; Pringle and Hamazaki, 1998) and mayfly larvae (Soluk and Craig, 1990). Burrowing invertebrates including Asellidae (crustaceans), Tubificidae (worms) and Chironomidae larvae (non-biting midges) can affect the structure and porosity of the bed sediment matrix, via bioturbation, sediment reworking and structure building (Mermillod-Blondin *et al.*, 2003, 2004; Mermillod-Blondin and Rosenberg, 2006). Crayfish potentially increase the entrainment of fine sediments through a combination of locomotion (foraging and fighting) and burrowing activities (Johnson *et al.*, 2010; Harvey *et al.*, 2014; Rice *et al.*, 2014). Rice *et al.* (2016) attributed a 32% (474 kg) increase in monthly base flow suspended sediment loads to crayfish activity.

Caddisfly zoogeomorphology

Caddisfly (Trichoptera: Insecta) are one of the most diverse orders of aquatic macroinvertebrates globally, with over 14 500 species (Zhou *et al.*, 2016). Caddisfly typically spend their larval stages in aquatic environments. Individual taxa are small (usually <30 mm in length) but may have disproportionately large zoogeomorphic effects due to their use of silk (Albertson and Allen, 2015). Caddisfly silk, a tough fibrous protein, has high specific strength and ability to stretch, and can more than double in length before breaking (Brown *et al.*, 2004; Tszdel *et al.*, 2009). Silk allows caddisfly larvae to create a wide variety of structures and Wiggins (1996) classified larvae into five groups (Figures 1i–v). These are larvae which: (i) construct retreats and silk filtration nets; (ii) bind together fine sediments into portable tubular cases; (iii) build domed (saddle-shaped) cases; (iv) construct purse-type cases, primarily composed of silk; and (v) are free living, building a case only for pupation.

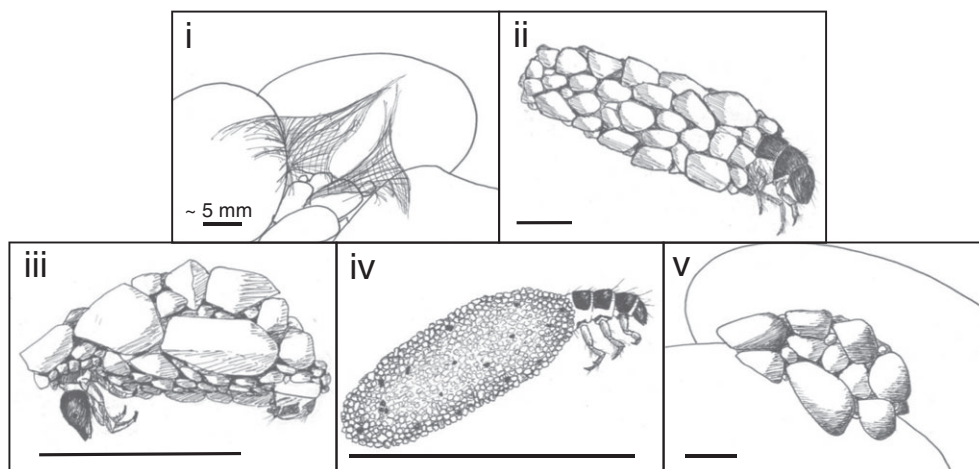


Figure 1. Diversity of caddisfly larval and pupal architecture (after Wiggins, 1996). (i) Nets filter food from flowing water, often accompanied by a static retreat in which the larvae reside (e.g. Hydropsychidae). (ii) Tubular cases which are usually mobile but may be fixed to stable particles for pupation (e.g. Limnephilidae). (iii) Domed/saddle cases are also usually mobile but fixed for pupation (e.g. Glossosomatidae). (iv) Purse cases (e.g. Hydroptilidae). (v) Pupal cases of free-living or retreat-building taxa (e.g. Rhyacophilidae or Hydropsychidae). The scale bar indicates approximately 5 mm.

Caddisfly larval structures can have measurable zoogeomorphic effects. The nets and retreats of Hydropsychidae (Figure 1i) can stabilize gravel beds by binding grains together, increasing their effective size and mass, and therefore the force required to move them (Figure 2N). Hydropsychidae larvae have been found to increase the critical shear stress required to initiate gravel movement by 10–40% (Statzner *et al.*, 1999; Cardinale *et al.*, 2004; Johnson *et al.*, 2009; Albertson *et al.*, 2014a). This consolidation can be increased further by the presence of multiple species (Albertson *et al.*, 2014b, 2019). Furthermore, caddisfly can stabilize cobbles (Takao *et al.*, 2006), with a single retreat increasing the force required to move a particle two to threefold (Nunokawa *et al.*, 2008).

However, caddisfly produce a range of structures (Figure 1) and to date, only the zoogeomorphic effects of nets and retreats have been considered. Most caddisfly species (Figures 1i–v) utilize fine sediment (~0.1 to 5 mm; Hansell, 1968a; Hansell 1968b; Tolkamp, 1980; Statzner *et al.*, 2005; Okano and Kikuchi, 2012; De Gispert, 2018) in the construction of mobile cases, fixed retreats or pupal cases at some point in their life cycle (Wiggins, 1996). We propose three potential mechanisms by which case-building caddisfly larvae may influence sediment transport and hydraulic processes in rivers (Figures 2A–C):

- (A) Caddisfly may modify the entrainment characteristics of sediments incorporated into their cases (Figure 2A). Case construction involves binding sediment particles together with silk (Hansell, 1968a; Okano *et al.*, 2016), producing a composite particle of reduced density and relatively large volume. The shear stress required to move caddisfly cases varies with species, case size and whether the case is occupied (Waringer, 1993; Statzner and Holm, 1989; Otto and Johansson, 1995), but there has been no systematic examination of the mobility of cases relative to their constituent grains.
- (B) Case-building caddisfly taxa may influence fluvial geomorphology by transporting sediment (Figure 2B). First, caddisfly may perturb sediment during locomotion (i.e. similar to the effect reported for stonefly larvae; Statzner *et al.*, 1996), or during case construction when they sort through and discard many particles (Hansell, 1968a). Second, many caddisfly species crawl large distances across the river bed (~1–4 m day⁻¹; Erman, 1986; Jackson *et al.*, 1999; Lancaster *et al.*, 2006), transporting their case and constituent sediment with them. In this manner, caddisfly transport sediment both

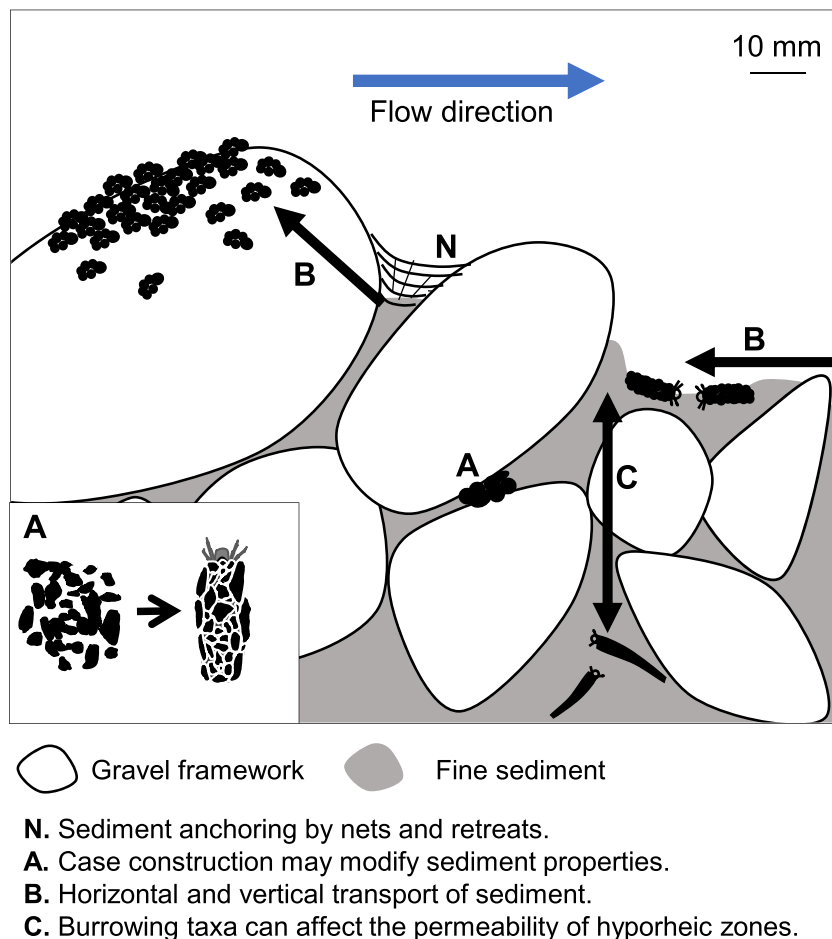


Figure 2. Conceptual diagram showing possible zoogeomorphic impacts of caddisfly in gravel-bed rivers. (N) nets and retreats strung between gravel particles increase bed stability (e.g. Johnson *et al.*, 2009). (A) all case-building caddisfly change the size, shape, weight and density of sediment particles by combining them into cases, with potential implications for the mobility of this sediment. (B) case-building taxa transport fine sediment both horizontally and vertically, with potential consequences for the flow exposure and mobility of this sediment. (C) burrowing taxa (e.g. Sericostomatidae) may affect the vertical sorting and hydraulic conductivity of gravel beds. [Colour figure can be viewed at wileyonlinelibrary.com]

upstream and downstream (Hart and Resh, 1980; Williams and Williams, 1993; Bergey and Ward, 1989).

- (C) Many burrowing invertebrates have been shown to increase the hydraulic conductivity of bed sediments (Mermillod-Blondin *et al.*, 2003, 2004), and this may also be true for some caddisfly (Figure 2C). For example, Sericostomatidae larvae burrow diurnally to approximately 12 cm (Wagner, 1990; Waringer, 1987), increasing the organic matter content of the substrate (Wagner, 1991) and reworking surface sediments (De Nadai-Monoury *et al.*, 2013).

Context of this study

The design of caddisfly structures has fascinated scientists and incited a large number of detailed studies (e.g. Hansell, 1968a; Tolkamp, 1980; Becker, 2001; Wiggins, 2004). However, research has focused largely on individual species and the functional importance of structures to the larvae (Otto and Johansson, 1995; Limm and Power, 2011; De Gispert *et al.*, 2018) rather than the effects of caddisfly case building on sediment stability and transport. The sedimentary implications are worthy of investigation because fine sediment availability is an important determinant of suspended and bed material transport. Sand fractions constitute the majority of the sediment flux in many rivers, and the sand content of gravel beds is a control on the movement of gravels as bedload (Jackson and Beschta,

1984; Ikeda and Iseya, 1988; Wilcock *et al.*, 2001; Wilcock and Crowe, 2003). Furthermore, while the geomorphic impact of individual caddisfly may be inconsequential, they are typically abundant (De Moor and Ivanov, 2008) and dominate invertebrate biomass in some rivers. Consequently, caddisfly communities can use substantial quantities of sand-sized sediment. For example, preliminary studies indicate that the saddle-cased species *Agapetus fuscipes* (Glossosomatidae, Figure 1iii) used approximately 1.4 tonnes km^{-1} of sand to build their cases on the River Dove, UK (Figure 3). Statzner *et al.* (2005) estimated that the pupal cases of Rhyacophilidae and Hydropsychidae (groups v and i, respectively in Figure 1) use between 1 and 3 kg m^{-2} (Statzner *et al.*, 2005; Statzner, 2011).

