The zoogeomorphology of case-building caddisfly larvae

by

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Abstract

Caddisfly (Trichoptera) are an abundant and widespread aquatic insect group. Caddisfly larvae of most species build cases from silk and fine sediment at some point in their lifecycle. Case-building caddisfly have the potential to modify the distribution and transport of sediment by: 1) altering sediment properties through case construction, and 2) transporting sediment incorporated into cases over the riverbed. This thesis investigates, for the first time, the effects of bioconstruction by case-building caddisfly on fluvial geomorphology. The research was conducted using two flume experiments to understand the mechanisms of caddisfly zoogeomorphology (case construction and transporting sediment), and two field investigations that increase the spatial and temporal scale of the research. Caddisfly cases varied considerably in mass between species (0.001 g - 0.83 g) and grain sizes used (D_{50} = 0.17 mm - 4 mm). As a community, caddisfly used a wide range of grain-sizes in case construction (0.063 mm – 11 mm), and, on average, the mass of incorporated sediment was 38 g m^{-2}, in a gravel-bed stream. This sediment was aggregated into biogenic particles (cases) which differed in size and shape from their constituent grains. A flume experiment determined that empty cases of some caddisfly species (tubular case-builders; Limnephilidae and Sericostomatidae) were more mobile than their incorporated sediment, but that dome shaped Glossosomatidae cases moved at the same entrainment threshold as their constituent grains, highlighting the importance of case design as a control on caddisfly zoogeomorphology. A second flume experiment found that crawling Glossosomatidae larvae transport sand vertically upwards, from sheltered interstices below gravel particles, onto the surface of armoured gravel-beds, increasing the hydraulic exposure of this sediment. As a result of both larvae crawling and case entrainment, case-building caddisfly were responsible for over 30% of coarse sand transport during low to medium discharge conditions in a gravel-bed stream. Tubular case-builders (especially Limnephilidae) and dome case-builders (Glossosomatidae) were particularly important zoogeomorphic agents, using and transporting substantial amounts of coarse sand and fine gravel. This research has shown that case bioconstruction by caddisfly larvae may have a destabilising effect on sand in gravel-bed rivers. The thesis uses case design to conceptualise and understand caddisfly zoogeomorphology under differing biotic and abiotic controls. Future research should consider sediment stabilisation associated with caddisfly pupation, and the relative importance of destabilisation and stabilisation across spatial and temporal gradients. The broad geographic spread, functional diversity, and commonly high abundances of case-building caddisfly mean that they may have important and widespread implications for sediment dynamics in rivers.

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Chapter 1. Introduction

1.1 Research context

Throughout history, rivers have been integral to human civilisation (Gani and Gani, 2011; Haidvogl, 2018). Rivers provide critical ecosystem services, including water supply, provision of food, power generation, navigation pathways, cultural and aesthetic value, and enhance human well-being (Böck *et al.,* 2018; Kaval, 2019). Estimates suggest that freshwater ecosystems deliver \$6.5 trillion USD a^{-1} worth of services, which is 20% of the global total, despite covering only 0.8% of the Earth's surface (Constanza *et al.,* 1997; Strayer and Dudgeon, 2010). Freshwater habitats are also extraordinarily biodiverse, supporting 9.5% of total described animal species (Balian *et al.,* 2008).

However, multiple pressures on rivers, including morphological and hydrological modification, urbanisation, pollution and climate change, have caused a global decline in freshwater biodiversity (Dudgeon *et al.,* 2006; Malmqvist and Rundle, 2002; Reid *et al.,* 2019; Strayer and Dudgeon, 2010). Freshwater flora and fauna have incurred an 81% reduction in abundance, compared to a global average of 58% across all habitats (1970-2012; WWF, 2016). This is concerning not only because of the intrinsic value of species, but also the loss of the ecosystem services that they provide (Cardinale *et al.,* 2012). Consequently, research into the geomorphological and ecological functioning of rivers is required to mitigate and reverse this decline (Auerbach *et al.,* 2014; Palmer and Ruhi, 2019; Wohl *et al.,* 2015).

Sediment (fragmentary material transported by or deposited in water; Edwards and Glysson, 1999), is an important control on river geomorphology and ecology. Sediment transport is a key driver of river morphology (Schumm, 1977), water quality (Hauer *et al.,* 2018), and provides the habitat template for a diverse array of plants and animals (Newson and Newson, 2000; Southwood, 1977). The erosion, deposition and transport of fluvial sediment is, therefore, a primary control on the ecosystem services provided by rivers and understanding sediment transport is essential for river management and restoration (Kondolf *et al.,* 2006; Sear, 1994). The influence of fluvial sediment on biological communities has been fundamental to research in aquatic ecology (Frissell *et al.,* 1986; Vannote *et al.,* 1980). More recently, however, research has demonstrated the reciprocal effects of biology on sediment dynamics in rivers (Atkinson *et al.,* 2018; Reinhardt *et al.,* 2010). Plants and animals have important impacts which can either reduce or increase sediment transport. For example, riparian vegetation stabilises river banks (Brooks

and Brierley, 2002; Gurnell *et al.,* 2019) while bioturbating invertebrates mix and erode sediment from the riverbed (Nogaro *et al.,* 2006).

Zoogeomorphology is the field of research that specifically considers the role of animals in geomorphology (Butler, 1995, 1992). It is increasingly recognised that animals can have substantial effects on sediment transport in rivers (Rice *et al.,* 2012; Statzner, 2012). Zoogeomorphic processes are important because animals may modify river sediment yields, morphology, and habitat. Signal crayfish, for example, increase suspension of fine sediment (Harvey *et al.,* 2014), which may reduce habitat quality for invertebrates (Mathers *et al.,* 2020). In addition, zoogeomorphic engineers may present a risk to lives or property. Burrowing of porcupines may have contributed to the collapse of a levee containing the Secchia river, Italy (Orlandini *et al.,* 2015; Taccari and Van Der Meij, 2016). In contrast, zoogeomorphic effects can potentially be used to enhance river ecosystem services (e.g. beaver rewilding to restore biodiversity; Law *et al.,* 2017), or to prioritise the conservation of species which usefully affect sediment dynamics or increase habitat diversity. Consequently, there are growing calls to understand the interactions between geomorphology and ecology to better manage and restore rivers (Auerbach *et al.,* 2014; Johnson *et al.,* 2019; Palmer and Ruhi, 2019).

Zoogeomorphic research in rivers has typically focussed on large charismatic taxa, especially beaver and salmonid fish (Atkinson *et al.,* 2018; Rice *et al.,* 2012; Statzner, 2012). Despite the recognised importance of invertebrates to geomorphic processes in terrestrial and marine systems (Cadée, 2001; Wilkinson *et al.,* 2009), they have received far less attention in rivers (Albertson and Allen, 2015). Caddisfly (Trichoptera: Insecta) have the potential to be important zoogeomorphic engineers. Caddisfly are diverse and ubiquitous in lotic habitats and can be extremely abundant, often occurring in very high densities (> 1000 larvae m^{-2}; Mcneely and Power, 2007; Wiggins, 2004). Furthermore, caddisfly may have disproportionately large zoogeomorphic effects due to their construction of filter-feeding silk nets and cases from fine sediment (Albertson and Allen, 2015). Whilst caddisfly nets have been found to bind together gravel particles and increase the critical shear stress required to initiate gravel movement by 10–40% (Statzner *et al.,* 1999; Cardinale *et al.,* 2004), the zoogeomorphic effects of case-construction by caddisfly larvae are unknown.

Most caddisfly species use fine sediment (~0.1 mm up to 5 mm; De Gispert, 2015; Hansell, 1968; Okano & Kikuchi, 2012; Statzner *et al.,* 2005; Tolkamp, 1980) in the construction of mobile cases, fixed retreats or pupal cases at some point in their life cycle (Wiggins, 1996). Both the construction of cases and the movement of sediment by caddisfly may modify the mobility

of incorporated sediment and its exposure to hydraulic forces. As a result, case-building caddisfly may affect sediment transport processes in rivers. This research is the first to consider the zoogeomorphic importance of case construction by caddisfly larvae. The aim of this thesis is to investigate and quantify the effect of case-building caddisfly on the distribution and transport of sand in rivers.

1.2 Fluvial zoogeomorphology

Recognition of the importance of organisms in shaping Earth surface processes is not new (Darwin, 1881) but it has seen a surge of research in the last 30 years, within the discipline of *biogeomorphology* (Viles, 1988). Biogeomorphology considers the two-way interaction between the biosphere and the geosphere to understand how plants and animals shape landforms (Naylor *et al.,* 2002; Viles, 2019). Biogeomorphology and the sub-discipline of zoogeomorphology have largely been studied by geomorphologists. Ecological interest in the closely related discipline of *ecosystem engineering* (Hastings *et al.,* 2007; Jones *et al.,* 1994) has also been growing (Butler and Sawyer, 2012). Ecosystem engineering investigates the physical modification, maintenance or creation of habitat by organisms (Jones *et al.,* 1994) and, as such, there is considerable overlap between the disciplines. Ecosystem engineers usually also have biogeomorphic effects (Jones, 2012). There has, however, been a lack of integration between geomorphologists and ecologists, which is required to address common interdisciplinary research questions (Reinhardt *et al.,* 2010; Rice *et al.,* 2010; Stallins, 2006).

The biogeomorphic effects of organisms can be broadly divided into five categories (Table 1.1) (Corenblit *et al.,* 2011; Naylor *et al.,* 2002; Viles, 2019). *Bioprotection* reduces erosion or weathering processes, stabilising sediment. *Bioconstruction* typically also has a stabilising effect (Viles, 2019), but may also destabilise sediment (Fei *et al.,* 2014). In contrast, *bioweathering*, *bioturbation* and *bioerosion* usually act to destabilise material. The diversity of organisms and their range of functional traits and behaviours can make conceptualising their zoogeomorphic effects difficult (Allen *et al.,* 2014). Individual species may also have both stabilising and destabilising effects depending on their biotic and abiotic context (Moore, 2006).

The dynamic nature and abiotic energy of many rivers may suggest that biogeomorphic effects in rivers are less important than in other ecosystems (Statzner, 2012). Biology, however, is proving to have large scale geomorphic effects that can dominate abiotic energy in some systems (Atkinson *et al.,* 2018; Coombes, 2016; Harvey and Bertoldi, 2015). Castro and Thorne (2019)

conceptualised biology as a primary driver of river typology (alongside geology and hydrology), highlighting the importance of plants and animals as major controls on river morphology and habitat.

The importance of vegetation and large woody material (large wood) to river geomorphology is evidenced by its now widespread use in river restoration (Cashman *et al.,* 2019; Grabowski *et al.,* 2019; Gurnell *et al.,* 2019). Vegetation and large wood can have large-scale effects on channel planform and longitudinal profiles (for reviews see; Corenblit *et al.,* 2007; Gurnell, 2014; Gurnell *et al.,* 2019; 2002; Montgomery and Piégay, 2003; Wohl, 2013). Usually, vegetation in rivers is associated with sediment stabilisation. Aquatic macrophytes, large-wood structures and riparian vegetation reduce local flow velocities and trap sediment, providing bioprotection (Table 1.1) to river beds and banks (Cotton *et al.,* 2006; Tal and Paola, 2010). When the spatial distribution of vegetation is patchy, however, flow is deflected around these biostabilised areas, leading to increased scour (Vandenbruwaene *et al.,* 2011). Vegetation can therefore increase the spatial complexity of geomorphic processes and the diversity of habitat provided.

Table 1.1. Mechanisms by which organisms affect geomorphic systems (adapted from Corenblit *et al.,* 2011; Viles, 2019) with definitions and the typical effect of each mechanism on sediment stability.

Mechanism	Definition	Typical geomorphic effect
(1) Bioconstruction	Allogenic (using material external to the organism) or autogenic (utilising self-generated tissue) structures built by organisms (Jones et al., 1994; Naylor et al., 2002).	Sediment stabilisation
(2) Bioprotection	Biological effects which lead to the accumulation or stability of sediment (Carter and Viles, 2005).	
(3) Bioweathering	Chemical weathering associated with biota (Dorn, 2014).	Sediment destabilisation
(4) Bioturbation	Biotic reworking of lose sediment (Meysman et al., 2006).	
(5) Bioerosion	Degradation of hard surfaces by organisms (Davidson et al., 2018).	

An increasing number of animals are documented to affect hydraulics, bed sediment sorting and sediment transport processes in rivers (see reviews; Rice *et al.,* 2012; Statzner, 2012; Albertson and Allen, 2015). Beaver (*Castor canadensis* and *Castor fiber*) have received the most research attention due to their construction of dams (bioconstruction; Table 1.1), which act as traps for water and sediment (Butler and Malanson, 2005; Gurnell, 1998; Naimen *et al.,* 1988; Puttock *et al.,* 2018; Ruedemann and Schoonmaker, 1938). Beaver dams can create multiple channels and a diverse mosaic of habitats, fundamentally changing the geomorphology of smaller rivers and riparian zones (Gurnell, 1998). Beaver are being reintroduced within their historical geographical range to restore habitat diversity, biodiversity and slow the downstream transport of sediment and water (Law *et al.,* 2017; Pollock *et al.,* 2015, 2014). Due to their dam construction, Beaver are usually sediment stabilisers, but burrowing by beaver can also erode river banks and input fine sediment into river systems (bioturbation, Table 1.1; Meentemeyer *et al.,* 1998).

Spawning Salmonidae (e.g. salmon and trout) also have strong zoogeomorphic effects (DeVries, 2012; Hassan *et al.,* 2011). Female salmon construct redds (nests) within gravel-beds during spawning, using strong undulations of their tail (Burner, 1951). Due to the vertical mixing and disturbance of stabilising gravel-bed sediment structures, redd construction locally destabilises bed sediment (Buxton *et al.,* 2015; Rennie and Millar, 2000). The landscape of pits and tail spills created by spawning salmonids is also vulnerable to erosion in high discharge (Gottesfeld *et al.,* 2004). A study in British Columbia estimated that bioturbation by salmon accounted for 30-50% of total annual bedload flux at spawning locations on four gravel-bed rivers (Hassan *et al.,* 2008). Salmonidae spawning may therefore influence the characteristics of river channels and sediment transport over large spatial and temporal timescales (Fremier *et al.,* 2017).

Benthivorous fish also bioturbate and destabilise sediment while foraging (reviewed by Rice *et al.,* 2019). Foraging by the Sonora sucker (*Catostomus insignis)*, for example, was responsible for diurnal cycles of up to 32% of daily suspended matter load (Booth *et al.,* 2020). Pledger *et al.,* (2014) determined that foraging Barbel (*Barbus barbus*) could increase gravel entrainment by 82% in a laboratory setting. Density (Barton *et al.,* 2000; Breukelaar *et al.,* 1994; Parkos III *et al.,* 2003), body size (Pledger *et al.,* 2016) and specific feeding behaviours (Rice *et al.,* 2019), are all important controls on the geomorphic effectiveness of benthivorous fish bioturbation. Consequently, both salmonids and benthivorous fish disturb water worked structures, increasing the likelihood of sediment erosion in subsequent high flows (Pledger *et al.,* 2014; Statzner *et al.,* 2003). Nest building (bioconstruction; Table 1.1) by non-salmonid species from river-bed sediment may also have geomorphic implications (Rice *et al.,* 2019).

1.3 Invertebrate zoogeomorphology

"Worms have played a more important part in the history of the world than most persons would at first suppose" (Charles Darwin, 1881 p. 305).

Moore (2006) hypothesised that the magnitude of an organism's zoogeomorphic effect is a function of its density, behaviour and body size. Using a meta-analysis of biogeomorphic studies in lotic environments, Albertson and Allen (2015) tested this hypothesis. While the biomass of individuals was associated with the scale of their potential zoogeomorphic work, when populations were considered, the effects of invertebrates were comparable to much larger vertebrates (Albertson and Allen, 2015). After controlling for biomass, the individual effects of some aquatic insects were 550 times greater than those of fish and crustaceans (Albertson and Allen, 2015). Therefore, whilst zoogeomorphic research in rivers has prioritised larger taxa with evident geomorphic impacts (Statzner, 2012), the less noticeable effects of invertebrates can be equally important. Rice *et al.,* (2012) called these 'Cinderella' taxa because their important geomorphic effects are not easily visible in rivers.

In terrestrial and marine environments, the zoogeomorphic importance of invertebrates has received more research than in lotic systems. Functionally, there are many similarities between invertebrates in these habitats with those in rivers (Meysman *et al.,* 2006), therefore a brief description and examples of terrestrial and marine invertebrate sediment engineers is included, as well as a more exhaustive review of literature on the zoogeomorphology of freshwater invertebrates. Literature from other disciplines, including ecosystem engineering, ichnotaxonomy (fossil animals) and geochemistry, is also re-interpreted from a zoogeomorphic context (following Statzner, 2012).

1.3.1 Terrestrial

In his seminal text on zoogeomorphology, Butler (1995 pp. 11) stated "*the geomorphic effects of invertebrates are apparent to even the most casual observer who has seen an ant mound or earthworm casting*". Perhaps because of their increased visibility, the zoogeomorphic effects of terrestrial invertebrates have been recognised for a considerable time. Darwins' (1881) book concerning the importance of earthworms in soil is often cited as the first reference to animal geomorphic agents (Coombes, 2016; Meysman *et al.,* 2006; Rice *et al.,* 2019). Darwin recognised, not only that worms bioturbate sediment, moving 0.53 t ha^{-1} a^{-1} upwards to the soil surface, but that this contributed to landform development (Feller *et al.,* 2003). Subsequently, considerable research

has considered the bioturbation effects of worms and their role in soil formation (*pedogenesis*; see reviews by Meysman *et al.,* 2006; Wilkinson *et al.,* 2009). Ants and termites also contribute to bioturbation (Dangerfield *et al.,* 1998; Whitford and Eldridge, 2013). Sediment excavation by ants is often 1–5 t ha^{-1} a^{-1} soil and occasionally exceeds 50 t ha^{-1} a^{-1} (Seal and Tschinkel, 2006; Wilkinson *et al.,* 2009).

Worms, ants, and termites construct sediment structures (mounds; Wilkinson *et al.,* 2009). Mounds of loose sediment may be easily eroded (such as Darwin's earthworm casts; Darwin, 1881) but some mounds, especially those of ants and termites, are maintained (Humphreys and Mitchell, 1983) and can be stabilising components of terrestrial landscapes (Wilkinson *et al.,* 2009). Ant mounds can persist as long as 100 years (Cowan *et al.,* 1985). Terrestrial invertebrates, therefore, bioturbate sediment below the ground surface, create mound structures above the surface and influence both soil formation and the flux and downslope erosion of fine sediment (Gabet *et al.,* 2003; Richards and Humphreys, 2010; Wilkinson *et al.,* 2009).

1.3.2 Marine

The significance of invertebrate zoogeomorphology is also recognised in marine environments (see reviews by Mermillod-Blondin and Rosenberg, 2006; Murray *et al.,* 2002; Shull, 2009). As for the terrasphere, bioturbation is an important process in marine environments (Mermillod-Blondin, 2011; Murray *et al.,* 2002). Bioturbators convey sediment upwards, downwards or internally within the substrate (François *et al.,* 1997; Shull, 2009). For example, burrowing crabs moved 0.375 kg m^{-2} of sediment per day to the surface of unvegetated mudflats (Wang *et al.,* 2010).

Filter feeding Polychaete worms build tubes from secreted material and often occur at high densities, creating tube 'lawns' and modifying the physical structure of soft sediment environments (Dudgeon, 1990). The effect of Polychaete tube lawns on sediment stability is still debated, however, with several studies documenting a destabilising effect caused by flow acceleration around the tubes (Eckman *et al.,* 1981; Luckenbach, 1986; Xie *et al.,* 2018) and others a stabilising effect (Meadows *et al.,* 1990; Meadows and Tait, 1989). Friedrichs *et al.,* (2000) suggest that polychaete tubes transition from having destabilising to stabilising effects based on population density, at 8.8 % of sediment surface coverage by their tubes, regularly recorded in the field. Similar zoogeomorphic activities are reported for amphipods, such as *Haploops nirae* which constructs tubes and stabilises soft bed sediment, facilitating colonisation by other invertebrates (Chaalali *et al.,* 2017).

1.3.3 Sediment destabilisation in freshwater habitats: bioturbation and bioerosion

Bioturbators redistribute sediment, changing both the physical structure of substrate and the chemical and biological processes occurring within it (Gautreau *et al.,* 2020; Mermillod-Blondin, 2011). The effects of bioturbators vary based on the functional characteristics of the organisms (Mermillod-Blondin *et al.,* 2002; Michaud *et al.,* 2005; Nogaro *et al.,* 2009) and the abiotic environment. Mermillod-Blondin and Rosenberg (2006) distinguish between diffusion dominated habitats: fine grained sediments with low hydraulic conductivity (typical of lakes and marine systems); and advection dominated substrates with high hydraulic connectivity and usually larger grain sizes (rivers). Bioturbation in diffusion dominated habitats has particularly strong effects on microbial and geochemical processes (Mermillod-Blondin, 2011). In advection dominated substrates, such as the hyporheic zone of most rivers, bioturbators can affect hydrological exchange with the surface (Nogaro *et al.,* 2009) and may be especially important geomorphologically by altering the exposure of sediment to erosive hydraulics at the sediment-water interface. Bioturbation in rivers is particularly strong when stabilising grain structures (such as armoured gravel-beds) are disturbed (Statzner, 2012).

Several species of crayfish cause substantial bioturbation via locomotion (foraging and fighting) including the rusty crayfish (*Faxonius rusticus*; Albertson and Daniels, 2016; Statzner *et al.,* 2000; Statzner and Peltret, 2006), red swamp crayfish (*Procambarus clarkii*; Arce and Diéguez-Uribeondo, 2015) and the signal crayfish (*Pacifastacus leniusculus*; Harvey *et al.,* 2014; Johnson *et al.,* 2010; Rice *et al.,* 2014). Crayfish locomotion in gravel substrates results in pits and mounds (Albertson and Daniels, 2016; Johnson *et al.,* 2010), affects near bed hydraulics (Han *et al.,* 2019) and leads to the suspension of fine sediment (Harvey *et al.,* 2014). Diurnal signals of high turbidity at night, when crayfish are more active, allowed Rice *et al.* (2016) to isolate the contribution of nocturnal signal crayfish to baseflow sediment yield for a low-order, lowland, UK stream. Signal crayfish added at least 32% (474 kg) to monthly baseflow sediment (Rice *et al.,* 2016). Bioturbation by signal crayfish can also can increase the infiltration (downwards transport) of fine sediment into interstices between gravel particles during foraging (Mathers *et al.,* 2019).

In the UK, where they are invasive, signal crayfish also contribute to bioturbation via burrowing into river banks. Faller *et al.* (2016) estimated that signal crayfish add approximately 3 t km^{-1} of sediment per burrowed bank in the Thames catchment, UK, but burrowing was patchy and occurred at only 10% of banks surveyed. Crayfish burrowing may also destabilise banks, causing

collapse and further fine sediment input into river channels (Arce and Diéguez-Uribeondo, 2015; Harvey *et al.,* 2019).

Other crustaceans also have bioturbation effects including Atyidae (shrimp) which reduce sedimentation (Pringle *et al.,* 1993; Pringle and Hamazaki, 1998) and Asellidae (water hoglouse) which mix and homogenise sediment within the river bed (Mermillod-Blondin *et al.,* 2002). As in terrestrial habitats, Oligochaeta (worms) convey sediment upwards, feeding on material up to 20 cm below the sediment surface, and transporting this to the surface as faecal pellets (Ciutat *et al.,* 2006; Dafoe *et al.,* 2011). Networks of burrows constructed by Tubificidae (Oligochaeta) increase interstitial flow within fine-grained benthic sediments (Nogaro *et al.,* 2006), modify lake sediment structure, and increase suspended sediment (Zhang *et al.,* 2014; Ciutat *et al.,* 2006).

Predatory stonefly larvae can transport substantial quantities of sand from gravel interstices whilst foraging for prey (up to 200 – 400 kg m^{-2} yr^{-1} for *Dinocras cephalotes;* Statzner *et al.,* 1996), with reduced prey availability increasing foraging activity, and therefore erosion (Statzner *et al.,* 1996; Zanetell and Peckarsky, 1996). Similarly, *Pseudiron centralis* (mayfly) larvae have been documented eroding sand furrows while hunting for buried Chironomidae (non-biting midge) prey (Soluk and Craig, 1990). Mayfly in lakes are also documented to have bioturbation effects (Charbonneau and Hare, 1998; Edmunds and Mccafferty, 1996), by burrowing or dwelling in interstices (Bae and McCafferty, 1995). Individual *Hexagenia limbate* (mayfly) larvae can move an average of 4 cm^3 sediment per day (Charbonneau and Hare, 1998).

Consequently, bioturbation is an important zoogeomorphological process in both lotic and lentic environments. In a pool of a small, low-order stream, bioturbation by the resident invertebrate communities resulted in 85% of the surface reworked after 4 days (De Nadaï-Monoury *et al.,* 2013). A number of taxa were responsible, but these included cranefly (Tipulidae), dragonfly (Odonata) and two caddisfly species; *Odontocerum albicorne* (Odontoceridae) and *Sericostoma sp.* (Sericostomatidae; De Nadaï-Monoury *et al.,* 2013).

Bioerosion (the removal of material from hard surfaces; Table 1.1; Davidson *et al.,* 2018), is documented for only a small number of taxa in freshwater habitats, largely within the fields of paleoecology and ichnotaxonomy. Uchman *et al.* (2017) documented recent U-shaped burrows of mayfly in consolidated sediment from the rivers Drwęca (Poland) and Ohře (Czech Republic). Similarly, Savrda (2019) found Chironomidae burrows, up to 40 mm deep in claystone in riffle habitats of the Conecuh River, USA. Caddisfly burrows were also documented, in both sandstone and claystone in riffles, with burrows also up to 40 mm deep and extended above the burrow by chimneys of fine-sediment (Figure 1.1; Savrda, 2019).

1.3.4 Sediment stabilisation in freshwater habitats: bioconstruction and bioprotection

There are fewer examples of stabilisation than destabilisation in lotic zoogeomorphology (Albertson and Allen, 2015), but thanks to their diverse behaviours, a number of aquatic invertebrates have stabilising effects. Silk is a protein secreted by several aquatic insects (Trichoptera, Diptera and Lepidoptera) and some arthropods (Wotton, 2011). Silk is used by organisms in tube construction, feeding nets, and to attach to substrate (Wotton, 2011). Silk can also affect the stability of benthic substrates, providing bioprotection. For example, the silk tubes constructed by Chironomidae larvae act to reduce suspension of fine sediment (Edwards, 1962).

Similarly, the construction of nets and retreats from silk by caddisfly larvae has been found to increase the critical shear stress required to initiate gravel movement by 10 to 40% (Albertson *et al.,* 2014a; Cardinale *et al.,* 2004; Johnson *et al.,* 2009; Statzner *et al.,* 1999; Figure 1.1). Several biotic factors are important controls on these zoogeomorphic effects. Larger taxa, with stronger silk result in greater sediment stabilisation. For example, *Arctopsyche californica* result in greater stabilisation than *Ceratopsyche oslari* (Albertson *et al.,* 2014b). *Stenopsyche marmorata* are even larger and can secure larger gravel particles (Nunokawa *et al.,* 2008; Takao *et al.,* 2006). Species interactions are also important. Further increases in sediment stability occur with *A. californica* and *C. oslari* polycultures, possibly because they inhabit different hydraulic niches (Albertson *et al.* 2014b; 2019).

Caddisfly nets therefore provide bioprotection by binding gravel particles together, increasing their effective size (Albertson *et al.,* 2014a), and modelling suggests nets may reduce near bed flow velocities by nearly 60% (Juras *et al.,* 2018). *Stenopsyche marmorata* retreats fixed with silk between large cobbles can increase the mean force required to move a cobble 2 – 3 fold for a single retreat (Nunokawa *et al.,* 2008). Furthermore, many caddisfly species fix gravel particles to cobbles in pupation cases (Statzner et al., 2005), which may stabilise sediment (Statzner, 2012). Attempts to upscale the zoogeomorphic effects of net-construction by caddisfly have included modelling (Albertson *et al.,* 2014b; Tashiro *et al.,* 2005) and large scale experiments. Albertson *et al.,* (2019) used 50 m^2 semi-natural outdoor river channels and found that *A. californica* and *C. oslari* increased gravel entrainment thresholds by 20%.

Freshwater mussels also stabilise sediment via the physical weight of the mussels reducing entrainment (Statzner, 2012), and the use of byssal threads by some species to attach themselves to substrate (Peyer *et al.,* 2009). Zimmerman and de Szalay, (2007) found that mucket (*Actinonaias ligamentina*) and kidney shell mussels (*Ptychobranchus fasciolaris*) stabilised sediment when they were

dormant but also had bioturbation effects whilst burrowing and reproducing. Mussel aggregations can be extensive in freshwater habitats (e.g. several thousand invasive zebra mussels (*Dreissena polymorpha*) per m^{-2} in the Hudson river, USA; Strayer, 1999) and can provide stable habitat for other invertebrates (Ricciardi *et al.,* 1997; Vaughn and Spooner, 2006). Furthermore, zebra mussels may reduce suspended sediment levels by filter feeding (Skubinna *et al.,* 1995; Strayer, 1999).

Invertebrate biostructures, including cases of caddisfly, can provide a stable spot for calcium carbonate to deposit (Roche *et al.,* 2019), resulting in bioherms (accretionary mounds consisting of fossilised remains surrounded by different geology; Cummings, 1932; Figure 1.1). In Western China, He *et al.* (2015) recorded caddisfly bioherms 3-5 m high stretching 400-500 m laterally. Similarly, bioherms predominantly composed of layers of caddisfly cases and calcium deposits line the shores of Lake Gosiute, Wyoming, USA (Leggitt and Cushman, 2001; Figure 1.1). These bioherms are extensive; 70 km in length, 9 m in height and 40 m in diameter (Leggitt and Cushman, 2001).

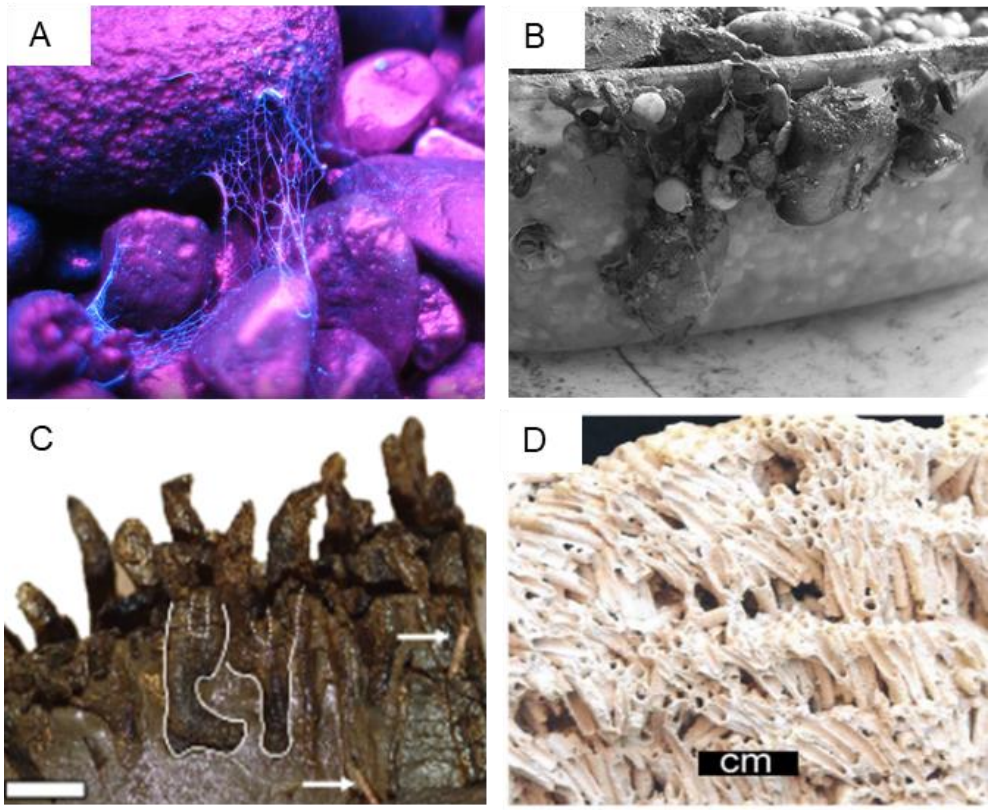


Figure 1.1. Examples of documented caddisfly zoogeomorphology to date. (A) Sediment stabilisation by caddisfly filter-feeding nets. (B) Caddisfly retreats can stabilise both coarse and fine gravel. (C) Bioerosion by caddisfly burrows which extend 40 mm into mudstone (white outline) accompanied by smaller Chironomidae burrows (white arrows) (Scale bar = 1 cm; Savrda, 2019). (D) Layers of caddisfly form calcium carbonate bioherms. Each caddisfly case is orientated vertically with the anterior end downwards (Leggitt & Cushman, 2001). (A) and (B) photos M. Johnson.

Therefore, many lotic invertebrates have been demonstrated to have zoogeomorphic effects, acting to both stabilise and destabilise sediment. A significant challenge for biogeomorphology is to understand the net effects of a vast range of organisms that vary widely in behaviour and may have complicated and often contradictory zoogeomorphic effects under different biotic and abiotic conditions. Zoogeomorphic research is usually undertaken at limited spatial and temporal scales (short term field or flume experiments) and few studies attempt to understand the effects of organisms at scales typically studied by geomorphologists (e.g. Rice *et al.,* 2016). There is also a need to study the zoogeomorphic effects of more taxa, particularly aquatic invertebrates which have received less research in rivers (Albertson and Allen, 2015; Rice *et al.,* 2012). Taxa which create bioconstructions or provide bioprotection using autogenic secretions are particularly effective sediment stabilisers in aquatic ecosystems, including Polychaete worms, mussel byssal threads, Chironomidae tubes and net-building caddisfly. In rivers, net building caddisfly have received a great deal of research for their stabilisation of gravel-beds with filter feeding nets. However, the zoogeomorphic effects of case construction by caddisfly larvae have not been considered.

1.4 Caddisfly biology and case-building behaviour

1.4.1 Caddisfly diversity and life history

Caddisfly (Trichoptera) are one of the most diverse orders of aquatic insects (Holzenthal *et al.,* 2007; Malm *et al.,* 2013). There are currently 16,267 extant caddisfly species recorded (Morse, 2020), of which, 198 are found in the UK (Wallace *et al.,* 2016). Caddisfly are found in all biogeographical regions except for the Antarctic (de Moor and Ivanov, 2008). They are abundant in most freshwater systems including rivers, lakes and ephemeral systems often occurring in densities of several thousand per meter square (Mcneely and Power, 2007; Wiggins, 2004; de Moor and Ivanov, 2008). Caddisfly larvae vary in size but are usually < 30 mm long (Wallace *et al.,* 2003). Caddisfly larvae are typically aquatic (with one exception in the UK; Wallace, 2016), and the adults are terrestrial (Figure 1.2).

The lifecycle of a caddisfly usually takes approximately one year in temperate latitudes (univoltine), although this varies with taxa and environment (Becker, 2005; Cudney and Wallace, 1980). Most of a caddisfly's lifecycle is spent as a larvae, during which time caddisfly go through a number of instars (larvae development stages; usually 5; Wiggins, 2004; Figure 1.2). For most species at temperate latitudes, metamorphosis from pupae to adult takes about three weeks

(Wallace *et al.,* 2003). The new adult uses its pupal mandibles (powered by the muscles of the adult) to cut its way out of the cocoon and case and swim (using pupal swimming legs) to the surface where it climbs onto emergent substrate or vegetation (Figure 1.2). Adult caddisfly do not have mandibles so either require liquid food (e.g. nectar or honeydew from aphids) or use energy stored from larval feeding (Wiggins, 2004). Typically female caddisfly dive into the water to lay eggs, or fly down to the water surface and release eggs (Figure 1.2).

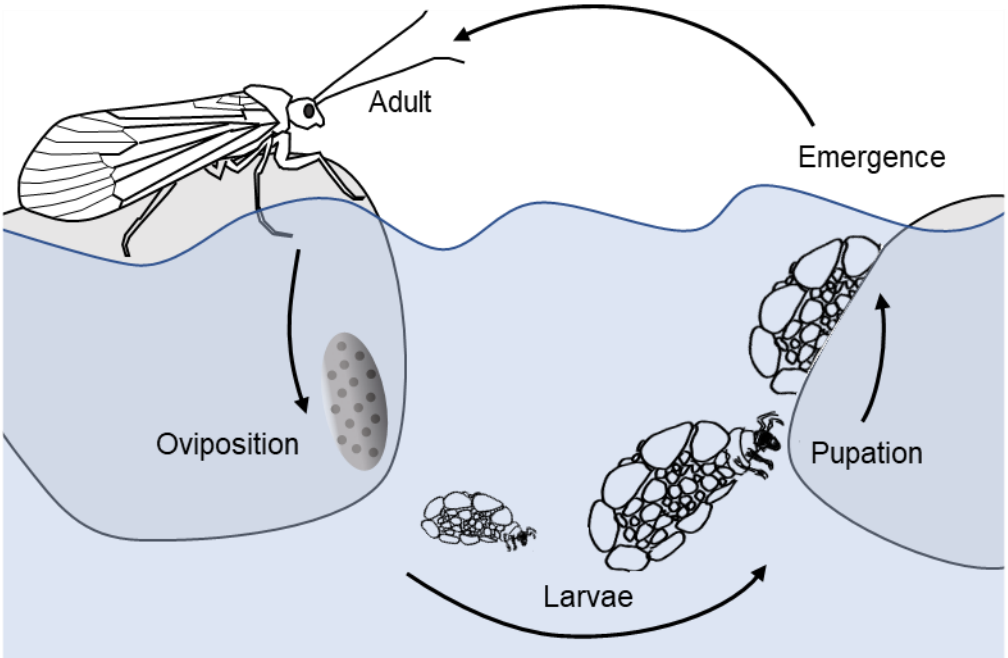


Figure 1.2. Lifecycle of a case-building caddisfly. Larvae are typically aquatic whilst the adult is terrestrial. Timings, number of larval instars and number of generations per year vary between species.

Caddisfly larvae are diverse in their functional behaviour. For example, caddisfly larvae vary in their feeding strategies (Cummins, 1995; Wiggins and Mackay, 1978). Scrapers and grazers use their specially adapted mandibles to feed on microscopic organisms (e.g. diatoms, other algae and protozoans; Wiggins, 2004). Shredders utilise vascular plant material and aid in leaf litter decomposition, a major source of energy in streams (Vannote *et al.,* 1980). Filter feeders construct nets to catch food from the water column. The abundance of filter feeders can be particularly high because they do not rely on resources from their immediate environment (Wallace *et al.,* 1977). A number of caddisfly are also predators of other invertebrates and occasionally larger organisms (e.g. eggs and tadpoles of wood frogs; Rowe *et al.,* 1994). Due to their feeding behaviour, caddisfly larvae perform essential roles in stream ecosystems, including processing of organic matter by shredders (Graça, 2001; Wallace and Webster, 1996), secondary

productivity as food for higher organisms (including fish), and affecting the structure of algal communities (Hart, 1985; Kohler, 1992; McNeely and Power, 2007). In addition caddisfly provide a number of ecosystem services (See Morse *et al.,* 2019). However, it is for their bioconstruction that caddisfly are of most interest to zoogeomorphologists.

1.4.2 Caddisfly architecture and bioconstruction

Caddisfly (Trichoptera) have evolved diverse strategies to survive and thrive in lotic habitats and the production of silk is believed to be central to their evolutionary success (Wiggins, 2004). Silk is a protein synthesized by the larvae and produced from silk glands at the tip of the labium (a mouth part; Holzenthal *et al.,* 2007). Caddisfly silk has high specific strength and ability to stretch and can more than double in length before breaking (Brown *et al.,* 2004; Tszydel *et al.,* 2009). Therefore, caddisfly structures can be strong and long lasting (Albertson and Daniels, 2016; Maguire *et al.,* 2020).

Silk allows caddisfly larvae to create a wide variety of structures. Wiggins (1996) classified larvae into five groups (Figure 1.3, i – v) 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. These architecture types broadly fit with the three typically recognised taxonomic caddisfly suborders; Annulipalpia (retreat builders), Integripalpia (tube case-builders) and Spicipalpia (free living, dome and purse cased caddis; de Moor and Ivanov, 2008; Holzenthal *et al.,* 2007; Wiggins, 2004). Most caddisfly species (Figure 1.3, all groups i-v including net builders and free-living taxa) construct or modify cases for pupation (Wiggins, 1996). Therefore, most caddisfly taxa build a case at some point in their lifecycle.

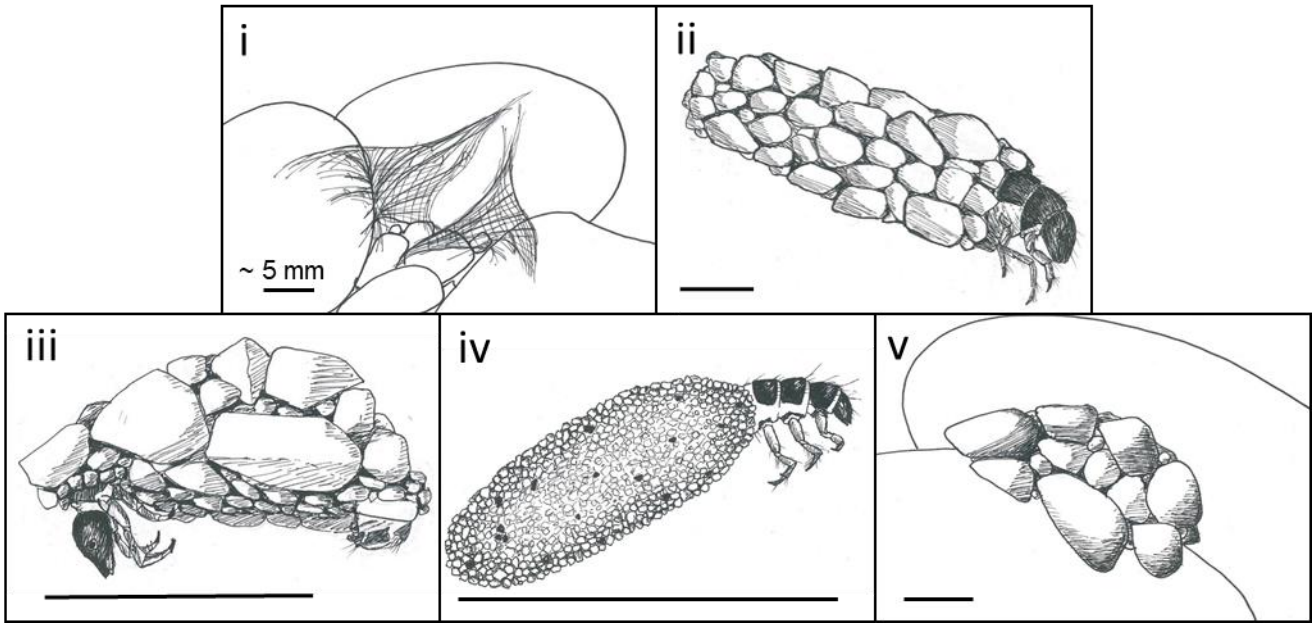


Figure 1.3. Diversity of caddisfly larval and pupal architecture (after Wiggins, 1996). (i) Nets filter food from flowing water, often accompanied by a static retreat in which the larvae resides (e.g. Hydropsychidae). (ii) Tubular cases which are usually mobile but may be fixed to stable particles for 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.

Case-building caddisfly use mineral and/or organic sediment in the construction of a wide range of case designs (e.g. Figure 1.3). The design of cases is largely dependent on the species and instar of caddisfly (Wallace *et al.,* 2003). The size of the overall case, and the individual sediment particles incorporated, typically becomes larger as the larvae grows (Statzner, 2011). Case design may also change with larvae instar, with some taxa only building cases in later instars or changing from organic to mineral sediment as they develop. For example, Hansell (1972) described the tubular case building (Figure 1.3ii) of *Lepidostoma hirtum* (Lepidostomatidae). *L. hirtum* builds a case from fine mineral grains shortly after hatching and periodically extends its case by adding material to the anterior (front end) and cutting material off the posterior (back end), during each instar. At the third instar, *L. hirtum* larvae added rectangular leaf panels, thus transitioning from a mineral to organic case (Hansell, 1972). Whilst most tube case-builders construct one case and modify it during their larval life stage (as for *L. hirtum*), dome/ saddle case-builders such as Glossosomatidae (Figure 1.3iii) build a new case at the start of each instar (Becker, 2005; Houghton and Stewart, 1998). Some caddisfly species are highly selective of the sediment that they incorporate into their cases and will sort through and discard many particles (Hansell 1968), assessing their size, shape, density and surface texture (Okano & Kikuchi 2012). Caddisfly larvae

can adapt their case design based on sediment availability (Okano *et al.,* 2010; Statzner and Dolédec, 2011), including the use of artificial particles such as plastic (Ehlers *et al.,* 2019). Some evidence suggests that larvae may also change their case design based on biotic context, such as the presence of predators (Boyero *et al.,* 2006), or abiotic context, such as differences in flow velocity (Delgado and Carbonell, 1997).

During pupation (Figure 1.2), tubular case-builders (Figure 1.3ii) modify their cases slightly, fixing them to stable substrate and adding silk to the anterior and posterior ends to reduce risk of predation but maintain water flow for respiration (Wiggins, 2004). Net and retreat taxa construct a chamber of mineral or plant material with a silk lining. This may be adapted from the retreat although most species abandon their existing retreat and build a new cocoon (Figure 1.3v; Holzenthal *et al.,* 2007; Wiggins, 2004). Dome case-builders often construct a new case, while free-living and net-building taxa build cases only for pupation. These pupal cases are attached to the river bed with silk (Holzenthal *et al.,* 2007).

Building cases is extremely costly for caddisfly larvae, requiring substantial energy investment to collect and orientate the constituent particles and for silk production. Otto (1975) determined that 12% of the total energy expended in the final instar of *Potamophylax cingulatus* (Limnephilidae; tubular case-builder) was used in silk production for case building and this comes at a cost of larvae growth (Stevens *et al.,* 1999). Cases must provide a benefit to caddisfly larvae to justify this investment. Cases act as camouflage, deterrent and provide protection if larvae are attacked (Johansson, 1991). For example Ferry *et al.* (2013) found that the presence of a case aided in caddisfly survival against larval dragonfly. Cases of many tube case-builders also aid in respiration because larvae perform undulations to pump water through the case (Feldmeth, 1970; Williams *et al.,* 1987). However, dome case-builders (e.g. Glossosomatidae) do not undulate within their case, instead building cases with many gaps and preferring fast flowing habitats to ensure that water circulates through the case and over the larvae's gills (Okano *et al.,* 2016; Williams *et al.,* 1987). Heavy, mineral cases may also provide useful ballast in lotic habitats, reducing the effort the larvae needs to put into avoiding entrainment and drift (Otto and Johansson, 1995; Statzner and Holm, 1989; Webster and Webster, 1943).

Previous research concerning sediment use by case-building caddisfly has focused largely on individual species and the functional importance of structures to the larvae (De Gispert *et al.,* 2018; Limm and Power, 2011; Otto and Johansson, 1995), rather than the effects of caddisfly case-building on sediment stability and transport.

1.5 Aim and objectives

Based on the literature reviewed above, the aim of this thesis is to investigate and quantify the effect of case-building caddisfly on the distribution and transport of sediment in rivers. To achieve this, the thesis will encompass two in-situ field studies and two ex-situ flume experiments. Research will be conducted across a range of spatial and temporal scales from the transport of individual caddisfly cases up to understanding seasonal variability in sediment transport by caddisfly at the reach scale. The thesis aims to address three specific objectives:

1) To quantify the mass and grain-size of sediment incorporated into caddisfly cases and identify the individual taxa responsible, in riffle habitats of a lowland stream (Chapter 2).
2) To determine the effect that case construction by caddisfly larvae has on the hydraulic force required to transport incorporated sediment (Chapter 3).
3) To ascertain the importance of caddisfly in transporting and redistributing sediment over the riverbed (Chapters 4 and 5).

1.6 Justification of aim and objectives

Animals can have important zoogeomorphic effects on the transport of sediment in rivers, with consequences for river morphology, habitat and ecosystem services. Whilst the zoogeomorphic effects of a wide range of lotic taxa have been examined, the effects of aquatic invertebrates are understudied in rivers, compared to terrestrial and marine habitats. Case-building caddisfly are widespread and often extremely abundant in rivers and exhibit behaviours with the potential to have important effects on sediment distribution and transport. However, the zoogeomorphic effects of caddisfly case-construction have received little research.

