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Title:

Increase in coarse sediment transport associated with disturbance of gravel river beds by signal crayfish (*Pacifastacus leniusculus*).

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Abstract (max. 300 words)

There is growing acknowledgement of the interaction between animals and the river bed on which they live and the implications of biological activity for geomorphic processes. It has been observed that signal crayfish (*Pacifastacus leniusculus*) disturb gravel substrates, potentially promoting sediment transport and impacting ecological communities. However, the mechanisms involved and the extent of their impact remain poorly understood, especially in relation to other processes that affect grain mobility in gravel-bed rivers. A series of flume experiments, using loose and water-worked gravel beds of narrowly-graded grain sizes that were exposed to six hours of crayfish activity under low-velocity flows, showed a substantial increase in the number of grains entrained by subsequent higher-velocity flows when compared with control runs in which crayfish were never introduced. Crayfish alter the topography of their substrate by constructing pits and mounds, which affect grain protrusion. When walking and foraging, they also alter gravel fabric by reorienting and changing the friction angle of surface grains. In water-worked surfaces, this fabric rearrangement is shown to lead to a statistically significant, partial reversal of the structuring that had been achieved by antecedent flow. For these previously water-worked surfaces, the increase in entrainment arising from disturbance by crayfish was statistically significant, with grain transport nearly twice as great. This suggests that signal crayfish, an increasingly widespread invasive species in temperate latitudes beyond their native NW North America, have the potential to enhance coarse-grained bedload flux by altering the surface structure of gravel river beds and reducing the stability of surface grains. This study illustrates further the importance of acknowledging the impact of mobile organisms in conditioning the river bed when assessing sediment entrainment mechanics in the context of predicting bedload flux.

Keywords:

Introduction

Bedload transport in rivers has been studied intensively for over 100 years (Du Buoys, 1879; Gilbert, 1914; Buffington and Montgomery, 1997). However, the vast majority of research on transport has been undertaken in isolation from ecological processes, despite the number and diversity of organisms that live on, above and within the channel bed and knowledge established in other aquatic environments that animals can modify substrate conditions (Murray *et al.*, 2002). There is growing acknowledgement in river science that mobile organisms can influence transport both directly and indirectly (Moore, 2006). However, this research is dominated by the study of relatively few species (viz. salmonid fish, beavers), which is surprising, given that many others have been observed to have potential geomorphic impacts, including the foraging and nesting of non-salmonid fish and the deliberate and inadvertent activity of many species of insect larvae and crustaceans (see Rice *et al.*, in review). Animals not only have the potential to disturb substrates but also stabilise them. So, for instance, hydropsychid caddisfly larvae bind bed material with the silk that they spin in order to construct filter nets and other structures, so increasing the shear stress required to entrain gravels (Statzner *et al.*, 1999; Cardinale *et al.*, 2004; Johnson *et al.*, 2009). Consequently, the interaction between organisms and the channel bed is likely to have substantial and varied impacts on geomorphic processes in many river reaches.

Crayfish are large, freshwater crustaceans which have an ecological impact that can be disproportionate to their biomass due to their role as shredders, breaking down organic matter into smaller pieces and so providing food for many other invertebrates (Momot, 1995; Nyström *et al.*, 1996; Schofield *et al.*, 2001). Crayfish also graze plants and algae. This can increase habitat heterogeneity which, when coupled with their shredding of organic matter and their predation of many invertebrate species, leads to complex interactions with other organisms. Crayfish occur on all continents, with the exception of Antarctica, and have become successful as invasive species outside their native range through introduction by humans, whether deliberate or inadvertent. Because of their important ecological interactions, their relatively large size, their long life and their high densities, crayfish are considered to be amongst the most notorious invasive species in freshwater environments, having significant and pervasive deleterious impacts on existing ecological communities (Lodge *et al.*, 1998; Gherardi *et al.*, 2006). A particular example is the signal crayfish (*Pacifastacus leniusculus*), which has become established in parts of western USA, Europe and Japan. In the British Isles, it has had not only important detrimental ecological impacts, killing or out-competing fish and removing plant cover, it has also spread a disease, to which

it is immune, that has led the native white-claw crayfish (*Austropotamobius pallipes*), which it also out-competes, to become endangered (Nyström and Strand, 1996; Guan and Wiles, 1997; Holdich *et al.*, 1999; Vorburger and Ribi, 1999; Usio *et al.*, 2001; Stenroth and Nyström, 2003; Crawford *et al.*, 2006).

In addition to their often detrimental ecological interactions, crayfish also affect the geomorphic environment, leading to habitat disturbance for native species. Signal crayfish have been found to burrow into cohesive bank material, sometimes extensively, and this has been reported to cause localised bank collapse where densities are high (Guan, 1994). They have also been found to rework gravels up to 38 mm in diameter in still-water experiments, creating topographic pits and mounds and rearranging surface grains after only a few hours of activity, potentially altering the stability of coarse-grained river beds (Johnson *et al.*, 2010). There is evidence that the activity of signal crayfish can affect the flux of fine-grained sediment in low-energy rivers of British lowlands, with plumes of suspended material recorded unexpectedly at night during periods of high crayfish activity but steady flow (Harvey *et al.*, *in press a; b*). Other crayfish species have also been found to have geomorphic impacts. In particular, Statzner *et al.* (2000, 2003a), found that the crayfish *Orconectes limosus* increased the mobility of mixed sand-gravel in an experimental channel and changed the depth of the channel-bed sediments, a feature interpreted as indicative of alterations made to the sand-gravel structure. These findings have been corroborated by field observations in New Zealand of Koura crayfish (*Paranephrops planifrons*) disturbing gravel grains when foraging (Parkyn *et al.*, 1997). Furthermore, several species have been observed to prevent fine sediment accumulation on the bed surface by encouraging low-flow winnowing as they look for food by probing interstices (Parkyn *et al.*, 1997; Creed and Reed, 2004; Usio and Townsend, 2004; Matsuzaki *et al.*, 2009).

Some of the most damaging invasions arise from the introduction of species that disturb or alter the physical environment. Not only do native organisms have to survive new pressures from competition and predation, they also must respond to an altered habitat (Vitousek, 1990). Consequently, understanding the extent to which signal crayfish affect geomorphological processes is also important for determining the nature of their impact on the native ecological community. Johnson *et al.* (2010) complemented early investigations by Stazner et al. (2000, 2003a), in a series of still-water experiments. These found that crayfish had a substantial impact on the topography of gravel substrates, moving large volumes of material both by brushing against grains when walking and by constructing pits

and mounds. This paper builds on that study, aiming to establish the link between the reworking of river-bed gravels by crayfish and changes in sediment stability. There are three specific objectives:

i) To quantify the impact of crayfish activity on the micro-topography and fabric of previously water-worked and loose gravels under low-velocity flows;

ii) To determine whether crayfish activity results in grain-scale structural change at the channel-bed surface, that has potential significance for sediment entrainment mechanics;

iii) To determine whether sediment reworking by crayfish has a significant impact on the stability and entrainment of gravels during high-velocity flows that are typical of rain-fed floods or freshets.