However, the quantity and size distribution of sediment used by the case-building caddisfly community has never been measured. Sediment use by caddisfly larvae is likely to vary with both the composition and abundance of the caddisfly community and within-species variability in case design. The distribution of caddisfly is a result of environmental controls (including flow velocity, oxygen availability and bed sediment characteristics), biological interactions (e.g. competition and predation) and historical factors (Southwood, 1977; Murphy and Davy-Bowker, 2005). The abundance and case designs of caddisfly larvae vary seasonally (e.g. some species only use mineral sediment grains when building pupal cases, Figure 1v; Wiggins, 2004). Furthermore, any impacts of case-building caddisfly on sediment stability will also depend on the geomorphic and hydrological context of the river environment. Consequently,

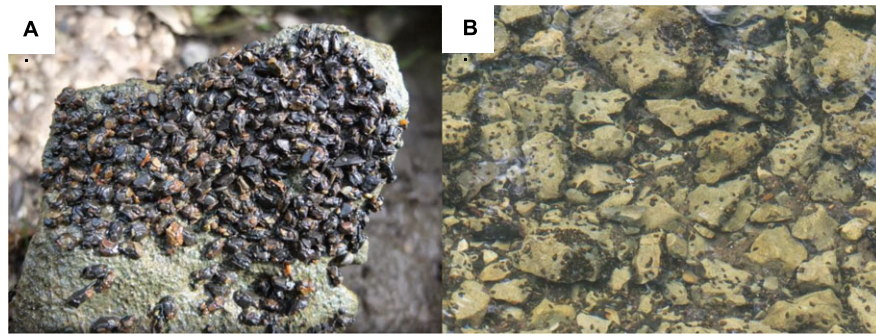


Figure 3. Glossosomatidae larvae in the River Dove, Derbyshire, UK. (A) Dense aggregations on the exposed face of a single cobble. (B) Cases visible on the upper surfaces of cobble and gravel particles across an area of approximately 1 m^2 . Sand and fine gravel-sized sediments have been transported from interstitial spaces to the surface of gravel and cobble clasts. [Colour figure can be viewed at wileyonlinelibrary.com]

both sediment use and the potential for zoogeomorphic effects are likely to vary spatially and temporally.

In this study, we quantified mineral sediment use by case-building caddisfly in a UK stream. Sampling was restricted to riffle habitats because these typically support a greater abundance and diversity of caddisfly taxa (Brown and Brussock, 1991) and the lowest quantity of fine bed sediments, due to bed armouring (Statzner, 2011). Specifically, we measured the grain size distribution and quantity of sediment used by each of the case-building taxa present and compared sediment use between taxa. We also investigated how sediment use varies in space, in relation to the abundance of caddisfly taxa and the availability of sediment in the bed; both likely to be important controls on case design and sediment use. These results provide important information necessary to design *ex-situ* experiments and field studies to investigate the potential zoogeomorphic role of case-building caddisfly (Figure 2). Furthermore, knowledge of the controls on sediment use by caddisfly larvae will begin to address the potential extent and importance of case-building caddisfly for fluvial geomorphology. For example, if caddisfly adapt their case design to local conditions, their presence

would be expected to be less constrained by the availability of specific grain size fractions and consequently they may have a more widespread zoogeomorphic impact. This paper addresses three specific questions:

1. What is the mass and grain size of sediment used in cases by different caddisfly taxa and by the whole caddisfly community?
2. How does the mass and grain size of sediment used by the caddisfly community and individual taxa vary spatially?
3. To what extent do variations in the mass and grain size of sediment used in cases reflect differences in taxon abundance and sediment availability?

Methods

Field sampling

Caddisfly and bed sediment samples were collected from riffle habitats in Wood Brook, Leicestershire, UK (Figure 4). Wood

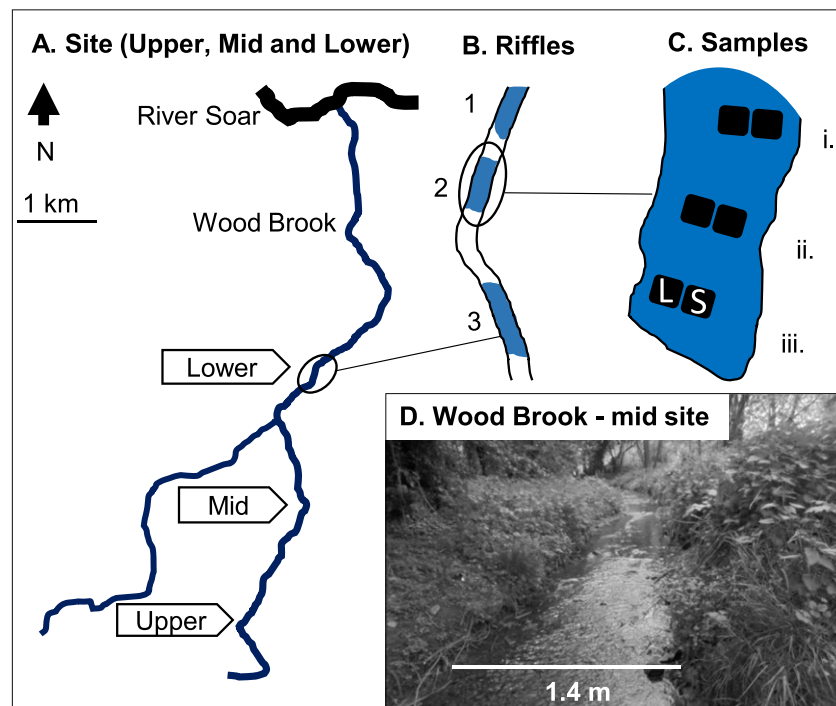


Figure 4. Study site and sampling strategy. (A) Wood Brook (drawn from EDINA, 2018). Three sites were sampled: upper, mid and lower. Mid site: $1^{\circ}13.4124'W$, $52^{\circ}45.0648'N$. (B) Three riffles were sampled, nested within these three sites. (C) Three samples were taken within each riffle. In each case, caddisfly larvae (L) and sediment (S) were sampled from proximate locations. (D) Wood Brook at the mid site, riffle 2. [Colour figure can be viewed at wileyonlinelibrary.com]

Brook is a first to second-order gravel-bed stream with an average width of 1.5 m and depth less than 0.1 m in the riffles studied. Wood Brook rises at an elevation of 200 m above sea level and flows for approximately 10 km to its confluence with the River Soar. The geology is largely mudstones and boulder clay underlain by Precambrian volcanic and intrusive igneous rocks (Greenwood *et al.*, 2001). The median discharge of Wood Brook for the five years prior to sampling was 0.03 m s^{-1} . This was calculated from 15-minute resolution stage data and a rating curve. The slope of Wood Brook over the study area was 0.02 and the mean D_{50} of surface sediment was 38 mm.

Caddisfly and sediment samples were collected from three sites along Wood Brook (referred to as upper, mid and lower; Figure 4) in order to capture variability in bed sediment availability and caddisfly communities, associated with longitudinal variations in grain size, channel morphology and local habitat characteristics. Nested within each site, three riffles were selected (each $>6 \text{ m}$ in length, Figure 4) and three longitudinally distributed samples collected from each riffle, making a total of 27 units (i.e. 3 samples \times 3 riffles \times 3 sites). Caddisfly communities and case characteristics are known to vary seasonally, therefore all samples were collected during a one-month period between 28 March and 26 April 2017, recognized as an optimum time for instream macroinvertebrate diversity in the UK and therefore likely to be the peak time for sediment use within caddisfly cases.

Caddisfly larvae samples were collected using a Surber sampler (Surber, 1937) with a basal area of 0.1 m^2 ($330 \times 310 \text{ mm}$ frame with a 1 mm diameter mesh net), providing a fully quantitative measure of macroinvertebrate density (Everall *et al.*, 2017). The surface sediment layer was agitated by hand so that macroinvertebrates were carried into the net by the current and larger particles were individually inspected for larvae and cases. A similar Surber sampler frame, with a 0.1 mm net to retain fine sediments, was used to collect a benthic sediment scoop from a location immediately adjacent to the caddisfly sample (Figure 4C). The bed sediment sample was used to estimate the sediment available to caddisfly for case building, although this will vary depending on the mobility of the individual species (Statzner, 2011). Both caddisfly larvae and sediment were sampled to a depth of 0.05 m (approximately $1.4 \times$ bed D_{50}).

Laboratory analysis

Caddisfly samples were preserved in 4% formaldehyde solution, washed through a 0.25 mm mesh sieve and manually processed for caddisfly larvae, pupae and cases, which were stored in 70% industrial methylated spirit. Most larvae were identified to species level (Edington and Hildrew, 1995; Wallace *et al.*, 1990), although early instar taxa (e.g. *Athripsodes* sp.) were not identified beyond genus. Larvae and case length were measured to the nearest millimetre (Tolkamp, 1980). When more than 10 individuals of a species were present, length was estimated for a random subsample (average $n = 12$). Cases in each sample were combined within each taxon for grain size analysis (regardless of size or instar). For most taxa, only cases that were complete and retained their original length and width were analysed, although Rhyacophilidae and Hydropsychidae pupae were included even if incomplete due to low total abundance. To break down the silk structure and disaggregate the mineral particles, caddisfly cases were immersed in 30% hydrogen peroxide (H_2O_2) at 80°C for at least 5 h and stirred periodically. For cases with high organic content, some larger organic particles were removed manually. H_2O_2 was removed by washing the samples with

deionized water through a 38 mm diameter, 0.063 mm aperture sieve and then dried overnight at 80°C . The disaggregated sediment was then mechanically sieved through 5.6–0.063 mm (38 mm diameter) sieves at half-phi intervals and weighed. Individual fractions were weighed on a four decimal place scale. To reduce sieving error, case samples with mass less than 0.01 g, or samples where the mass lost during the sieving process exceeded 5%, were removed from the analysis (9 and 1 removed, respectively, leaving 151 samples). Bed sediment samples were dried at 105°C for 12 h and then sieved into half-phi intervals down to 0.063 mm using a mechanical sieve shaker.

Data Analysis

Sediment use by individual caddisfly taxa

The grain size distribution of an average individual case of each taxon in each sample, was calculated by dividing the mass of each grain size fraction by the number of cases in that sieved sample. Percentiles were determined for each of these grain size distributions. The mass of an average individual case was estimated as the sum of all size fractions divided by the number of cases sieved. To compare the mass and size distribution of sediment used in individual cases of different taxa at the river scale (question 1), the grain size distributions, percentiles and mass were averaged across all samples in which that taxon used sediment. The mean and standard deviation of larvae length, case length, case mass, \overline{D}_{50} , \overline{D}_5 and \overline{D}_{95} are reported for each taxon, where the bar indicates the mean of all values across the river. \overline{D}_5 and \overline{D}_{95} are used to give a measure of the range of grain sizes used by each taxon, excluding the most extreme sizes.

Sediment use by the caddisfly community

To calculate the total mass of sediment used by each taxon in each Surber sample, the sediment use by an individual of that taxon was multiplied by the number of cases recorded in the Surber sample (*note*: not all cases in a sample were subject to sieve analysis). The fragility of Glossosomatidae cases meant that the number of larvae recorded was typically greater than the number of surviving cases. Therefore, the total sediment used by this taxon was determined by multiplying the average sediment use per case by the number of larvae present. The total sediment mass used by the case-building caddisfly community in each Surber sample was then calculated as the sum of the totals for each taxon. The grain size distribution was similarly calculated, multiplying the mass of each grain size fraction in an individual case by the number of cases (or larvae for Glossosomatidae) present. The community grain size distribution was calculated as the sum of each grain size fraction used by each taxon. The mean and standard deviation, percentiles, skew and kurtosis were calculated for community sediment use. The mass of sediment used by caddisfly larvae in each sample was scaled from 0.1 m^2 Surber samples to 1 m^2 for ease of interpretation.