The mass and grain size of sediment used by caddisfly is known for individual cases of some species (e.g. Tolkamp, 1980). However, the quantity of sediment used by the whole caddisfly community at a single site has never been measured. The grain-size used by caddisfly varies between species from fine sand to fine gravel (Statzner *et al.,* 2005; Tolkamp, 1980). Therefore, it is important to identify the mass and grain size distribution of sediment which may be directly affected by case-building caddisfly (i.e. tied up in cases). Objective 1 will address this research gap by quantifying both the mass and grain size characteristics of mineral sediment used by case-building caddisfly. It also helps to understand the potential spatial scale and variability of case-building caddisfly zoogeomorphic effects.

Some case-building caddisfly are known to bioturbate sediment by burrowing (De Nadaï-Monoury *et al.,* 2013) and caddisfly cases can promote precipitation of tufa in calcareous environments (Leggitt and Cushman, 2001), but case-building caddisfly may have a much broader range of unstudied zoogeomorphic mechanisms, hypothesised in Figure 1.4. Case construction involves binding sediment particles together with silk (Hansell, 1968; Okano *et al.,* 2016), producing a composite particle of reduced density and relatively large volume. Caddisfly may therefore modify the entrainment characteristics of sediments incorporated into their cases (Figure 1.4A). The shear stress required to move caddisfly cases varies with species, case size and whether the case is occupied (Otto & Johansson, 1995; Statzner and Holm, 1989; Waringer, 1993), but there has been no systematic examination of the mobility of cases relative to their constituent grains. It is unknown whether case construction will increase or reduce the mobility of constituent sediment; fundamental to understanding the zoogeomorphic effects of case construction. Objective 2 will address this research gap through ex-situ flume experiments, considering three species of empty caddisfly cases, and their constituent mineral grains.

Unlike caddisfly nets and retreats, or mounds built by ants and worms, caddisfly case bioconstructions are often transported around with the larvae. Many caddisfly species crawl large distances (~ 1 – 4 m day^{-1}, Erman, 1986; Jackson *et al.,* 1999; Lancaster *et al.,* 2006), transporting their case and constituent sediment with them. Case-building caddisfly may therefore directly transport sediment, vertically and horizontally over the river-bed (Figure 1.4B & C) and may move sediment upstream (Williams and Williams, 1993; Bergey, 1989; Hart and Resh, 1980). Sediment movement by caddisfly may be an important flux of sediment itself or it may modify the exposure of this sediment to hydraulic forces and affect sediment transport. Therefore, it is important to understand the transport of sediment by caddisfly larvae and the consequences of this movement for sediment distributions and bedload transport in rivers (objective 3).

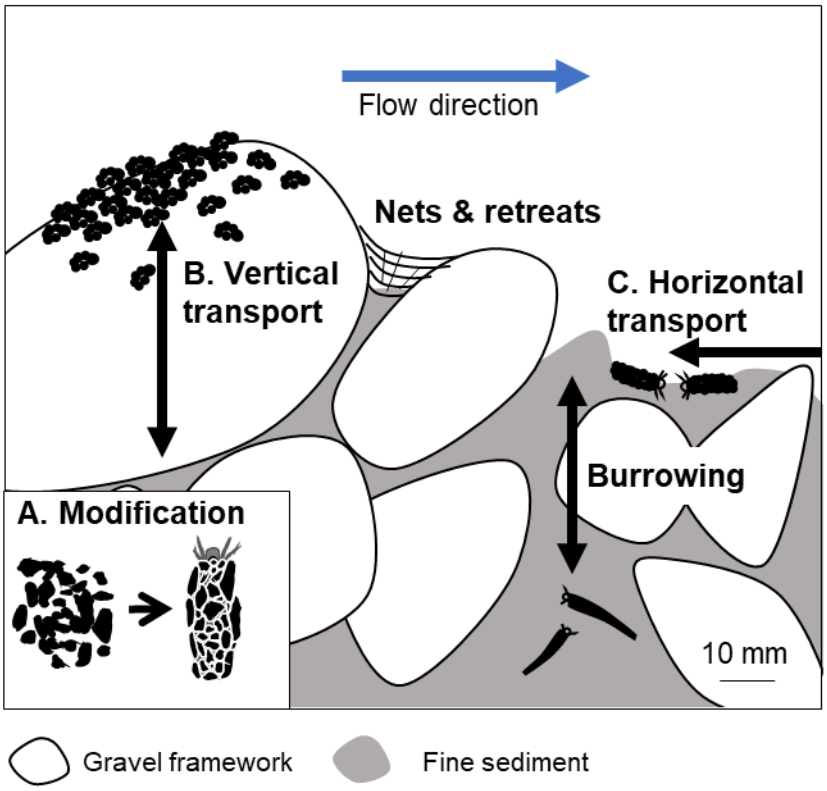


Figure 1.4. A conceptual diagram showing possible zoogeomorphic impacts of caddisfly in gravel-bed rivers. Previous research has considered nets and retreats and burrowing taxa. This thesis will examine the zoogeomorphic effects of case construction. (A) All case-building caddisfly change the size, shape, mass and density of sediment particles by combining them into cases with potential implications for the mobility of this sediment. (B) Case-building taxa may transport fine sediment vertically, with potential consequences for the flow exposure and mobility of this sediment. (C) Case-building taxa may also transport sediment horizontally over the riverbed.

1.7 Thesis structure

This thesis is comprised of 6 chapters (Figure 1.5). Following the introduction and literature review (This Chapter), the thesis research is divided into four separate projects (Chapters 2-5) which address the thesis aim and objectives. Chapter 2 measures the mass and spatial variability of sediment used by the case-building caddisfly larvae community. This was achieved using a field study to quantify sediment in caddisfly case samples collected from riffle habitats, spaced along a UK stream. Furthermore, Chapter 2 identifies the caddisfly taxa which have the potential to be important to zoogeomorphology, based on their abundance, sediment mass used and behaviour, providing the focus of future chapters. Chapter 2 also considers the importance of abundance and sediment availability in controlling sediment used by the caddisfly population. Chapter 2 therefore addresses thesis objective 1.

Chapters 3 and 4 are both laboratory flume experiments designed to better understand specific mechanisms by which case-building caddisfly may affect sediment transport. Chapter 3 addresses objective 2, investigating whether the construction of cases by caddisfly alters the hydraulic force required to move the sand incorporated into the case. This study is a small-scale flume experiment which compares critical entrainment thresholds for individual empty cases to the sand the cases were constructed from. This was examined for three species with differing case designs and considered the importance of case mass and shape in their entrainment thresholds.

Based on the importance of one species, Glossosomatidae *Agapetus fuscipes*, in Chapters 2 and 3, it was hypothesised that sediment movement by this taxon may be substantial and change the hydraulic exposure of transported sediment. Chapter 4 employs a flume study to measure sediment movement by *A. fuscipes* larvae, under low and high flow velocity and in gravel-beds with high and low grain protrusion. Chapter 4 therefore focusses on objective 3, documenting sediment movement by one caddisfly species in detail.

Chapter 5 expands the temporal and spatial scale of previous chapters to determine the role of case-building caddisfly in sediment transport, seasonally and at the reach scale. Chapter 5 uses bedload traps placed in a lowland stream to isolate and compare the geophysical and case-building caddisfly contributions to bedload transport over an annual period. Chapter 5 further addresses objective 3; considering seasonal variations and the contribution of different caddisfly taxa to sediment transport.

Chapter 6 discusses the results of Chapters 2-5. The fulfilment of thesis objectives are reviewed, followed by an updated version of Figure 1.4; discussing additional understanding of the

mechanisms of case-building caddisfly zoogeomorphology as a result of this thesis research. Subsequently the zoogeomorphic effects of caddisfly taxa from each architecture group (Figure 1.3) are discussed. Last, the challenges in upscaling the thesis results and the potential implications of caddisfly zoogeomophology for river geomorphology and ecology are examined.

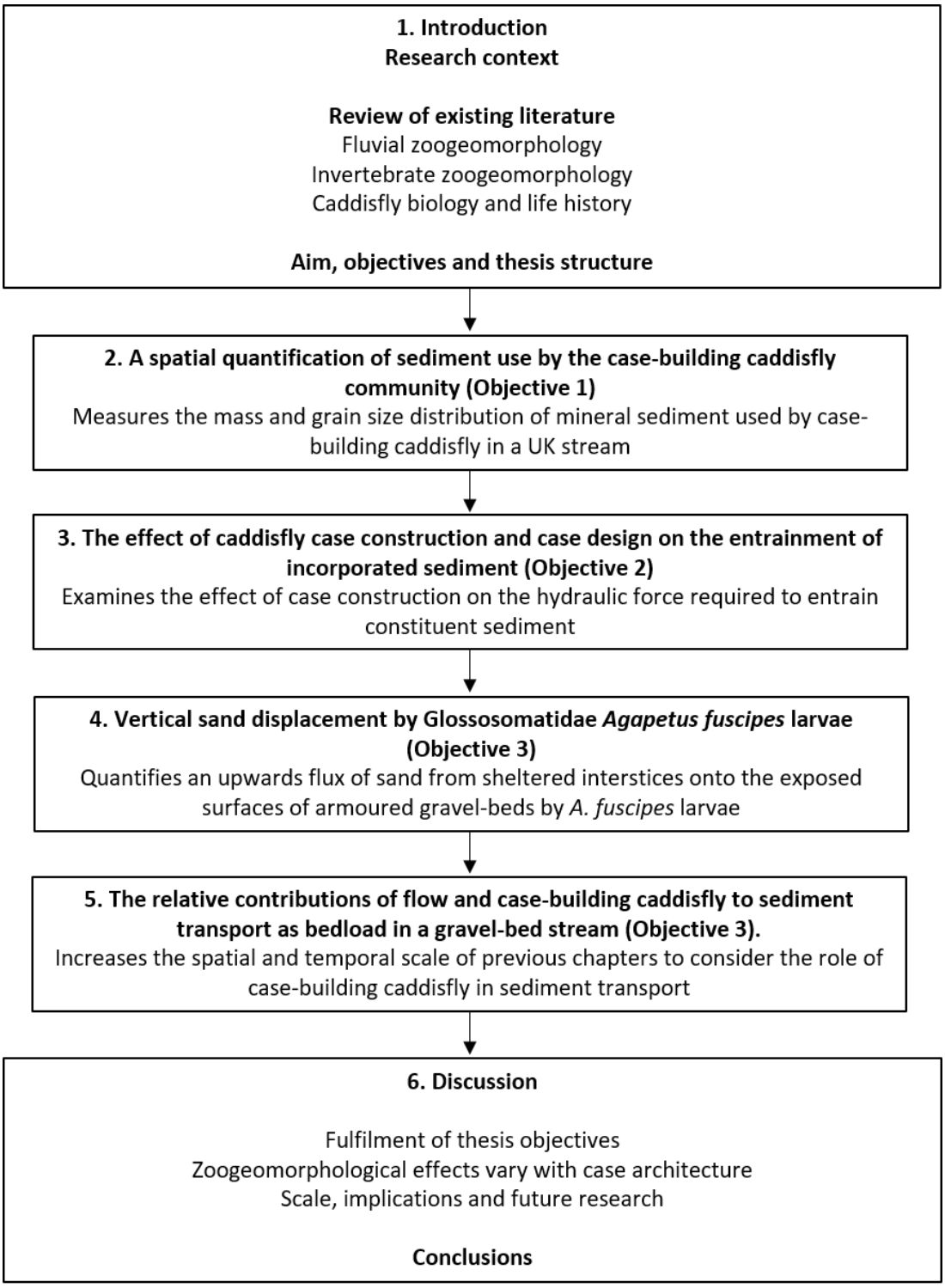


Figure 1.5. Structure of the thesis outlining the six chapters.

Caddisfly in an alpine river, near Briançon, France.

Note: Figures at the head of each chapter are not included in the figure list or referred to in the text because they are not part of the scientific argument, rather are used to enhance the presentation and provide a break between each chapter.

Chapter 2. A spatial quantification of sediment use by the case-building caddisfly community

This chapter is based largely on a published manuscript but has been adapted to fit the thesis.

Published as: Mason, R.J., Rice, S.P., Wood, P.J., Johnson, M.F., 2019. The zoogeomorphology of case-building caddisfly: Quantifying sediment use. Earth Surface Processes and Landforms. 44, 2510 – 2525. DOI: 10.1002/esp.4670.

This chapter differs from the published version in the following ways:

1) Paper introduction has been shortened and elements of the published version have been included in the thesis introduction.
2) Minor edits have been made to the methods, results and discussion.

Author contributions:

Richard J Mason: Study design, field work, laboratory and data analysis, and chapter write-up.

Stephen P Rice, Paul J Wood and Matthew F Johnson: Advised with fieldwork, laboratory procedure, data analysis, and reviewed the published manuscript and chapter.

2.1 Introduction

Gravel-bed rivers are characterised by coarse sediment (>2 mm diameter) but often contain substantial quantities of fine sediment (< 2 mm), with bed sediment sometimes exceeding 30% sand by mass (Church, 2010). This fine sediment is important to sediment transport (Wilcock and Kenworthy, 2002), near-bed hydraulics (Laronne *et al.,* 2001) and habitat structure and availability (Wharton *et al.,* 2017; Wilkes *et al.,* 2019). 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). Therefore, understanding the transport and distribution of sand in rivers is important.

During case construction, caddisfly cement sand-sized sediment together with silk, creating aggregate particles, with potential zoogeomorphic implications (Figure 1.4). In many streams and rivers where caddisfly are abundant, case construction could involve the use of substantial quantities of sand. Previous research has considered the sediment used by individual caddisfly larvae for several species (e.g. Hansell, 1972; Tolkamp, 1980), but there has been little research on sediment used by groups of individuals and communities. Statzner *et al.,* (2005) estimated that the pupal cases of Rhyacophilidae and Hydropsychidae (groups v and i respectively, Figure 1.3) use between 1 and 3 kg m^{-2} (Statzner, 2011; Statzner, *et al.,* 2005). Preliminary studies indicate that the saddle-cased species *Agapetus fuscipes* (Glossosomatidae, Figure 1.3iii) used approximately 1.4 tonnes km^{-1} of sand to build their cases on the River Dove, U.K.

From a zoogeomorphological perspective, it is important to measure the mass of sand used by case-building caddisfly communities, to determine the mass of sediment which may be affected by their bioconstruction activities. Furthermore, it is important to understand which grain sizes are most affected by caddisfly bioconstruction. Individual caddisfly species use a wide range of grain sizes (~0.105 mm up to 5 mm; Statzner *et al.,* 2005; Tolkamp, 1980, Hansell, 1968; De Gispert *et al.,* 2018; Okano & Kikuchi, 2012) and its unknown what size range the caddisfly community will predominantly use. Knowing the species of caddisfly which dominate sediment use is also important because different taxa vary considerably in behaviour and therefore their potential zoogeomorphic effects.

The mass and grain sizes used by the caddisfly community will be controlled by the composition and abundance of caddisfly larvae as well as any variability in case design between individuals of the same species. 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 varies seasonally (e.g. some species only use mineral sediment grains when building pupal cases; Figure 1.3v; 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, both sediment use and the potential for zoogeomorphic effects are likely to vary spatially and temporally.

This chapter quantifies the mineral sediment use by case-building caddisfly in a UK stream (thesis objective 1). 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, the grain size distribution and quantity of sediment used by each of the case-building taxa present are measured and compared to sediment use between taxa. The spatial variation of sediment was investigated 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 1.4). 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 chapter addresses objective 1 of the thesis via 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?

2.2 Methods

2.2.1 Field sampling

Caddisfly and bed sediment samples were collected from riffle habitats in Wood Brook, Leicestershire, UK (Figure 2.1). Wood Brook is a 1st – 2nd order gravel-bed stream with an average width of 1.5 m and depth of 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 surficial geology is largely mudstones, siltstone and alluvium. The median discharge of Wood Brook for the five years prior to sampling was 0.03 $m^3 s^{-1}$. This was calculated from 15 minute resolution stage data and spot discharge measurements, fitted with a rating curve, provided by the Environment Agency. The slope of Wood Brook over the study area was 0.02 and the mean D_{50} of surface sediment was 38 mm.

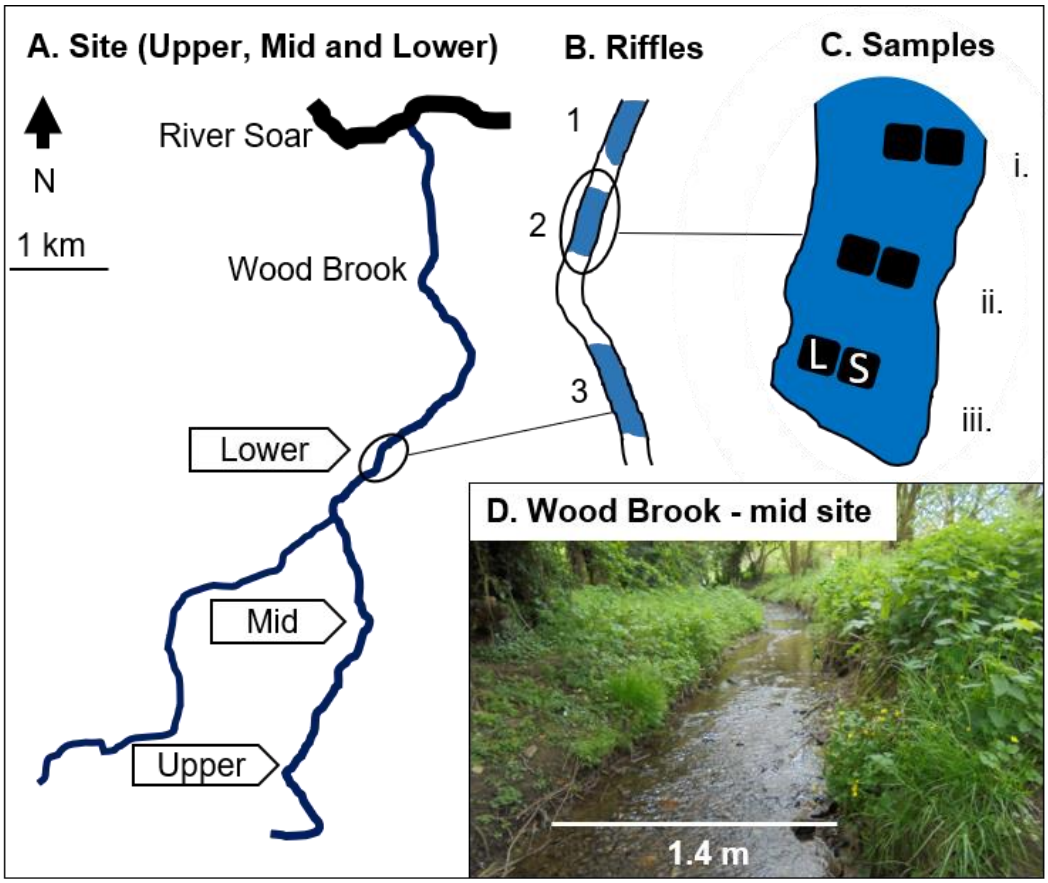


Figure 2.1. Study site and sampling strategy. (A) Wood Brook (drawn from EDINA, 2018). Three sites were sampled; upper, mid and lower. Mid site: 1° 13.4124' W, 52° 45.0648' N. (B) Three riffles were sampled, nested within these three sites. (C) Three samples were taken within each riffle (i. – iii.). In each case, caddisfly larvae (L) and sediment (S) were sampled from proximate locations. (D) Wood Brook at the mid site, riffle 2.

Caddisfly and sediment samples were collected from three sites along Wood Brook, (referred to as upper, mid and lower; Figure 2.1) 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 m in length; Figure 2.1) and three longitudinally distributed samples collected from each, making a total of 27 units (i.e. 3 samples x 3 riffles x 3 sites). Caddisfly communities and case characteristics are known to vary seasonally, therefore all samples were collected during a one-month period between 28th March and 26th April 2017, recognised as an optimum time for instream macroinvertebrate diversity 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 x 310 mm frame with a 1 mm 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 2.1C). 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 x bed D_{50}).

2.2.2 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 (using Edington and Hildrew, 1995 and Wallace *et al.,* 2003), although early instar taxa (e.g. *Athripsodes* sp.) were not identified beyond genus. Larvae and case length were measured to the nearest mm (Tolkamp, 1980). When more than 10 individuals of a species were present, length was estimated for a random subsample (mean 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.

After preliminary trials, a methodology was developed to break down the silk structure of cases to disaggregate the mineral particles without damaging them. First, caddisfly cases were immersed in 30% hydrogen peroxide (H_2O_2) at 80°C for at least five hours and stirred periodically. For cases with high organic content some larger organic particles were removed manually. H_2O_2 was then removed by washing the samples with deionised water through a 38 mm diameter, 0.063 mm aperture, sieve and then dried overnight at 80°C. The disaggregated sediment was finally mechanically sieved through 5.6 mm to 0.063 mm (38 mm diameter sieves), at half phi intervals and weighed. Individual fractions were weighed on a 4 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 samples removed respectively, leaving 151 samples). Bed sediment samples were dried at 105°C for 12 hours and then sieved into half-phi intervals down to 0.063 mm using a mechanical sieve shaker.

2.3 Data Analysis

2.3.1 Sediment use by individual taxa

The grain size distribution (GSD) 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 GSDs. 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 GSDs, 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, $\overline{D50}$, $\overline{D5}$ and $\overline{D95}$ are reported for each taxon, where the bar indicates the mean of all values across the river. The $\overline{D5}$ and $\overline{D95}$ are used to give a measure of the range of grain sizes used by each taxon that excludes the most extreme sizes.

2.3.2 Sediment use by the whole caddisfly community in a Surber sample

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 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 GSD 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 GSD 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 samples, to 1 m^2 for ease of interpretation.

2.3.3 Spatial variability in sediment use by the caddisfly community

In order to address Question 2, the mean mass and GSD of sediment used by the caddisfly community in each sample were grouped into the three sites (upper, mid and lower), with nine samples in each (i.e. 3 replications in 3 riffles within each site). A Shapiro-Wilk test revealed that these predominately 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 from each other. Shapiro-Wilk, Kruskal-Wallis and Dunn's tests were conducted using the *stats* package in R Studio (version 3.3.3, R Core Team, 2017).

2.3.4 Is caddisfly abundance a control on the mass of sediment used?

To address this question, I assumed that differences in the total sediment mass used in different locations (i.e. variability between samples) reflect: 1) differences in the abundance and composition of the 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). The relative importance of these factors was investigated using linear regression between abundance (independent variable) and the total mass of sediment used (dependant 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 and therefore that within species variability in case mass is low. Samples without sediment use by a particular taxon were excluded from the regression analysis but samples with sediment use (cases), but no larvae (larvae may have been lost in sampling or emerged as adults), were included. *Agapetus fuscipes* (Glossosomatidae) were the focus of further investigation of within species variability 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 with variability in the size of sediment used, the mean and standard deviation of GSDs were plotted for each site.

Furthermore, the correlations between mean case mass, mean case D_{50} and mean larvae length across all sites for this taxon were used to investigate potential explanations for the variability in case mass.

2.3.5 Relation between sediment availability and sediment use

To investigate how sediment use varied with sediment availability, the GSDs 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.

2.4 Results

2.4.1 Sediment use by individual caddisfly taxa

There was considerable variability in the mass and size distribution of cases of individual taxa (Table 2.1, Figure 2.2). The tubular cases of Leptoceridae and Lepidostomatidae used fine sand (D_{50} = 0.17 mm) and 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 (Table 2.1, Figure 2.2). Goeridae cases were unusual because coarser particles secured to the case edges resulted in a bimodal sediment distribution. The size distribution of Glossosomatidae cases (dome 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 2.1, Figure 2.2). Therefore, case-building caddisfly exhibited considerable variability in larvae and case size, particle size distribution and case mass, not just between structure groups (Figure 1.3) but also between families and species (Table 2.1, Figure 2.2).

2.4.2 Sediment use by the whole caddisfly community

A diverse caddisfly community was recorded with twenty-four taxa from ten families (Table 2.2) 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

2.2), but 94% of individual caddisfly larvae recorded. All taxa combined, the average total mineral mass used by case-building caddisflies was 37.57 g m^{-2}, but it varied across the 27 samples, ranging from 3.74 to 138.83 g m^{-2} (Figure 2.3A).

Due to the differences in case GSDs between taxa, the size range of mineral sediment used by the community was broad, from 0.063 mm to 11 mm (Figure 2.2). Therefore, caddisfly utilise the entire sand size range as well as fine gravel particles for case construction (0.063 mm < sand <2 mm < gravel; Wentworth, 1922). On average, sediment use was 84% sand and 16% fine gravel. The average particle-size distribution of sediment used (Figure 2.3B) was bimodal with a primary mode between 1 – 1.4 mm and another mode at 4 – 5.6 mm. The 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 2.3B), followed by pupae of Rhyacophilidae and Hydropsychidae (15%), and Limnephilidae (11%) with other taxa using less than 5%.

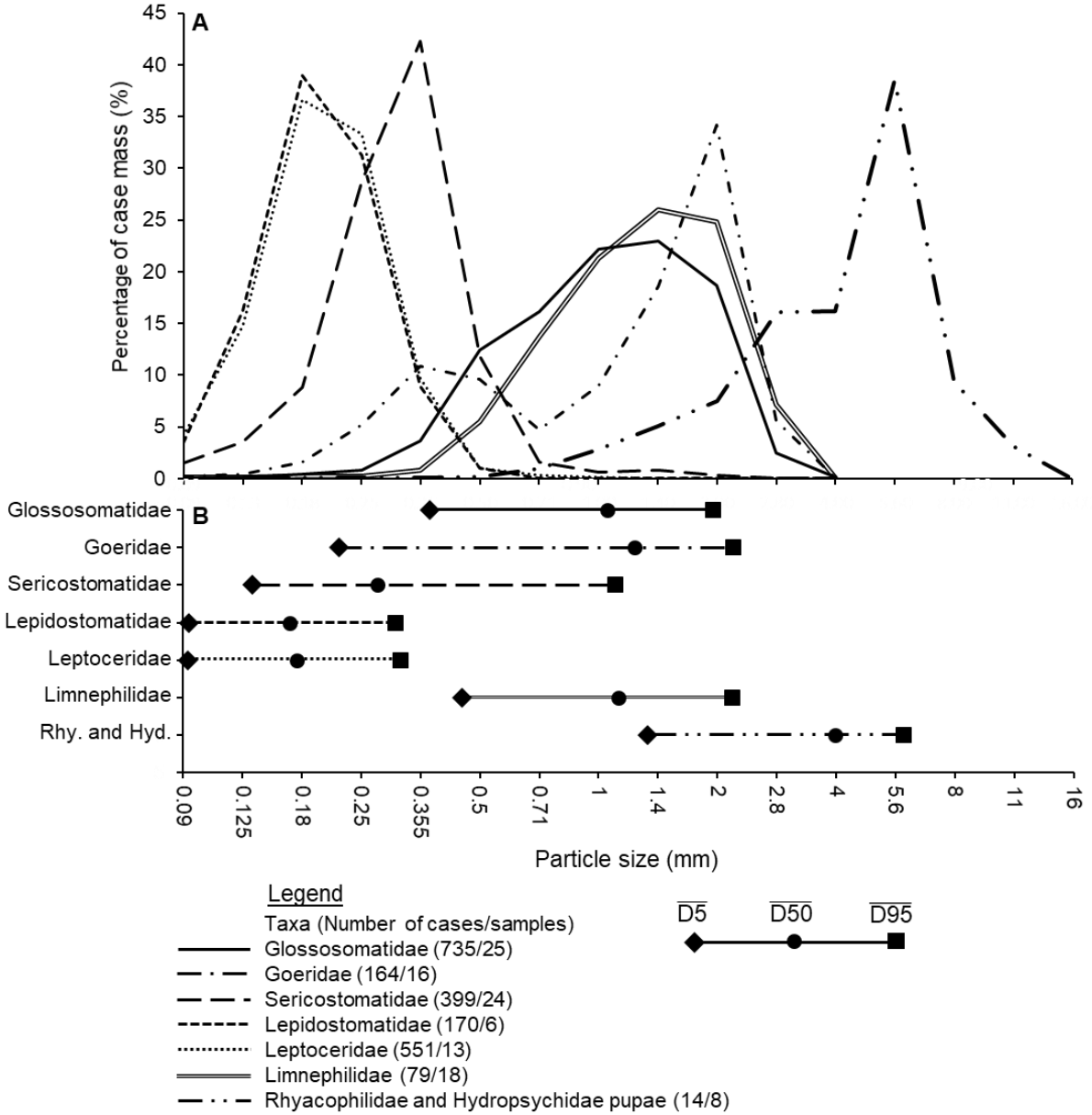


Figure 2.2. Particle size distribution of the cases of caddisfly taxa. (A) Grain size distribution averaged across all samples, for the six case-building families and for the pupal cases of Rhyacophilidae and Hydropsychidae combined. Particle size for (A) refers to the upper limit or passing sieve. (B) Spread ($\overline{D5}$ – $\overline{D95}$) and median ($\overline{D50}$) 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).

Table 2.1. Characteristics of larvae and cases for each case-building caddisfly taxonomic group and individual species of Limnephilidae. Values shown are the mean of all 27 samples, with standard deviation in brackets (only one incidence of *H. radiatus* and *C. villosa*). †Pupal cases of Rhyacophilidae and Hydropsychidae larvae.

	Larvae		Case				
Family	Number	Length (mm)	Length (mm)	Weight (g)	$\overline{D50}$ (mm)	$\overline{D5}$ (mm)	$\overline{D95}$ (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†	-	-	-	0.83 (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)
Potamophylax cingulatus	-	-	-	0.16 (0.05)	1.12 (0.14)	0.47 (0.05)	2.13 (0.25)
Potamophylax latipennis	-	-	-	0.17 (0.01)	1.31 (0.17)	0.48 (0.05)	2.24 (0.36)
Micropterna sequax	-	-	-	0.11 (0.05)	0.93 (0.37)	0.40 (0.11)	1.77 (0.53)
Halesus radiatus	-	-	-	0.063	1.39	0.51	2.64
Chaetopteryx villosa	-	-	-	0.028	0.57	0.30	1.04

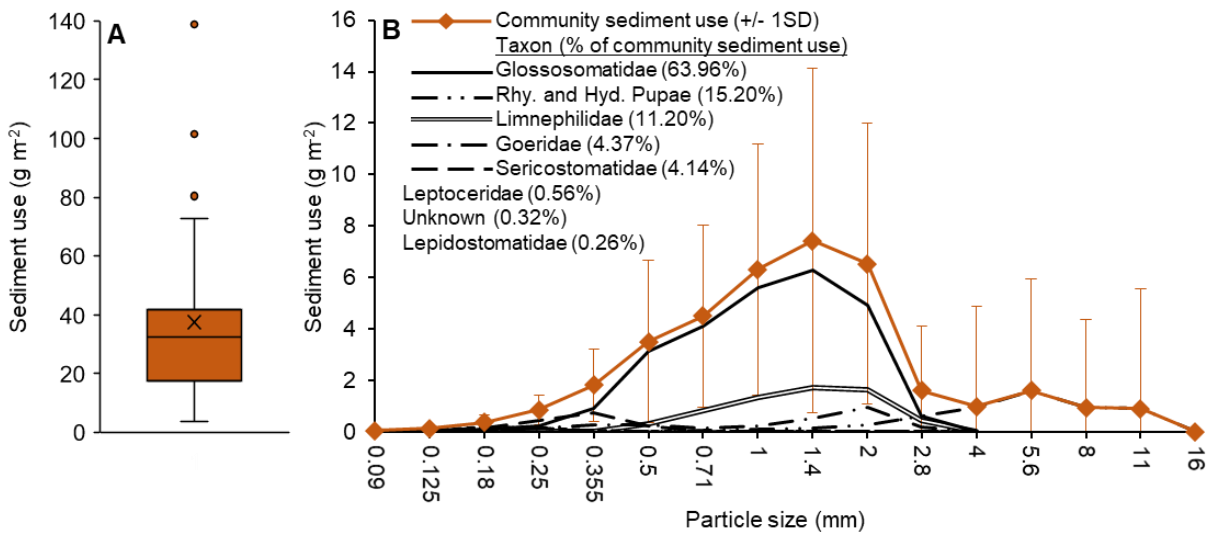


Figure 2.3. Total sediment use by the case-building caddisfly community and constituent taxa. (A) Boxplot of total community sediment use from all samples. The box denotes the median and interquartile range (inclusive of median), whiskers show interquartile range multiplied by 1.5 and the mean is indicated by x (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.

Table 2.2. Caddisfly taxa found in this chapter. Taxa are sorted according to their behaviour (after Wiggins, 1996); (1) taxa that used mineral sediments in their cases were included in sediment analysis and (2) cases that were not analysed for sediment content. †Cases for which a larvae 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. ‡Pupal cases of Hydropsychidae and Rhyacophilidae were identified only to family level but are likely to be the same species found elsewhere.

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

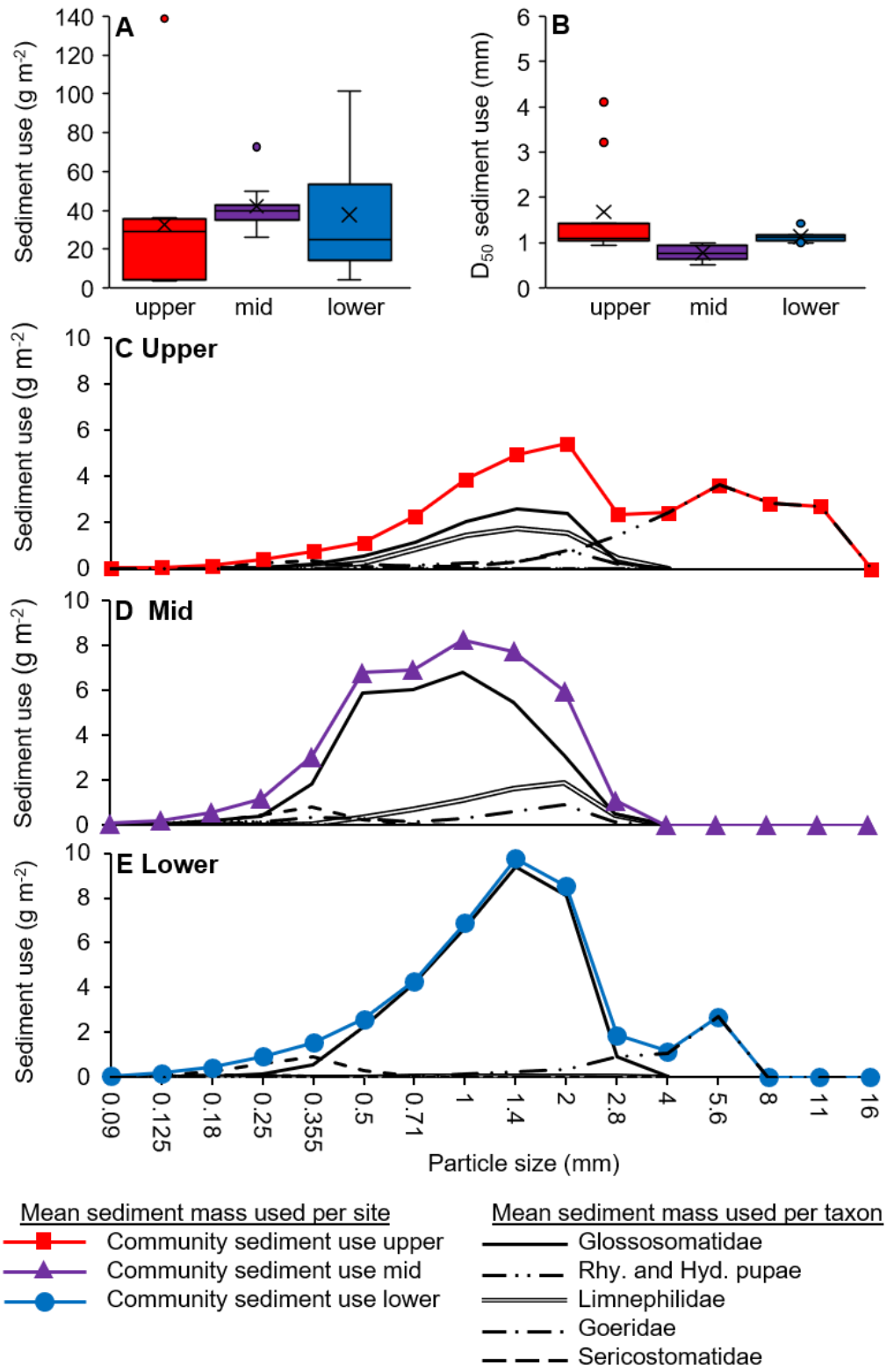


Figure 2.4. Variability in sediment use between sites (upper, mid and lower). (A) Boxplot showing the mass of sediment used by the caddisfly community at each site. (B) Boxplot showing the D_{50} of sediment used at each site. For both boxplots, the box denotes the median and interquartile range (inclusive of median), whiskers show interquartile range multiplied by 1.5 and the mean is indicated by x. (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.

2.4.3 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 2.3, mean at the upper site = 29.59, mid = 38.02, lower = 34.11 g m^{-2}, Figure 2.4A). However, the size of sediment used was significantly finer at the mid site than the upper and lower sites for D_{50}, D_{84} and D_{16} (Table 2.3, Figure 2.4B, mean D_{50} at the upper site = 1.61, mid = 0.79, lower = 1.11 mm). The upper and lower site were not significantly different for any grain size parameter (Table 2.3). The mass of sediment used by each taxon varied between sites (Figure 2.4C-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 GSDs 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.

Table 2.3. 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. 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.

Parameter	Kruskal-Wallis (K)	Dunns (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

2.4.4 Relation between abundance and sediment use

Abundance of the caddisfly community (all taxa) was a poor predictor of the mass of sediment used, explaining only 17% of variation (Table 2.4). This means that differences in case mass between individuals are important at a community level. When considering each taxon separately, for some taxa their 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 the mid (Table 2.4, Figure 2.5A). 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. 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 2.5B). There was a negative association between Glossosomatidae larvae abundance and mean case mass across all sites (R = -0.55, Figure 2.5C). However, in samples with low abundance, case mass varied substantially, whereas case mass was always lower at high abundance. A very strong correlation exists between Glossosomatidae mean case mass and D_{50} (Figure 2.5D) and between case mass and mean larvae length (Figure 2.5E). Overall, the abundance of most taxa, particularly Glossosomatidae, is a poor predictor of sediment mass used by this taxon due to within-taxon variations in the mass of cases built and the grain sizes used.

2.4.5 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 at upper and lower sites (38 and 40 mm respectively). Considering only the size range used by case-building caddisfly in this study, the average mass of bed sediment availability increased with grain size (Figure 2.6A). 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 2.6B). Sediment availability for all size fractions greatly exceeded the mass of sediment used by caddisfly larvae, resulting in a low percentage used overall (Figure 2.6C). 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 2.6B). 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 to taxa at all sites. Despite this, use of sediment by the case-building caddisfly community and Glossosomatidae were both skewed towards finer sediment at the mid site where this sediment was more abundant.

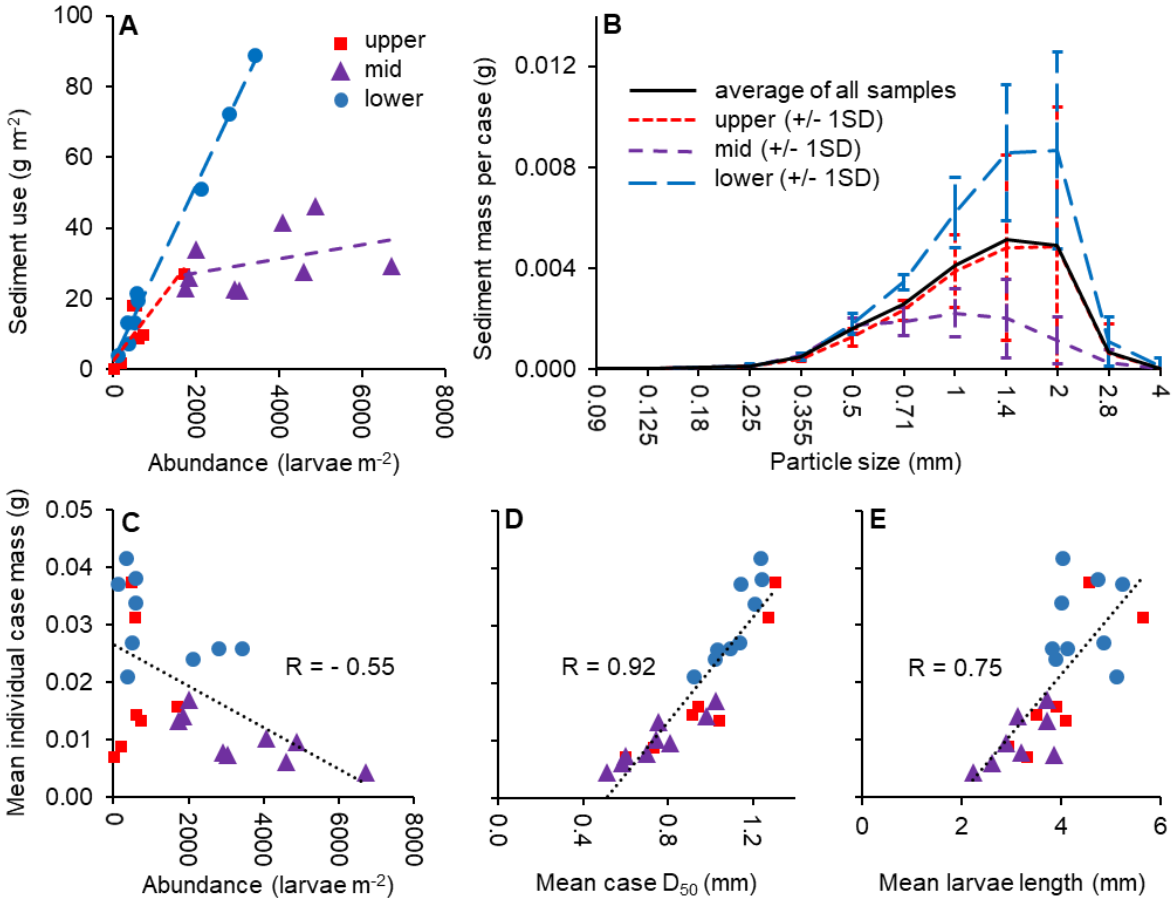


Figure 2.5. Variability in sediment use by *A. fuscipes* (Glossosomatidae) individuals between sites. (A) Plot of the relation between abundance and sediment use by this taxon giving the R^2 values in Table 2.4. Within each site abundance is a good indicator of sediment mass used but all sites combined 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.

Table 2.4. 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. 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.

	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)***

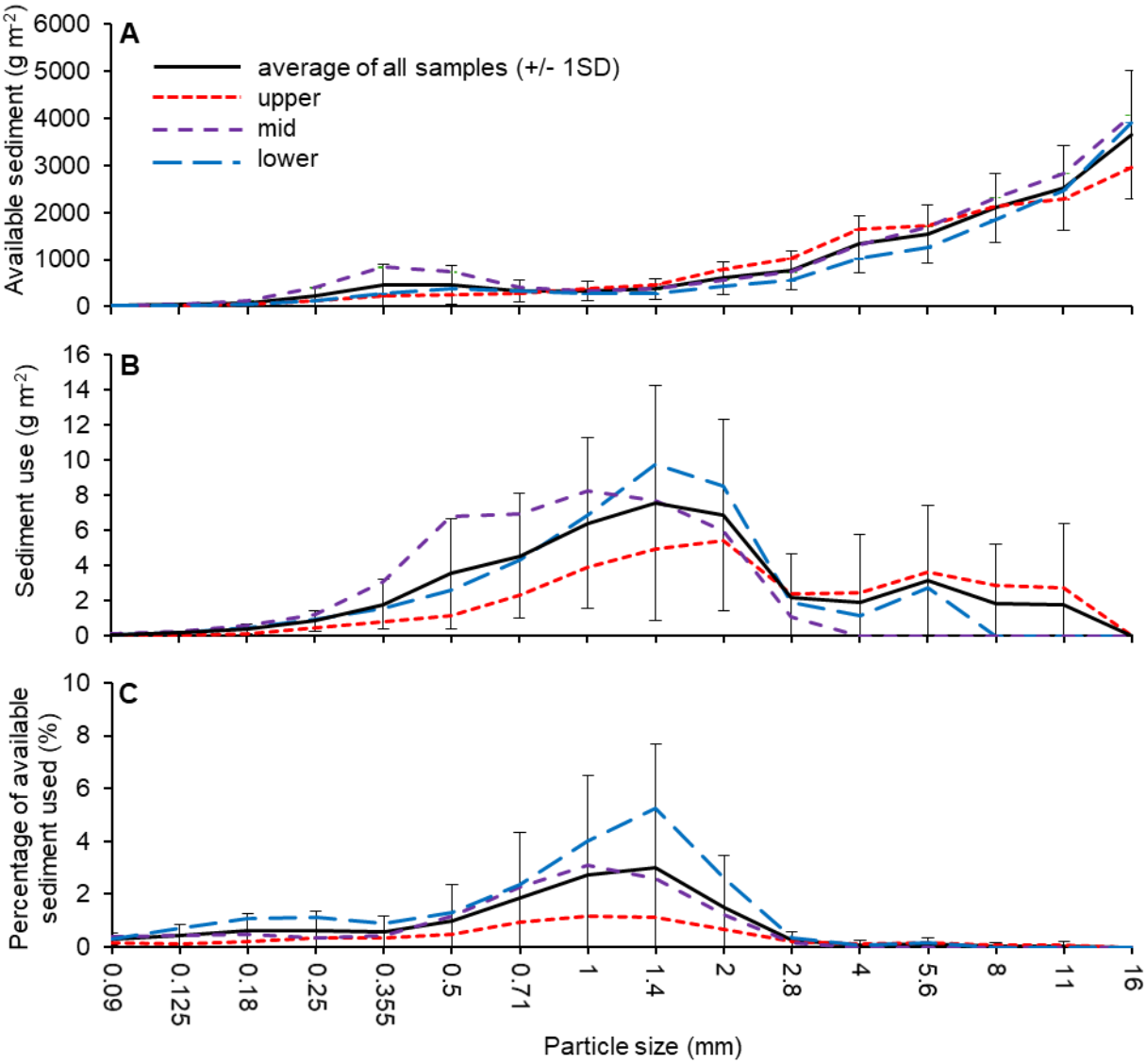


Figure 2.6. Sediment use in relation to available sediment in the river-bed. Particle-size distributions shown as a mean for the river as a whole (with standard deviation) and each site independently. (A) Mass of bed sediment available to case-building caddisfly. (B) Mass of sediment used by case-building 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.

2.5 Discussion

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

The caddisfly community of Wood Brook was diverse, both in terms of species richness and the design of silk structures, with all five case categories recorded (Figure 1.3, Table 2.2). About half of taxa were case-building caddisfly utilising mineral sediments, but due to their high abundance they accounted for over 90% of individuals. This suggests that if the mechanisms identified in Figure 1.4 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 2.2) probably reflects differences in the function of the larval cases (Otto and Svensson, 1980; Wiggins, 2004). For example, the fine grains used in Sericostomatidae cases (D_{50} = 0.27, Table 2.1) result in smooth, tapered cases, which may facilitate burrowing. Most taxa in this study used predominantly mineral sediments (Table 2.2), 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 (Otto and Johansson, 1995; Statzner and Holm, 1989; Webster and Webster, 1943). The results of this study demonstrate that both the size and magnitude of mineral sediment used is 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 caddisfly taxa, the community used sediment from 0.063 to 11 mm in diameter (Figure 2.3B). 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 2.3B), which are important size fractions geomorphologically, as they are often the most mobile bed-material size fractions (Ashworth and Ferguson, 1989; Jackson and Beschta, 1984; Kuhnle, 1993).

