

## Topographic disturbance of subaqueous gravel substrates by signal crayfish (*Pacifastacus leniusculus*)

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### ARTICLE INFO

#### Article history:

Received 15 March 2010

Received in revised form 11 July 2010

Accepted 22 July 2010

Available online 1 August 2010

#### Keywords:

Biogeomorphology

Bioturbation

Gravel-bed rivers

Signal crayfish

Surface roughness

### ABSTRACT

The impact of signal crayfish (*Pacifastacus leniusculus*) on the topography and fabric of six narrowly graded, gravel substrates was investigated using repeat laser scanning of sediment surfaces in still-water aquaria. Digital Elevation Models (DEMs) of the gravel surfaces were obtained before and after exposure to crayfish for five predetermined periods. The impact on the substrate was quantified by establishing topographic and volumetric changes using DEMs of difference (DoD). The presence of an individual, medium sized crayfish for 24 h resulted in an average volume change in surface topography of 450 cm<sup>3</sup> over an area of 2400 cm<sup>2</sup>, giving a sediment displacement of 1.7 kg m<sup>-2</sup> d<sup>-1</sup>. The majority (78%) of this volume change was associated with small scale ( $\leq 1$  median grain diameter) movements of surface grains. This fabric adjustment altered grain orientations and friction angles. Crayfish also constructed pits and mounds that increased significantly the roughness of the gravel substrates and altered the protrusion of individual grains. Crayfish were able to move material up to 38 mm in diameter that had a submerged weight six times that of the individuals used in this study. By modifying the arrangement of grains on the surface of fluvial substrates, signal crayfish may counteract the low flow physical consolidation of gravel beds and reduce the entrainment stresses required to move river bed material. The results of this study suggest that signal crayfish, an internationally widespread invasive species, may have substantial impacts on the physical environment of streams and rivers, as well as on local benthic ecological communities.

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### 1. Introduction

There is a need to gain a better understanding of the dynamic roles of biota in promoting physical processes. The in situ mixing of substrates by burrowing organisms, termed bioturbation, has long been recognized (Murray et al., 2002; Meysman et al., 2006). Where reworking by organisms results in a net loss or gain of material (i.e. erosion or deposition), the collective processes have been termed “zoogeomorphology” (Butler, 1995). When changes in physical status impact the ecological community through, for instance, a modification in the flux of resources, it can be described as “ecosystem engineering” (Jones et al., 1994, 1997).

Within fluvial geomorphology, we particularly require a mechanistic understanding of how animals affect sediment dynamics. The impact of reworking gravelly fluvial substrates by organisms has been studied to a lesser extent than it has in sedimentary environments characterised typically by finer clastic materials. However, there are notable exceptions. For instance, spawning salmonids disturb river beds by altering the topography, structure and permeability of gravels

which can increase bedload transport during subsequent high flows (Kondolf et al., 1993; Montgomery et al., 1996; Hassan et al., 2008).

In this context of sediment disturbance, comparatively small alterations of grain–grain geometry (often referred to as bed-material fabric) have a substantial impact on bed stability during flood flows. Gravel substrates are often heterogeneous in terms of grain shape and size (Carling et al., 1992; Rice and Church, 1998), and this results in some grains protruding higher into the flow than others, increasing the stresses they experience (Fenton and Abbott, 1977). A mixture of different grain shapes produces a range of friction angles that dictate the ease with which grains can roll or slide downstream (Kirchner et al., 1990; Buffington et al., 1992). Grain orientation also influences critical shear stresses by dictating the projected area that is subjected to fluid drag (Carling et al., 1992). Subtle changes in attitude can have a significant impact on grain stability and, thereby, lead to changes in surface roughness, which, in turn, alters the near-bed hydraulic environment and, ultimately, determines the incidence and nature of bedload transport. Consequently, a key question is whether organisms are capable of altering the geometrical relations of coarse surface grains, so affecting substrate structure, near-bed hydrodynamics and, hence, bedload sediment transport.

A number of invertebrate species have been found to modify and rework river gravels and their interstitial matrices. Some species of

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insect larvae and freshwater shrimp winnow fine material (Pringle et al., 1993; Zanetell and Peckarsky, 1996; Statzner et al., 1996) and others act like “tiny bulldozers” as they move through interstices, redistributing fine material within the substrate (Boulton, 2000, p. 56). Invertebrates have also been found to increase the stability of gravel substrates. Hydropsychid caddisfly larvae can bind grains together with silk that is spun to construct filter nets and retreats within which they shelter (Statzner et al., 1999; Cardinale et al., 2004). These silk threads have been found to increase by 38% the shear stress required to entrain gravels of 4–6 mm (Johnson et al., 2009) and this increase in river bed stability helps facilitate the presence of other invertebrates by reducing the risks of entrainment along with bed material as well as dislodgement by the collision impact of clasts that have been mobilized upstream.

Crayfish—large freshwater crustaceans—have been found to be important geomorphic agents in both rivers and riparian terrestrial environments (Statzner et al., 2000; Butler, 2002). Some species, including signal crayfish, burrow extensively into river bank and bed materials (Holdich, 2002a; Barbaresi et al., 2004), and this can destabilise banks (Guan, 1994) and increase turbidity of the flow (Angeler et al., 2001). They can also cause winnowing of fine material from the bed (Parkyn et al., 1997; Creed and Reed, 2004; Usio and Townsend, 2004). In a series of experiments in small artificial channels, more material was found to be eroded from a sand–gravel substrate where crayfish (*Orconectes limosus*) had been active than from substrates without crayfish. The microtopography of the bed was also found to have been modified (Statzner et al., 2000, 2003).

The present study focuses on signal crayfish (*Pacifastacus leniusculus*), a species native to northwestern North America, but now widely invasive throughout western North America, Europe, and Japan (Holdich, 2002b; Lewis, 2002). Invasive populations have been established in many thousands of rivers and lakes where density and biomass are often greatest on noncohesive, cobble substrates (Guan and Wiles, 1996; Flint and Goldman, 1977; Lewis and Horton, 1997; Lewis, 2002), due to the abundance of potential shelters beneath and between coarse clasts (Guan and Wiles, 1996; Parkyn and Collier, 2004). Signal crayfish have been the subject of much ecological research because of the impacts they have had on the ecology of regions they have invaded and particularly because of their detrimental impact on native crayfish populations (Nyström and Strand, 1996; Guan and Wiles, 1997; Holdich et al., 1999; Usio et al., 2001; Stenroth and Nyström, 2003). Signal crayfish are omnivorous, mainly consuming plant detritus, algae, and other invertebrates (Guan and Wiles, 1998; Lewis, 2002). Individuals have been found to move long distances in upstream and downstream directions (Bubb et al., 2002; Light, 2003; Bubb et al., 2004, 2006). They are known to shelter either in burrows or between grains in coarse bed material, both of which they defend aggressively (Vorburger and Ribi, 1999). Previous studies have examined how disturbance by crayfish is influenced by abiotic and biotic interactions (Statzner et al., 2000, 2003; Statzner and Peltret, 2006; Statzner and Sagnes, 2008). However, without a detailed understanding of how, and the extent to which, crayfish move material, it is difficult to draw conclusions about their potential impact on physical processes such as sediment transport.