Spatial variability in sediment use by the caddisfly community

In order to address question 2, the mean mass and grain size distribution of sediment used by the caddisfly community in each sample was combined by site (upper, mid and lower),

with nine samples in each (i.e. three replications in three riffles within each site). A Shapiro–Wilk test revealed that these predominantly displayed non-normal distributions and therefore a non-parametric Kruskal–Wallis test was used to compare the variability in the mass and grain size percentiles (D_{50} , D_{16} and D_{84}) of the community-level data between sites. Subsequently, Dunn's tests were used to determine which sites were significantly different. Shapiro–Wilk, Kruskal–Wallis and Dunn's tests were conducted in R studio (version 3.3.3, R Core Team, 2017).

Relation between abundance and sediment use

To address this question, we assumed that differences in the total sediment mass used in different locations (i.e. variability between samples) reflect: (1) differences in the abundance and caddisfly taxa present and (2) differences in the mass of cases built by individuals of the same species (potentially reflecting unknown biotic and abiotic drivers, including sediment availability). To explore the relative importance of these factors, we conducted linear regression between abundance (independent variable) and the total mass of sediment used (dependent variable) for each taxon and the whole community. A high value (R^2) indicates that spatial variability in sediment use is associated with the abundance of each taxon. A low value means that within-species variability explains differences in sediment use between samples. Samples without sediment use by a particular taxa were excluded from the regression analysis while samples with sediment use (cases) but no larvae (larvae may have been lost in sampling or emerged as adults) were included. To further investigate within-species variability in case building we concentrated on *A. fuscipes* (Glossosomatidae) because they were the most abundant taxon and accounted for most sediment use at the river scale. To determine if variability in *A. fuscipes* case mass corresponded to variability in the size of sediment used, we plotted the mean and standard deviation of grain size distributions for each site. Furthermore, to investigate potential explanations of variability in case mass we examined the correlations between mean case mass, mean case D_{50} and mean larvae length across all sites for this species.

Relation between sediment availability and sediment use

To investigate how sediment use varied with sediment availability, the grain size distributions of mean sediment use by the

caddisfly community were compared to the bed sediment availability, both at the river scale and for each site. The mass of sediment used by the caddisfly community was divided by the mass of available sediment and multiplied by 100 to give the percentage of sediment used. This was done for each grain size, for each sample, and averaged for each site and the whole river.

Results

Sediment use by individual caddisfly taxa

There was considerable variability in the mass and size distribution of cases of individual taxa (Table I, Figure 5). The tubular cases of Leptoceridae and Lepidostomatidae (Figure 1ii) used fine sand ($D_{50} = 0.17$ mm) and the mean mass for both taxa was only 0.001 g, less than 1% of the mean Limnephilidae case mass (0.146 g), which used coarser sediment ($D_{50} = 1.12$ mm). Pupal cases of Rhyacophilidae (free living) and Hydropsychidae (net and retreat builder) were substantially heavier (mean mass = 0.83 g) and coarser ($D_{50} = 4$ mm) than all other taxa (Figure 5). Goeridae cases are unusual because they secure coarser particles to the case edges. This resulted in a bimodal sediment distribution (Figure 5). The size distribution of Glossosomatidae cases (saddle cases, $D_{50} = 0.94$ mm) was similar to Limnephilidae (tube cases), but the mean mass of each individual case was less (0.02 g, Table I, Figure 5). Therefore, case-building caddisfly exhibited considerable variability in larvae and case size, particle size distribution and case mass, not just between structure groups (Figure 1) but also between families and species (Table I, Figure 5).

Sediment use by the whole caddisfly community

A diverse caddisfly community was recorded with 24 taxa from 10 families (Table II) and a mean taxonomic richness of 7.4 taxa per sample (minimum 3, maximum 12). Mean abundance was 2250 larvae m^{-2} , but this varied from 180 to 7460 larvae m^{-2} . Caddisfly using mineral sediments for case building accounted for approximately 50% of the taxa present (Table II), but 94% of individual caddisfly larvae recorded. All taxa combined, the average total mineral mass used by case-building caddisfly was 37.57 g m^{-2} , but this varied across the 27 samples, ranging from 3.74 to 138.83 g m^{-2} (Figure 6A).

Table I. Characteristics of larvae and cases for each case-building caddisfly taxonomic group and individual species of Limnephilidae

Family	Larvae		Case				
	Number	Length (mm)	Length (mm)	Weight (g)	\overline{D}_{50} (mm)	\overline{D}_5 (mm)	\overline{D}_{95} (mm)
Glossosomatidae	180 (178)	3.6 (1.04)	4.6 (1.13)	0.020 (0.012)	0.94 (0.24)	0.37 (0.07)	1.82 (0.36)
Goeridae	6 (5)	5.4 (0.93)	5.7 (1.15)	0.027 (0.011)	1.18 (0.22)	0.22 (0.02)	2.10 (0.31)
Sericostomatidae	12 (14)	6.5 (3.59)	8.4 (2.55)	0.012 (0.007)	0.27 (0.03)	0.13 (0.03)	0.53 (0.20)
Lepidostomatidae	18 (15)	3.1 (1.53)	5.4 (0.60)	0.001 (0.0003)	0.17 (0.01)	0.09 (0.004)	0.29 (0.03)
Leptoceridae	21 (23)	1.8 (1.05)	3.5 (0.36)	0.001 (0.0004)	0.17 (0.02)	0.09 (0.01)	0.30 (0.03)
Rhy. and Hyd. Pupae ^a	-	-	-	0.828 (0.68)	4.00 (1.29)	1.34 (0.33)	5.95 (2.24)
Limnephilidae (Average)	4 (3)	16.5 (1.68)	17.2 (2.27)	0.146 (0.050)	1.12 (0.15)	0.46 (0.06)	2.14 (0.26)
<i>Potamophylax cingulatus</i>	-	-	-	0.158 (0.05)	1.12 (0.14)	0.47 (0.05)	2.13 (0.25)
<i>Potamophylax latipennis</i>	-	-	-	0.166 (0.01)	1.31 (0.17)	0.48 (0.05)	2.24 (0.36)
<i>Micropterna sequax</i>	-	-	-	0.112 (0.05)	0.93 (0.37)	0.40 (0.11)	1.77 (0.53)
<i>Halesus radiatus</i>	-	-	-	0.063	1.39	0.51	2.64
<i>Chaetopteryx villosa</i>	-	-	-	0.028	0.57	0.30	1.04

Values shown are the mean of all 27 samples, with standard deviation in brackets (only one incidence of *H. radiatus* and *C. villosa*).

^aPupal cases of Rhyacophilidae and Hydropsychidae larvae.

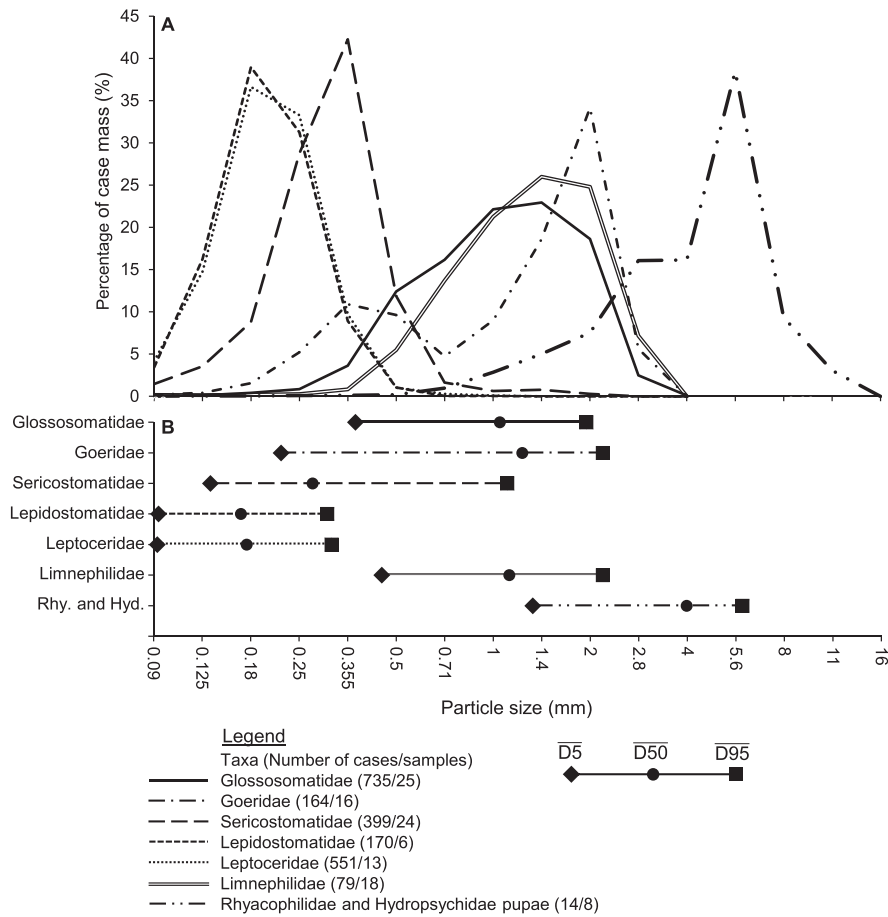


Figure 5. Particle size distribution of the cases of caddisfly taxa. (A) Grain size distribution, averaged across all samples, for the six case-building families and for the pupal cases of Rhyacophilidae and Hydropsychidae combined. Particle size for A refers to the upper limit or passing sieve. (B) Spread ($D_5 - D_{95}$) and median (D_{50}) of the particle size distribution for each taxonomic group, averaged across all samples. In the legend, brackets indicate the total number of cases analysed and the number of samples in which the taxa were present (out of a total of 27).

Due to the differences in case grain size distributions between taxa, the size range of mineral sediment used by the community was broad, from 0.063 to 11 mm (Figure 5). Therefore, caddisfly utilize the entire sand size range as well as fine gravel particles for case construction ($0.063\text{ mm} < \text{sand} < 2\text{ mm}$ gravel; Wentworth, 1922). On average, sediment use was 84% sand and 16% fine gravel. The average particle size distribution of sediment used (Figure 6B) was bimodal with a primary mode at 1–1.4 mm and another mode at 4–5.6 mm. D_{50} was 1.06 mm and the distribution is fairly symmetrical (skew Sk : -0.008) and leptokurtic (kurtosis K : 1.238). The total mass of sediment used by case-building caddisfly (all samples combined) was dominated by Glossosomatidae (64%, Figure 6B), followed by pupae of Rhyacophilidae and Hydropsychidae (15%) and Limnephilidae (11%), with other taxa accounting for less than 5%.

Spatial variability in community sediment use

Kruskal–Wallis tests confirmed that there were no significant differences in the total mass of sediment used between the three sites (Table III, Figure 7A, mean at the upper site = 29.59, mid = 38.02, lower = 34.11 g m^{-2}). However, the size of sediment used was significantly finer at the mid site than at the upper and lower sites for D_{50} , D_{84} and D_{16} (Table III, Figure 7B, mean at the upper site = 1.61, mid = 0.79, lower = 1.11 mm). The upper and lower sites were not significantly different for any grain size parameter (Table III). The mass of sediment used by each taxon varied between sites (Figures 7C–E).

At the upper site, Glossosomatidae and Limnephilidae accounted for a similar proportion of the 0.5–4 mm size fraction while at the mid and lower sites, sediment use was dominated by Glossosomatidae. Both the upper and lower sites have community grain size distributions skewed towards coarser particles due to (1) pupal cases of Rhyacophilidae and Hydropsychidae which dominated sediment use at larger grain sizes (2.8–11 mm), and (2) differences in the size distribution of sediment used by Glossosomatidae.

