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Stabilization of fine gravels by net-spinning caddisfly larvae

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Title:

**The influence of net-spinning caddisfly larvae on the
incipient motion of fine gravels: an experimental field and
laboratory flume investigation**

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Abstract

We examined the impact of Hydropsychidae caddisfly larvae on the incipient motion of two sizes of narrowly graded fine-gravel (4-6 and 6-8 mm). This impact was assessed relative to the collective impact of other abiotic and biotic processes that are potentially important conditioning agents of fine-gravels. Trays of gravel were placed in the River Soar, Leicestershire, UK, where they were colonised to natural densities by caddisfly larvae. Identical trays that were surrounded by a 250 µm mesh were also deployed, preventing colonisation but allowing field conditioning of sediments, including minor reworking of grains and biofilm development. After 21 days in the river, trays were removed to a laboratory flume where grain entrainment stresses were established. In addition to the colonised and conditioned treatments, critical shear stresses were measured for identical sediments that were not placed in the river (laboratory gravels). Gravels that were colonised by Hydropsychidae required significantly greater shear stresses for entrainment than conditioned trays ($p \leq 0.002$), however, there was no significant difference between conditioned and laboratory gravels. This implies that the presence of caddisfly can be a more important influence on fine-gravel stability than some conditioning processes. Shields parameter was compared across treatments and across the two gravel size-fractions using two-way ANOVA. No significant differences or interactions were observed, indicating that 4–6 mm gravel was stabilised to a similar degree as 6–8 mm gravel by conditioning and colonisation processes. Our results extend earlier studies in two important ways: (1) entrainment stresses were established for fine gravels that were colonised at natural densities, under natural stream conditions and (2) the caddisfly effect was measured relative to both field-conditioned and unconditioned laboratory controls. The temporal and spatial

distribution of silk-spinning caddisfly larvae suggests that they have the potential to influence fine-sediment mobility in many rivers, worldwide.

Key words: ecosystem engineering, Shields parameter, Hydropsychidae, entrainment threshold, biofilm.

Introduction

Organisms that modify and help to structure their physical habitat are referred to as ecosystem engineers (Jones *et al.*, 1994; Stallins, 2006). Many plants and animals engage in ecosystem engineering and their individual and cumulative activities can have substantial impacts on sediment fluxes and landform development (Viles, 1988; Butler, 1995; Dietrich & Perron, 2006), as well as on wider ecosystem structure and functioning (Moore, 2006). In rivers, a variety of plants and animals are known to be ecosystem engineers. The growth of instream and riparian vegetation can stabilise stream banks and benthic sediments, dramatically changing local sedimentological and hydraulic conditions (Green, 2005; Cotton *et al.*, 2006). Within productive lowland rivers, aquatic macrophytes (e.g., *Ranunculus* spp.) have been found to modify significantly instream hydraulic conditions, reducing flow velocity within individual stands and leading to fine sediment deposition of up to $0.085 \text{ m}^3 \text{ m}^{-2}$ in a single month (Wharton *et al.*, 2006). The creation of spawning redds by salmonid fish removes fine sediment from the surface layers of the substrate, changing the local bed material grain-size distribution (Kondolf *et al.*, 1993; Moore *et al.*, 2004) and, at popular spawning sites, redd construction can substantially affect vertical sediment sorting, armour development and bedload flux (Gottesfeld *et al.*, 2004). The foraging activities of other fish species may have significant cumulative impacts on the presence of macrophyte and local substratum composition (Power, 1990; Flecker, 1996; Statzner *et al.*, 2003b). Mammals such as beavers also affect river morphology by constructing dams that alter flow and sedimentation patterns (Gurnell, 1998) and beaver ponds are estimated to trap between 10^8 and 10^{10} m^3 of sediment in North America alone (Butler & Malanson, 2005). In addition, the trampling of channel margins by domestic

livestock, particularly cattle, reduces bank strength and is a well-known cause of channel widening (Trimble & Mendel, 1995).