The aim in this paper is to quantify the impact of crayfish bioturbation on the topography of gravel substrates. In contrast to previous experiments, the impact of individual crayfish has been assessed whilst keeping all other factors constant. There are three specific objectives: (i) to determine whether crayfish can alter the microtopography of gravel substrates and assess the mechanisms of disturbance; (ii) to determine the influence of grain size on the degree of crayfish impacts; and (iii) to determine how reworking of gravel substrates by crayfish is influenced by the length of time they are present.

## 2. Methods

### 2.1. Crayfish aquaculture

Crayfish used in this set of experiments were caught with baited crayfish traps in Wood Brook, near Loughborough, UK (1°13'41" W., 52°45'24" N.), and transported to the laboratory under licence from the Environment Agency of England and Wales and the Department for Environment, Food and Rural Affairs (DEFRA). To limit the variability of impact that might be associated with differing size and age, only individuals with a carapace length (measured from tip of rostrum to end of carapace) of  $50 \pm 5$  mm (~100 mm total length, including tail) and having a subaerial weight of  $55 \pm 10$  g were selected. Signal crayfish typically attain a maximum carapace length of 50–70 mm, although individuals up to 95 mm have been recorded in the UK (Holdich, 2002a). Selected individuals were also without obvious injury (such as the loss of legs, claws, or antennae) as this affects their exploratory behaviour (Basil and Sandeman, 2000; Koch et al., 2006). Deselection also included crayfish with small claws relative to their body size because this indicates previous loss of a claw that is in the process of growing back. The sex of the crayfish was recorded. However, both males and females exhibit no significant differences in activity (Guan, 1994), so the influence of this was not considered in the experiments.

The animals were housed individually, each in an aquarium constructed from a plastic box (0.6×0.4×0.4 m) that had black, opaque sides, as it is known that crayfish survival increases in dark environments (Lewis, 2002) and darkness avoided the experimental complications associated with shadows or movements within the laboratory. Each aquarium had a secure lid with a central opening of 480×240 mm that was covered in wire mesh to prevent escape. Ten aquaria were used simultaneously. The investigation of intra-specific interaction was not an aim of these experiments, as contact between crayfish can lead to behaviour that is highly variable and this would incorporate increased variability into the results, potentially confounding the identification and analysis of trends relating the impact of crayfish to the length of exposure on the gravel bed and grain size.

Water temperature was not controlled, but it was monitored and remained consistent between the 10 aquaria, staying between 15 and 21 °C for the duration of the experiments. This is well within the temperature range of signal crayfish (Nakata et al., 2002) and is similar to recorded temperatures in other laboratory studies (Crawshaw, 1974; Mundahl and Benton, 1990; Basil and Sandeman, 2000). Each aquarium had a filter pump that circulated water through the tank, removing waste and aerating the water. No shelter was provided for the crayfish whilst experiments were running in order to encourage activity. Pellet fish food had been provided before the start of each experiment and every other day when individuals were not involved in experiments.

### 2.2. Experimental procedure

The gravel surface in each aquarium was screeded flat to form a 0.1 m deep, planar substrate, sufficiently deep for crayfish to burrow without reaching the base of the aquarium. A digital elevation model (DEM) of the initial surface was interpolated from a laser scan obtained using a Konica Minolta tripod-mounted laser scanner. Water was then introduced to a depth of 0.2 m above the gravel surface with great care to avoid rearrangement of substrate grains. The filter pump was activated and a single crayfish was released ~50 mm above the gravel surface, allowing it to drift slowly onto the bed. Each crayfish was left on a prepared gravel surface in the aquarium for a predetermined period, after which it was removed by hand and the water drained slowly through a tap in the base so as not to disturb the gravel. Once drained, the gravel surface was scanned for a second time.

Three-dimensional spot-height data were obtained from a single laser scan in each case, the axis of the scanner being perpendicular to the gravel surface, yielding ~240 000 irregularly spaced *x*, *y*, and *z* coordinates with an average *xy* spacing of 1 mm. This surface was gridded to form a raster DEM using a kriging interpolation in ArcGIS. All surface analysis was undertaken on raster DEMs in ArcGIS. The difference between DEMs before and after crayfish activity was calculated by subtracting one surface from the other to create a new surface where *z*-values represent the topographic change between surfaces. This DEM of difference (DoD), had a zero plane that represented no topographic change. The roughness of surfaces was parameterized and compared using the standard deviation of elevations from the raster models (Nikora et al., 1998; Aberle and Smart, 2003). In order to estimate the number of grains that were displaced by the crayfish on each substrate, half of the total volume change was divided by the average grain volume of each grain size fraction, after allowing for a porosity of 0.3 (Bunte and Abt, 2001). Half of the total change was used because the DoDs reflect a volume change associated with the new location of a transported grain as well as the void it has left. Grain volume was approximated by assuming an ellipsoid and using average values of the principal axes measured on a subsample of grains from each grain size fraction.

### 2.3. Experimental variables

Three series of experiments were conducted, all following the procedure described above. The first (series 1) examined how gravel disturbance changed with the length of time that a crayfish was left on a substrate. Screened, 8–11 mm (3–3.5  $\phi$ ), marine gravel was used. This consists mainly of chert with a grain density of 2650 kg m<sup>-3</sup>. Clasts were predominantly compact-bladed (Sneed and Folk, 1958) and rounded (0.6 particle roundness; Krumbein, 1941). Crayfish were left on this substrate for either 6, 24, 48, 72, or 96 h, with 10 replications for each period.