Relation between abundance and sediment use

The abundance of the caddisfly community (all taxa) was a poor predictor of the mass of sediment used, explaining only 17% of variation (Table IV), meaning that differences in case mass between individuals are important at a community level. When considering each taxon separately, for some, abundance displayed a strong association with sediment mass used (Leptoceridae, $R^2 = 0.79$ and Goeridae, $R^2 = 0.75$), but for others the association was weak (Glossosomatidae, $R^2 = 0.34$). When grouped by site, the association between abundance and sediment use was stronger for some taxa, including Glossosomatidae, which displayed a strong linear association between sediment mass and abundance at the upper and lower sites but not at the mid site (Table IV, Figure 8A). Within each of the three sites, Glossosomatidae larvae built cases of similar mass and consequently Glossosomatidae abundance had a strong association with total Glossosomatidae sediment use.

Table II. Caddisfly taxa found in this study. Taxa are sorted according to their behaviour (after Wiggins, 1996) and use in this study: (1) taxa that used mineral sediments in their cases which were included in sediment analysis and (2) cases that were not analysed for sediment content

	Behaviour group	Family	Genus and Species
(1) Cases included in sediment analysis	Saddle case makers	Glossosomatidae	<i>Agapetus fuscipes</i>
	Tube case makers	Goeridae	<i>Silo pallipes</i>
		Sericostomatidae	<i>Sericostoma personatum</i>
		Lepidostomatidae	<i>Lepidostoma hirtum</i>
		Leptoceridae	<i>Athripsodes sp.</i>
		Limnephilidae	<i>Potamophylax cingulatus</i>
			<i>Potamophylax latipennis</i>
			<i>Micropterna sequax</i>
			<i>Halesus radiatus</i>
			<i>Chaetopteryx villosa</i>
		Empty Limnephilidae cases	
(2) Not included		Unknown ^a	
	Net spinners	Hydropsychidae	<i>Hydropsyche siltalai</i> , <i>pellucidula</i> and <i>instabilis</i> ^b
	Free living	Rhyacophilidae	<i>Rhyacophila dorsalis</i> ^b
	Tube case makers	Leptoceridae	<i>Mystatices longicornis</i>
			<i>Mystatices azurea</i>
		Limnephilidae	<i>Stenophylax sp.</i>
			<i>Limnephilus lunatus</i>
	Purse case makers	Hydroptilidae	<i>Hydroptila sp.</i>
	Net spinners	Hydropsychidae	<i>Hydropsyche siltalai</i>
			<i>Hydropsyche pellucidula</i>
		<i>Hydropsyche instabilis</i>	
	Polycentropidae	<i>Polycentropus flavomaculatus</i>	
		<i>Polycentropus kingi</i>	
	Free living	Rhyacophilidae	<i>Rhyacophila dorsalis</i>

^aCases for which a larva was never found and therefore could not be identified were classified as unknown. Unknown cases were all similar in architecture and are believed to be discarded pupal cases of Leptoceridae species.

^bPupal cases of Hydropsychidae and Rhyacophilidae were identified only to family level but are likely to be the same species found elsewhere.

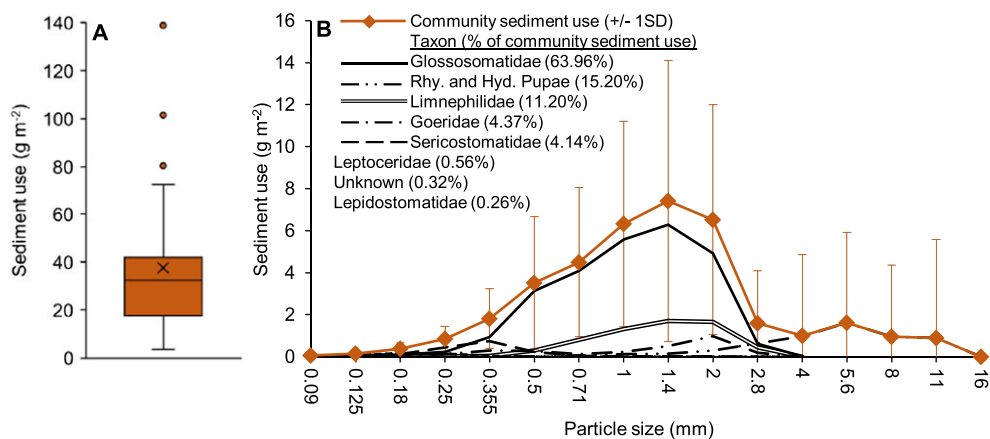


Figure 6. Total sediment use by the case-building caddisfly community and constituent taxa. (A) Boxplot of total community sediment use from all samples. The box denotes the median and interquartile range (inclusive of median), whiskers show the interquartile range multiplied by 1.5 and the mean is indicated by \times (37.57 g m^{-2}). (B) Size distribution of mean mass of sediment use across all sites for the entire case-building caddisfly community and for each taxon, including only those which accounted for $>3\%$ of total sediment use. The standard deviation in community sediment use is also shown and indicates substantial variability between samples. Legend indicates community and taxon with percentage of total sediment use in brackets. Particle size indicates passing sieve. [Colour figure can be viewed at wileyonlinelibrary.com]

However, at the river scale there was considerable inter-site variability in case mass.

In addition to having lower mass, Glossosomatidae cases at the mid site contained finer sediment particles (Figure 8B). Correlations between mean case mass and larvae abundance across all samples revealed that there was a negative association ($R = -0.55$, Figure 8C). However, in samples with low abundance, case mass varied substantially, while at high abundance, mass was always lower. A very strong correlation exists between mean case mass and D_{50} (Figure 8D) and between case mass and mean larvae length (Figure 8E). Overall, the abundance of

most taxa, and particularly Glossosomatidae, is a poor predictor of sediment mass used by this taxa due to within-taxa variations in the mass of cases built and the grain sizes used.

Relation between sediment availability and sediment use

The mean D_{50} of bed material samples was lowest at the mid site (32 mm) and similar between the upper and lower sites (38 and 40 mm, respectively). Considering only the size range

Table III. Results of Kruskal–Wallis and Dunn’s post-hoc tests to determine the variability in sediment use by caddisfly larvae between sites (upper, mid and lower) relative to within-site variability

Parameter	Kruskal–Wallis (K)	Dunn’s (Z)		
		lower–mid	mid–upper	upper–lower
D_{50}	16.5***	3.44***	–3.59***	–0.15
D_{16}	7.3*	1.96*	–2.58**	–0.62
D_{84}	13.5**	2.94**	–3.39***	–0.45
Mass	4.0	–1.34	1.96*	0.62

Chi-squared values reported for Kruskal–Wallis and Z-statistic for Dunn’s test. For both, significance is indicated by * $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$.

used by case-building caddisfly in this study, the average mass of bed sediment availability increased with grain size (Figure 9A). Some samples displayed a bimodal distribution with a second peak in the 0.25–0.5 mm size range, particularly at the mid site. Sediment use was also skewed towards finer sediment at the mid site (Figure 9B). Sediment availability for all size fractions greatly exceeded the mass of sediment used by caddisfly larvae, resulting in a low percentage used overall (Figure 9C). As an average across all samples, the percentage of sediment use peaked at the 1–1.4 mm size range with a mean of 2.99% (matching the mode of sediment use, Figure 9 B). In this size fraction, the percentage used ranged considerably from 0.25% up to 24.86% of available sediment. Therefore, sediment of all grain sizes was abundant and available

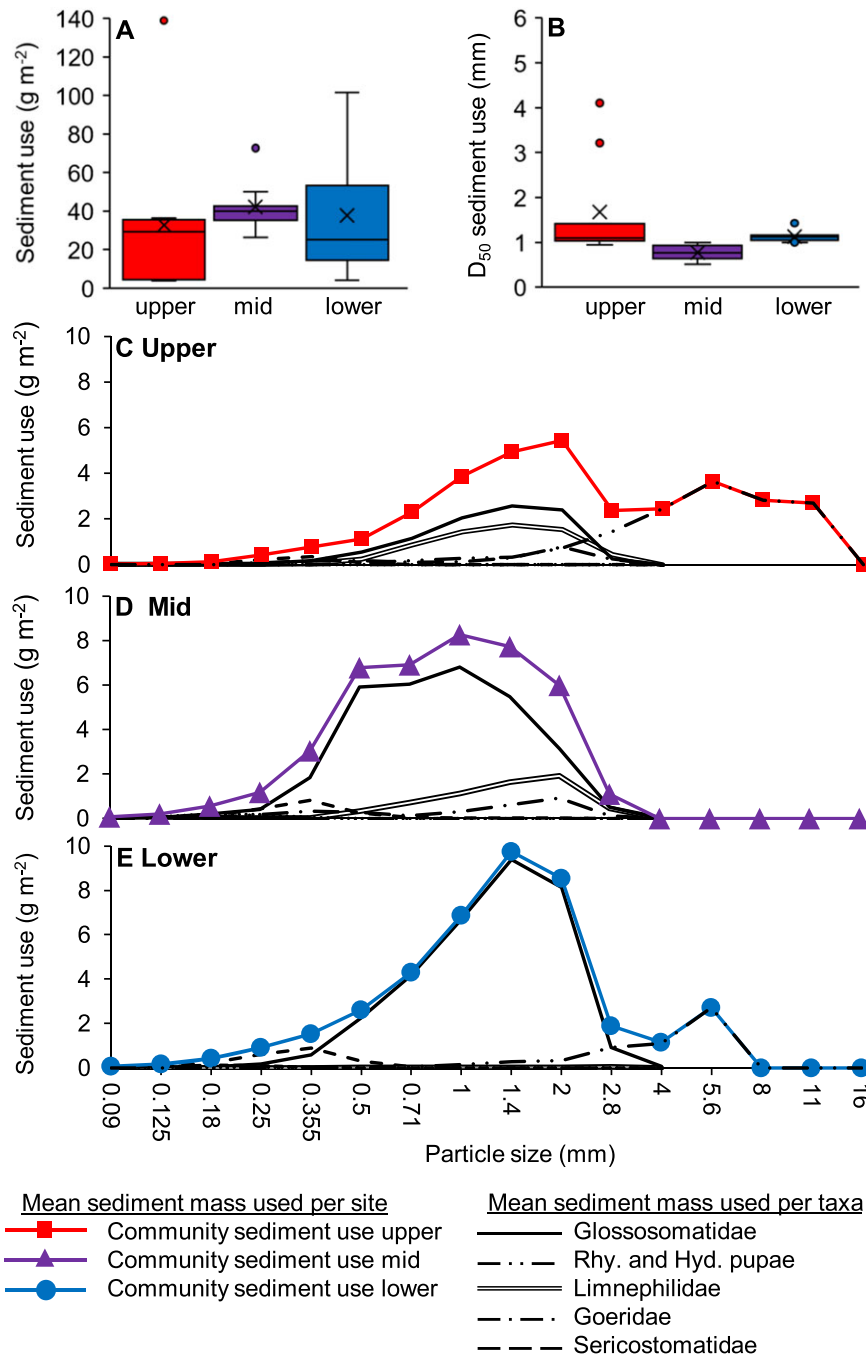


Figure 7. Variability in sediment use between sites (upper, mid and lower). (A) Boxplot showing the mass of sediment used by the caddisfly community at each site. (B) Boxplot showing the D_{50} of sediment used at each site. For both boxplots, the box denotes the median and interquartile range (inclusive of median), whiskers show the interquartile range multiplied by 1.5 and the mean is indicated by \times . (C–E) Particle size distribution of mean total sediment use for the caddisfly community and constituent taxa, for each site. Only taxa which account for more than 3% of total sediment use are shown. Particle size indicates passing sieve. [Colour figure can be viewed at wileyonlinelibrary.com]

Table IV. R^2 values for linear regression between abundance (independent) and the mass of sediment used (dependent) for each taxon across all samples (whole river) and for each site (upper, mid and lower) independently. The regression was also conducted for the whole caddisfly community

	All	Upper	Mid	Lower
Glossosomatidae	0.34(25)**	0.71(7)*	0.15(9)	0.99(9)***
Goeridae	0.75(16)***	0.80(6)*	0.75(9)**	(1)
Sericostomatidae	0.38(24)**	0.05(6)	0.78(9)**	0.25(9)
Lepidostomatidae	0.52(6)	(0)	(0)	0.52(6)
Leptoceridae	0.79(13)***	(2)	0.84(9)***	(2)
Limnephilidae	0.55(18)***	0.25(9)	0.93(8)***	(1)
Community	0.17(27)*	0.09(9)	0.14(9)	0.97(9)***

The number of samples included in each regression (n) is shown in brackets (regression not conducted when $n < 5$). Significance is indicated by * $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$.

to taxa at all sites. Despite this, the use of sediment by both the case-building caddisfly community and Glossosomatidae was skewed towards finer sediment at the mid site where this sediment was more abundant.