Methods

Experimental overview

Experiments were conducted under controlled flow conditions in a glass-walled, tilting, 0.6m wide laboratory flume. Narrowly-graded gravels (11–16, 16–22 mm) were placed in the experimental section of the flume and screeded flat (Figure 1). Both upstream and downstream of this experimental area, a 0.1 m deep bed of 25–35 mm river gravels was used to generate a boundary layer similar to that found in natural gravel-bed rivers. In half of the experimental runs, the surface of the experimental area was left as a loose, random arrangement of gravel (*series 1*) and, in the other half, the surfaces were water-worked. Crayfish were then introduced in both *series* under a low-velocity flow and left for six hours, their behaviour being continuously recorded with submerged digital video cameras. Laser scans of the gravel surfaces before and after water-working, as well as before and after crayfish activity, were obtained and compared in order to assess both micro-topographic and grain-structure alterations. The patches of gravel were then entrained in the flume under a high-velocity flow and the mobility quantified from digital video recordings. Grain movements on surfaces which had been disturbed by crayfish were then compared with those of control runs, the surfaces of which had been subject to the same pre-conditioning but on which no crayfish had been present.

Selection of the two grain-size fractions (11–16, 16–22 mm) was based on the results of experiments in still-water aquaria, which revealed a distinct change in the nature and magnitude of bed disturbance at a grain size of about 16 mm (Johnson *et al.*, 2010). By using these size fractions, this behavioural change could be further studied. The gravel was derived from the River Lune, NW England, and was predominately bladed (Sneed and Folk, 1958) and well rounded (0.8; Krumbein, 1941). Grain density was 2650 kg m^{-3} (Graham *et al.*, 2005).

Crayfish were trapped in Wood Brook, a small gravel-bed stream near Loughborough, UK (1°13'41'' W., 52°45'24'' N.), under licence from the Environment Agency of England and Wales and the Department for Environment, Food and Rural Affairs (DEFRA) and housed individually in large aquaria (see Johnson *et al.*, 2010 for additional details). Only crayfish without obvious injury, with a carapace length of 55 ± 5 mm and a subaerial weight of 55 ± 10 g were selected for use in these experiments.

When crayfish were deployed in the flume, they were kept within the experimental area using a thin-wire, 10 mm mesh cage 0.6 m long, 0.4 m wide and 0.3 m high (Figure 1). The cage was only used during low-velocity flows and was not left in the flume during the grain-structuring or entrainment stages of the experiments. The cage was seated on four fixed reference points to ensure that it covered exactly the same area in all runs. These reference points were also used to rectify laser-scanned images. The location of the cage provided a 0.1 m wide buffer on each flank of the experimental area; these were intended to prevent activity in the zones most affected by side-wall drag and to deny the crayfish use of the flume walls.

Experimental procedure and hydraulic conditions

All flows were turbulent and sub-critical, with a water surface parallel to the bed surface. During each run, flow measurements were taken with an acoustic Doppler velocimeter 0.1 m downstream from the experimental area. Five velocity profiles were measured for each of the three flows in order to quantify the hydraulic environment and assess the replicability of the flow conditions. Bed shear stress (τ_i) was estimated according to the law of the wall as:

$$\tau_i = \rho \, v^{*2} \tag{eq. 1}$$

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

$$v^* = \frac{c}{b}$$ (eq. 2)

where c = 2.5 and is the reciprocal of the von Karman constant for clear water flows, κ = 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 ranged from 0.953 – 0.997). To enable a comparison of the shear stresses for both grain sizes, the dimensionless Shields' parameter (θ_i) was calculated as:

$$\theta_i = \frac{\tau_i}{(\rho s - \rho)g D_i}$$ (eq. 3)

where τ_i is the shear stress at each flow over grain size D_i, g is the acceleration due to gravity (= 9.81 m s^{-2}) and ρ_s is sediment density (= 2650 kg m^{-3}).

Initially, the experimental area was filled with one of the grain-size fractions and gently screeded flat. The surface was then laser-scanned and the data used to create a DEM. To water-work the test-beds in *series 2* experiments, the flume channel was slowly filled with water, ensuring no disturbance, then the tail weir and pump were altered to generate moderate bed particle movement (average velocity [v] = 0.4 m s^{-1}; local boundary shear stress [τ] = 2.18 Nm^{-2}; Shields' dimensionless shear stress parameter [θ] = 0.01; *series 2*; Table 1). The flume was left running for two hours to structure the surface, after which discharge was gradually reduced to zero and the flume channel was slowly drained. During the two hours, gravel was fed upstream of the experimental area at a similar rate to its transport out of the patch. The water-worked surfaces were then laser scanned. After scanning the initially loose (*series 1*) or water-worked surfaces (*series 2*), the cage was placed over the experimental area.

Once the cage was in place, the flume was slowly filled with water and a flow suitable for crayfish occupation was established (v = 0.1 m s^{-1}; τ = 0.14 Nm^{-2}; θ = 0.0005; Table 1) which was unable to disturb the surface gravels or limit the movement of crayfish. A single animal was then released approximately 0.05 m from the channel bed and allowed to drift down to the surface. A total of 20 crayfish were used in the 40 flume runs that involved crayfish, each animal being used twice. While crayfish were in the flume, the channel was covered to

create a dark environment because crayfish are nocturnal and covering avoided complications associated with moving shadows. A large water cooler was used to keep water temperature between 15°C and 20°C. The crayfish were left in this constant flow for six hours after which they were removed by hand and the flume was slowly drained. The cage was then removed and the surface laser scanned again.

Finally, the flume was re-filled and a high-velocity flow was imposed (v = 0.9 m s^{-1}; τ = 10.5 Nm^{-2}; θ = 0.05; Table 1). This entrainment flow was established consistently for each run and was imposed for two hours, during which the experimental area was continuously monitored with video cameras. After two hours, the flume was slowly drained and another laser scan of the surface was obtained.

This procedure was replicated 10 times for each of the four crayfish-modified substrate types (loose and water-worked 11–16 and 16–22 mm grain sizes). In order to provide control runs, the procedure was also replicated without crayfish a further ten times for each substrate type, giving a total of 80 runs. During control runs, the cage was placed in the flume and left for six hours of low-velocity flow but, in each case, no crayfish were introduced.

Analysis of laser scanned surfaces

Surface models were each obtained from two laser scans, both perpendicular to the bed. These scans were merged to form a single surface. Surfaces were then cropped, orientated, rectified and imported into ArcGIS where they were interpolated into raster digital elevation models (DEMs) and detrended following the same procedure described by Johnson *et al.* (2010). Topographic changes due to crayfish activity were obtained by calculating DEMs of difference (DoDs). This was achieved by subtracting the *z*-values of each cell of the surfaces before and after water-working or crayfish activity. Error analysis (Johnson *et al.*, 2010) haspreviously established that a minimal discernable difference of ± 1 mm is appropriate.

Geostatistical analyses of the surface structure were performed in ArcGIS. The surface roughness was paramaterised by the standard deviation of elevation measurements (*z* values; Aberle and Smart, 2003). The granular structure (fabric) was characterised by quantifying the inclination of slopes in a stream-wise and cross-stream direction using the

inclination index (I_l) derived by Smart *et al.* (2004). Inclination is defined as the slope between points at a predetermined distance. Water-worked surfaces are expected to have an asymmetric distribution of inclinations in a stream-wise direction due to imbrication (Smart et al., 2004; Hodge *et al.*, 2009). In a cross-stream direction there should be an equal number of positive and negative inclinations, as there is expected to be no structure in this direction. The inclination index is calculated as:

$$I_l = \frac{p_l - n_l}{p_l + n_l + z_l} \qquad \text{(eq. 4)}$$

where l is the lag distance (= 2 mm), p is the number of positive inclinations, n is the number of negative inclinations and *z* is the number of paired points which define zero slope. Consequently, an equal number of positive and negative inclinations will give a result of zero and, as asymmetry increases, I_l will increase to maxima of ± 1 (Smart *et al.*, 2004; Millane *et al.*, 2006).