Despite their comparatively small size, aquatic macroinvertebrates also have significant impacts on their physical environment by removing fine sediments from interstitial spaces (Pringle *et al.*, 1993; Zanetell & Peckarsky, 1996; Parkyn *et al.*, 1997; Statzner *et al.*, 2003a), modifying local hydraulic conditions (Thomson *et al.*, 2004) and increasing the porosity and permeability of bed sediments (Mermillod-Blondin *et al.*, 2003; Nogoro *et al.*, 2006). In addition, some silk-producing, caseless, caddisfly larvae can stabilise bed sediments in the 2-8 mm size range (Cardinale *et al.*, 2004) by constructing silk nets for feeding galleries (Alstad, 1987a; 1987b; Statzner & Bretschko, 1998; Edler & Georgian, 2004; Brown *et al.*, 2005) and retreats (Statzner *et al.*, 1999). The silk binds fine sediment together thereby increasing critical entrainment stresses. This engineering activity benefits the individuals involved by providing stable feeding sites, but, potentially, it has ecological benefits for the wider community because patches of stable bed material can act as refugia from hydraulic disturbance (Winterbottom *et al.*, 1991; Lancaster & Hildrew, 1993; Lancaster, 2000). Moreover, the ecological engineering activities of these organisms may add to the complex set of interacting factors that are known to affect particle entrainment from non-cohesive river beds, including grain size, density and shape, particle protrusion and the geometric arrangement of surrounding grains (e.g. Fenton and Abbott, 1977; Komar and Li, 1986; Carling *et al.*, 1992; Buffington & Montgomery, 1997).

Experimental investigations using artificial channels (0.1 m wide, 0.1 m deep and 1.0 m long) have demonstrated that the presence of caddisfly larvae from the family Hydropsychidae can increase particle stability (Cardinale *et al.*, 2004). In these experiments, caddisfly were seeded at particular densities onto clean gravels that were

unaffected by other natural, in-stream, processes that might also reduce particle stability: for example, natural flow variations that organise bed materials into more or less stable configurations and the presence of natural biofilms and periphyton. Statzner *et al.* (1999) attempted to examine the influence of caddisfly on entrainment in natural settings, but interpretation of their results was complicated by flood disturbance during the experiment. Takao *et al.* (2007) found that filter-feeding caddisfly biomass was correlated to clast stability; however, this does not imply that these clasts had been engineered, because filter-feeding caddisfly are known to live preferentially in stable areas due to their sedentary life style.

Aims

To extend understanding of the role of silk-producing caddisflies (from the family Hydropsychidae) on particle entrainment, this study compares thresholds of incipient motion for colonised and river-conditioned but uncolonised sediments using combined field and laboratory flume experiments. In contrast to previous work, we examine the incipient motion of fine-gravel substrates that have been colonised to natural densities, without isolating the animals from those abiotic and biotic interactions inherent in field environments that may influence engineering potential (Moore, 2006; Statzner and Sagnes, 2008). We are able, therefore, to examine the caddisfly impact relative to the collective effects of some other ambient, abiotic and biotic processes that are potentially important conditioning agents of fine-gravel entrainment.

There is an expectation that coarse gravel entrainment is not affected by caddisfly silk because the influence of particle weight is thought to be over-riding as grain size increases. However, the lower grain-size limit of this effect is unknown. We examine, therefore, the

entrainment of two size fractions of fine gravel (4-6 and 6-8 mm) in order to evaluate whether caddisfly impact is grain size-dependent. Within our general aim of quantifying the degree to which silk producing caddisflies (Hydropsychidae) stabilise fine-gravel bed materials, we test the following specific hypotheses:

1. Fine-gravel patches colonised by Hydropsychidae larvae require higher shear stresses for entrainment than uncolonised gravels of the same size that are conditioned by natural, instream biotic and abiotic processes.
2. Fine-gravel patches not colonised by Hydropsychidae, but conditioned by natural biotic and abiotic processes, require higher shear stresses for entrainment than clean laboratory gravels of the same size.
3. As gravel size increases in a narrow range from 4 to 8mm, the relative differences between entrainment stresses for these three treatment groups declines due to the increasing importance of particle inertia.

Methods

Overview

To test these hypotheses, a combined field and flume investigation has been undertaken. Trays of narrowly graded sediments (4-6 mm and 6-8 mm) were placed in a local river where caddisfly larvae from the family Hydropsychidae are abundant. Some trays were left open to allow colonisation (dubbed “colonisation” trays) and an equal number were

covered with 250 μm mesh to prevent colonisation but allow other influences and processes (“conditioned” trays). After 21 days, these trays were carefully removed from the field site and placed in a laboratory flume where the shear stress required to mobilise the sediment in each tray was measured through assessment of the near-bed flow velocity profile. In the field, both sets of trays were subject to several processes that might condition sediment entrainment (in addition to the caddisfly effect in the case of the colonised trays), including biofilm development and small-scale sediment reworking under low-flow conditions. To assess the collective role of these conditioning factors, entrainment stresses were also established for a third set of “laboratory” trays that contained the same sediment mixtures but that were not placed in the river. Comparisons of the entrainment stresses for the colonisation versus conditioned and conditioned versus laboratory trays provide tests of hypotheses 1 and 2. Comparison of these results for the 4–6 and 6–8 mm gravels provides a test for hypothesis 3. A fourth set of open, “enumeration” trays was placed in the river but not subjected to entrainment measurements. These provided information about colonisation densities of Hydropsychidae larvae and other benthic taxa and allowed qualitative evaluation of hydropsychid silk producing activity and other stream conditioning processes.