2.5.2 Sediment use by key taxa and potential zoogeomorphological importance

Several taxa are of particular zoogeomorphic 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 (Becker, 2001; Marchant, 1988; Statzner, 2011) and usually reside on the exposed upper surfaces of larger gravel particles where the flow of water facilitates respiration (Becker, 2005; Morris *et*

al., 2015; Morris and Hondzo, 2013a). Glossosomatidae may therefore have important effects on sand availability and hydraulic exposure at the bed-surface, where they are likely to affect downstream sediment transport

Despite their low abundance in this study, Rhyacophilidae and Hydropsychidae pupal cases were constructed from large particles and, therefore accounted for 15% of the overall sediment used by case-building caddisfly by mass (Figure 2.3B), and nearly 50% of sediment used at the upper site (Figure 2.4C). Statzner (2011) and Statzner *et al.* (2005) measured sediment use by these taxa in the Furan river, France, and found them to use substantial quantities of sediment (up to ~3 kg m^{-2}). They found considerably higher abundances of pupal cases (250 m^{-2} for *H. siltalai*; Statzner, 2011*),* compared to the average of 3 cases m^{-2} in this study. This is probably due to both higher abundances of larvae in the Furan river 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.,* 2003). 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 1.1). 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 (Nunokawa *et al.,* 2008).

2.5.3 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 2.4), even within this relatively narrow range of environmental conditions (riffle habitats in ~3.6 km of stream; Figure 2.1A). There was considerable variability in the mass of sediment used (4 – 139 g m^{-2}) but this was not structured by site (Figure 2.4A). 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 (Southwood, 1977; Cummins and Lauff, 1969). The size of sediment used by the caddisfly community was significantly lower at the mid site than the upper and lower sites (Table 2.3, Figure 2.4B). This is interesting because the greatest environmental difference would be expected between the upper and lower sites (Rice and Church, 1998; Vannote *et al.,* 1980). Nevertheless, the mid site had the lowest slope, bed sediment D_{50} and 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 2.4D, Figure 2.5B). 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 2.4C). The upper site had, on average, the lowest abundance of Glossosomatidae and the mass of each case was very variable (Figure 2.5C). 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.

2.5.4 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 2.4) is unsurprising because the mass of cases varied by several orders of magnitude between taxa (Table 2.1). Therefore, to achieve a 0.85 g increase in sediment use would require just one Rhyacophilidae or Hydropsychidae pupal case but 850 Leptoceridae cases (0.001g each, Table 2.1). Interestingly, abundance of many individual taxa was also only weakly related to the mass of sediment used by that taxa at the river scale (Table 2.4). This indicates that within taxon differences in case mass between samples explained more variability in total sediment use than the abundance of that taxon. In this study, differences in case mass between individuals of the same taxon 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 2.1) 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 (Figure 2.5B and C). *A. fuscipes* larvae at the mid site were also smaller (Figure 2.5E), and less-developed (early instar) larvae are likely to build smaller cases with lower mass. The greater abundances of *A. fuscipes* at this site may increase competition for resources and stunt larvae development. Alternatively, the greater availability of fine sediment at the mid site (Figure 2.6A) may cause larvae to build cases which contain more fine sediment and consequently weigh less (Figure 2.5D). At the river scale only a small percentage of available sediment was used (average 1 – 1.4 mm fraction = 2.99%; Figure 2.6C) 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). Whilst specific size fractions are not limiting at any site, the greater availability of finer fractions at the mid site may, therefore, 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), at an average of 2.99% compared to 15 – 25% for the dominant case 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.

2.5.5 Methodological discussion

This chapter presents the first quantification of sediment use by a whole case-building caddisfly community, rather than small numbers of individuals or species. This presented several methodological challenges and required amalgamation of techniques used previously to measure GSDs of individual caddisfly cases (Statzner *et al.,* 2009; Tolkamp, 1980), with those used in assessment of much larger quantities of sediment in geomorphology (Bunte and Abt, 2001). 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, 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 the grain size estimates are broader than many in the literature (e.g. Tolkamp, 1980). Last, the mass and size distribution characteristics of Rhyacophilidae and Hydropsychidae pupal cases are likely to be less accurate than those for the other taxa, due to their low abundance and therefore the low number of individuals analysed. This also necessitated combining the two families which are 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.

2.6 Summary

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 (Albertson *et al.,* 2014a; Cardinale *et al.,* 2004; Johnson *et al.,* 2009). 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 1.3), 2) families (Figure 2.2), 3) species (Table 2.1) and, 4) individuals of the same species (Table 2.4, Figure 2.5). Case mass ranged from 0.001 g to 0.85 g and D_{50} from 0.17 mm 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 caddisfly zoogeomorphic impact (Figure 1.4) for small gravel-bed streams.

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 localised 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, their abundance or availability of particular grain-size fractions for case construction. 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. It follows that if caddisfly

cases do have geomorphic effects (mechanisms in Figure 1.4), then these are likely to be widespread across a range of habitats in which case-building taxa are known to be common.

This study provides insights into the size and quantity of sediment use by case-building caddisfly, essential to guide further research on caddisfly zoogeomorphology. Future work is required to understand the specific mechanisms of zoogeomorphic effects (Figure 1.4) and to quantity the effects of case construction by caddisfly on sediment transport in rivers.

Caddisfly cases during laboratory analysis.

Chapter 3. The effect of caddisfly case construction and case design on the entrainment of incorporated sediment.

3.1 Introduction

3.1.1 Controls on sediment transport

Sediment transport is an important control on the morphology of rivers and fluvial habitat, with implications for the ecosystem services they provide and the risks they pose to society. Therefore, understanding and predicting sediment dynamics remains a primary focus of fluvial geomorphology. The transport of sediment is controlled by many variables reflecting characteristics of both the sediment (e.g. size, shape, grain interactions) and the hydraulic environment (Wilcock *et al.,* 2009; Church *et al.,* 1998). Particle size is a dominant control on sediment transport (e.g. Shields, 1936) because larger particles typically have greater mass and consequently require larger, less frequent, hydraulic forces to entrain them (Bridge and Bennett, 1992; Wilcock *et al.,* 2009). Particle shape is also important because it influences how particles respond to the forces applied to them (Perret *et al.,* 2017). Rods and spherical shapes are transported more easily than disc and blade shapes because they are able to roll which reduces friction with the river bed (Carling *et al.,* 1992; Oakey *et al.,* 2005). In river-beds, particles do not exist in isolation and grain interactions, including imbrication, packing, sorting and hiding, substantially modify the mobility of river-beds (Parker and Sutherland, 1990). These factors affect the *critical* or *threshold* shear stress; the hydraulic force at which sediment particles begin to move (Dey and Papanicolaou, 2008; Simões, 2014).

Animals can affect sediment transport processes by modifying both sediment characteristics and local hydraulics (Chapter 1; Rice *et al.,* 2012; Statzner, 2012). Biological processes can modify the size, shape and density of sediment (Dudgeon, 1990), with implications for sediment transport. For example, faecal pellets produced by aquatic invertebrates, such as those of the marine Polychaete *Amphicteis scaphobranchiata,* are easily entrained due to their relatively high protrusion above the bed (pellet D_{50} approximately 0.5 - 2.5 mm; Taghon *et al.,* 1984). Pellets produced by *Hydrobia ulvae* in intertidal mudflats of the Danish Wadden Sea, lose their cohesion to the clay mudflats on which this snail lives and are therefore preferentially entrained (Austen *et al.,* 1999).

Aggregate particles are also produced in dryland environments by physical processes including the expansion and contraction of soils containing swelling clays, salt efflorescence and the

breakup of mud curls (Rust and Nanson, 1989; Simon and Gibling, 2017). In rivers, these aggregates (D_{50} = 0.13 mm; Maroulis and Nanson, 1996) commonly move as bedload; maintaining frequent contact with the bed by rolling, hopping or saltating (Maroulis and Nanson, 1996; Rust and Nanson, 1989), although their constituent clay particles would otherwise usually be transported in suspension. The combination of sediment into an aggregate, whether by biological or physical processes, can therefore substantially alter the entrainment and transport of incorporated particles.

During the construction of cases, caddisfly larvae combine grains of sand and fine gravel into a single aggregate (Figure 1.4A). Caddisfly cases are heavier, but larger and less dense than the original grains used in case construction. Furthermore, caddisfly case designs are often shapes that rarely occur in natural river mineral sediments; such as the long hollow cylinders built by tubular case makers (Figure 3.1A&B). Therefore, case construction is likely to modify the hydraulic force required to transport the constituent grains. Caddisfly are abundant and can incorporate substantial quantities of sediment in their cases (Figure 2.3). If case construction changes the mobility of sediment involved in case construction this could be an important zoogeomorphic effect.

3.1.2 Entrainment of caddisfly and the role of the case

Previous research on the entrainment of caddisfly larvae and cases has been approached primarily from an ecological perspective. Drift (downstream transport) is an important means of migration and relocation for many species of aquatic invertebrates in rivers (Naman *et al.,* 2016). Uncontrolled drift can be detrimental (e.g. increasing vulnerability to predation) and therefore aquatic invertebrates have evolved a wide variety of strategies for reducing unintentional entrainment (Statzner *et al.,* 1988). Caddisfly can resist drift *passively*, via adhesive or static friction (due to weight and case roughness), or *actively* via the effort of the larvae to remain attached (Waringer, 1989).

The role of the caddisfly case in reducing entrainment of larvae is much debated (Dodds and Hisaw, 1925; Limm and Power, 2011; Otto and Johansson, 1995). For mineral case-building caddisfly, an increase in case mass does not necessarily increase passive drift resistance. For example, coarse grains stuck to the edges of Goeridae cases are commonly believed to increase ballast. However, these 'ballast' particles contributed little to total current resistance (empty cases with stones = 10.3 cm s^{-1}, without stones = 8.7 cm s^{-1}; Otto and Johansson, 1995) because the increase in ballast from the added weight of particles was offset by the increased lift the particles provided (Otto and Johansson, 1995; Statzner and Holm, 1989). Nevertheless, due to their much

greater mass, mineral cases presumably provide more passive resistance to drift than organic cases (Dodds and Hisaw, 1925; Webster and Webster, 1943). This would allow larvae to expend less energy actively resisting drift (Waringer, 1989) and reduce the drift distance if larvae are entrained. *Potamophylax latipennis* (Limnephilidae) larvae build large mineral cases (Figure 3.1B) and are usually only entrained for short periods, moving akin to a saltating grain (Lancaster *et al.,* 2006).

Caddisfly case designs vary considerably in shape, size and weight (Figure 3.1), factors which are likely to effect their entrainment thresholds. Even between taxa which build tubular cases, the velocity required to entrain cased caddisfly larvae varies considerably. For example, passive resistance to drift (case and dead larvae) for 5th instar larvae of tubular case-builders (all Limnephilidae) *Chaetoteryx fusca, Drusus monticola* and *Metanoea rhaetica* was between 8 and 10 cm s^{-1}, *Allogamus auricollis* was 21 cm s^{-1}, whilst the larger *P. cingulatus* required 71 cm s^{-1} (Waringer, 1993). Therefore, the design of caddisfly cases is an important control on their entrainment thresholds.

Whilst considerable research has been conducted on the transport of sand and gravel in rivers, this past work tends to neglect the importance of biology. Similarly, research conducted on entrainment of caddisfly larvae has not considered the consequences of case construction for geomorphology. Caddisfly create aggregate particles which are likely to vary in mobility from their constituent grains. This chapter investigates the effects of case construction by three species with different case designs, on the entrainment of the constituent sand particles. In doing so it adds a geomorphic perspective to existing literature on caddisfly entrainment and drift. This chapter aims to determine what effect case construction by caddisfly larvae has on the hydraulic force required to entrain the fine sediment incorporated in the cases. Entrainment thresholds were measured for empty cases in order to assess the zoogeomorphic effects of the case construction process (thesis objective 2), rather than sediment transport by live larvae (thesis objective 3). Specifically, the following research questions are investigated:

1) Is there a difference between the critical entrainment threshold of caddisfly cases and the loose sediment incorporated in the cases?
2) How do critical entrainment thresholds vary between species with differing case designs and what aspects of case design (e.g. mass or shape) influence entrainment?

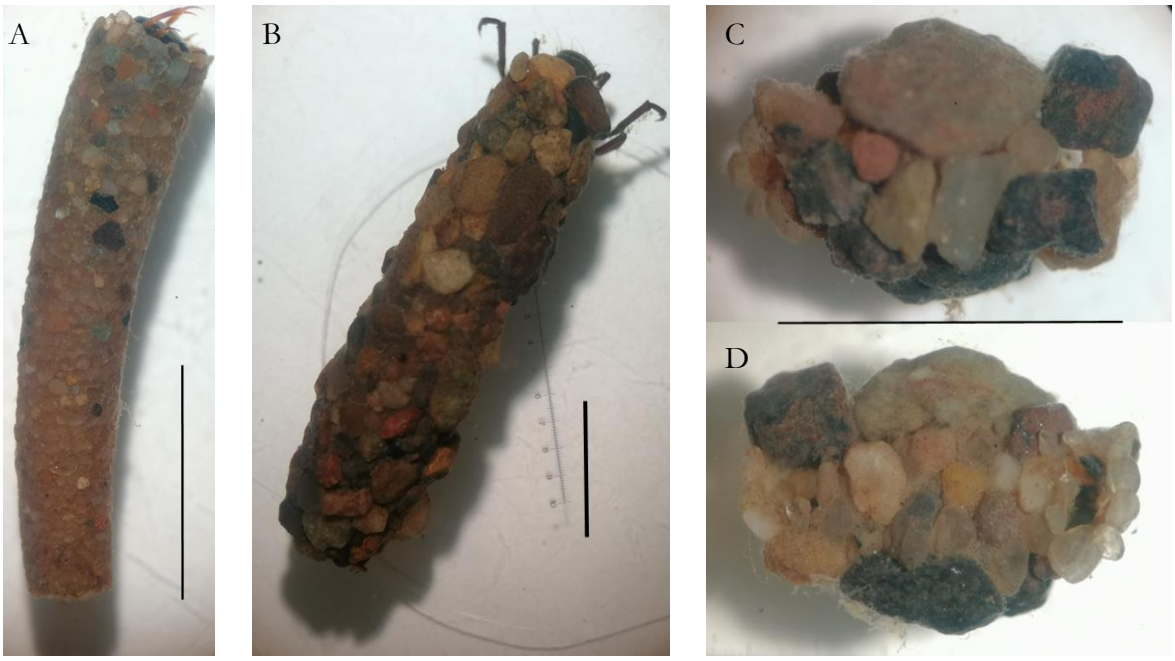


Figure 3.1. Examples of case architecture from the three caddisfly species used in this experiment. (A) Sericostomatidae *Sericostoma personatum* constructs a tubular, curved case from fine sand. (B) Limnephilidae *Potamophylax latipennis* uses coarser sand and fine gravel. Cases of both these species are tubular in shape and lined internally with silk. (C) Glossosomatidae *Agapetus fuscipes* dorsal view and (D) ventral view. *A. fuscipes* constructs cases from a similar sediment size range as *P. latipennis* but the case design is different. *A. fuscipes* cases weigh less and have a domed shape with a flat base of finer sediments, similar to a turtle shell. Bar indicates 5 mm.

3.2 Methods

3.2.1 Selection of species

Three caddisfly species building mobile cases were selected based on their case design (Figure 3.1), and potential zoogeomorphic importance (Chapter 2). Sericostomatidae (*Sericostoma personatum*) cases are tubular in shape, narrowing towards the posterior and slightly curved (Figure 3.1A). *S. personatum* cases are constructed from fine sand (D_{50} = 0.27 mm, Table 2.1). Whilst Sericostomatidae contributed a small amount to total sediment use in Chapter 2, they used a substantial proportion of fine sand and also have zoogeomorphic implications; Sericostomatidae burrow diurnally (Wagner, 1991, 1990) and bioturbate fine sediment (De Nadaï-Monoury *et al.,* 2013).

Limnephilidae probably exhibit the greatest diversity in case design of all caddisfly families (Wiggins, 2004). The Limnephilid *P. latipennis* (Figure 3.1B) builds large cases from coarse sand (D_{50} = 1.31 mm; Table 2.1). *P. latipennis* construct cases from both mineral and organic sediment

(Table 2.2), but in this experiment their cases were exclusively mineral. Limnephilidae contributed 11% to total sediment use in Wood Brook (Figure 2.3) and are highly mobile so may have zoogeomorphic effects by transporting sediment horizontally (Figure 1.4C).

Glossosomatidae *Agapetus fuscipes* were responsible for 64% of sediment mass used by caddisfly larvae in Wood Brook (Figure 2.3) and primarily used coarse sand (D_{50} = 0.94 mm; Table 2.1). Glossosomatidae larvae usually occupy locations with high flow velocity (Morris and Hondzo, 2013b) and therefore, the entrainment threshold of their cases is geomorphologically important. The shape of *A. fuscipes* cases differ from the other two species being domed, with a flat base, rather than tubular (Figure 3.1C).

S. personatum and *P. latipennis* were collected from Black Brook (a second order gravel-bed stream; 52°46'33.4"N 1°17'57.6"W) on 17th June 2019 and preserved in 70% industrial methylated spirit (IMS). Glossosomatidae are very difficult to remove from their fragile cases when preserved, so *A. fuscipes* larvae were collected more locally from a similar stream on 18th August 2019 (Burleigh Brook, 52°45'47.5" N 1°14'32.8" W), and whilst alive, were gently removed from their cases with tweezers. *S. personatum* and *P. latipennis* larvae were removed from their cases after preservation. Cases were then soaked in deionised water to ensure that no IMS remained and to remove any air trapped within the case. Entrainment experiments were conducted between 20th August and 20th September 2019.

3.2.2 Flume setup

Experiments were conducted in a 10 m long by 0.3 m wide Armfield S6 flume, with parallel glass sides (Figure 3.2A). A raised bed of fixed gravel (D_{50} = 15 mm) was constructed at 0.08 m height along the entire flume length. Large cobbles at the flume inlet broke up initial flow structures and ensured well-mixed and fully turbulent flow conditions. Experiments were conducted 7 m from the flume inflow. A flat circular platform (0.065 m in diameter) was fixed so that its surface was 0.1 m from the flume base (thus approximately level with the surfaces of D_{90} particles on the bed; Figure 3.2B & Figure 3.3A). The flat platform standardised variation in hiding or protrusion of cases and sediment (compared to a gravel-bed) and improved observations of entrainment. A sediment trap was located 0.6 m downstream of this platform (depth 0.065 m, length 0.18 m) to collect entrained material (Figure 3.2B). Caddisfly cases and sediment were placed individually on the platform and hydraulic force gradually increased until entrainment occurred.

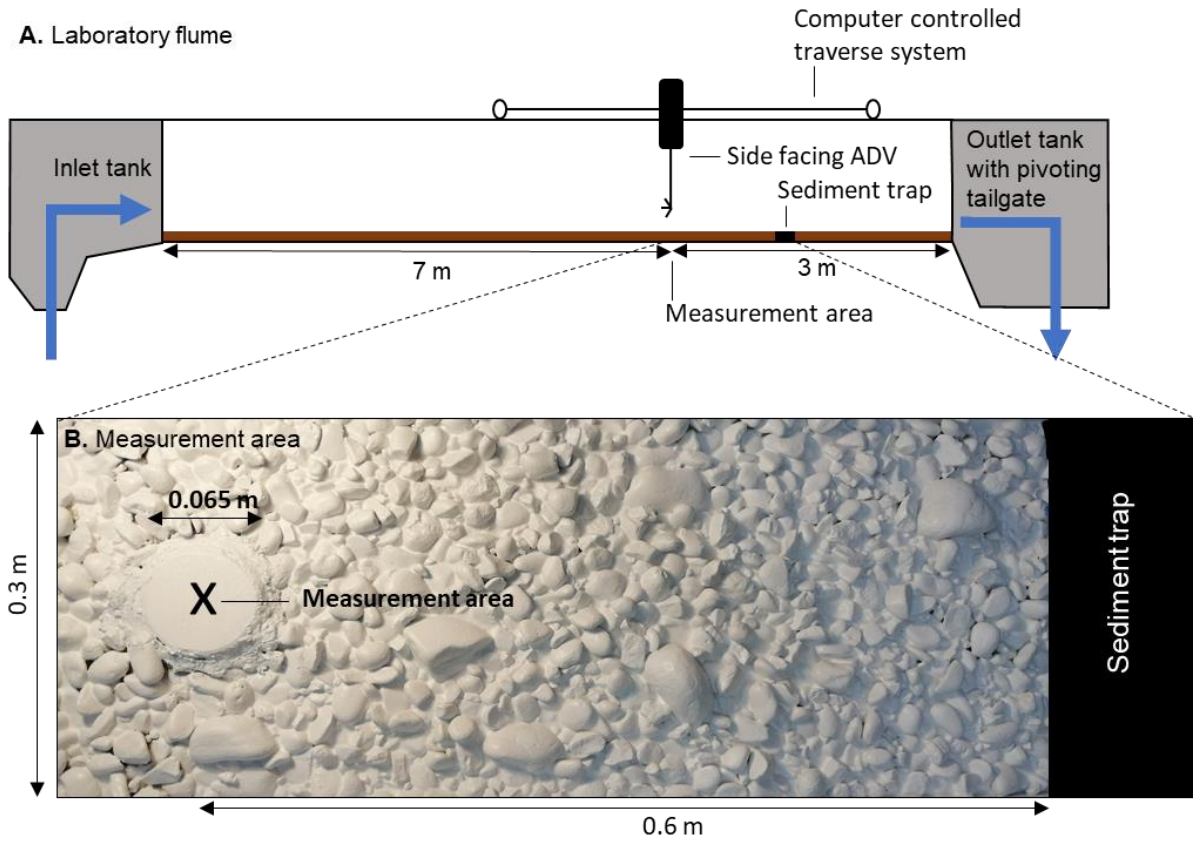


Figure 3.2. The laboratory flume setup. (A) Water recirculates over a raised gravel-bed. Entrainment was measured from a flat platform located 7 m down the flume. A sediment trap was positioned 0.6 m downstream of this platform. Discharge (pump speed), tail gate and slope were all adjusted to produce a series of 11, reproducible, flow stages with constant depth and increasing velocity and bed shear stress. (B) plan view of the measurement platform, fixed gravel bed and sediment trap.

Eleven flow stages with increasing flow velocity and shear stress were determined *a-priori* (Table 3.1). Pump discharge was increased between each flow stage, and the tail gate and slope were adjusted to maintain a constant depth of 0.08 m and uniform flow over the test area. A side facing Nortek 10 MHz acoustic Doppler velocimeter (ADV) was used to simultaneously measure the three orthogonal components of water velocity in the centre of the experimental platform (X, Figure 3.2B). These velocity measurements were used to determine near bed velocity and to calculate bed shear stress for each flow stage. Velocity measurements were recorded for 120 s at a sampling frequency of 50 Hz. The cylindrical volume over which velocity measurements were taken was 6 mm in height and centred 10 mm above the bed (thus velocity was measured between 7-13 mm above the bed ; Nortek, 2009). The horizontal length of the measured area (measurement length) was adjusted to increase data quality but for most runs was 7 mm. Six replicates of each flow stage (two measurements taken before, two during and two after the experimental period) were conducted for calculation of bed shear stress. This provided

an estimate of the variability in flow conditions within and between flow stages (Table 3.1). An additional velocity measurement taken at 60% depth was used to estimate depth averaged velocity (n = 3).

Table 3.1. Flume and hydraulic measurements for each flow stage (1-11). Discharge, velocity and bed shear stress increased with each run, whilst depth remained constant. Depth average velocity (U) was based on a single point taken at 60% depth (independent of TKE estimates) and was not collected for the last stage due to an oversight. Near bed U was centred at 10 mm above the bed. For the Reynolds calculations $^{+}$ indicates flow is transitional according to 500<Re<2500. All other runs were fully turbulent. Froude numbers reveal that all runs were subcritical (Fr<1). Mean bed shear stress (τ_b) was calculated using the turbulent kinetic energy approach.

Flow stage	Bed slope (%)	Depth (m)	Discharge (m^3s^{-1})	Depth Average U (ms^{-1})	Near bed U (ms^{-1})	Reynolds	Froude	Mean τ_b ($N\ m^{-2}$)
1	0.02	0.081	0.0005	0.02	0.02	1152 $^{+}$	0.025	0.0030
2	0.02	0.081	0.0010	0.04	0.03	2199^{+}	0.047	0.0114
3	0.02	0.081	0.0018	0.08	0.06	3976	0.085	0.0412
4	0.02	0.079	0.0025	0.11	0.08	5532	0.121	0.0668
5	0.02	0.082	0.0032	0.13	0.10	6918	0.147	0.1125
6	0.02	0.080	0.0042	0.18	0.13	9091	0.197	0.1599
7	0.02	0.082	0.0051	0.21	0.15	10900	0.229	0.2287
8	0.03	0.081	0.0060	0.27	0.18	12955	0.276	0.2830
9	0.05	0.082	0.0070	0.29	0.19	15118	0.320	0.3432
10	0.06	0.081	0.0085	0.35	0.24	18351	0.393	0.4907
11	0.08	0.080	N/A	N/A	0.28	N/A	N/A	0.7277

3.2.3 Flume procedure

A single case was added to the centre of the measurement platform (Figure 3.2B) during flow stage 1 (mean water velocity = 0.02 ms^{-1}, Table 3.1). Cases were orientated facing upstream as case positioning is important to entrainment (Waringer, 1993; Figure 3.3A). Each flow stage was maintained for 270 seconds, at which point the discharge was increased and the tail gate and slope adjusted. This changeover process was completed in 30 seconds so that each flow stage took approximately five minutes. A GoPro camera positioned above the measurement platform was used to observe entrainment.

After 8 replicates had been completed for each caddisfly species, cases were broken down into their constituent sediment grains (hereafter *sediment*). Cases were dried at 70°C for 3 hours and weighed. Subsequently, 30% hydrogen peroxide (H_2O_2) was added at 80°C and cases were stirred to facilitate the breakdown of silk (following Chapter 2). The remaining case sediment was

washed through a 0.063 mm sieve and dried. Subsequently, the sediment for each case was individually sieved into half phi intervals. Despite the low mass of sediment, small diameter sieves (38 mm diameter) resulted in a mean mass loss of only 0.7% and max 2.4% (0.0006 g) per case.

The flume experimental procedure was then repeated with the loose case sediment. After soaking in deionised water, loose sediment was added to the flume through a small funnel, which prevented entrainment before the experiment began. Sediment was spread over an approximately circular patch, 1 grain thick in the centre of the measurement platform (Figure 3.3B).

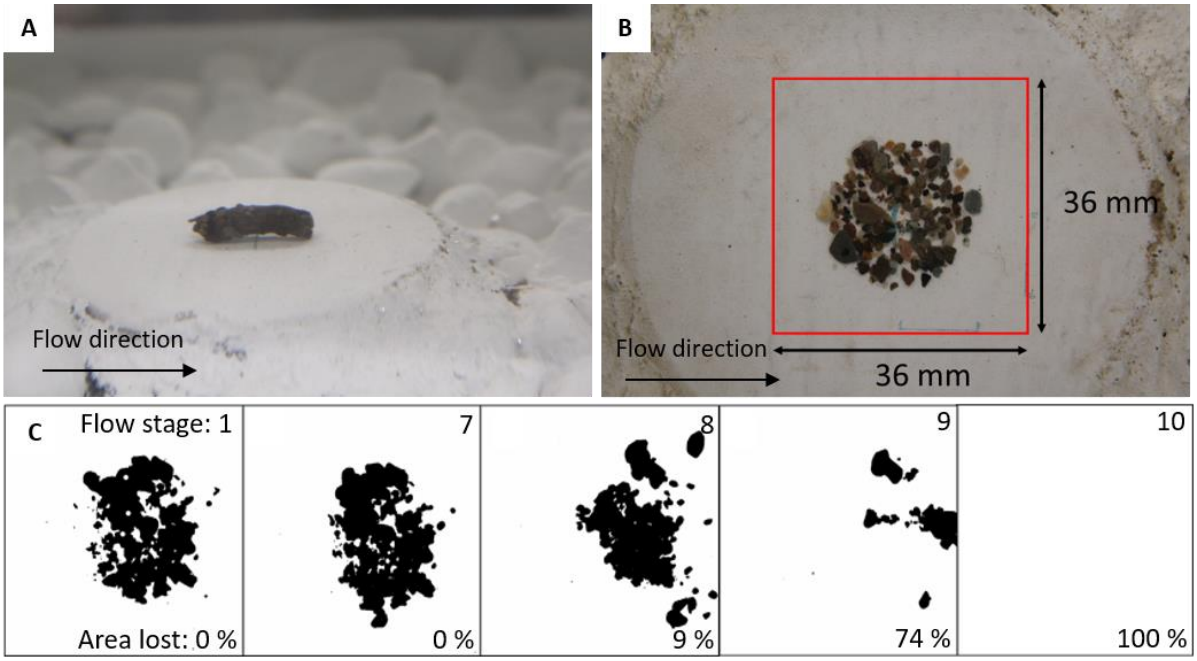


Figure 3.3. Entrainment of cases and sediment from measurement platform. (A) *Potamophylax latipennis* case position during the first flow stage. Case were orientated parallel to the flow direction and facing upstream. (B) *P. latipennis* sediment during the first flow stage. Sediment was spread over a wider area, one grain thick. For both cases and sediment, transport out of an area 36 mm^2 (red box) was classified as entrainment. (C) Image analysis was used to remove subjectivity from the classification of entrainment thresholds for sediment runs. The surface area of particles entrained during each flow stage was calculated as a percentage of the initial area of sediment.

3.3 Data Analysis

3.3.1 Hydraulic stages

Velocity time series data were post-processed using phase-space thresholding to remove spikes, which were replaced by linear interpolation (Biron *et al.,* 2004; Goring and Nikora, 2002) using the Velocity Signal Analyser tool for Matlab (Jesson *et al.,* 2015). Velocity measurements had to be taken close to the bed, to estimate hydraulics close to those experienced by caddisfly larvae. Velocity measurement close to the bed using ADVs is difficult due to the increased turbulence, shear and reflection near boundaries (Martin *et al.,* 2002; McLelland and Nicholas, 2000; Goring and Nikora, 2002; Voulgaris and Trowbridge, 1998). Data with correlation less than 60% and signal to noise ratio (SNR) less than 10 were removed. Whilst these thresholds are lower than recommended for turbulence calculations (recommended correlation = 70%, SNR = 15; Nortek, 2009), they are an acceptable compromise when working close to boundaries (McLelland and Nicholas, 2000). Any velocity time series with more than 20% data removed from any axis was discarded. This left 5-6 replicates of 2 minute, 50Hz, time series velocity data for each flow stage.

Bed shear stress was calculated via the turbulent kinetic energy (TKE) approach. TKE was calculated from the intensity of the velocity fluctuations in three dimensions (the second order moment statistics; Equation 1 and Equation 2). This method requires turbulence data from a single point close to the bed (e.g. 0.1 of flow depth; Biron *et al.,* 2004) and has been consistently found to give a good estimate of bed shear stress (Kim *et al.,* 2000). Although more susceptible to errors in measurement than methods relying on mean velocities (e.g. Law of the Wall; Karman, 1931) the TKE method has been found to be less susceptible to error in vertical elevation (Kim *et al.,* 2000) and sensor orientation (Biron *et al.,* 2004). TKE (*E*) was calculated according to Equation 1.

$$E = \frac{\rho(\mathrm{u}'^2 + v'^2 + w'^2)}{2} \tag{1}$$

Where ρ was water density = 1000 kg m^{-3} and u'^2, v'^2 and w'^2 were the second order moment statistics for velocity in the long-stream, cross-stream and vertical directions, respectively.

Subsequently, bed shear stress τ_b (N m^{-2}) was estimated by multiplying TKE (*E*) by a constant C_1 = 0.19 (Soulsby, 1983; Stapleton and Huntley, 1995), Equation 2.

$$\tau_b = C_1 E \tag{2}$$

τ_b calculated via the TKE approach increased exponentially with flow stage. A Tukey Honest Significance Difference test indicated that the bed shear stress of the four lowest flow stages were not significantly different from their neighbours, but later stages were different (adjusted $P < 0.05$, Figure 3.4A). All flow stages were significantly different for mean streamwise bed velocity (Figure 3.4B). For further analysis the mean τ_b and mean near bed velocity (u) for each flow stage were extracted (Table 3.1). Statistics were conducted in the *stats* package for R Studio (version 3.5.1, R Core Team, 2018).

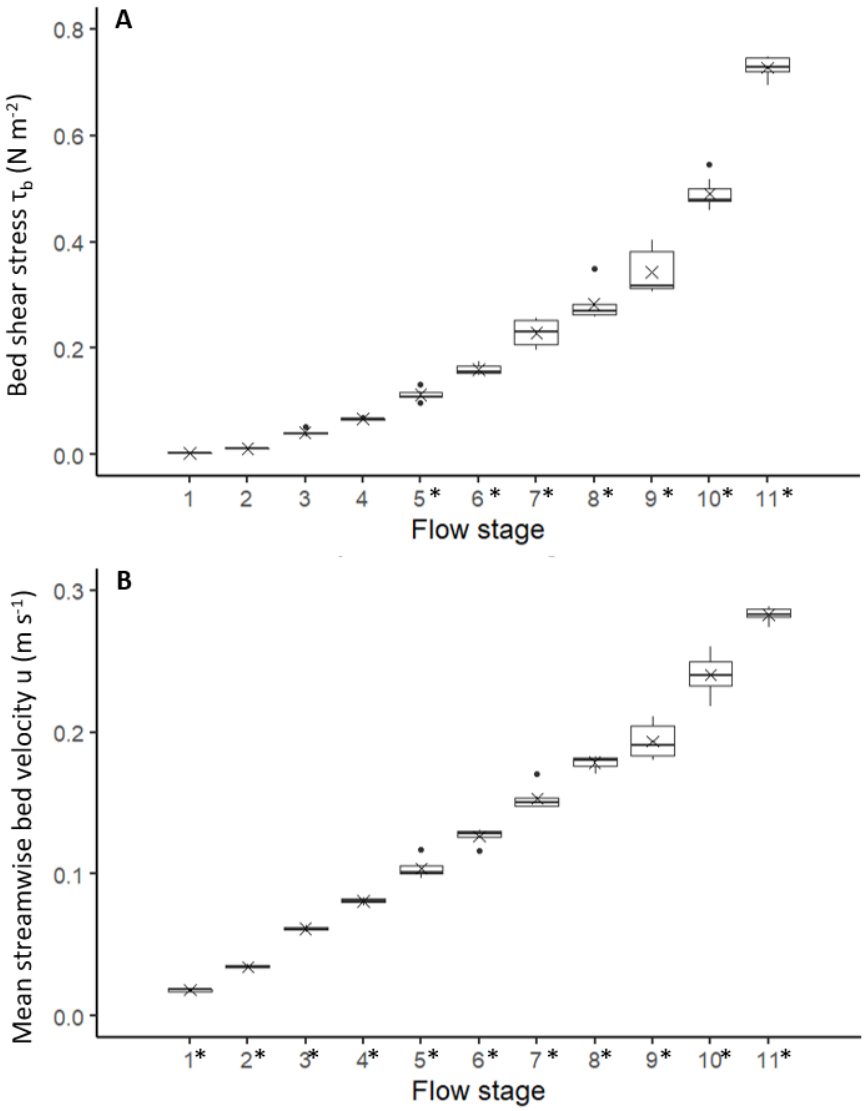


Figure 3.4. Hydraulic conditions during successional flow stages 1-11. (A) Bed shear stress replicates at each flow stage calculated using the turbulent kinetic energy approach. Demonstrates exponentially increasing bed shear stress with flow stage. (B) Mean near bed velocity. Boxes show the median and interquartile range, whiskers show the interquartile range multiplied by 1.5 and the mean is indicated by ×. * indicates that the stage was significantly different from both neighbouring flow stages according to a Tukey Honest Significant Difference test (adjusted $P<0.05$).

3.3.2 Entrainment

Establishing entrainment thresholds is subjective, resulting in difficulty comparing between studies (Perret *et al.,* 2015; Garcia, 2008). To remove some of this subjectivity, cases and sediment were required to move > 18 mm (approximately the longest case length of the three species; *P. latipennis*) to classify as entrainment. For loose sediment this was complicated by many grains moving at different entrainment thresholds. Photographs were used to measure the proportion of sediment which was entrainment under each flow stage. Photographs were taken 240 seconds into each flow stage (immediately prior to adjusting flume setup for the next stage). Photos were later analysed in ImageJ (Figure 3B & 3C; Abramoff *et al.,* 2004), following this procedure:

1) The image was scaled and then cropped to a 36 mm diameter square centred on the sediment (18 mm x 2; Figure 3.3B).
2) The image was thresholded to identify sediment particles from the white background (Figure 3.3C).
3) The image was edited to remove the scale bar and then the surface area of particles remaining was calculated.

These steps were repeated for photographs of each flow stage. The surface area of sediment was used as an estimate of sediment remaining. The percentage difference between the area of sediment in the initial image (flow stage 1) and each subsequent flow stage was calculated (Figure 3.3C). This gave a quantitative estimate of sediment entrained during each flow stage.

For each experimental run the initiation of movement and cumulative sediment entrained during each flow stage were determined. To compare sediment entrainment thresholds to those of caddisfly cases, the flow stage during which 90% sediment area had been entrained was used. Because a case moves as a single particle, case movement is equivalent to 100% of sediment entrainment. However, the 90% threshold allows a few particles to remain and therefore provides a conservative measure of entrainment for sediment.

Entrainment threshold data for cases and sediment of each species was mostly non-normal (Shapiro-Wilk $P<0.05$ for all except *A. fuscipes* cases). Therefore, non-parametric statistics were used to test each of the research questions. Question 1 examined whether a significant difference existed between the entrainment thresholds of cases and their constituent sediment. These data were paired because the same material was used as a case and as disaggregated sediment. Therefore, Wilcoxon signed-rank tests were used with a Bonferroni adjustment. To determine if a significant difference existed between species, for either case or sediment entrainment,

(Question 2) a Kruskal-Wallis test was conducted followed by post-hoc Mann-Whitney (Wilcoxon rank sum) tests.

3.3.3 Caddisfly case design

To assess the role of case shape on entrainment between species with different case designs it was important to measure the case dimensions. An image taken prior to flume experiments was analysed in ImageJ to measure the length and width of each case used in the flume experiments (a and b axis respectively). After the flume experiment, it became evident that case volume was important. Therefore, a separate sample of 8 cases of *P. latipennis* and *S. personatum* were measured for all three axes, using electronic callipers (checked with a microscope eyepiece graticule and stage micrometer). Measured caddisfly were collected from the same site on the same date as those used in the flume experiments. *A. fuscipes* cases were extremely variable in shape, and therefore 16 cases were measured (Figure 3.5). A linear association between the b and c axis of each species was then used to estimate the c axis for the cases used in the flume experiment (R^2 values for *S. personatum* = 0.99, *P. latipennis* = 0.64, *A. fuscipes* = 0.15; Figure 3.5). The dimensions of cases of all three species were very different, so this method was a sufficiently accurate estimate of case-volume to differentiate between species.

To compare differences in shape between the cases of each species, Corey shape factor (Corey, 1949) was determined (Equation 3).

$$SF = \frac{c}{\sqrt{ab}} \tag{3}$$

Where a, b and c (mm) were the major, intermediate, and minor axis of the case, respectively.

Shields criterion (Shields, 1936) is widely used to nondimensionalise entrainment thresholds (Yang *et al.,* 2019). Shields parameter (τ_{*c}) was calculated according to Equation 4, for cases and sediment of each species.

$$\tau_{*c} = \frac{\tau_c}{(\rho s - \rho)gD} \tag{4}$$

Where τ_c was bed shear stress (τ_b) during the flow stage at which the case or sediment was entrained (N m^{-2}), ρ was water density = 1000 kg m^{-3}, ρs was sediment density = 2650 kg m^{-3} for both cases and sediment, g was acceleration due to gravity = 9.81 m s^{-2} and D was particle diameter (D_{50} for sediment or b axis for cases, m). This was plotted against grain Reynolds

number (Re_* Equation 5, dimensionless) to compare case and sediment entrainment thresholds to the curve developed by Shields (1936).

$$Re_* = \frac{u_* \mathrm{D}}{\mathrm{v}} \tag{5}$$

Where u_* was the shear velocity (Equation 6), D particle diameter (m), and v, kinematic viscosity = 1×10^{-6} m^2 s^{-1}.

$$u_* = \frac{\tau_c}{\rho} \tag{6}$$

Shields dimensionless criteria is widely used in studies of particle entrainment (Yang *et al.,* 2019). However, it is less appropriate for caddisfly cases because it uses particle size (D) multiplied by density as a proxy for particle mass (because sediment size is more commonly measured than mass in rivers; Wolman, 1954). This is an issue for caddisfly cases because their size to mass ratios are not consistent between species (compare *S. personatum* large but lightweight cases to *A. fuscipes* cases, which are small but more dense; Figure 3.1; Table 2.1). Furthermore, caddisfly cases are hollow, so that if density were calculated from their external dimensions and mass, without allowing for their hollow centre, their density is less than that of water and they should float. For this reason, case density was taken to be the same as sediment density (2650 kg m^{-3} the density of quartz sand). For particle diameter (D in Equation 4) case width (b axis) was used for cases and mean D_{50} for sediment.

As an alternative standardisation method, better suited to hollow particles, cases were standardised by mass; τ_c values were divided by mass (τ_c/m). If differences in entrainment thresholds between cases still exist, they can therefore be attributed to case shape (Question 2). As for entrainment threshold data (τ_c) Kruskal Wallis followed by Wilcoxon rank sum tests were then conducted for differences between species (for cases and sediment) for $\frac{\tau_c}{m}$ and τ_{*c} and Wilcoxon signed rank for paired case versus sediment data.

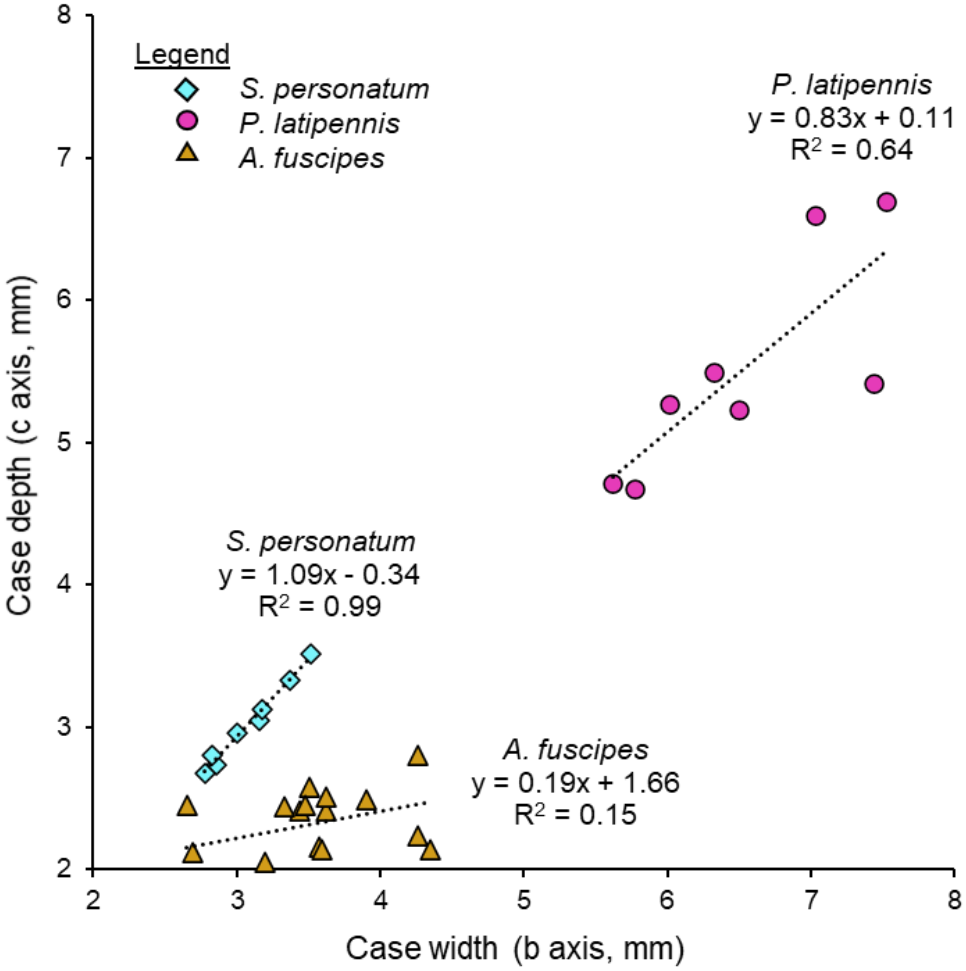


Figure 3.5. Association between width (b axis) and depth (c axis) of cases of each species. A linear trend between b and c was used to estimate the unknown c axis of caddisfly used in the flume experiments. The trend is weaker for *P. latipennis* and particularly *A. fuscipes* due to variability in case design between species. However, it provides a sufficiently accurate method to calculate case volume for the analysis in this chapter because it distinguishes between species.

3.4 Results

3.4.1 Entrainment of cases versus constituent sediment

The construction of cases resulted in composite particles which were much larger than the constituent sediment (Table 3.2). *S. personatum* used the finest sediment (mean D_{50} = 0.27 mm), converting this to a case of mean width (B axis) of 3.07 mm and length 14.57 mm. *P. latipennis* and *A. fuscipes* used larger coarse sand particles with similar size distributions (mean width = 1.16 and 0.98 mm respectively; Figure 3.6) but *P. latipennis* cases were considerably larger and heavier than both of the other species (Table 3.2).

Comparing entrainment of cases and sediment (Question 1) both *S. personatum* and *P. latipennis* cases moved at significantly lower critical shear stress thresholds than their loose case sediment (Figure 3.7A, Table 3.3). All cases of *S. personatum* or *P. latipennis* were entrained below the shear stress required to entrain their respective sediment grains (Figure 3.8). *A. fuscipes* cases however, moved over a similar range of τ_c as their constituent sediment (Figure 3.7A) and critical entrainment was not significantly different between cases and constituent grains (Table 3.3B). For *A. fuscipes*, the range of case movement overlaps that of sediment, although a few sediment particles moved at lower and higher shear stress than cases (Figure 3.8C). Shields criterion indicates that case critical entrainment was much lower than would be expected from particle size for all species (Figure 3.10).

Table 3.2. Size and shape characteristics for cases and sediment. Mean with standard deviation in brackets. a, b, and c indicate major, intermediate and minor particle axes respectively. D_{50} reported as b axis for loose sediment. *Minor (c axis) were not measured on these specimens but 8 cases (16 for *A. fuscipes*), collected from the same sites on the same date were used to construct a regression model between b and c axis to predict the c axis of these individuals (Figure 3.5). SF is the dimensionless Corey shape factor.

		a (mm)	b or D_{50} (mm)	c* (mm)	SF	Volume (mm^3)	Mass (g)
Case	*S. personatum*	14.57 (0.66)	3.07 (0.11)	3.01 (0.11)	0.45 (0.01)	134.57 (12.13)	0.03 (0.004)
	P. latipennis.	21.75 (0.86)	5.73 (0.42)	4.84 (0.37)	0.43 (0.01)	608.11 (110.33)	0.26 (0.04)
	A. fuscipes	6.01 (0.32)	3.63 (0.59)	2.34 (0.11)	0.51 (0.03)	51.70 (12.79)	0.03 (0.01)
Sediment	*S. personatum*		0.27 (0.02)				0.03 (0.004)
	P. latipennis.		1.16 (0.15)				0.25 (0.04)
	A. fuscipes		0.98 (0.2)				0.03 (0.006)

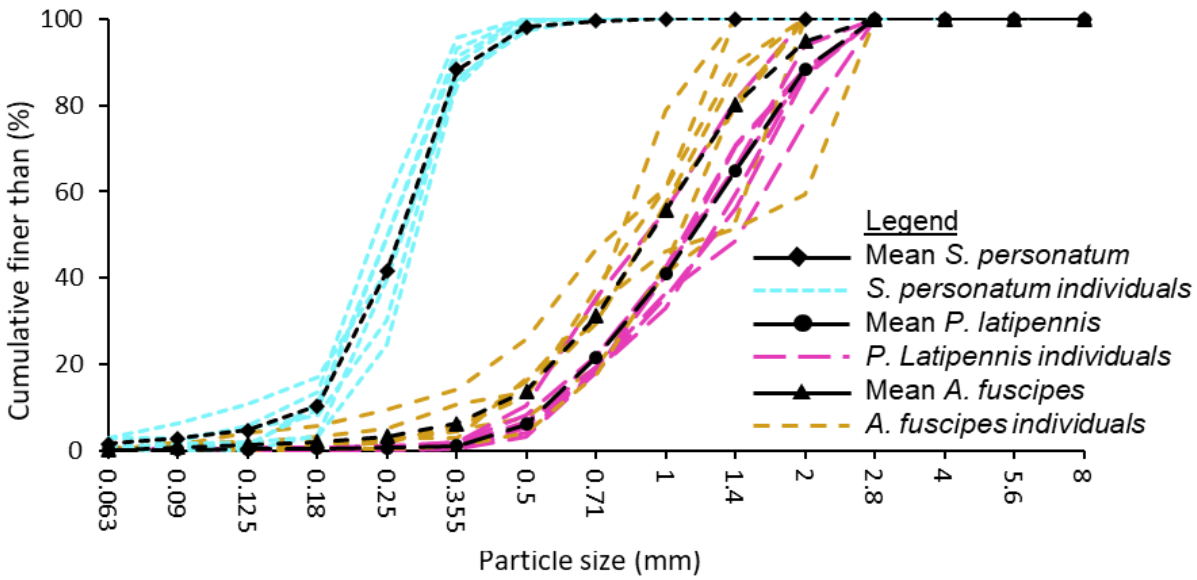


Figure 3.6. Cumulative particle size distribution for case sediment of each of the three species. Mean indicated by line with markers. Particle size indicates passing sieve.