Analysis of videography

Videography was used to analyse the mobilisation of gravel grains during high-velocity flows. Establishment of entrainment thresholds is inherently subjective and as a result there have been numerous definitions of incipient motion and threshold transport (Neill and Yalin, 1969; Buffington and Montgomery, 1997). Any linear relation between size of grains moved and time-averaged flow stress is obscured by the influence of surface geometry and stochastic fluctuations in stress intensity due to turbulence and, consequently, a particular grain can be entrained by a range of flows rather than at a single discrete threshold (Grass, 1971; Paintal, 1971; Lavelle and Mofjeld, 1987; Wilcock and McArdell, 1993; 1997). For this reason, rather than trying to determine a single entrainment threshold, the movement of grains was counted over a two-hour period. The imposed flow was chosen to be the lowest which was sufficient to induce bedload transport over the entire experimental patch (i.e. moving more than a few isolated grains). Although more grains were inevitably entrained from 11–16 mm than 16–22 mm materials, it was decided that this entrainment flow was suitable for both, because lesser flows did not regularly or frequently entrain bed material and higher flows induced scour.

Video cameras were not used underwater during the entrainment runs because they would have altered the hydraulic environment. Instead, they were set up to record through the

glass side-wall of the flume. The number of mobile grains was counted by a single operator (MFJ) and binned in discrete periods. A grain was defined as mobile if it was displaced a distance greater than a single grain diameter. This gives a gross measure of surface stability and does not take into consideration the length of grain movement. Because a single operator analysed all videos, the results are expected to be consistent between runs. This was tested by analysing the same 120-minute video five times. The surface used was of 11–16 mm loose gravels, as this was the most mobile and the most difficult to analyse. Nearly all error was associated with the first 20 minutes of entrainment because the large number of grains moving at the same time made counting difficult, even when played back frame-by-frame. After 20 minutes, bedload was associated with individual grains moving infrequently, either in isolation or in groups of two or three, which were relatively easy to count. The total cumulative number of grains counted as moved differed by a maximum of 24 (mean = 16; σ = 5). This is 5% of the total number moved over the entire 120-minute period and was insufficient to modify the trends of changing mean entrainment.

Results

Micro-topographic change

Similar to previous experiments conducted in still-water aquaria (Johnson *et al*., 2010), the volume of material moved by crayfish was partitioned into two types, based on the magnitude of change. Videography showing substrate disturbance by signal crayfish can be found at Johnson (www. 2010). Any topographic difference greater than ±1 D_{50} was considered pit and mound construction and any change greater than the minimal discernable difference of ±1 mm but less than ±1 D_{50} was considered fabric adjustment and was associated with crayfish brushing past surface grains when moving or foraging. Whilst pits and mounds were more apparent visually, the majority of disturbance was associated with fabric adjustment in all cases (Figure 2). However, whilst the dominance of fabric adjustment had also been observed in still-water experiments (78%), it was found to be less pronounced in the flume (61%).

The difference in the impact of crayfish on loose (*series 1*) and water-worked surfaces (*series 2*) in a low-velocity flow was highly significant for 11–16 mm material (ANOVA, *p* = 0.002). Construction of pits and mounds and fabric rearrangement were both substantially reduced by prior water-working (Figure 3). However, in 16–22 mm gravels, there was no statistically significant difference in topographic change between loose and water-worked

surfaces (ANOVA; p = 0.823). Of further interest is that water-working of 11–16 mm surfaces reduced the volume of material moved by crayfish to a level which was not significantly different from that of water-worked 16–22 mm material (ANOVA; p = 1.000).

Grain-structure change

The fabric adjustment achieved by two hours of structuring flow was quantified using geostatistical analysis. Loose surfaces had no asymmetry in inclination frequency in either stream-wise or cross-stream directions, whereas water-worked surfaces had strong asymmetry in a stream-wise, but none in a cross-stream direction (Figure 4). Here, the values of the inclination index (I_l = 0.07 - 0.1) are consistent with those of studies in gravel-bed rivers, where values have been found to lie between 0.03 – 0.18 (Millane *et al.*, 2006). This suggests that the flow conditions used here were successful in developing an appropriate bed structure.

When crayfish were placed on an initially loose surface (*series 1*) they did not have a significant impact on inclination index (Figure 4a) and I_l values remained very close to zero, indicating that animal disturbance simply produced a slightly different random arrangement of grains. In contrast, six hours of crayfish activity on water-worked surfaces (*series 2*) had a statistically significant impact on the stream-wise inclination index (Table 2). In 11–16 and 16–22 mm gravels, the index was reduced by 37% and 20%, respectively (Figure 4b) demonstrating that crayfish have the potential to counteract prior structuring of substrates by the flow, partially randomising surface inclinations. These reductions were insufficient to return the surfaces to I_l values characteristic of an unstructured state, (paired *t*-test; 11–16 mm p = 0.001; 16–22 mm p < 0.001).

Six hours of exposure to signal crayfish increased surface roughness, but paired *t*-tests indicate that this was not statistically significant for initially loose (*series 1;* 11–16 mm p = 0.214; 16–22 mm p = 0.701) or water-worked surfaces (*series 2;* 11–16 mm p = 0.135; 16–22 mm p = 0.534). This counters the results of the still-water experiments (Johnson *et al.*, 2010), which found a significant correlation between surface roughness and the proportional area of pit and mound construction. The difference is likely to be due to the limited time crayfish were at work on a surface in the flume and the lack of solid side-walls, which would otherwise have reduced the degree of slumping of material, allowing pits to be dug deeper.

Sediment entrainment

As might be anticipated, water-worked surfaces were considerably more stable than loose surfaces during entrainment tests. In 11–16 mm gravels, three times more grains were moved on average from loose surfaces than from those which had been water-worked. At the start of experimental runs, the number of grains mobilised rose rapidly before reaching an asymptote. The initial steep rise was associated with entrainment of susceptible grains, which were especially common on the surface of the loose, unstructured gravel. These vulnerable grains were either entrained and transported out of the patch, or moved to less vulnerable positions within the patch. As a result, the number of grains entrained per unit interval declined as the substrate became increasingly structured. Not surprisingly, the water-worked control surfaces had substantially fewer grains entrained during the initial period because grains in vulnerable positions or orientations had already been moved to more stable positions by the previous structuring flow (Figure 5).

Six hours of exposure to crayfish had a substantial impact on the stability of gravel patches, with considerably more grains moved from crayfish-disturbed than from control surfaces (Figure 5). The impact of crayfish is most noticeable in the first 20 minutes of entrainment with more grains entrained from crayfish-disturbed substrates in comparison to control equivalents. This is particularly evident across previously water-worked surfaces where there is a large difference in the mean number of grains entrained after 20 minutes between crayfish-disturbed and control surfaces. On average over the two-hour period, 1.8 times more material was moved from previously water-worked, crayfish-disturbed surfaces than from water-worked control surfaces. Whilst there is a substantial difference in the mean number of grains entrained between controls and crayfish-disturbed surfaces for both initially loose (*series 1*) and water-worked substrates (*series 2*), it was only statistically significant for those that had been water-worked (Figure 6; Table 3).