Discussion

Sediment use by individual taxa and the case-building caddisfly community

Caddisfly are a widespread, abundant and diverse group of invertebrates. Caddisfly larvae build complex structures from fine sediment and silk (Wiggins, 2004). Whilst case building by individual caddisfly taxa has received attention from an ecological perspective, this is the first study to focus on the granulometry of cases from a geomorphic perspective and to

measure sediment use (mass and grain sizes) by a range of taxa and for entire communities.

The caddisfly community of Wood Brook was diverse, both in terms of species richness and the design of silk structures, with all five categories recorded (Table II, Figure 1). About half of taxa were case-building caddisfly utilizing mineral sediments, but due to their high abundance they accounted for over 90% of individuals. This suggests that if the mechanisms identified in Figure 2 are significant, case-building caddisfly could be important zoogeomorphic engineers in this stream. The considerable variability in the size of sediment used by different taxa in this study (Figure 5) probably reflects differences in the function of the larval cases (Otto and Svensson, 1980; Wiggins, 2004; Boyero *et al.*, 2006). For example, the fine grains used in Sericostomatidae cases ($D_{50} = 0.27$, Table I) result in smooth, tapered cases, which may facilitate burrowing. Most taxa in this study used predominantly mineral sediments (Table II), which require a much greater investment of energy than organic cases (Otto and Svensson, 1980). Consequently, using mineral sediment must be advantageous to larvae in gravel-bed rivers, perhaps providing ballast, protection from crushing by moving sediment and reduced risk of predation (Webster and Webster, 1943; Statzner and Holm, 1989; Otto and Johansson, 1995). The results of this study demonstrate that both the size and magnitude of mineral sediment used are dependent on the caddisfly taxa present, and consequently any geomorphic effect is likely to vary between taxa. As a result of the diversity in grain size used by different taxa, the caddisfly community used sediment from 0.063 to 11 mm in diameter (Figure 6B). Consequently, caddisfly have the potential to directly affect the distribution and mobility of a broad sediment size range. However, sediment use was predominantly coarse sand and fine gravel (Figure 6B), which are important size fractions geomorphologically, as they are often the most mobile bed material size fractions (Jackson and Beschta, 1984; Ashworth and Ferguson, 1989; Kuhnle, 1993).

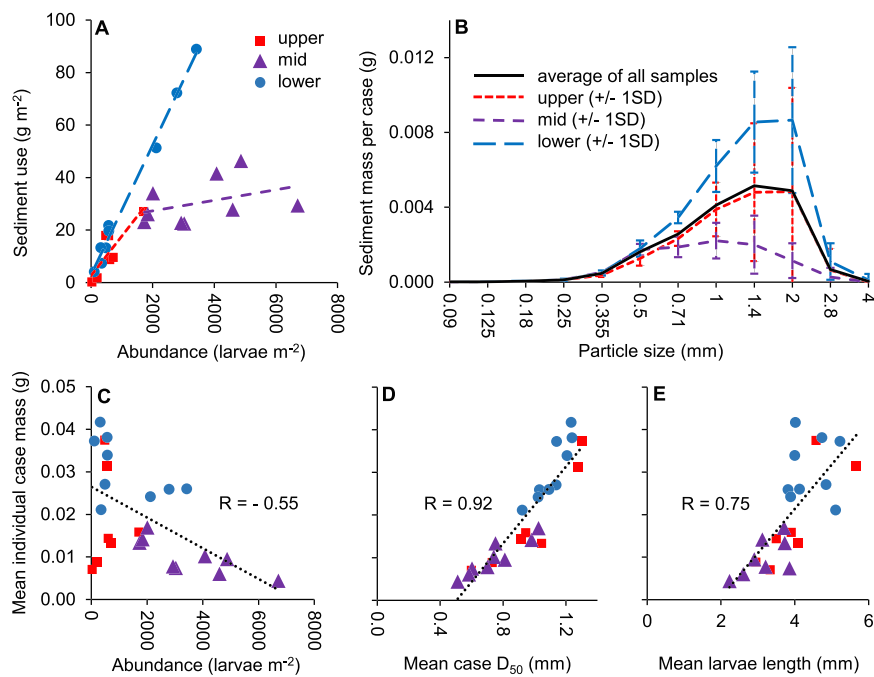


Figure 8. Variability in sediment use by *A. fuscipes* (Glossosomatidae) individuals between sites. (A) Plot of the relation between abundance and sediment use by this taxon, giving the R^2 values in Table IV. Within each site, abundance is a good indicator of sediment mass used, but for all sites combined it is poor. (B) Particle size distribution for individual *A. fuscipes* cases as a mean of all samples and for each site independently. Particle size refers to passing sieve. (C–E) Correlation plots between mass of an individual *A. fuscipes* case and variables expected to explain spatial variability in case mass: (C) mean *A. fuscipes* abundance; (D) mean case D_{50} ; and (E) mean larvae length. [Colour figure can be viewed at wileyonlinelibrary.com]

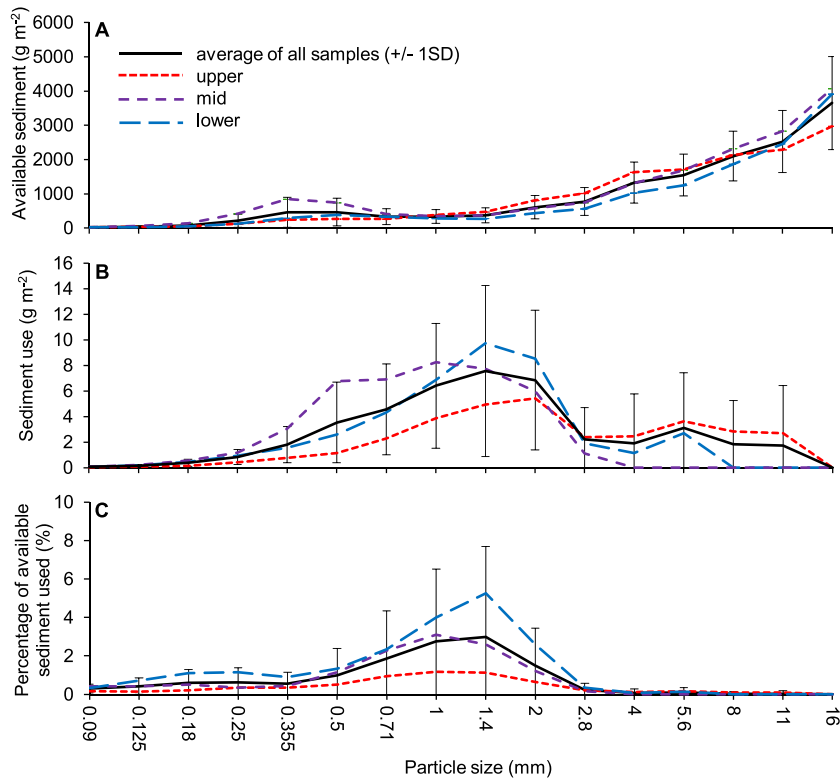


Figure 9. Sediment use in relation to available sediment in the river bed. Particle size distributions shown as a mean for the river as a whole (with standard deviation) and each site independently. (A) Mass of bed sediment available to case-building caddisfly. (B) Mass of sediment used by case-building caddisfly communities. (C) Percentage of available sediment that is used by case-building caddisfly. Note that due to the use of 0.1 mm diameter net, the quantity of sediment available and percentage of sediment used are not accurate below 0.125 mm. Particle size indicates passing sieve. [Colour figure can be viewed at wileyonlinelibrary.com]

Sediment use by key taxa and potential zoogeomorphological importance

Despite the abundance and diversity of case-building caddisfly larvae in Wood Brook, several taxa are of particular interest. Glossosomatidae accounted for over 60% of sediment use and were by far the most abundant taxa (up to 6710 larvae m^{-2}). Glossosomatidae cases are built from sediment particles accessible to them on the bed surface (Marchant, 1988; Becker, 2001; Statzner, 2011; Hansell, 1968b) and they may therefore have a disproportionate effect on sand availability at the bed surface. In particular, Glossosomatidae usually reside on the exposed upper surfaces of larger gravel particles where the flow of water facilitates respiration (Figure 3; Nijboer, 2004; Becker, 2005; Morris and Hondzo, 2013; Morris *et al.*, 2015). Glossosomatidae therefore redistribute surface particles vertically, potentially increasing the exposure of constituent sand grains by transporting them from interstitial spaces and sheltered patches onto the upper surfaces of larger cobbles. This study showed that Glossosomatidae used on average 25.95 but up to 88.92 $g m^{-2}$ of sand. On average, this represents a vertical redistribution of 1 kg of sand for every 40 m^2 of occupied river bed.

Despite their low abundance in this study, Rhyacophilidae and Hydropsychidae pupal cases were constructed from large particles and, by mass, therefore accounted for 15% of the overall sediment used by case-building caddisfly (Figure 6B) but nearly 50% at the upper site (Figure 7C). Statzner *et al.* (2005) and Statzner (2011) measured sediment use by these taxa in the River Furan, France and found them to use substantial quantities of sediment (up to $\sim 3 kg m^{-2}$). They found considerably higher abundances of pupal cases (250 m^{-2} for *Hydropsyche siltalai*; Statzner, 2011) compared to the average

of 3 m^{-2} in this study. This is probably due to both higher abundances of larvae in the River Furan than Wood Brook, and the time of year sampled. Statzner *et al.* (2005) sampled in June and August, while our study was conducted in April, prior to pupation for most species (Wallace *et al.*, 1990). In situations where pupal cases of free-living and net-building taxa are abundant (>1000 larvae m^{-2} ; Cardinale *et al.*, 2004), sediment use is expected to be skewed towards coarser particles. During pupation, these taxa may have geomorphic effects by modifying the hydraulic properties of coarse sand and gravel (Figure 2A). Pupal cases are usually attached to more stable particles (unlike mobile cases) and consequently the mobility of constituent sediment is likely to be reduced. Cases may also reduce the mobility of the larger particles they are attached to (Figure 1i; Nunokawa *et al.*, 2008).

Spatial variability in community sediment use and the distribution of case-building caddisfly taxa

Both the size and mass of sediment used were spatially variable at the river scale (Figure 7), even within this relatively narrow range of environmental conditions (riffle habitats in ~ 3.6 km of stream; Figure 1). There was considerable variability in the mass of sediment used (4–139 $g m^{-2}$) but this was not structured by site (Figure 7A). This is potentially related to the patchy distribution of benthic invertebrates in rivers (Pringle *et al.*, 1988); a result of habitat variability and biological controls (Cummins and Lauff, 1969; Southwood, 1977). The size of sediment used by the caddisfly community was statistically lower at the mid site than at the upper and lower sites (Table III, Figure 7B). This is interesting because the greatest environmental difference would be expected between the upper and lower

sites (Vannote *et al.*, 1980; Rice and Church, 1998). Nevertheless, the mid site had the lowest slope, bed sediment D_{50} and water depth, suggesting that it was distinct from the other sites in terms of habitat characteristics.

