Rice, Stephen P. and Johnson, Matthew F. and Mathers, Kate and Reeds, Jake and Extence, Chris (2016) The importance of biotic entrainment for base flow fluvial sediment transport. Journal of Geophysical Research: Earth Surface, 121 (5). pp. 890-906. ISSN 2169-9011

DIEL BIOTURBATION REVEALS THE IMPORTANCE OF BASEFLOW BIOTIC ENTRAINMENT IN FLUVIAL SEDIMENT TRANSPORT

Stephen P Rice[1]

Matthew F Johnson[2]

Kate Mathers[1]

Jake Reeds[3]

Chris Extence[3]

1. Department of Geography, Loughborough University, Loughborough, Leics., LE11 3TU, UK (corresponding author, s.rice@lboro.ac.uk)
2. School of Geography, University of Nottingham, Nottingham, NG7 2RD, UK
3. Environment Agency, Waterside House, Waterside North, Lincoln, LN2 5HA, UK

KEY POINTS

1. The contribution of crayfish bioturbation to monthly and annual suspended sediment loads was measured
2. Biotic entrainment was important at baseflow but floods dominated the annual yield
3. Energy from life contributes to sediment fluxes and requires investigation

ABSTRACT

Sediment transport is regarded as an abiotic process driven by geophysical energy, but zoogeomorphological activity indicates that biological energy can also fuel sediment movements. It is therefore prudent to measure the contribution that biota make to sediment transport, but comparisons of abiotic and biotic sediment flux are rare. For a stream in the UK, the contribution of crayfish bioturbation to suspended sediment flux was compared with the amount of sediment moved by hydraulic forcing. During baseflow periods, biotic fluxes can be isolated because nocturnal crayfish activity drives diel turbidity cycles, such that night-time increases above day-time lows are attributable to sediment suspension by crayfish. On average, crayfish bioturbation contributed at least 36% (430 kg) to monthly baseflow suspended sediment loads; this biotic surcharge added between 4.7 and 13.54 t (0.19 to 0.55 t km^{-2} yr^{-1}) to the annual sediment yield. As anticipated, most sediment was moved by hydraulic forcing during floods and the biotic contribution from baseflow periods represented between 0.43 and 1.24% of the annual load. Crayfish activity is nonetheless an important impact during baseflow periods and the measured annual contribution may be a conservative estimate because of unusually prolonged flooding during the measurement period. In addition to direct sediment entrainment by bioturbation, crayfish burrowing supplies sediment to the channel for mobilization during floods so that the total biotic effect of crayfish is potentially greater than documented in this study. These results suggest that in rivers, during baseflow periods, bioturbation can entrain significant quantities of fine sediment into suspension with implications for the aquatic ecosystem and baseflow sediment fluxes. Energy from life rather than from elevation can make significant contributions to sediment fluxes.

Keywords: zoogeomorphology, ecogeomorphology, signal crayfish, diel bioturbation, suspended sediment

INTRODUCTION

Animals play a significant role in geomorphological systems [*Viles*, 1988; *Butler*, 1995; *Butler and Sawyer*, 2012; *Johnson and Rice*, 2014; *Holtmeier,* 2015; *Albertson and Allen*, 2015] often via complex ecogeomorphological feedbacks [*Naiman et al.*, 2000; *Hall and Lamont*, 2003; *Wheaton et al.*, 2011; *Beschta and Ripple*, 2012] that have implications for the responsible organisms and the wider ecosystem [ecosystem engineering: *Jones et al.*, 1994; *Wright and Jones*, 2006; *Moore,* 2006; *Jones*, 2012]. Despite increasing recognition of zoogeomorphological activity there is a pervasive but untested assumption that the impact of animals on sediment flux is minor relative to geophysical forcing. Sediment transport continues to be predominantly regarded as an abiotic process driven by the conversion of potential energy derived from relief to kinetic energy across elevation gradients. With only a few exceptions in fluvial geomorphology [*Tashiro and Tsujimoto*, 2006; *Albertson et al.*, 2014] and rare occurrences in other domains [*Borsje et al.*, 2008], sediment transport formulations do not recognize animal activity or the potential contributions of biological energy. In the absence of clear supporting evidence it is prudent to test this orthodoxy by investigating what relative contribution fauna make to the movement of sediment at the Earth's surface. A recent report from the U.S. National Academy of Sciences [*NRC*, 2009] pointed out the need for such research, given that purely abiotic models are often insufficient to predict geophysical processes.