Sediment test trays

Twenty-four, rigid, moulded-plastic containers (0.19 m long, 0.14 m wide and 0.05 m deep) were filled with 4–6 mm gravel and twenty-four of the same ‘trays’ were filled with 6–8 mm gravel. For each grain-size fraction, six replicates were used for each experimental treatment (colonisation, conditioned, laboratory) and six additional trays were used for enumeration. All sides of all trays were perforated with 4 mm diameter holes to allow

colonisation laterally through the substrate as well as across the surface via drifting or crawling. The 250 μm mesh netting used to exclude Hydropsychidae larvae and other macroinvertebrates allowed colonisation by smaller invertebrates (meiofauna) but, because of their size and life-style, they are not thought to be a significant factor in the stability of gravels in this study.

Field Procedure

The colonisation, conditioned and enumeration trays were deployed on a large riffle in the River Soar, Leicestershire UK ($1^{\circ} 11.0' \text{ W}$, $52^{\circ} 46.8' \text{ N}$) for 21 days in July -August 2006. This period provided sufficient time for colonisation and is consistent with other investigations that consider substrate colonisation by benthic macroinvertebrates (Mackey, 1992; Cardinale *et al.*, 2002). The riffle has a relatively uniform geomorphic and hydraulic environment and supports high densities of several hydropsychid caddisfly larvae species (*Hydropsyche angustipennis* [Curtis, 1834], *H. contubernalis* [McLachlan, 1865] and *H. pellucidula* [Curtis, 1834]). The River Soar is a gravel-bed channel with a well-developed alluvial floodplain and a meandering planform. Average channel width at the study site is approximately 15 m and mean water depth during the study was approximately 0.5 m. The mean discharge at Pillings Lock, 3.5 km upstream and the closest gauging station to the field site, is $9.8 \text{ m}^3 \text{ s}^{-1}$ and the Q_{10} flow (that which is exceeded 10% of the time) is $22.0 \text{ m}^3 \text{ s}^{-1}$. Thirty-six trays were introduced to the river over a ten-day period in July 2006.

Deployment of trays was staggered so that entrainment measurements for a particular tray could be made in the flume on the same day that the tray was removed from the river. This was necessary to prevent the degradation of silk structures, biofilms and other biological

materials. The total field deployment lasted 34 days and during that period there were no major flow events. The mean daily discharge at Pillings Lock was $3.9 \text{ m}^3 \text{ s}^{-1}$, with daily averages ranging between 2.7 and 7.4 and a standard deviation for the period of $1.1 \text{ m}^3 \text{ s}^{-1}$. Although tray deployment was staggered, trays were inserted in triples (colonisation, conditioned, enumeration) so that the small variations in flow did not bias one particular treatment.

Small rectangular slots were excavated in the bed with minimal disturbance, so that the trays could be placed in the river with their surface conformable with that of the local bed material surface (Figure 1). Trays were distributed throughout the riffle in such a way as to avoid disturbance when retrieving trays. When removing the trays from the river and transporting them back to the laboratory, great care was taken not to disturb the sediments. A large deflector was placed in the river upstream of the trays to block the flow and prevent fine material and invertebrates from being washed out of the trays as they were removed from the river. The rigidity of the trays meant that there was minimal disturbance as they were lifted out of the river and returned to the laboratory.

Flume set-up and procedures

A tilting laboratory flume was used to determine entrainment thresholds. The flume has a 10 m working section that is 0.3 m wide, with parallel, glass walls. Depth, velocity and energy slope are controlled by adjusting flume gradient, the elevation of the outflow weir and pump discharge. Through the lower-central length of the flume, a false bed was constructed to a height of 0.05 m and this incorporated a cavity that allowed snug insertion

of the experimental trays. A ramp, 2.8 m upstream from the test site, linked the flume bed to the false bed over a distance of 0.3 m. To reproduce natural, near-bed flow conditions and ensure a fully developed boundary-layer, roughness was added to the flume bed, including the raised portion, in the form of rigid panels to which a complete, uniform covering of gravel particles (8-10 mm) was fixed using adhesive. Once in place, the lip of each experimental tray was flush with the rough surface on the false bed. The cavity accommodating the test trays was positioned 5.48 m down the flume from the inlet. Depth and velocity measurements in the test section showed the flow to be uniform and steady.

