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Invasive crayfish as drivers of fine sediment dynamics in rivers: field and laboratory evidence

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ABSTRACT

Despite increasing recognition of the potential of aquatic biota to act as ‘geomorphic agents’, key knowledge gaps exist in relation to biotic drivers of fine sediment dynamics at microscales and particularly the role of invasive species. This paper explores the impacts of invasive signal crayfish on suspended sediment dynamics at the patch scale through laboratory and field study. Three hypotheses are presented and tested: (1) that signal crayfish generate pulses of fine sediment mobilisation through burrowing and movement that are detectable in the flow field; (2) that such pulses may be more frequent during nocturnal periods when signal crayfish are known to be most active; and (3) that cumulatively the pulses would be sufficient to drive an overall increase in turbidity. Laboratory mesocosm experiments were used to explore crayfish impacts on suspended sediment concentrations for two treatments: clay banks and clay bed substrate. For the field study, high frequency near-bed and mid-flow turbidity time series from a lowland river with known high densities of signal crayfish were examined. Laboratory data demonstrate the direct influence of signal crayfish on mobilisation of pulses of fine sediment through burrowing into banks and fine bed material, with evidence of enhanced activity levels around the mid-point of the nocturnal period. Similar patterns of pulsed fine sediment mobilisation identified under field conditions follow a clear nocturnal trend and appear capable of driving an increase in ambient turbidity levels. The findings indicate that signal crayfish have the potential to influence suspended sediment yields, with implications for morphological change, physical habitat quality and the transfer of nutrients and contaminants. This is particularly important given the spread of signal crayfish across Europe and their presence in extremely high densities in many catchments. Further process-based studies are required to develop a full understanding of impacts across a range of river styles.

KEY WORDS: invasive species; *Pacifastacus leniusculus*; suspended sediment dynamics; turbidity; river management

INTRODUCTION

Fine sediment, comprising sand, silt and clay, accounts for the majority of total fluvial sediment flux, and has important implications for catchment water resource management, particularly since changes in fine sediment dynamics can modify sediment yields and initiate morphological adjustments downstream (Walling and Collins, 2008). Such changes may have implications for channel morphology and conveyance capacity, aquatic ecosystem health and chemical water quality. For instance, aggradation of fine sediments can degrade aquatic habitats, reduce survival rates of fish and aquatic invertebrates (Marks and Rutt, 1997; Heywood and Walling, 2006), alter community structure (Wood and Armitage, 1997) and undermine river restoration efforts (Kondolf, 1998) as well as reduce flow conveyance, with the potential to increase flood risks (Singer et al., 2008). In addition, fine sediments play a significant role in the transport of both nutrients and pollutants within fluvial environments (Bowes et al., 2003; House, 2003; Carter et al., 2006), with implications for water quality.

Fine sediment dynamics can be classified into three domains with associated modes of explanation (Naden, 2010). At the catchment scale, fine sediment flux is determined primarily by the geomorphological characteristics of the fluvial system and the history of erosion and sediment transfer (e.g. Trimble, 1983). Time-scales of interest in determining catchment fine sediment fluxes may range from years to centuries, and catchment sediment budgets may be created from estimates of fine sediment storage and the apportionment of sediment sources (e.g. using fingerprinting techniques; Oldfield et al., 1979). At the reach-scale of river systems, fine sediment flux is usually explored through measurement of suspended sediment concentrations (and/or water turbidity) and discharge. The amount of fine sediment transported by rivers typically follows a power law relationship with discharge (e.g. Bogardi, 1974), but often with large amounts of scatter in the relationship resulting from factors such as seasonal variability (e.g. associated with the growth and senescence of aquatic vegetation; Cotton et al., 2006) and hysteresis effects over the course of an individual hydrological event (Walling 1977; Williams, 1989). At small spatio-temporal scales in river channels (e.g. channel cross section; seconds to minutes), the physical factors that determine fine sediment dynamics are the physical properties of fine sediments and the high-frequency properties of the flow. Examination of such characteristics requires high-frequency sampling of water turbidity and flow velocities, and such studies have illustrated the role of turbulent flow structures in initiating short duration, high magnitude bursts of fine sediment transport (Lapointe, 1992; 1996; Clifford et al., 1996).

Recent literature has also given increasing attention to the complexity introduced into sediment entrainment and transport processes by the presence of aquatic organisms acting as ‘geomorphic agents’ or ‘ecosystem engineers’ (Jones et al., 1994). This includes aquatic and riparian vegetation (e.g. Gurnell and Petts, 2006; Bertoldi et al., 2009; Gurnell et al., 2012), aquatic invertebrates (Statzner et al., 2003; Wharton et al., 2006; Johnson et al., 2009), fish, particularly through spawning activities (e.g. salmonids; Hassan et al., 2008; 2011) and mammals (e.g. Wright et al., 2002). Within this context, the influence of aquatic organisms on fluvial sediment dynamics may be particularly pronounced for invasive species; these may be present at high densities, and represent a disturbance to which the river system may not be resilient (Harvey et al., 2011). The susceptibility of natural communities to further invasions is likely to increase, exacerbated by the interacting stressors of habitat loss and climate change (Macdonald and Burnham, 2010). A sound understanding of the ways in which invasive aquatic biota influence fine sediment dynamics from the patch to the catchment scale of river systems is vital for catchment sediment budgeting and management efforts, but represents a new and under-developed research area.

This paper focuses on the signal crayfish (*Pacifastacus leniusculus*), a species endemic to North America, that has been introduced to over 20 countries in Europe since the 1960s (Lewis, 2002). It has rapidly colonised river systems in Britain since the mid-1970s (Holdich, 2000). Much of the research on signal crayfish to date has focused on biotic interactions. As relatively large bodied omnivores they are typically detrimental to other invertebrates and fish in the recipient community via predation, competition, or habitat alteration via consumption of aquatic macrophytes (Guan and Wiles, 1997; 1998; Crawford et al., 2006). Native white-clawed crayfish (*Austropotamobius pallipes*) populations in the UK have been decimated by the arrival and rapid spread of signals over the last few decades (Alderman et al., 1990; Holdich, 2003; Bubb et al., 2005, Haddaway et al., 2012). Signal crayfish are known to burrow extensively (Lewis, 2002), can achieve extremely high densities - up to 20 individuals m^2 (Abrahamsson and Goldman, 1970; Bubb, 2004) and are known to inhabit a range of environments including stillwaters (Ruokonen et al., 2013).

Several species of crayfish, including signal crayfish, are known to act as ‘geomorphic agents’, impacting directly upon the physical environment of river systems (Newton, 2010). This includes bioturbation of sediments through movements such as walking and tail flips (Statzner and Sagnes, 2008); alteration of bedform roughness and modifying bed material particle size distributions and particle consolidation (Statzner et al., 2000; 2003); changes in the composition of fine sediments associated with the processing of organic matter (Usio, 2000); and extensive burrowing into soft river banks which may increase bank erosion and associated increased inputs of fine sediments (Lewis, 2002). Much of this detailed research on sediment mobilisation, however, focuses on experimental laboratory streams and on coarser (gravel-sized) bed material. Reaches characterised by fine bed and bank material may be more susceptible to these geomorphic impacts, and hence there is a pressing need for improved process understanding at local scales in order to inform up-scaling and assess the nature and extent of potential implications for catchment-level sediment management, water quality and physical habitat. Such insights are particularly important given that currently there are no effective measures for control or mitigation available for signal crayfish (Holdich et al., 1999). Harvey et al. (2011) review the existing knowledge base for the impacts of signal crayfish on fine sediment dynamics through their interactions with bed and bank material through a range of activities. They suggest that patch scale impacts on fine sediment dynamics through burrowing, movement and feeding activities may lead to changes in bed material size and structural arrangement, microtopography, bank erosion, flow resistance and hydrodynamics. Such patch scale impacts may in turn influence sediment yields, morphology, conveyance capacity and transport of sediment-associated nutrients and contaminants at larger spatio-temporal scales, and hence it is recommended that further research is urgently required at the interface between freshwater ecology, fluvial geomorphology and hydraulics at various spatiotemporal scales in order to quantify the significance of different impacts (Harvey et al., 2011).

This paper presents findings from combined field and laboratory work which aims to explore signal crayfish impacts on fine sediment dynamics at the patch scale. In particular, three hypotheses are tested:

1. Signal crayfish generate pulses of fine sediment mobilisation through their interactions with river bed and bank material (burrowing and movement) that are detectable in the flow.

2. The frequency of pulsed sediment mobilisation events is greater during nocturnal periods when crayfish in general, and signal crayfish in particular are known to be most active (Hill and Lodge, 1994; Lozan, 2000; Styrishave et al., 2007; Grey and Jackson, 2012).

3. The cumulative influence of sediment pulses is sufficient to result in a change to ambient turbidity levels during nocturnal periods.

RESEARCH DESIGN AND METHODS

Research design

A combination of laboratory and field study was employed to test the research hypotheses. Laboratory mesocosm experiments focused on interactions with fine bed sediment and artificially created banks. Laboratory mesocosms provided controlled conditions under which detectable changes in suspended sediment concentration could be directly related to crayfish interacting with artificial banks and substrates constructed from fine sediments. This was designed to provide ‘proof of concept’ for impacts on fine sediment mobilisation. The field study then addressed whether similar patterns in turbidity were identifiable under field conditions, providing an indication of the real-world relevance of the process. Given the episodic nature of bank erosion processes (and burrowing activity) and hence the complexities of exploring bank erosion processes in the field, field experiments focused on sediment mobilisation in the near-bed region.

In both laboratory and field studies, turbidity sensors were used to indicate suspended sediment concentrations. Turbidity is a measure of the degree to which light passing through a water body is scattered and/or absorbed by particulate matter held in suspension and has been used to indicate suspended sediment concentrations in a range of field applications (e.g. Clifford et al., 1995; Gippel, 1995; Brasington and Richards, 2000; Harvey and Clifford, 2010). The focus on continuous measurement of turbidity rather than time-integrated suspended sediment sampling is appropriate in this application, since it allowed continuous high frequency sampling (Lapointe, 1992; Clifford and French, 1996) and minimised the disturbance to flow and fine sediments at sampling locations. Turbidity was recorded using Partech IR40 and/or IR100 infrared turbidity sensors connected to a Campbell Scientific CR10X data logger, recording data at a frequency of 5Hz. The 0-5 mA signal produced by the turbidity sensors is converted to a voltage by placing a resistor in the current loop (Clifford et al., 1995). The IR40 and IR100 have path lengths of 40 mm and 100 mm, and suspended sediment concentration detection ranges of 0-200 mgl^{-1} and 0-1500 mgl^{-1}, respectively.