Comparisons between biological and geophysical contributions to sediment transport can be made using the mass transfer rate or the energy expended to accomplish that transport. *Phillips* [2009] estimated the contribution of biological energy to landscape evolution at global and regional scales. Net primary production was compared with potential energy derived from elevation differences across terrestrial landscapes and showed that the contribution to geomorphological work from biotic energy almost certainly exceeds that from geophysical sources. However, this is the only study of its kind and the refined analysis that *Phillips* [2009] invited, which amongst other improvements would seek to establish the proportion of biological energy that is geomorphologically relevant and the proportion of geophysical energy that accomplishes geomorphological change, has not yet been developed. Direct attempts to compare biotic and abiotic contributions to sediment transport are equally rare. Many studies have extrapolated local *in-situ* measurements to make inferences about the magnitude of zoogeomorphic sediment transfers, including for earthworms [e.g. *Darwin*, 1881; *Jouquet et al.*, 2010], marine macrozoobenthos [e.g. *Davison*, 1891; *de Backer et al.*, 2011], beavers [e.g. *Butler and Malanson*, 2005; *Visscher et al.*, 2014], and fossorial mammals [e.g. *Hall et al.*, 1999; *Eriksson & Eldridge* 2014]. Other studies have bench-marked biotic impacts on sediment flux, relative to abiotic controls, in *ex-situ* [e.g. Statzner *et al.*, 1999; Pledger *et al.*, 2014] and *in situ* field experiments [e.g. *Moore et al*., 2004]. However, very few studies have isolated and compared faunal and geophysical fluxes in the field at spatial and temporal scales sufficient to provide a robust perspective on their relative importance. The only example we are aware of is *Hassan et al.*'s [2008] comparison of the cumulative bed load transport accomplished by geophysical forcing (flood events) and biological activity (salmonid spawning) in the interior of British Columbia, Canada, which found that bed material displacements caused by spawning can dominate bed load transport in small mountain catchments.

In this paper we quantify the contribution of crayfish bioturbation to the suspended sediment load in a lowland river in the UK and compare this biotic flux with the amount of sediment moved by hydraulic forcing. Numerous studies have demonstrated that bioturbation by fish, crustaceans and macroinvertebrates affects the retention, hyporheic movement and interstitial storage of fine river bed sediments [*Flecker*, 1997; *Power*, 1990; *Zanetell and Peckarsky*, 1996; *Statzner et al.*, 1996; *Pringle and Hamazaki*, 1998; *Mermillod-Blondin*, 2003; *Usio and Townsend*, 2004; *Helms and Creed*, 2005; *Fortino*, 2006; *Cross et al.*, 2008; *Statzner and Sanges*, 2008; *Nogaro et al.*, 2009]. However, there are no published measurements of the suspended sediment flux caused by bioturbation in rivers or any evaluation of the magnitude of this biotic effect relative to hydraulically-driven sediment entrainment. Herein, bioturbation refers to the direct entrainment of fine sediment into the water column by the expenditure of energy by crayfish. Relevant activities include the construction and maintenance of burrows, foraging for food on the river bed and fighting with or maneuvering away from other crayfish during resource conflicts. In addition to directly entraining sediment, burrowing by crayfish also recruits new sediment to the river system because excavated bank materials are transferred to the river bed where they are available for subsequent transport. Where burrow densities are high, bank integrity may be lost, accelerating mass failure and the recruitment of more sediment. This paper does not consider these recruitment aspects of burrowing, which may be substantial, and is focused solely on bioturbation.

Rice et al. [2014] used a four-week dataset from the Brampton Branch of the River Nene, UK to demonstrate how bioturbation fluxes might be isolated from those driven by hydraulics. Numerous studies in UK rivers have demonstrated that the invasive signal crayfish, *Pacifasticus leniusculus* (Dana) is predominantly nocturnal [*Guan and Wiles*, 1998; *Bubb et al.*, 2002]; for example, on the River Bain, Lincolnshire, only 6% of crayfish movements between July and November 2009 occurred during daylight hours [*Johnson et al.*, 2014]. It is therefore reasonable to assume that any bioturbation impact on sediment flux would predominantly occur at night, with negligible daytime contributions. Monitoring on the Brampton Branch revealed increases in night-time turbidity and, in the absence of any hydraulic cause, it was argued that the most likely cause was bioturbation by the nocturnal activities of signal crayfish, which have infested this river. It was then possible to estimate the contribution of bioturbation to the total sediment load by comparing daytime with night-time sediment fluxes, which for the month in question amounted to 47% of the yield between floods and 20% of the yield when flood events were included. *Rice et al.*'s [2014] argument for a causal link between increased night-time bioturbation and nocturnal crayfish activity was based on several lines of evidence: (1) mesocosm experiments [*Harvey et al.*, 2014] confirming an earlier suggestion [*Harvey et al.*, 2011] that nocturnal burrowing by signal crayfish increases turbidity at night; (2) aquarium experiments showing that a variety of crayfish activities including walking, tail-flipping and fighting increase turbidity [*Rice et al.*, 2014]; and (3) the lack of a credible hydraulic explanation for the diel turbidity pattern. In addition, previous investigations of similar diel turbidity in streams favour bioturbation as the most likely explanation [*Gillain*, 2005; *Richardson et al.*, 2009; *Loperfido et al.*, 2010] or, at least, a potential explanation [*Williams et al.*, 2011]. While this set of arguments is robust, direct field evidence linking crayfish activity to increased turbidity was not collected. Moreover, the single month of sediment flux data cannot be assumed representative of the annual bioturbation effect because of anticipated seasonal variations in crayfish activity and flood forcing.