A second series of experiments (series 2) also investigated the influence of the period of potential substrate reworking. In this case, shorter intervals of animal occupance were used to obtain a higher resolution data set, but without replication of each time period. A single crayfish was again left on a screeded, 8–11 mm (3–3.5  $\phi$ ), gravel bed for a set period. These periods increased in length by 30 min up to 24 h and then by 60 min up to 96 h. Ten crayfish were used in these experiments and, for each animal and any run of the series, the set period was varied. In each case, DEMs were obtained at the beginning and end of the set period, giving a total volume of disturbance for that period. An accumulating increase in the volume change could not be measured as it was necessary to drain aquaria before laser scanning. Consequently, after each period, the surface was re-set to planar by screeding and a different crayfish was left on this re-set surface for a new set period.

The third series of experiments (series 3) aimed to determine what grain sizes could be moved. To establish this limit, individuals were left on one of six narrowly graded and screeded grain sizes (Table 1). These grain size fractions were determined after

considering the *b*-axis diameter and particle weight. The gravel was predominately bladed (Sneed and Folk, 1958) and well rounded (0.8 particle roundness; Krumbein, 1941), allowing for an incidental consideration of the influence of grain shape through comparison with series 1, as well as size, on substrate reworking by crayfish. The gravel used in series 3 was obtained from the River Lune, England, it consists mainly of limestone with minor contributions of sandstone, and it has a grain density of 2580–2620 kg m<sup>-3</sup> (Graham et al., 2005; Table 1). Crayfish were left on each screeded substrate for 24 h, with 10 replications for each grain size.

### 2.4. Error analysis

An analysis was undertaken of the error associated with measurements derived from DoDs. The general experimental procedure described above was repeated 10 times with 8–11 mm (3–3.5  $\phi$ ) gravel, but without adding crayfish. Consequently, the two DEMs obtained for each of the 10 experiments should be identical, and the DoDs should be flat surfaces on the zero plane. The results showed that errors ranged between -0.96 and 0.79 mm, with a mean value of -0.05 mm. The distribution of errors was leptokurtic and, as a result, significantly non-normal (Kolmogorov–Smirnov  $p < 0.001$ ), indicating that a relatively small proportion of the distribution was associated with its tails. The distribution of error was not biased towards particular regions of the DoD surface; and the laser scanner does not produce systematic distortions, such as those associated with conventional photography, so no corrections are required. The measured error is associated partly with the mechanical error of the laser scanner (quoted by the manufacturer as 0.4 mm in the *z*-axis) and partly with the experimental procedure, including small scale dilation or consolidation of the substrate when submerged and subsequently drained. The interpolation of height values between measured points during DEM construction may also introduce small errors to the overall analysis, but because of the density of data in this study (1 point per mm over a surface of 600 × 400 mm), this source of error is likely to be negligible. The measurement error was taken into account in the analysis of results by using  $\pm 1$  mm as the minimum discernable difference. Consequently, differences  $\leq \pm 1$  mm were considered to indicate no topographic change.

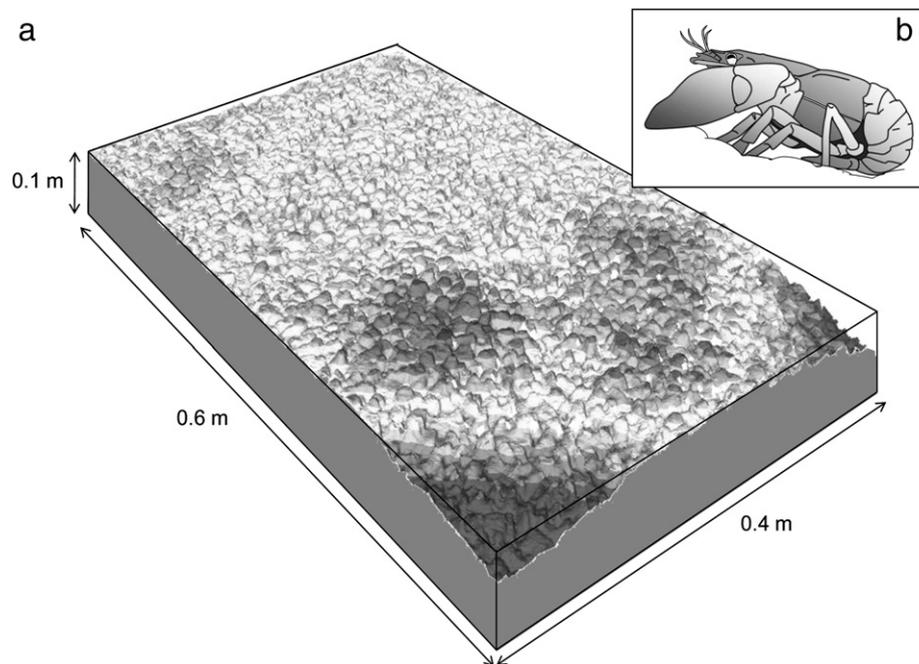
## 3. Results

### 3.1. Methods of bed sediment disturbance by crayfish

Crayfish were observed to disturb the substrate in two distinct ways. The first was a rearrangement of surface grains that resulted in subtle adjustments of grain fabric. This was associated with walking and foraging. The second was visually more dramatic and was associated with the construction of pits and mounds for shelter (Fig. 1). These two types of disturbance have been quantified by partitioning the topographic change to the initial planar surface. Fabric adjustment—the rearrangement of surface grains—has been defined as the volume of topographic change in those areas beyond pits and mounds where change in surface height exceeded the minimum discernable difference of  $\pm 1$  mm, but was  $\leq \pm 1$  median grain diameter ( $D_{50}$ ); for areas where elevation changes were  $\geq \pm 1 D_{50}$ , calculated volumes have been attributed to pit digging and mound building, respectively. Whilst the incorporation of some mound material and pit excavation in the fabric adjustment volume is possible, the adoption of  $1 D_{50}$  as the height change discriminator has ensured that this is minimized, given that all grains were narrowly graded and superimposition of a single grain on the screeded surface or removal of a single grain from the pit precinct would, on average, produce a height change  $> 1 D_{50}$ .

**Table 1**  
Characteristics of gravels. The submerged weight was measured from a 100 grain subsample of material from each grain size fraction.