While the relationship between turbidity and suspended sediment concentration is affected by particle size, shape and colour, it can be calibrated with respect to either *in situ* particles (Clifford et al., 1995) or Formazin Turbidity Units (FTU) using a formazin solution (HMSO, 1984). Calibration curves are generally S-shaped and can be described by linear relationships for a large part of the range. For the laboratory experiments, turbidity was converted to sediment concentration (mgl^{-1}) by calibration with suspended sediment samples collected across a range of concentrations during the experiments. Samples were filtered through 2.5µm papers and dried at 100^{o}C to obtain dry weight. Regression curves were fitted to the relationship between voltage output and suspended sediment concentration (R^2 = 0.99). Results for the laboratory study are reported as suspended sediment concentration (mgl^{-1}). For the field study, turbidity was converted to FTU through calibration with formazin solution across a range of concentrations (0-1200 FTU). Regression curves were fitted to the relationship between voltage output and FTU ($R^2 = 0.99$). Results for the field study are reported as turbidity (FTU). Suspended sediment concentration was not directly measured in the field as this would have necessitated disturbing the water column to obtain water samples, potentially compromising the experiment.

Laboratory mesocosms

Laboratory experiments were conducted within replicate treatment and control mesocosm tanks (0.24 x 0.45 x 0.3m) filled with 10l of tap water. There was no flow through the tanks so both treatment and control tanks were aerated using standard aquarium air stones and tubing and an AirBlow 100 pump unit. The tanks were maintained at 15^{o}C under a fixed light regime of 12 hours light (07:00-19:00) followed by 12 hours of darkness (19:00-07:00). Experiments comprised two treatments: artificial clay banks and artificial clay substrates, both prepared using bentonite clay. Each treatment was replicated three times, giving a total of six experimental runs. For the bank experiments, replicate artificial banks were created by moulding damp sediment and placing it under weights for several days to create solid clay blocks of a consistent volume (0.08 x 0.10 x 20.5 m) and shear strength (0.05kg/cm^3; measured using a shear vane). Banks were held in place at each side of the tank using wooden panels. For bed substrate experiments, the base of each tank was covered with bentonite to a depth of 0.03 m and compressed under weights in the same ways as artificial banks. This was necessary to minimise mobilisation of substrate during filling of tanks with water. The substrate was also covered with plastic sheeting as the tanks were filled to prevent disturbance of the sediment. Signal crayfish were collected and identified from field sites within the Greater London area. One medium-sized crayfish (carapace length 22.5 – 36 mm) was placed into each treatment tank and no crayfish were present within the control tanks. Crayfish were not sexed but had both claws intact. Crayfish were stored within holding tanks with food for several days prior to the experimental runs. Turbidity sensors were positioned 10 cm above the bed in each of the control and treatment tanks. Figure 1a illustrates the experimental design.

Field study

High-frequency turbidity records were obtained from a site on the eastern arm of the River Windrush (UK grid reference SP 401 050; Figure 2) on 1 and 2 July 2009. The Windrush drains an area of 362.6 km^2 from its source in Gloucestershire to its confluence with the River Thames at Newbridge. The majority of the catchment is underlain by pervious Oolitic limestone and land use is predominantly agricultural, although extensive gravel workings and the town of Witney (population 22,265) are prominent features of the lower valley. The mean annual rainfall in the catchment is 743 mm (1961-90) and the mean daily flow of the Windrush at Newbridge is 3.35 m^{3}s^{-1} (1950-2009). The Windrush has a large population of signal crayfish. The native white-clawed crayfish are no longer present in the majority of the catchment and are confined to its headwaters which have yet to be invaded by the signal crayfish. The field site forms part of a wider project by the Wildlife Conservation Research Unit, University of Oxford, researching signal crayfish movements, growth rates and removal strategies (Moorhouse and Macdonald 2011a, b, c) which provides quantitative data on signal crayfish densities in the study reach. Channel width at the study location was approximately 5.5 m. Signal crayfish densities at the time of the study were extremely high. From the 500 m section surrounding the turbidity monitoring station 6158 individual crayfish were captured from 35 traps set for a total of 24 nights between April and September 2009 (for further information see Moorhouse and Macdonald, 2010). Accurate estimation of crayfish densities is impossible from these trapping data, due to low recapture rates, small nightly home-ranges of crayfish (modal nightly movement size in these rivers 0-5 m; Moorhouse and Macdonald, 2011) and biases towards the capture of the largest individuals (Moorhouse and Macdonald 2010). Both of these latter issues mean that the majority of the population would likely remain untrapped with traps employed at the spacing used in this study. The captured individuals, therefore, only represent a small fraction of the actual population present during the study period. An approximate calculation of Catch Per Unit Effort (catch per trap per night) reveals > 7 individuals per trap. Assuming that each trap captured and retained every individual within a 2.5 m radius this would equate to a minimal density of one crayfish per 3 m^2 of river bed. Given the known trap bias towards capturing only the largest individuals (those with a carapace of 50 mm or greater; Moorhouse and Macdonald 2010), and the likelihood that the majority of even large bodied crayfish within this radius will remain untrapped or escape (e.g. Holdich et al., 1999) this minimal estimate almost certainly excludes a large number of crayfish.

Turbidity monitoring equipment was deployed for a period of 16 hours, encompassing approximately nine hours of daylight and seven hours of darkness between 5pm on 1st July 2009 and 9am on 2nd July 2009, incorporating the nocturnal period when signal crayfish are typically most active (Styrishave et al., 2007). Crayfish activity is also known to be greatest during warmer summer periods (Lozan, 2000; Johnson et al., 2010). Due to uncertainties associated with the expected field range of suspended sediment concentrations, two types of turbidity sensor with differing ranges (IR40C and IR100C) were mounted as a pair at 0.8 of the water depth from the surface (flow depth of 0.14 m above the bed) in order to capture-near bed turbidity variations. A further IR40C sensor was mounted at 0.6 of the water depth from the surface (flow depth of 0.28 m above the bed) to record mid-flow turbidity levels. The monitoring equipment was positioned within a ‘glide’ physical biotope unit (Bisson et al., 1981; Newson and Newson, 2000), characterised by homogeneous smooth boundary turbulent surface flow conditions and water depths, and a bed substrate consisting of sand and silt (grain size < 2mm diameter). Turbidity sensors were installed at a point in the channel cross section that was expected to be associated with high levels of crayfish movement: towards the bank, adjacent to overhanging marginal vegetation that provides cover (Jowett et al., 2008). Figure 1b illustrates the experimental design.

Hydrological conditions were stable for the duration of the monitoring period: discharge and water depth at the monitoring location were 0.46 m^3s^{-1} and 0.7 m respectively and remained constant. Flow stage was low, reflecting the meteorological conditions encountered at the time of the study: maximum daytime air temperatures exceeded 28°C and no rainfall was detected at Met Office operated rain gauges in the surrounding catchment for at least four days prior to the experimental period. Discharge records from a downstream gauging station at Newbridge, below the confluence of the eastern and western forks of the Windrush, confirm stationarity in flow conditions throughout the monitoring period (Figure 3).

High frequency flow properties were sampled over the period of record on an approximately hourly basis in order to identify changes in turbulent bursting and event-driven boundary layer organisation (McQuivey, 1973; Clifford et al., 1993; Ashworth et al., 1996) which can result in short-term sediment suspension (Lapointe, 1992; 1996). High frequency flow measurements were taken immediately adjacent to turbidity sensors, in the near-bed region (0.8 of the flow depth from the surface), using a Sontek field 10 MHz 3D Acoustic Doppler Velocimeter (ADV) sampling streamwise (U), cross stream (V) and vertical (W) velocities at a frequency of 16Hz for a sampling period of 5 minutes.

Data analysis

The first stage of analysis involved visual examination of calibrated turbidity traces to check for data quality issues and anomalies, and to identify scales of variation the data set and detrending requirements. For both field and laboratory data sets, shorter-duration pulsed turbidity events superimposed on longer-term trends were visually identifiable on time series plots. Pulses were isolated from low amplitude trends in ambient suspended sediment concentration/turbidity in order to estimate the number of pulses, their duration and the maximum turbidity value achieved for each pulse. For geophysical time series characterised by a variety of higher frequency fluctuations superimposed onto low amplitude, low frequency variations, detrending is required, and commonly takes the form of a low-order polynomial regression (e.g. Gordon, 1974; Clifford and French, 1993; French et al., 1993). This is achieved through visual inspection of model fit, since the nature of high magnitude fluctuations in such time series will limit the utility of traditional measures of fit such as R^2. Following detrending, a conservative analytical regime was adopted based on identification of an appropriate threshold value to delimit sediment pulses and to focus analysis on the more pronounced suspension events. For laboratory data, visual inspection of fitted regression curves confirmed that a moving average filter was most effective in detrending the time series and this was used to detrend the series. A threshold value of 1.5 was applied to residuals based on visual inspection of remaining variance in ambient suspended sediment concentration. Pulses were less discrete for laboratory time series as a result of the non-circulatory nature of the tanks, and hence pulses separated by less than 2 seconds were combined into a single event. For field data the low amplitude trend was more subtle relative to the magnitude of discrete turbidity pulses and detrending involved downweighting of high magnitude values to within the ambient turbidity range (as identified visually from timeplots; see Chatfield, 2004). Visual inspection of fitted regression curves revealed that 4th order polynomial regressions best described the low amplitude trend in field data and these were used to detrend the time series.

Turbidity residuals were derived from the low magnitude trends and downweighted values were reinstated within the field time series to allow analysis of turbidity pulse characteristics. The same threshold value of 1.5 was applied to delimit pulses in the field time series in order to remove remaining variance in ambient turbidity as identified by visual inspection. The threshold value chosen will necessarily influence the estimated absolute number of events and their duration but allows comparability across data sets. Non-parametric Mann-Whitney U tests were used to identify statistically significant differences between control and treatment laboratory time series, and between darkness and daylight hours in the field ambient turbidity data set.