Table 3.3. Results of statistical tests performed on (A) Difference between entrainment of each species, for both cases and loose sediment and (B) Difference between case and sediment. Chi-squared values reported for Kruskal Wallis and W and V statistics for Wilcoxon rank and signed rank respectively. Significance is indicated by * 0.05 > *P* > 0.01; ** 0.01 > *P* > 0.001; *** *P* < 0.001. Each test was done for critical bed shear stress (τ_c), bed shear stress divided by mass ($\frac{\tau_c}{m}$) and shields dimensionless shear stress (τ_{*c}).

A. Species

Parameter	Case or sediment	Kruskal-Wallis (K)	Wilcoxon rank (w)		
			A. fuscipes - *S. personatum*	*S. personatum* – *P. latipennis*	*P. latipennis* – *A. fuscipes*
τ_c (N m^{-2})	Case	18.8***	0***	0***	8*
	Sediment	16.8***	43	4**	64***
$\frac{\tau_c}{m}$ (N m^{-2} kg^{-1})	Case	20.5***	0***	0***	64***
	Sediment	16.6***	46	64***	0***
τ_{*c}	Case	19.3***	0***	4**	0***
	Sediment	17.5***	64***	64***	53*

B. Sediment versus case

Parameter	Wilcoxon signed rank (v)		
	S. personatum	*P. latipennis*	*A. fuscipes*
τ_c (N m^{-2})	0*	0*	3
$\frac{\tau_c}{m}$ (N m^{-2} kg^{-1})	0*	0**	3*
τ_{*c}	0**	0**	0**

3.4.2 Differences in case entrainment between species

The shear stress required to entrain cases was significantly different between each species (Table 3.3A, Figure 3.7A; Question 2). *S. personatum* moved under the lowest shear stress (mean τ_c = 0.06 N m^{-2}). *P. latipennis* required 0.18 N m^{-2} to move and *A. fuscipes* required the greatest shear stress to entrain (mean τ_c = 0.28 N m^{-2}; Figure 3.7A). Qualitative observation of the method of movement for cases indicated variability between species. As shear stress increased, tubular cases (*S. personatum* and *P. latipennis*), 1) rocked in situ, 2) spun so that they were transverse to the flow and, 3) rolled off the measurement area. In contrast, *A. fuscipes* initially moved by sliding followed by either continued sliding or, occasionally, by rolling.

3.4.3 Differences in constituent sediment entrainment between species

Unlike cases which moved as one particle, loose sediment particles moved over a much wider range of τ_b (Figure 3.8). For example, transport of *S. personatum* sediment was initiated as early as 0.11 N m^{-2} but reached the 90% threshold at 0.34 N m^{-2} (Figure 3.8A). *P. latipennis* sediment required significantly greater shear stresses to entrain than that of the sediment associated with other two species, which were not significantly different from one another (Table 3.3; Figure 3.7A).

Observing the method of movement for loose sediment runs was considerably harder than for cases and many particles were too small to identify. Larger particles of sediment of all species moved by a mixture of rolling and sliding (dependant on the sphericity of the particle). Loose sediment also showed signs of grain interactions, with sediment patches moving together and areas of smaller grains building up behind larger grains. This was particularly true for *A. fuscipes* and *P. latipennis* which had a greater range of particle sizes than *S. personatum* (Figure 3.6).

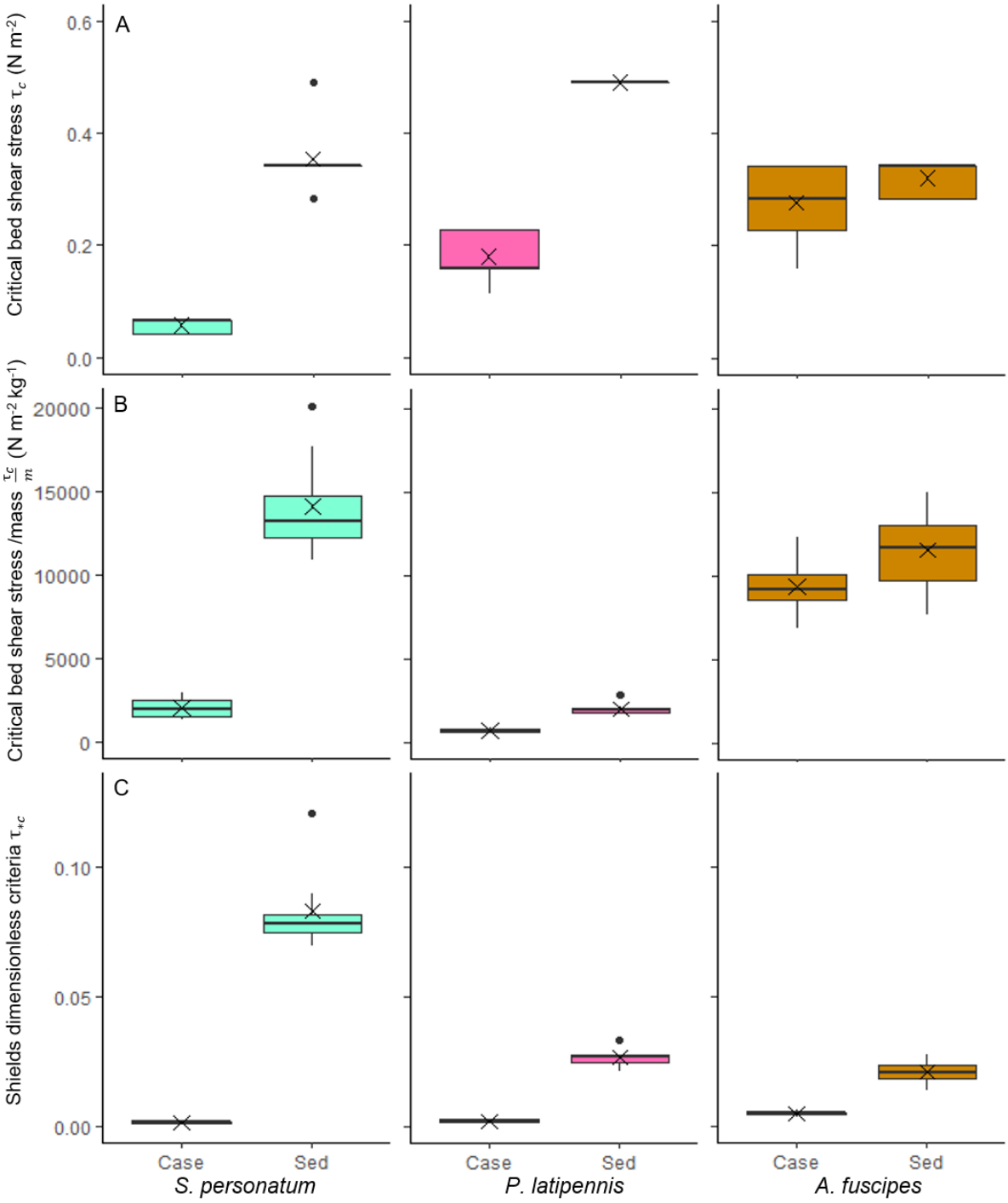


Figure 3.7. Parameters for the entrainment of cases and 90% of constituent sediment for each species. (A) Critical bed shear stress (τ_c). (B) Critical bed shear stress divided by mass, τ_c/m. (C) Shields dimensionless critical shear stress, τ_{*c}. Boxes show the median and interquartile range, whiskers show the interquartile range multiplied by 1.5 and the mean is indicated by ×.

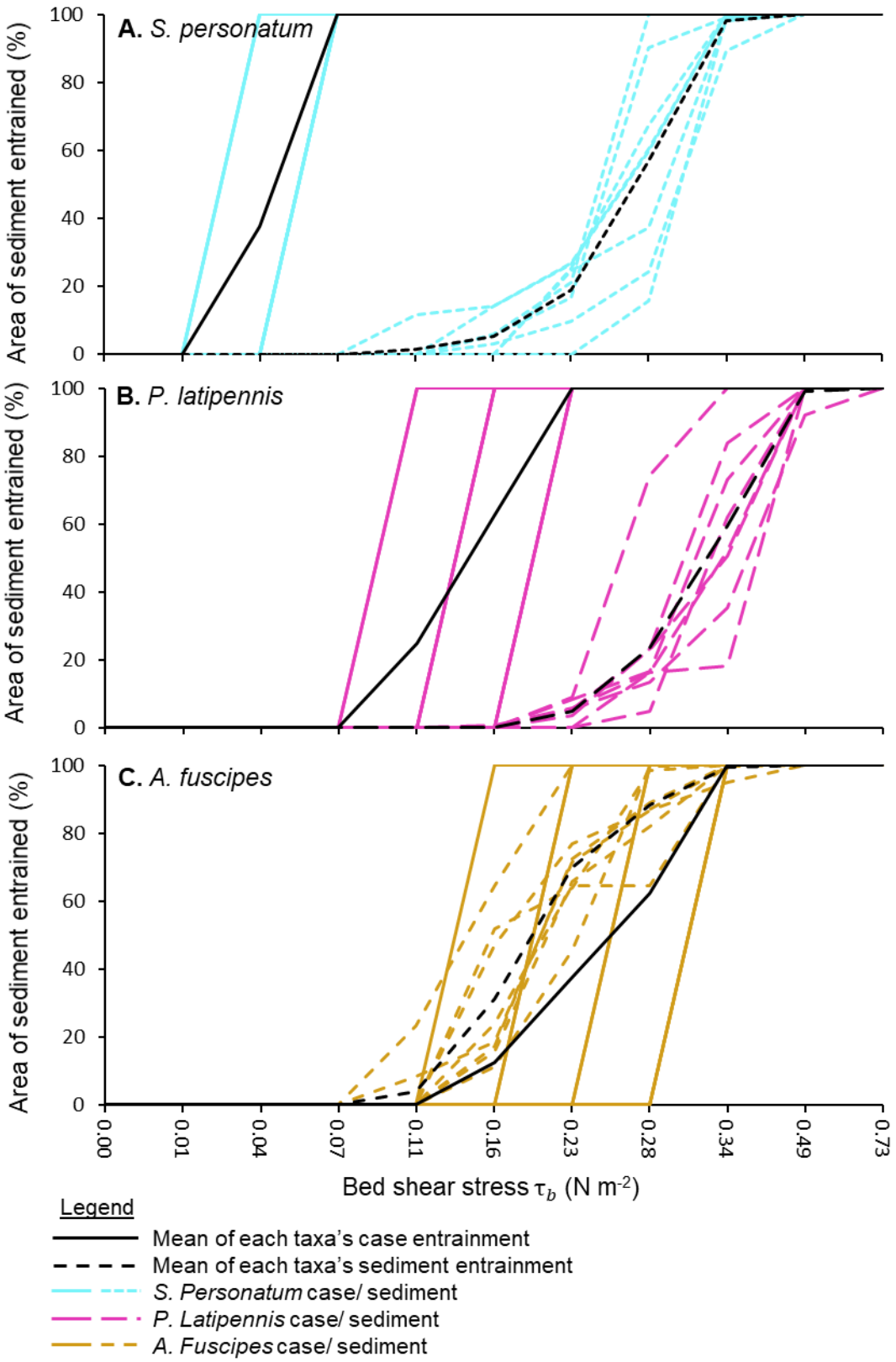


Figure 3.8. Percent of sediment entrained by the end of each flow stage for cases (solid line) and sediment (dashed line) of each species (A-C). Percent calculated as the spatial area of grains remaining (following Figure 3.3C).

3.4.4 The role of case shape for case entrainment

The case designs of each species were very different (Figure 3.1; Table 3.2). *P. latipennis* built cases both substantially heavier and of greater volume than the other two species (Table 3.2). *S. personatum* and *A. fuscipes* built cases of similar mass (both 0.03 g; Table 3.2) but *S. personatum* cases were more than twice as long. Using the Zingg classification indicated a notable difference in shape between cases of *A. fuscipes* and the other species (Figure 3.9). *A. fuscipes* cases had lower c/b and higher b/a ratios and consequently a more spherical shape. Both *S. personatum* and *P. latipennis* have similar b and c axis dimensions which were far exceeded by their a axis, and were both therefore rod shaped (Figure 3.9). Importantly for their entrainment, *S. personatum* cases had a circular cross section while *P. latipennis* cases were roughly oval. *A. fuscipes* cases were elongated hemispheres with a flat base and sharp angles between the base and sides; they were spherical (Figure 3.9) but the edges were not rounded.

After dividing by mass ($\frac{\tau_c}{m}$), the entrainment threshold of each species were still significantly different (Table 3.3; Figure 3.7B). This indicates that differences between species are at least partly due to case shape, not solely related to their relative mass. Per unit mass, *P. latipennis* cases were entrained at significantly lower shear stress than *S. personatum* (Figure 3.7B; Table 3.3). This suggests that differences in mass are largely responsible for the significantly higher entrainment threshold of *P. latipennis* than *S. personatum* (Figure 3.7; Table 3.3). After controlling for mass, *A. fuscipes* remains significantly more difficult to entrain than the other species (Figure 3.7B; Table 3.3). This suggests that shape, not mass, was largely responsible for the difference between dome shaped *A. fuscipes* and the tubular cases of the other species. Using Shields dimensionless criterion (τ_{*c}) entrainment thresholds of cases of all species were still significantly different, although dwarfed by the much higher values of τ_{*c} for loose sediment (Figure 3.7C).

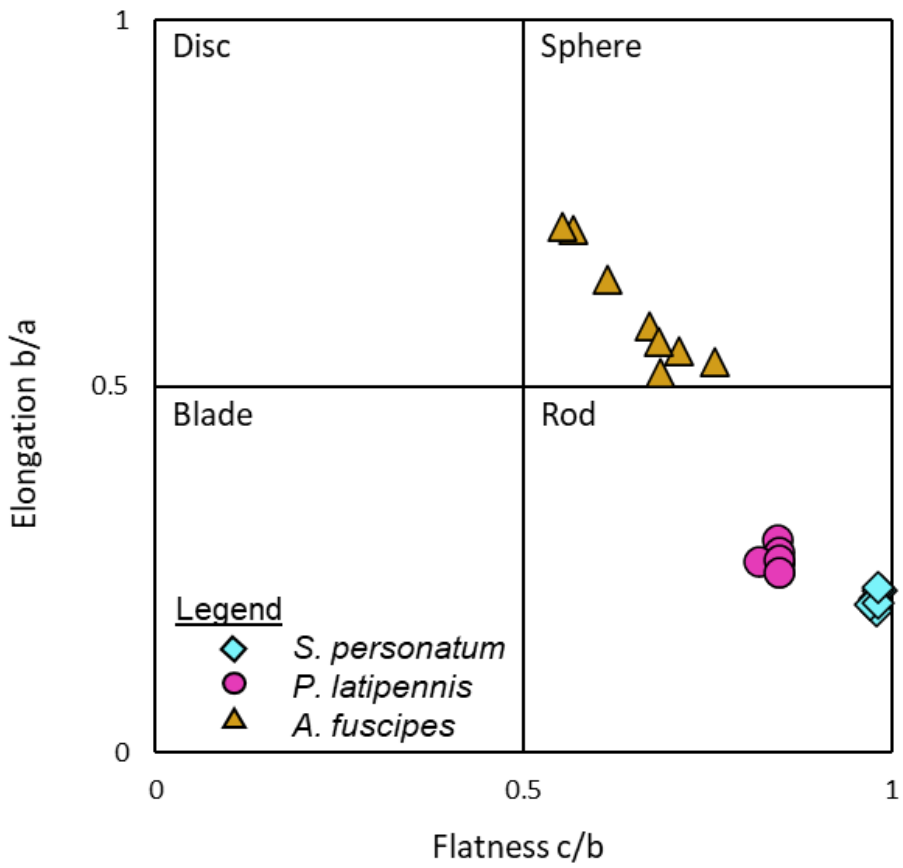


Figure 3.9. Zingg classification of particle shape for cases of the three species (Mclean 1982). Distinct differences in shape are evident between *A. fuscipes* cases, which more closely resemble spheres and the rod-shaped cases of *P. latipennis* and *S. personatum*.

3.5 Discussion

This chapter has examined the bed shear stress required to entrain empty cases of three species of caddisfly and the loose sediment the cases were constructed from. Cases and sediment were entrained from a measurement plate (simulating a flat-topped cobble) within a gravel-bed. Consequently, hydraulic conditions were analogous to those of gravel-bed streams, where high densities of these species typically occur (including Black Brook and Burleigh Brook where larvae were collected, and Wood Brook studied in Chapter 2). The experiment successfully identified and replicated a series of flow stages, which provide a stepped increase in near bed velocity and bed shear stress. (Figure 3.4). This enabled precise determination of critical entrainment thresholds, evidenced by the fact that the entrainment thresholds of sediment particles match those predicted by Shields (1936; Figure 3.10).

Cases built by two species; *P. latipennis* and *S. personatum* were entrained at significantly lower shear stresses than their case sediment (Table 3.3). This might be expected from the fact that caddisfly case construction increases the size and therefore protrusion of sediment into flow (Table 3.2). This fits with previous studies on the mobility of other naturally occurring agglomerates, including Polychaete faecal pellets (Taghon *et al.,* 1984) and clay aggregates (Rust and Nanson, 1989). Therefore, caddisfly bioconstructions may increase the potential for sediment transport. In contrast, cases of *A. fuscipes* were entrained at similar shear stresses to their incorporated sediment (Figure 3.8C). This result is particularly interesting and suggests that case shape, at least partly, affects the difference in entrainment between caddisfly species. Whilst the experiment is limited in the generality of the results, which are specific to empty cases of three species, it provides an important step towards understanding the mechanisms by which case-building caddisfly may affect sediment transport in rivers.

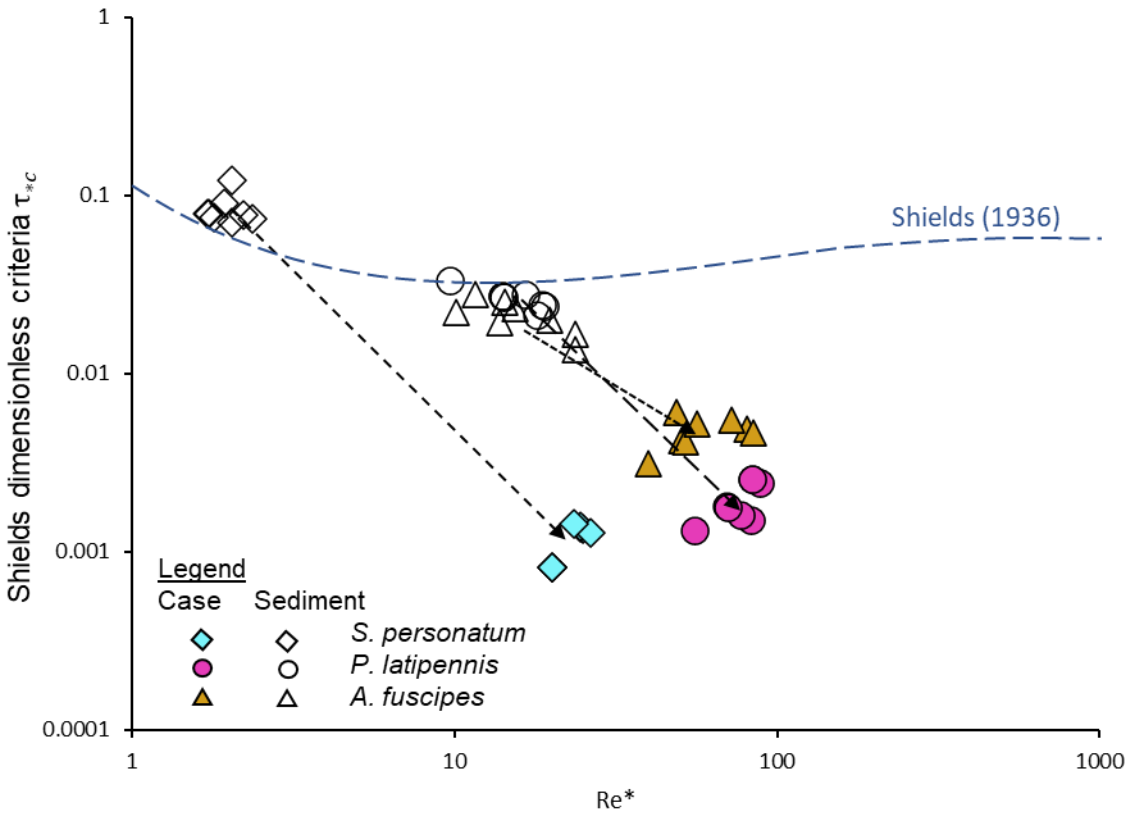


Figure 3.10. Shields criteria for cases and sediment for each species. Loose sediment plots approximately on the Shields line (based on the empirical work of Shields (1936) and generally accepted (Paphitis, 2001)), giving confidence in the methodological approach of this chapter. However, cases were moved at τ_{*c} far below expected for the size of these particles. Arrows indicate approximate reduction in Shields criteria and increase in Reynolds which occurs when cases are constructed from loose sediment.

3.5.1 Transport of caddisfly cases versus sediment (Question 1)

Caddisfly of all three species created cases with very different size and shape characteristics to the sediment grains used in construction. All three species incorporated fine sand to fine gravel sized mineral sediment (Figure 3.6), into much larger aggregate particles. *P. latipennis,* for example, built the largest cases which were on average 22 mm long and 6 mm wide from sediment with an average diameter of 1.16 mm (Table 3.2). Hydraulic force increases rapidly with distance above the riverbed and therefore larger particles experience higher drag. For mineral sediment grains, this increased exposure is usually offset by the increase in particle mass, meaning that larger particles require higher shear stress to entrain (Shields, 1936). Caddisfly cases are substantially heavier than the individual sand grains incorporated but are also hollow, and therefore weigh considerably less than a solid mineral particle of the same size. *S. personatum* and *P. latipennis* both constructed large tubular cases which were easier to entrain than their constituent sediment (Table 3.3) suggesting that the increased exposure to hydraulic force due to protrusion, outweighed the increase in mass resulting from the cementing of many small sediment grains together.

A. fuscipes also substantially increased the effective size of sediment during case construction, building a case which was a similar mass to *S. personatum* (both 0.03 g; Table 3.2) from sediment of a similar size to *P. latipennis* (Table 3.2). However, entrainment of *A. fuscipes* cases did not differ from their incorporated sediment (Table 3.3). This was also true after standardising for case mass (Table 3.3; Figure 3.7B), suggesting that case shape is responsible for the difference in entrainment thresholds between *A. fuscipes* and the tubular case-builders.

Entrainment was measured from a flat platform (Figure 3.2) and therefore the transport of cases and sediment over a rough gravel-bed are unknown. Qualitative observations of case entrainment showed that, once entrained, cases quickly came to rest in the first sheltered pocket between gravel particles. It is probable, however, that due to their size and shape *S. personatum* and *P. latipennis* cases will be transported over gravel beds at lower shear stresses than their constituent sediment. Cases of all three species are larger than their constituent sediment grains and are therefore less likely to find sheltered pockets, resulting in overpassing. Furthermore, rod shaped particles (e.g. *S. personatum* and *P. latipennis* cases) are more mobile than platy or spherical particles, because they can twist around obstacles and are less likely to find pockets in bed topography where they are stable (Demir, 2000). Hollow rods of mineral sediment are rarely found in riverbeds, so these species of caddisfly construct a particle with novel entrainment properties.

3.5.2 Entrainment of loose sediment

Unlike caddisfly cases which moved as one item, loose sediment moved over a wide range of shear stresses (Figure 3.8). The critical bed shear stress required to move 90% of case sediment was similar for *A. fuscipes* and *S. personatum* but higher for *P. latipennis* (Figure 3.7A). This is probably a combination of grain size and the total mass of grains. *P. latipennis* used the largest sediment grains (Figure 3.6) but *A. fuscipes* used only marginally smaller grains (Figure 3.6) and was entrained at significantly lower shear stress (Table 3.3). Therefore, grain size is not the only factor affecting the entrainment of sediment. *P. latipennis* cases were considerably larger than *A. fuscipes*. The greater number of particles probably increased the importance of grain interactions and armouring was evident for *P. latipennis* sediments, with larger particles hiding smaller particles. The entrainment of smaller grains is therefore dependent on the entrainment of larger particles, causing sediment to be transported at a higher shear stress threshold.

A 90% entrainment threshold of loose sediment was used to compare to entrainment of cases (100% of sediment moved at once) because often a small number of particles persisted to much higher shear stresses, presumably largely due to chance (Figure 3.8). 90% did not relate to a step change in sediment movement (as is commonly used in entrainment studies; Buffington and Montgomery, 1998; Simões, 2014; Perret *et al.,* 2015) but is approximately equivalent to 'general movement' (Perret *et al.,* 2015; Petit 1994). As the overall effect of caddisfly on sediment stability was of primary interest, comparing general sediment movement was probably more valuable than incipient motion. In any case, both *P. latipennis* and *S. personatum* cases had been transported before the incipient movement of loose sediment (Figure 3.8A & B).

3.5.3 Movement of cases, role of mass and shape (Question 2)

The difference in entrainment thresholds between cases of different species will be a result of both difference in mass and the size and shape of cases. The difference between *P. latipennis* and *S. personatum* cases appears to be largely related to the difference in case mass (Figure 3.7B). The shape is broadly similar between the two species, both being tubular (Figure 3.1) but they differ considerably in mass (mean *P. latipennis* = 0.26 g, *S. personatum* = 0.03 g; Table 3.2). However, small differences in shape may be important to case entrainment; *S. personatum* cases are narrower and therefore protrude less into the flow, reducing their exposure to turbulent hydraulics. In addition, the slightly curved profile of *S. personatum* cases may reduce rolling as the case has to be lifted (and in loose sediment the ends would dig in). Cases of *P. latipennis* are made from much coarser sediment (Figure 3.6) and therefore have a rougher surface texture (Figure 3.1). Particles

sticking out from the case may increase case protrusion and facilitate entrainment but may also make the case less inclined to roll along the bed.

The shape of *A. fuscipes* cases was very different to cases of *S. personatum and P. latipennis* (Figure 3.1; Figure 3.9), resembling domes over a flat base instead of tubes. Consequently, whilst they had a similar mass to *S. personatum* and were considerably lighter than *P. latipennis*, they were much harder to entrain than either species (Figure 3.7A). The tubular shape and rounded profile of *S. personatum* and *P. latipennis* meant that, while they remained facing upstream until entrainment, once turned sideways they rolled easily off the platform. In contrast, the flat base of *A. fuscipes* probably increased friction, reduced tendency to roll, and therefore required much greater shear stress for entrainment.

These results suggest that different case designs might serve different purposes for the larvae. *S. personatum* burrow diurnally (Wagner, 1987) and therefore may avoid entrainment by burrowing, facilitated by an externally smooth case of small sand grains. Glossosomatidae are rheophilic species, adapted to life on the exposed upper surfaces of gravel beds (Olden *et al.,* 2004). *A. fuscipes* cases may therefore be designed to reduce entrainment. Furthermore, *A. fuscipes* appear to be flexible with the grain size used in case construction (Figure 2.5). If flow resistance is a key objective of their case design, perhaps they are more likely than other species to adapt their case to the hydraulic environment. Whilst cases may not be designed purely as anti-entrainment devices they may still play an important role by; 1) reducing energy required for active resistance and, 2) keeping entrained larvae near the bed surface where they are likely to move only short distances into more sheltered areas, unlike uncased larvae which, once active resistance has failed, are more likely to move in suspension

3.5.4 Geomorphological implications of caddisfly case construction

Therefore, empty cases of *S. personatum* and *P. latipennis* are likely to be preferentially transported over other grains on the river-bed surface. However, this experiment is limited to entrainment of empty cases off a flat platform. Entrainment of cases with live larvae over a mobile gravel-bed are likely to be different. The tightly controlled nature of this experiment prohibited the use of live larvae. For example, the baseboard was fixed and painted white in order to increase sediment contrast for photographing entrainment (Figure 3.2; Figure 3.3). Experimental trials with live larvae under low flows resulted in larvae walking downstream (probably as the quickest way to escape a highly unnatural environment) and in higher flows clinging to the flume edges where velocities were reduced.

The presence of a live larvae in a case considerably increases the force required to move the case. Otto and Johansson (1995) found that cases of *Silo spp.* (Goeridae) moved at 10.3 cm s^{-1} but with the addition of a live larvae this increased to 64.4 cm s^{-1}. Live larvae are able to actively reduce drift via a number of mechanisms including clinging on, changing case orientation (e.g. facing into flow to reduce exposure), fixing their case or themselves with silk threads and moving to avoid high exposure areas (Olden *et al.,* 2004; Rice *et al.,* 2007; Waringer, 1989). Active resistance to entrainment varies between species; for *A. auricollis* active resistance accounted for 55% of current resistance (Waringer, 1989) compared to 90% for *Potamophylax cingulatus* (Otto, 1976). Larvae may also be able to sense increasing shear stresses and seek refuge pre-emptively to avoid entrainment (Townsend and Hildrew, 1994). Therefore, it is possible that when the larvae is alive the sediment is transported further by walking than by drift (Figure 1.4B). Furthermore, if the addition of a larvae increases the shear force required to move *A. fuscipes* cases, these would become more stable than their constituent sediment.

The results of this experiment apply only to empty cases. This scenario is most likely to occur following pupation of adult caddisfly or when cases are abandoned by the larvae. Pupal cases of Limnephilidae are typically attached to the undersides of larger particles or stable wood material. Sericostomatidae pupal cases have been found buried just below the surface in fine sediment and anchored to larger grains. However, both find their way onto the bed surface and were found scattered across the bed of Black Brook, in various states of decay.

3.6 Summary

Via the construction of cases from mineral and organic sediment caddisfly create composite particles of sediment particles bound together with silk (Hansell, 1968; Okano *et al.,* 2016). Caddisfly created an agglomerate particle with greater mass than any individual incorporated grain, but cases were also much larger and hollow and therefore effectively less dense. The effect of case construction on the entrainment threshold of incorporated sediment varied between the three species. *S. personatum* and *P. latipennis* cases were entrained at significantly lower bed shear stresses than their constituent grains. This effect is also likely to be seen in the movement of cases over gravel-beds as they can more easily pivot and roll over obstacles. In contrast, *A, fuscipes* cases were entrained over the same range of shear stress as their constituent grains. This fits with the rheophilic nature of *A. fuscipes* larvae and their preference for living on exposed surfaces in fast flowing streams.

Both weight and shape were important in explaining the difference in entrainment between case designs. The difference between *S. personatum,* which moved earliest (mean τ_c = 0.06 N m^{-2}), and *P. latipennis* (mean τ_c = 0.18 N m^{-2}) was largely a result of differences in mass between the two cases. *A. fuscipes* cases were relatively lightweight but significantly more difficult to entrain than other species (mean τ_c = 0.28 N m^{-2}). Observations of case movement revealed that once entrainment thresholds were reached, *S. personatum and P. latipennis* turned perpendicular to the flow direction and rolled. However, the flat base and sharp edges of *A. fuscipes* reduced their propensity to roll and most cases slid, increasing friction with the bed and therefore entrainment thresholds.

These are important results for understanding the effect of bioconstruction by caddisfly larvae on the mobility of sediment in rivers. More research is required to determine the role of live larvae in the mobility of its case sediment, via resisting or initiating entrainment as well as transporting sediment while crawling. All three species studied in this chapter occur in large numbers (particularly *A. fuscipes*) and use substantial quantities of sediment (Chapter 2). Consequently, increased mobility of these sediments could affect the distribution and transport of sediment in rivers.

Glossosomatidae Agapetus fuscipes in an experimental flume (Chapter 4)

Chapter 4. Vertical sand displacement by Glossosomatidae *Agapetus fuscipes* larvae

4.1 Introduction

4.1.1 Sand transport in armoured gravel-bed rivers

Substrate surfaces are important zones for sediment transport in rivers. Gravel-bed rivers typically develop armoured surface layers, in which coarser grains are overrepresented compared to the subsurface (Dietrich *et al.,* 1989; Pitlick *et al.,* 2008). Entrainment is size selective, so fine sediment is preferentially winnowed from gravel-beds (Shields, 1936). Fine sediment also infiltrates into the interstices between the gravel framework, resulting in a downwards movement of particles; a process which is accelerated when gravel particles are mobilised and voids become available (Mao *et al.,* 2011). The fine sediment content of gravel-beds is therefore hidden below the surface in interstices and in the lee of obstacles, where it is sheltered from hydrodynamic forces at the surface (Laronne *et al.,* 2001).

The development of armoured substrate surfaces means that only high discharge events can break up and mobilise the coarse surface layer of gravel-beds. Consequently, under most flow conditions bedload transport is dominated by finer grained sediments including sand (Church, 2010). However, although it may be hidden, fine sediment plays important roles in gravel-bed river geomorphology. The sand fraction in gravel-bed rivers can also promote or inhibit the transport of larger gravel clasts, depending on fine sediment proportion (Grams *et al.,* 2007; Venditti *et al.,* 2010; Wilcock *et al.,* 2001). Therefore, the quantity and distribution of fine-sediment within gravel-beds is geomorphologically important. The transport of fine sediment in armoured gravel-bed rivers is limited by supply of this sediment on the surface and, the steep gradient in hydraulic exposure between the surface and subsurface of armoured gravel-beds mean that displacement of fine sediment over small vertical distances can have substantial effects on the exposure of that sediment and its contribution to bedload transport (Garcia *et al.,* 1999; Powell, 1998).

Caddisfly of the family Glossosomatidae are characteristic of gravel surfaces in fast flowing gravel-bed streams and rivers (Figure 4.1A; Houghton and Stewart, 1998; Morris and Hondzo, 2013b; Nijboer, 2004; Wood and Armitage, 1999). Observations of Glossosomatidae species indicate a preference for positioning themselves on the exposed upper faces of gravel-bed

particles (Figure 4.1B & C; Kovalak, 1976; Olden *et al.,* 2004). These zones of high hydraulic shear and exposure to predators are avoided by many aquatic macroinvertebrates, due to the energetic cost of maintaining position in turbulent conditions (Statzner *et al.,* 1988; Statzner and Higler, 1986). However, Glossosomatidae larvae are well adapted to high velocity locations due to their case mass (relative to body weight; Becker, 2001; Waringer, 1989), case shape (Figure 3.7), and their use of silk to fix their case in position on gravel surfaces (Olden *et al.,* 2004).

Respiration is an important factor structuring the distribution of Glossosomatidae larvae in gravel-bed streams (Kovalak, 1976). Unlike many caddisfly taxa, Glossosomatidae rely on flow velocity to flush oxygenated water through gaps in the dome of their case (Zwick *et al.,* 2011). Glossosomatidae cases act to reduce predation and allow them to better exploit periphyton on exposed gravel surfaces than 'unarmoured' grazers (Kohler and McPeek, 1989).

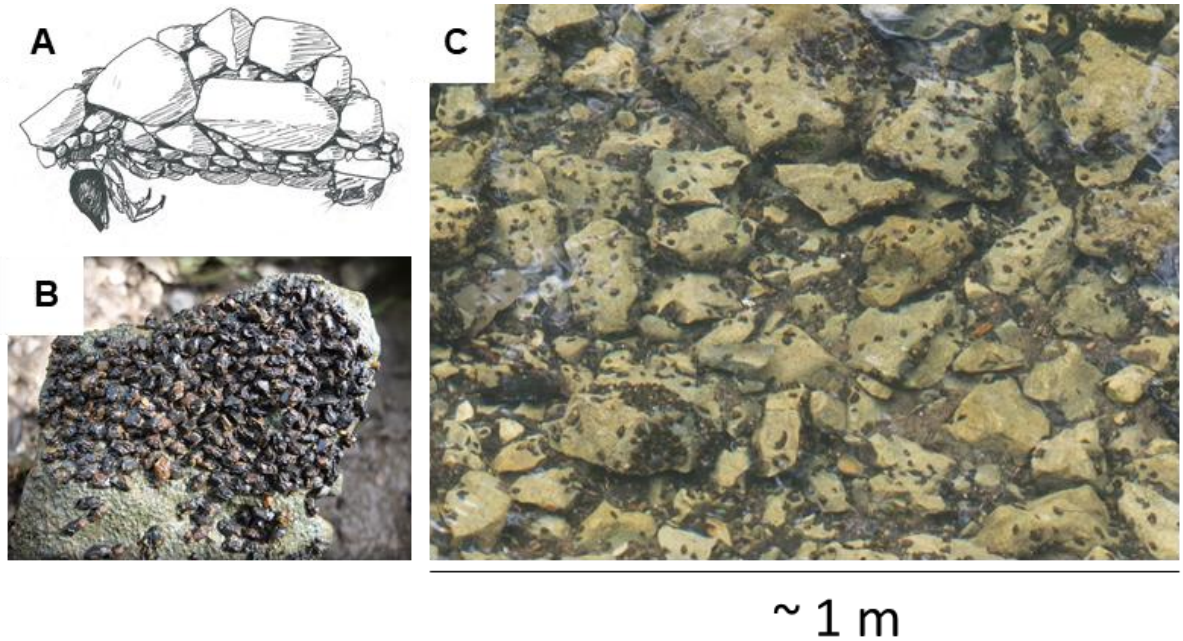


Figure 4.1. Glossosomatidae larvae in the River Dove, Derbyshire, U.K. (A) Sketch of *Agapetus fuscipes* case design, note the use of a relatively broad range of sand sizes, often with larger particles on the case sides and the ring of fine sediment around the case opening, characteristic of *Agapetus* species (Wallace *et al.,* 2003). (B) Dense aggregations on the exposed face of a single cobble, (C) Cases visible on the upper surface of gravel particles on the riverbed.

Glossosomatidae larvae therefore exhibit 'conflicting resource requirements' (*sensu.* Statzner, 2011; Statzner *et al.,* 2005), requiring both fine sediments for case construction (Becker, 2001; Marchant, 1988) and exposed gravel surfaces for food and respiration (Kovalak, 1976). This suggests that Glossosomatidae larvae construct cases from fine sediment available in sheltered areas (interstices and sheltered patches), and then move with their case onto the gravel surface. This flux of sediment could be geomorphologically important because;

1) By transporting their case sediment from sheltered patches and interstices to the surface of gravel particles, Glossosomatidae potentially increase the exposure of fine sediment to entraining flows. 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 (Figure 4.1C).

2) Similar movements are repeated by many individuals. Glossosomatidae are a widespread caddisfly family and under the appropriate environmental conditions, can reach extremely high abundances (Hickin, 1967; McNeely and Power, 2007). In Wood Brook, Glossosomatidae *Agapetus fuscipes* larvae were found at abundances up to 6710 larvae m^{-2}, making it by far the dominant caddisfly taxa (Chapter 2). As a result, Glossosomatidae accounted for 64% of total sediment mass used by caddisfly (Figure 2.3). At some sites, this could represent a substantial flux of sediment in a single direction; onto the riverbed surface.

3) Glossosomatidae larvae use sand, with a D_{50} of 0.94 mm (Table 2.1). Sand is often the most mobile sediment fraction, accounting for a substantial proportion of bedload in many rivers (Church, 2010). The transport of sand out of interstices may also have implications for gravel transport (Wilcock and Kenworthy, 2002).

The potential displacement of sediment by Glossosomatidae larvae is likely to vary based on larvae behaviour and the abiotic conditions, particularly the hydraulic and sediment characteristics of the environment. Whilst Glossosomatidae have a wide range of flow tolerances, their behaviour under high flow velocity is important because larvae may move their case (and sediment) back to sheltered areas, or the larvae may abandon the case and drift. Glossosomatidae larvae have been found to migrate to less exposed locations on gravel particles during floods, resulting in reduced entrainment (Brooks, 1998 In: Lake, 2000). However, other studies have documented Glossosomatidae species drifting under hydraulic stress (Houghton and Stewart, 1998), potentially leaving their case exposed and easily transported downstream.

The nature of the gravel-bed is also likely to affect the movement of Glossosomatidae larvae. In particular, the size and protrusion of individual surface particles into the flow, as well as having geomorphological implications (Masteller and Finnegan, 2017), will dictate the space and hydraulic landscape available to larvae. Gravel-beds with higher grain protrusion will provide more opportunity for larvae to find sites suitable for feeding and respiration but will also increase the separation distance between exposed particle surfaces and available fine sediment required for case construction and modification, potentially forcing larvae to migrate further.

4.1.2 Context of this chapter

Transport of sediment at moderate flows is dictated by the availability and character of fine sediment on the bed surface, the distribution of which is of interest to fluvial geomorphologists (Curran and Waters, 2014; Laronne *et al.,* 2001; Wilcock and Kenworthy, 2002). However, the role of biology in modifying sediment sorting processes has received far less research attention (Rice *et al.,* 2012; Statzner, 2012). Many species of case building caddisfly are very mobile, transporting their case sediments several metres per day (Rice *et al.,* 2007; Elliott, 1971; Figure 1.4B & C) but active transport of sediment by caddisfly larvae has not been studied. Glossosomatidae caddisfly have the potential to affect the distribution of fine sediment by transporting sand from sheltered locations to the surface of gravel-beds. However, the movement of Glossosomatidae larvae has only been studied from a habitat preference perspective (Kovalak, 1976; Morris *et al.,* 2011; Morris and Hondzo, 2013b). This is the first attempt to understand movement of fine sediment by a caddisfly larva and the implications for zoogeomorphology. This chapter uses a laboratory flume to compare Glossosomatidae *A. fuscipes* movement behaviour under two flow velocities and two bed roughness scenarios. This chapter addresses thesis objective 3. Specifically, the following research questions were investigated:

1) To establish if *A. fuscipes* larvae transport sediment vertically upwards, from interstices onto the surfaces of gravel particles and to quantify any flux of sediment.
2) To determine if the vertical migration of *A. fuscipes* larvae is influenced by flow velocity or the grain protrusion of the gravel-bed.

4.2 Methods

4.2.1 Flume setup

Experiments were conducted in an Armfield S6 Flume, with a working section 10 m long and 0.3 m wide (Figure 4.2A, as for Chapter 3). A bed of gravel particles (16 – 64 mm diameter, D_{50} = 38 mm) cemented to a plywood base ensured fully turbulent flow with bed roughness and turbulence comparable to the stream from which caddisfly larvae were sourced. The bed was raised from the flume base by 0.08 m to allow a tray filled with loose sediment (length = 0.21 m, width = 0.14 m, area = 0.0294 m^{-2}; Figure 4.2B) to be inserted flush with the bed. The sediment tray was located 7 m from the flume inflow and 3 m from the tailgate. A net (1 mm aperture) was placed 0.7 m downstream of the tray to catch drifting larvae. Four treatments were studied with varying flow velocity and gravel protrusion. Two velocities, low (mean velocity = 0.14 m s^{-1}) and high (mean velocity = 0.6 m s^{-1}) were used, whilst gravels were selected to be either large (high protrusion; b axis = 45 – 65 mm) or small (low protrusion; b axis = 32 – 45 mm). Gravel sizes and velocities chosen were representative of the range of conditions in the shallow gravel-bed stream from which larvae were collected and the upper velocity was the maximum achievable in the flume whilst maintaining stable flow conditions.

Velocity was measured using an electromagnetic current meter located 1 m upstream of the sediment tray at 0.05 m elevation from the bed (Figure 4.2). Velocity was manipulated by adjusting the discharge, flume slope and outflow weir to maintain a water depth of 0.1 m. Oxygen availability was measured at the start and end of each run and remained above 99% saturation. Water temperature was controlled between 13 – 15.6°C and light was provided over the focus area using a Fluval aquasky LED between 04:30 and 22:00 to mimic the natural daylight cycle in June - July.

A. fuscipes larvae were sourced from a local stream; Black Brook (52°46'33.4"N 1°17'57.6"W). Larvae were collected the evening before experiments and then acclimatised overnight in aerated aquaria with physiochemical conditions similar to those in the flume. Experiments were conducted between mid-June and mid-July 2018.

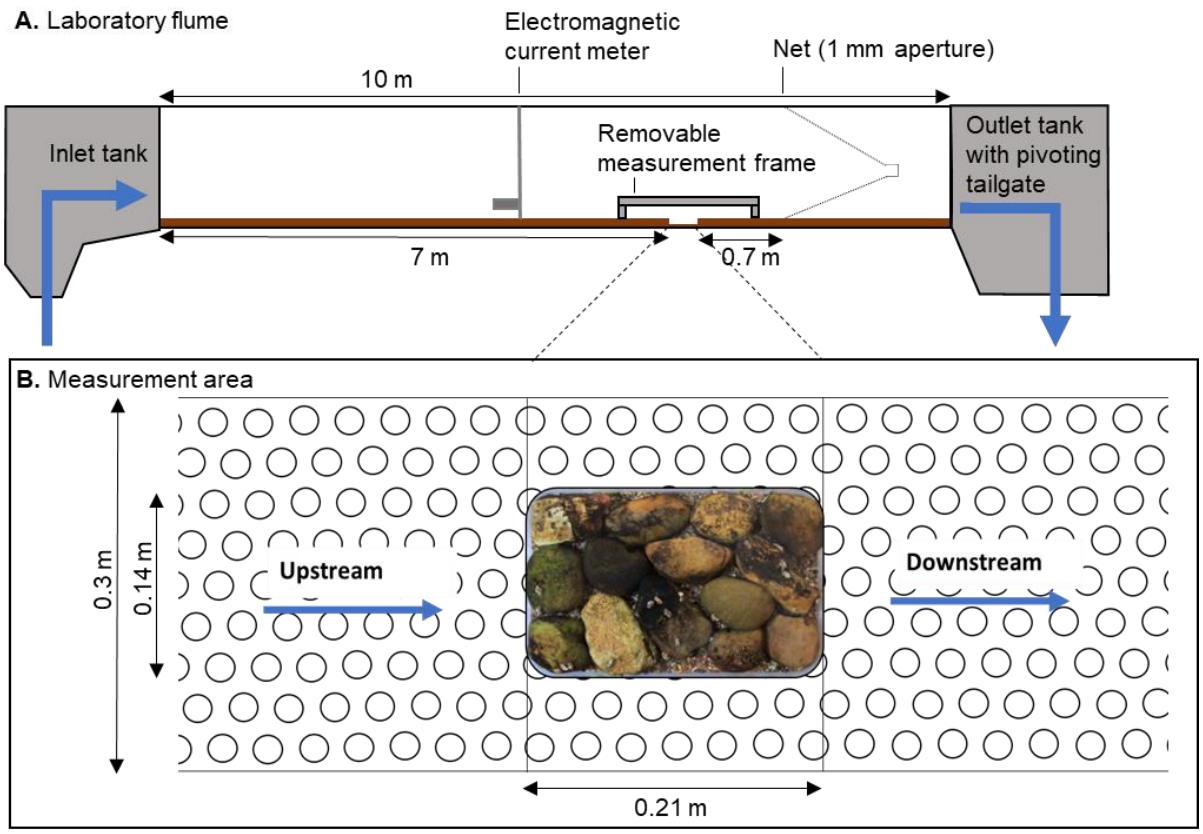


Figure 4.2. The laboratory flume setup. (A) Experiments were conducted in the same flume as Chapter 3. An uneven fixed gravel bed (D_{50} = 38 mm) was placed throughout the flume length. (B) This was raised to allow a tray (length = 0.21, width = 0.14 m) to be inserted flush with the bed. An aluminium frame could be placed over the tray area facilitating accurate measurement of *A. fuscipes* locations but was removed during the flume runs.

4.2.2 Sediment tray setup

The sediment tray (Figure 4.3) was first filled with gravel and sand, collected from local streams and then dried at 130°C, until level with the tray rim (Figure 4.3A). Sand was sieved to be between 0.355 - 2.8 mm to include the D_5-D_{95} range used by *A. fuscipes* locally (Table 2.1), with a size distribution shown in Figure 4.3C. In addition, fresh gravel particles were collected the previous day from the surface of a local stream and added to the tray surface to simulate an armoured gravel-bed (Figure 4.3A). This gravel was placed in the sediment tray with algae covered faces uppermost (as they were positioned in the river).