The greater use of fine sediments by the caddisfly community at the mid site is the result of both the absence of Rhyacophilidae and Hydropsychidae pupal cases and the use of finer sediments by Glossosomatidae larvae (Figure 7D). The upper site had the coarsest D_{50} where Rhyacophilidae and Hydropsychidae pupae used a greater proportion of coarse-sediment grains, resulting in a bimodal sediment distribution with a primary peak in the coarse sand range and a second peak of fine gravel for the site (4–5.6 mm, Figure 7C). The upper site had, on average, the lowest abundance of Glossosomatidae and the mass of each case was very variable (Figure 8C). This could be due to shading by riparian vegetation reducing the availability of their algae food source (Mcneely and Power, 2007) and increasing inputs of allochthonous organic matter, favouring shredders (Vannote *et al.*, 1980), such as the Limnephilidae larvae present.

Sediment use in relation to the abundance of taxa and availability of sediment

The weak association between the abundance of the whole case-building caddisfly community and the total mass of sediment used (Table IV) is unsurprising because the mass of cases varied by several orders of magnitude between taxa (Table I). Therefore, to achieve a 0.85 g increase in sediment use would require just one Rhyacophilidae or Hydropsychidae pupal case but 850 Leptoceridae cases (0.001 g each, Table I). Interestingly, the abundance of many individual taxa was also only weakly related to sediment mass used at the river scale (Table IV). This indicates that within-taxa differences in case mass between samples explained more variability in total sediment use than the abundance of that taxa. In this study, differences in case mass between individuals of the same taxa may be explained to some extent by the presence of multiple instars of larvae, which were combined for grain size analysis. Furthermore, within the Limnephilidae family, the presence of multiple species (with different case designs) and differing use of organic material (Table I) also explains this weak association.

A. fuscipes (Glossosomatidae) cases had lower mass and used finer sediment at the mid site than the upper and lower sites (Figures 8B and C). This difference was associated with smaller *A. fuscipes* larvae (Figure 8E) and less developed (early instar) larvae are likely to build smaller cases with lower mass. The greater abundance of *A. fuscipes* at this site may increase competition for resources and limit larvae development. Alternatively, the greater availability of fine sediment at the mid site (Figure 9A) may cause larvae to build cases which contain more fine sediment and consequently weigh less (Figure 8D). At the river scale only a small percentage of available sediment was used (greatest at the 1–1.4 mm fraction where mean percentage used = 2.99%; Figure 9C) and therefore, it is unlikely that taxa are limited in their case design by access to their preferred grain sizes. Glossosomatidae larvae, however, typically use easily accessible sediment (Becker, 2001) and therefore, while specific size fractions are not limiting at any site, the greater availability of finer fractions at the mid site may explain the lower D_{50} of *A. fuscipes* cases here.

Overall, the percentage of available sediment used in this study is considerably lower than that of Statzner (2011); 2.99% compared to 15–25% for the dominant sediment size. This is likely to be at least partly due to a difference in sampling

technique. Statzner (2011) sampled surface sediments and the first subsurface layer and, whilst they do not specify a precise depth, this is unlikely to be as deep as the 5 cm sampled in this study. In addition, Wood Brook drains agricultural lands and consequently contains a high quantity of fine sediment. There is, however, considerable variability in the proportion of sediment used, up to 25% of the 1–1.4 mm size fraction was used at one lower sample. This is explained by a low quantity of fine sediment in this sample, rather than high caddisfly use of sediment. Therefore, in rivers with lower quantities of fine sediment, such as mountain streams (Church, 2010) or downstream of reservoirs (Brandt, 2000), case-building caddisfly may use substantial proportions of the available fine sediment.

Limitations

Quantifying sediment use by a caddisfly community presented multiple methodological challenges. Determining the size distribution of very small masses of sediment (as low as 0.01 g) was difficult, but the use of small-diameter sieves (38 mm) reduced sediment loss and allowed comparison with sieved bed sediment samples (unlike photographic methods; Statzner *et al.*, 2009). Quantifying sediment use for enough individuals and sites necessitated combining taxa of different instars within each sample. However, sediment distributions are known to change with larvae development, which means that our grain size estimates are broader than many in the literature (e.g. Tolkamp, 1980). Last, the size distribution of Rhyacophilidae and Hydropsychidae pupal cases is likely to be less accurate than those for the other taxa, due to the low number analysed and the combination of two families, known to differ in pupal case design (Statzner *et al.*, 2005). Nevertheless, within these constraints, the results present an important step towards understanding the magnitude of sediment use by case-building caddisfly and the effect of cases on fine-sediment sorting and transport in rivers.

Conclusions

This study quantifies sediment use by the case-building caddisfly community from riffle habitats in a small stream. In doing so it extends research on both the ecology of case building and the zoogeomorphic role of caddisfly in rivers (Cardinale *et al.*, 2004; Johnson *et al.*, 2009; Albertson *et al.*, 2014b). Considerable variability was found in the mass and size distribution of cases between caddisfly taxa at every taxonomic level, between (1) silk structure design groups (Figure 1), (2) families (Figure 5), (3) species (Table I) and (4) individuals of the same species (Table IV, Figure 8). Case mass ranged from 0.001 to 0.85 g and D_{50} from 0.17 to 4 mm. Therefore, the mechanisms and extent of caddisfly zoogeomorphic effects are likely to vary between taxa. Community sediment use was on average 37.57 g m^{-2} , and was 84% sand and 16% fine gravel. *A. fuscipes* (Glossosomatidae) accounted for over 60% of sediment use, Rhyacophilidae and Hydropsychidae (15%) and Limnephilidae (11%). These taxa should therefore be the focus of future research concerning the mechanisms of zoogeomorphic impact outlined in Figure 2.

Due to considerable variability in case mass between sites, abundance was weakly related to sediment use for the caddisfly community and for most taxa at the river scale. In this stream, caddisfly used a small percentage of the total sediment available to them for all size fractions (on average <3%), suggesting that access to preferred sediment was not a limiting

factor in case design. Nevertheless, *A. fuscipes* cases varied in case design between sites, with a lower D_{50} at the mid site where finer sediment was more readily available. Intraspecific variability is rarely considered in zoogeomorphology (Albertson and Allen, 2015). This raises important questions about the replicability of localized biogeomorphic studies which consider only a few individuals, or individuals from a singular site.

Despite variability in community composition, abundance and case architecture, the caddisfly community used sediment in all 27 samples. Consequently, within the riffle habitats studied, sediment use by the caddisfly community is not constrained in space by the presence of a particular species, abundance or sediment availability. It follows that if cases do have geomorphic effects (mechanisms in Figure 2), then these are likely to be widespread across a range of habitats in which case-building taxa are known to be common. Furthermore, individual taxa appear to be adaptable in their use of sediment. The distribution of *A. fuscipes*, in particular, is not limited by the availability of a specific range of grain sizes and consequently may have widespread zoogeomorphic effects.

Small streams, such as Wood Brook, make up 70–80% of the total channel length of river networks and are an important but often neglected waterbody in catchment geomorphology research (Downing, 2012; Wohl, 2017). Caddisfly are abundant in most small streams and rivers and consequently, their zoogeomorphic role could be widespread. Future work is required to characterize sediment use by caddisfly larvae at larger spatial and temporal scales, as well as to quantify the effects of case building on the mobility of sediment particles (Figure 2). This study provides insights into the size and quantity of sediment use by case-building caddisfly, essential to guide further research on caddisfly zoogeomorphology.

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References

- Albertson LK, Allen DC. 2015. Meta-analysis: abundance, behavior, and hydraulic energy shape biotic effects on sediment transport in streams. *Ecology* **96**: 1329–1339. <https://doi.org/10.1890/13-2138.1>.
- Albertson LK, Sklar LS, Pontau P, Dow M, Cardinale BJ. 2014a. A mechanistic model linking insect (Hydropsychidae) silk nets to incipient sediment motion in gravel-bedded streams. *Journal of Geophysical Research: Earth Surface* **119**: 1833–1852. <https://doi.org/10.1002/2013JF003024>.
- Albertson LK, Cardinale BJ, Sklar LS. 2014b. Non-additive increases in sediment stability are generated by macroinvertebrate species interactions in laboratory streams. *PLoS One* **9**: 1–11. <https://doi.org/10.1371/journal.pone.0103417>.
- Albertson LK, Sklar LS, Cooper SD, Cardinale BJ. 2019. Aquatic macroinvertebrates stabilize gravel bed sediment: a test using silk net-spinning caddisflies in semi-natural river channels. *PLoS One* **14**: e0209087. <https://doi.org/10.1371/journal.pone.0209087>.
- Ashworth PJ, Ferguson RI. 1989. Size-selective entrainment of bed load in gravel bed streams. *Water Resources Research* **25**: 627–634. <https://doi.org/10.1029/WR025i004p00627>.
- Becker G. 2001. Larval size, case construction and crawling velocity at different substratum roughness in three scraping caddis larvae. *Archiv für Hydrobiologie* **151**: 317–334. <https://doi.org/10.1127/archiv-hydrobiol/151/2001/317>.
- Becker G. 2005. Life cycle of *Agapetus fuscipes* (Trichoptera, Glossosomatidae) in a first-order upland stream in central Germany. *Limnologia* **35**: 52–60. <https://doi.org/10.1016/j.limno.2005.01.003>.
- Bergey EA, Ward JV. 1989. Upstream–downstream movements of aquatic invertebrates in a Rocky Mountain stream. *Hydrobiologia* **185**: 11–82. <https://doi.org/10.1007/BF00006069>.
- Boyero L, Rincón PA, Bosch J. 2006. Case selection by a limnephilid caddisfly [*Potamophylax latipennis* (Curtis)] in response to different predators. *Behavioural Ecology and Sociobiology* **59**: 364–372. <https://doi.org/10.1007/s00265-005-0059-y>.
- Brandt SA. 2000. Classification of geomorphological effects downstream of dams. *Catena* **40**: 375–401. [https://doi.org/10.1016/S0341-8162\(00\)00093-X](https://doi.org/10.1016/S0341-8162(00)00093-X).
- Brown AV, Brussock PP. 1991. Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia* **220**: 99–108. <https://doi.org/10.1007/BF00006542>.
- Brown SA, Ruxton GD, Humphries S. 2004. Physical properties of *Hydropsyche siltalai* (Trichoptera) net silk. *Journal of the North American Benthological Society* **23**: 771–779. [https://doi.org/10.1899/0887-3593\(2004\)023<0771:PPHST>2.0.CO;2](https://doi.org/10.1899/0887-3593(2004)023<0771:PPHST>2.0.CO;2).
- Butler DR, Malanson GP. 2005. The geomorphic influences of beaver dams and failures of beaver dams. *Geomorphology* **71**: 48–60. <https://doi.org/10.1016/j.geomorph.2004.08.016>.
- Buxton TH, Buffington JM, Yager EM, Hassan MA, Fremier AK. 2015. The relative stability of salmon redds and unspawned streambeds. *Water Resources Research* **51**: 6074–6092. <https://doi.org/10.1002/2015WR016908>.
- Cadée GC. 2001. Sediment dynamics by bioturbating organisms. In *Ecological Comparisons of Sedimentary Shores*, Reise K (ed), Vol. **151**. Springer: Berlin; 127–148. *Ecological Studies (Analysis and Synthesis)*.
- Cardinale BJ, Gelmann ER, Palmer MA. 2004. Net spinning caddisflies as stream ecosystem engineers: the influence of *Hydropsyche* on benthic substrate stability. *Functional Ecology* **18**: 381–387. <https://doi.org/10.1111/j.0269-8463.2004.00865.x>.
- Church M. 2010. Gravel-bed rivers. In *Sediment Cascades: An Integrated Approach*, Burt TP, Allison RJ (eds). Wiley: Chichester; 241–269.
- Corenblit D, Tabacchi E, Steiger J, Gurnell AM. 2007. Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. *Earth-Science Reviews* **84**: 56–86. <https://doi.org/10.1016/j.earscirev.2007.05.004>.
- Cotton JA, Wharton G, Bass JAB, Heppell CM, Wotton RS. 2006. The effects of seasonal changes to in-stream vegetation cover on patterns of flow and accumulation of sediment. *Geomorphology* **77**: 320–334. <https://doi.org/10.1016/j.geomorph.2006.01.010>.
- Cummins KW, Lauff GH. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. *Hydrobiologia* **34**: 145–181. <https://doi.org/10.1007/BF00141925>.
- De Gispert Q, Alféns G, Bonada N. 2018. Grain size selection in case building by the mountain cased-caddisfly species *Potamophylax latipennis* (Curtis, 1834). *XVII Congress of the Iberian Association of Limnology Santander*, 6–11 July.
- De Moor FC, Ivanov VD. 2008. Global diversity of caddisflies (Trichoptera: Insecta) in freshwater. *Hydrobiologia* **595**: 393–407. <https://doi.org/10.1007/s10750-007-9113-2>.
- De Nadaï-Monoury E, Lecerf A, Canal J, Buisson L, Laffaille P, Gilbert F. 2013. A cost-effective method to quantify biological surface sediment reworking. *Hydrobiologia* **713**: 115–125. <https://doi.org/10.1007/s10750-013-1497-6>.
- Downing J. 2012. Global abundance and size distribution of streams and rivers. *Inland Waters* **2**: 229–236. <https://doi.org/10.5268/IW-2.4.502>.
- EDINA. 2018. *1:25 000 Scale Colour Raster* [NTF geospatial data]. Updated: December 2017, Ordnance Survey (GB). Using: EDINA Digimap Ordnance Survey Service. Available online at: <http://digimap.edina.ac.uk/> (accessed 29 March 2018).