An initial set of observations, guided by prior competence calculations, was used to establish a flume set-up that generated shear stresses which were marginally insufficient to entrain clean gravel particles of either size fraction (slope = 0.001, water depth = 0.07 m, mean velocity = 0.43 m s^{-1}). By gradually increasing pump discharge, without changing the gradient and while maintaining constant water depth through adjustment of the tail weir, higher shear stresses eventually capable of entraining the test gravels were obtained.

Some of the colonised trays containing 4–6 mm gravel had experienced small amounts of scour during field deployment. This meant that when placed in the flume, the sediment surface in these trays was below the level of the false bed. This discordance could have generated hydraulic differences sufficient to affect the entrainment stresses that were measured. To assess this, we measured entrainment stresses for a fourth set of six trays containing clean 4–6 mm gravels which were first scoured in the flume to a depth that mimicked the observed field scour (up to 0.01 m). Comparison between the entrainment thresholds for these scoured trays and the standard laboratory trays provided a test of whether scour-generated discordance is likely to have affected the entrainment stresses measured for those colonised trays that had experienced scour.

Entrainment measurements and analysis

For each flume run, a single tray (colonised, conditioned, laboratory or scoured) was carefully fitted into the cavity in the raised bed. After 15 minutes of low flow, pump discharge was increased in stepped increments whilst maintaining a constant water depth and slope, to give successive flow stages. The mean velocity increased from 0.43 m s^{-1} to 0.84 m s^{-1} over 13 flow stages; each flow stage was maintained for 300 seconds.

Preliminary observations had indicated that initiation of grain movement was most likely to occur within this period.

Bed material entrainment is not easily correlated with gross hydraulic properties due to the heterogeneity of gravelly bed materials and the spatial and temporal variability of hydraulic forces impinging on the bed (Buffin-Bélanger *et al.*, 2006). Therefore, a single threshold of motion, although practicably desirable, is not easily determined or appropriate and it has been suggested that multiple thresholds (Wilcock & McArdell, 1993) or no specific threshold (Paintal, 1971; Newson, 1992) may be more realistic. The difficulty of identifying incipient motion is greater for sediment containing a range of grain sizes. This is the reason we have used two narrowly-graded grain-size fractions in our experiments.

In accordance with a large body of previous work on entrainment, we have utilised a pragmatic definition of entrainment threshold based on visual observation (Wilcock, 1988; Buffington and Montgomery, 1997). As flow strength was increased, entrainment began with small, occasional movements of isolated grains. However, in all our experimental runs, a step-change was clearly observed as flow was increased, whereby this occasional

single-grain movement was replaced by general movement of the majority of surface grains, mimicking direct observations made in the field, where the bed has been water-lain and naturally conditioned (Garcia *et al*, 2007). We used the start of this latter, widespread movement of grains as our definition of the entrainment threshold. Like many earlier studies, this direct, visual method does not depend on a formal flux criterion (Neill and Yalin, 1969; Wilcock, 1988). In order to ensure consistency of judgement, a single operator (MFJ) assigned all entrainment thresholds. Such a method is considered particularly appropriate when applied to discrete textural patches like those used in this study (Buffington & Montgomery, 1997).

When the entrainment threshold was reached in each case, a detailed velocity profile was obtained 0.02 m upstream of the tray. A Nixon propeller flow meter (impeller diameter = 10 mm) was used to obtain mean streamwise velocity over 30-second periods at 0.01 m depth increments throughout the flow depth. Once the measurements were completed, the flume was drained slowly and the tray was carefully removed and photographed.

The critical bed shear stress at incipient motion τ_{ci} for grain size D_i , was estimated from the observed velocity profiles according to the law of the wall as:

$$\tau_{ci} = \rho v^{*2} \quad (1)$$

where ρ is water density ($= 1000 \text{ kg m}^{-3}$) and v^* is shear velocity. Shear velocity was estimated from:

$$v^* = c/b \quad (2)$$

where $c = 2.5$ and is the reciprocal of the von Karman constant for clear water flows, $\kappa = 0.41$, and the parameter b is the slope of a linear least-squares regression of velocity (m s^{-1}) on the logarithm of depth (m) in the measured profile (R^2 values ranging from 0.919 – 0.993). To enable direct comparison of the stresses required to entrain 4–6 mm and 6–8 mm sediments, the dimensionless Shields parameter (θ_{ci}) was also calculated for each case as:

$$\theta_{ci} = \tau_{ci} / (\rho_s - \rho) / g D_i \quad (3)$$

where τ_{ci} is the shear stress at incipient motion for grain size D_i , g is the acceleration due to gravity ($= 9.81 \text{ m s}^{-2}$) and ρ_s is sediment density ($= 2650 \text{ kg m}^{-3}$).