For the field data set only, the character of pulsed turbidity events was explored further by classifying pulses separately by shape and magnitude through application of Principal Components Analysis (PCA) and Hierarchical Cluster Analysis (HCA). The approach has been used by Hannah et al. (2000) to classify hydrographs. In order to classify pulses according to event 'shape', a varimax PCA was applied to a data matrix of N columns of pulses by n rows of sequential turbidity values. In order to achieve a matrix of turbidity pulses with an equal number of rows for each pulse, events were artificially extended to the length of the longest duration pulse in the time series using the ambient turbidity threshold value. In this case, the process of applying PCA reduces the matrix of empirical turbidity response curves into a smaller number of generalised curves representing pulses of similar character. PC loadings, therefore, describe the correlation between empirical turbidity response curves and the derived generalised curves. Nine Principal Components (PCs) with eigenvalues greater than 1 cumulatively explained 94% of the variance in the IR40C turbidity series. These represent 9 generalised turbidity response curves. HCA (average linkage method) was then applied to the PC loadings for each pulse, hence grouping pulses with similar loadings on the nine PCs (i.e. those with similar shape; Hannah et al., 2000). The number of clusters within the data set was identified from breaks in the dendrogram. The second process of classifying pulses according to their magnitude involved performing a separate HCA (Ward's method) on a set of variables used to describe the 'magnitude' characteristics for each event: mean turbidity; turbidity range; standard deviation of turbidity; and time to peak. The two HCA outputs were combined to yield a series of shape-magnitude clusters (Hannah et al., 2000). Following the identification and analysis of sediment pulses in the field data, the individual pulses were removed from the time series in order to explore the presence of a nocturnal trend in ambient turbidity levels outside of pulsed events.

RESULTS

Visual inspection of laboratory and field time series

Replicate time series for the bank and substrate laboratory experiments are presented in Figure 4. For each of the two experiments, there was a clear distinction between control and treatment time series, with evidence of considerable mobilisation of sediment within the treatment tanks in the form of both shorter duration, higher magnitude 'pulses' of sediment mobilisation and/or extended duration lower magnitude increases, superimposed on an overall trend of increasing suspended sediment concentration following the start of the experimental period. For the bank treatment, control traces did show some fluctuations over time which reflects localised bank collapse as a result of saturation. This is negligible in relation to the treatment tanks, however, and Mann-Whitney U tests confirm statistically significant differences in suspended sediment concentration between control and treatment pairs for both bank and bed experiments ($p<0.001$). Further analysis focuses on treatment time series only.

Bank treatment time series were characterised by higher overall suspended sediment concentrations, greater prominence of shorter-duration fluctuations and greater similarity between runs compared to substrate time series. No clear nocturnal trend was apparent for either treatment, but time series data suggest a tendency towards a reduction in suspended sediment concentration following the end of the night-time period (Figure 4). For the substrate treatment, there was a considerable difference in the character of sediment traces between runs. A large number of high magnitude, short duration pulses occur on one of the runs while the remaining two were characterised by a series of more prolonged, lower magnitude increases in suspended sediment concentration.

These trends in suspended sediment concentration correspond with visual observation of crayfish behaviour in the two treatment tanks. Example still photographs and video clips are provided in Figure 5 and in the supplementary video material respectively. For substrate treatments, crayfish dug pits in corners of the tank in which they positioned themselves for periods of time (Figure 5a and b; and see supplementary video material). For bank treatments, crayfish created and inhabited burrows in the artificial banks (Figure 5c and d) but the displacement of sediment through burrowing was combined with associated periodic, localised collapse of bank material which also mobilised sediment (Figure 5e and f), contributing to suspended sediment concentrations. Crayfish also mobilised sediment by walking across the sediment (see supplementary video material).

Field turbidity time series derived from the near-bed and mid-flow sensors are presented in Figure 6 and reveal two key features. First, a large number of high magnitude turbidity pulses were detected in the near-bed region by both sensors. In contrast, the mid-flow sensor fails to detect these with the exception of one pulse which appears to have been detected by all three sensors. Second, there was a clear increase in the frequency of near-bed turbidity pulses between approximately 21:00 and 06:00, corresponding closely with the period of darkness between sunset (21:20) and sunrise (04:48). High frequency flow data presented in Figure 7 demonstrate stationarity in U V and W velocity components throughout the sampling period in terms of both average velocity values and variation around the mean. This suggests that no significant changes in flow variability occurred during the sampling period, at either low or high frequencies, that would indicate a turbulence-induced change in pulsed turbidity events during the monitoring period.

Pulsed turbidity events

Discrete suspended sediment pulses occurring within the laboratory data sets are explored in Figure 8. The number of pulses differed considerably between experimental runs for the same treatment, suggesting that crayfish behaviour varied between runs and exerted a considerable influence on the character of turbidity time series. Overall, the total number of pulses was higher for the bank treatments (between 743 and 1941 pulses; with a cumulative duration of between 7 and 10 hours of the record) relative to the substrate treatment (between 398 and 737 pulses; with a cumulative duration between 1 and 7 hours of the record). A small amount of bank collapse occurred under the control treatment suggesting that saturation of artificial banks played a small role, but bank collapse was greatly increased by crayfish burrowing. Two of the substrate time series showed less evidence of high magnitude pulsed events, but instead were characterised lower magnitude, longer duration periods of elevated suspended sediment associated with crayfish activity occurring further from the sensor (in corners of the tanks; see Figure 5 and supplementary video material).

The number of pulses occurring in each hour of the monitoring period varied between runs and ranged from zero to 300. There was no clear nocturnal trend in the number of pulsed events as identified previously from time plots, although both bank and substrate experiments showed evidence of an enhanced number of pulses between 00:00 and 03:00 which then declines. For the substrate treatment there was considerable variability between runs, but a total of 421 pulses were recorded across the three runs between 00:00 and 03:00 (mean 35 pulses per hour; standard error 6.4) compared to 245 pulses during the period of light between 07:00 and 10:00 (mean 26 per hour; standard error 6.0). For the bank treatment a total of 917 pulses were recorded across the three runs between 0:00 and 03:00 (mean 76 pulses per hour; standard error 10.8) compared to 331 between 07:00 and 10:00 (mean 28 per hour; standard error 7.3). The vast majority of pulses were short in duration (across bank runs median = 3.75s and upper quartile = 8.75s; for substrate runs median = 3.25s and upper quartile = 10.75s), and with maximum suspended sediment concentration values up to 5.4 mgl^{-1} (for bank runs median 3.75 mgl^{-1} and upper quartile = 5.14 mgl^{-1}; for substrate runs median = 3.95 mgl^{-1} and upper quartile = 5.40 mgl^{-1}). A smaller number of pulses endured for over 1 minute, up to a maximum of 20 minutes, reflecting periods of more sustained crayfish activity. Likewise a small number of short duration, high magnitude pulses with peak suspended sediment concentration values exceeding 100mgl^{-1} occurred in the record for both treatments, indicating sediment mobilisation events closer to the turbidity sensor. Since the pulse characteristics for the laboratory time series will be strongly controlled by tank hydraulics, and hence may be considerably different in magnitude and duration to crayfish-induced sediment mobilisation events occurring under field conditions, pulse characteristics for laboratory data were not analysed in further detail.

Figure 9 plots characteristics for each pulsed turbidity event identified on the IR40 near-bed sensor for the field turbidity series. Since several high magnitude turbidity pulses detected by the IR100C sensor resulted in the readings outside of the sensor range, and only one pulse was detected on the mid-flow IR40C sensor, turbidity pulse analysis focused on the near-bed IR40C sensor only for field data. In total, 88 events were identified for the IR40C near-bed sensor, an order of magnitude below the values identified in laboratory data. This was expected given the small surface area of the laboratory tanks and the absence of flow to diffuse and advect sediment plumes. One pulse was removed from the time series for the IR40C since it was over 15 minutes in length (compared to <40 s for all other events) and of similar magnitude throughout. This was considered to represent a temporary sensor obstruction such as a piece of organic debris, rather than a discrete sediment suspension event.

Figure 9a illustrates a clear nocturnal trend in pulse frequency for the field data set: no pulses were detected between 17:00 and 19:00 and the number of pulsed events per hour then increased from 1 between 19:00 and 19:59 to a peak of 23 between 23:00 and 23:59, and subsequently decreased to zero by 07:00 the following day. Pulse duration and maximum turbidity revealed a large degree of scatter through the period of record (Figure 9c and d), although there appeared to be a tendency towards higher variability in pulse duration/ magnitude towards the mid-point of the nocturnal period (particularly around 24:00 and 03:00). The relationship between pulse duration and magnitude (Figure 9b) shows a tendency for higher peak turbidity values to be associated with longer duration pulses, but there is considerable scatter observed for the longest duration pulses. The majority of pulses were associated with durations between 1s and 15s and maximum turbidity values up to 1500 FTU, with a smaller cluster of much longer duration events up to a maximum of 37s and with a maximum turbidity up to 2600 FTU.

Figure 10 plots turbidity time series for individual pulses classified according to the shape-magnitude clusters derived from PCA and HCA. Each plot in Figure 10 corresponds to a shape cluster and uses symbology to differentiate between magnitude clusters for each. In total, eight pulse ‘shape’ clusters (A-H) were identified by applying HCA to the PC loadings that described correlation between empirical turbidity response curves and the generalised curves derived from the PCA. In a separate process, three pulse ‘magnitude’ clusters (1-3 describing low, intermediate and high magnitudes respectively) were identified based on pulse magnitude characteristics (mean turbidity; turbidity range; standard deviation of turbidity; and time to peak). Clusters A and B (Figure 10a and b) contained the lowest magnitude and shortest duration pulses; these pulse shapes were associated only with the lowest ‘magnitude’ cluster. The pulses in cluster B have a longer lag time, higher overall event magnitude and lower level of negative skewing relative to cluster A. The shapes of pulses in clusters C, D and E (Figure 10c,d,e) were more complex than A and B, and demonstrate intermediate durations and variable magnitudes. Most pulses falling within these clusters show a lag in peak turbidity of up to 7 seconds from the onset of the event. Clusters F, G, and H described a small number of pulse events (3, 1 and 2 pulses respectively) and are therefore plotted together for brevity in Figure 10f. Together, they represent longer duration pulses with long lags and multiple peaks. Clusters E, F and G all contained pulses in which a secondary peak occurred following a delay of between 15 and 30 s from the onset of the pulse. These secondary peaks could represent a new, potentially unrelated turbidity event but since there is not a complete return to ambient turbidity, these pulses were treated as an individual event for the purposes of this analysis. Given their close proximity in time and similarity in shape, it is possible that these pulses may represent a repetition of the same phenomenon occurring in the same spatial location. The occurrence of the different shape-magnitude pulse clusters varied throughout the period of record. Events belonging to cluster A were distributed throughout the period between 19:00 and 06:00 but the period of greatest variability in cluster type occurred between 22:00 and 03:00, and almost all of the events associated with clusters B, C, D and E, G and H fell within this period.