To ensure differences in gravel size resulted in differing protrusions between the treatments, only gravel that was not platy, elongated or bladed was selected, with a deviation from compactness value ($S = c/a$) greater than 0.3 (where c and a are the minor and major particle axis respectively, Bunte and Abt, 2001). Analysis of variance followed by post-hoc Tukey Honest

Significant Difference tests conducted in R Studio 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 (Figure 4.3D), but not between runs of the same gravel treatment. As particles were placed in stable positions, with c axis orientated vertically, this indicates that the larger gravel size also resulted in a difference in bed protrusion.

Flow velocity depth profiles were collected for an example of each treatment to characterise in more detail the velocity larvae were exposed to and investigate interactive effects between gravel size and flow velocity (e.g. does larger gravel also increase flow velocity by forcing flow to accelerate over the bed surface?). Velocity profiles were measured using a Nixon low speed propeller set at five locations over the sediment tray. Velocity profiles were collected at 10 mm vertical intervals from the bed (10 mm being the area measured by the propeller). At each vertical interval six, ten second measurements were taken and averaged. Velocity profiles demonstrated that flow was different between flow treatments but not between gravel treatments (Figure 4.4).

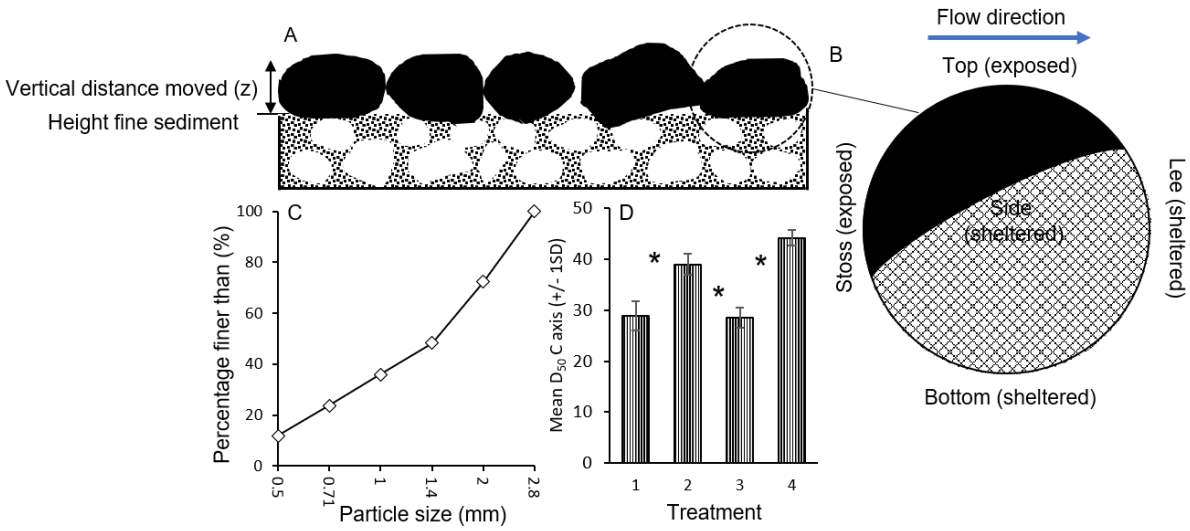


Figure 4.3. Sediment tray setup. A tray of loose sediment was added to the flume, flush with the bed. (A) Side profile of the sediment tray, containing a framework of gravel particles infilled with fine sediment. Fresh, algae coated gravel particles were placed on the surface to simulate an armoured gravel-bed. (B) The position of each larvae following the flume experiment was recorded according to their relative exposure zones. (C). Size distribution of fine sediment in the tray. (D) Mean of D_{50} of the minor (c) axis of gravels within each run demonstrates a significant difference in bed protrusion/roughness between small gravel treatments (1 and 3) and large gravel treatments (2 and 4), indicated by * (Tukey HSD, $P < 0.05$).

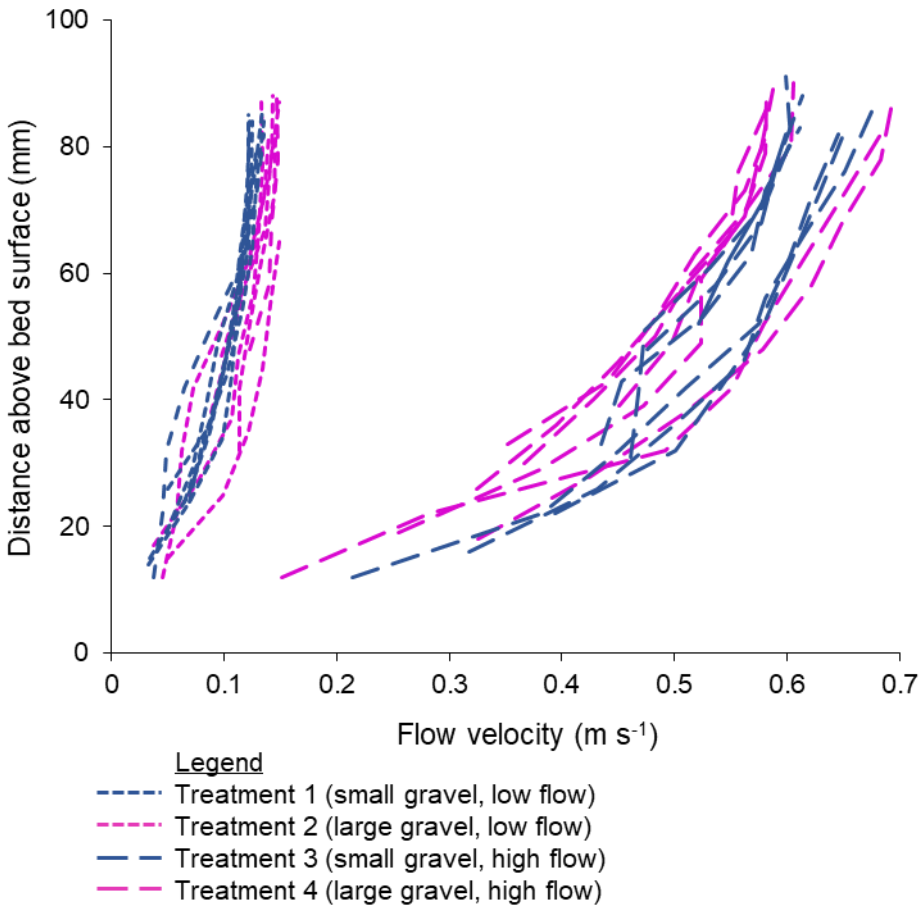


Figure 4.4. Flow velocity profiles for a representative run from each treatment. Indicates a difference in velocity between velocity treatments, but not between gravel protrusion treatments.

4.2.3 Experimental procedure

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). X and Y location were determined using rulers on the frame, while 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 area for Z of mean = 0.3 mm (max = 1.25 mm, n = 204). this accounts for error in the placement of the measurement frame and the precision of the digital callipers.

Prior to each experiment the sediment tray was installed, and gravel particles placed on top (Figure 4.3A). The measurement frame was used to measure the height of fine sediment within the tray at 10 locations. The measurement frame was then removed during the experiment so that it did not affect flow conditions. 50 *A. fuscipes* larvae were added in each flume run in order

to reproduce a population density in the sediment tray equivalent to that in the field (Chapter 2). *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 = 0.111 m s^{-1}, depth = 82 mm) which were maintained for 2 hours, with larvae contained within the sediment tray by a plastic surround. This two hour period was identified in trials to allow larvae to settle and begin case construction (*sensu.* Houghton and Stewart, 1998). Subsequently, the plastic surround was removed, and discharge was gradually increased, and the tail gate lowered to maintain a constant depth of 100 mm until the desired velocity was reached. This velocity was maintained until the following morning (11 am), a total of 21 hrs. At this point discharge was reduced and a series of measurements were taken:

1) Larvae location were obtained using the measurement frame and callipers. For larvae which had migrated outside of the sediment tray only X and Y were recorded using a tape measure.
2) The position of each larvae with respect to the gravel particle they were located on was recorded according to Figure 4.3B, allowing flow exposure to be inferred (*sensu.* Kovalak, 1976).
3) Following the measurement of the visible larvae, the entire base board 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 recorded.

A total of 13 flume runs were conducted (using 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 (Table 4.1), and one run of treatment 2 had to be discounted because flow conditions changed overnight.

4.2.4 Caddisfly and case analysis

Cases removed from the larvae prior to flume experiments were dried and stored. Caddisflies and cases built during flume runs were stored in 70% Industrial Methylated Spirits. Larvae were then removed from their cases, identified (all larvae were identified 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. All cases from each flume run were amalgamated to determine their mass and grain-size characteristics to determine the mass and size fractions of sediment transported by *A. fuscipes*. Cases were included in sediment analysis if they were considered complete (not missing any obvious sections or large

grains) and cases that were attached to the gravel particles were not included as they tended to break up when removed from the gravel they were attached to. The results from analysed cases were later extrapolated to the count of all cases found within the sediment tray to calculate the total quantity of sediment used. Cases were thoroughly rinsed in deionised water and then dried at 105°C overnight to obtain mass. Subsequently, case sediment was sieved through 38 mm diameter sieves at half phi intervals down to 0.063 mm, giving a sediment size distribution for cases built in the field and in the flume, for each run.

4.2.5 Data analysis

The X Y and Z of each larvae location were used to ascertain whether the larvae had stayed within the tray or moved downstream or upstream from the tray (as all larvae started in the sediment tray). For longitudinal movement, distance travelled was calculated for each larva from the respective upstream or downstream edge of the sediment tray. Distance travelled in a vertical direction was of primary interest for this experiment. This 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 (Figure 4.3A), according to Equation 1.

$$Z_{dist} = Z_{larvae} - Z_{fine\ sediment} \tag{5}$$

Where Z_{dist} was the vertical distance moved, Z_{larvae} the height of larvae at the end of the run and $Z_{fine\ sediment}$ was the height of the fine sediment surface prior to the flume run.

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. 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 for the final model).

4.3 Results

The experiment studied larvae position and movement under four treatments, differing in gravel size /protrusion (Figure 4.3) and flow velocity (Figure 4.4), whilst controlling other physiochemical conditions (Table 4.1). Temperature was slightly higher in the high flow velocity treatments due to the difficulty the coolers had in maintaining a low water temperature when pumps were operating at higher output, but this was not reflected in oxygen saturation, which remained high (Table 4.1). The mean head width of *A. fuscipes* in each run ranged between 0.47 and 0.51 mm, indicating that larvae were final instar (Wallace *et al.,* 2003). Once added to the sediment tray, larvae crawled over the bed surface, sometimes for several tens of minutes before beginning case construction. Several abandoned "emergency" cases were found. These were built from finer sediment than the final cases and had little structural integrity. Final cases were morphologically similar to those built in the field. The number of larvae remaining in the sediment tray (from the original 50), ranged between 13 and 39, averaging 66% although this figure was lower in treatment 4 (Table 4.1). Upstream migration was greater in low flow runs and downstream movement was more common at the high flow velocity (Figure 4.5).

Table 4.1. Details of each treatment. (A) Four treatments were conducted; 1) small gravel, low velocity, 2) large gravel, low velocity, 3) small gravel, high velocity and 4) large gravel, high velocity. For each treatment (B) physiochemical conditions and, (C) details of larvae which stayed within the sediment tray are given. Only those larvae which remained in the sediment tray had their vertical (Z) movement measured. Numbers of larvae remaining are the sum of all runs. Percent remaining is the number of larvae remaining compared to the number added (Number of runs x 50 larvae) and gives an indication of *A. fuscipes* migration out of the sediment tray.

A. Treatment details				B. Physiochemical conditions				C. Larvae in sediment tray	
Treatment	Gravel b axis (mm)	Velocity (m s^{-1})	Number of runs	Temp (°C)	pH	Dissolved O_2 (mg L^{-1})	EC (µS cm^{-1})	Larvae remaining	Percent remaining
1	32 - 45	0.14	4	13.80	7.39	10.71	324.63	121	69.14
2	45 - 65	0.14	2	13.88	7.48	10.63	314.75	67	71.28
3	32 - 45	0.60	3	15.25	7.48	10.22	314.00	96	69.57
4	45 - 65	0.60	4	14.60	7.36	10.78	315.00	68	53.13
All			13					352	65.79

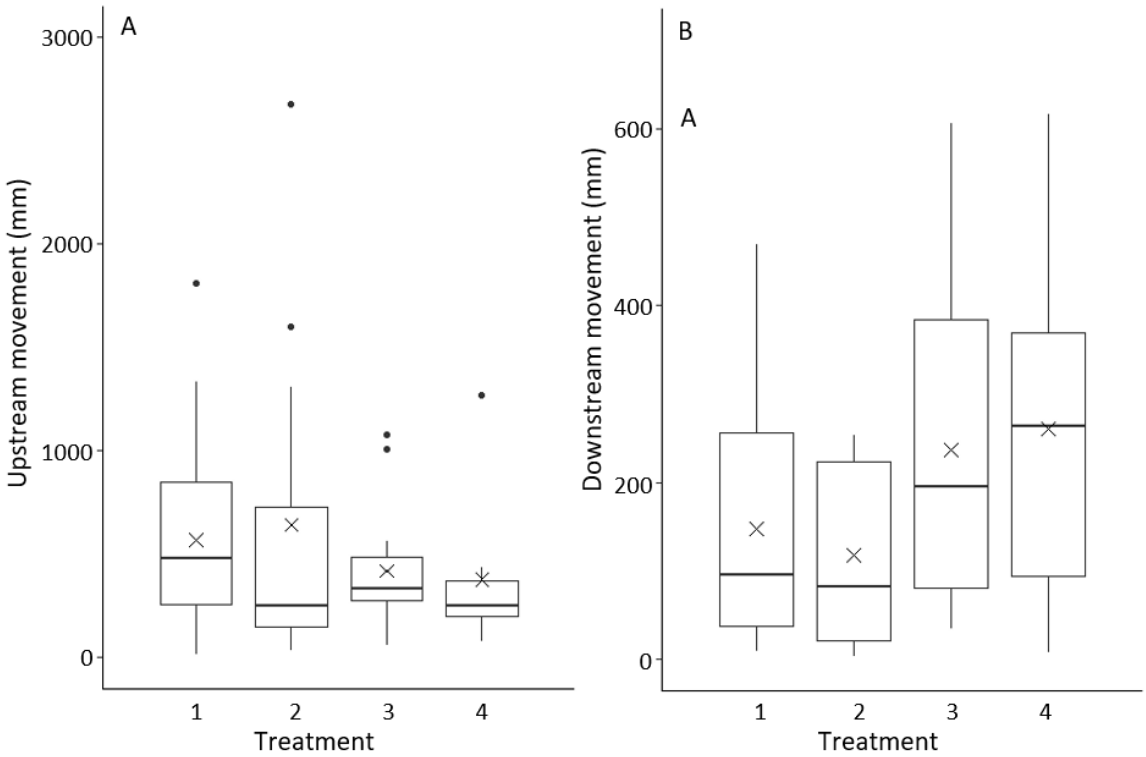


Figure 4.5. Longitudinal movement of *A. fuscipes* larvae within each treatment. (A) Upstream, and (B) downstream. Only larvae which moved either upstream or downstream of the sediment tray are included. Boxes indicate interquartile range, lines extend within 1.5 times IQR beyond box. Median indicated by a line, mean by x.

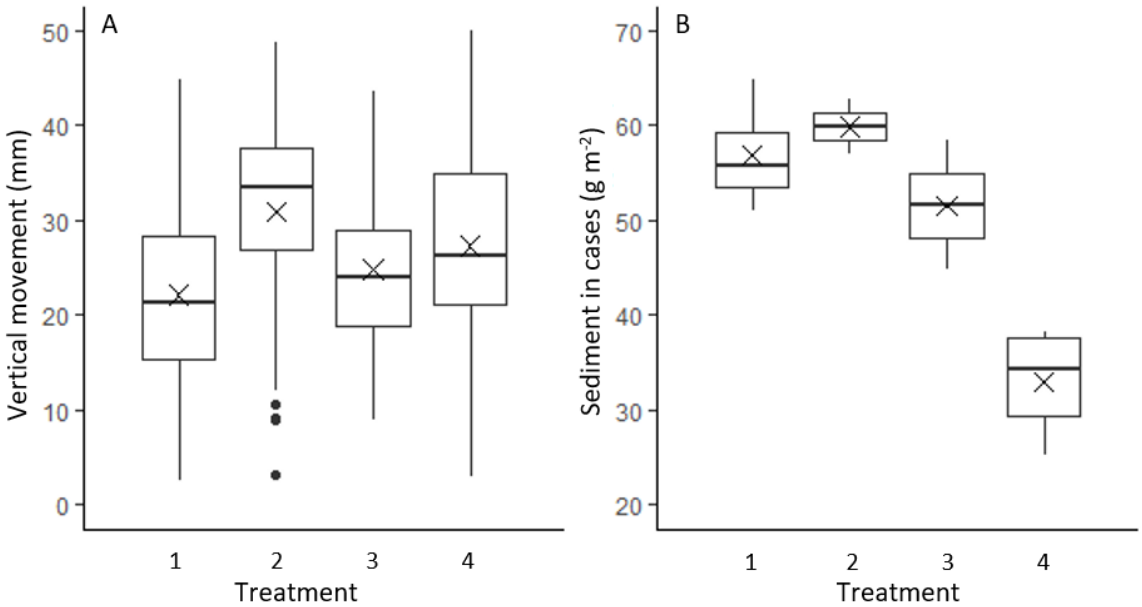


Figure 4.6. Vertical sediment transport by Glossosomatidae *A. fuscipes* larvae. (A) Larvae transport sediment upwards, from interstices onto the surfaces of gravel particles. This was true for all treatments and larvae elevation increased with gravel size but not flow velocity. (B) The amount of sediment displaced was largely dependent on the percentage of larvae remaining within the sediment tray and was similar during treatments 1-3 but lower in treatment 4. Boxes indicate interquartile range, lines extend within 1.5 times IQR beyond box. Median indicated by a line, mean by x.

Table 4.2. Characteristics of *A. fuscipes* cases and sediment use within each treatment. (A) Case characteristics; Mean case mass and D_{50}, (B) Sediment displacement; Mean vertical distance moved (Z distance) and sediment flux. Sediment flux is calculated by multiplying the number of larvae remaining in the sediment tray (Table 4.1C) by the mass of their cases (Table 4.2A).

	A. Case characteristics		B. Sediment displacement	
Treatment	Weight (g)	D_{50} (mm)	Z distance (mm)	Sediment flux (g m^{-2})
1	0.055	1.33	21.83	56.88
2	0.053	1.29	30.95	59.88
3	0.054	1.43	24.43	58.19
4	0.057	1.40	27.05	32.95
All	0.055	1.37	25.40	50.28

When all experimental runs and treatments were considered, the vertical elevation of 352 larvae was measured (from an original 650 larvae added to the flume; Table 4.1). The mean vertical migration was 25.40 mm upwards from the level of fine sediment (Table 4.2) and only 6 larvae travelled less than 5 mm vertically (Figure 4.6). Some larvae moved up to 50 mm upwards (Figure 4.6). Consequently, *A. fuscipes* transport sediment upwards by incorporating it into their cases and crawling upwards (Question 1). The quantity of sediment used by larvae in the sediment tray was lower in high flow velocity runs, particularly run 4, as a result of increased larvae migration out of the tray (Table 4.2).

Mixed effects models indicated that bed protrusion affected the vertical distance travelled by *A. fuscipes* larvae (p = 0.01, Chi^2 = 6.56), with larvae moving on average 5.49 +/- 2.14 mm (standard error, SE) higher when larger gravel particles were present (Question 2; Figure 4.6). Flow velocity did not significantly affect vertical distance travelled (p = 0.93, Chi^2 = 0.007), during the low flow velocity runs vertical distance travelled was increased by only 0.18 mm +/- 2.13 (SE). The interaction between gravel size and flow velocity was not significant.

Case characteristics varied between treatments (Figure 4.7; Table 4.2). The size of mineral particles used by larvae during high flow velocity experiments (Treatments 3 and 4) were larger, reflected in the particle size distribution (Figure 4.7A) and the case D_{50} (Figure 4.7B). However, case mass showed no pattern among treatments (Figure 4.7C). The number of larvae occupying sheltered and exposed locations was broadly similar between treatments 1-3, with slightly more larvae in exposed locations than sheltered in each treatment (Figure 4.8). However, during treatment 4 (high flow, large particles) the number of larvae in sheltered locations remains similar but there are far fewer in exposed locations (Figure 4.8). Furthermore, in treatment 4, larvae

were largely recorded in the downstream half of the sediment tray, unlike other treatments where they were more evenly spread (Figure 4.9).

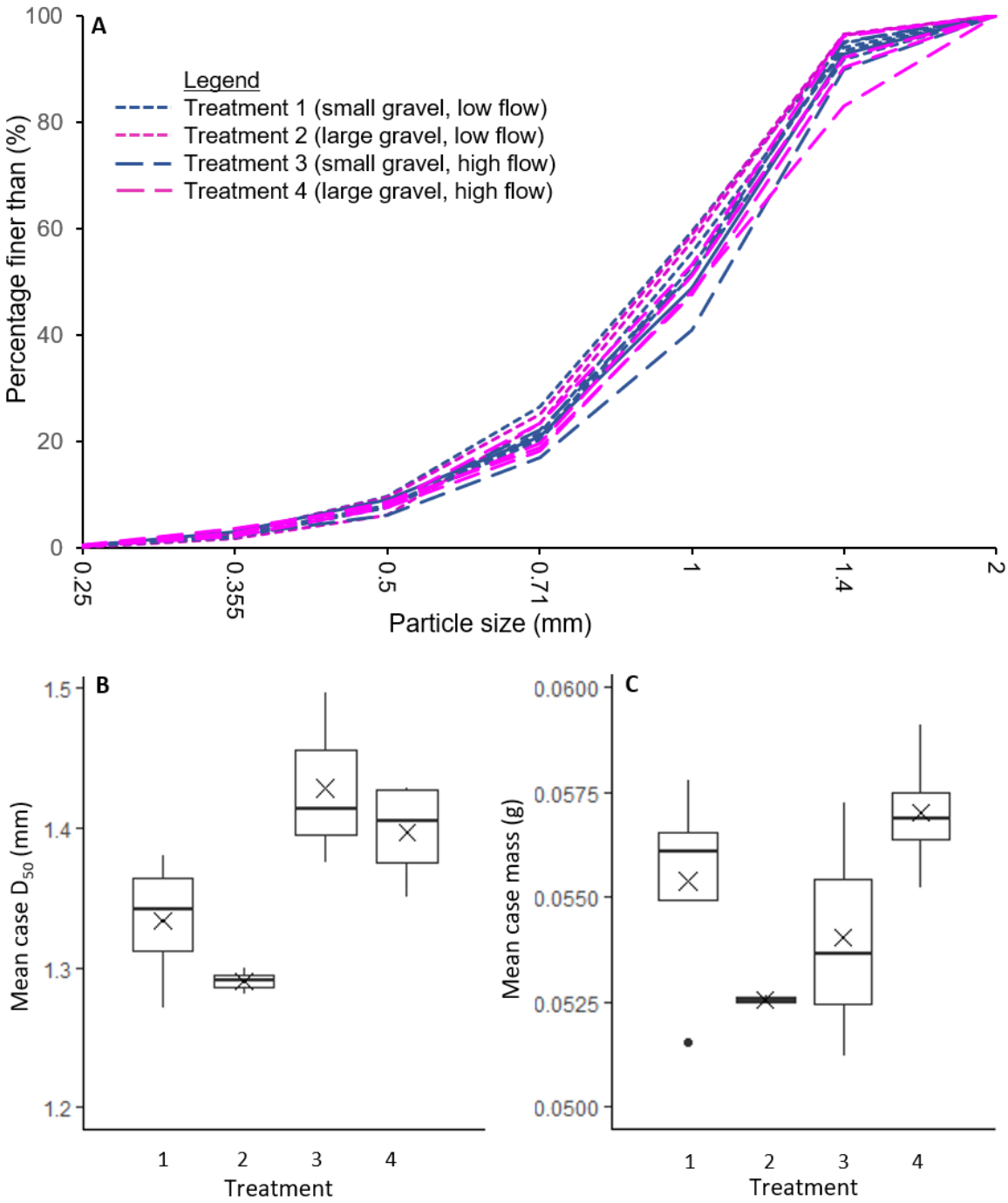


Figure 4.7. Case architecture of *A. fuscipes* larvae from each treatment. (A) particle size distribution for *A. fuscipes* cases from each run with legend indicating treatment. Particle size indicates passing sieve. (B) Case D_{50} for each treatment. (C) Case mass for each treatment. For boxplots, boxes indicate interquartile range, lines range within 1.5 times IQ beyond box. Median indicated by a line, mean by x.

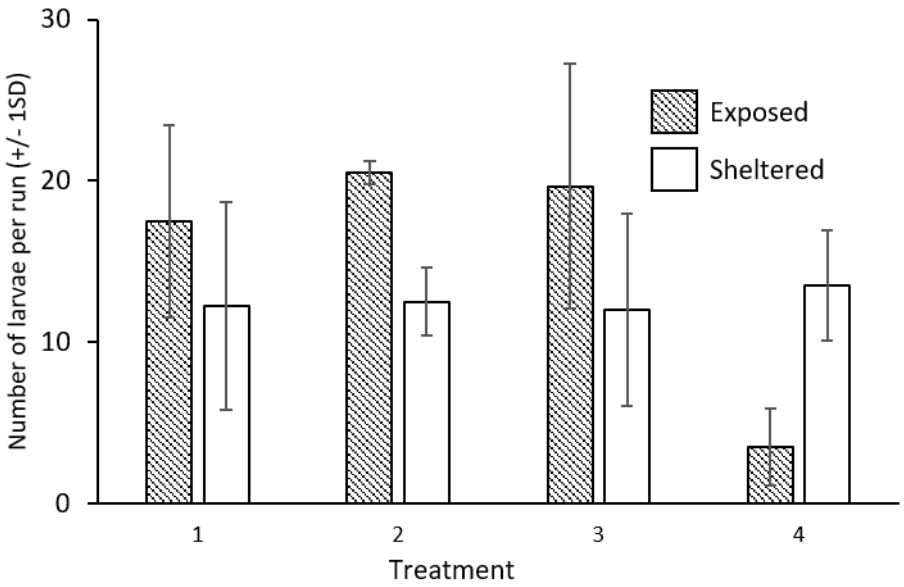


Figure 4.8. The relative hydraulic exposure of *A. fuscipes* larvae, inferred from the position of larvae (Figure 3B). Larvae on the top or stoss of particles were classified as exposed while larvae on the bottom, side or in the lee of gravels were sheltered. Error bars indicate standard deviation between replicate runs.

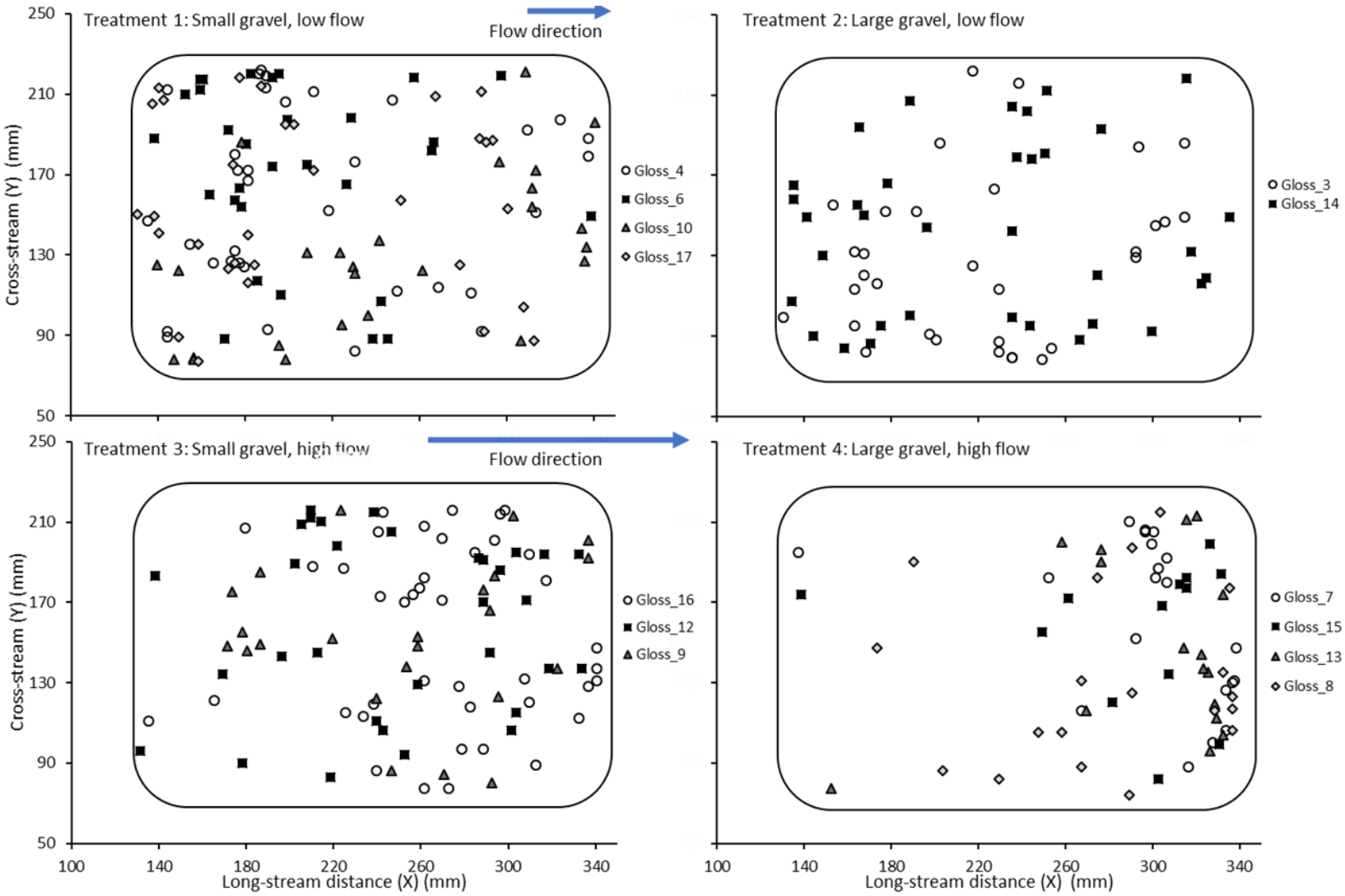


Figure 4.9. The location of each larvae (which remained within the sediment tray) for each run within each treatment. Each run had a different gravel particle configuration so precise positions of larvae are not useful. In treatment 4 (and possibly 3) there are more larvae in the downstream end of the sediment tray compared to a more even spread in treatments 1 and 2. Legends show the symbol for larvae of each run.

4.4 Discussion

4.4.1 Vertical displacement of sand by Agapetus fuscipes larvae

The positioning of *A. fuscipes* larvae on the gravel particles was nearly universal (99% of larvae), with only a few individuals found on the fine sediment. During all treatments there was a wide range of vertical elevations of larvae (Figure 4.6A), but larvae predominantly occupied the upper half of gravel particle surfaces (compare Figure 4.3D and Figure 4.6A). Each larvae carried with them a case constructed from sand (mean D_{50} = 1.37 mm), resulting in the mean displacement of 0.055 g, 25.40 mm upwards for each *A. fuscipes* individual (Figure 4.7; Table 4.2). Cumulatively, *A. fuscipes* larvae resulted in a substantial flux of sediment from sheltered interstices and onto the gravel surface (Figure 4.6B; 25 – 71 g m^{-2}). The abundance of *A. fuscipes* larvae in this study and the quantity of sediment used by these larvae were both representative of the field (sediment use by *A. fuscipes* in Wood Brook Chapter 2, mean = 25.95 g m^{-2} max = 88.92 g m^{-2}).

The biotic sediment flux is dependent on the mass of each *A. fuscipes* case and the number of individual larvae exhibiting this behaviour. The mean case mass was greater in this study than Chapter 2 (this chapter = 0.055 g; Table 4.2, Chapter 2 = 0.020 g; Table 2.1), due to the selection of final instar larvae for the experiment. Case mass was broadly similar between treatments, but fewer larvae stayed in the sediment tray during treatment 4, resulting in less sediment displacement within the sediment tray (Table 4.2) and more displaced downstream (Figure 4.5B). Interestingly, whilst there was no difference in case mass between treatments, cases were built from coarser particles in the high flow velocity treatments (Figure 4.7; Table 4.2). Larvae may have used coarser particles to increase their resistance to entrainment, but as case mass was not increased, this would have little effect on case stability. Alternatively, higher flow velocities may have preferentially transported finer sediment particles downstream, effectively armouring the fine sediment surface and leaving only coarser particles available to the larvae. *A. fuscipes* were found to vary the sediment size used in case construction in the field (Figure 2.5) and are believed to adapt their cases to the sediment sources available. Therefore, this study and Chapter 2 suggest that the size range of sediment displaced by Glossosomatidae may be related to the sand size fractions most readily available to larvae.

This study demonstrates that Glossosomatidae larvae move sediment from where it is available (i.e. sheltered interstices) to more exposed gravel surfaces. The positioning of *A. fuscipes* on the upper surfaces of gravel beds has been widely observed in the field (e.g. Figure 4.1). Furthermore, this behaviour has been documented in the field for a number of other Glossosomatidae species including *Glossosoma nigrior* (Kovalak, 1976), *Glossosoma boltoni* (Scott,

1958) and *Agapetus boulderensis* (Olden *et al.,* 2004; Wellnitz *et al.,* 2001). Therefore, this is a widespread behaviour among Glossosomatidae taxa and suggests that the findings of this experiment using *A. fuscipes* may be applicable to other species and beyond laboratory conditions. This also suggests that the behaviour observed in this flume experiment is analogous to that in the field, an important consideration for mesocosm experiments using live organisms (Skelly, 2002; Thomas *et al.,* 2014). This experiment was carefully designed to represent as closely as possible the conditions in Black Brook from which larvae were collected. The use of field conditioned gravels means that food availability was comparable to the field and physiochemical conditions were carefully monitored (Table 4.1). It was important to conduct experiments with large numbers of larvae (650 total) to reduce individual behavioural differences. Furthermore, hydraulics were representative of small streams with low depth in which *A. fuscipes* are commonly abundant (Morris *et al.,* 2015, 2011; Morris and Hondzo, 2013b).

4.4.2 Influence of grain protrusion on sand displacement

Increased bed protrusion resulted in larvae moving to relatively higher elevations (Figure 4.6A). During the low gravel protrusion treatments, the mean elevation of *A fuscipes* larvae was 22 and 24 mm (Table 4.2), compared to a mean particle c axis of 29 mm (Figure 4.3D). Mean larvae elevations during the high protrusion run were 31 and 27 mm compared to mean gravel c axis of 40 and 44 mm (Treatments 2 and 3 respectively; compare Figure 4.6A and Figure 4.3D). Therefore, larvae moved higher up gravel particles but were not restricted to the highest surfaces and occupied a wide range of elevations at all bed protrusions (Figure 4.6A).

Conditions on the top of particles might be preferable to *A. fuscipes* for several reasons, especially respiration efficiency and food availability (Wellnitz *et al.,* 2001). Initial trials for this experiment used clean gravels without an algae coating but most *A. fuscipes* larvae migrated out of the sediment tray. Using fresh algae coated gravels greatly increased larvae retention, suggesting that food is an important control on *A. fuscipes* horizontal 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.

A. fuscipes positions, relative to flow exposure, are a compromise between oxygen availability and flow velocity. Kovalak, (1976) recorded that *G. nigrior* occupied more exposed locations as temperature increased (and therefore dissolved oxygen content decreased) and as flow velocity

decreased. In the current experiment, the action of the pumps and tail gate, and oxygenation in the tanks, maintained high oxygen levels even during low flow runs (Table 4.1). Whilst marginally elevated temperatures during high flow runs may have required larvae to occupy more exposed locations to satisfy oxygen demand, this is unlikely as oxygen concentrations were not reduced during these treatments (Table 4.1). Consequently, oxygen availability was high and therefore is unlikely to be the reason for *A. fuscipes* larvae occupying exposed locations.

4.4.3 Influence of flow velocity on sand displacement

Flow velocity did not affect the vertical elevation of *A. fuscipes*; larvae moved to exposed locations regardless of flow velocity (Figure 4.6A). Whilst vertical distance travelled was not affected by flow velocity, larvae occupied more sheltered positions when flow velocity was high and when the gravel-bed had high protrusion (treatment 4; Figure 4.8). Some previous research has documented Glossosomatidae larvae occupying less exposed locations as flow velocity increases (Brooks, 1998 In: Lake, 2000; Kovalak, 1976; Houghton and Stewart, 1998). For example, flume experiments conducted by Brooks (1998 In: 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 refugia. However, Glossosomatidae larvae are well adapted to maintain their positions in areas of high hydraulic stress by virtue of their case design and, under hydraulic stress are able to attach directly to gravel surfaces and can move and change direction whilst remaining attached to stable particles (Olden *et al.,* 2004). Consequently, it is probable that the high flow treatment used in this experiment (0.6 m s^{-1}; Figure 4.4) was not enough to restrict larvae movements. Kovalak, (1976) found that Glossosomatidae larvae sought less exposed locations at velocities over 0.7 m s^{-1}.

4.4.4 Combined influence of gravel protrusion and high flow velocity on larvae positioning

A. fuscipes larvae preferred exposed locations on gravels (top and stoss) rather than sheltered locations (bottom, side and lee) during treatments 1-3 (Figure 4.8). However, in treatment 4 (high flow, large particles) most larvae occupied sheltered positions, although the elevation of these positions was unchanged (Figure 4.6A). Treatment 4 also differed from other treatments by increased *A fuscipes* larvae migration outside of the sediment tray (largely downstream; Figure 4.5) and positioning of larvae in the downstream half of the sediment tray (Figure 4.9).

It is interesting that treatment 4 was different to the other treatments, which had either particle size or flow velocity in common. This suggests that an interaction effect between high flows and

high particle protrusion affects the exposure of larvae positions, although not their vertical elevation. During high flow runs some transport of fine sediment occurred from between gravel particles and this was greater during treatment 4. The increased gravel-bed protrusion may have caused flow to accelerate over the sediment tray, resulting in increased near-bed velocities. However, this was not reflected in the velocity profiles (Figure 4.4) which show similar near bed velocities and velocity slopes under both high flow treatments, regardless of particle size. Further research is therefore required to characterise *A. fuscipes* case building behaviour (do they use larger sediment?) and positioning (do they seek shelter?) under flow velocities at the upper limit of their tolerance.

4.4.5 Zoogeomorphic effects of sand displacement

In armoured 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 riverbed surface where transport of finer sediment is limited by its availability on this surface (Church, 2010). Glossosomatidae larvae may affect bed armouring by transporting previously sheltered sand particles out of voids and onto the surface of the gravel-bed, thereby increasing the flow exposure of this sediment (Figure 4.10). Furthermore, Glossosomatidae larvae may move fine sediments in low flow conditions, conditioning the bed and potentially increasing the transport of this sediment during subsequent high flows.

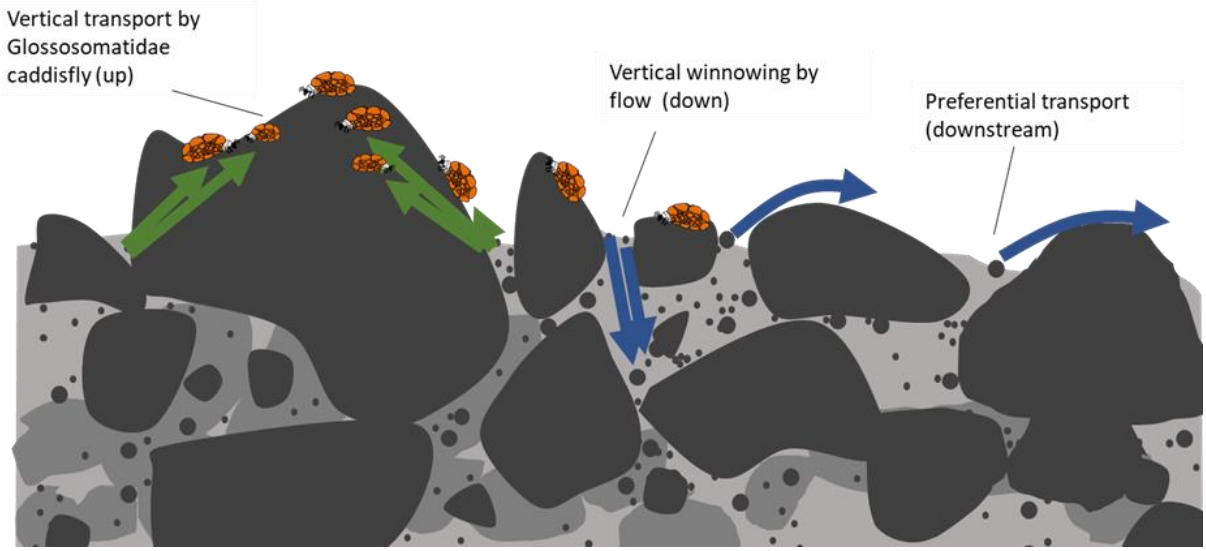


Figure 4.10. Physical bed armouring processes (blue) and Glossosomatidae movement of sediment (green) occurring in an armoured gravel-bed. Movement of sediment, even small distances can substantially alter the exposure of this sediment to entraining flows and may affect downstream sediment flux in rivers. Glossosomatidae transport opposes vertical winnowing and increases the hydraulic exposure of case sediment.

In this study, the cumulative impacts of many individuals resulted in the displacement and increased flow exposure of 25 to 71 g m^{-2} (Figure 4.6B) by 25.40 mm. The zoogeomorphic significance of this sediment flux will depend on the stability of sand in its exposed location. The stability of Glossosomatidae sediment in these exposed locations is controlled by 1) the hydraulic and sedimentological conditions in the river and 2) the exposure of the case and 3) the passive and active resistance of the case and larvae to entrainment (Figure 4.11). Passive resistance of *A. fuscipes* cases is much higher than that of tubular case species (Figure 3.7A). *A. fuscipes* larvae can also 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; Treatment 4 - Figure 4.9).

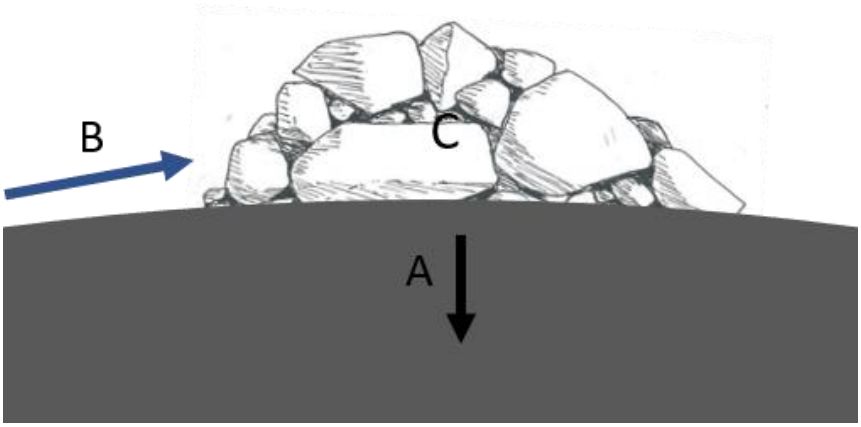


Figure 4.11. The stability of an *A. fuscipes* case (C) is dependent upon anchoring of the case by the larvae, (A) and hydraulic force (B). *A. fuscipes* cases may be anchored passively due to case mass and friction (Chapter 3) and actively, due to the larvae clinging on or attaching the case with silk. During pupation cases are attached securely with silk which is likely to substantially increase the stability of the sediment.

The resistance of *A. fuscipes* to drift increases with instar (Van Der Lee *et al.,* 2020), and therefore, cases of early instar Glossosomatidae are more easily eroded whilst, late instar larvae are well adapted to mitigating entrainment (Van Der Lee *et al.,* 2020). Glossosomatidae may fix their cases under hydraulic stress (Olden *et al.,* 2004) and also fix their pupal cases on cobbles in flowing water, often on the upstream face (Anderson and Bourne, 1974). Fixing their cases will considerably increase the hydraulic force required to entrain the constituent sediment (Figure 4.11A). Consequently, sand displaced by Glossosomatidae larvae may be resistant to entrainment and downstream transport, despite the increase in its hydraulic exposure. However, Glossosomatidae are unusual among caddisfly because they build a new case at each instar (Becker, 2005) and under adverse conditions, including low oxygen availability (Morris and Hondzo, 2013a) and fine sediment deposition (Wagner, 1987), Glossosomatidae larvae have

been observed to abandon their case to drift (far more readily than most other caddisfly species; Merrill, 1969; Wagner, 1987). Abandoned Glossosomatidae cases are likely to be more susceptible to entrainment. The stability of the sand displaced by Glossosomatidae larvae is therefore dependent on the behaviour and life stage of the larvae.

4.5 Summary

This experiment demonstrated that Glossosomatidae *A. fuscipes* larvae transport sediment vertically upwards through armoured gravel-bed surfaces. An experimental flume was used to study the movement of Glossosomatidae *A. fuscipes* larvae and the sediment incorporated in their cases. When added to the flume, caseless *A. fuscipes* larvae began to construct cases from the fine sediment available to them below the gravel surface. Larvae transported these cases from sheltered interstices onto surface grains, resulting in a flux of sand (Mean D_{50} =1.37 mm; Table 4.2) vertically upwards by a mean distance of 25.40 mm (Table 4.2; Figure 4.6A). The vertical displacement was greater in treatments with greater bed protrusion, but flow velocity did not affect the vertical distances moved (Figure 4.6A). This behaviour was exhibited by 99% of larvae, resulting in an upwards flux of 25 – 71 g m^{-2} (Figure 4.6B) This is the first study to quantify the direction and magnitude of sediment transport caused by active movement of a caddisfly larvae.

The experimental results are comparable to field observations and previous research on positioning of Glossosomatidae spp. on gravel-bed surfaces. Consequently, this displacement of sediment is expected to occur at most sites where *A. fuscipes* and other Glossosomatidae species are abundant, but this will require field validation. Glossosomatidae sediment transport may have zoogeomorphic importance because 1) sediment transport is repeated by 99% of individuals and Glossosomatidae are often abundant, 2) while distances moved are small (25.40 mm) larvae increase the exposure of the sediment they transport, and 3) Glossosomatidae use sand, an important size fraction in gravel-bed rivers. Sediment transport by Glossosomatidae larvae could have consequences for the mobility of the sand involved, but more research is required to consider the entrainment of displaced sediment and how this varies with larval behaviour, including positioning on particles and fixing of larval or pupal cases with silk. This will be required to understand whether Glossosomatidae have a stabilising or destabilising effect on sand sediments in gravel-bed rivers.

Glossosomatidae caddisfly on the River Dove, Peak District, U.K. Photo: S. Rice & M. Johnson.

Chapter 5. The relative contributions of hydraulics and case-building caddisfly to bedload transport in a gravel-bed stream

5.1 Introduction

Measuring and predicting the sediment load of rivers is a fundamental objective of fluvial geomorphology. River sediment loads ultimately determine channel morphology, habitat provision and fluvial landscape denudation (Church, 2006; Schumm, 1977). Sediment load is a combination of wash load and bedload (Gordon *et al.* 2004). Bedload maintains frequent contact with the river bed, moving either as contact load (rolling or sliding) or by saltation (hopping; Parker, 2008). The transport of bedload sediment is a function of the force provided by the water and the availability of sediment to be transported. Sediment transport is also controlled by animals and plants (Chapter 1). Many studies have demonstrated the small scale effects of a wide range of animals on sediment transport in rivers (Chapter 1; Rice *et al.,* 2012; Statzner, 2012) but the larger-scale effects on sediment loads in streams are rarely considered.

Case-building caddisfly may affect bedload sediment transport by several mechanisms outlined in Chapter 1 (Figure 1.4). Many species of case-building caddisfly taxa are extremely mobile and directly transport the sand incorporated into their cases. For example, during a flume experiment, *Potamophylax latipennis* (Limnephilidae) crawled 93% of the time (reducing to 78% at high discharge), equivalent to several metres per hour (Lancaster *et al.,* 2006). Furthermore, Limnephilidae larvae may move sediment in their cases large distances. Erman (1986) found that *Chyrnda centralis* migrated first upstream (up to 56.9 m), possibly in response to environmental conditions, and later downstream, prior to pupation. Individual *C. centralis* larvae crawled at up to 1.4 m per hour (Erman, 1986). However, the movement dynamics of aquatic invertebrates are much less studied than their spatial distribution (Lancaster *et al.,* 2008; 2006). Due to their high abundance and relatively high mobility, case-building caddisfly taxa may account for a substantial flux of sediment.