The entrainment thresholds relating to tray treatments were compared using paired t-tests (independent) and a two-way analysis of variance (ANOVA), with particle size (4–6 mm and 6–8 mm) and treatment (colonised, conditioned and laboratory) as the fixed factors.

Enumeration Trays

Upon removal from the field, trays intended to enumerate macroinvertebrates and silk structures were preserved in 70% industrial methylated spirit (IMS) until analysis. Analysis involved detailed inspection and photography of the sediment surface for evidence of Hydropsychidae larvae silk structures. Subsequently, the trays were dissected and Hydropsychidae larvae counted and identified to species level. Other macroinvertebrate taxa present in the trays were recorded and enumerated. Grain-size distributions of the sediment that was recovered in the enumeration trays were obtained by standard sieving techniques.

Results

Macroinvertebrate colonisation and silk constructions

The total abundance of macroinvertebrates recorded in each set of six enumeration trays ranged between 1240 and 4737 m⁻² for the 4–6 mm gravel and 1842 and 3797 m⁻² for the 6–8 mm gravel. Mean abundance values were not significantly different between the two grain sizes ($t = -0.373$, $p = 0.724$, $n = 6$). Hydropsychid caddisfly larvae and their silk constructions were recorded in all enumeration trays but were present in greater numbers in those with 6–8 mm gravel. Hydropsychidae larvae comprised 21% (4-50%) of the total macroinvertebrates recorded, with three species being represented: *Hydropsyche angustipennis* [Curtis, 1834], *H. contubernalis* [McLachlan, 1865] and *H. pellucidula* [Curtis, 1834]. *H. contubernalis* was the most abundant, comprising 71% of all hydropsychids, followed by *H. pellucidula* (12%) and *H. angustipennis* (10%). Dissection of the preserved enumeration trays indicated that retreats were constructed by tying together approximately six to seven clasts in the 4–6 mm trays, whereas, in the 6–8 mm colonisation trays, retreats were predominately constructed from only two or three clasts. Caddisfly nets were mainly found anchored to coarser particles or to the edges of the tray (Figure 5). A greater abundance of nets was found in the 6–8 mm trays, but nets were less common than retreats in all trays.

Evidence of other conditioning processes

No evidence of macroinvertebrate colonisation was found in the conditioned trays (those covered in netting whilst in the field). However, both the field-conditioned and the colonised trays were affected by other natural conditioning processes that may have affected the entrainment thresholds of the fine gravels.

First, the discharge during field deployment induced bedload within the riffle. Sediment mobility was evidenced by the deposition of thin, superficial patches of fine sediment (predominantly medium–coarse sand) in colonised trays as well as the occasional larger clast (Figure 1). Sediment in the trays underwent low-flow reworking that may have increased grain stability (cf. Carling *et al.*, 1992). In addition, some test grains were eroded from the trays (Figure 1) and there was minor scouring, as described above. In addition, from an initially random fabric, the test gravels became bedded down, such that the grains interlocked and presented a more compact surface, without conspicuously proud grains.

Second, patches of algae (biofilms) grew on the surface clasts, developing in association with the fine sediment deposited in the trays. There is a lack of clear information regarding the impact of biofilms on the entrainment of non-cohesive sediments in riverine settings. However, they are known to influence the stability of cohesive sediments (Gerbersdorf *et al.*, 2008) and it is probable, therefore, that they increased stability via envelopment and agglutination of individual grains (Heinzelmann and Wallisch, 1991; Naylor and Viles, 2002).

The changes in grain size characteristics in the field-deployed trays requires further consideration in the context of the impacts of those changes on the subsequent experimental treatments. That fine sediment was added to most trays is of little consequence because the

thin patches of sand were removed at low flow stage during entrainment tests in the flume. However, the deposition of larger particles of up to 22 mm was restricted to the colonised trays because the netting excluded them from the conditioned trays. We did not remove these clasts prior to the entrainment tests because of concern that this might disrupt silk bonds and destabilise the test grains. However, we were careful to observe that there were no obvious effects on entrainment during the experimental runs. This is likely to be because these clasts were rare (between 4 and 10 particles, representing 3 to 6 % of the surface area). We were able to estimate the likely changes in grain size within the colonised trays by measuring those that occurred within the twelve enumeration trays, where post-deployment sieve analysis provided volume-by-weight grain-size distributions. The original test gravels dominated the final content, constituting an average of 82% (standard deviation 2%, n=12); the percentage of imported coarser grains was approximately 10% (Table 1).