There was a significantly greater variance in number of grains entrained in runs with initially loose surfaces (*series 1*) than in runs where the bed had been water-worked (*series 2*) for both 11–16 mm and 16–22 mm bed materials (Table 3). This was not unexpected in the case of water-worked surfaces, because they had been structured under the same conditions and, therefore, had all developed a similar fabric under the imposed stress of the

structuring flow. In contrast, loose surfaces all had different structures, as they were randomly oriented distributions of grains, and this resulted in the greater range of entrainment counts in each series of runs. The activity of crayfish did not alter significantly the variance of entrainment counts within any bed type, despite increasing the total average number of grains entrained (Table 3). Had crayfish completely reversed the imbrication induced by water-working, then the variance in entrainment would have been expected to increase, along with the total number of grains entrained.

Discussion

The introduction of a single signal crayfish to a narrowly-graded gravel channel bed for six hours under low-velocity flow resulted in substantial alteration to the micro-topography and grain structure. The nature of this disturbance is similar to that previously described for still-water experiments (Johnson *et al.*, 2010). In general, these results corroborate those of other studies, which have suggested that other species of freshwater crayfish have impacts on the mobility of their substrates through their activity (Statzner *et al.*, 2000; 2003a).

Across all surfaces, crayfish-induced alterations were dominated by fabric adjustment. This led to partial reversal of the structuring induced by water-working (*series 2*) as crayfish walked and foraged. Crayfish activity did not structure initially unstructured, loose gravels (*series 1*): although the surface arrangement of grains was modified, it remained predominately random. Therefore, the magnitude of restructuring by crayfish, whilst statistically significant, is relatively subtle in comparison to structuring by the flow. However, the structuring of substrates by the flow will only occur occasionally when the bed is mobile. Whereas, crayfish will reverse structuring whenever they are active and cumulatively may have a substantial impact, especially where they occur in high densities. Also, the experiments demonstrate that restructuring by crayfish, when coupled with changes in protrusion due to the excavation of pits and building of mounds, was responsible for a substantial increase in the number of grains subsequently entrained by higher-velocity flow, though the impact was statistically significant only for previously water-worked surfaces.

The impacts of topographic changes made by signal crayfish

The greater grain entrainment from water-worked surfaces is due to reductions in grain interlock and friction angle and an increase in protrusion and resulting fluid drag. However, there will be a proportion of grains which will have increased friction angles through minor rearrangement into more stable niches. There will also be those grains in pits which will be 'hidden' from the flow or will have higher friction angles because they rest on slopes that incline downstream. Consequently, it is difficult to determine the exact impact of pit and mound topography or fabric adjustment on transport without more detailed, grain-by-grain observations, even though the overall impact of crayfish activity has been shown to be a reduction in the stability of the bed.

The path length of grains transported from crayfish-disturbed surfaces was not quantified. A grain on the upstream 'lip' of a pit may be considered unstable but it is likely to be moved only the short distance into the pit, where it would occupy a relatively stable position, sheltered from the flow. Therefore, pits may act as temporary bedload traps. Under high bedload flux, displacement and entrapment would result in the topography of the bed quickly becoming planar, with mounded material eroded and transported into pits immediately downstream. If crayfish were to occur in high density then, when constructing a pit, they may also push mounded material into adjacent pits. In this context, Gottesfeld *et al.* (2008) found that, as the density of Chinook salmon (*Oncorhynchus tshawytscha*) increased, bed morphology changed from the dune form characteristic of salmonid spawning reaches to a more uniform, plane bed. Similarly, crayfish density may influence the geometry of pits and mounds, which would also have a substantial impact on the magnitude of substrate disturbance. It is unlikely that the impact of crayfish will increase linearly with density due to the hierarchical structuring of crayfish populations with dominant crayfish digging and foraging more than subordinate individuals (Goessmann *et al.*, 2000; Herberholz et al., 2003). It is currently unknown how interactions between signal crayfish influence their geomorphic impacts, but, Rice *et al.* (in review) have found that where two crayfish are present simultaneously in experiments identical to those presented here, the magnitude of impact does not increase in comparison to a single crayfish.

The presence of pits and mounds will also have a hydraulic impact. We have shown that they increase surface roughness (Figure 2), although not significantly so after only six hours, and mounded material may create leeside zones of recirculating flow that are similar to those found in the vicinity of other protruding sedimentary micro-forms, such as pebble clusters (Hassan and Reid, 1990; Buffin-Bélanger and Roy, 1998; Lawless and Robert, 2001). These

hydraulic impacts will have implications for the entrainment and entrapment of grains. In addition, mounds will increase form drag. Montgomery *et al.* (1996) found that the construction of redds by spawning salmonids created drag on the flow, which reduced bed sediment mobility, counteracting the loosening of the bed that had been achieved previously through redd excavation. A similar effect will also arise from the pits and mounds constructed by crayfish, so limiting the differences in entrainment between crayfish-worked and control beds (Figures 5 and 6). However, without detailed hydraulic measurements, it is difficult to ascertain exactly how these undulations in the bed topography influence entrainment mechanics.

Impact of water-structuring of gravels on crayfish activity

For 11–16 mm gravels, substantially more material was moved by crayfish on loose (*series 1*) than on water-worked surfaces (*series 2*). As might be expected, this implies that the structuring of gravel substrates reduces their vulnerability to disturbance by crayfish. However, the same pattern is not true of coarser 16–22 mm material, where similar volumes of material were moved by crayfish on both loose and water-worked surfaces. It is suggested that this difference between beds of different grain-size reflects both grain inertia in the context of accidental contact and the exertion required to excavate grains of different submerged weight. The accidental rearrangement of grains is common in the case of the finer fraction used here, where the body weight of a mobile crayfish is sufficient to disturb the orientation and friction angle of individual grains. However observations suggested that even in this case, water-worked surface grains did not move as readily as did those on loose surfaces due to the increased stability imparted by greater grain interlock and higher friction angles. In coarser, 16–22 mm gravels, where the submerged weight of individual grains was about 0.8 times that of individual crayfish, accidental rearrangement of grains was less and this resulted in significantly lower volumes of moved material. The fabric adjustment that occurred on these coarser beds tended to result from foraging, digging and purposeful probing of interstices. The fact that water-working did not reduce the volume of material moved implies that grain weight was already an over-riding factor limiting crayfish activity.

Significantly less material was moved in pit and mound construction in water-worked than initially loose surfaces of 11–16 mm gravels. This is likely to be due to the difficulty of dislodging grains from a structured surface where grains are more interlocked. Initial conditions had less impact in the coarser material because, again, grain weight was a limiting

factor. It was found that crayfish did not give up digging completely on the coarser, water-worked surfaces, but, instead, they dug for shorter periods than they did on loose 11–16 mm surfaces. This suggests that, despite the fact that crayfish can dig into 16–22 mm material, they limit themselves, perhaps because pit digging is not a good investment of energy in substrates which are difficult to manipulate. To summarise, water-working limited the accidental reorganisation of surface fabrics by walking and foraging and reduced pit and mound construction by making it more difficult for crayfish to dislodge grains from the surface. This difference was more pronounced in finer material, if only because crayfish disturbance was already limited by the weight of individual grains in the coarser substrate.