Using data from a different location on the Brampton Branch, we advance the initial analysis of *Rice et al.* [2014] in two important ways. First, we examine field evidence linking daily variations in crayfish activity to diel turbidity cycles over a four-month period, which strengthens the argument that nocturnal increases in bioturbation drive diel turbidity. Second, we use a sediment flux record extending over 12 months to quantitatively compare the suspended sediment mobilized by bioturbation with that mobilized by hydraulic forcing and establish the relative contribution of each to monthly and annual sediment loads.

During floods, crayfish may be responsible for a proportion of the sediment that is mobilised via their sediment recruitment role, but we anticipate direct entrainment by bioturbation to be a factor that affects fine sediment fluxes predominantly during baseflow, rather than during floods. This is based on two arguments. First, in our pilot work [*Rice et al.*, 2014] individual floods moved substantially larger quantities of sediment than the typical night-time increase in suspended sediment flux that we associated with crayfish activity. This was because floods sustained higher average suspended sediment concentrations (100s mg l^{-1} vs 10s mg l^{-1}) for longer periods (days vs hours). Second, crayfish activity generally declines as water depth increases [*Johnson et al.* 2014], so it is reasonable to assume that the potential for crayfish to cause sediment suspension is diminished during floods. Because floods are likely to dominate total sediment flux, we therefore expect that direct entrainment will have a relatively small impact on annual sediment flux, but an important impact during baseflow periods.

2. METHODS

2.1 Field Site

The Brampton Branch is a headwater tributary of the River Nene, Northamptonshire, UK. It drains approximately 233 km^2 of small, rolling hills and well-developed floodplains across a total relief of 147 m. Dominant land uses according to the UK Land Cover Map 2000 [*Fuller et al.*, 2002] are arable farming (54%) and grassland (28%), some of which supports sheep and cattle grazing. Close to the catchment outlet, mean flow is 1.15 m^3 s^{-1}, Q_{10} (90th percentile) flow is 2.35 m^3 s^{-1} and Q_1 is approximately 10 m^3 s^{-1} (St Andrews gauging station, Ordnance Survey grid reference SP749613). Catchment geology is dominated by Jurassic mudstones and siltstones. Monitoring focused on a headwater reach approximately 100 m in length near the village of Hanging Houghton (SP742741; Figure 1) where catchment area is 24.5 km^2. The land use in this part of the catchment is predominantly arable farming and mixed woodland and there were no grazing stock along the river, upstream of the study site. The channel has a pool-riffle structure, is between 2 and 4 m wide and has an average bed slope of 0.0023. The subsurface bed material (based on pooling eight individual McNeil samples [*McNeil and Ahnell*, 1964]) has a weakly bimodal grain size distribution with: D_{16} = 0.5 mm, D_{50} = 6.5 mm, D_{84} = 32.3 mm and 32% by mass finer than 2 mm. Wolman sampling of the surface bed material [*Wolman*, 1954] yielded a log-normal grain size distribution with: D_{16} = 6.6 mm, D_{50} = 20.1 mm, D_{84} = 41.8 mm and 14.9% by count finer than 4 mm.

Invasive signal crayfish *(P leniusculus)* are the primary zoogeomorphic agent in the study river. This species is a large (10-15 cm long) and aggressive decapod crustacean that is now widespread and abundant following successful colonization of streams and rivers across the UK and 26 other European territories [*Souty-Grosset et al.*, 2006; *Holdich et al.*, 2014; *James et al.*, 2014]. The role of these animals as agents of sediment recruitment [*Guan*, 1994; *Harvey et al.*, 2014], bed destabilization [*Johnson et al.* 2011] and bioturbation [e.g. *Usio and Townsend*, 2004; *Creed and Reed*, 2004] is reviewed in *Harvey et al.*, [2011]. Benthic macroinvertebrate sampling at four sites on the Brampton Branch has been completed twice each year since 1985 by the Environment