Critical entrainment shear stresses

Greater shear stresses were required to entrain fine gravel of both sediment sizes from the colonised trays than from both the uncolonised, conditioned trays and the laboratory trays (Figure 2). The critical shear stress for entrainment of 4–6 mm gravels from colonised trays was 35% greater than that for conditioned trays and 38% greater than that required to entrain grains within the laboratory trays (Figure 2a). The equivalent figures for 6–8mm gravels were 23% and 31%, respectively (Figure 2b). The difference in critical entrainment stress between colonised and conditioned trays was significant for both 4–6 mm ($t = 8.186$, $p = 0.000$, $n = 6$) and 6–8 mm sediments ($t = 6.027$, $p = 0.002$, $n = 6$).

Interestingly, the difference in critical shear stress between the conditioned and laboratory trays was not significant for either the 4–6 mm ($t = 1.206$, $p = 0.282$, $n = 6$) or 6–8 mm ($t = 1.801$, $p = 0.132$, $n = 6$) test sediments (Figures 3a and 3b).

There was also no significant difference in the shear stress required to entrain 4–6 mm gravels from trays mimicking scour and the laboratory trays ($t = -0.248$, $p = 0.814$, $n = 6$), suggesting that scour of some colonised trays is unlikely to have affected measured entrainment stresses. This result is supported by the observation that entrainment thresholds were very consistent between colonised trays of 4–6 mm gravel despite varying amounts of scour (of between 0 and 0.01 m; Figure 2).

Shields parameter

The Shields parameter was calculated so that comparisons could be drawn between the two grain-size fractions when determining if hydropsychid silk preferentially stabilises the finer gravel fraction (4–6mm). A two-way ANOVA shows that differences in the mean Shields parameter between tray treatments were significant ($F = 88.969$, $p = <0.001$), while Tukey's post-hoc multiple comparison indicates that the colonised trays were significantly different from the other treatments ($p = <0.001$). There was not, however, a significant difference in the Shields parameter between the two grain-sizes ($F = 0.954$, $p = 0.336$) and no significant interaction between the two factors (treatment and grain size) occurred ($F = 1.870$, $p = 0.172$). This suggests that 4–6 mm gravels were stabilised to a similar degree as corresponding 6–8 mm gravel by conditioning and colonisation processes (Figure 4).

Discussion

Fine gravel in the colonised trays required significantly higher forces before entrainment than either field conditioned but uncolonised or unconditioned laboratory gravels. Our results lead us, therefore, to accept hypothesis 1 and to conclude that the presence of Hydropsychidae caddisflies increases the critical shear stress. Evidence of Hydropsychidae larvae silk was found in all enumeration trays and was observed to be an effective stabilising agent both in the field and flume. The threshold of incipient motion for the sediment in the conditioned trays was not significantly different from that of sediment in the laboratory trays that were not subject to river conditioning. Therefore, we reject hypothesis 2 and conclude that the sediment reworking and biofilm development observed in the field had no measurable effect on the stability of the fine gravel under test. Counter to hypothesis 3, the 4–6 and 6–8 mm gravels were stabilised to a similar degree and we conclude that, for this marginal but significant difference in grain size, there is no demonstrable impact of Hydropsychidae caddisflies: both grain-size fractions experienced similar increases in the dimensionless threshold of incipient motion.

In general, these results support the findings of earlier work (Statzner *et al.*, 1999; Cardinale *et al.*, 2004), but they also extend that work in two important ways: we have established elevated thresholds of incipient motion for fine gravels that have been colonised at *natural* densities and under *natural* stream conditions; and we have measured caddisfly impact relative to both laboratory *and* field-conditioned controls.

Natural colonisation densities and the impact of Hydropsychidae as ecosystem engineers

Likely controls on the importance of ecosystem engineering include biological interactions such as competition and predation (Statzner & Peltret, 2006; and Statzner & Sagnes, 2008) as well as the body size and behaviour of individuals (Moore, 2006). Although we have not examined such additive effects (cf. Statzner and Sagnes, 2008), the use of natural field sites at least provided scope for unfettered interaction between organisms, not least in terms of natural colonisation densities: Hydropsychidae larvae numbers presumably reflect local competition and other biological and physical factors. In their flume experiment, Cardinale *et al.* (2004) also found that the presence of these organisms increased bed-grain stability, but their seeded densities were much higher than those in the current study. At their “low” hydropsychid density (904 larvae m⁻² remaining after experiment), the substrate required a 10% increase in velocity before entrainment. At their highest density (2542 larvae m⁻² remaining after the experiment) this increase rose to 30%. Our colonisation densities were only 113–564 larvae m⁻² for 4–6 mm sediment and 489–1053 larvae m⁻² for 6–8 mm sediment, but the impact on entrainment was still highly significant. This implies that high densities of hydropsychids are not required to increase the threshold of incipient motion.