Potential impact of crayfish on sediment transport

Gravel river beds are known to develop transport-limiting structures at low flows, progressively stabilising as grains are moved into less vulnerable positions. Reid and Hassan (1992) showed that the entrainment threshold in Turkey Brook, England, increased as a function of increasing interval since the last bed-disturbing flood, indicating a strong time-dependence of low-flow structuring. This supports previous results in Turkey Brook that found bedload transport peaked on the recession limb of flood hydrographs when an event followed an extended period of low flow, the rising limb having altered bed structure and winnowed fine material from surface interstices, loosening it before entrainment on the recession limb (Reid *et al.*, 1985). Alternatively, when a flood closely followed a previous event, bedload transport peaked on the rising limb because the pre-flood bed surface was relatively unconsolidated and comparatively loose (Frostick *et al.*, 1984; Reid *et al.*, 1985). Laboratory experiments have confirmed that antecedent flows can significantly increase the shear stress required to entrain bed material (Paphitis and Collins, 2005; Haynes and Pender, 2007). Oldmeadow and Church (2006) found that, in reaches of East Creek, British Columbia, where the surface structure had been destroyed, bedload transport rates were 32% higher than in undisturbed reaches, highlighting the differences in strength between loose and structured beds. These results have been corroborated by Lamarre and Roy (2008) in Moras Creek, Québec. The modification of channel-bed micro-topography and grain structure by crayfish undoubtedly acts to oppose this consolidation of gravel-bed rivers. This had been implicit in the still-water experiments reported by Johnson *et al.* (2010) and it is fully supported by the results of the flume experiments reported here, where exposure to crayfish substantially increased sediment mobility.

The conflict of opposing processes (crayfish disturbance *versus* low-flow stabilisation) leads to speculation about the changing dominance of each. Most imbrication and grain clustering will be achieved fairly rapidly on the recession limb of the flood hydrograph and minor fabric adjustments of framework grains and the intrusion of fine-grained matrices will continue at various low levels of intensity for the extended periods of low-flow that intervene between floods. Crayfish will take refuge during floods, but will be active in disturbing bed sediment during the comparatively long inter-flood periods of low flow. Invasion of signal crayfish could act to modify this dynamic pattern, promoting looseness of the bed even during long inter-flood intervals, so encouraging entrainment and increasing annual bedload sediment yield. The impact of crayfish will depend on whether their activities counter the hydraulic and sedimentary processes of consolidation and this will be determined by the interval between successive floods and levels of crayfish activity which are associated with biological and abiotic controls. For example, in many temperate-zone streams, gravel-bed consolidation associated with prolonged low-flow periods tends to occur in summer months. This coincides with periods of warm temperatures which encourages increased crayfish activity.

Considerations like this highlight the important need to now develop a fuller understanding of how experimental results can be applied at larger landscape scales and over appropriate time scales. This is true of all zoogeomorphic impacts, but particularly so of abundant but small "Cinderella" geomorphic agents which do not have obvious visible impacts on the landscape, like beaver ponds, but which are known to affect geomorphic processes and which, cumulatively, must expend very large amounts of energy in modifying the physical environment (Rice et al., 2010). It therefore seems reasonable to assume that invertebrates, like crayfish, are important agents of change with as yet unquantified impacts on river channel geomorphology and sediment fluxes. An ancillary study in the River Bain, Lincolnshire, UK (Johnson, 2010) has confirmed that crayfish occupy gravel patches with grain-size characteristics similar to those used in the laboratory experiments. This establishes the potential for crayfish to have an impact on coarse sediment movements in natural rivers and is a first step in linking laboratory results to field scales.

Several aspects of the sediment setup need to be considered when transposing processes elucidated in the experiments conducted here to natural rivers. Because the water-worked surfaces used were narrowly-graded, they cannot be taken as representative of the naturally heterogeneous bed materials that are typical of most gravel-bed rivers. Despite this, several lines of evidence can be used to suggest that crayfish are likely to have a significiant impact

on sedimentary processes in natural rivers. It is known that crayfish burrow against coarse grains (Parkyn *et al.*, 1997), implying that a heterogeneous sediment mixture inclusive of cobbles or large pebbles may encourage greater amounts of digging. A heterogeneous sediment mixture may also make it easier for crayfish to dislodge grains, because smaller grains can be moved in order to dislodge a medium-sized grain and, in addition, crayfish can exert leverage on large grains which project from the surface. Second, the homogeneous substrate and flow characteristics in the experiments did not permit development of a coarse surface layer, typical of many gravel river beds. This may have acted to oppose disturbance by crayfish by making the surface more difficult to disturb. Although many rivers have armour layers composed of grains well within the range of sizes that crayfish can disturb, it remains unclear how the additional structuring of a heavily armoured surface would limit their impact.. Third, no fine sediment was included in the test beds. This matrix material is known to reduce the friction angle of surface grains as well as tightening the packing of the bed. Reorientation of surface grains during structuring disturbs fines, which then settle back onto the bed, while suspended sediment transported from upstream also settles, further consolidating the packing arrangement (Frostick *et al.*, 1984). Given the greater strength imparted to the bed by the presence of fines, the impact of crayfish might be reduced. However, set against this, crayfish have been found to winnow substantial quantities of fine material while foraging. Fine sediment can also be mobilised by the movement of legs and by contact between the abdomen and substrate when walking (Usio and Townsend, 2004). Furthermore, when frightened, crayfish escape by backwards swimming, which exerts considerable force on the bed and disturbs fine sediments (Webb, 1979; Cooke and McMillan, 1985). Indeed, a number of studies have noted that less fine material accumulates in substrates where crayfish are present (Parkyn *et al.*, 1997; Creed and Reed, 2004; Usio and Townsend, 2004).

Crayfish-sediment interactions as a disturbance to invaded environments.

The impact of signal crayfish on physical processes will occur within a framework of abiotic and biotic controls. Crayfish will be active at certain times due to changes in water temperature and flow stage and will be limited to particular river reaches associated with suitable habitats. Crayfish activity, and consequently their geomorphic impact, will be further influenced by ecological interactions. Whilst crayfish activity is known to be affected by predatory fish, hunger levels and competition (Stein and Magnusson, 1976; Shave *et al.*, 1994; Stocker and Huber, 2001; Herberholz *et al.*, 2003), the effect of these variables on their geomorphic impact is currently unknown although attempts have been made to relate

bed disturbance by the crayfish *O.limosus* to fish predators (Statzner and Sagnes, 2008). One of the important current challenges in this area of research is linking these non-trophic interactions into more traditional frameworks of organism interactions, such as food-webs (Jones *et al.*, 1994; Wilby *et al.*, 2001).

Invasive species offer an interesting and potentially important example of a geomorphic agent as they have been removed from many of the limiting biotic and abiotic controls in their native range (Cuddington and Hastings, 2004). The geomorphic disturbance associated with invasive species in freshwater environments is only beginning to be acknowledged (Harvey *et al.* in review). Invasive species are already considered to be one of the largest threats to biodiversity in global freshwater environments (Lodge *et al.*, 1998; Gherardi *et al.*, 2006) before factoring in the potential geomorphic impacts of some alien species, such as zebra mussels (*Dreissena polymorpha*) and crayfish (i.e. *Pacifastacus*, and *Orconectes* sp.) in Europe and salmonid fish (*Salmo* sp.) introductions in New Zealand. The signal crayfish provides a prime example in the UK where the favourable climatic conditions, lack of aquatic predators and limited competition from other species, has allowed it to spread rapidly and establish dense colonies, in excess of 10 m^{-2} in some areas. The impact of bed disturbance on the native community is currently unknown but would be significant if crayfish substantially altered bed stability. This would be in addition to the well documented detrimental impacts of crayfish on native organisms through ecological interactions.