Grain size ( <i>b</i> -axis, mm)	Average clast volume (cm <sup>3</sup> )	Average clast submerged weight (g)	Average clast submerged density
8–11	0.6	0.97	1.62
11–16	1.7	3.4	1.65
16–22	4.7	7.5	1.6
22–32	14.2	21.4	1.58
32–38	32.1	53.7	1.62
38–45	76.2	121.9	1.6



**Fig. 1.** a) Digital Elevation Model (DEM) of an 11–16 mm gravel surface after 72 h of exposure to a signal crayfish. The surface was originally planar and horizontal. Note the two pits in the bottom corners of the DEM that are surrounded by shallow mounds (shaded). b) Cartoon of the posture of a crayfish when sitting in a pit.

Pits were generally larger in volume than associated mounds (paired *t*-test;  $p < 0.001$ ), but only because excavated material tended to be spread fairly widely across the substrate surface and, using the definitions given above, part has been unavoidably incorporated within the measure of fabric adjustment. The spreading of material was a combination of effort to push gravel away from pits to avoid slumping and an incidental result of activity associated with the brushing of grains when walking during forays. After 24 h on 8–11 mm gravel, pits were, on average, 21 mm ( $2.2 D_{50}$ ) deep, increasing to 29 mm ( $3.1 D_{50}$ ) after 96 h. Conversely, mounds were 16 mm high after 24 h and 17 mm high after 96 h, an increase of only 1 mm despite the same lapse of time. This is because crayfish aim at rapidly deepening pits for shelter, but derive no benefit from increasing the height of mounds. Indeed, distributing mound material widely, even if some or most of this is inadvertent, reduces its height and may ensure that both predators and competitors are seen earlier.

### 3.2. Substrate reworking and length of exposure

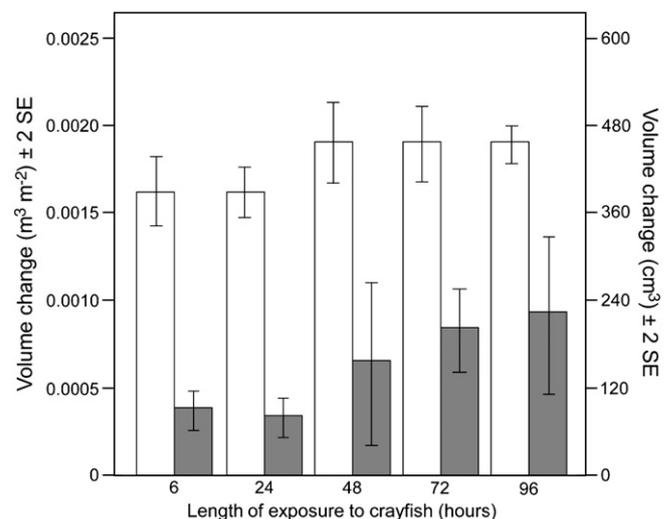
Crayfish were able to move substantial volumes of 8–11 mm gravel within 6 h of being introduced to the substrate (series 1; Fig. 2). Length of time of activity was significant for both fabric adjustment (ANOVA;  $p = 0.047$ ) and pit and mound construction (ANOVA;  $p = 0.041$ ). However, Tukey post-hoc tests do not extract which time period is significantly different due to the discrepancy in statistical power between the two tests (Table 2). Fig. 2 shows that the majority of grain displacements occurred in the first 6 h. It also shows a stepped increase in volume change at 48 h for both fabric adjustment and pit and mound construction. Of interest is that pit and mound construction accounts for a relatively small proportion of the volume change, by comparison with fabric rearrangement. Indeed, in this series of experiments on 8–11 mm substrates, an average of 22% (range: 4–56%) of the material that was moved was associated with the excavation of pits and the construction of mounds, the remainder being associated with fabric adjustments.

Fig. 3 shows the volume of material moved by crayfish over periods ranging from 0.5 to 96 h (series 2). Each data point represents a single surface, with volume changes from an individual crayfish plotted against the length of time of exposure. Ten crayfish were used

in these experiments, and the impact of each is indicated by a different symbol. The results show an initial period of disturbance followed by a prolonged period when the total volume of material moved did not significantly increase further. The greatest rate of activity was in the first 3–5 h and the majority of bed disturbance occurred within the first 10–15 h of crayfish presence. Beyond about 15 h, the total volume change was generally indiscernible, except in those few cases where significant proportions (>10%) of the surface were associated with late-stage pit and mound construction.

### 3.3. Grain size and the movement of gravel

Crayfish moved a wide range of grain sizes, but did not move grains coarser than 38 mm in diameter (series 3; Fig. 4). These 38 mm



**Fig. 2.** Mean (and two standard errors,  $n = 10$ ) of surface volume change arising from the introduction of a single crayfish to a screeded, planar, submerged, 8–11 mm gravel surface ( $2400 \text{ cm}^2$ ) for each of five intervals (6, 24, 48, 72, and 96 h) (series 1 experiments). For each interval, unshaded bars indicate fabric adjustment and grey bars indicate pit and mound construction.

**Table 2**

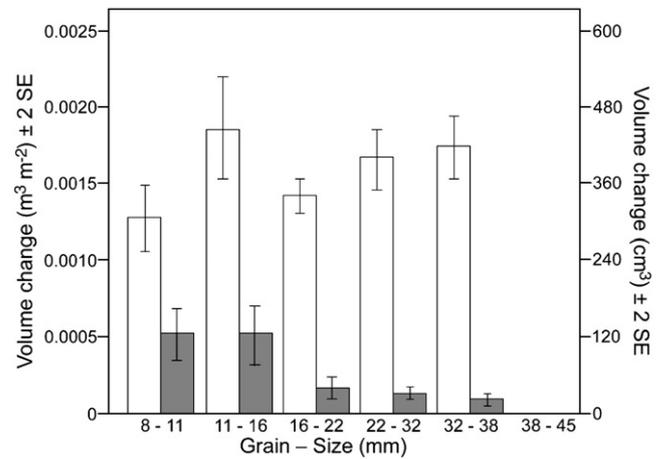
Tukey post-hoc *p* levels of differences in the volume change in gravel surfaces exposed to crayfish for one of five time periods: 6, 24, 48, 72 and 96 h. The length of time present is statistically significant (ANOVA; *p* = 0.047) but Tukey post-hoc does not determine which variables are significantly different, hence all *p* values > 0.05.

	6	24	48	72	96
6		1.000	0.360	0.142	0.090
24	1.000		0.297	0.110	0.068
48	0.360	0.297		0.985	0.946
72	0.142	0.110	0.985		0.999
96	0.090	0.068	0.946	0.999	

grains had a mean submerged weight of 54 g, corresponding to six times the mean submerged weight of the crayfish. Of interest is that pit and mound construction became less prevalent as grain size increased (Fig. 4). Indeed, it became indiscernible where the gravel exceeded 22 mm, at least for the size of crayfish used in these experiments (Fig. 5).