That low densities of caddisflies are able to reduce grain entrainment from relatively unstable patches of fine gravel is interesting when it is considered that the highest densities of these larvae are typically found on large, stable particles. Stable locations with high densities are relatively safe but competition for food, space and other resources is relatively high. It may be the case that, on finer-grained patches, the engineering activities of these larvae are sufficient to substantially offset the apparent disadvantage of living on an

unstable substrate and, indeed, offer comparable benefit overall, given the greater abundance of food and individual space relative to more stable, but densely occupied sites.

In any case, the stabilisation of these otherwise unattractive locations by relatively low numbers of larvae illustrates the fundamental importance of ecosystem engineering activity, i.e. the creation of a habitat that would not otherwise be available (cf. Gutiérrez *et al.*, 2003). The presence of caddisfly silk would not be significant on substrates which are already stable enough to support high densities of macroinvertebrates. However, the stabilisation of bed grains benefits the sedentary lifestyle of this organism and other macroinvertebrates.

The relative importance of Hydropsychidae larvae and other conditioning factors

The similarity of the entrainment stresses in the field-conditioned but uncolonised and laboratory trays is interesting and unexpected. It implies that exposure to several potentially important stabilising mechanisms (other than Hydropsychidae larvae silk) had no significant effects on the trays of sediment deployed in the river. These include: (1) exposure of the unstructured gravels to twenty-one days of natural flows with daily discharges that varied between 2.7 and 7.4 m³ s⁻¹; and (2) the development of algal biofilm. Many studies have argued that, after a flood event when the bed is relatively loose, low-flow conditions organise the substrate by moving vulnerable grains and arranging the surface particles into a more flow resistant pattern (e.g. Carling *et al.*, 1992; Wilcock & McArdell, 1993). Although low-flow reworking of sediment was observed in this study, the

uniform size of each fine gravel used probably limited the impact on grain stability of any reworking. It is possible that experiments utilising larger ranges of grain-size would have let us find a larger difference between entrainment stresses between field-conditioned and laboratory trays.

Biofilm development was also found to have no impact in this study. There is no evidence that by covering and by bonding together surface grains, biofilm offer protection from the flow and increased entrainment stresses. There is some evidence that biofilms are not effective in stabilising grains greater than 2 mm in diameter (Heinzelmann, 1992; Statzner, 1999) and the muddy biofilm present on our fine-gravels was quickly eroded in the flume at low-flow stages, leaving the underlying grains exposed to the flow.

Grain-size effects and the role of silken retreats versus nets

The experimental flow-channel study of Cardinale *et al.* (2004) found that Hydropsychidae larvae stabilised finer (2 and 4mm) sediment fractions to a greater extent than coarser fractions (8mm). In this study, both fractions were stabilised to a similar degree, although the Shields parameter was slightly greater for the finer gravels. Cardinale *et al.* (2004) hypothesised that silk nets were the main stabilising agent. In the present study, although the 4–6 mm sediment had a lower density of Hydropsychidae larvae than the 6–8 mm sediment, the 4–6 mm enumeration trays had more caddisfly retreats because there were more interstices than found in the 6–8 mm observation trays. These retreats were observed to be effective stabilising agents both in the flume and in the field: when trays were removed from the river, large quantities of adjacent substrate remained attached to the tray edges (Figure 5). The apparent importance of retreats, rather than nets, in the River Soar contrasts with the observations of Cardinale *et al.* (2004). However, there is evidence that

the construction of nets and/or retreats may reflect local hydraulic conditions and may be influenced by competition between individuals for space and food resources (Statzner & Bretschko, 1998). This may help explain the contrasting observations, because the naturally colonised larvae densities in our study (113–1053 larvae m⁻²) are substantially lower than the seeded densities (904–2542 larvae m⁻² remaining after the experiment) in the study of Cardinale *et al.* (2004).

Scaling-up the local geomorphological effect of caddisfly larvae

It is interesting to consider the large-scale, geomorphological implications of ecosystem engineering activities. Moore (2006) estimated that, in small Alaskan streams, spawning sockeye salmon (*Oncorhynchus nerka*) collectively disturb in excess of 30% of the substrate surface every year and Gottesfeld *et al.* (2004) found that cumulative sockeye effects had the same relative importance for bedload transport as some flood events.