Conclusions

There is a need for better understanding of the dynamic interaction between biota and their physical domain, not just in assessing the creation and maintenance of suitable habitats, but also in understanding the role of organisms in affecting physical processes. The overlap between biological and Earth sciences has led recently to the development of unified frameworks for studying these interactions (Naiman *et al.*, 2000; Paola *et al.*, 2006; Stallins, 2006; Reinhardt *et al.*, 2010; Rice *et al.*, 2010). Signal crayfish have the potential to disturb water-worked gravel, altering grain structure and micro-topography and, as a consequence, nearly doubling bed material entrainment during subsequent high-velocity flows. Signal crayfish dig into substrates, creating pits and mounds. However, the predominant volumetric disturbance by crayfish is the rearrangement of individual surface grains when walking and foraging for food. This fabric adjustment has been shown to bring a partial reversal of the imbrication that arises from water-working through some degree of randomisation in grain

arrangement. This illustrates the importance of recognizing the physical interactions of organisms and their substrates in assessing river sediment transport. However, it also alerts us to the deleterious impact on physical processes that can be a consequence of the introduction of non-native species to regions outside their natural range.

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Tables

Table 1: *Average flow parameters (n = 10) for each of the three flows used in the experimentsfor the two substrate sizes.*

Purpose of flow	Grain-size (mm)	Discharge ($m^3 s^{-1}$)	Depth (m)	Water-surface slope	Velocity ($m s^{-1}$)	Shear stress (Nm^{-2})	Shields' parameter (θ)
Grain structuring	11–16	0.06	0.25	0	0.4	2.14	0.01
	16–22					2.21	0.01
Crayfish activity	11–16	0.016	0.25	0	0.1	0.14	0.0006
	16–22					0.14	0.0005
Entrainment	11–16	0.11	0.2	0.005	0.8	10.47	0.05
	16–22					10.77	0.04

Table 2: *The mean and standard deviation (n = 10) of inclination index for water-worked surfaces before and after crayfish activity (series 2 experiments). Significance levels (p values) derived from paired t-tests indicate the difference between water-worked surfaces before and after crayfish activity.*

Direction of traverse		11 – 16 mm			16 – 22 mm		
		Mean	St.de	*p*-value	Mean	St.dev	*p*-value
Stream-wise I_I	Before crayfish	0.074	0.021	0.019	0.106	-0.013	0.029
	After crayfish	0.046	0.023		0.083	0.034	
Cross-stream I_I	Before crayfish	-0.008	-0.009	0.812	-0.013	0.015	0.534
	After crayfish	-0.010	0.016		0.004	0.014	

Table 3: *The mean and standard deviation of the number of entrained grains in 120 minutes for the four substrates by grain-size and by crayfish disturbance. Significance levels (p-values) in the mean number of grains moved between control and crayfish disturbed surfaces are derived from an ANOVA (Tukey post-hoc test). Significance levels of the difference in variance in the number of grains mobilised are derived with Levene's test.*

Antecedent bed condition	Treatment	*p*-values

and grain-size (mm)		Control		Crayfish			
		Mean	**St.dev**	**Mean**	**St.dev**	**Mean**	**Variance**
Loose	**11 – 16**	465	124	576	165	0.107	0.327
	16 – 22	195	31	207	39	0.464	0.455
Water-worked	**11 – 16**	147	50	264	30	< 0.001	0.359
	16 – 22	64	15	125	22	< 0.001	0.498