In addition to directly transporting sediment themselves, case-building caddisfly may modify the exposure or stability of sediment, affecting entrainment thresholds and transport by hydraulic processes. Case construction by *P. latipennis* and *Sericostoma personatum*, reduces the entrainment thresholds of incorporated sediment when empty (Figure 3.7A), potentially resulting in preferential entrainment of cases over other river bed sediment. Furthermore, even relatively small movements of sediment by caddisfly larvae may be geomorphologically important if they

alter the exposure of sediment grains to entrainment by hydraulic processes. Glossosomatidae move sand from sheltered interstices upwards onto the exposed surface of gravel-beds (Figure 4.6). Therefore, caddisfly larvae may both directly transport sediment and modify its exposure to hydraulic processes. This thesis has identified and examined several mechanisms by which caddisfly may affect sediment dynamics in rivers, using small scale flume experiments (Chapters 3 & 4). However, the wider scale effect of these processes on river sediment load has not been considered.

Biogeomorphological research is often limited by its narrow spatial and temporal scale (Naylor *et al.,* 2002). This is particularly true of zoogeomorphology; most studies are conducted at the scale of organisms (or small communities) over short time periods (hours – weeks; Albertson and Allen, 2015; Rice *et al.,* 2012; Statzner, 2012). As a consequence, the geomorphic implications are often hard to interpret and communicate to geomorphologists who typically work at the scale of river reaches or catchments. Relatively few attempts have been made to measure the zoogeomorphic effects at larger scales in rivers. Rice *et al.* (2016) measured the contribution of signal crayfish to suspended sediment load for a tributary of the River Nene, UK, over a 13-month period and compared this to sediment load due to hydraulic forces. Signal crayfish accounted for at least 32% of suspended sediment during base flow (Rice *et al.,* 2016). Furthermore, Hassan *et al.,* (2008) determined that salmonids were responsible for 35% of the bedload transport over a 3 year period at spawning locations on four Creeks draining into Takla Lake, British Columbia, Canada.

A handful of studies have used statistical methods to extrapolate the zoogeomorphic consequences of fish. Rice *et al.* (2019) scored benthivorous fish species according to their zoogeomorphic effectiveness, based on field and flume experiments. They then applied these scores to fish population data to assess the cumulative effects of benthivorous fish at the catchment scale (Rice *et al.,* 2019). Fremier *et al.,* (2017) considered salmonid impacts on river long profiles over geological timescales. However, extrapolating from small scale experiments is subject to considerable error and both studies serve to give only a general indication of the role of the zoogeomorphic effects of fish at larger scales.

Estimates of the zoogeomorphic effects of animals at scales beyond the microhabitat are rare, particularly for smaller organisms such as invertebrates (Rice *et al.,* 2012; Statzner, 2012). Furthermore, whilst they allow for tightly controlled analysis, mesocosm and flume experiments cannot fully replicate the river environment (Kirkegaard *et al.,* 2011; Thomas *et al.,* 2014), thus measuring the impact of caddisfly in the field is vital to understand their zoogeomorphic effects.

This chapter presents a reach scale investigation of the proportion of bedload sediment transport that is directly attributable to case-building caddisfly for a small lowland stream (Thesis objective 3). The relative importance of hydraulic and biotic (caddisfly) controls on bedload transport are evaluated and compared to seasonal changes in discharge and caddisfly larvae development over an annual cycle. The chapter also considers the whole caddisfly community, rather than being limited to a single (Chapter 4) or small selection of species (Chapter 3). Consequently, this chapter represents an attempt to increase the spatial, temporal and taxonomic scope of the thesis. This chapter addresses thesis objective 3 via three specific research questions:

1) What is the mass and grain size distribution of sediment transport in caddisfly cases, and how does this vary seasonally?
2) What is the contribution of individual caddisfly taxa to sediment transport, and how does this vary seasonally?
3) How does the magnitude of caddisfly sediment transport compare to mineral and organic sediment transported by hydraulic processes, and how does this vary seasonally?

5.2 Methods

5.2.1 Field site

Sampling was conducted on a 2nd order gravel-bed stream (Black Brook, near Loughborough, U.K. 52°46'33.4"N 1°17'57.6"W; Figure 5.1). Black Brook is separated from arable fields by a wide margin of vegetation including mature trees which shade the site (Figure 5.1A). Discharge in Black Brook is primarily controlled by Black Brook reservoir, 3 km upstream. The study site consisted of two riffles separated by a pool (Figure 5.1B & C).

A detailed reconnaissance of the site was conducted in Summer 2017 during low discharge conditions. Depth and flow velocity were measured at two cross sections where traps were to be located, prior to deployment (Figure 5.2). Velocity was measured using an electromagnetic flow meter at 0.05 m above the bed, averaged over 30 seconds. The bed surface particle size distribution was determined according to Wolman (1954). This demonstrated similar particle size distributions in each riffle (Upper D_{50} = 31.50 mm, n = 112, Lower D_{50} = 35.60 mm, n = 120).

5.2.2 Pit trap design and deployment

Pit traps were used to collect sediment transported as bedload, and to isolate the contributions of: 1) hydraulically transported mineral and organic sediment and, 2) sediment transported in caddisfly cases. Pit traps have been used extensively as measures of bedload transport (Einstein,

1944; Poreh *et al.* 1970; Reid, *et al.,* 1980) and allow the collection of long term data (unlike temporary sediment samplers like the Helley-Smith). Pit traps are also used in terrestrial habitats to sample mobile invertebrates (Drake *et al.,* 2007). However, the use of pit traps in rivers has been limited to ephemeral rivers during their dry phases (Corti *et al.,* 2013) because many invertebrates can swim or drift. Case-building caddisfly (particularly those using mineral sediment) travel rarely and only short distances by drift (De Brouwer *et al.,* 2017; Lancaster *et al.,* 2006) and therefore pit traps can be used to sample mobile case-building caddisfly. Pit traps allowed simultaneous sampling of hydraulically transported bedload sediment, mobile caddisfly and caddisfly sediment transported in caddisfly cases, providing a measure of the mass and proportion of bedload flux which is directly attributable to caddisfly.

Circular sediment traps were used so that the direction of travel of sediment and caddisfly did not affect collection efficiency (Sterling and Church, 2002). Traps were formed of an outer tube buried flush with the bed surface, with an inner plastic bucket which could be removed with minimal disturbance to the surrounding bed. The width of each trap at the bed surface was 0.19 m and the depth was 0.22 m which was infilled by 0.04 m of concrete to weigh down empty traps. Traps for the estimation of bedload in rivers are typically larger to catch more saltating grains which may pass over smaller trap diameters (Sterling and Church, 2002). However, traps used for invertebrate sampling are typically much smaller (cup sized; Corti *et al.,* 2013). The size of traps used here was a compromise to ensure trap efficiency, whilst keeping the volume of material collected low enough for subsequent laboratory analysis. Initial burial of the traps caused disturbance to the bed of the river and therefore traps were buried in June 2017 and sampled between March and December 2018.

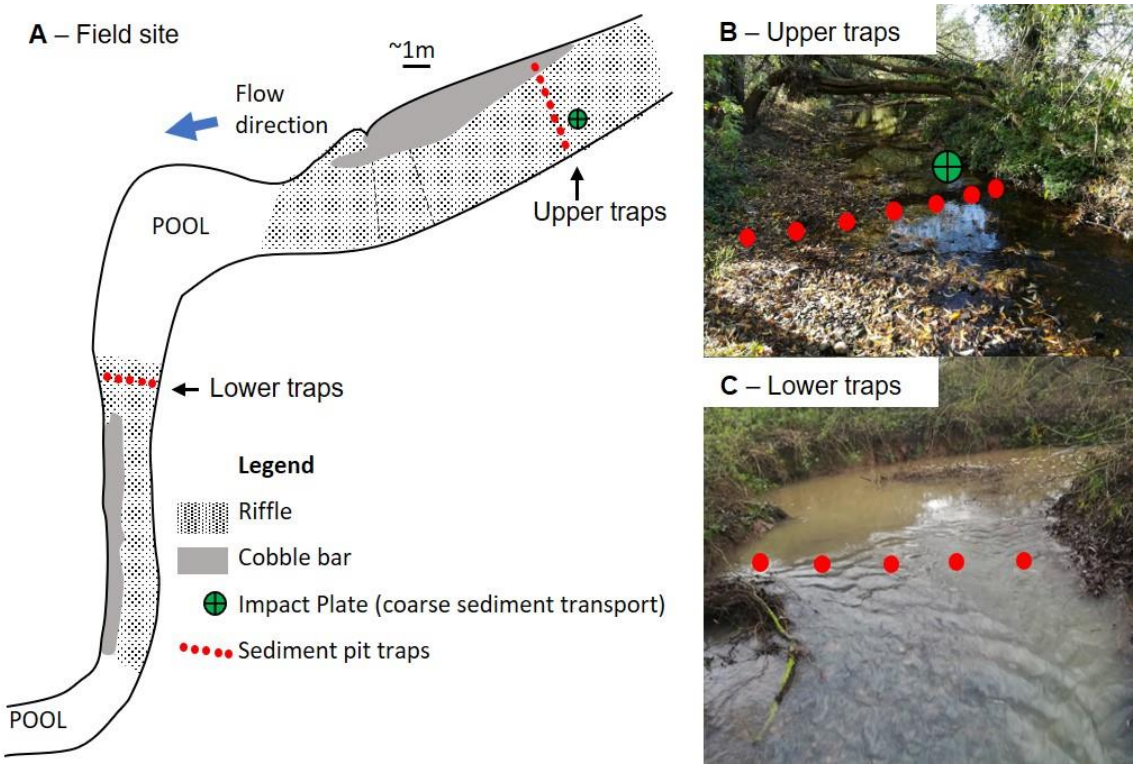


Figure 5.1. Sampling location on Black Brook near Loughborough. (A) Map showing the sampling site. The upper and lower riffles were separated by a pool. The upper traps were situated midway down the upper riffle in a row of 7. The downstream traps were placed at the head of the lower riffle in a row of 5. An impact plate was placed in the thalweg, upstream of the upper traps. Figure drawn from EDINA 2018 and field reconnaissance. (B) Photograph looking upstream towards the upper riffle traps and impact plate, October 2018. Note that only 4 of the 7 traps are in the active channel at this discharge. (C) Lower traps, looking upstream into pool, December 2018.

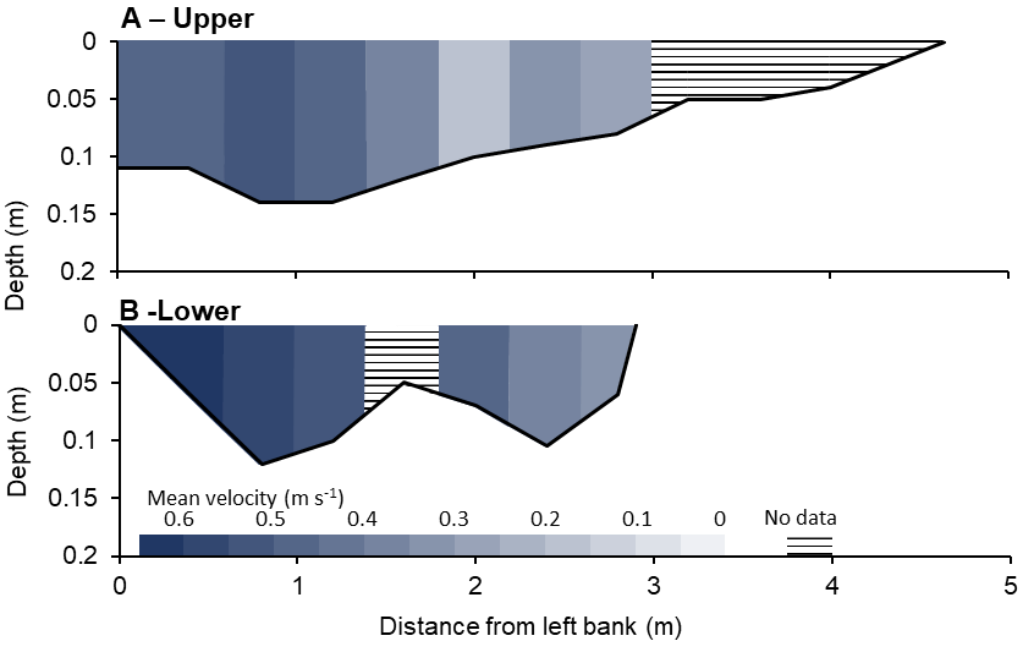


Figure 5.2. Depth and velocity profiles for sediment trap cross sections, looking downstream. (A) Upper traps and (B) Lower traps. The upper riffle was wider, with thalweg close to the river left bank and a gravel bar to the right which periodically dried under low discharge. The lower riffle was narrower and flow was funnelled out of the pool resulting in higher velocities. The lower riffle had two thalwegs with a slightly raised bar in the centre which never dried out. Velocity measurements could not be taken when water depth was less than the depth of the flow meter (0.05 m).

Two rows of pit traps were used, with spacing between traps within each row approximately 0.4 m. A row of 7 traps was located mid-way down the upper riffle. At these upper traps, Black Brook had an asymmetric cross-section with a steep left-hand bank and thalweg close to that bank (depth = 0.14 m, Figure 5.2A). Depth gradually decreased towards the right bank, with a gravel bar fully submerged during high discharge but, exposed under low flow conditions (Figure 5.1B). The lower riffle was narrower than the upper (upper width = 4.6 m, lower = 2.9 m) so 5 traps were used. Traps were located at the riffle head, where flow was funnelled out of the pool (Figure 5.1C). Depth was similar and flow velocities slightly higher than at the upper traps (Figure 5.2B). The two sets of traps were separated by a long riffle and deep pool (Figure 5.1A) and the presence of both erosional and depositional environments between the traps meant that sediment trapping in the upper traps was unlikely to have any effect on sediment transport at the lower traps. Traps were thus located in different geomorphological locations, with the upper traps providing an estimate of sediment transport over a riffle and the lower traps situated immediately downstream of a pool, together giving a reach scale estimate of sediment transport

5.2.3 Pit trap sampling

Pit traps were deployed on 6 occasions between February and December 2018 to collect bedload transport and isolate the caddisfly and hydraulic constituents (Table 5.1). Evenly spaced sampling intervals were used to capture seasonal variation in caddisfly sediment use and the abiotic environment, including discharge and hydraulic bedload transport. Traps were usually deployed for 14 days (exceptions are 19 days in August samples and 13 in December; Table 5.1). The contents of all 5 lower traps were aggregated in the field. For the 7 traps at the upper site, only traps within the active channel at the time of collection were sampled (this varied between 4 and 7; Figure 5.1B shows dry gravel bar) and these were also aggregated. Trap samples were sieved using a 0.063 mm mesh in the field and preserved in 4% formaldehyde solution. This resulted in 12 detailed bedload samples; two sets of amalgamated traps (upper and lower) for 6 temporal sampling periods.

Between these detailed sampling periods, trap contents were collected to allow estimation of the annual sediment flux of the stream. Traps were usually emptied before they were 2/3 full because once material builds up inside a pit trap, flow recirculation can cause sediment to be lost (Laronne *et al.,* 2002). This was not possible on one occasion in mid-March because the traps filled within a single flood event. These samples were dried at 105°C overnight and weighed.

Table 5.1. Details of the six sampling occasions. (A) Detailed bedload trap samples were collected on six occasions over the year (date emptied), having been in place for approximately 14 days (19 in August, 13 in December). All lower traps were sampled on each occasion but some upper traps were not in the channel under low discharge (Figure 5.1B) so only 4 were sampled in August and October. Daily discharge indicates the mean for the sampling period, with standard deviation in brackets. (B) Caddisfly species richness and abundance for each sample for upper and lower traps.

A. Sample characteristics					B. Caddisfly	
Sample Number	Date emptied	Days sampled	Number upper traps	Daily discharge ($m^3 s^{-1}$)	Species richness upper/lower	Abundance upper/lower (larvae m^{-1} day^{-1})
Feb	1.3.18	14	7	0.70 (0.06)	7/6	11.98/17.67
April	3.5.18	14	7	0.75 (0.07)	10/6	134.65/15.71
June	28.6.18	14	7	0.67 (0.004)	9/4	16.81/1.79
August	29.8.18	19	4	0.64 (0.05)	7/6	48.89/122.77
October	22.10.18	14	4	0.66 (0.07)	7/10	185.34/110.30
December	20.12.18	13	7	0.71 (0.08)	10/9	165.82/146.23

5.2.4 Environmental measurements

To provide environmental context, continuous measurement of discharge and bedload transport were required. In addition to the pit trap samples of bedload transport, an impact plate sensor was positioned in the channel thalweg upstream of the upper traps (Figure 5.1A). Impact sensors are steel plates placed flush with the riverbed and equipped with an accelerometer which can measure the impact of moving particles greater than 3 mm diameter (Richardson *et al.,* 2003). They provide good estimates of the timings of bed movement and a less accurate measure of intensity as they can only record three hits per second (Reid *et al.,* 2006). The impact sensor was set to record the number of hits in 5-minute intervals.

Discharge was estimated from an Environment Agency gauge, 1.79 km downstream of the study site. A rating curve was generated from 37 discharge measurements, also collected by the Environment Agency. This was best characterised by two separate linear trends for values above and below 0.5 m depth. Some negative discharge values were predicted by this rating and were assigned a low discharge value of 0.05 $m^3 s^{-1}$.

5.2.5 Laboratory analysis of detailed samples

When the wet mass of the 12 detailed samples exceeded 1 kg, sub sampling was necessary due to the complexity of the laboratory analysis. To do this, the sample was mixed well, and then 1 kg of wet mass was randomly extracted. Samples were subsequently washed and all material > 0.063 mm retained. Material > 0.25 mm was spread out in trays and caddisfly larvae, cases and case fragments removed manually. Many samples contained extremely high abundances of Glossosomatidae larvae. For these samples, this taxon was subsampled by picking ¼ of each tray

to estimate the abundance of larvae and sediment in their cases. The remaining sediment, with caddisfly removed (hereafter, *hydraulic* sediment), was dried at 105°C and sieved through 42 mm – 0.063 mm sieves in half phi intervals. The proportion of mineral and organic sediment was measured for gravel (> 2mm) by manually separating organic and mineral sediment. Finer fractions underwent loss on ignition at 550°C for 3 hrs to determine the mass of organic material.

The removed caddisfly and cases (hereafter *caddisfly* sediment) were stored in 70% industrial methylated spirits until they could be identified to the lowest practical level (usually species unless early instar larvae, as for Chapter 2). Caddisfly cases of each species, within each sample, were combined for further analysis. Case samples were rinsed in deionised water and added to test tubes with 30% hydrogen peroxide H_2O_2 at 70°C and stirred periodically. In contrast to Chapter 2, this was also conducted for cases which were partially or wholly organic. Therefore, as soon as silk had broken down, samples were removed from H_2O_2 to prevent further degradation of organic material (OM). While some mass of OM is likely to have been removed by this process, observations suggest this was minimal. Case samples were then rinsed through a 0.063 mm aperture, 38 mm diameter sieve and dried at 70°C for two days. Samples were sieved through 5.6 – 0.063 mm (38 mm diameter) sieves to ascertain grain size distribution (GSD). Subsequently, loss on ignition was conducted for each caddisfly species sample (there was insufficient material to do each size fraction individually).

Therefore, for each of the 12 detailed samples (6 upper and 6 lower) this data analysis established: 1) the mass and GSD used by each caddisfly species and the organic content of the whole sample for each species, and 2) the mass and GSD of hydraulic sediment in the traps, with organic content known for each size fraction. In addition, the mass of sediment in upper and lower traps is known for approximate two-week intervals (less frequently during low discharge periods) between 2nd January and 20th December 2018.

5.3 Data Analysis

5.3.1 Calculating caddisfly sediment flux

First, caddisfly sediment in the traps was standardised to allow comparison between upper and lower trap sites. Within each sample, for each grain size fraction (i), of each species, the mass of caddisfly sediment found in traps was standardised to a flux, g_{ci} (g m^{-1} day^{-1}; Equation 1).

$$g_{ci} = \frac{G_{ci}}{W \times t} \tag{6}$$

Where, G_{ci} = the mass of caddisfly sediment of each grain size fraction (i) collected from traps in grams, W = width of traps sampled in m (Equation 2) and t = time traps deployed for (days; usually 14 days; Table 5.1A).

$$W = d \times n \tag{7}$$

Where d = trap diameter (0.19 m), n = number of traps sampled (5 at the lower site and between 4 and 7 at the upper; Table 5.1A).

The mass of sediment used in the cases of each caddisfly species was then determined as the sum of the individual grain size fractions (g_{ci}) for that species. For subsequent analysis, species were also summed into respective caddisfly families (following Chapter 2). The total mass of sediment used by caddisfly (g_c) was calculated by summing the mass of each caddisfly family. To evaluate the contribution of each caddisfly family to the total caddisfly sediment mass (Question 2), the percentage of total caddisfly sediment (g_c) which was attributable to each caddisfly family was determined. The mass of caddisfly sediment which was organic was determined for each caddisfly family, by summing the mass of organic material used by each caddisfly species. This was then converted to a percentage of total caddisfly sediment for each family and subsequently the percentage of caddisfly sediment which was organic across all caddisfly families was calculated.

5.3.2 Calculating hydraulic sediment flux

As for caddisfly, the mass of total hydraulic sediment, was standardised by the width of traps sampled (W, metres) and sampling time (t, days), for each size fraction (i), to give a flux g_{hi} (g m^{-1} day^{-1}; Equation 3).

$$g_{hi} = \frac{G_{hi}}{W \times t} \tag{8}$$

Where, G_{hi} = the mass of hydraulic sediment of each size fraction (i) collected from traps in grams. Total hydraulic sediment flux (g_h) was calculated by summing the individual size

fractions. The percentage of hydraulic bedload which was organic was determined for each size fraction.

5.3.3 Calculating total sediment flux

Bedload flux (g_{bi}) was then calculated for each size fraction (i) by summing caddisfly sediment (g_{ci}) and hydraulic sediment (g_{hi}) (Equation 4).

$$g_{bi} = g_{hi} + g_{ci} \tag{9}$$

In addition, the percentage of the total flux in each individual grain size fraction (i) that was recovered from caddisfly cases ($c_{i\%}$) was calculated as the bedload flux in that fraction (g_{bi}) divided by the sum of the corresponding g_{ci} across all species in the sample, multiplied by 100.

5.4 Results

5.4.1 Seasonal discharge and bedload transport in Black Brook

Discharge in Black Brook during the study period was flashy with the highest flows occurring in winter and spring (December 2017 – April 2018; Figure 5.3A). Discharge between May and December was generally low and stable, with a few minor peaks (Figure 5.3A). The mean daily discharge (calculated from the sum of the 15 minute interval data) averaged between December 2017 and December 2018 was 0.72 m^3 s^{-1}. The average daily discharge during detailed sampling periods varied from 0.64 to 0.75 m^3 s^{-1}. The average of all sampling periods (grey shading; Figure 5.3C) was 0.68 m^3 s^{-1}. The max mean daily discharge during a detailed sampling period was 0.93 m^3 s^{-1} (April) which was approximately the Q10 (10 % equalled or exceeded) of the annual mean daily discharge. Therefore, the detailed sampling periods represented 90% of the hydrograph range experienced over the full year. However, the highest discharges of the year (max mean daily discharge = 1.50 m^3 s^{-1}) were not sampled and it was during these periods that the majority of bedload transport occurred (Figure 5.3).

There was good corroboration between bedload transport as measured by the impact plate (Figure 5.3B) and traps (Figure 5.3C). Most annual bedload sediment transport in this stream occurred in March and April, with minimal bedload movement after April (Figure 5.3B &C). Bedload transport displays a strong association with discharge (Figure 5.3). The total annual sediment load was 488.64 kg yr^{-1} for the upper traps and 333.40 kg yr^{-1} for the lower traps. This

represents a minimum budget because sampling did not begin until 2nd January 2018 (missing 20th Dec to 2nd Jan) and traps were full during the bedload transport peak on 15th March, so some transported sediment was almost certainly not captured by the traps.

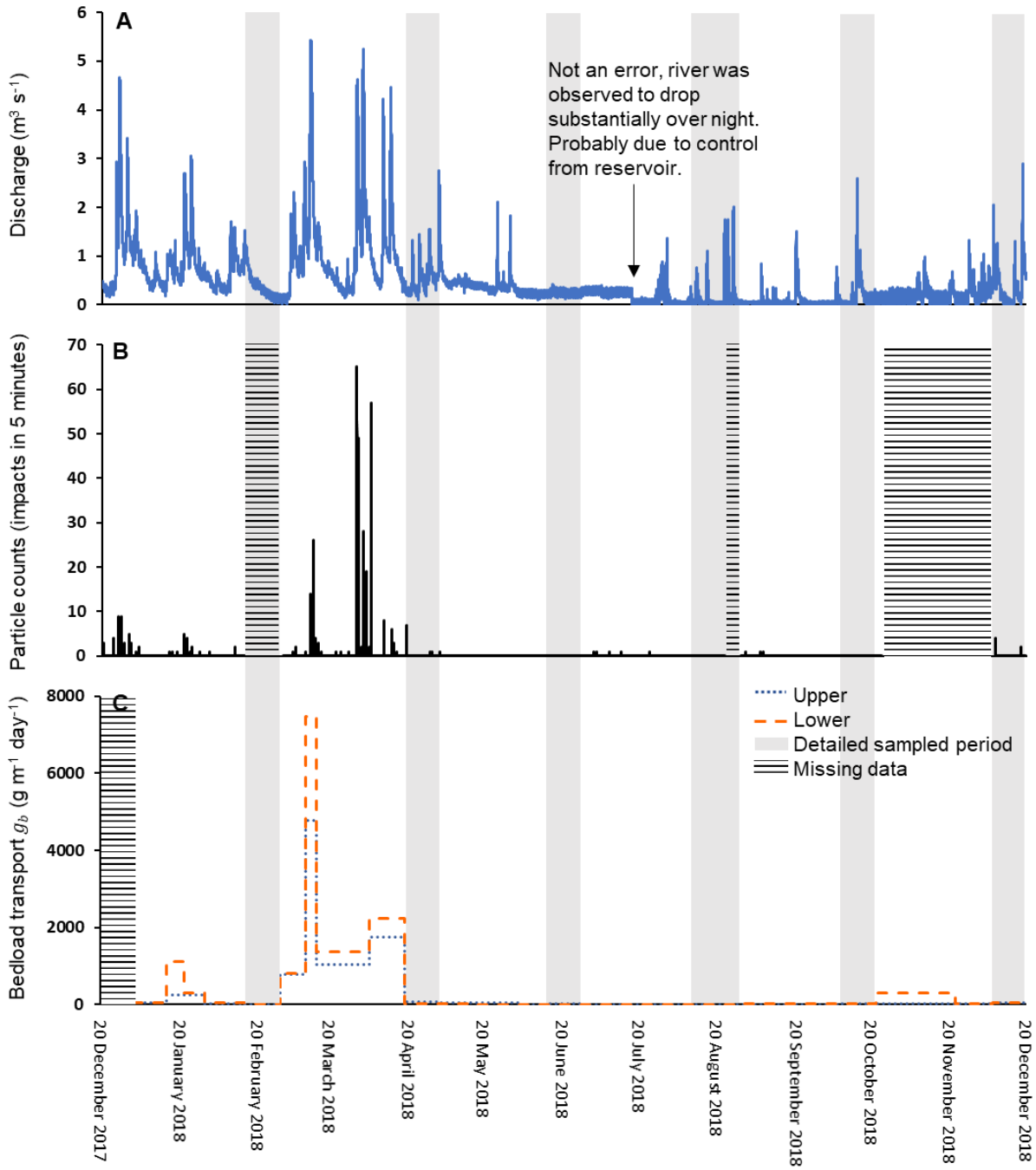


Figure 5.3. Discharge and bedload transport estimations for the study period. The six periods of detailed sampling are indicated by shading. (A) Discharge from Environment Agency gauge 1.79 km downstream, (B) bedload estimate from impact plate deployed at the site. (C) Bedload transport estimate from bedload traps in the upper and lower riffles. Missing data indicated by stripes.

5.4.2 What is the mass and GSD of sediment transport in caddisfly cases, and how does this vary seasonally?

14 species of caddisfly were found in the bedload traps; almost exclusively case-building taxa. Three caddisfly species that do not build cases during the larval stage were found; *Polycentropus flavomaculatus* (net builder), *Lype reducta* (fixed retreats/galleries) and a single *Rhyacophila dorsalis* pupal case (architecture groups in Figure 1.4). Species richness in the traps varied between 4 and 10 (mean = 7.25) and abundance in samples from 19 – 2867 (mean = 1139 larvae sample^{-1}; Table 5.1). This was equivalent to an average flux of 81.50 larvae m^{-1} day^{-1} (range = 1.79 – 185.34 larvae m^{-1} day^{-1}) Caddisfly larvae abundance was generally lower in February to June and much higher in August, October and December (Table 5.1). However, April also had a high abundance of larvae in the upper traps (Table 5.1).

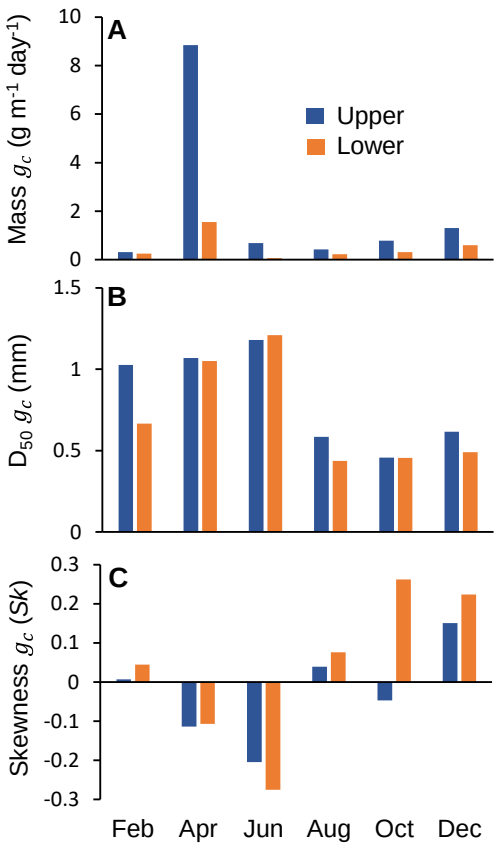


Figure 5.4. Characteristics of sediment used by caddisfly (g_c) in each sampling period. (A) Mass, (B) Size distribution and (C) Skewness. In general, there is a strong association between upper and lower traps. There is also a change in the size and skew of sediment between June and August.

The mass of caddisfly sediment was always higher in the upper traps than the lower (Figure 5.4A). The greatest mass of caddisfly sediment at both sites occurred in April (Figure 5.4A), despite low abundance compared to winter months (Table 5.1). The upper traps had a particularly high caddisfly mass at 8.85 g m^{-1} day^{-1}, compared to a mean annual caddisfly sediment flux 1.27 g m^{-1} day^{-1}.

Caddisfly predominantly used sediment in the medium to coarse sand size range (mean D_{50} = 0.91 mm). Both unimodal and bimodal distributions were present in the caddisfly sediment (Figure 5.5). There is also a notable fining of caddisfly sediment between June and August when the D_{50} dropped substantially from approximately 1 mm to approximately 0.5 mm (Figure 5.4B). This is accompanied by an abrupt change in the skew of the GSD of caddisfly sediment from negative to positive, reflecting the transition from predominantly coarse to fine sediment (Figure 5.4C).

In all samples, caddisfly sediment was predominantly mineral (Figure 5.6). At the upper site, the lowest mineral content was 80.07% in February (Figure 5.6A). At the lower traps the lowest mineral content in caddisfly sediment was 96.91% (Figure 5.6B). As an average across all samples, 93.78% of caddisfly sediment was mineral.

5.4.3 What is the contribution of individual caddisfly taxa to sediment transport?

Glossosomatidae were the most abundant caddisfly taxa and dominated caddisfly sediment, accounting on average for 56.11% of sediment mass in each sample (Figure 5.7). The mass of Limnephilidae sediment exceeded Glossosomatidae in some spring samples but was much reduced after June, resulting in a mean contribution to caddisfly sediment of 35% (Figure 5.7). Glossosomatidae dominated the finer sand fractions (up to 1.4 mm) and Limnephilidae the fine gravel fractions (1.4 – 5.6 mm; Figure 5.7). Goeridae used a bimodal range of sediment sizes, but only accounted for 4.67% of caddisfly sediment (Figure 5.7). Sericostomatidae contributed up to 20% of fine sand caddisfly sediment, but overall contributed only 2.67% to total caddisfly sediment transport (Figure 5.7).

The contribution of each caddisfly family to total sediment use varied seasonally with similar trends at both sites (Figure 5.8B). In winter and early spring (December and February) Glossosomatidae and Limnephilidae contributed similar amounts to the total sediment used by caddisfly. The contribution of Limnephilidae peaked in April at both sites but then decreased relative to Glossosomatidae between June and October (Figure 5.8B). This swap from Limnephilidae to Glossosomatidae sediment therefore matches the notable change in larvae abundance (Figure 5.8A) and D_{50} sediment size and skew occurring between June and August (Figure 5.4B &C).

Glossosomatidae, Sericostomatidae and Goeridae used entirely mineral sediment in their cases (Figure 5.6). Limnephilidae used a mixture of mineral and organic sediment. As a family, the organic proportion of Limnephilidae cases varied from 64% - 99% by mass (Figure 5.6). Limnephilidae in the upper traps used a higher proportion of organic material than those in the lower (Figure 5.6).

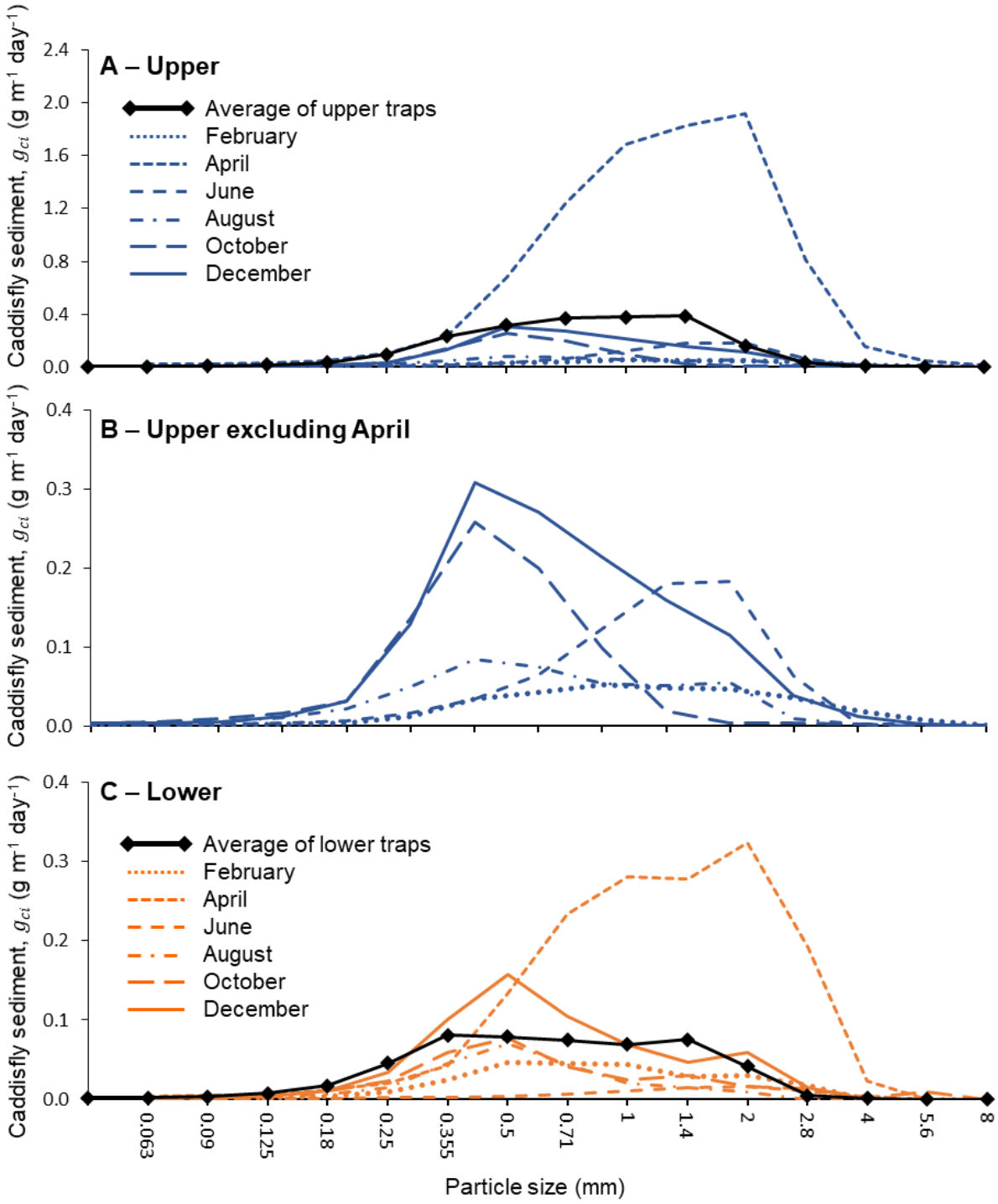


Figure 5.5. Grain size distribution of sediment use by caddisfly (g_{ci}) in each sampling period. (A) Upper traps; April has by far the most caddisfly sediment. (B) In the upper traps with April excluded, caddisfly sediment transport in other months was comparable to the lower traps. (C) Lower traps; April again has the greatest mass of sediment transported by caddisfly. Particle size indicates passing sieve.

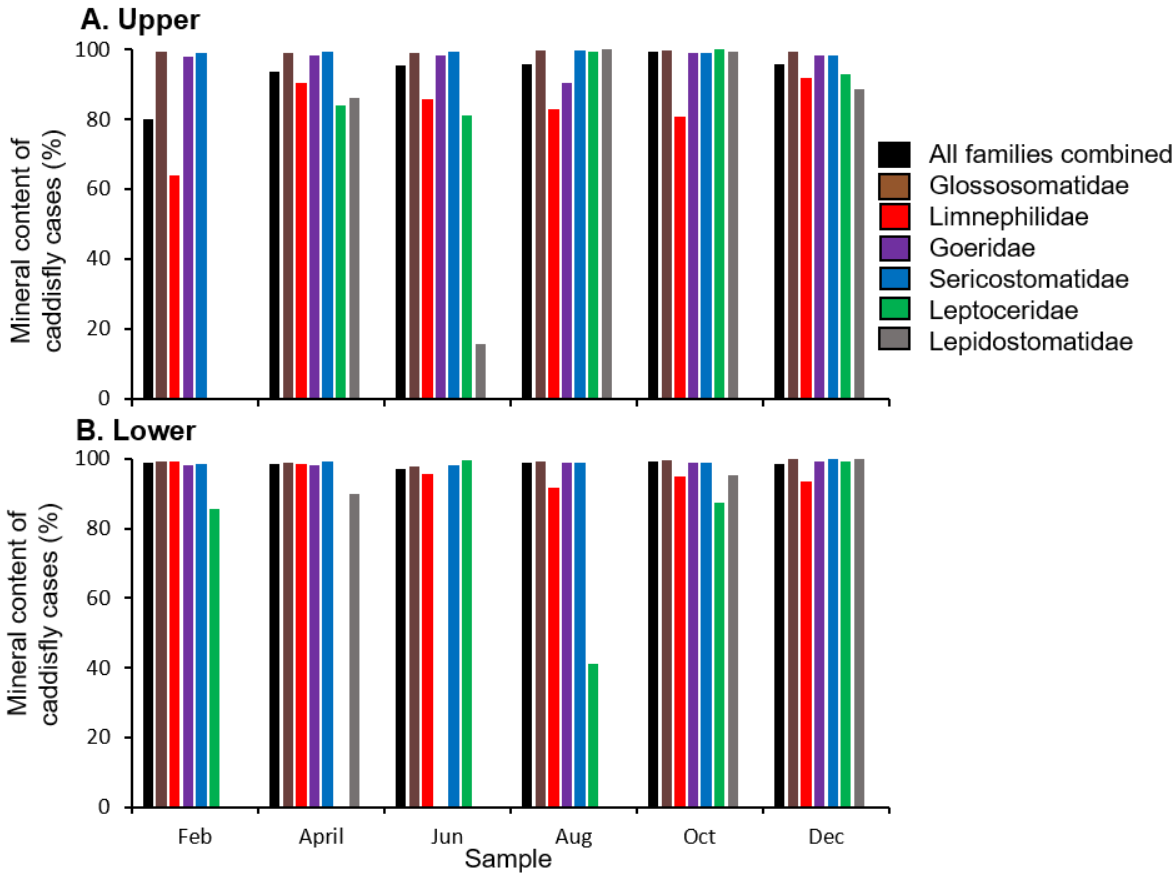


Figure 5.6. The mineral content of caddisfly sediment for upper (A) and lower traps (B) and split into each caddisfly family. For most species and all families combined, caddisfly sediment transport was predominantly mineral. This was measured by loss on ignition.

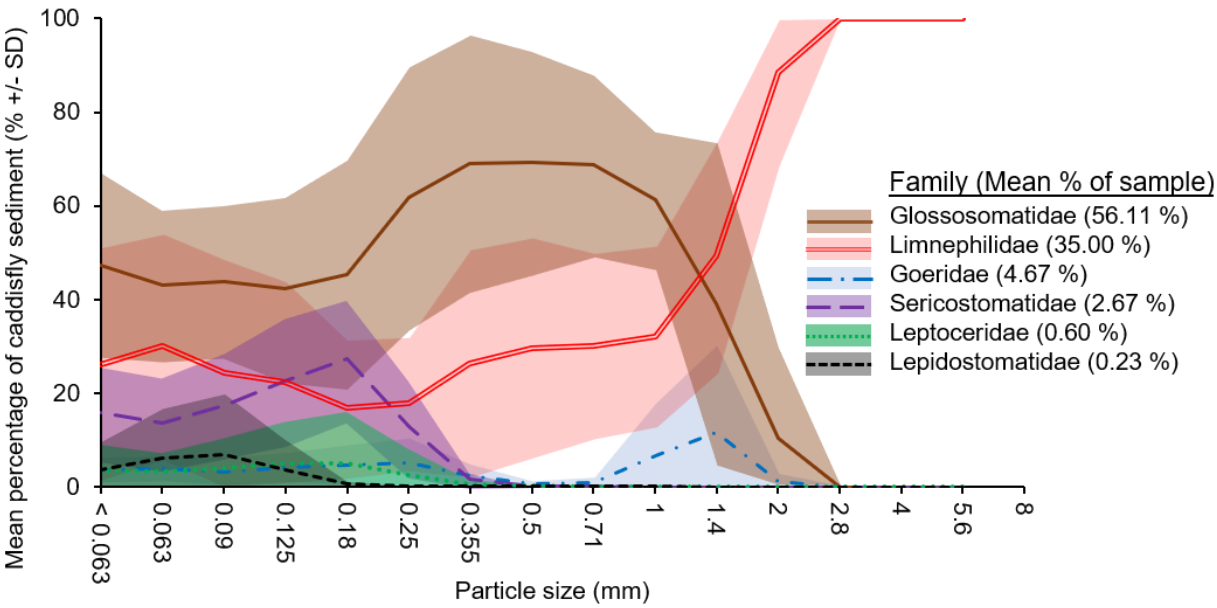


Figure 5.7. Percentage of caddisfly sediment use in each size fraction contributed by each caddisfly family (Mean across all samples). The average contribution of each family to total caddisfly transport in each sample is shown in brackets on the legend. Particle size indicates passing sieve.

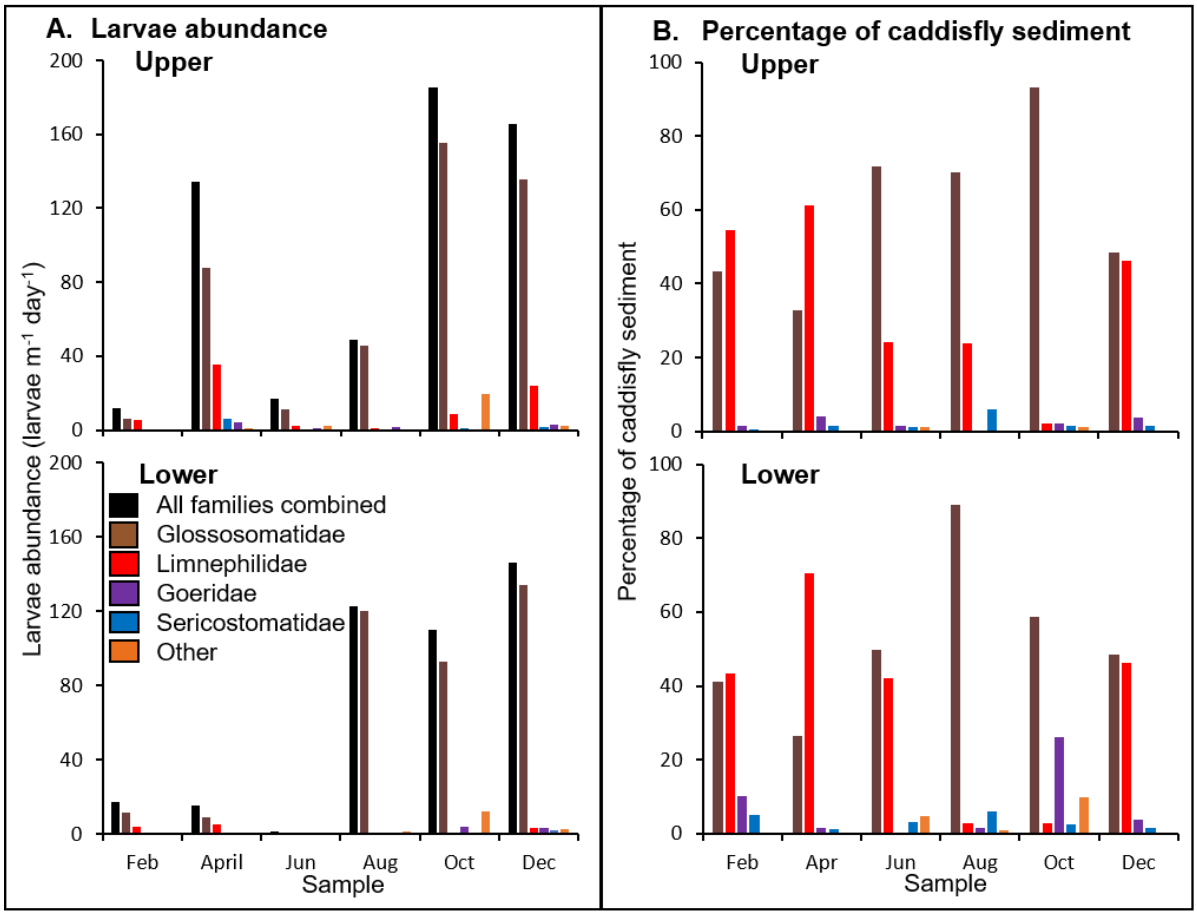


Figure 5.8. (A) The abundance of caddisfly larvae of each family within each sample for upper and lower traps. (B) the contribution of each caddisfly family to total caddisfly sediment mass in each sample. Taxa accounting for less than 1% of caddisfly sediment (Figure 5.7) were categorised as other.

5.4.4 Hydraulic mineral and organic sediment

Hydraulically transported sediment was divided into mineral and organic components (Figure 5.9). Most samples showed a bimodal size distribution by mass of hydraulic transported sediment, with a mode at medium sand (varying between 0.18 – 0.5 mm) and a mode at gravel (>4 mm; Figure 5.9). Therefore, in most samples there was a lower amount of coarse sand (~0.5 – 2 mm) transported by the flow (Figure 5.9). Of the detailed samples, the most sediment was transported in April in the upper traps and February and April in the lower (Figure 4A). April corresponds to increased discharge (Figure 5.3A), but bedload transport during these samples was still low compared to bedload transport during the interval between detailed sampling periods (Figure 5.3B &C).