Nocturnal trend in ambient turbidity for field data

Figure 11 plots average hourly turbidity values for the low magnitude trend in ambient turbidity in field data (i.e. following the removal of discrete high magnitude turbidity pulses) for all three sensors. An abrupt increase in turbidity at around 19:50 which lasted for approximately 50 minutes on the IR100C sensor only was considered to represent an anomalous event associated with a piece of debris becoming trapped around the sensor and was therefore excluded from the ambient data set. For the near-bed sensors there was a clear nocturnal trend associated with an increase in ambient turbidity from approximately 21:00 up to around 02:00, which then receded to approximately the original level by around 08:00. This trend was more pronounced for the IR100C which is more sensitive at the lower part of the turbidity range, thereby affording greater resolution (Henshaw, 2009). The mid-flow IR40C sensor curve demonstrated a slightly different character from the near-bed sensor curves, rising from around 21:00 until reaching a peak around 04:00, but failing to return to the original level during the period of record and remaining approximately 5 FTU higher than the starting turbidity value. In order to test the statistical significance of these nocturnal variations, Mann Whitney U tests were performed on light and darkness groupings of minute-averaged ambient turbidity values for each of the three turbidity sensors according to the timing of sunset and sunrise. This confirmed statistically significant differences in the mean daylight and darkness ambient turbidity values for each of the three sensors ($p < 0.001$).

DISCUSSION

The analysis of high frequency suspended sediment and turbidity time series from laboratory and field studies revealed a number of interesting features that support the research hypotheses. First, signal crayfish were able to mobilise fine sediment through different types of movement, creating pulsed sediment suspension events of varying magnitude and duration under controlled laboratory conditions. These pulsed events were sufficient to drive a statistically significant increase in suspended sediment concentrations in still-water tanks. A higher total number of pulses were recorded for the bank treatment and this reflects a combination of factors. First, there was greater potential for burrowing into the artificial banks relative to the bed substrate due to the greater depth and width of consolidated material. For bank treatments, crayfish were observed to burrow extensively into artificial clay banks, consistent with field observations of dense networks of burrows in invaded habitats (Guan, 1994; Holdich et al., 1999). In addition, the occurrence of sediment pulses in the bank treatment reflects the combined contribution of ‘direct’ impacts of burrow excavation activity transferring sediment into water column and the ‘indirect’ impacts associated with periodic partial bank collapse as a result of burrowing. This was combined with crayfish movements across destabilised material. For substrate treatments, pulsed suspension events were associated with crayfish movements across the bed and the digging of pits in the corner of the tanks. Other species of crayfish have also been observed to mobilise fine sediment during walking, foraging and swimming (e.g. *Paranephrops planifrons*: Parastacidae; Parkyn et al., 1997) and signal crayfish are known to mobilise larger gravel-sized sediment particles (Johnson et al., 2010). Signal crayfish have also been shown to create pit and mound features in coarse sediment beds under laboratory conditions (Johnson et al., 2010), similar to those observed in fine sediment beds for this study. This may partly reflect a lack of cover in substrate tanks, leading to the crayfish adopting a defensive position. While there is no clear nocturnal trend in laboratory data, the number of pulses was enhanced between 00:00 and 03:00 and declined into the subsequent period of light at the end of the night-time period (see Figure 4 and Figure 8). Across the three experimental runs, the number of pulses in the period between 00:00 and 03:00 was almost three times higher than the period of light between 07:00 and 10:00 for the bank treatment, and almost two times higher for the substrate treatment.

The laboratory experiments provide clear evidence of the ability of signal crayfish to mobilise fine sediment under controlled conditions. However, relationships between crayfish behaviour and suspended sediment concentrations for laboratory experiments will be greatly influenced by both the hydraulic conditions of the tanks and the altered behaviour of the crayfish as a result of their placement in a different environment. Tanks were not recirculating, meaning that pulsed suspension events were not subject to advection and diffusion processes that would be significant under field conditions (Rutherford, 1994). This will increase overall suspended sediment levels and limits the potential for detailed analysis and interpretation of sediment pulse characteristics for laboratory time series. The artificial lighting and temperature control as well as the lack of cover, food sources, predation, competition and other biotic interactions will have influenced crayfish behaviour during the experimental period. For example, crayfish are known to cease or curtail various behaviours in the presence of conspecific alarm odours (Hazlett, 2003), and in the absence of such odours (as would be the case in laboratory conditions) it is likely that variations signal crayfish activity may not conform to a nocturnal pattern (e.g. Lozan, 2000).

The field data set reveals pulsed turbidity events similar to those identified in laboratory data. These occur in the near-bed region and are detected by two separate sensors, but similar pulses are not detected in the mid-flow region at the same location. Fewer pulses are identified in the field time series relative to laboratory data. This was expected, given the small surface area of laboratory mesocosms and the influence of advection and diffusion processes under field conditions. Importantly, turbidity pulses identified on field time series appear tightly constrained to the period of darkness between sunset and sunrise. The pulsed events vary in duration, magnitude and ‘shape’ but can be grouped statistically into distinct clusters of similar magnitude and shape characteristics. There is a notable lack of short duration (<5 s) high magnitude observations characteristic of turbulence-induced sediment suspension events (McQuivey 1973; French and Clifford, 1992; Lapointe, 1996; Roy et al., 1996; Buffin-Belanger and Roy, 2005), and few extended duration (>15 s) events. The turbidity pulses are most frequent and most varied in their characteristics towards the mid-point of nocturnal period. These temporal trends correlate with known nocturnal increases in signal crayfish activity including movement, burrowing, fighting and feeding (Flint, 1977; Guan and Wiles, 1998; Lozan, 2000; Styrishave et al., 2007).

Observational data on crayfish activity during the monitoring period are not available for the field study, limiting direct process inference. However, the known behavioural characteristics of signal crayfish, combined with their presence in extremely high densities at the field site (Moorhouse and Macdonald 2011a, b, c), and the similar features identified in laboratory data sets, implies they are likely to be responsible for the observed trends in field data. Importantly, the turbidity increases are not explained by temporal variations in high frequency velocity characteristics, and seem independent of discharge variations or possible enhanced supply from catchment run-off events in the immediate past. Additionally, the turbidity increases are more marked near to the river bed, indicating a local origin, and the nocturnal pattern observed in field data, with clear onset and cessation aligned with sunset and sunrise implies a causal or generating mechanism which was biological rather than physical in origin. The data also complement previous research that links bioturbation by the red swamp crayfish (*Procambarus clarkii*) with increased suspended solids and dissolved nutrients in a wetland enclosure study (Angeler et al., 2001).

The occurrence of pulsed turbidity events within the nocturnal period of the field time series corresponds with a statistically significant increase in ambient turbidity values (i.e. excluding pulses) in the near-bed region for the same period. Furthermore, a statistically significant increase in ambient turbidity is also recorded in the mid-flow region which appears time-lagged relative to the near-bed trends. These data suggest a combined effect of localised turbidity events occurring both within the immediate vicinity of the sensors and upstream that was sufficient to drive a statistically significant increase in ambient turbidity both at the bed and also in the mid-flow region. The difference between the near-bed and mid-flow trends could reflect the cumulative effects of crayfish activity upstream and the diffusion and downstream advection of mobilised sediments which may have a time-lagged influence in the mid-flow region.

The combined field and laboratory approach taken in this paper was designed to overcome some of the extreme practical difficulties associated with process-based research at the geomorphology-ecology interface. For this study, laboratory experimentation provides a controlled environment for a proof of concept study that identifies detectable pulsed sediment suspension events of varying character that can be directly attributed to crayfish interacting with bed and bank material through movement and burrowing. However, crayfish behaviour will be influenced by the artificial surroundings of the laboratory, and the non-recirculatory nature of the tanks does not provide an accurate description of the character and significance of the pulsed mobilisation events under field conditions. Observational evidence is much more difficult to secure in the field as a result of a number of practical constraints, notably the need to isolate hydrological and hydraulic influences, maintenance, power and data storage constraints of field equipment, and the nocturnal behaviour of signal crayfish. In this case the field data set complements the laboratory data set by identifying similar pulsed sediment suspension features in a reach with extremely high densities of crayfish. This suggests real world significance, with the potential to drive an overall increase in turbidity and hence influence sediment dynamics at larger spatio-temporal scales (Harvey et al., 2011). While the signal crayfish is of particular interest due to its relatively large body size and aggressive nature, other invasive species of crayfish in the UK are also known to burrow into river banks (e.g. red swamp crayfish *Procambarus clarkii* and spiny-cheeked crayfish *Orconectes limosus)* and hence may have similar impacts upon mobilisation of fine sediment from the river bed and banks.

The results presented in this paper suggest that further research into the impact of signal crayfish on fine sediment dynamics is warranted. Future studies may incorporate in situ enclosure/ exclosure field experiments (removing animals in order to help identify the extent of impacts (e.g. localised versus significant downstream advection)) across sites with different fine sediment bed material characteristics and for different hydrological conditions. Opportunities for paired control-impact studies may also be identified at invasion fronts, allowing a comparison of fine sediment dynamics across reaches with similar physical characteristics in the presence and absence of a crayfish population. Observational data may be collected alongside suspended sediment monitoring through Passive Integrated Transponder (PIT) technology in order to detect animal movement patterns at the reach scale (e.g. see Bubb et al., 2006) and/or underwater videography in order to directly observe movements at a local scale. This may allow relationships between rates of movement across the bed and suspended sediment concentrations to be explored, and different types of activity (e.g. movement, feeding, fighting) to be linked to different styles of sediment mobilisation.

CONCLUSION

This paper presents findings from combined field and laboratory studies that demonstrate the potential for signal crayfish to act as drivers of fine sediment dynamics at the patch scale of river systems. Results support the three research hypotheses presented. Signal crayfish generate pulses of fine sediment mobilisation through interactions with river bed and bank material (burrowing and movement) that are detectable in the flow. Pulsed sediment mobilisation events are tightly constrained to the nocturnal period in which signal crayfish are known to be most active under field conditions, and show evidence of enhanced frequencies in the nocturnal period under laboratory conditions. For both data sets, pulsed events appear sufficient in their cumulative magnitude and frequency to drive a change to ambient suspended sediment/ turbidity levels. Whilst similar activities and associated sediment disturbances could be associated with native species, the larger body size and more aggressive nature of the signal crayfish, and its presence in many catchments in extremely high densities, may lead to more significant sediment disturbance compared to that which may be expected for native species. Furthermore, signal crayfish are known to burrow much more extensively in invaded environments relative to both their native range and to other species such as the UK's native white-clawed crayfish.