Figures

Figure 1: The flume set-up showing in-channel camera positions (camera 1a and 2a) and the cage when crayfish are in the flume channel and the camera position behind the glass side-wall (camera 1b and 2b) when entraining substrates. The two laser scanner positions are also indicated.
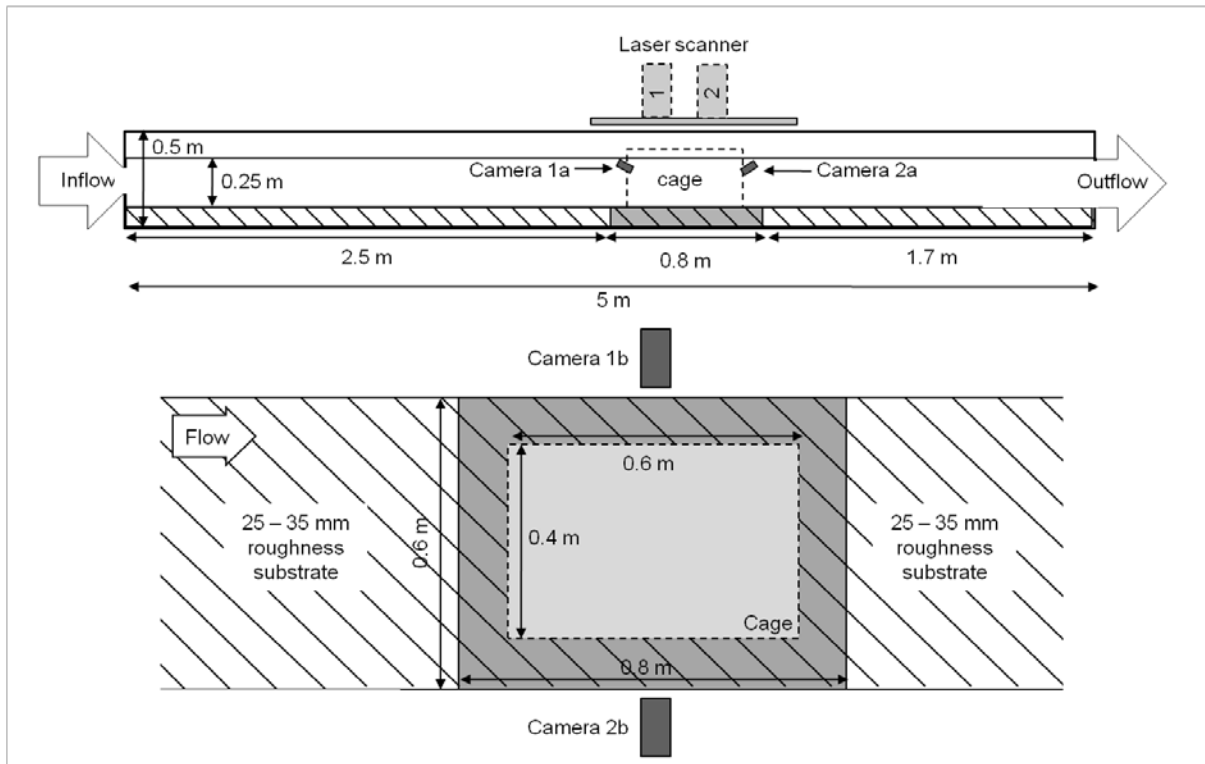
Figure 2: DEM of an 11–16 mm initially water-worked surface after six hours of crayfish activity. Note the four distinct areas of pit construction (blue areas) and the ridges of mounded material (brown) which network between pits. The surface was originally planar.
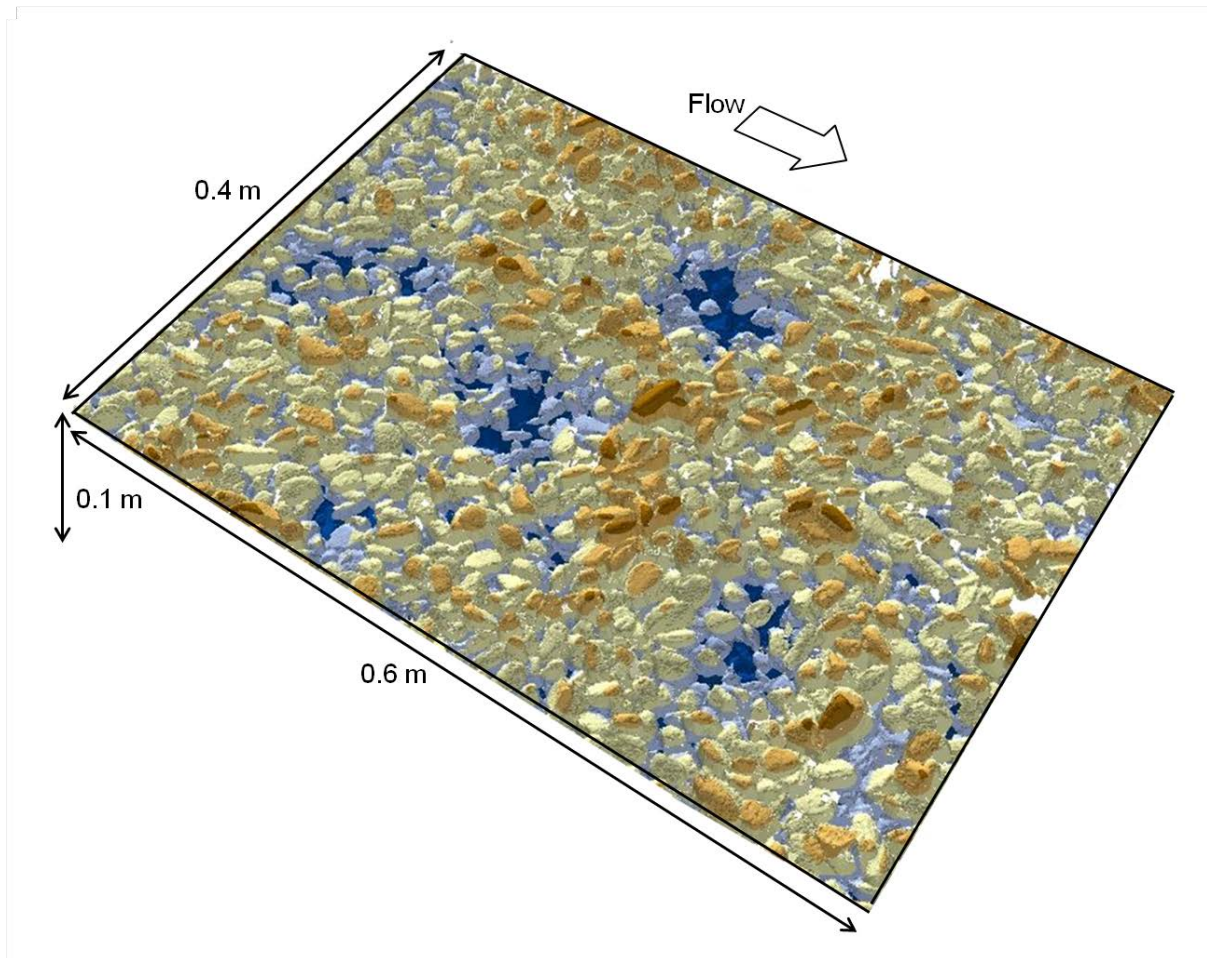
Figure 3: The mean (± 2 SE, *n* = 10) volume change between surfaces before and after crayfish activity for loose (*series 1*) and water-worked (*series 2*) surfaces of both grain sizes. Grey bars indicate fabric rearrangement and white bars indicate pit and mound construction. Significant differences occur between columns A and B ($p < 0.001$) and a and b ($p = 0.002$).
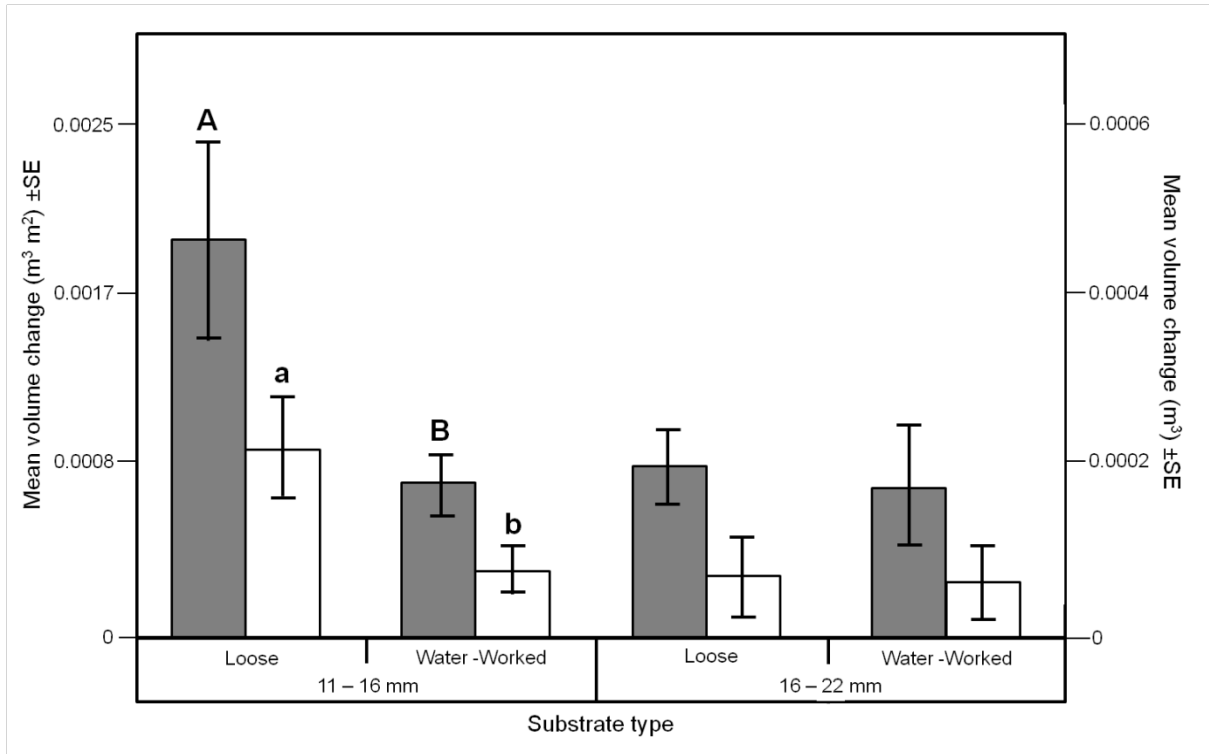