The volume change differs between grain size fractions for both fabric adjustment (ANOVA; *p* = 0.003) and pit and mound construction (ANOVA; *p* < 0.001) (Fig. 4). Whilst the only significant difference identified by post-hoc tests for fabric adjustment was that between 8–11 mm and 32–38 mm substrates (Tamhane T2; *p* = 0.48), Fig. 4 suggests a greater volume of 11–16 mm material has been moved than is the case with fractions both finer and coarser. As this cannot be explained by particle weight alone, it is suggested that it is a function of the relation between grain weight and volume (Table 1). The 8–11 mm grains were light enough for crayfish to cause widespread disturbance, but were each of such small volume (0.6 cm<sup>3</sup>) that the cumulative volumetric impact was limited. The 16–22 mm grains were heavy enough to limit crayfish disturbance, but each had a large volume (4.7 cm<sup>3</sup>) so that only a few grains needed to be disturbed to match the volume of displaced 8–11 mm material. In contrast, the 11–16 mm grains are both light enough for crayfish to move easily whilst also having a large enough volume (1.7 cm<sup>3</sup>) to account cumulatively for the large volume of moved material.

Estimates of the number of grains displaced by the crayfish on each substrate are presented in Fig. 5, where the inverse exponential relation between mobilized grain numbers and grain diameter reflects the direct relation between individual grain weight and the cube of its

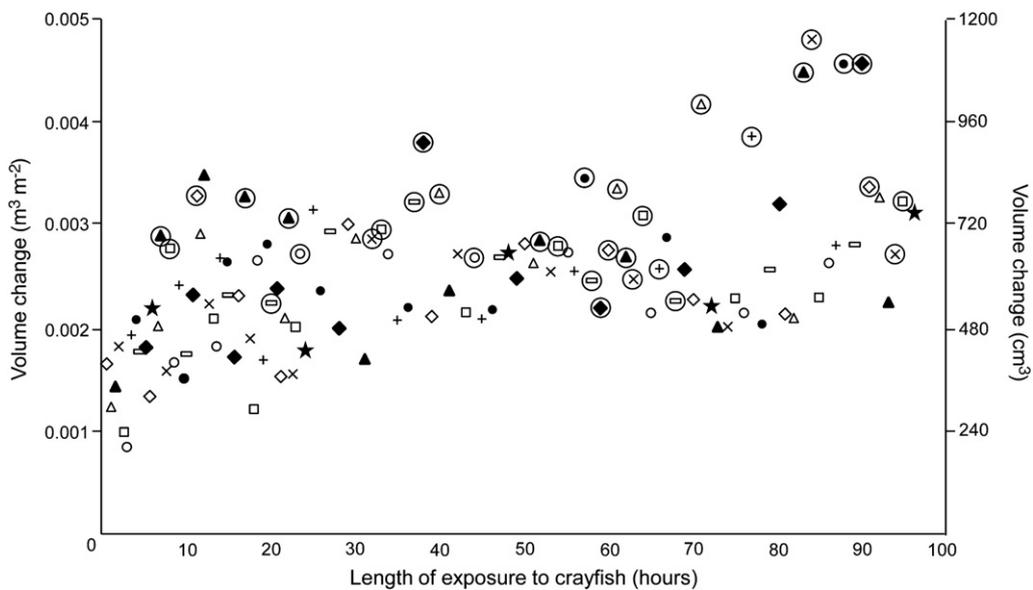


**Fig. 4.** Mean (and two standard errors, *n* = 10) of surface volume change arising from the introduction of single crayfish on a screeded, graded, planar, submerged, gravel surface (2400 cm<sup>2</sup>) of specified grain size for 24 h (series 3 experiments). For each gravel grade, unshaded bars indicate fabric adjustment and grey bars indicate pit and mound construction.

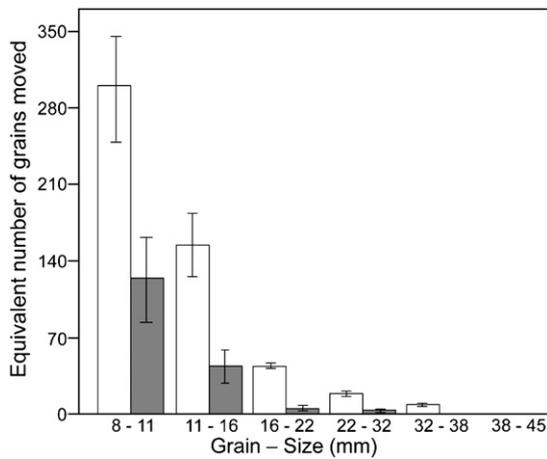
radius, size-fraction by size-fraction. A grain size of 16 mm appears to be a break-point, with considerably fewer equivalent grain volumes moved from surfaces composed of larger and, therefore, heavier grains. Also to be noted is the small number of grains that were moved as pit and mound construction in substrates where grain size lies between 16 and 32 mm. Furthermore, notice should be taken of the fact that no disturbance at all was recorded where grain submerged weight exceeded 54 g (i.e. >38 mm), not even minor amounts of fabric adjustment.

**3.4. Changes to surface roughness**

The surface roughness of gravel, parameterised as the standard deviation of bed elevations from DEMs, increased with the length of time crayfish were present (Fig. 6). However, only those surfaces that had had at least 72 h of exposure to crayfish activity were significantly different from control surfaces (which are shown at time equals zero in Fig. 6; Tamhane T2, *p* = 0.011). The increase in morphological



**Fig. 3.** The total surface volume change arising from the introduction of a single crayfish to a screeded, planar, submerged, 8–11 mm gravel surface (2400 cm<sup>2</sup>) for a predetermined period. Ten crayfish (each identified by a specific symbol) were deployed for periods ranging from 0.5 to 96 h (series 2 experiments) after which they were removed and the surface scanned. After scanning, the surface was re-set to planar by screeding. Stars represent the mean volume change derived from series 1 experiments (Fig. 2). Those surfaces with ≥ 10% of their area associated with pit and mound construction are circled.