Here, the geomorphological implications of fine-gravel stabilisation by Hydropsychidae larvae are difficult to gauge. In particular, the spatial extent and seasonality of their influence are currently unquantified and we have no systematic understanding of the limits of their impact in terms of both the flow magnitudes and the grain sizes above which their effect disappears. Without such information it is only possible to speculate about their cumulative impact. It is likely that their effect is spatially patchy at the local level as a function of other abiotic and biotic controls on the distribution of the larvae and because only relatively fine sediment fractions are likely to be strongly affected. Similarly, it seems unlikely that they play a role during large flood events that mobilise a large proportion of

the river-bed material. However, the cumulative impact of hydropsychid caddisflies on the redistribution of fine-grained sediments between large floods could be both widespread and persistent because they are one of the most diverse families of lotic invertebrates worldwide (Wallace & Merritt, 1980) and developing larvae of Hydropsychidae are present within riverine systems all year round in the UK (Boon, 1979; Edington and Hildrew, 1995).

Notwithstanding our inability to quantify the impact of hydropsychid caddisfly silk on sediment flux, we can draw attention to the reminder brought by Leopold (1992) and further developed by Lisle (1995) that bedload is often dominated by sand in many river environments. Here, an increase in entrainment threshold due to hydropsychid caddisfly silk of c. 30% might be reducing fine-grained bedload yield by a significant amount. Indeed, the impact of such a restraining mechanism might add a new dimension to the findings of Reid *et al.* (1985, 1986) that entrainment and ‘distrainment’ thresholds differ significantly during the passage of a flood wave, a phenomenon they attributed to the binding effects of interstitial fines in the absence of knowledge of ecosystem engineering by invertebrates. Looked at the other way, an absence of the effects of hydropsychid caddisfly silk might lead to larger flux of fine-grained bedload and have considerable cumulative consequences for nuisances such as reservoir sedimentation.

Conclusions

The combined field and flume experiments described here support the findings of earlier work in this area (Statzner *et al.*, 1999; Cardinale *et al.*, 2004) and extend that work in two important ways. First, we have established that there are elevated thresholds of incipient

motion for fine gravels that are colonised in a natural river setting as distinct from gravels seeded with larvae in small, experimental channels. The colonisation densities that were observed are much lower than in flume experiments and are the product of a suite of abiotic and biotic processes that influence colonisation in natural settings. The strong impact of the Hydropsychidae caddisflies on entrainment (for example, an increase in critical shear stress of 35% for 4–6 mm fine gravels) indicates that they might have a substantial effect on fine-grained bedload flux in natural settings. Second, we have measured the caddisfly effect alongside both field-conditioned, uncolonised and unconditioned, uncolonised laboratory controls. This has allowed us to assess the importance of the caddisfly relative to the combined impact of other factors that condition the bed and may influence particle entrainment. Somewhat surprisingly, we found that in-stream conditioning processes, such as biofilm development and the reworking of grains by low flows, had no measurable impact on incipient motion of fine gravels. Consequently, we conclude that these larvae are locally very important for stabilising fine-grained patches. Ecologically, this benefits both the Hydropsychidae larvae and other sedentary macroinvertebrates by creating habitats that would not otherwise be available. This makes these organisms important ecosystem engineers. The cumulative impact of silk-spinning caddisflies at larger, geomorphological scales is difficult to quantify. However, given their global distribution and the staggered nature of their life histories it is likely that they influence the downstream redistribution of fine sediments much of the time and in many rivers worldwide.

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Table 1. Percentage weights of material in observation trays in relation to the original size fraction

Tray	Grain size	% finer	% original	% coarser
1	4–6 mm	10.1	84.7	5.2
2	4–6 mm	8.9	84.1	7.1
3	4–6 mm	7.0	83.8	9.2
4	4–6 mm	8.4	80.0	11.7
5	4–6 mm	8.2	79.0	12.8
6	4–6 mm	7.5	82.4	10.1
Mean		8.3	82.3	9.3
1	6–8 mm	6.5	83.1	10.4
2	6–8 mm	8.6	80.5	10.8
3	6–8 mm	7.9	82.8	9.2
4	6–8 mm	8.9	82.0	9.1
5	6–8 mm	9.4	80.0	10.6
6	6–8 mm	8.1	79.6	12.4
Mean		8.2	81.3	10.4

List of Figures

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Figure 1

Figure 2

Figure 3

Figure 4

Figure 5