If the impacts of signal crayfish on fine sediment mobilisation and transport become significant in specific reaches and/or for certain periods of time, downstream impacts could include morphological change, increased turbidity levels, and the mobilisation and transport of sediments and sediment-associated nutrients and contaminants. Such impacts could have detrimental effects for the ecological status of water bodies, and for flood risk through changes in conveyance capacity. Further process-based studies are required to develop a full understanding of relationships between fine sediment mobilisation and transport associated with the various mechanistic abilities of crayfish; relationships between impact and body size/sex; interspecific interactions; the influence of additional habitat-related variables such as food sources and refugia; temporal variations in activity levels including seasonal (temperature) as well as diurnal; and the nature and scale of potential impacts across a range of river styles.

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REFERENCES

Abrahamsson SAA and Goldman CR (1970) Distribution, density and production of the crayfish Pacifastacus leniusculus Dana in Lake Tahoe, California – Nevada. *Oikos* **21**: 83–91.

Alderman DJ, Holdich DM, and Reeve I. (1990) Signal crayfish as vectors in crayfish plague in Britain. *Aquaculture* 86: 3–6.

Ashworth PJ, Bennett SJ, Best JL and McLelland SJ. (1996) Coherent flow structures in open channels. John Wiley and Sons Ltd, Chichester.

Bertoldi W, Gurnell AM and Drake NA (2011) The topographic signature of vegetation development along a braided river: results of a combined analysis of airborne lidar, colour air photographs and ground measurements. *Water Resources Research* **47**: W06525

Bisson PA, Nielson JL, Palson RA, Grove LE. (1981) A system of naming habitat in small streams, with examples of habitat utilization by salmonids during low streamfl ow. In Acquisition and Utilization of Aquatic Habitat Inventory Information: Proceedings of a Symposium. American Fisheries Society Western Division: Bethesda, MD.

Bogardi J. (1974) Sediment Transport in Alluvial Streams. Akadémiai Kiadô, Budapest

Bowes MJ, House, WA, and Hodgkinson, RA. (2003) Phosphorous dynamics along a river continuum. *Science of the Total Environment* **313:** 199-212.

Brasington J and Richards KS. (2000) Turbidity and suspended sediment dynamics in the Nepal Middle Hills. *Hydrological Processes* **14**: 2259-2274.

Bubb DH, Thom TJ, and Lucas MJ (2004) Movement and dispersal of the invasive signal crayfish Pacifastacus leniusculus in upland rivers. *Freshwater Biology* **49**: 357–368.

Bubb DH, Thom TJ, and Lucas MC (2005) The within catchment invasion of the non-indigenous signal crayfish (Dana) in upland rivers. *Bulletin Francais de Peche et de Pisciculture* **376–377**: 665–673.

Bubb DH, Thom TJ, Lucas MC. (2006) Movement patterns of the invasive signal crayfish determined by PIT telemetry. *Canadian Journal of Zoology* **84**: 1202–1209.

Buffin-Belanger T and Roy AG. (2005) 1 min in the life of a river: selecting the optimal record length for the measurement of turbulence in fluvial boundary layers. *Geomorphology* **68**: 77-94.

Carter J, Walling DE, Owens PN and Leeks GJL. (2006) Spatial and temporal variability in the concentration and speciation of metals in suspended sediment transported by the River Aire, Yorkshire, UK. *Hydrological Processes* **20**: 3007-3027.

Chatfield C. (2004) The Analysis of Time Series: An Introduction. CRC Press LLC: Boca Raton, Florida.

Clifford NJ, Richards KS, Brown RA and Lane SN. (1995) Scales of variation of suspended sediment concentration and turbidity in a glacial meltwater stream. *Geografiska Annaler* **77A**(1-2), 45-65.

Clifford NJ, French JR and Hardisty J. (1993) Turbulence: Perspectives on Flow and Sediment Transport. Chichester, John Wiley and Sons Ltd.

Clifford NJ, Richards KS, Brown RA, Lane SN. (1995) Laboratory and field assessment of an infrared turbidity probe and its response to particle size and variation in suspended sediment concentration. *Hydrological Sciences Journal* **40(6)**: 771–791.

Clifford NJ and French JR. (1996) Criteria for suspended sediment monitoring in river environments: field evaluation of contrasting turbidity sensor types using simulated sediment transport events. In Maxwell WHC, Preul HC and Stout GE (eds.) *Proceedings Rivertech96: 1st International Conference on New/emerging Concepts for Rivers*: 754-761.

Cotton JA, Wharton G, Bass JAB, Heppell CM and Wotton RS. (2006) Plant-water-sediment interactions in lowland permeable streams: investigating the effect of seasonal changes in vegetation cover on flow patterns and sediment accumulation. *Geomorphology* **77**: 320-334.

Crawford L, Yeomans WE, and Adams CE (2006) The impact of introduced signal crayfish Pacifastacus leniusculus on stream invertebrate communities. *Aquatic Conservation: Marine and Freshwater Ecosystems* **16**: 611–621.

Flint RW. (1977) Seasonal activity, migration and distribution of crayfish, Pacifastacus leniusculus, in Lake Tahoe. *American Midland Naturalist* **97**: 280-292.

French JR and Clifford NJ. (1992) Characteristics and "Event-Structure" of near-bed turbulence in a macrotidal saltmarsh environment. *Estuarine, Coastal and Shelf Science* **34**: 49-69.

Gippel CJ (1995) Potential of turbidity monitoring for measuring the transport of suspended solids in streams. *Hydrological Processes* **9**: 83-97.

Grey J and Jackson MC. (2012) 'Leaves and eats shoots': direct terrestrial feeding can supplement invasive red swamp crayfish in times of need. *PLoS ONE* **7(8)**: e42575.

Guan RZ and Wiles PR. (1997) Ecological impact of introduced crayfish on benthic fishes in a British lowland river. *Conservation Biology* 11: 641–647.

Guan RZ and Wiles PR. (1998) Feeding ecology of the signal crayfish Pacifastacus leniusculus in a British lowland river. *Aquaculture* **169**: 177-163.

Gurnell AM and Petts GE. (2006) Trees as riparian engineers: the Tagliamento River, Italy. *Earth Surface Processes and Landforms* **31:** 1558-1574.

Gurnell AM, Bertoldi W and Corenblit D. (2012) Changing river channels: the roles of hydrological processes, plants and pioneer fluvial landforms. *Earth Science Reviews* **111**: 129-141.

Haddaway NR, Wilcox RH, Heptonstall REA, Griffiths HM, Mortimer RJG, Christmas M, and Dunnet AMl. (2012) Predatory functional response and prey choice identify predation differences between native/invasive and parasitised/unparasitised crayfish. *PLoS ONE* **7(2)**: e32229.

Hannah DM, Smith BPG, Gurnell AM and McGregor GR. (2000) An approach to hydrograph classification. *Hydrological Processes* **14**: 317-338.

Harvey GL and Clifford NJ. (2009) Microscale hydrodynamics and coherent flow structures in rivers: Implications for the characterization of physical habitat. *River Research and Applications* **25**: 160-180.

Harvey GL and Clifford NJ. (2010) Experimental field assessment of suspended sediment pathways for characterising hydraulic habitat. *Earth Surface Processes and Landforms* **35**: 600–610.

Harvey GL, Moorhouse TP, Clifford NJ, Henshaw AJ, Johnson MF, Macdonald DW, Reid I and Rice SP. (2011) Evaluating the role of invasive aquatic species as drivers of fine sediment-related river management problems: the case of the signal crayfish (Pacifastacus leniusculus). *Progress in Physical Geography* **35**: 517–533.

Hassan MA, Petticrew EL, Montgomery DR, Gottesfeld AS and Rex JF. (2011) Salmon as biogeomorphic agents in gravel bed rivers: the effect of fish on sediment mobility and spawning habitat. *Geophysical Monograph Series* 194: 337-352.

Hassan MA, Gottesfeld AS, Montgomery DR, Tunnicliffe JF, Clarke GKC, Wynn G Jones-Cox H, Poirier R, MacIsaac E, Herunter H, and Mcdonald SJ. (2008) Salmon-driven bedload transport and bed morphology in mountain streams. *Geophysical Research Letters* 35: L04405.

Hazlett BA. (2003) The effects of starvation on crayfish responses to alarm odor. *Ethology* **109**: 587-592.

Henshaw AJ. (2009) Impacts of land use changes and land management practices on upland catchment sediment dynamics: Pontbren, mid-Wales. Unpublished PhD thesis. University of Nottingham.

Heywood MJT and Walling DE. (2006) The sedimentation of salmonid spawning gravels in the Hampshire Avon catchment, UK: implications for the dissolved oxygen content of intragravel water and embryo survival. *Hydrological Processes* **21**: 770-788.

Hill AM and Lodge DM. (1994) Diel changes in resource demand - competition an predation in species replacement among crayfishes. *Ecology* **75**: 2118-2126.

Holdich DM, Rogers WD and Reynolds JD. (1999) Native and alien crayfish in the British Isles. In: Gherardi F and Holdich DM.(Eds.) *Crayfish in Europe as alien species: how to make the best of a bad situation?* 221–236. Balkema, Rotterdam.

Holdich DM. (2000) The Development of Ecological Requirements to inform the Production of Conservation Objectives for white-clawed crayfish. English Nature, Peterborough.

House WA. (2003) Geochemical cycling of phosphorous in rivers. *Applied Geochemistry* 18: 739-748.

HMSO (1984) Methods for the examination of waters and associated materials: Colour and turbidity of waters – 1981 Tentative methods. HMSO, London.

Johnson MF, Reid I, Rice SP and Wood PJ (2009) Stabilization of fine-gravels by net-spinning caddisfly larvae. *Earth Surface Processes and Landforms* **34**: 413 - 423.

Johnson MF, Rice SP and Reid I (2010) Topographic disturbance of subaqueous gravels by signal crayfish (*Pacifastacus leniusculus*). *Geomorphology* **123**: 269-278.

Jones CG, Lawton JH, and Shachak M (1994) Organisms as ecosystem engineers. *Oikos* **69**: 373–386.

Jowett IG, Parkyn SM and Richardson J. (2008) Habitat characteristics of crayfish (Paranephrops planifrons) in New Zealand streams using generalized additive models (GAMs). *Hydrobiologia* **596**: 353 – 365.

Kondolf GM (1998) Lessons learned from river restoration projects in California. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**:39-52.

Lane SN, Tayefi V Reid SC, Yu D, Hardy RJ. (2007) Interactions between sediment delivery, channel change, climate change and flood risk in a temperate upland environment. *Earth Surface Processes and Landforms* **32**: 429-446

Lapointe M. (1992) Burst-like sediment suspension events in a sand bed river. *Earth Surface Processes and Landforms* **17**:253-2970.

Lapointe MF. (1996) Frequency spectra and intermittency of the turbulent suspension process in a sand- bed river. *Sedimentology* **43**: 439–449.