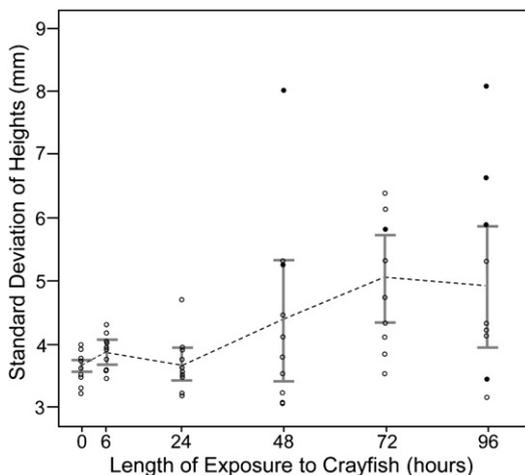
**Fig. 5.** Mean (and two standard errors,  $n=10$ ) of the equivalent number of grains moved by a single crayfish on a screeded, graded, planar, submerged gravel surface ( $2400 \text{ cm}^2$ ) of specified grain size for 24 h (series 3 experiments). For each gravel grade, unshaded bars indicate fabric adjustment and grey bars indicate pit and mound construction.

roughness associated with crayfish is due to the construction of pits and mounds, which increase in volume through time (Fig. 2). Thus, a strong correlation exists between the morphological roughness of the surface and the total fractional area occupied by pits and mounds ( $r^2 = 0.675$ ,  $p < 0.001$ ; Fig. 7).

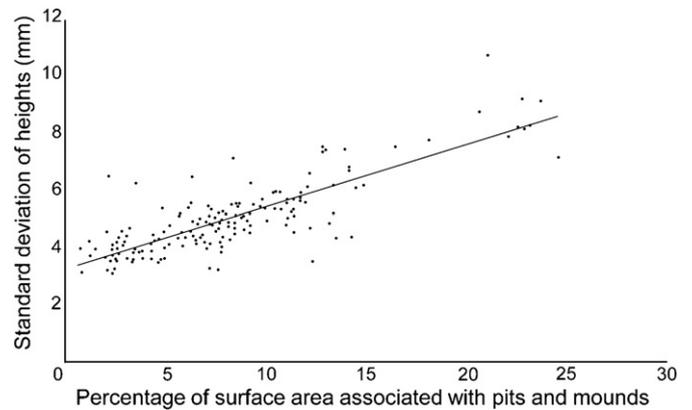
#### 4. Discussion

##### 4.1. Linking the still-water experimental results to gravel bed rivers

Crayfish moved grains up to 38 mm in diameter, each weighing six times that of each of the individuals used in these experiments and reflecting significant amounts of work, especially since much of the displacement involved upslope movements from within a pit. However, in this study, grains were moved from narrowly graded substrates, and it is possible that similar-sized crayfish might be capable of moving coarser grains with ease if these were in a bed of mixed sizes, where coarse clasts would have smaller pivot angles if they were sitting relatively proud on a finer bed. It should also be remembered that these experiments were conducted in still-water



**Fig. 6.** Morphological roughness, defined as the standard deviation of spot heights (mm spacing) of a screeded, submerged, 8–11 mm gravel surface exposed to the actions of a single crayfish for intervals of 6, 24, 46, 72, and 96 h (series 1). The roughness of control surfaces unaffected by exposure to crayfish is given at time zero. Surfaces with significant pit and mound construction ( $\geq 10\%$  surface area) are marked by filled circles. The pecked line links the means of each experimental interval.



**Fig. 7.** Relation between surface roughness, defined as the standard deviation of spot heights (mm spacing), of initially screeded, planar, 8–11 mm gravel surfaces, each exposed while submerged to a single crayfish for varying intervals up to 96 h, and the percentage of the surface area associated with pit and mound construction. The linear regression ( $y = 0.2119x + 3.1982$ ) has an  $r^2$  value of 0.675 ( $p < 0.001$ ).

aquaria and alteration of gravel microtopography might differ in lotic environments. Here, crayfish might need to exert a reduced force in order to mobilise grains in comparison with that required in still-water due to the simultaneous impact of the flow, at least when moving grains in a downstream direction. The opposite would obtain, of course, were material being moved in an upstream direction. Another factor not present in these experiments is inter- and intra-specific interactions. These impact on the activity of crayfish and are, consequently, likely to affect the nature and magnitude of substrate reworking by crayfish. For instance, the presence of a predator might instigate the digging of a shelter. Also, signal crayfish form a hierarchical social structure where dominance increases burrowing and a suppression of burrowing is found in subordinates (Herberholz et al., 2003). Therefore, biotic interactions, including social contact between crayfish, are likely to have complex effects on the extent and significance of their geomorphic impact.

##### 4.2. The impact of crayfish on the microtopography of substrates

The impact of crayfish on the microtopography of gravel river beds can be assigned to two distinct types. First, pits and mounds were found on the majority of surfaces where grain size was finer than 16 mm and, despite representing a relatively small proportion of the overall volume of disturbance, they produced the most obvious topographic change. Pits are dug to provide shelter by either piling up grains using the first two pairs of walking legs and then pushing the body into the pile, “bulldozing” these grains forward, or pushing the large claws (chelae) into the gravel and levering or pushing grains out from the bed. While burrowing by crayfish into cohesive sediments has been widely reported (Guan, 1994; Barbaresi et al., 2004), the excavation of noncohesive bed material has not been examined in detail, despite having been observed in both the field and laboratory (Itagaki and Thorp, 1981; Parkyn et al., 1997; Herberholz et al., 2003). In the experiments reported here, the majority of pits were situated in the corners of the aquaria, but some were dug in central regions. However, while crayfish were in holding tanks between experiments, we also observed them excavating gravel (8–11 mm) from between coarse clasts in order to increase the suitability of such crevices as shelters. This is consistent with field observations of the species *Paranephrops planifrons* in New Zealand (Parkyn et al., 1997). It implies that heterogeneous substrates, which are not uncharacteristic of many gravel bed rivers, may provide different opportunities for digging due to the presence of such coarse grains.

We hypothesise that pits excavated in the current experiments are makeshift shelters that are constructed when more appropriate

retreats, such as macrophyte stands or burrows in cohesive banks, are not available. This implies that more bed material will be excavated by crayfish when these other shelters are not available. In support of this, [Statzner et al. \(2000\)](#) found that the total erosion of material from artificial channels where crayfish were provided with shelters was  $2.8 \text{ kg m}^{-2}$ , whereas this increased to  $4 \text{ kg m}^{-2}$  when shelters were removed. They interpreted this as being due to an increase in aggression associated with lack of shelter. However, the results of the present study suggest that the cause of the increased bedload flux observed by [Statzner et al. \(2000\)](#) might be due, at least in part, to increased excavation and destabilization of the substrate by crayfish constructing shelters.