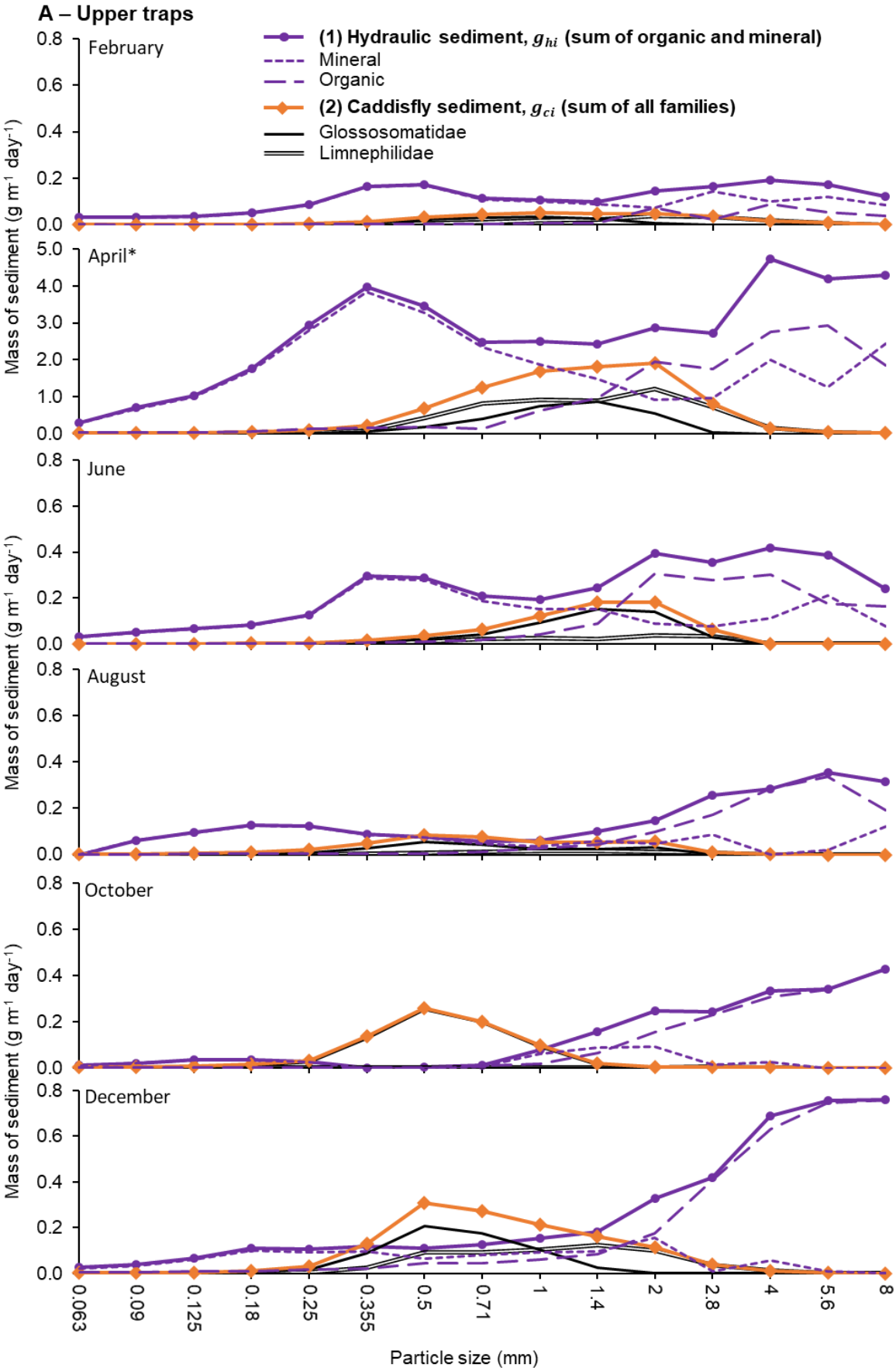
Most hydraulically transported sediment < 0.5 mm was mineral as opposed to organic (Figure 5.10). Therefore, the peak in bedload transport of medium sand was predominantly mineral (Figure 5.9). This mode was particularly distinct in the lower traps (Figure 5.9B). The organic

content of sediment increased with grain size up to 2mm; approximately 50% > 2 mm (by mass) was organic (Figure 5.10). The upper traps had larger quantities of coarse organic sediment than the lower (Figure 5.9). This was seasonally variable with greatest percentage of organic sediment transported in late August – December (Figure 5.9A).

5.4.5 How does the magnitude of caddisfly sediment transport compare to mineral and organic sediment transported by hydraulic processes?

Caddisfly transported primarily coarse sand which, in many samples, corresponds with the size range under-represented in hydraulic sediment transport (Figure 5.9). Consequently, sediment in caddisfly cases contributed a substantial proportion of bedload transport (Figure 5.10). On average across all samples at both trap sites, the proportion of sediment used by caddisfly was also unimodal, peaking at coarse sand (36.5 %) and skewed towards smaller particle sizes (Figure 5.10).

The percentage of bedload associated with caddisfly cases varied seasonally (Figure 5.11). At the upper site, caddisfly were responsible for the greatest proportion of bedload transport later in the year (particularly October and December). In October, caddisfly transported 100% of the 0.355 – 0.71 mm bedload (Figure 5.11A). At both sites the percentage of sediment transport which was caddisfly peaked at smaller grain sizes as the year progressed (Figure 5.11). The caddisfly contribution to bedload also varied spatially. In general, the proportion of caddisfly sediment was lower at the lower traps than upper (Figure 5.11). The percentage of caddisfly sediment peaked in the lower traps during April with 72% of 2 mm sediment present in cases.


A – Upper traps
(1) Hydraulic sediment, g_{hi} (sum of organic and mineral)
Mineral
Organic
(2) Caddisfly sediment, g_{ci} (sum of all families)
Glossosomatidae
Limnephilidae
February
April*
June
August
October
December
Mass of sediment (g m-1 day-1)
Particle size (mm)
0.063
0.09
0.125
0.18
0.25
0.355
0.5
0.71
1
1.4
2
2.8
4
5.6
8

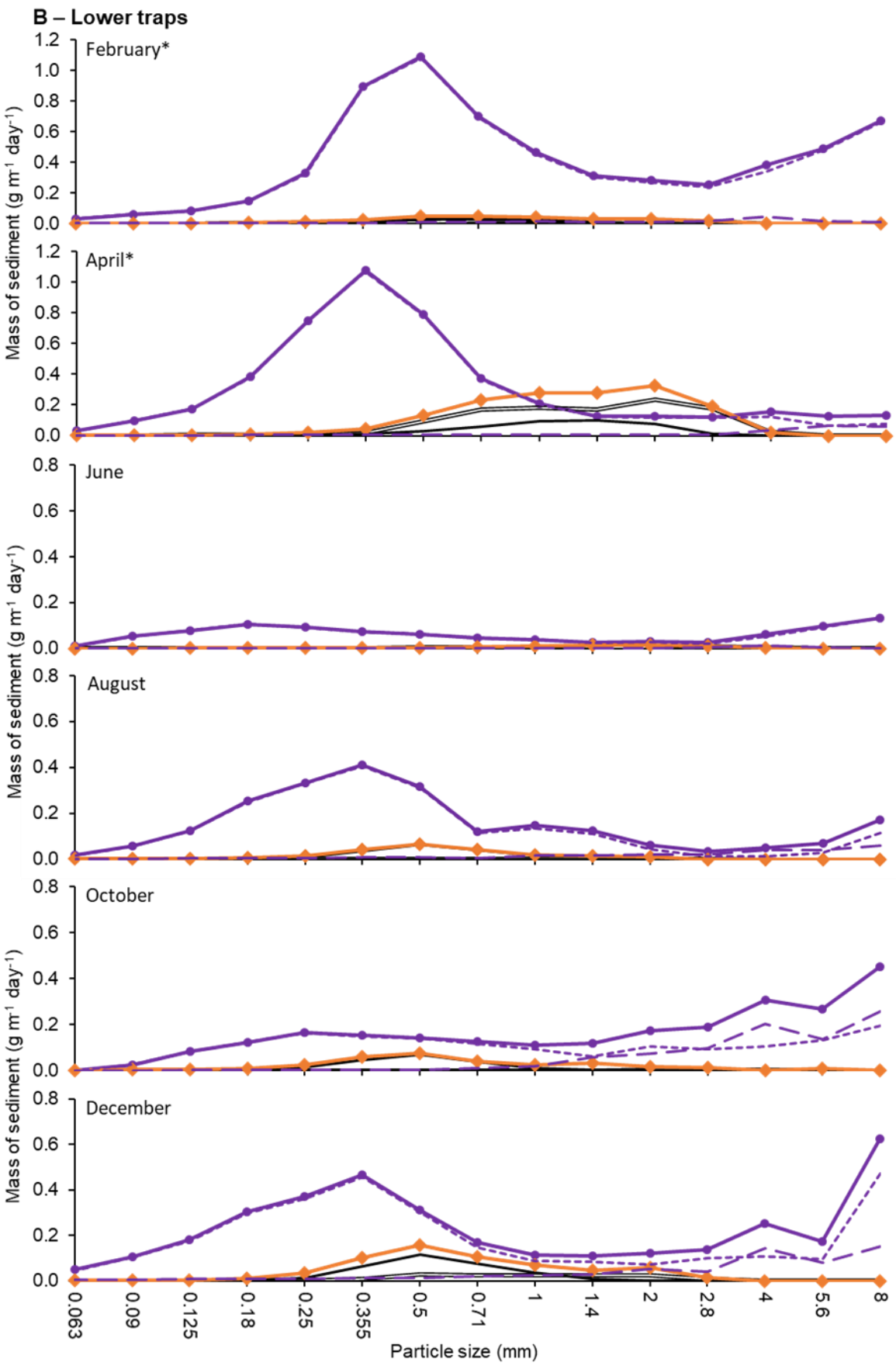


Figure 5.9. Hydraulic and caddisfly sediment content of traps at each detailed sampling occasion for upper traps (A) and lower traps (B). *Note differing y axis scale. Particle size indicates passing sieve.

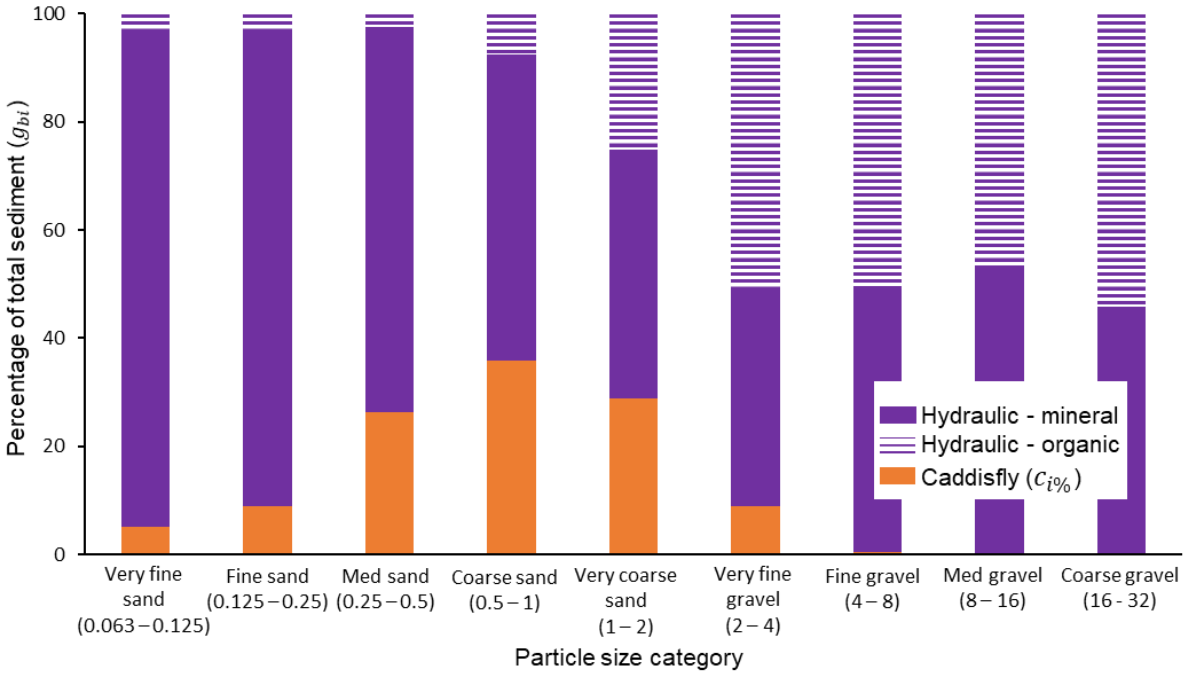


Figure 5.10. Contribution of case-building caddisfly ($c_{i\%}$) and hydraulic (mineral and organic) sediment to bedload sediment flux as a mean across both sets of traps and all sampling occasions. Split into particle size categories for simplicity.

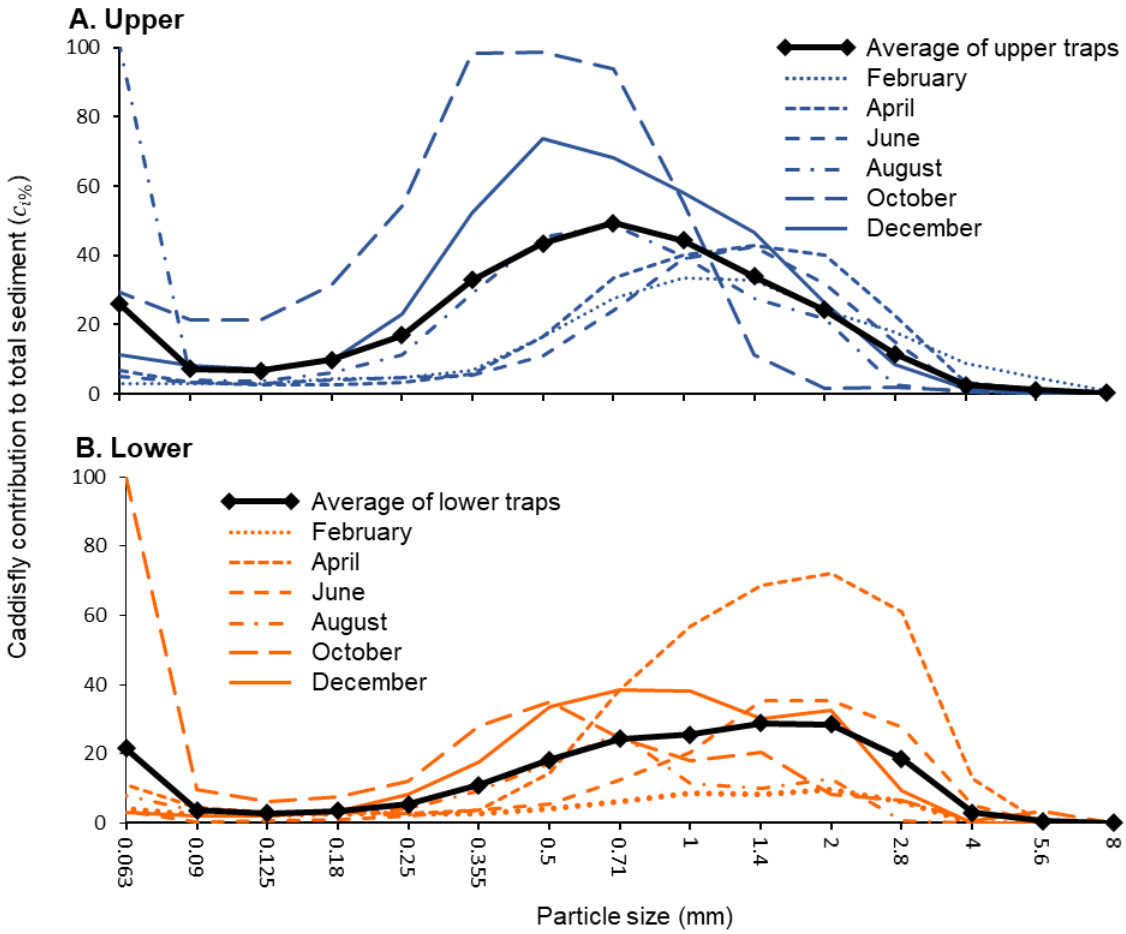


Figure 5.11.Percentage of total bedload transport that was caddisfly sediment, for each size fraction in each sample ($c_{i\%}$). Particle size indicates passing sieve.

5.5 Discussion

The effects of aquatic fauna on sediment transport in rivers are poorly understood, particularly for invertebrate taxa (Rice *et al.,* 2012; Statzner, 2012). Case-building caddisfly have important effects on the distribution and entrainment of sand (Chapters 3 and 4), but the implications for sand transport in rivers were unknown. This chapter measured the contribution of case-building caddisfly larvae (caddisfly sediment) and geophysical processes (hydraulic sediment) to bedload transport, during low to medium discharge conditions for a small UK stream. Case-building caddisfly contributed, on average, 1.27 g m^{-1} day^{-1}, which equates to 464.72 g m^{-1} a^{-1}. This accounted for 30% of the bedload transport of medium-coarse sand in bedload samples. The importance of caddisfly sediment transport under high discharge and high hydraulic sediment transport conditions is unknown. Nevertheless, under low to medium discharge conditions case-building caddisfly transport substantial proportions of sand in this stream, with potential implications for instream habitat provision.

5.5.1 What is the mass and GSD of sediment transport in caddisfly cases, and how does this vary seasonally?

The results of this study demonstrate that caddisfly larvae contribute to the downstream displacement of bed material; that is, they contribute to bedload sediment flux. During the year-long study period, case-building caddisfly accounted for an average of 1.27 g m^{-1} day^{-1}. The maximum mass of caddisfly sediment occurred in April at 8.85 g m^{-1} day^{-1} for the upper traps, which equates to 42 g day^{-1} transported at this cross section, over this two-week period. Caddisfly sediment was largely medium and coarse sand (Figure 5.5; D_{50} = 0.91 mm). In most caddisfly samples, sediment use was unimodal, although some samples had a bimodal distribution with a peak at fine sediment (about 0.5 mm) and coarser sand (about 2 mm). The size of sediment transported by caddisfly was similar to the sizes used by caddisfly in Wood Brook (D_{50} = 1 mm; Table 2.1).

Two mechanisms could be responsible for the caddisfly sediment transport recorded in this chapter. Caddisfly may have crawled into the traps or they may have been entrained by the flow and deposited in the traps (Figure 5.12). Active crawling by caddisfly is likely to be an important factor because caddisfly accounted for substantial amounts of bedload sediment transport even when discharge was very low and there was little hydraulic bedload (*cf.* Figure 5.11 & Table 5.1). Limnephilidae are mobile crawlers which follow hydraulically sheltered pathways, related to the

micro-topography of the river bed (Lancaster *et al.,* 2006; Erman, 1986). This mobility could explain their high abundance in traps, which far exceeded their population density in the nearby and similar Wood Brook (Chapter 2). Glossosomatidae, the caddisfly family accounting for the largest proportion of caddisfly sediment, are not known to move large distances horizontally. However, in Chapter 4, *A. fuscipes* larvae moved several metres around the flume in a 24hr period, despite their algae food source only being available in a small test area (Figure 4.5). Large Glossosomatidae populations migrating short distances for food and case building (Chapter 4) could, therefore, account for their high contribution to bedload flux.

Caddisfly larvae and cases may also have been transported into the traps by the flow (Figure 5.12). Whilst this study has differentiated between hydraulic and caddisfly transported bedload, some caddisfly sediment is also likely to have been transported by hydraulic processes. Empty cases of *P. latipennis* were found to be easily entrained (more so than their constituent sand grains; Figure 3.7A). Furthermore, Lancaster *et al.* (2006) found that *P. latipennis* larvae crawled more slowly and shorter distances under high discharge but did not attempt to shelter from increased flow velocity and consequently were moved via entrainment. Without larvae taking active measures to avoid drift, the increase in weight due to a larval inhabitant would probably have minimal effect in reducing entrainment. Therefore, it is likely that empty tubular cases, and those occupied by larvae that do not seek shelter, are preferentially transported over bed sediment (Chapter 3). In Chapter 4, downstream movement of Glossosomatidae increased at high flow velocity (Figure 4.5B; Figure 4.9D), and larvae were observed to be entrained off cobbles and settle in the next interstice. Entrainment of mineral caddisfly cases usually occurs over short distances (Elliott, 1971; Lancaster *et al.,* 2006; Otto, 1976) and whilst probably not detrimental to the larvae it could carry them into the traps in this study.

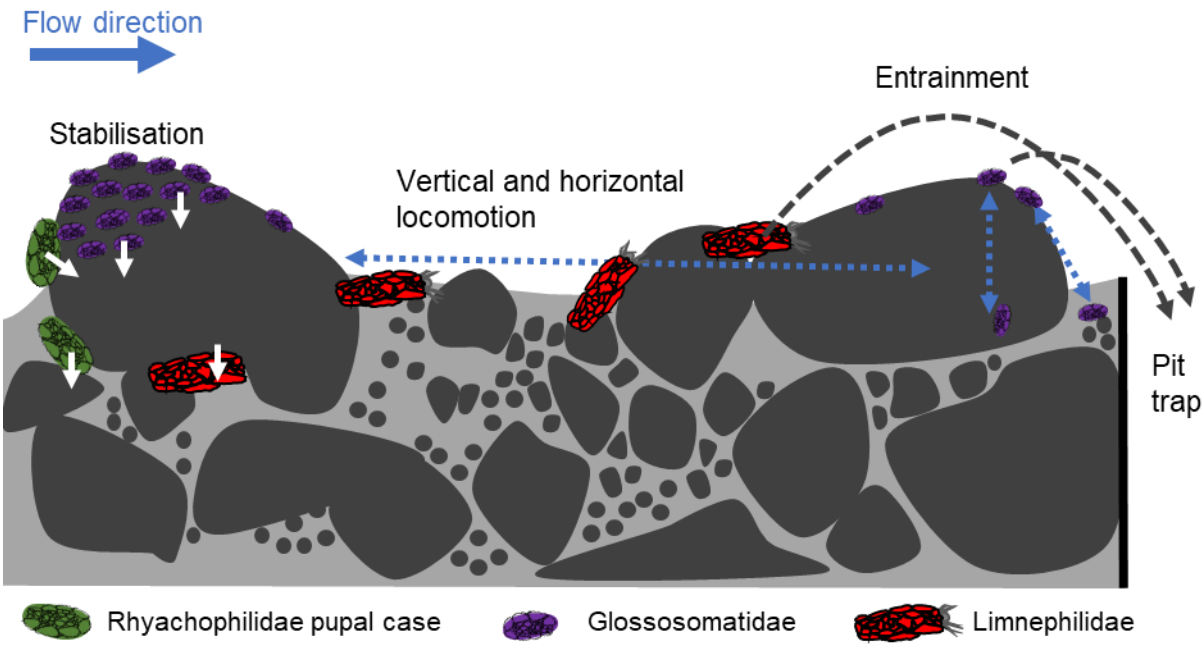


Figure 5.12. Conceptual model of sediment transport processes applying to caddisfly sediment. Caddisfly and cases may have been transported into the pit traps either by crawling (vertical and horizontal locomotion; blue arrows) or by entrainment (black arrows). The pit traps do not cover the full spectrum of cased caddisfly zoogeomorphic effects because they do not measure stabilisation of sediment by larvae which fix their cases (e.g. for pupation; white arrows).

Bedload traps do not capture the full zoogeomorphic effects of case-building caddisfly. Many caddisfly secure sediment, reducing the potential for entrainment and transport into traps (Figure 12). Rhyacophilidae and Hydropsychidae pupal cases are fixed to large stable particles, increasing the entrainment threshold of incorporated fine sediment (Statzner, 2012). These two families accounted for 15.20% of caddisfly sediment mass in Chapter 2 (Figure 2.3B). Most tubular case-builders (e.g. Limnephilidae and Sericostomatidae) also fix their cases for pupation and Glossosomatidae may fix their case earlier in their life cycle (Olden *et al.,* 2004). For example, for pupation, *P. latipennis* fix their case to the underside of large particles (often aggregating in groups of 40 or more; Otto and Svensson, 1981). *P. latipennis* cases are therefore unlikely to be mobilised again until flow is sufficient to move these large particles (Figure 5.12). Therefore, in addition to the sediment transport by caddisfly larvae identified in this chapter, a substantial amount of sediment may also be stabilised, particularly during late spring-autumn when most taxa pupate.

The low contribution of caddisfly families to sediment transport (Figure 5.7) does not suggest their zoogeomorphological contribution is less, rather that they are not responsible for transporting sediment horizontally. Net, retreat and pupal case building activities stabilise gravel and fine sediment. Their absence from these traps suggests they do so effectively, as personal observation revealed that Hydropsychidae, at least, were abundant in this stream. Burrowing taxa such as Sericostomatidae may still bioturbate bed sediments (e.g. De Nadaï-Monoury *et al.,* 2013)

but their vertical rather than lateral movements (Wagner, 1991) mean that they are less likely to end up in traps.

5.5.2 Contribution of caddisfly families

This is, to my knowledge, the first use of pit traps to sample macroinvertebrates in active river channels. The abundance of caddisfly and the associated mass of sediment in their cases was unexpectedly high (mean flux of larvae = 81.50 larvae m^{-1} day^{-1}). However, functional diversity was low; the vast majority of caddisfly found were case-builders. Presumably, caseless taxa are either less abundant, less mobile (e.g. fix themselves to the bed with silk) or were able to swim or drift out of traps. The energy invested in case construction, coupled with the functional benefits of the case (e.g. protection from predation), mean that most caddisfly species are reluctant to abandon their case (Dobson *et al.,* 2000), and are therefore unlikely to escape from traps. Furthermore, the presence of a heavy, mineral case, reduces the tendency to drift and the length of drift events. For example, when entrained in their cases, *P. latipennis* larvae travel only short distances (about 13 cm), saltating over the river bed (Elliott, 1971; Lancaster *et al.,* 2006; Otto, 1976), and are therefore unlikely to drift out of sediment traps. Therefore, whilst pit traps are not suitable for most aquatic invertebrate taxa, they proved to be very effective for case-building caddisfly. Pit trap contents are dependent on a combination of population density, the movement dynamics of individuals, and the characteristics of the trap and surrounding landscape (Jansen and Metz, 1979). Consequently, using these results to infer population density would be challenging, and require a detailed understanding of the mobility of each taxon. However, when the mobility of larvae is of interest, pit traps provide an excellent sampling method (Corti *et al.,* 2013). In this study, traps were particularly useful as they allowed a direct comparison with hydraulic sediment transport.

Glossosomatidae were the most abundant caddisfly in every sample, however due to the smaller mass of their cases (Table 2.1) the total sediment mass contributed by the much larger Limnephilidae larvae was often greater (Figure 5.7A & B). Glossosomatidae larvae more readily leave their cases, particularly under adverse environmental conditions, such as fine sediment deposition (Nijboer, 2004), which may allow them to drift out of traps. This might account for the number of cases (estimated from the mass of case sediment) outweighing the number of larvae, in some samples. The opposite was found in Chapter 2 (Wood Brook Surber samples) where the abundance of larvae exceeded cases, presumably due to the relative fragility of Glossosomatidae cases. It is therefore possible that the mass of Glossosomatidae sediment

found in traps in the present study is an underestimate because larvae abandoned their cases and drifted out of the traps and the cases subsequently disintegrated. Glossosomatidae sediment transport may also be underestimated because they were also the only taxa found attached to the vertical trap sides. Presumably Glossosomatidae were able to escape from the trap by using silk to attach their case to the smooth plastic sides (*sensu.* Olden *et al.,* 2004).

Limnephilidae, whilst less abundant than Glossosomatidae, dominated caddisfly sediment in February and April (Figure 5.8B). There was a drop in the median grain size of caddisfly sediment between June and August (Figure 5.4B), associated with a transition from Limnephilidae to Glossosomatidae dominating caddisfly sediment (Figure 5.8B). This transition between April and August is probably related to the pupation of Limnephilidae taxa at this time. In a Swedish stream *P. latipennis* mostly hatched in October, reached instar IV by February, V in May and pupated between July and August (Otto, 1971). Otto (1971) also documented an increase in movement, both upstream and downstream of *P. latipennis* prior to pupation, hypothesised to be a result of increased food requirements at this time. Therefore, the peak in Limnephilidae sediment may be a combination of increased crawling prior to pupation and the high mass of sediment contained within each final instar Limnephilidae case. Glossosomatidae used a substantial amount of sediment all year round, without the clear seasonal pattern found for Limnephilidae (Figure 5.8B). This is likely to be largely because of overlapping cohorts of larvae of different instars. Figure 5.13 shows four *A. fuscipes* cases from the same sample demonstrating that several instars of this species are present at the same time.

By virtue of their case construction, the caddisfly element of sediment transport could be measured. Isolating biotic turbation activities has only been done a handful of times, but via a number of methods. Rice *et al.* (2016) were able to isolate the fine sediment bioturbation of crayfish temporally, as crayfish were largely active at night and there were few other reasons for a nocturnal peak in sediment. Hassan *et al.* (2008) separated bedload transport due to Salmonidae because this occurred at discharges well below those required for fluvial entrainment of sediment. The disturbance of markers (Rice *et al.,* 2019), tagged particles (Gottesfeld *et al.,* 2004) and characteristic sediment (De Nadaï-Monoury *et al.,* 2013) have also been used to measure bioturbation. Thus, case bioconstruction provided a unique opportunity to study bioturbation caused by caddisfly larvae.

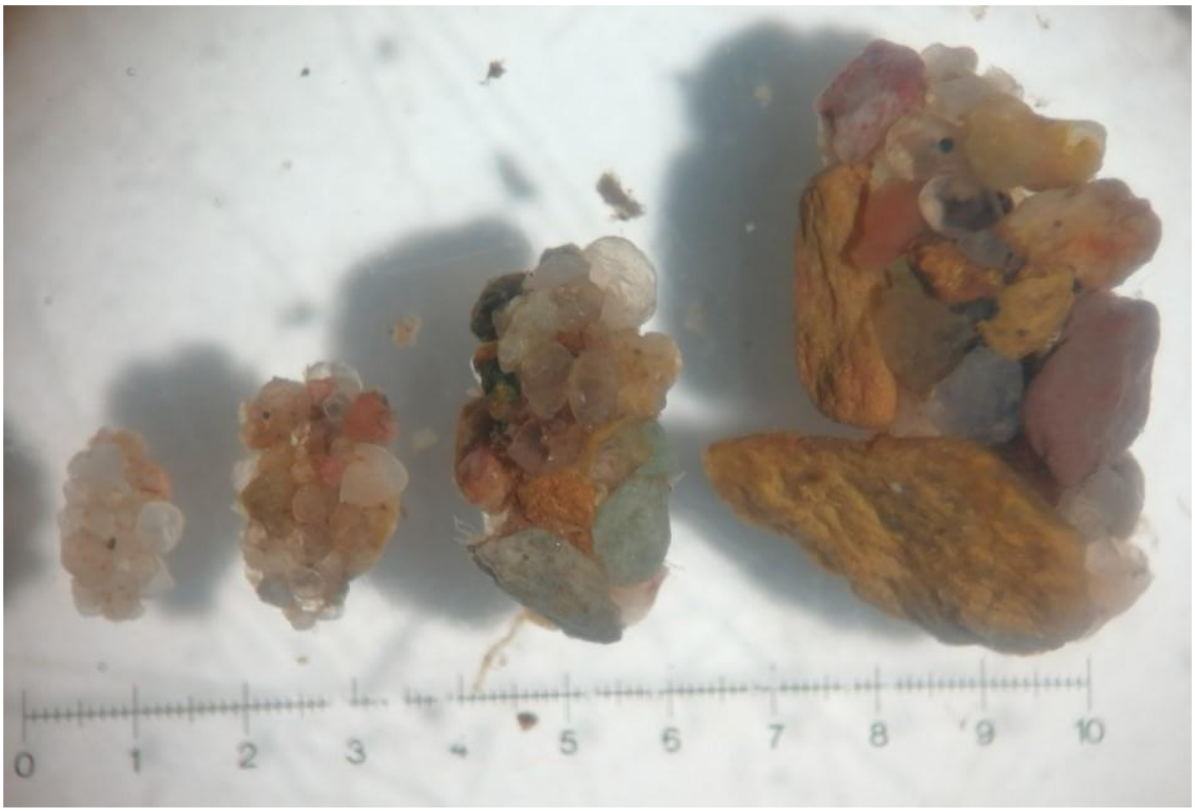


Figure 5.13. Glossosomatidae *A. fuscipes* cases of different sizes from the same sample. Scale in mm.

5.5.3 How does the magnitude of caddisfly sediment transport compare to hydraulically transported mineral and organic sediment?

During periods of low to medium discharge, caddisfly were responsible for the transport of 30% of the medium to coarse sand (0.25 – 2 mm; Figure 5.10). Caddisfly transported sediment peaked at coarse sand (Figure 5.5). There was no seasonal pattern in either the mass of caddisfly sediment or the proportion of bedload sediment transport that could be attributed to caddisfly, other than a peak in late spring (April).

The sampling periods were determined *a-priori*, to ensure an even spread across the year. Unfortunately, it is not known what the proportion of caddisfly bedload transport was during the large discharge / sediment transport events in spring which were responsible for most bedload transport (Figure 5.3). It is likely that the percentage of caddisfly sediment in traps was reduced because, once the armour layer is disturbed, mass sediment transport often occurs (Parker, 2008). Furthermore, high discharge and bedload movement may trigger caddisfly larvae to seek refugia, reducing their transport of sediment. Consequently, caddisfly bedload transport probably represents a small fraction of total annual bedload transport by mass.

However, discharge was highest in April (Figure 5.3) and this sample also had the largest amount of caddisfly sediment. This suggests that increasing discharge increases the number of caddisfly falling into the trap, presumably via entrainment, although caddisfly activity may also be highest at this time for Limnephilidae (Otto, 1971). The two are not mutually exclusive, an increase in time spent crawling will likely also increase the potential for entrainment.

The next step is to understand the contribution of caddisfly to bedload transport during high sediment transport events. Repeating this research with detailed sampling periods stratified to cover a range of discharges (rather than evenly spread across the year) would address this. However, this would be complicated by the difficulty of predicting sediment transport events *a-priori* and an uneven spread of samples might complicate understanding of seasonal changes in caddisfly communities and sediment use.

5.5.4 Consequences for fluvial zoogeomorphology

Sediment transport by caddisfly larvae is important because it does not conform to traditional understanding of how sediment moves in rivers. Bedload transport begins when shear forces provided by the flow reach a critical value sufficient to transport surface particles (Shields, 1936; Chapter 3) and transport rate is a function of excess shear stress. In contrast, sand transport by caddisfly larvae occurs even under low discharge, far below the critical threshold for bed mobilisation (compare Figure 5.4 and Figure 5.3A). Therefore, even though caddisfly sediment transport is probably only a small fraction of total bedload transport over the full year, transport of sand during low-medium flow conditions could be geomorphologically important.

Unlike hydraulic transport, caddisfly transport cannot be assumed to be in a downstream direction. Caddisfly movements are a combination of entrainment (downstream) and locomotion, which may be in any direction, but is often upstream (Elliott, 2003; Erman, 1986). Caddisfly movements may not be random, and consequently could result in a systematic transport of sediment in specific directions, related to their biological needs and season. Some evidence exists for mass migrations, rather than just random walks. For example, (Erman, 1986) found that C. *centralis* migrated downstream prior to pupation. Similarly, *Brachycentrus subnubilis* (Brachycentridae) spends most of the year sheltered underneath beds of the macrophyte *Ranunculus*, emerging in spring to more exposed positions for pupation (Gunn, 1985). Furthermore, many caddisfly, including *P. latipennis*, also aggregate for pupation (Martin and Barton, 1987; Otto and Svensson, 1981). Such migrations could result in sand fluxes, with more consistent impacts than if sand is moved randomly over the riverbed.

Black Brook is a small lowland stream with a high abundance and diversity of caddisfly fauna, typical of many European lowland streams. Whilst discharge in Black Brook is to some extent controlled by a reservoir, the stream still experienced flood peaks during the sampling period (Figure 5.3A). Both the mass of sediment used and transported by caddisfly will vary between rivers. In streams with more fluvial disturbance, the importance of sediment movement by caddisfly may be less. Nevertheless, it is likely that similar magnitudes of sediment transport by caddisfly larvae occur in many streams with comparable caddisfly communities.

5.6 Summary

A key challenge for research in biogeomorphology is to measure the effects of organisms at spatial and temporal scales sufficiently large to provide comparison with geophysical processes (Rice *et al.,* 2019). The results of this chapter provide evidence that case-building caddisfly contribute to reach-scale bedload transport during all seasons. Pit traps, commonly used to estimate both bedload transport in rivers and invertebrate communities, provided a novel method to sample and isolate biotic (*caddisfly sediment*) and abiotic (*hydraulic sediment*) components of bedload in a comparable manner. In result, the chapter provides the first reach scale seasonal assessment of zoogeomorphic effects of aquatic insects as well as the first use of pit traps to sample macroinvertebrates in an active river environment.

Case-building caddisfly contributed to the bedload flux of Black Brook during the low to medium flow conditions sampled, an average of 1.27 g m^{-1} day^{-1} which equates to 464.72 g m^{-1} a^{-1}. For Black Brook, over an annual period, this was equivalent to 3.5 kg a^{-1} at the upper traps and 0.7 kg a^{-1} at the lower. Many caddisfly species are active crawlers (Lancaster, 2008; Rice *et al.,* 2007) and consequently, caddisfly transported sediment even during the lowest discharge periods. The mass of caddisfly sediment peaked in spring. Caddisfly and empty cases may also have been preferentially entrained into traps. Caddisfly sediment was predominantly coarse sand (D_{50} = 0.91 mm) and over 90% was mineral sediment (by mass).

During base flow periods case-building caddisfly accounted for 1/3 of coarse sand transport in this stream on average, although they were responsible for over 60% of some size fractions in several samples. However, the majority of bedload transport in this stream occurred in spring between sampling periods and so the importance of case-building caddisfly during periods with high sediment mobility is unknown.

Pit traps capture a combination of taxa abundance and mobility. Glossosomatidae (*A. fuscipes*) accounted for over half of sediment transport and Limnephilidae (predominantly *P. latipennis*) a further 1/3rd. Limnephilidae show a strong seasonal pattern, ramping up their sediment contribution until pupation in late spring. Taxa which build static cases and nets were notably rare in the traps, suggesting that their stabilisation of sediment may prevent it from moving as bedload, although the abundance of these taxa in this stream is unknown.

Sediment transport in rivers is typically viewed as a physical phenomenon. The results of this chapter add to increasing literature on the importance of biology in sediment processes and provide the first reach-scale quantification of bedload movement by an insect engineer. Furthermore, the movement of sediment by caddisfly does not conform to traditional understanding of bedload dynamics. Sediment may move upstream as well as downstream and although likely influenced by hydraulic processes, high discharge events may reduce caddisfly sediment transport. It is therefore important to better understand sediment engineering roles by invertebrates in gravel-bed streams.

Black Brook, location of Chapter 5, March 2018.

Chapter 6. Discussion

6.1 Introduction

Whilst sediment dynamics in rivers have traditionally been considered a largely physical phenomenon (Reinhardt *et al.,* 2010), it is increasingly recognised that plants and animals can have substantial effects on sediment transport processes (Rice *et al.,* 2012; Statzner, 2012; Wilkes *et al.,* 2018). Most zoogeomorphic research has focussed on vertebrate taxa, but invertebrates also extensively bioturbate and stabilise sediment (Chapter 1). Caddisfly have prompted geomorphological research for their construction of nets and retreats, which stabilise gravel substrates (e.g. Albertson *et al.,* 2019; Johnson *et al.,* 2009), resulting in zoogeomorphic effects as important as those of much larger taxa (Albertson and Allen, 2015). However, documented zoogeomorphic effects of case-building caddisfly are limited to a few examples of bioturbation (*Sericostoma personatum*; De Nadaï-Monoury *et al.,* 2013), bioerosion (sp. unknown; Savrda, 2019) and the formation of calcium carbonate bioherms (e.g. Leggitt and Cushman, 2001). It is therefore important to assess the zoogeomorphic effects of case construction by caddisfly larvae.

The results of this thesis demonstrate that case-building caddisfly redistribute substantial quantities of fine sediment over riverbeds. This discussion chapter will first evaluate how each of the thesis objectives have been met (Section 6.2). Second, the chapter will consider the zoogeomophic effects of case-construction in more detail (Section 6.3) and how these vary between case architecture groups (Figure 1.3; Section 6.4) and the relative importance of stabilising and destabilising zoogeomorphic mechanisms (Section 6.5). The challenge presented by scaling zoogeomorphic processes is discussed in Section 6.6 and the possible implications for fluvial geomorphology and ecology are discussed in Section 6.7.

6.2 Fulfilment of thesis objectives

The primary aim of this thesis was to investigate and quantify the effect of case-building caddisfly on the distribution and transport of sediment in rivers. This was addressed via three specific objectives;

1) To quantify the mass and grain-size of sediment incorporated into caddisfly cases and identify the individual taxa responsible, in riffle habitats of a lowland stream (Chapter 2).
2) To determine the effect that case construction by caddisfly larvae has on the hydraulic force required to transport incorporated sediment (Chapter 3).
3) To ascertain the importance of caddisfly in transporting and redistributing sediment over the riverbed (Chapters 4 and 5).

The aim and objectives of this thesis were addressed by two field studies and two laboratory flume experiments.

6.2.1 Objective 1 – Quantifying sediment use by case-building caddisfly

The characteristics of sediment used in individual caddisfly cases had been studied for a range of species (e.g. De Gispert *et al.,* 2018; Gaino *et al.,* 2002; Otto and Svensson, 1980). Statzner *et al.,* (2005) and Statzner (2011), however, were the only published studies which spatially quantified sediment use by case-building caddisfly and they only considered a few species. Previous research had also primarily investigated caddisfly case-building from an ecological perspective, to understand the process of case construction (Hansell, 1972; Rowlands and Hansell, 1987), the purpose of cases (Ferry *et al.,* 2013; Otto and Johansson, 1995; Williams *et al.,* 1987) or adaptation of case design to the biotic or abiotic environment (Boyero *et al.,* 2006; Statzner, 2011; Statzner *et al.,* 2005). To understand the geomorphological effects of case-building caddisfly it was necessary to measure sediment use at larger spatial scales, for all taxa living at the site. Objective 1 was addressed using a field study which quantified the sediment used by the caddisfly community found in riffle habitats in a lowland stream (Chapter 2). There was a wide variability in the mass of sediment used in caddisfly cases (mean = of 38 g m^{-2}, range 4 – 139 g m^{-2}). Despite variability in local habitat and caddisfly sediment use, all sites supported diverse case-building caddisfly communities utilising mineral sediment. Consequently, geomorphological effects of case-building caddisfly are potentially widespread. Whilst caddisfly examined in Chapter 2 primarily used coarse sand in case construction (D_{50} = 1 mm), the range of sediment caddisfly used varied from very fine sand to gravel (0.063 to 11 mm; Figure 2.3), reflecting the grain size requirements or preferences of different species (Figure 2.2.). Therefore, this chapter

indicated that case-building caddisfly may have zoogeomorphic effects across a wide range of grain sizes.

The results of Chapter 2 also demonstrated the diversity of case-building caddisfly behaviour and sediment use within and between species. The average mass of an individual caddisfly case varied between species by several orders of magnitude (0.001 g for early instar Leptoceridae and Lepidostomatidae cases to 0.828 g for Rhyacophilidae and Hydropsychidae pupal cases; Table 2.1). Further research (Chapters 3 & 4) focussed on taxa which used a large amount of sediment or exhibited behaviours which may have zoogeomorphic effects, including crawling with their cases. The taxa which accounted for the most sediment use (e.g. Glossosomatidae = 64%, Rhyacophilidae & Hydropsychidae = 15%, Limnephilidae = 11%) were primarily surface dwellers and therefore, may affect interactions between sediment and hydraulics at the sediment-water interface, potentially affecting the entrainment of this sediment.

Moore (2006) suggested that the size of an organism's zoogeomorphic effect is a function of its abundance, body size and behaviour. Caddisfly were abundant in Wood Brook (mean abundance = 2250 larvae m^{-2}), and 90% of these individuals were case-builders rather than net building or free-living taxa. Whilst case-building caddisfly have a small body size (typically < 30 mm), other similar sized taxa have been shown to have important zoogeomorphic effects (e.g. net-building caddisfly - Albertson and Allen, 2015; stonefly - Statzner *et al.,* 1996; Chironomidae - Xing *et al.,* 2018). Chapter 2 concludes that caddisfly case-building effect a substantial amount of surface sediment over a wide range of grain sizes including sand and fine gravel.

6.2.2 Objective 2 – Effects of case construction on sediment entrainment

To understand the zoogeomorphic effect of case-building caddisfly it is necessary to know, not only how much sediment is used in cases, but also how case construction affects the mobility of sediment incorporated within them. Caddisfly cases can be considered composite particles which are substantially larger and comparatively less dense than their constituent sediment grains. Whilst some researchers have investigated the entrainment of caddisfly cases of different species (Otto, 1976; Otto and Johansson, 1995; Waringer, 1993, 1989), the effect of caddisfly bioconstruction on the geomorphological properties of amalgamated sediment had not been examined previously. Chapter 3 presented the result of a detailed flume experiment designed to understand the effect of case construction on sediment entrainment and address thesis objective 2. Chapter 3 compared the entrainment thresholds of empty cases and the loose sediment grains from which individual cases were constructed, for three species with different case designs. The tubular cases of *P. latipennis* and *S. personatum* required significantly less shear stress to move

(mean case τ_c = 0.06 and 0.18 N m^{-2} respectively), than their loose constituent sediment (mean sediment τ_c = 0.35 and 0.49 N m^{-2} respectively, Figure 3.7A). There was no difference in the entrainment threshold of *A. fuscipes* cases compared to the loose sediment from which they were constructed (mean case τ_c = 0.28, sediment = 0.32 N m^{-2}). This was hypothesised to be a result of *A. fuscipes* domed case shape and flat base, which increased friction with the riverbed.

The results of Chapter 3 suggest that empty cases of *P. latipennis* and *S. personatum* are more easily entrained than their constituent grains and therefore, by incorporating sediment into their cases, these species may increase the mobility of this sediment. However, these results are limited to empty caddisfly cases, which might occur following case abandonment or emergence of an adult caddisfly from a pupation case. Additional research is required to understand how the behaviour of a live occupant would affect case entrainment. Previous research suggests that caddisfly are effective at avoiding entrainment, by clinging on or moving to more sheltered locations (Waringer, 1989), however larvae may be regularly entrained short distances (Lancaster *et al.,* 2006).

The large numbers of case-building caddisfly collected in sediment traps in Chapter 5 also suggests that caddisfly and their cases are highly mobile (Figure 5.4A & Figure 5.9A). It is likely that entrainment of caddisfly was an important factor in their movement into traps, in addition to larvae crawling. This is supported by the fact that the number of Limnephilidae found in traps, including *P. latipennis,* was highest during periods with the highest discharges (April samples; Figure 5.3 & Figure 5.4), although this may also have coincided with increased locomotive activity prior to pupation. Although the act of case construction by *A. fuscipes* did not reduce the hydraulic force required to transport constituent sediment (as was the situation for *S. personatum* and *P. latipennis*), immediately after case construction, *A. fuscipes* typically transport this sediment vertically upwards, increasing its hydraulic exposure (Chapter 4). This may increase the vulnerability of cases to entrainment and explain why *A. fuscipes* also constituted a substantial proportion of sediment transport in bedload traps in Chapter 5 (Figure 5.7).

6.2.3 Objective 3 – Sediment redistribution by case-building caddisfly

Caddisfly are mobile animals and many species transport their cases with them. Chapters 4 and 5 investigated sediment redistribution by case-building caddisfly (objective 3). The flume experiment reported in Chapter 4, demonstrated a vertical flux of sediment by *A. fuscipes* larvae from sheltered interstices within an armoured gravel-bed, on to the exposed upper surface of gravel particles. On average, each Glossosomatidae larvae was found to transport 0.055 g of sediment upwards by 25.40 mm. Combining this result with the sediment use by

Glossosomatidae populations in Wood Brook (Chapter 2), this flux represents a mean vertical movement of 25.95 gm^{-2} (up to 88.92 g m^{-2}) of sediment; equivalent to 1 kg of sand for every 40 m^2 of riverbed. Therefore, Glossosomatidae relocate sediment to more exposed locations which may increase downstream transport of this sediment.