Lewis SD. (2002) Pacifastacus Biology of freshwater crayfish. In: Holdich DM. (Ed.) Biology of Freshwater Crayfish: 511–540. Blackwell, Oxford.

Lozan JL. (2000) On the threat to the European crayfish: A contribution with the study of the activity behaviour of four crayfish species (Decapoda: Astacidae). *Limnologica* **30**: 156-161.

Macdonald D and Burnham D. (2010) The state of Britain’s mammals: a focus on invasive species. People's Trust for Endangered Species: London. ISBN 0-9545711-5-0.

Marks SD and Rutt GP. (1997) Fluvial sediment inputs to upland gravel bed rivers draining forested catchments: potential ecological impacts. *Hydrology and Earth System Sciences* **1**: 499-508.

McQuivey RS. (1973) Summary of turbulence data from rivers, conveyance channels and laboratory flumes. United States Geological Survey Professional Paper, 802B.

Moorhouse, T.P., Macdonald, D.W. (2011a). The effect of manual removal on movement distances in populations of signal crayfish (*Pacifastacus leniusculus*). *Freshwater Biology* **56**: 2370-2377.

Moorhouse, T.P., Macdonald, D.W. (2011b). The effect of removal by trapping on body condition in populations of signal crayfish. *Biological Conservation* **144**: 1826-1831.

Moorhouse, T.P., Macdonald, D.W., (2011c). Immigration rates of signal crayfish (*Pacifastacus leniusculus*) in response to manual control measures. *Freshwater Biology* **56**: 993-1001.

Naden PS. (2010) The fine-sediment cascade. In: Burt T and Allison R. (eds) *Sediment Cascades*. Wiley-Blackwell, Chicester.

Newson MD and Newson CL. (2000) Geomorphology, ecology and river channel habitat; mesoscale approaches to basin-scale challenges. *Progress in Physical Geography* **24(2)**: 195–217.

Newton A. (2010) Geomorphology: Crayfish at work. *Nature Geoscience* **3**: 592.

Oldfield F, Rummery TA, Thompson R and Walling DE. (1979) Identification of suspended sediment sources by means of magnetic measurements: some preliminary results. *Water Resources Research* **15**: 211-218.

Parkyn SM, Rabeni CF, and Collier KJ (1997) Effects of crayfish (Paranephrops planifrons: Parastacidae) on in-stream processes and benthic faunas: A density manipulation experiment. *New Zealand Journal of Marine and Freshwater Research* **31**: 685–692.

Roy AG, Buffin-Bélanger T and Deland S. (1996) Scales of turbulent coherent flow structures in a gravel-bed river. In: Ashworth P J, Bennett SJ, Best JL and McLelland SJ (eds.) *Coherent Flow Structures in Open Channels*, Chichester, John Wiley and Sons Ltd pp. 147-164.

Ruokonen TJ, Kiljunen M, Karjalainen J and Hämäläinen H. (2012) Invasive crayfish increase habitat connectivity: a case study in a large boreal lake. *Knowledge and Management of Aquatic Ecosystems* **407**, 08.

Rutherford JC. (1994) *River Mixing*. John Wiley & Sons: Chichester.

Singer, MB, Aalto, R and James, LA. (2008) Status of the Lower Sacramento Valley flood-control system within the context of its natural geomorphic setting. *Natural Hazards Review*, **9**: 104-115.

Statzner B, Fievet E, Champagne JY, Morel R and Herouin E. (2000) Crayfish as geomorphic agents and ecosystem engineers: Biological behavior affects sand and gravel erosion in experimental streams. *Limnology and Oceanography* **45**: 1030-1040.

Statzner B, Peltret O and Tomanova S. (2003) Crayfish as geomorphic agents and ecosystem engineers: effect of a biomass gradient on baseflow and flood-induced transport of gravel and sand in experimental streams. *Freshwater Biology* **48**: 147-163.

Statzner B and Sagnes P. (2008) Crayfish and fish as bioturbators of streambed sediments: Assessing joint effects of species with different mechanistic abilities. *Geomorphology* **93**: 267-287.

Styrishave B, Bojsen BH, Witthofft H and Andersen O. (2007) Diurnal variations in physiology and behaviour of the noble crayfish Astacus astacus and the signal crayfish Pacifastacus leniusculus. *Marine and Freshwater Behaviour and Physiology* **40**: 63-77.

Trimble SW. (1983) A sediment budget for Coon Creek Basin in the Driftless area, Wisconsin, 1853-1977. *American Journal of Science* **283**: 454-474.

Usio N (2000) Effects of crayfish on leaf processing and invertebrate colonisation of leaves in a headwater stream: decoupling of a trophic cascade. *Oecologia* **124**: 608-617.

Walling DE. (1977) Limitation of the rating curve technique for estimating suspended sediment loads, with particular reference to British rivers. In: Erosion and Solid Matter Transport in Inland Waters (Proc. Paris Symp., July 1977), IAHS Publ. no. 122, 34-48.

Walling DE and Collins AL. (2008) The catchment sediment budget as a management tool. *Environmental Science and Policy* **11**: 136-143.

Wharton G, Cotton JA, Wotton RS, Bass JAB, Heppell CM, Trimmer M, Sanders IA and Warren L. (2006) Macrophytes and suspension-feeding invertebrates modify flows and fine sediments in the Frome and Piddle catchments, Dorset (UK). *Journal of Hydrology* **330**: 171-184.

Williams GP. (1989) Sediment concentration versus water discharge during single hydrologic events in rivers. *Journal of Hydrology* **111**: 89-106.

Wright JP, Jones CG and Flecker AS. (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* **132**: 96-101.

FIGURES

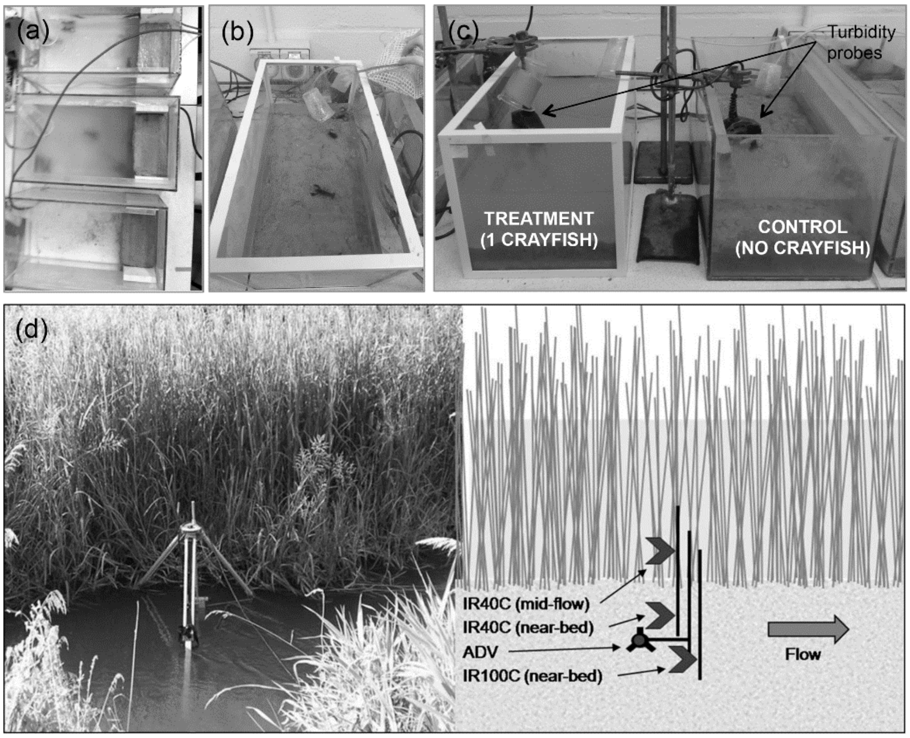


Figure 1 Experimental design for laboratory mesocosm experiments and field study: (a) mesocosm tanks with artificial clay banks; (b) mescosm tanks with artificial clay substrate; (c) control and treatment tanks; and (d) photography of monitoring location at the field site on the River Windrush with diagram to show the equipment set-up.

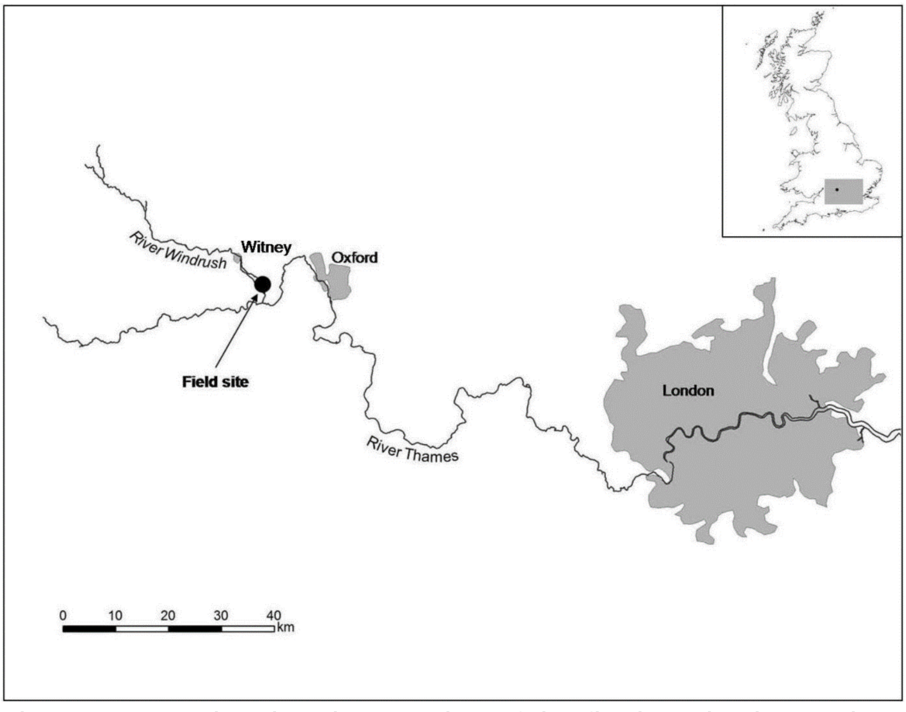


Figure 2 Map showing the location of the field study site on the River Windrush, Oxfordshire, UK.