The importance of the second type of disturbance by crayfish became evident only after the DoDs were analysed. This was associated with the more subtle rearrangement of surface grains as the crayfish brushed past them when walking and foraging. Grains that protruded on the substrate surface were particularly susceptible to being knocked. Fabric adjustment accounted for the majority of the volume change in gravels finer than 38 mm. The majority of this rearrangement involved in situ movement of grains, such as changes in orientation and friction angle. Previous studies have also suggested that body contact by crayfish is important in promoting sediment transport, particularly for fine material ([Statzner et al., 2000](#); [Usio and Townsend, 2004](#)). Crayfish also rearranged surface gravels by probing the bed. They were observed to stop walking and push the small claws on their first and second pairs of walking legs into interstitial spaces. In addition, they would occasionally pick up grains finer than 16 mm with their first pair of legs and rotate them in front of their mouth before dropping them back onto the substrate. This is likely to be a foraging behaviour and is similar to that observed in *P. planifrons* which “lift and jostle small stones” with walking legs when looking for food ([Parkyn et al., 1997](#), p. 689). All of these actions caused a reorientation and displacement of grains finer than 16 mm by distances of generally  $<1 D_{50}$ . As the grain size increased (series 3), the disturbance caused by probing was reduced because crayfish could fit their legs into interstitial spaces with less, or no, disturbance of the surrounding grains.

#### 4.3. The impact of grain size and length of exposure on topographic alterations by crayfish

By expressing the movement of material in terms of the equivalent number of grains, it is apparent that disturbance involved many more grains in substrates finer than 16 mm ([Fig. 5](#)). This was expected, given the submerged weight of individual clasts in each of the graded beds. In addition, there appeared to be an abandonment of any attempt at pit and mound construction in substrates coarser than 16 mm. This is almost certainly because larger grains are much more difficult to dislodge. However, in addition to weighing more, larger grains also require the simultaneous dislodgement of similar-sized neighbours because of restraint by grain–grain interlock. It is not surprising, therefore, that there is a limit to the size of material that can be moved ([Fig. 4](#)). As a result, grains coarser than 16 mm were rarely displaced, whereas grains finer than 16 mm were regularly displaced through distances of multiple  $D_{50}$ . This implies that the extent of reworking by signal crayfish will be greater on gravels finer than 16 mm, at least for animals of the size used here, despite their ability to move coarser grains.

A substantial volume of gravel was moved within 6 h of the introduction of crayfish to a surface. Little extra material was moved with further exposure except where significant pit and mound construction took place later ([Fig. 3](#)). This pattern of behaviour is consistent with qualitative observations made by others ([Basil and Sandeman, 2000](#); [Patullo and Macmillan, 2006](#)). Crayfish initially explored a new habitat—in this case aquaria with subdued illumination—by walking along the edges of the substrate and then crossing

into the central area of the gravel surface. This initial exploration led to a rapid alteration of the surface grain fabric. After a few hours, individuals selected a location, normally a corner, where they remained at rest, sometimes for an extended period. During this phase, crayfish often excavated a pit, within which they sheltered. From this shelter, crayfish continued to venture periodically, exploring the aquarium, usually returning to the pit after a period of several minutes. After approximately 38 h, there was often a noticeable amount of renewed activity that was sometimes associated with substantial expansion of a pit. This lapse might reflect the period of time it took crayfish to acclimatize to the substrate and it is this renewed activity, coupled with pit and mound construction, which accounts for the increase in volume change at 48 h and beyond in the experimental runs of series 1 ([Fig. 2](#)) and the late-stage outliers in series 2 ([Fig. 3](#)).

The total volume of topographic change between initial and crayfish disturbed surfaces during a 24 h period (series 3) was consistent for all grain sizes except 11–16 mm, with an overall mean of  $450 \text{ cm}^3$  (S.D. =  $123 \text{ cm}^3$ ) from surfaces, each of  $2400 \text{ cm}^2$ . Interestingly, this volume change is consistent with the time-series experiments of series 1, where an average change of  $469 \text{ cm}^3$  (S.D. =  $89 \text{ cm}^3$ ) was recorded for the same period. As different shaped gravels were used in these two series, the similarity of the quantity of material moved suggests that the work performed was not affected by grain shape. Crayfish would have had to move only  $225 \text{ cm}^3$  of gravel to create an average, 24 h, volume change of  $450 \text{ cm}^3$ . Given a bulk density of  $1830 \text{ kg m}^{-3}$ , this equates to a disturbance of  $1.7 \text{ kg m}^{-2} \text{ d}^{-1}$ . We can compare and contrast this with the results of [Statzner et al. \(2000\)](#), who found that the activity of 10 crayfish in a small flow channel resulted in maximum transport of a sand–gravel mixture of  $4 \text{ kg m}^{-2} \text{ d}^{-1}$ . In this context, our still-water experiments, each run involving a single animal, suggest that the actions of the crayfish in either directly displacing or preparing material for movement by the flow could be of considerable significance.

#### 4.4. Potential impact on sediment transport of topographic changes induced by crayfish

The changes in surface roughness from pit and mound construction undoubtedly influence the local near-bed hydraulic environment. Protuberances on the bed have a significant influence on flow resistance through form drag ([Brayshaw et al., 1983](#); [Hassan and Reid, 1990](#); [Robert, 1990, 1997](#); [Lawless and Robert, 2001](#)) and also induce a complex and variable hydraulic environment, including local reversal of the boundary shear stress vector ([Buffin-Bélanger et al., 2006](#); [Garcia et al., 2007](#)). A heterogeneous near-bed hydraulic environment has a significant impact on the presence and behaviour of benthic organisms that reside on the substrate ([Carling, 1992](#); [Lancaster et al., 2006](#); [Rice et al., 2008](#)) and on the entrainment of bed material ([Schvidchenko and Pender, 2001](#)). Pit and mound construction results in changes to the local bed slope which have an impact on gravel entrainment through an increase or decrease in friction angle ([Hardisty and Whitehouse, 1988](#)). Pits and mounds also alter the degree of protrusion or “hiding” of grains. [Fenton and Abbott \(1977\)](#) found that changes in grain protrusion of less than  $1 D_{50}$  in an otherwise planar bed alters the critical shear stress by an order of magnitude. Here, in 8–11 mm material, mounds were, on average,  $1.8 D_{50}$  high and pits were  $2.7 D_{50}$  deep, which would, in flowing water, entail significant alterations to the stresses exerted on protruding or “hiding” grains.