- Edgington JM, Hildrew AG. 1995. *Caseless Caddis Larvae of the British Isles with Notes on their Ecology*, 2nd edn. Freshwater Biological Association: Ambleside.
- Erman NA. 1986. Movements of self-marked caddisfly larvae, *Chymda centralis* (Trichoptera: Limnephilidae), in a Sierran spring stream, California, U.S.A. *Freshwater Biology* **16**: 455–464. <https://doi.org/10.1111/j.1365-2427.1986.tb00988.x>.
- Everall NC, Johnson MF, Wood P, Farmer A, Wilby RL, Measham N. 2017. Comparability of macroinvertebrate biomonitoring indices of river health derived from semi-quantitative and quantitative methodologies. *Ecological Indicators* **78**: 437–448. <https://doi.org/10.1016/j.ecolind.2017.03.040>.
- Fremier AK, Yanites BJ, Yager EM. 2017. Sex that moves mountains: the influence of spawning fish on river profiles over geologic timescales. *Geomorphology* **305**: 163–172. <https://doi.org/10.1016/j.geomorph.2017.09.033>.
- Gottesfeld AS, Hassan MA, Tunnicliffe JF, Poirier RW. 2004. Sediment dispersion in salmon spawning streams: the influence of floods and salmon redd construction. *Journal of the American Water Resources Association* **40**: 1071–1086. <https://doi.org/10.1111/j.1752-1688.2004.tb01068.x>.
- Greenwood MT, Bickerton MA, Petts GE. 2001. Assessing adult Trichoptera communities of small streams: a case study from Charnwood Forest, Leicestershire, UK. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**: 93–107. <https://doi.org/10.1002/aqc.435>.
- Gurnell AM. 1998. The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography* **22**: 167–189. <https://doi.org/10.1191/030913398673990613>.
- Gurnell AM. 2014. Plants as river system engineers. *Earth Surface Process and Landforms* **39**: 4–25. <https://doi.org/10.1002/esp.3397>.
- Hansell MH. 1968a. The house building behaviour of the caddis-fly larva *Silo Pallipes Fabricius*: II. Description and analysis of the selection of small particles. *Animal Behaviour* **16**: 562–577. [https://doi.org/10.1016/0003-3472\(68\)90052-3](https://doi.org/10.1016/0003-3472(68)90052-3).
- Hansell MH. 1968b. The selection of house building materials by the caddis-fly larva, *A. fuscipes* Curtis. *Revue du Comportement Animal* **2**: 91–102.
- Hart DD, Resh VH. 1980. Movement patterns and foraging ecology of a stream caddisfly larva. *Canadian Journal of Zoology* **58**: 1174–1185. <https://doi.org/10.1139/z80-162>.
- Harvey GL, Henshaw AJ, Moorhouse TP, Clifford NJ, Holah H, Grey J, Macdonald DW. 2014. Invasive crayfish as drivers of fine sediment dynamics in rivers: field and laboratory evidence. *Earth Surface Processes and Landforms* **39**: 259–271. <https://doi.org/10.1002/esp.3486>.
- Hassan MA, Gottesfeld AS, Montgomery DR, Tunnicliffe JF, Clarke GKC, Wynn G, Jones-Cox H, Poirier R, Macisaac E, Herunter H, Macdonald SJ. 2008. Salmon-driven bed load transport and bed morphology in mountain streams. *Geophysical Research Letters*: 35. <https://doi.org/10.1029/2007GL032997>.
- Huser BJ, Bajer PG, Chizinski CJ, Sorensen PW. 2016. Effects of common carp (*Cyprinus carpio*) on sediment mixing depth and mobile phosphorus mass in the active sediment layer of a shallow lake. *Hydrobiologia* **763**: 23–33. <https://doi.org/10.1007/s10750-015-2356-4>.
- Ikeda H, Iseya F. 1988. *Experimental study of heterogeneous sediment transport*, Environmental Research Center Paper No. 12. University of Tsukuba: Japan.
- Jackson JK, Mcelravvy EP, Reshy VH. 1999. Long-term movements of self-marked caddisfly larvae (Trichoptera: Sericostomatidae) in a California coastal mountain stream. *Freshwater Biology* **42**(3): 525–536. <https://doi.org/10.1046/j.1365-2427.1999.00503.x>.
- Jackson WL, Beschta RL. 1984. Influences of increased sand delivery on the morphology of sand and gravel channels. *Water Resources Bulletin* **20**: 527–533. <https://doi.org/10.1111/j.1752-1688.1984.tb02835.x>.
- Johnson MF, Reid I, Rice SP, Wood PJ. 2009. Stabilization of fine gravels by net-spinning caddisfly larvae. *Earth Surface Processes and Landforms* **34**: 413–423. <https://doi.org/10.1002/esp.1750>.
- Johnson MF, Rice SP, Reid I. 2010. Topographic disturbance of subaqueous gravel substrates by signal crayfish (*Pacifastacus leniusculus*). *Geomorphology* **123**: 269–278. <https://doi.org/10.1016/j.geomorph.2010.07.018>.
- Krantzberg G. 1985. The influence of bioturbation on physical, chemical and biological parameters in aquatic environments: a review. *Environmental Pollution* **39**: 99–122. [https://doi.org/10.1016/0143-1471\(85\)90009-1](https://doi.org/10.1016/0143-1471(85)90009-1).
- Kuhnle RA. 1993. Fluvial transport of sand and gravel mixtures with bimodal size distributions. *Sedimentary Geology* **85**: 17–24. [https://doi.org/10.1016/0037-0738\(93\)90072-D](https://doi.org/10.1016/0037-0738(93)90072-D).
- Lancaster J, Buffin-Bélanger T, Reid I, Rice S. 2006. Flow and substratum-mediated movement by a stream insect. *Freshwater Biology* **51**: 1053–1069. <https://doi.org/10.1111/j.1365-2427.2006.01554.x>.
- Limm MP, Power ME. 2011. The caddisfly *Dicosmoecus gilvipes*: making a case for a functional role. *Journal of the North American Benthological Society* **30**: 485–492. <https://doi.org/10.1899/10-028.1>.
- Marchant R. 1988. Vertical distribution of benthic invertebrates in the bed of the Thomson River, Victoria. *Australian Journal of Marine and Freshwater Research* **39**: 775–784. <https://doi.org/10.1071/MF9880775>.
- Mcneely C, Power ME. 2007. Spatial variation in caddisfly grazing regimes within a northern California watershed. *Ecology* **88**: 2609–2619. <https://doi.org/10.1890/06-0796.1>.
- Mermillod-Blondin F, Rosenberg R. 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. *Aquatic Sciences* **68**: 434–442. <https://doi.org/10.1007/s00027-006-0858-x>.
- Mermillod-Blondin F, Gaudet JP, Gérino M, Desrosiers G, Creuzé des Châtelliers M. 2003. Influence of macroinvertebrates on physicochemical and microbial processes in hyporheic sediments. *Hydrological Processes* **17**: 779–794. <https://doi.org/10.1002/hyp.1165>.
- Mermillod-Blondin F, Gaudet JP, Gerino M, Desrosiers G, Jose J, Creuzé des Châtelliers M. 2004. Relative influence of bioturbation and predation on organic matter processing in river sediments: a microcosm experiment. *Freshwater Biology* **49**: 895–912. <https://doi.org/10.1111/j.1365-2427.2004.01233.x>.
- Montgomery DR, Piégay H. 2003. Editorial. Wood in rivers: interactions with channel morphology and processes. *Geomorphology* **51**: 1–5. [https://doi.org/10.1016/S0169-555X\(02\)00322-7](https://doi.org/10.1016/S0169-555X(02)00322-7).
- Moore JW. 2006. Animal ecosystem engineers in streams. *Bioscience* **56**: 237–246. [https://doi.org/10.1641/0006-3568\(2006\)056\[0237:AEIS\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)056[0237:AEIS]2.0.CO;2).
- Morris MWL, Hondzo M. 2013. Double-averaged rough-bed open-channel flow with high Glossosoma (Trichoptera: Glossosomatidae) abundance. *Environmental Fluid Mechanics* **13**: 257–278. <https://doi.org/10.1007/s10652-012-9265-0>.
- Morris M, Mohammadi MH, Day S, Hondzo M, Sotiropoulos F. 2015. Prediction of Glossosoma biomass spatial distribution in Valley Creek by field measurements and a three-dimensional turbulent open-channel flow model. *Water Resources Research* **51**: 1457–1471. <https://doi.org/10.1002/2014WR015887>.
- Murphy JF, Davy-Bowker J. 2005. Spatial structure in lotic macroinvertebrate communities in England and Wales: relationship with physicochemical and anthropogenic stress variables. *Hydrobiologia* **534**: 151–164.
- Naimen RJ, Johnston CA, Kelley JC. 1988. Alteration of North American streams by beaver. *Bioscience* **38**: 753–762. <https://doi.org/10.2307/1310784>.
- Nijboer R. 2004. The ecological requirements of *Agapetus fuscipes* Curtis (Glossosomatidae), a characteristic species in unimpacted streams. *Limnologia* **34**: 213–223. [https://doi.org/10.1016/S0075-9511\(04\)80046-X](https://doi.org/10.1016/S0075-9511(04)80046-X).
- Nunokawa M, Gomi T, Negishi JN, Nakahara O. 2008. A new method to measure substrate coherent strength of *Stenopsyche marmorata*. *Landscape and Ecological Engineering* **4**: 125–131. <https://doi.org/10.1007/s11355-008-0044-5>.
- Okano J, Kikuchi E. 2012. Effect of current velocity and case adaptations on the distribution of caddisfly larvae (Glossosoma, Trichoptera). *Limnology* **13**: 37–43. <https://doi.org/10.1007/s10201-011-0353-5>.