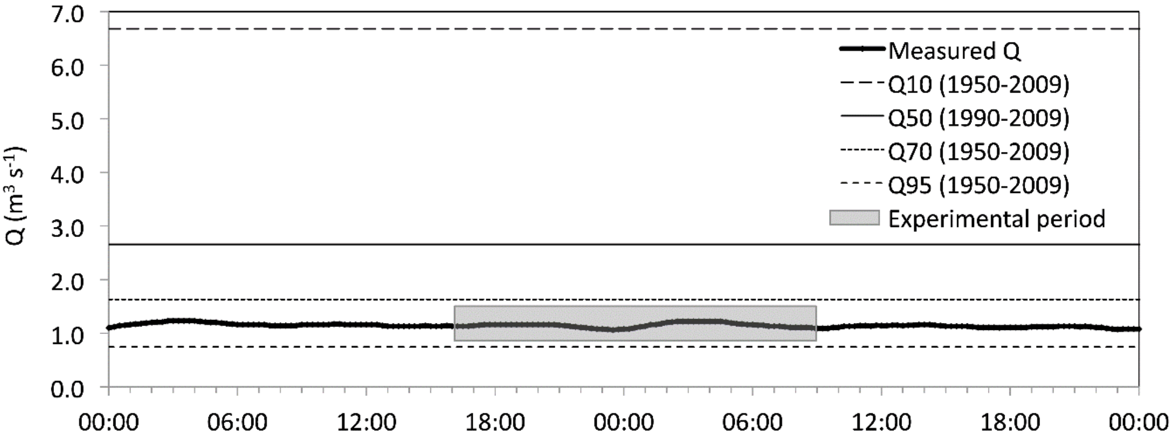


Figure 3 Time series of 15-minute discharge data for the River Windrush at Newbridge during the monitoring period, showing long-term flow percentiles. Source: Environment Agency.

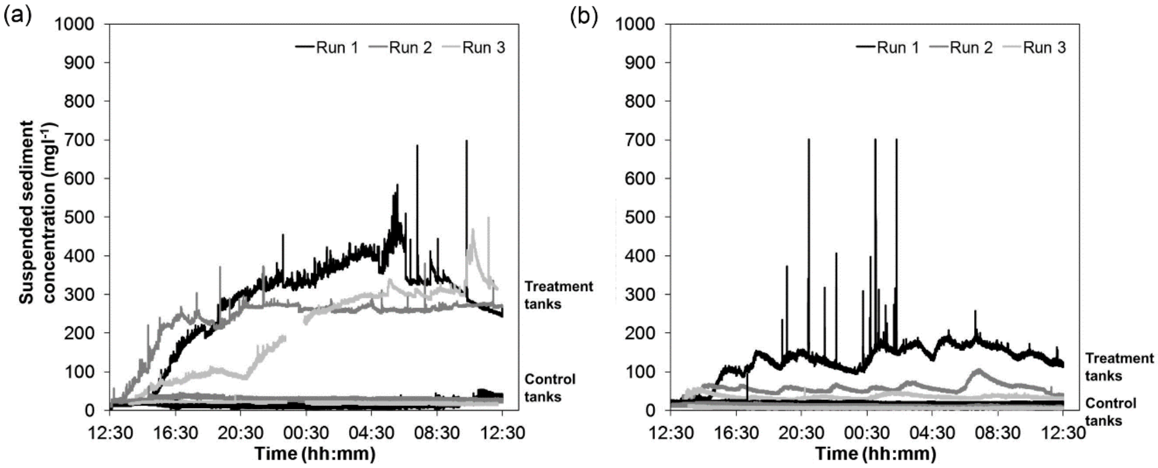


Figure 4 Suspended sediment concentration time series for laboratory mesocosm experiments, showing each of the three runs for (a) bank treatments; and (b) substrate treatments.

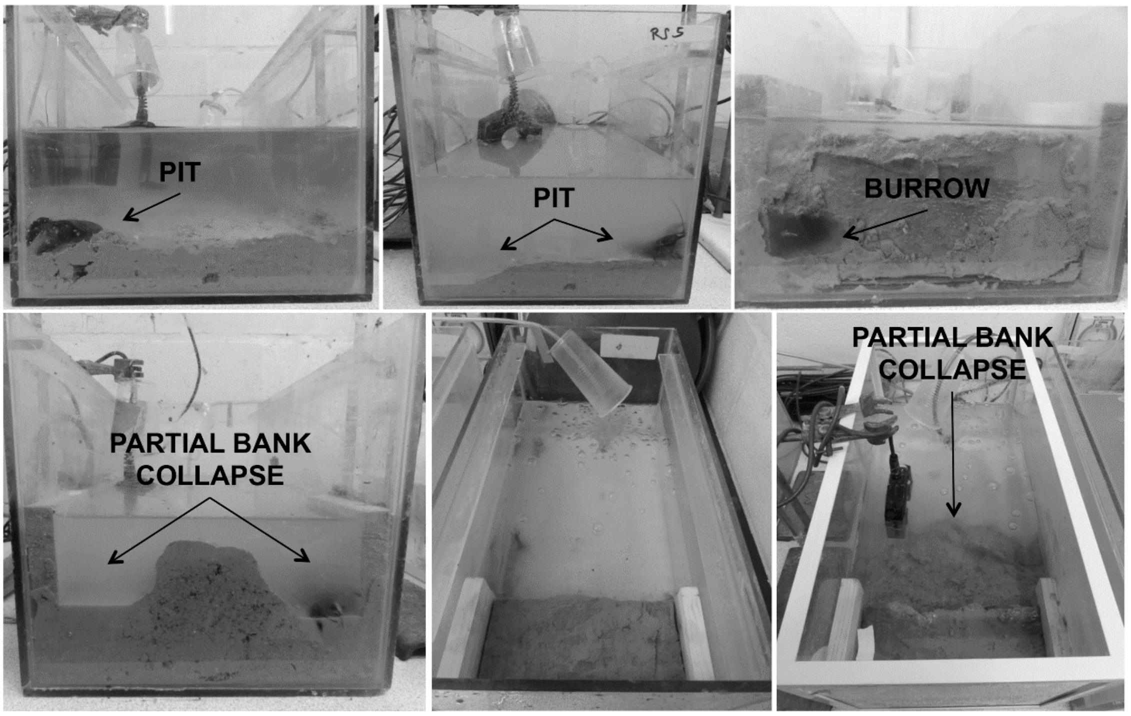


Figure 5 Photographs illustrating key crayfish interactions with bank and bed material observed during the laboratory mescosm experiments: (a) crayfish digging a pit in the left corner of the tank; (b) crayfish digging a pit in the right corner of the tank, with a previously created pit visible in the left corner; (c) burrow visible in the artificial bank; (d) partial collapse of bank following extensive burrowing. (e) and (f) show the artificial bank treatment before the start of the experiment, and following removal of the crayfish at the end of the monitoring period respectively.

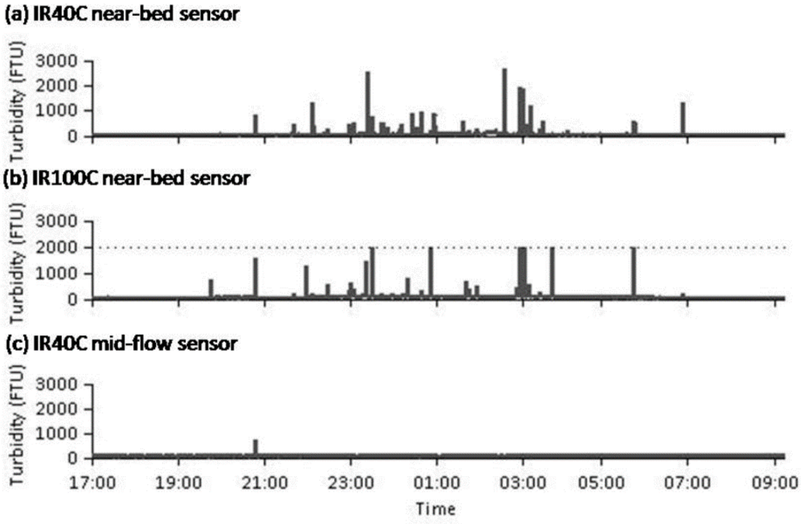


Figure 6 Turbidity time series for: (a) IR40C near-bed; (b) IR100C near-bed; and (c) IR40C mid-flow. The dotted line in (b) represents the upper limit of the IR100C range – turbidity values which meet the line indicate turbidity levels beyond the range of the sensor. All field readings were within range for the IR40C.

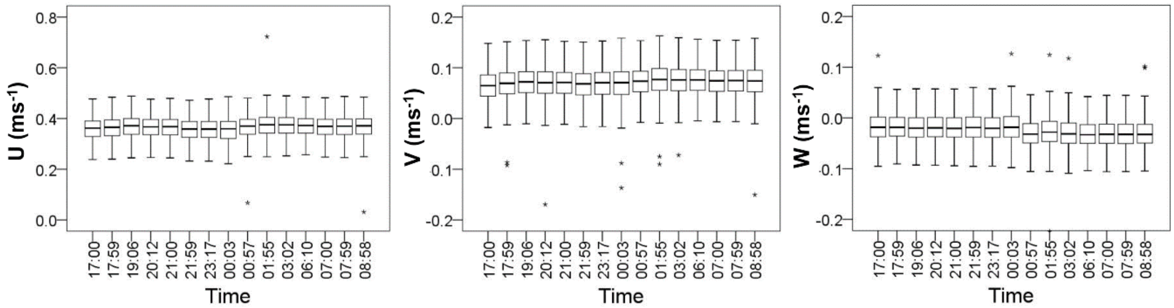
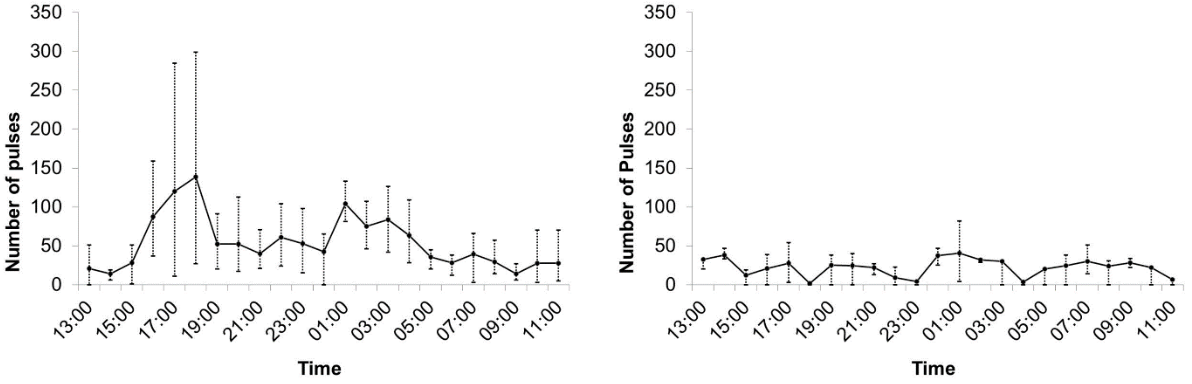
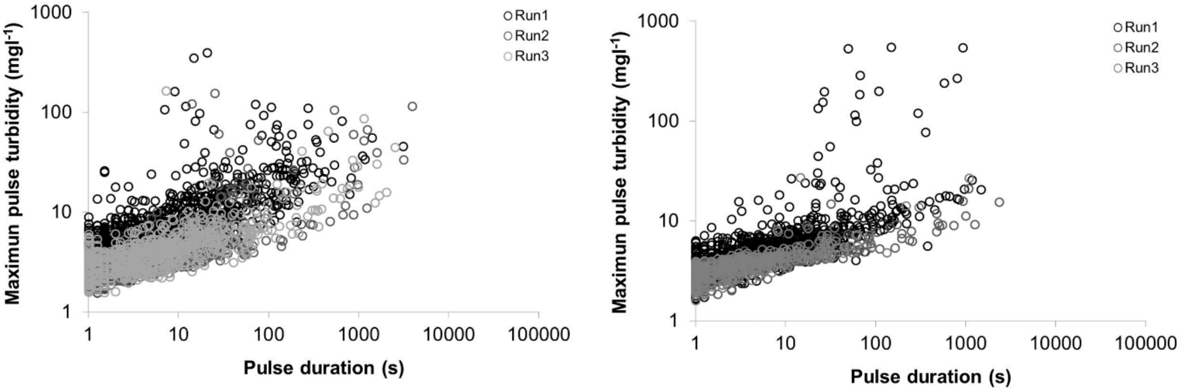