Although less material was moved through distances  $\geq 1 D_{50}$  in substrates coarser than 16 mm, the ability of crayfish to dislodge larger grains might be of significance in preparing the river bed for sediment transport, given the limited entrainment of coarse, framework grains by marginally competent flows, the majority of which transport only fine material over and between the more stable framework ([Church et al., 1991](#); [Lisle and Madej, 1992](#); [Wilcock and](#)

McArdell, 1997). In field experiments, Church and Hassan (2002) found that 16–45 mm grains were mobilised only when boundary shear stress exceeded  $27 \text{ N m}^{-2}$ . In a Scottish river with a surface  $D_{50}$  of 32–45 mm, Wathen et al. (1995) similarly found that material coarser than 16 mm rarely moved except in the largest flood events and that it made up <50% of the bedload even when shear stress exceeded  $30 \text{ N m}^{-2}$ . These examples remind us that coarse bed material in the range that crayfish can displace is only infrequently moved by the flow and, consequently, this leads us to speculate that crayfish may be an important force acting on material coarser than 16 mm, especially during extended periods of low to modest flow that typically occur between flood events or flood seasons. While such disturbance will not in itself result in downstream displacement, it might act to reduce the integrity of surface structure, thereby enhancing the potential for subsequent displacement of coarser grains as part of the bedload by reducing critical entrainment stresses. Disturbance of these coarse grains might then promote the mobilisation of finer clasts which had formerly been sheltering in sub- and adjacent positions beneath and between the now displaced coarse clasts.

Because they alter grain fabric and protrusion, and because they are not limited to movement in a downstream direction, crayfish might significantly counter the structuring and consolidation of gravels by the flow. So, where active, they might oppose abiotic factors that have been identified as accounting for differences in entrainment mechanics at the start and finish of bedload transport, such as grain clustering, matrix development and the length of time for granular consolidation between bed-disturbing flows (Reid and Frostick, 1984; Reid et al., 1985; Reid and Hassan, 1992). They might also reduce the impact of other biotic factors that add strength to the bed, such as the production of silk bonds by caddis larvae (Johnson et al., 2009) and the growth of algal films (Gerbersdorf et al., 2008). The consolidation and structuring of gravel substrates occurs during extended periods of low flow, and it is during these periods that crayfish will be most active (Light, 2003). So, extended periods of minimal hydraulic disturbance will allow the cumulative impact of crayfish to increase. It is known that crayfish can significantly reduce the accumulation of fines in gravel substrates by winnowing sand grains (Parkyn et al., 1997; Statzner et al., 2000, 2003; Creed and Reed, 2004; Usio and Townsend, 2004) and the present study has found that crayfish can modify the protrusion, orientation, and friction angle of surface framework grains. It follows, therefore, that crayfish may have substantial impact in preparing bed material for entrainment during subsequent floods.

#### 4.5. The ecological implications of disturbance by signal crayfish

Crayfish have a complex influence on the ecological community structure. They have an important functional role in aquatic ecosystems, shredding coarse organic matter into finer pieces, which facilitates the presence of other invertebrate taxa (Schofield et al., 2001; Usio and Townsend, 2001). The beneficial impact of crayfish in providing fine organic material counters the negative impacts on species diversity and abundance that are associated with their efficiency as predators (Parkyn et al., 2001). Where they are invasive, they are known to have substantial negative ecological impacts on juvenile fish, native crayfish and other invertebrate species, which they predate and out-compete for resources, such as shelter (Guan and Wiles, 1997; Holdich et al., 1999; Vorbürger and Ribi, 1999; Usio et al., 2001; Stenroth and Nyström, 2003; Crawford et al., 2006). They also significantly reduce macrophyte and algal cover, removing sources of food and shelter used by other animals (Creed, 1994; Lodge et al., 1994; Nyström et al., 1996).

Besides these ecological impacts, signal crayfish also alter substantially the physical environment by reducing bank stability, increasing water-column turbidity and discouraging the accumula-

tion of fine sediment (Guan, 1994; Statzner et al., 2000; Angeler et al., 2001; Usio and Townsend, 2004) and, as shown by the present study, modifying the microtopography and grain-grain fabric of gravel substrates. These physical alterations may impact the ecological community directly or indirectly, further complicating the role of signal crayfish in invaded environments, particularly where they occur at high densities, which can exceed  $10^1 \text{ m}^{-2}$ .

## 5. Conclusions

The impact of large invertebrates on the fabric and topography of subaqueous gravelly substrates is significant. The presence of a signal crayfish for 24 h has been shown to produce an average volume change in surface topography of  $450 \text{ cm}^3$  in an area of  $2400 \text{ cm}^2$ , equating to a displacement of  $1.7 \text{ kg m}^{-2} \text{ d}^{-1}$ . Crayfish do not act uniformly over a substrate, nor do they act steadily over time. The impact of any organism is conditioned by its behaviour in relation to its life cycle, by environmental factors such as substrate grain size distribution, flow regime, and temperature, and by the presence or absence of other organisms, especially predators and competitors. The interaction of all these will make some gravelly river beds more susceptible to crayfish disturbance than others. It is also likely that the impact of crayfish will be greatest when disturbance by the flow is highly episodic, leaving long intervening periods for their effects to build. During such extended periods of low flow, gravel substrates are thought to consolidate. This study suggests that invasive crayfish may oppose this stabilisation process, jostling grains into less stable positions and increasing grain exposure through the mounding of material excavated from pits. Both will affect gravel stability during subsequent flood events, and we hypothesize that beds subjected to the activity of crayfish are likely to be less stable than those which are not.

Signal crayfish are a widespread, internationally important, invasive species, which is known to have detrimental impacts on native plants, fish, and invertebrate populations, including other species of crayfish. This study shows that they also have potentially significant effects on the streambed physical environment, adding to the catalogue of geomorphic impacts attributed to biota.

## Acknowledgments

We would like to thank three anonymous reviewers for their extensive commentaries, which have helped us improve the clarity of the paper. We would also like to thank Barry Kenny, Stuart Ashby, and Dr. Julian Green for help with equipment, Dr. David Graham and Mark Szegner for their advice regarding analysis of DEMs, and Richard Gravelle, Sally Little, and Mary Sattenstall for help catching crayfish. MFJ was in receipt of a Loughborough University Postgraduate Studentship.

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