Chapter 5 examined the relative contribution of caddisfly and abiotic processes to bedload transport in a small gravel-bed river and therefore considered the net effect of caddisfly sediment transport via 1) locomotion (e.g. *A fuscipes*, Chapter 4) and 2) entrainment (Chapter 3). The importance of caddisfly to total annual bedload transport was not measured because the highest discharges did not occur during sampled periods. However, during the low to medium discharge conditions when caddisfly contributions to bedload were sampled, case-building caddisfly were unexpectedly mobile; an average of 82 larvae entered the pit traps m^{-1} day^{-1} and case-building caddisfly accounted for 30% of medium to coarse sand transport. Therefore, case-building caddisfly actively contributed to sediment transport in this gravel-bed stream.

6.3 Bioconstruction by case-building caddisfly larvae

Five mechanisms are commonly used to conceptualise an organism's biogeomorphic effects (Table 1.1; Corenblit *et al.,* 2011; Naylor *et al.,* 2002; Viles, 2019). The results of this thesis and previous published research provide evidence that caddisfly undertake at least four of these biogeomorphic mechanisms (Figure 6.1). Caddisfly nets provide *bioprotection* (e.g. Johnson *et al.,* 2009), whilst burrowing taxa cause *bioturbation* of soft substrates (De Nadaï-Monoury *et al.,* 2013) and *bioerosion* of hard substrates (Savrda, 2019). An example of caddisfly *bioweathering* remains to be found. This thesis has evaluated the zoogeomorphic effects of *bioconstruction* by caddisfly larvae (Figure 6.1).

Caddisfly cases are unique compared to most bioconstructions documented in the zoogeomorphic literature. First, cases are often transported by the larvae (Chapters 4 & 5). This is common for autogenic bioconstructions (e.g. mussel and snail shells), but far less common for allogenic engineering, (e.g. caddisfly cases). Second, bioconstructions are constructed by individual larvae rather than colonies (e.g. ants), although many individuals may exhibit similar behaviours (Chapter 4) or aggregate (e.g. for pupation; Otto and Svensson, 1981). Case-building caddisfly were found to have destabilising effects on sand distributions in rivers. The cases of some species were intrinsically more mobile than incorporated sediment (Chapter 3) and are

transported by the larvae (Chapter 4), processes which together result in a flux of sediment which can be directly attributed to caddisfly larvae (Chapter 5).

However, sediment destabilisation by case-building caddisfly is very different from most documented bioturbation. Previous research concerning bioturbation has chiefly described movements of particles short, vertical or horizontal distances (François *et al.,* 1997) causing mixing, which in rivers may affect hydraulic connectivity and sediment exposure in relation to potentially entraining flows in coarser river sediments (Johnson *et al.,* 2011; Rice *et al.,* 2019). In contrast, caddisfly transport their case sediment long distances (relative to organism length). Furthermore, caddisfly larvae may transport sediment in specific directions (e.g. Glossosomatidae move sediment vertically upwards). Consequently, the effects of case-building caddisfly on sediment transport processes are likely to be unique.

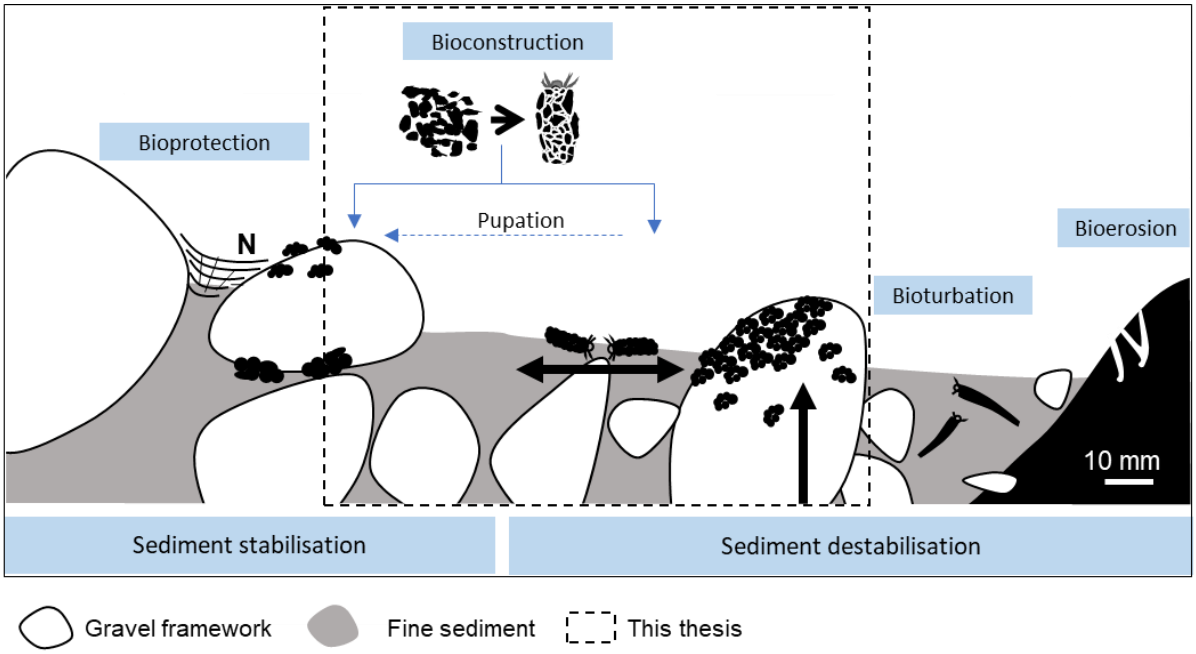


Figure 6.1. Conceptual zoogeomorphology of caddisfly larvae. Case construction (bioconstruction) may destabilise sediment by 1) modifying the entrainment threshold of the incorporated sediment and 2) moving the case sediment vertically and horizontally. However, case construction can also stabilise sediment if cases are moved to areas of lower hydraulic stress or if cases are fixed in place with silk (bioprotection). Cases are typically fixed for pupation so that many caddisfly species may destabilise sediment for much of their larval life but then stabilise sediment during pupation. The focus in this thesis on bioconstruction adds to the literature on existing caddisfly zoogeomorphic effects (bioprotection by caddisfly nets and retreats and bioturbation and bioerosion by burrowing larvae).

It is also expected that cases fixed to the substrate will stabilise sediment (Figure 6.2). This has been documented for pupal cases of *H. siltalai* (Statzner, 2012), and most species of tubular and dome case-building caddisfly also fix their cases for pupation (Figure 6.2). This process presumably stabilises the constituent sediment particles by fixing the small grains to large and immobile clasts. Therefore, case-building caddisfly may have either destabilising and stabilising effects on river sediment depending on species, life -stage and case-building behaviour.

6.4 Effect of case architecture on caddisfly zoogeomorphology

The behaviour of an organism is a key control on their zoogeomorphic effect (Moore, 2006). However, living organisms exhibit a wide variety of behaviours, which makes conceptualising and understanding their different biogeomorphic effects challenging (Allen *et al.,* 2014). Caddisfly are taxonomically and functionally a very diverse order of aquatic insects (Morse *et al.,* 2019). Nearctic Trichoptera have more genera and occupy a broader range of habitats and trophic categories than many other aquatic insect groups (e.g. Ephemeroptera, Odonata and Plecoptera; Wiggins and Mackay, 1978). Case-building caddisfly are diverse taxonomically and, in their behaviour, and sediment use (Chapter 2), as well as their zoogeomorphic effects (Chapter 3).

Case architecture, therefore, is an important caddisfly behaviour and control on their zoogeomorphic effect. Wiggins (1996) described five broad caddisfly architecture groups (Figure 1.3), four of which were found to have potential zoogeomorphic effects. The fifth group, purse case makers, were low in abundance and used very little sediment in the field studies (Table 2.2; Figure 5.7).

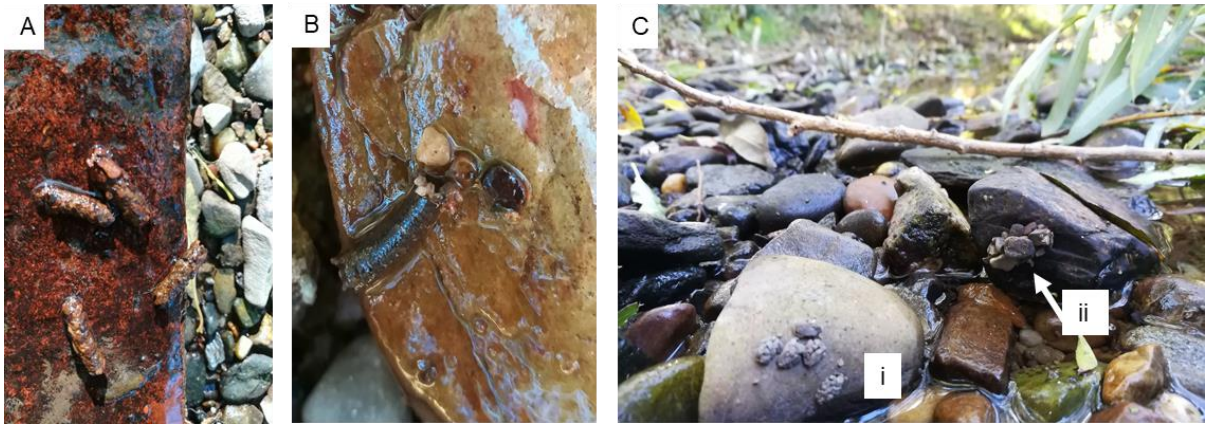


Figure 6.2. Examples of sediment stabilisation by case building caddisfly observed in Black Brook (location of the work reported in Chapter 5) September 2018. (A) Limnephilidae cases fixed to the underside of a brick for pupation. (B) Sericostomatidae case with a trail of larger gravel and fixed to the underside of a large cobble for pupation. (C) Fixed pupal cases of (i) free living or net building taxa like Rhyacophilidae and (ii) Glossosomatidae, left dry after sudden drop in water levels.

6.4.1 Tube case-builders

Tubular case-builders were the most species diverse of the case architecture types in Wood Brook (13 out of 24 taxa identified; Table 2.2). Tubular case-builders typically construct mobile cases which are carried around with the larvae (Figure 6.3) until pupation at which stage they are often fixed to larger, stable cobbles (Figure 6.2; Wiggins, 2004). Case architecture was found to be very variable between species in this group (case mass varied from 0.001 g for early instar Lepidostomatidae and Leptoceridae to 0.146 g for Limnephilidae; D_{50} from 0.17 to 1.12 mm; Table 2.1). Of the tube case-builders, Limnephilidae used most sediment (11% by mass; Figure 2.3) while other tube case-builders each used less than 5%.

Bioconstruction by tubular case-builders destabilises sediment, as tubular cases were inherently more mobile than their constituent grains (Figure 3.7A). Furthermore, larvae may crawl over the riverbed, transporting their case and constituent sediment with them (Figure 5.9). In Black Brook, Limnephilidae accounted for, on average 35% of sediment transport, and up to 70% in April prior to pupation (Figure 5.8B). The transport of sediment by tubular case-builders involves movement of a small number of grains, large distances (relative to organism size) over the riverbed surface. However, tube case-builders may also stabilise sediment. Tube case-builders typically secure their cases to large stable particles for pupation (Figure 6.1A &B).

Whilst bioturbation by burrowing tubular case taxa was not examined in this thesis, previous research has demonstrated that *S. personatum* and *Odontoceridae* larvae cause vertical mixing of fine sediment (De Nadaï-Monoury *et al.,* 2013). Sericostomatidae larvae burrow diurnally to approximately 12 cm depth (Wagner, 1990), increasing the organic matter content of the substrate (Wagner, 1991). *S. personatum* were widespread in riffle habitats (Chapter 2) as well as the pools studied by De Nadaï-Monoury *et al.,* (2013). Bioturbation by burrowing is widely documented in terrestrial, marine and freshwater habitats and therefore is likely to be important in rivers, particularly as sediment disturbed on the surface may then be transported by the flow.

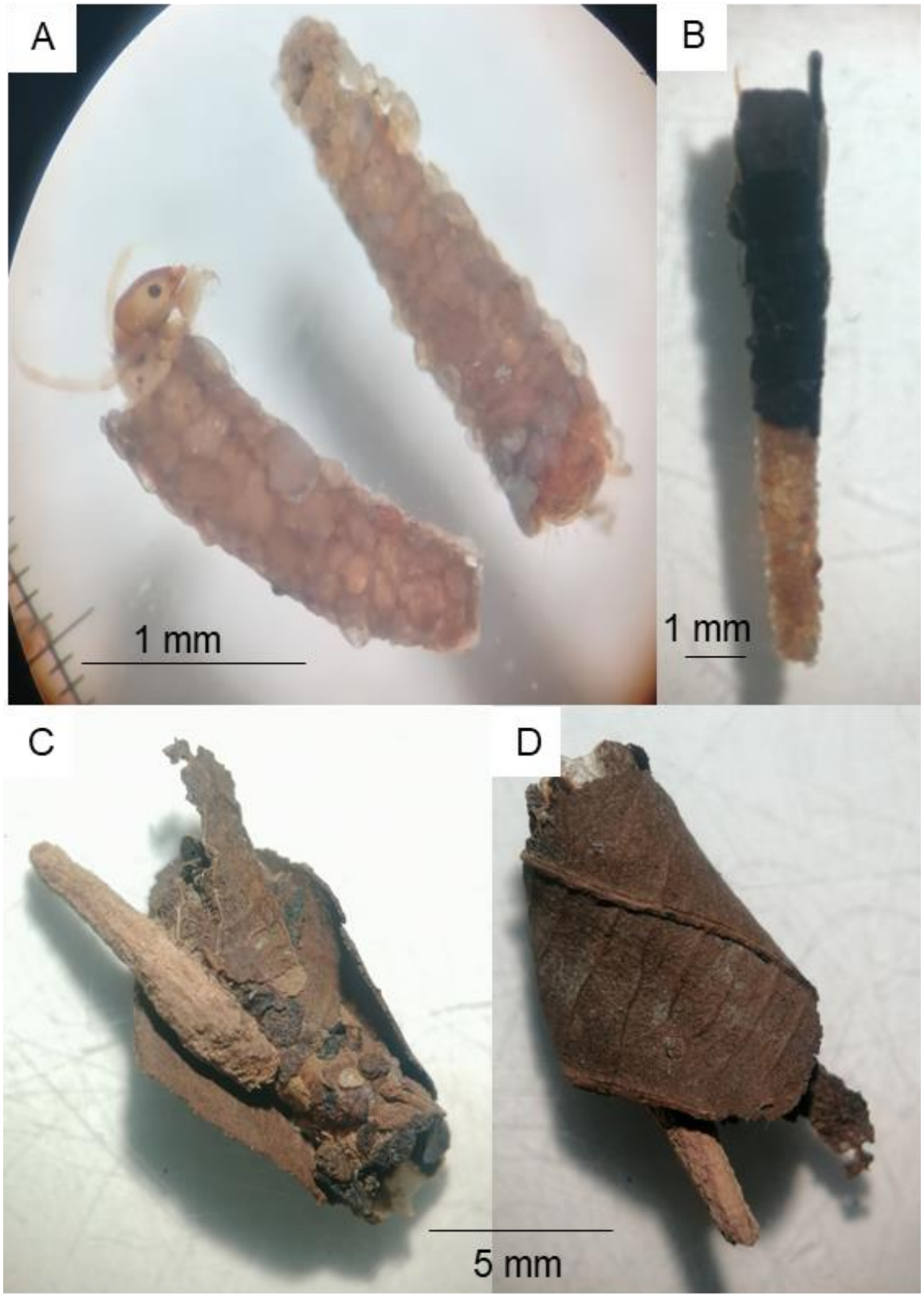


Figure 6.3. Further examples of case construction architecture by tubular case-building caddisfly larvae. (A) Cases of early instar *Athripsodes* sp. (Leptoceridae, left) and *Lepidostoma hirtum* (Lepidostomatidae, right) were the lightest cases recorded in Chapter 2 (mean mass = 0.001 g; Table 2.1). (B) Lepidostomatidae larvae transition from fine mineral grains to a square sectioned organic case. (C) Many organic cases were also found during the work for Chapter 5, particularly for early to mid instar Limnephilidae, ventral view (D) dorsal view of the same case.

6.4.2 Dome case-builders

Glossosomatidae (*Agapetus fuscipes*) were the most abundant taxa in the two field studies (mean density = 1805, max = 6710 larvae m^{-2}; Chapter 2). Glossosomatidae also used the most sediment, despite the mean mass of each case being relatively low (0.02 g; Chapter 2). *A. fuscipes* cases required more shear stress to move than cases of tubular caddisfly (Chapter 3), again despite their relatively low mass. The design of *A. fuscipes* cases is hypothesised to increase the hydraulic force required to entrain them, because their flat base increases friction with the substrate and hinders rolling, which is the main mechanism for transport of tubular cases (Chapter 3).

Glossosomatidae *A. fuscipes* were responsible for the upwards vertical displacement of sediment (Chapter 4), which opposes the geophysical processes partly responsible for bed armouring (downwards winnowing and infiltration of fine sediment). This increases the exposure of transported sediment, but the effect of this transport for sediment flux in rivers depends on the behaviour of larvae under high flows because they may be entrained, move to sheltered areas or fix their sediment to stable particles with silk. Unlike most tube-building taxa which only fix their cases prior to pupation, Glossosomatidae larvae may fix their cases earlier (Olden *et al.,* 2004). Furthermore, Glossosomatidae often fix their cases into hydraulically exposed locations, rather than under stones (as for many tube-case makers; Figure 6.1Ci). Even Glossosomatidae adults use and cement sediment in rivers, by collecting small capstones which are secured on top of egg masses, presumably to provide protection (Figure 6.3; Anderson, 1973). *A. fuscipes* display a preference for high flow velocities and therefore their sediment interactions have the potential to be particularly zoogeomorphologically important because they move sediment around on the surface and into more exposed areas. In Chapter 5 Glossosomatidae were responsible for 56% of caddisfly sand transport. Therefore, due to their behaviour and abundance, Glossosomatidae are particularly important zoogeomorphic engineers.

Figure 6.4. Glossosomatidae (believed to be *A. fuscipes*) attach their eggs to small gravel particles in the shallow margins of Black Brook (Chapter 5) and cover them with a capstone, fastened in place. Each female *A. fuscipes* larvae caps an average of six egg masses in this manner (Anderson, 1973). Whilst unlikely to have zoogeomorphic effects, this behaviour provides another example of the close-knit interactions between invertebrate life histories and fluvial geomorphology.

6.4.3 Pupal cases of net and retreat building and free-living taxa

This thesis has focused on case construction so has not looked at the sediment stabilisation effect of nets and retreats which are well documented (Johnson *et al.,* 2009). Net and retreat building and free-living taxa have been combined for this discussion because both only build a case for pupation purposes (Figure 1.3). Very few pupal cases of these taxa were recorded in Wood Brook, but they were by far the heaviest cases found (mean mass = 0.83 g; Table 2.1). The caddisfly families Rhyacophilidae and Hydropsychidae, combined accounted for 15% of overall sediment use by mass (Figure 2.3). Pupal cases of these taxa also expanded the size range of sediment used by caddisfly into the fine gravel size range (mean D_{50} = 4 mm; Table 2.1).

Statzner, (2012) suggest that pupal cases of *Hydropsyche siltalai* fixed between cobbles decrease the entrainment of the fine gravel incorporated in the cases and the cobbles themselves (Figure 6.4). Therefore, net and retreat building and free-living taxa are primarily sediment stabilisers. In situations where these species are abundant (Statzner, 2011 found 250 *H. siltalai* larvae per m^{-2}) they are likely to stabilise considerable mass of fine gravel, as well as the larger particles to which these pupal cases are fixed.

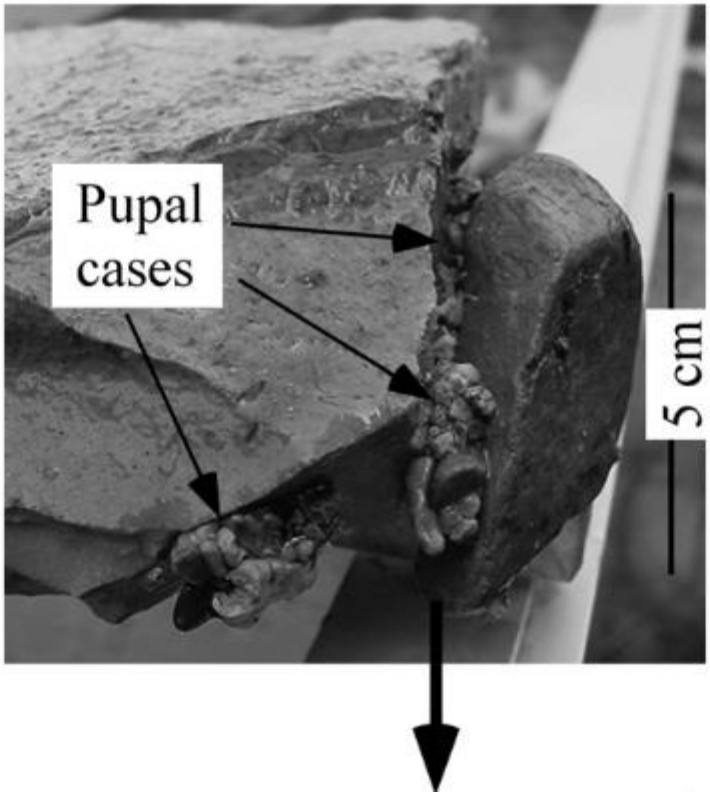


Figure 6.5. Sediment stabilisation by pupal cases of *Hydropsyche siltalai* (Hydropsychidae). Reproduced from Statzner (2012). These cases increase the entrainment thresholds of 1) the fine incorporated into cases, and 2) the ~5 cm diameter gravel particle secured to the much larger clast (and may also reduce the mobility of the larger stone).

Case-building caddisfly may therefore both destabilise and stabilise sediment, based on the case architecture and life stage. Therefore, the zoogeomorphic consequences of case-building caddisfly depend on the net effect of these potentially conflicting processes (Figure 6.1). If transport and stabilisation occur simultaneously, the net effect could be limited. However, if they are separated in space, time, or by the size of sediment affected, the impact could be large. The effects of stabilising and destabilising zoogeomorphic mechanisms may be separated by the hydraulic energy under which they are important (Figure 6.6). Chapter 5 identified sediment transport via caddisfly bioturbation during low to medium flow periods. During the high discharge events which caused general sediment movement (April, Figure 5.3), caddisfly are unlikely to have had a substantial effect, relative to abiotic transport. In contrast, sediment stabilisation behaviours (net/retreat building or fixing of pupal cases) are only geomorphologically important at hydraulic forces above the original entrainment threshold of incorporated sediment (i.e. sediment would have been transported in the absence of caddisfly activities). The effects of sediment stabilisation persist until the hydraulic force overwhelms the silk structure or transports the larger sediment particles that cases are fixed to. Therefore, as a

community, caddisfly larvae may increase sediment mobility under low flows but decrease it under high flows (Figure 6.6).

Furthermore, there is also likely to be a seasonal transition from sediment destabilisation to stabilisation as many species pupate (and fix their sediment) in spring/summer. For example, Limnephilidae (largely *P. latipennis*) were responsible for about 60 – 70 % of caddisfly sediment transport in traps in April but this substantially declined by August to less than 30% (Figure 5.8), presumably due to pupation and anchoring of this sediment.

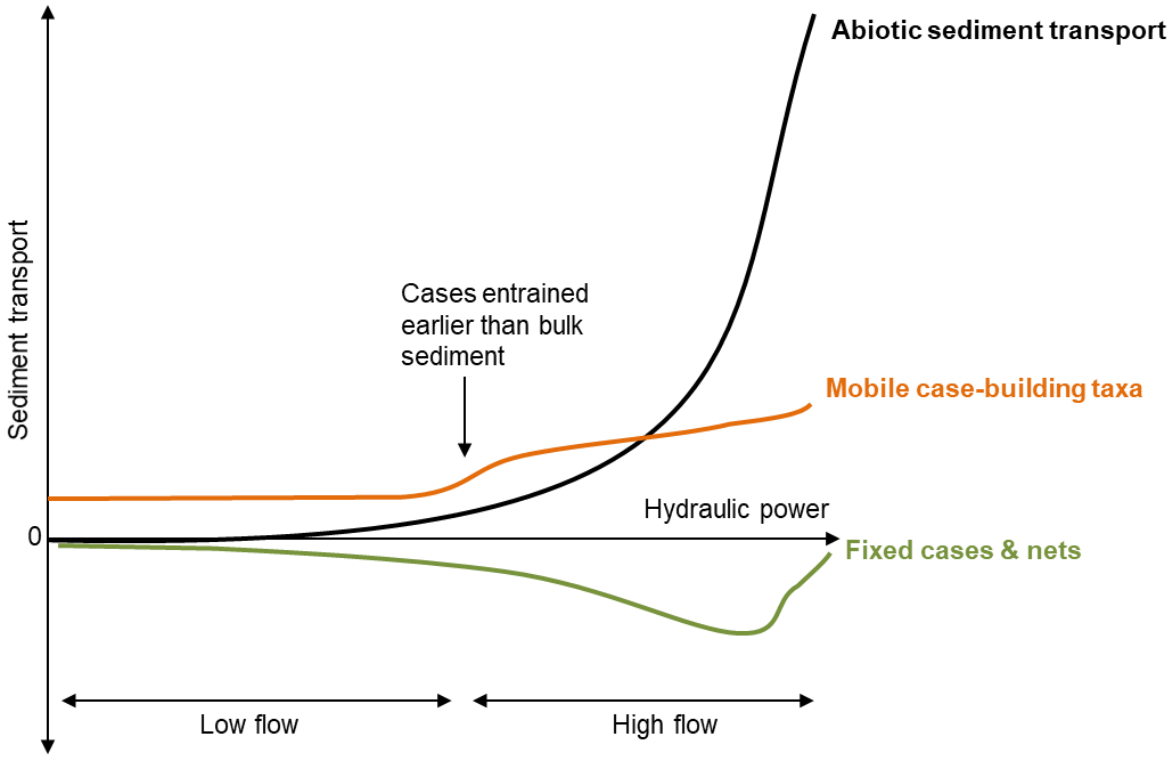


Figure 6.6. Hypothesised relationship between zoogeomorphic effects (sediment transport) of mobile case building taxa (destabilisation) and fixed cases and nets (stabilisation) with increasing hydraulic power, in gravel-bed rivers. Abiotic sediment transport increases non-linearly with hydraulic power. The stabilising influence of fixed cases and nets becomes important when the entrainment threshold reaches that of fixed sediment and reduces when hydraulic power is sufficient to break apart the stabilisation or entrain the larger particles which sediment is secured to. Mobile case-building caddisfly transport sediment even at the lowest discharges (which occur most of the time). With increasing hydraulic power cases are potentially mobilised earlier than the surrounding riverbed, but their importance in high flows is unknown but probably minimal (Chapter 5).

The zoogeomorphic effects of caddisfly may also be separated by the diameter of sediment affected. Caddisfly used a bimodal grain size distribution of sediment in Wood Brook with mobile case building caddisfly responsible for the mode at 1.4 mm and pupal cases of Rhyacophilidae and Hydropsychidae the mode at 5.6 mm was (Figure 2.3B). This is likely related to the need for mobile taxa to transport their cases whilst caddisfly which build their pupal cases

in situ, do not need to move grains very far (Statzner, 2011). Therefore, caddisfly taxa with different biogeomophic mechanisms could affect different sized grains, with nets and retreats stabilising the gravel framework (e.g. 11- 22 mm; Albertson *et al.,* 2014a), whilst pupal cases of these taxa and free living species stabilise smaller gravel particles (D_{50} = 4 mm; Table 2.1) and mobile case-builders destabilise predominantly coarse sand and fine gravel (D_{50} = 0.91 mm; Chapter 5), until pupation. Therefore, caddisfly may predominantly increase the mobility of sand, but reduce entrainment of gravel and cobbles.

Destabilising and stabilising effects could also be spatially discrete. At the river segment scale (Figure 6.7), predominantly case-building and net and retreat-building taxa may prefer different environments. However, many individual caddisfly taxa found to be important in this thesis change their case architecture with life stage (e.g. fixing cases for pupation) and therefore, it is likely that both bioturbation and biostabilisation occur at the same sites. Consequently, future research is required to consider the relative importance of stabilisation and destabilising zoogeomorphic effects of case-building caddisfly over spatial, temporal and environmental gradients.

6.5 Scaling up caddisfly zoogeomorphology and future research directions.

This thesis has considered the zoogeomorphic effects of caddisfly across a range of scales (Figure 6.7). At the scale of individual sediment grains, caddisfly construct cases that can increase sediment mobility (Chapter 3; grain scale Figure 6.7), but which can also reduce grain entrainment (Figure 6.5). At the microhabitat scale, case-building caddisfly redistribute grains vertically and horizontally, sometimes altering grain exposure to entrainment (Chapter 4). Furthermore, sediment use by caddisfly larvae varied considerably at the habitat patch scale (the smallest spatial scale investigated in Chapter 2). A flux of caddisfly sediment was documented at the pool/riffle and reach scales (Chapter 5). However, in common with the effects of other zoogeomorphic agents where effects can be identified and demonstrated at small scales (Rice *et al.,* 2019; Statzner, 2012), the zoogeomorphic effects of case-building caddisfly at larger spatial scales remain unknown (Figure 6.7).

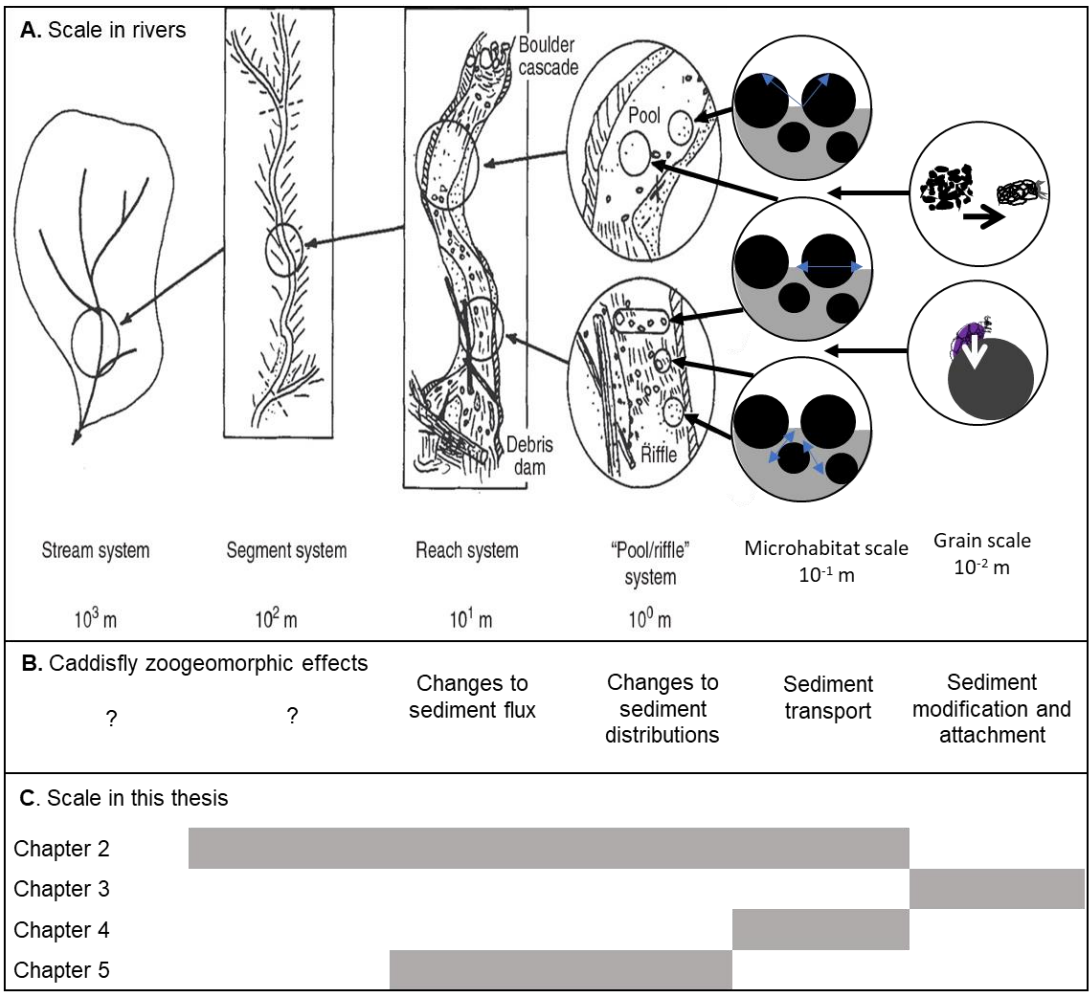


Figure 6.7. The role of spatial scale in this thesis and zoogeomorphology more broadly. (A) Scale in rivers, modified from Frissell *et al.* (1986). (B) The zoogeomorphic effects of case-building caddisfly at each scale. At larger spatial scales the effects are unknown. (C) The scale considered in each thesis chapter.

Case-building caddisfly are extremely widespread, found in all biogeographical regions except for the Antarctic (de Moor and Ivanov, 2008), often at high abundances (Morse *et al.,* 2019). Whilst the spatial distribution and abundance of caddisfly taxa are controlled by habitat characteristics (particularly flow velocity and bed sediment) and ecological processes such as dispersal and competition (Murphy and Davy-Bowker, 2005), the diversity of case-building caddisfly mean that taxa with similar case architecture to those found in this thesis are present in most lotic, lentic and even terrestrial habitats (Wallace *et al.,* 2003). It is therefore likely that the zoogeomorphic effects documented in this thesis are spatially widespread.

Similarly, Chapter 5 indicates that sediment transport by case-building caddisfly is not limited by season. Although the individual caddisfly taxa responsible changes (Figure 5.8B), zoogeomorphic effects continue over the entire year (Figure 5.4A). Furthermore, caddisfly cases may be long lasting constructions, surviving beyond pupation. Preliminary results from ongoing experiments

on caddisfly case decay indicate that unoccupied *A. fuscipes* cases fixed to the surface of bricks in rivers remain intact for several months in the absence of large-scale bed movement (Figure 6.8). Cases of *S. personatum* and *P. latipennis* are even more durable. The longevity of caddisfly cases is particularly high in areas with alkaline geology, where cases can become tufarised (Figure 6.9), further stabilising incorporated sediment. Therefore, the spatial and temporal scale of case-building caddisfly zoogeomorphological effects may be widespread and pervasive and long lasting; worthy of additional research.

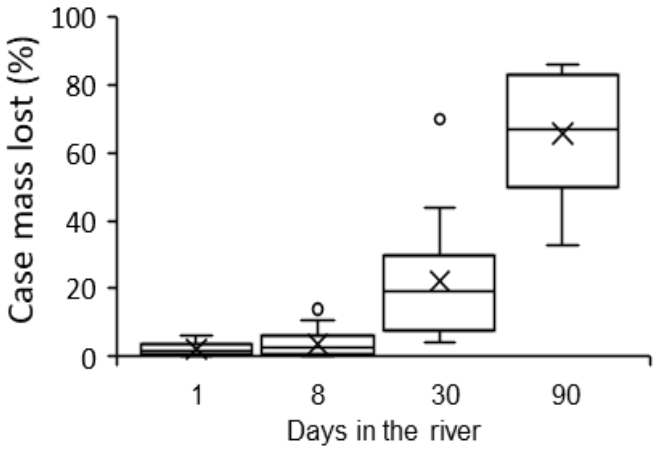


Figure 6.8. Caddisfly case longevity. Preliminary results from an ongoing experiment to understand how quickly Glossosomatidae *A. fuscipes* cases break down in rivers. Empty larval cases were either attached to bricks using glue to simulate silk or placed within mesh bags and protected from physical erosion. Initial results suggest that, in the absence of high discharge and bed movement, cases break down predominantly by biological or chemical processes rather than physical erosion. Furthermore, for the whole case to degrade usually takes more than 90 days.

Figure 6.9. Empty caddisfly cases from Little Stour River, Kent UK provide surfaces for calcium carbonate deposition.

Scale is a substantial challenge for biogeomorphological research (Naylor *et al.,* 2002). Fluvial processes propagate upstream and downstream (Ward, 1989), and therefore, fluvial geomorphology is typically considered at large spatial scales, from pool-riffle sequences to whole catchments. However, biogeomorphology must consider the behaviour of organisms, often in controlled environments, requiring work at much smaller scales. The focus of fluvial geomorphology on large scale processes may be one reason that zoogeomorphic research in rivers has chiefly been concerned with larger taxa, whilst understanding of the geomorphic importance of invertebrates comes largely from other disciplines (De Nadaï-Monoury *et al.,* 2013b; Mermillod-Blondin, 2011; Mermillod-Blondin and Lemoine, 2010; Savrda, 2019). However, consideration of multiple scales is essential for successful geomorphological research (Thoms and Parsons, 2002). For example, sediment transport at the reach or catchment scale is the result of numerous particle interactions at the grain scale. The challenge is therefore to build a zoogeomorphic framework which can integrate geomorphology and ecology across scales and allow for the complex mechanisms and geomorphic effects of different taxa.

Future research therefore needs to understand the relative importance of stabilisation and destabilisation effects of case-building caddisfly at larger scales. Upscaling the quantification of sediment transport by case-building caddisfly larvae could be done using pit traps as for Chapter 5, considering more rivers and isolating the zoogeomorphic effects of case-building caddisfly during high bedload transport events. To investigate potential stabilisation of sediment by pupating caddisfly might be relatively easy to achieve in the flume at small scales (*sensu.* Johnson *et al.,* 2009), but upscaling stabilisation effects in the field presents challenges. For example, it is difficult to quantify how much sediment would have been transported without caddisfly activity. The largest spatial scale caddisfly stabilisation experiment to date was conducted by Albertson *et al.* (2019) in 50 m^2 semi-natural outdoor river channels, facilities which are rare and would make the necessary spatial and temporal timescales prohibitively expensive. Mobile flumes which can manipulate water velocities over patches of river-bed in the field may provide the best mechanisms for upscaling the results of this thesis. For example, whether *A. fuscipes* increase the entrainment of sediment by moving it to more exposed locations (Chapter 4) could be determined by manipulating discharge above patches of river bed and measuring whether caddisfly cases or bed sediment moves first. The scale could be increased by undertaking these experiments at nested spatial scales (*sensu.* Chapter 2) and at various intervals over time (*sensu* Chapter 5).

Upscaling zoogeomorphic research via statistics and modelling should proceed with caution. There is likely to be some intrinsic bias upscaling from small-scale flume and field experiments because the latter are deliberately conducted at the spatial and temporal scales over which the zoogeomorphic effect in question is suspected to be important. For example, Chapter 4 evaluated the transport of sediment by *A. fuscipes* larvae at population densities equivalent to the average in Wood Brook (Chapter 2). However, densities in Wood Brook varied from 30 to 6710 larvae m^{-2} and therefore their zoogeomorphic effects are also considerably more variable than considered in Chapter 4. A related challenge is intra-specific variability. Both field chapters indicated that *A. fuscipes* case mass varied considerably in space (Figure 2.5) and even at the same site (Figure 5.13). Therefore, more research is required to assess the difference in biogeomophic effects between individuals of the same species. These effects are rarely considered, with researchers typically focusing on the largest (as in Chapter 4) or average-sized animals (Albertson and Allen, 2015).

6.6 Implications for river geomorphology and ecology

Case-building caddisfly affect the transport and distribution of coarse sand and fine gravel in rivers. Whilst it is unknown whether case-building caddisfly significantly modify total sediment flux over larger spatial and temporal scales and they are unlikely to affect large scale landform development, they may nevertheless, have equally important smaller scale effects on fluvial geomorphology and ecology (Figure 6.7). The potential geomorphological implications of caddisfly sediment engineering are discussed in more detail in Chapters 2-4, but a summary and additional ecological effects are proposed here.

Sand transport; Case building caddisfly transport sand during low to medium discharge conditions (Chapter 5). Although the magnitude of sand transported during high discharge events is unknown it is unlikely that caddisfly significantly affect the total sediment flux of Black Brook. However, caddisfly may increase the transport of coarse sand size fractions, changing the grain size distribution of the sediment flux.

Gravel transport; Changes to fine sediment distributions are also important for the transport of coarser, gravel particles. As the proportion of sand increases over 30%, riverbeds become dominated by the sand matrix which may partially bury gravel particles, reducing their exposure to entraining flows. However, the fine sediment reduces the roughness of the bed surface meaning that, if gravels are entrained, they may travel further (overpassing; Carling, 1990; Isla, 1993). Therefore, the sand fraction in gravel-bed rivers can also promote or inhibit the transport of larger gravel clasts, depending on fine sediment proportion (Grams *et al.,* 2007; Venditti *et al.,* 2010; Wilcock *et al.,* 2001). Statzner (2012) estimated that stonefly bioturbating and removing fine sediment from interstices could increase cobble critical entrainment thresholds by 50% (following Wilcox & Kenworthy, 2002). Therefore, it is likely that by creating agglomerate particles from sand (Chapter 3), case-building caddisfly affect the interaction between sand and gravel fractions in rivers and the subsequent transport of both sediment size fractions.

Colmation; Clogging of gravel-bed pore spaces with fine sediment is a widespread problem in rivers (Waters, 1995; Wharton *et al.,* 2017). Colmation reduces the porosity and flow connectivity of substrates and can disconnect riverbed surfaces from subsurface (hyporheic) habitats with negative consequences for biodiversity (Descloux *et al.,* 2013). Bioturbation by fish, crayfish and invertebrates can promote decolmation (Mermillod-Blondin, 2011; Nogaro *et al.,* 2006; Wharton *et al.,* 2017). It is likely that caddisfly also promote decolmation by moving substantial amounts of sediment over the bed surface. The upwards vertical transport of sand by Glossosomatidae larvae (Chapter 4) for example, will reduce the sand content of interstices. Furthermore, locomotive activity of case-building caddisfly will disturb fine sediment on the surface, reducing compaction and potentially increasing entrainment of these size fractions (*sensu*. Statzner, 1996).

Particle surface roughness; Caddisfly cases in exposed locations may change microscale hydraulics and facilitate habitation of these environments by other taxa. Glossosomatidae, in particular, usually inhabit exposed locations where they may add to flow resistance by increasing the roughness of otherwise smooth gravel particles. For example, Poff and Ward (1988) found that *Baetis* sp. (Baetidae Mayfly) nymphs occurred in and on occupied G*lossosoma verdona* (Glossosomatidae) cases in greater abundance than on rock surfaces without these cases. Furthermore, McCabe and Gotelli, (2003) found that aggregations of *Brachycentrus* (Brachycentridae) and *Neophylax* (Thremmatidae) pupal cases increased the species richness of macroinvertebrates 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 construction of a fixed case.

Zoochory; One further result of this thesis was the observation of seeds incorporated into the cases of caddisfly in the sediment traps in Chapter 5 (Figure 6.9). Seeds were mostly incorporated by Limnephilidae larvae (largely *P. Latipennis*). A wide range of seeds types were found. Some of the seeds are believed to be *Rubus* (blackberry; Figure 6.9E) and *Sambacus* (Elderflower; Figure 6.9G). This is the first recorded instance of seed use by caddisfly larvae in case construction. This could be important because *Potamophylax* larvae could disperse seeds (zoochory) within streams. Caddisfly larvae transport could be one of relatively few methods by which seeds could move upstream in rivers. It is unknown whether the seeds were viable as the cases were preserved in formaldehyde. Bio-transportation in caddisfly cases could also be important for other materials such as pollutants, including plastics (Ehlers *et al.,* 2019).

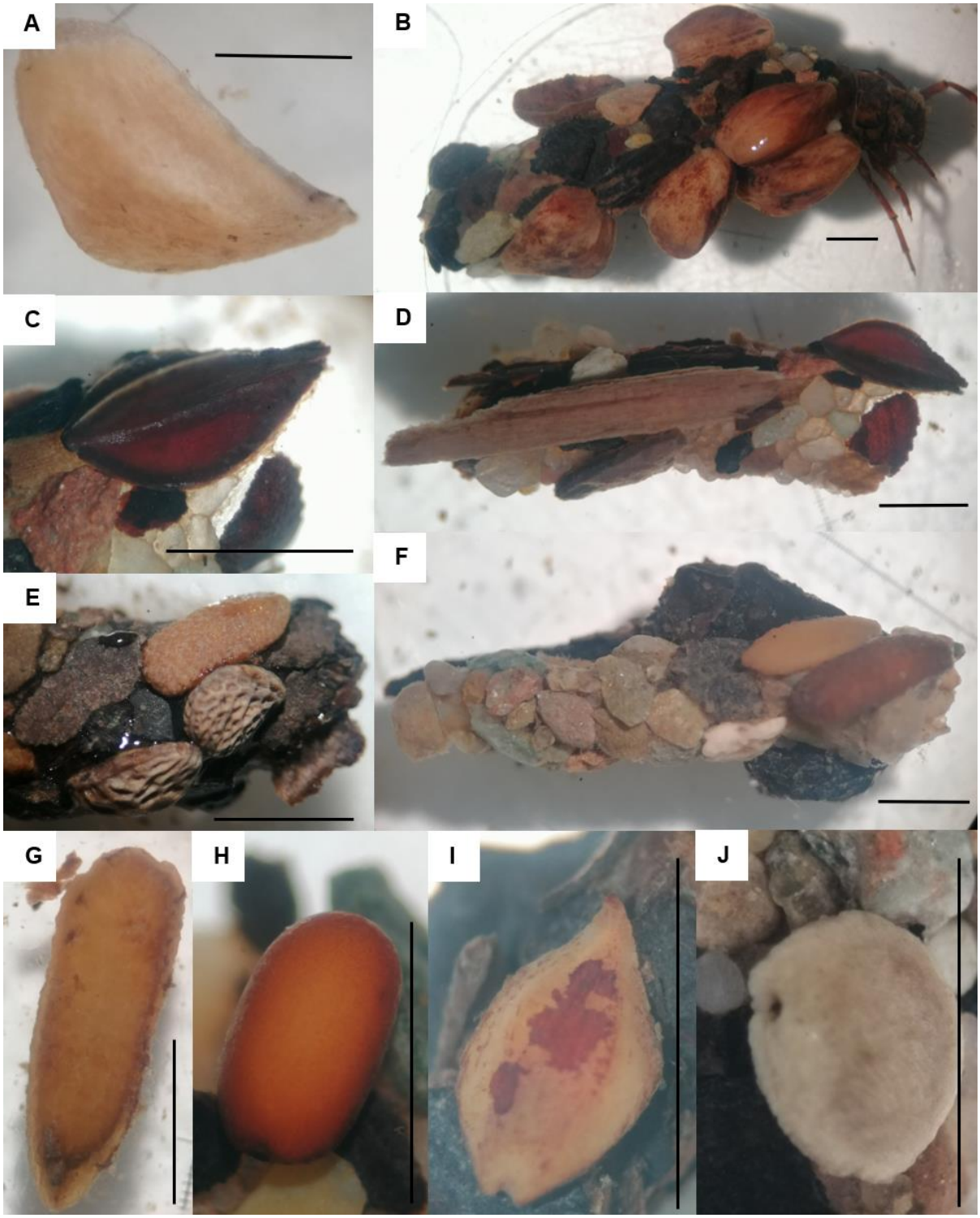


Figure 6.10. Examples of seeds in caddisfly cases observed in samples collected for Chapter 5. Several morphologically distinct seed types were found. Seeds of type G were the most common and were often used by caddisfly whose cases were otherwise largely mineral. Seeds were also used in strategic locations, such as along the sides of cases as in B. Caddisfly may disperse seeds within riverbeds and potentially allow plants to colonise upstream locations. Scale bar indicates approximately 2 mm.

6.7 Concluding remarks

At the beginning of this PhD research the effects of case-building caddisfly on sediment distribution and transport in rivers were unknown. This thesis has demonstrated via flume and field studies at a range of spatial and temporal scales that case-building caddisfly affect the distribution and transport of sediment within gravel-bed rivers.

Case construction by caddisfly larvae resulted in composite particles, which for tubular case-building species, reduced the hydraulic force required to mobilise incorporated sediment. Case-building caddisfly also transported sediment over the riverbed via crawling and entrainment. As a result of these processes, case-building caddisfly contributed substantially to the transport of coarse sand in low to medium discharge conditions. The zoogeomorphic effects of caddisfly were variable between case architecture types, species and even-within species.

Case-building caddisfly, with similar behaviours to those considered in this thesis are widespread, ubiquitous to rivers and zoogeomorphic effects are not limited to specific seasons. They therefore have the potential to be important zoogeomorphic taxa. Future research is required to understand these effects at larger spatial and temporal scales. The zoogeomorphic effects of case-building caddisfly may have implications for sediment transport and habitat provision in rivers.

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