Figure 7 High frequency velocity data for the field site on the River Windrush. Box-plots show median, interquartile range (boxes), 1.5 times the interquartile range (whiskers) and outliers (points) for streamwise (U), cross stream (V) and vertical (W) velocities.



(a) Bank treatment

(b) Substrate treatment



(c) Bank treatment

(d) Substrate treatment

Figure 8 Characteristics of suspended sediment pulses identified in the laboratory time series, showing: (a) number of pulses per hour for bank treatments (mean, maximum, minimum; n=3 runs); (b) number of pulses per hour for bank treatments (mean, maximum, minimum; n=3 runs); (c) duration and maximum turbidity of individual pulses for bank treatments (across the 3 runs); (d) duration and maximum turbidity of individual pulses for bed treatments (across the 3 runs).

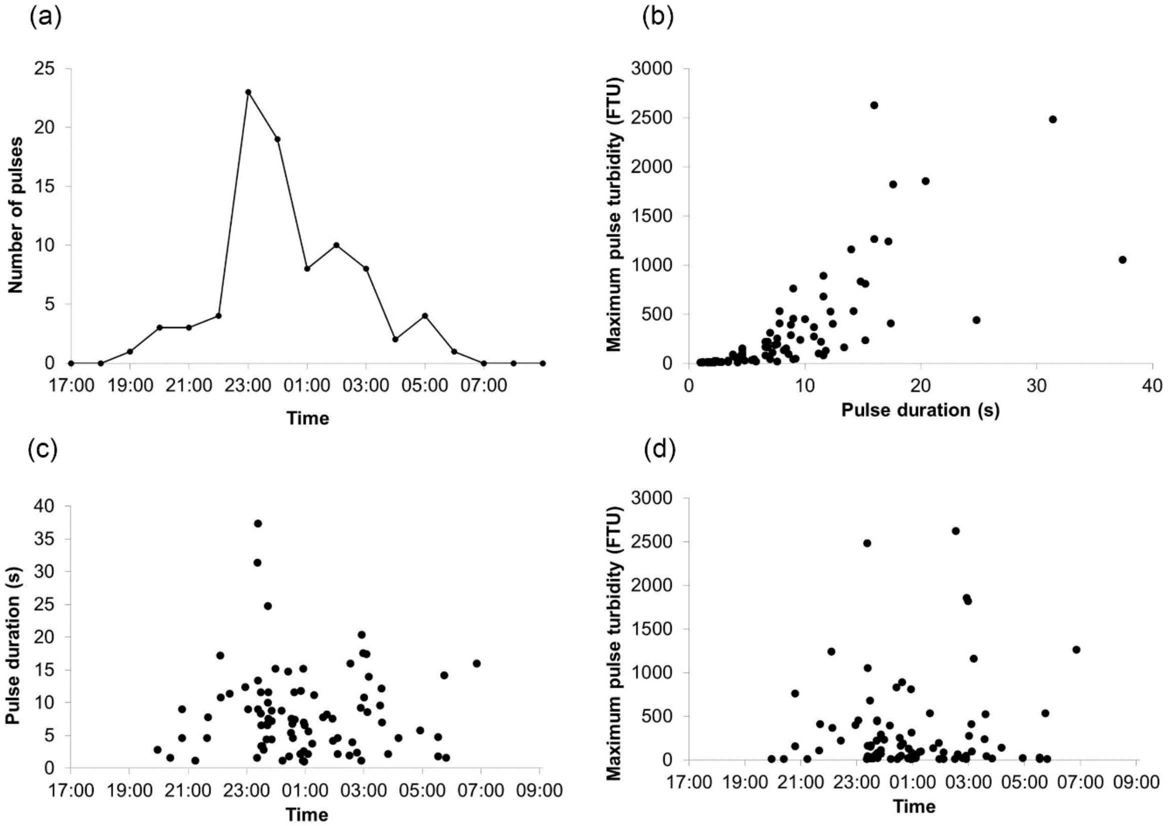


Figure 9 Characteristics of turbidity pulses identified in the field turbidity time series for the IR40C near-bed sensor, showing: (a) number of pulses per hour of the record; (b) duration and (c) maximum turbidity of pulses according to their position in the record; and (d) the relationship between pulse duration and maximum turbidity.

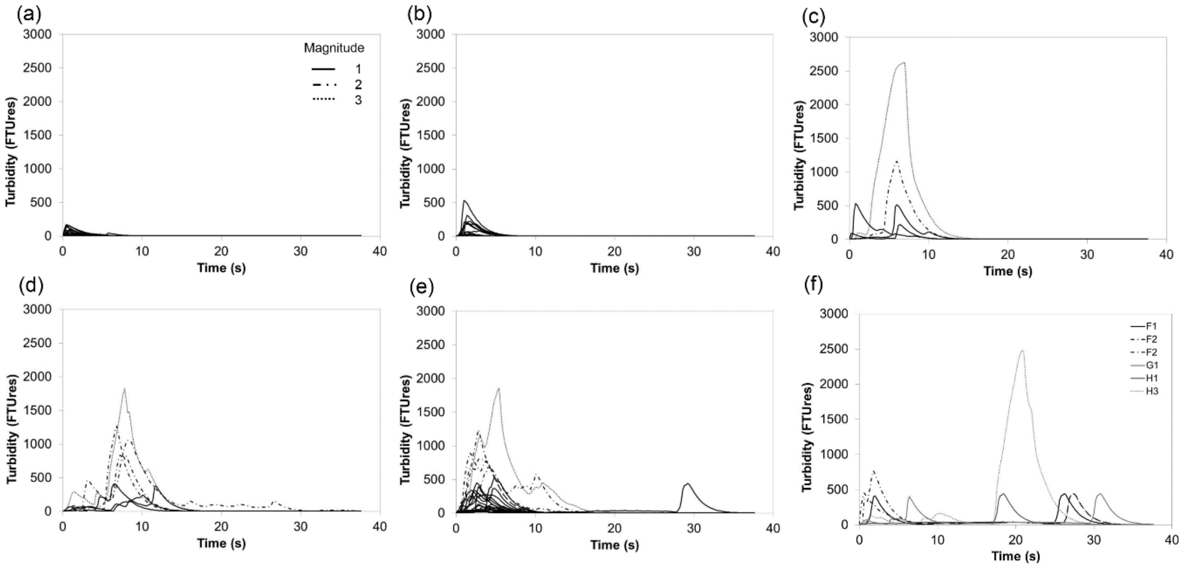
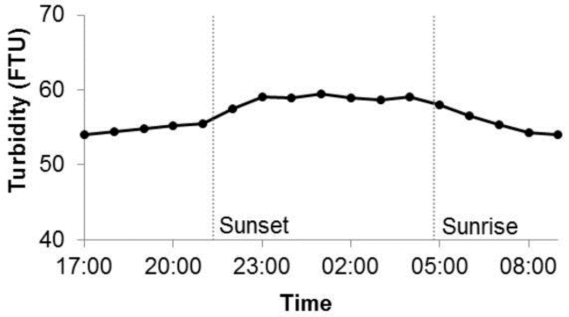
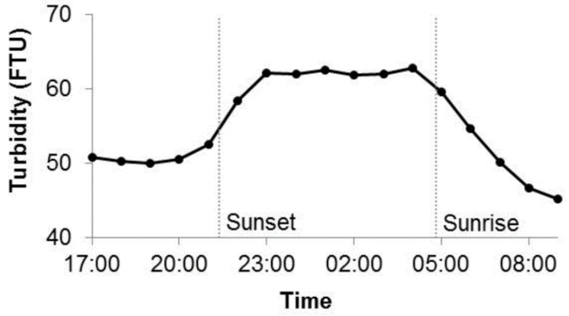


Figure 10 Event time-plots presented in shape-magnitude clusters. For (a) to (e), each plot represents a ‘shape’ cluster (A – E respectively), and within each plot solid lines represent low magnitude, dashed lines intermediate magnitude and dotted lines high magnitude pulses (identified from the magnitude HCA). For (f), a series of clusters that describe a small number of pulse events are plotted together for brevity, with a separate legend.

(a) IR40 near-bed



(b) IR100 near-bed



(c) IR40 mid-flow

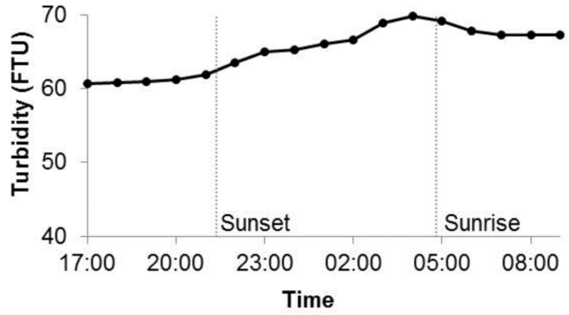


Figure 11 Trends in ambient turbidity, following removal of short-term pulsed events for: (a) IR40C near-bed sensor; (b) IR100C near-bed sensor; and (c) IR40C mid-flow sensor. Vertical dotted lines mark the timing of sunset and sunrise.