Figure 4: Mean (±2 SE; *n* = 10) alterations to the inclination index between substrates before and after water-working and after crayfish activity in both stream-wise (black circles) and cross-stream (open circles) directions. Significance levels are derived from paired *t*-tests. a) 11–16 mm. b) 16–22 mm. – rewrite, draw attention to scale difference and lose vertical dashed lines and make vertical solid line dashed. Same on below figures.
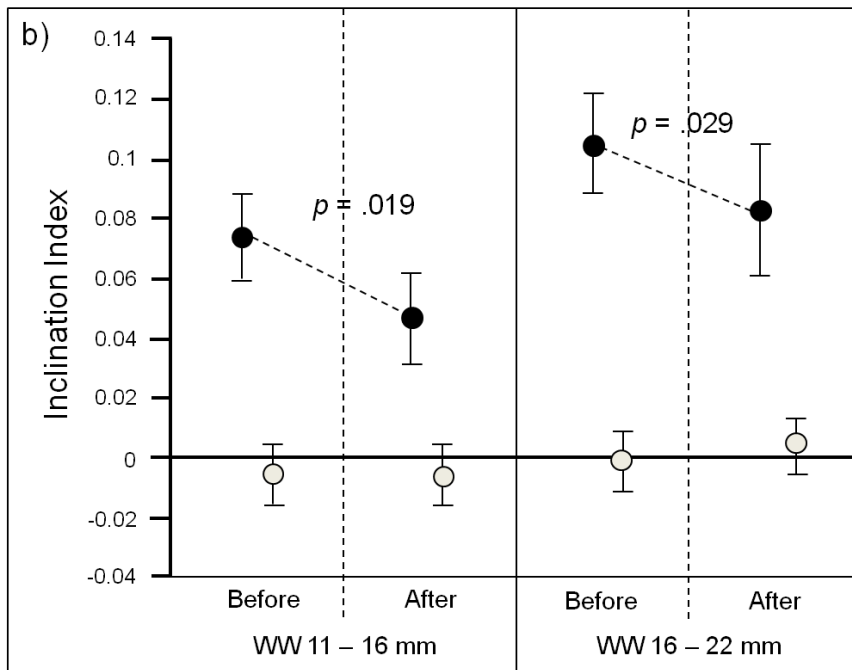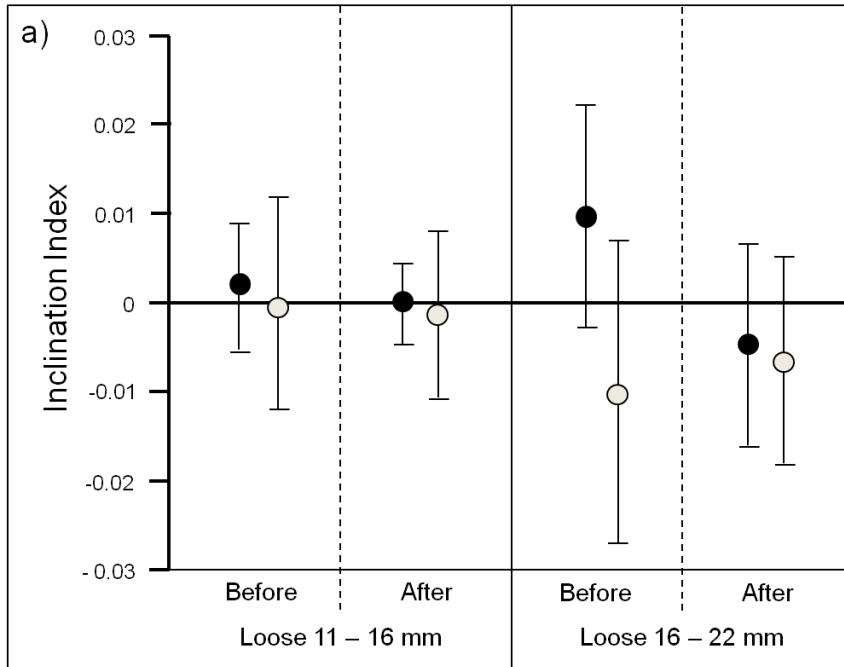
Figure 5: The cumulative number of grains moved with time under the entrainment flow. Lines indicate the mean, shaded regions are ± 2 SE of the mean (n = 10) a) 11–16 mm b) 16–22 mm. Lines were constructed from 10 second grain counts for the first 10 minutes and one minute counts for the following 110 minutes.
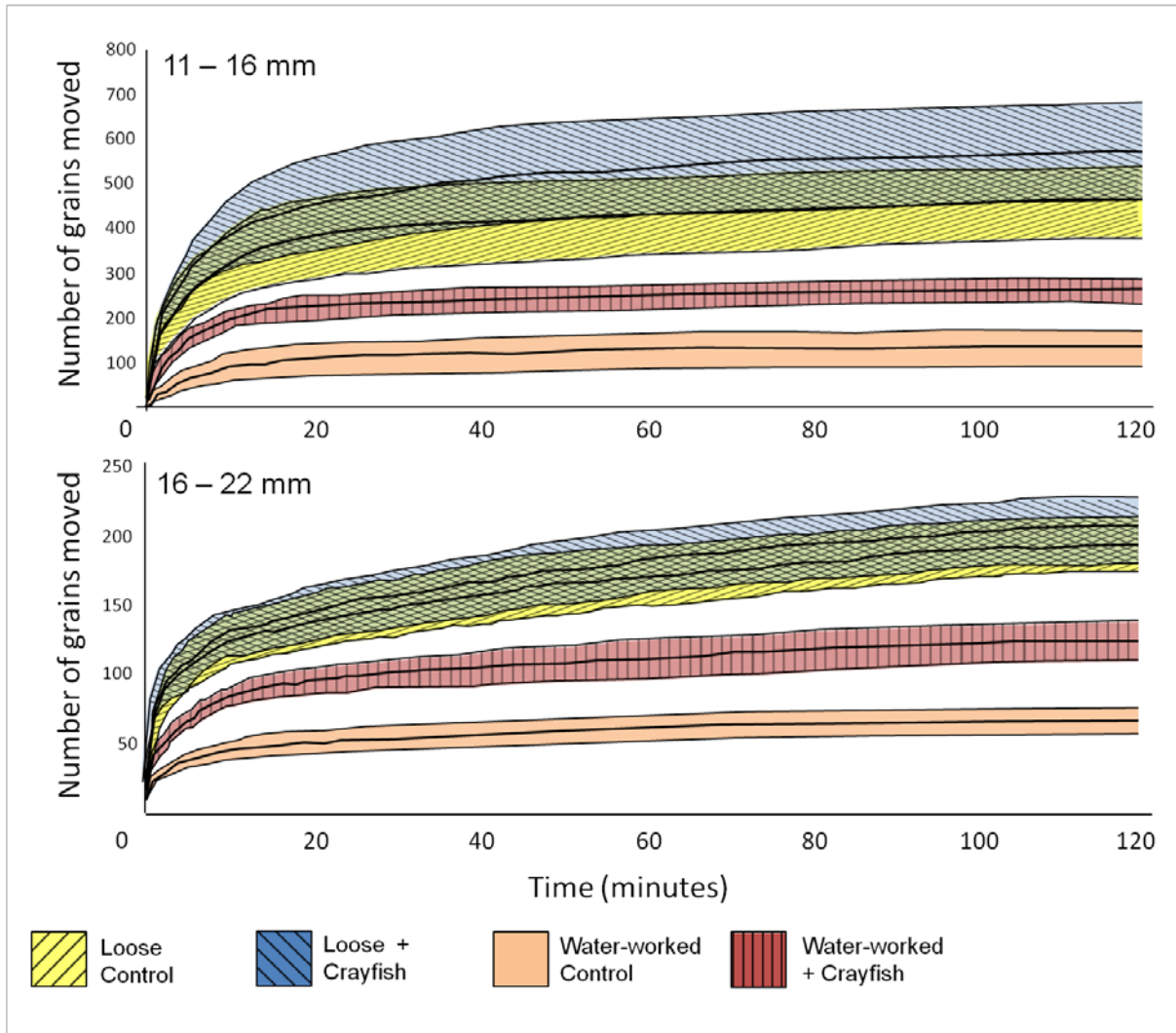
Figure 6: The mean (± 2 SE, *n* = 10) number of grains moved during a two hour entrainment period across a 2400 cm^2 area for loose and water-worked surfaces after six hours of low velocity flow with crayfish (crayfish) and without crayfish (control). a) 11–16 mm surfaces and b) 16–22 mm surfaces. Significant differences are labelled with a p value.