- Okano J, Sasaki O, Kano H. 2016. The effects of surface roughness of sediment particles on the respiration of case-bearing caddisfly larvae. *Freshwater Science* **35**: 611–618. <https://doi.org/10.1086/685713>.
- Otto C, Johansson A. 1995. Why do some caddis larvae in running waters construct heavy, bulky cases? *Animal Behaviour* **49**: 473–478. <https://doi.org/10.1006/anbe.1995.0061>.
- Otto C, Svensson B. 1980. The significance of case material selection for the survival of caddis larvae. *Journal of Animal Ecology* **49**: 855–865. <https://doi.org/10.2307/4231>.
- Pledger AG, Rice SP, Millett J. 2014. Reduced bed material stability and increased bedload transport caused by a foraging fish: a flume study with juvenile Barbel (*Barbus barbus*). *Earth Surface Processes and Landforms* **39**: 1500–1513. <https://doi.org/10.1002/esp.3592>.
- Pledger AG, Rice SP, Millett J. 2017. Foraging fish as zoogeomorphic agents: an assessment of fish impacts at patch, barform, and reach scales. *Journal of Geophysical Research: Earth Surface* **122**: 2105–2123. <https://doi.org/10.1002/2017JF004362>.
- Pringle CM, Hamazaki T. 1998. The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects. *Ecology* **79**: 269–280. [https://doi.org/10.1890/0012-9658\(1998\)079\[0269:TROOIA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[0269:TROOIA]2.0.CO;2).
- Pringle CM, Naiman RJ, Bretscroco G, Karr JR, Oswooo MW, Webster JR, Welcomme RL, Winterbourn MJ. 1988. Patch dynamics in lotic systems: the stream as a mosaic. *Journal of the North American Benthological Society* **7**: 503–524. <https://doi.org/10.2307/1467303>.
- Pringle CM, Blake GA, Covich AP, Buzby KM, Finley A. 1993. Effects of omnivorous shrimp in a montane tropical stream: sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. *Oecologia* **93**: 1–11. <https://doi.org/10.1007/BF00321183>.
- R Core Team. 2017. *A language and environment for statistical computing*. Vienna, Austria. <https://www.R-project.org/>.
- Reinhardt L, Jerolmack D, Cardinale BJ, Vanacker V, Wright J. 2010. Dynamic interactions of life and its landscape: feedbacks at the interface of geomorphology and ecology. *Earth Surface Processes and Landforms* **35**: 78–101. <https://doi.org/10.1002/esp.1912>.
- Rice SP, Church M. 1998. Grain size along two gravel-bed rivers: statistical variation, spatial pattern and sedimentary links. *Earth Surface Processes and Landforms* **23**: 345–363. [https://doi.org/10.1002/\(SICI\)1096-9837\(199804\)23:4<345::AID-ESP850>3.0.CO;2-B](https://doi.org/10.1002/(SICI)1096-9837(199804)23:4<345::AID-ESP850>3.0.CO;2-B).
- Rice SP, Johnson MF, Reid I. 2012. Animals and the geomorphology of gravel bed rivers. In *Gravel-Bed Rivers: Processes, Tools, Environments*, Church M, Biron PM, André GR (eds). Wiley: Oxford; 225–241.
- Rice SP, Johnson MF, Extence C, Reeds J, Longstaff H. 2014. Diel patterns of suspended sediment flux and the zoogeomorphic agency of invasive crayfish. *Cuadernos de Investigación Geográfica* **40**: 7–27. <https://doi.org/10.18172/cig.2508>.
- Rice SP, Johnson MF, Mathers K, Reeds J, Extence C. 2016. The importance of biotic entrainment for base flow fluvial sediment transport. *Journal of Geophysical Research: Earth Surface* **121**: 890–906. <https://doi.org/10.1002/2015JF003726>.
- Seal JN, Tschinkel WR. 2006. Colony productivity of the fungus-gardening ant *Trachymyrmex septentrionalis* (Hymenoptera: Formicidae) in a Florida pine forest. *Annals of the Entomological Society of America* **99**: 673–683. [https://doi.org/10.1603/0013-8746\(2006\)99\[673:CPOTFA\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2006)99[673:CPOTFA]2.0.CO;2).
- Soluk DA, Craig DA. 1990. Digging with a vortex: flow manipulation facilitates prey capture by a predatory stream mayfly. *Limnology and Oceanography* **35**: 1201–1206. <https://doi.org/10.4319/lo.1990.35.5.1201>.
- Southwood TRE. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46**: 337–365. <https://doi.org/10.2307/3817>.
- Statzner B. 2011. Mineral grains in caddisfly pupal cases and streambed sediments: assessing resource use and its limitation across various river types. *International Journal of Limnology* **47**: 103–118. <https://doi.org/10.1051/limn/2011004>.
- Statzner B. 2012. Geomorphological implications of engineering bed sediments by lotic animals. *Geomorphology* **157&158**: 49–65. <https://doi.org/10.1016/j.geomorph.2011.03.022>.
- Statzner B, Holm TF. 1989. Morphological adaptation of shape to flow: microcurrents around lotic macroinvertebrates with known Reynolds numbers at quasi-natural flow conditions. *Oecologia* **78**: 145–157. <https://doi.org/10.1007/BF00377150>.
- Statzner B, Fuchs U, Higler LWG. 1996. Sand erosion by mobile predaceous stream insects: implications for ecology and hydrology. *Water Resources Research* **32**: 2279–2287. <https://doi.org/10.1029/96WR00977>.
- Statzner B, Arens MF, Champagne JY, Morel R, Herouin E. 1999. Silk-producing stream insects and gravel erosion: Significant biological effects on critical shear stress. *Water Resources Research* **35**: 3495–3506. <https://doi.org/10.1029/1999WR900196>.
- Statzner B, Sagnes P, Champagne JY, Viboud S. 2003. Contribution of benthic fish to the patch dynamics of gravel and sand transport in streams. *Water Resources Research* **39**. <https://doi.org/10.1029/2003WR002270>.
- Statzner B, Méricoux S, Leichtfried M. 2005. Mineral grains in caddisfly pupal cases and streambed sediments: resource use and its limitation through conflicting resource requirements. *Limnology and Oceanography* **50**: 713–721.
- Statzner B, Dolédec O, Sagnes P. 2009. Recent low-cost technologies to analyse physical properties of cases and tubes built by aquatic animals. *International Review of Hydrobiology* **94**: 625–644. <https://doi.org/10.1002/iroh.200911165>.
- Surber EW. 1937. Rainbow trout and bottom fauna production in one mile of stream. *Transactions of the American Fisheries Society* **66**: 193–202. [https://doi.org/10.1577/1548-8659\(1936\)66\[193:RTABFP\]2.0.CO;2](https://doi.org/10.1577/1548-8659(1936)66[193:RTABFP]2.0.CO;2).
- Takao A, Negishi JN, Nunokawa M, Gomi T, Nakahara O. 2006. Potential influences of a net-spinning caddisfly (Trichoptera: Stenopsyche marmorata) on stream substratum stability in heterogeneous field environments. *Benthol. Soc* **25**: 545–555.
- Tolkamp HH. 1980. *Organism-substrate relationships in lowland streams*. Agricultural Research Reports: Wageningen, The Netherlands.
- Tsydel M, Sztajnowski S, Michalak M, Wrzosek H, Kowalska S, Krucińska I, Lipp-Symonowicz B. 2009. Structure and physical and chemical properties of fibres from the fifth larval instar of caddisflies of the species *Hydropsyche angustipennis*. *Fibres & Textiles in Eastern Europe* **17**(6): 7–12.
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130–137. <https://doi.org/10.1139/f80-017>.
- Viles HA. 1988. *Biogeomorphology*. Blackwell: Oxford.
- Wagner R. 1990. A laboratory study on the life cycle of *Sericostoma personatum* (Kirby & Spence), and light dark-dependent food consumption. *Hydrobiologia* **208**: 201–212. <https://doi.org/10.1007/BF00007785>.
- Wagner R. 1991. The influence of the diel activity pattern of the larvae of *Sericostoma personatum* (Kirby & Spence) (Trichoptera) on organic matter distribution in stream-bed sediments – a laboratory study. *Hydrobiologia* **224**: 65–70. <https://doi.org/10.1007/BF00006862>.
- Wallace ID, Wallace B, Philipson GN. 1990. *A Key to the Case-Bearing Caddis Larvae of Britain and Ireland*. Freshwater Biological Association: Ambleside.
- Wallace JB, Whiles MR, Webster JR, Cuffney TF, Lugthart GJ. 1993. Dynamics of inorganic particles in headwater streams: linkages with invertebrates. *Journal of the North American Benthological Society* **12**: 112–125. <https://doi.org/10.2307/1467341>.
- Waringer JA. 1987. Spatial distribution of Trichoptera larvae in the sediments of an Austrian mountain brook. *Freshwater Biology* **18**: 469–482. <https://doi.org/10.1111/j.1365-2427.1987.tb01332.x>.
- Waringer JA. 1993. The drag coefficient of cased caddis larvae from running waters: experimental determination and ecological applications. *Freshw. Biol.* **29**: 419–427.
- Webster DA, Webster PC. 1943. Influence of water current on case weight in larvae of the caddisfly, *Goera Calcarata* Banks. *The Canadian Entomologist* **75**: 105–108. <https://doi.org/10.4039/Ent75105-6>.
- Wentworth CK. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology* **30**: 377–392.
- Wiggins GB. 1996. Trichoptera families. In *An Introduction to the Aquatic Insects of North America*, Merritt RW, Cummins KW (eds). Kendall/Hunt Publishing: Dubuque, IA; 309–349.
- Wiggins GB. 2004. *Caddisflies: The Underwater Architects*. University of Toronto Press: Toronto.

- Wilcock PR, Crowe JC. 2003. Surface-based transport model for mixed-size sediment. *Journal of Hydraulic Engineering* **129**: 120–128. [https://doi.org/10.1061/\(ASCE\)0733-9429\(2003\)129:2\(120\)](https://doi.org/10.1061/(ASCE)0733-9429(2003)129:2(120)).
- Wilcock PR, Kenworthy ST, Crowe JC. 2001. Experimental study of the transport of mixed sand and gravel. *Water Resources Research* **37**: 3349–3358. <https://doi.org/10.1029/2001WR000683>.
- Wilkes MA, Gittins J, Mathers KL, Mason R, Casas-Mulet R, Vanzo D, Mckenzie M, Murray-Bligh J, England J, Gurnell A, Jones IJ. 2018. Physical and biological controls on fine sediment transport and storage in rivers. *WIREs Water* **6**: e1331. <https://doi.org/10.1002/wat2.1331>.
- Williams DD, Williams NE. 1993. The upstream/downstream movement paradox of lotic invertebrates: quantitative evidence from a Welsh mountain stream. *Freshwater Biology* **30**: 199–218. <https://doi.org/10.1111/j.1365-2427.1993.tb00802.x>.
- Wohl E. 2013. Floodplains and wood. *Earth-Science Reviews* **123**: 194–212. <https://doi.org/10.1016/j.EARSCIREV.2013.04.009>.
- Wohl E. 2017. The significance of small streams. *Frontiers of Earth Science* **11**: 447–456. <https://doi.org/10.1007/s11707-017-0647-y>.
- Zanetell BA, Peckarsky B. 1996. Stoneflies as ecological engineers – hungry predators reduce fine sediments in stream beds. *Freshwater Biology* **36**: 569–577. <https://doi.org/10.1046/j.1365-2427.1996.00132.x>.
- Zhou X, Frandsen PB, Holzenthal RW, Beet CR, Bennett KR, Blahnik RJ, Bonada N, Cartwright D, Chuluunbat S, Cocks GV, Collins GE, DeWaard JR, Dean J, Flint OS, Hausmann A, Hendrich L, Hess M, Hogg ID, Kondratieff BC, Malicky H, Milton MA, Morinière J, Morse JC, Mwangi FN, Pauls SU, Gonzalez MR, Rinne A, Robinson JL, Salokannel J, Shackleton M, Smith B, Stamatakis A, StClair R, Thomas JA, Zamora-Muñoz C, Ziesmann T, Kjer KM. 2016. The Trichoptera barcode initiative: a strategy for generating a species-level Tree of Life. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**: 20160025. <https://doi.org/10.1098/rstb.2016.0025>.