Agency of England. *P. leniusculus* were first recorded in these surveys in1995 at the site closest to the field site. A small population of indigenous white-clawed crayfish, *Austropotamobius pallipes* (Lereboulle, 1858) were present until the early 1990s but they were expunged following signal invasion. Signal crayfish are difficult to detect using routine sampling protocols [*Hiley*, 2003; *Peay*, 2003] so their presence in these samples indicates an abundant and well-established population, almost certainly at a density exceeding 1.0 m^{-2}. Because of the sampling difficulties, density is often represented by catch per unit effort (CPUE) metrics, which are useful for defining relative abundances and have been shown to correlate well with other measures [*Dorn et al.,* 2005]. Trapping estimates along the Brampton Branch in 2013 and 2014 revealed abundances of 3.3 to 9.6 adults per trap day.

2.2 Crayfish activity and turbidity

Crayfish activity levels were monitored and related to local variations in turbidity over a four month period from 1 June to 30 September 2013. Activity was monitored by tracking individual animals using Passive Integrated Transponder (PIT) tags (12 mm long, 2 mm wide) that were attached to the cephalothorax of locally-trapped adults using Cyanoacrylate. In April 2013, along a 20 m section of the study reach, 16 circular antennae (0.25 m diameter) were buried equidistantly, just beneath the bed surface close to a bank with abundant crayfish burrows. Antennae were connected to a multi-point decoder that logged the time whenever a tagged crayfish moved over or within 20 mm of an antenna. By late May, after several mobile bed events, we judged that the bed had recovered from installation and the number of tagged crayfish was maintained at approximately 7 until the end of September. Because crayfish periodically left the reach, we replenished numbers of tagged crayfish every month, tagging a total of 50 individuals over the monitoring period. Activity was measured as the total number of movements recorded by all antennae in each hour. This does not represent all crayfish journeys in the study section because crayfish could pass between the antennae without triggering a record and because it was only feasible to tag a fraction of the resident population. However, there is no reason to assume any temporal bias in these unrecorded movements, so the time series provides a consistent measure of crayfish activity. In the center of the antennae array a YSI sensor, located approximately 0.15 m from the bed, recorded turbidity at 30-minute intervals. These measurements were averaged over the same one-hour periods as those used to quantify crayfish movements.

Eight consecutive days in September when turbidity measurements were affected by debris build-up were removed from the time series. The resulting set of hourly measurements were analyzed in two ways. First, time series were examined to identify dominant periodicities by calculating the periodograms of the movement and turbidity data. A periodogram is a graphical representation of the discrete Fourier transform that estimates the relative importance (power) of all possible frequencies, thereby identifying dominant periodicities in a complex time series. Second, for the 24 hourly measurements in each calendar day, rank correlation analysis was used to examine the association between local turbidity and crayfish activity.

2.3 Sediment flux estimation

Suspended sediment flux Qs (mg s^{-1}) was estimated as the product of suspended sediment concentration C (mg l^{-1}) and discharge Q (l s^{-1}) at the downstream end of the study reach for each 5-minute period between 19 July 2013 and 18 July 2014. C was estimated from a high-resolution time series of turbidity (T, NTU) measurements, using an empirical rating between the sediment concentration in collected water samples and concurrent turbidity measurements. T was measured along with water depth Y (m) at five-minute intervals using a Measurement Specialities, Eureka 2 Manta sonde fitted with a self-wiping turbidity sensor (ISO 7027; 0 to 3000 NTU, quoted error ±1 %) and a vented pressure transducer (0-10 m, quoted error ±0.03 %). The sonde was mounted horizontally, 0.1 m above the bed with the sensors 0.3 m from the left bank. During the 365-day study period, measurement or data recording problems were rare, and affected only 6.7 days (1.8%).

The performance of the turbidity sensor was tested to ensure that its measurements were not adversely affected by local environmental conditions. In particular, it was important to demonstrate that any daily fluctuations in stream turbidity were not associated with daily variations in incident radiation and temperature. Incident light is a specific concern because the ISO 7027 standard is based on measuring the scatter of an emitted light pulse, in this case at an infrared wavelength, and measurements can be corrupted by incident infrared in shallow water. In August 2014, a second, identical sonde was installed immediately adjacent to the main sensor, but was placed inside a rectangular Perspex container (internal dimensions 0.13m wide x 0.75m long x 0.40m high) fixed to the river bed, watertight at the base and around the sides, but without an upper surface. This sonde experienced the same daily fluctuations in temperature and light, but was filled with clean tap water. In the absence of any temperature or incident light effect, it was anticipated that the boxed instrument would record constant low turbidity in contrast to a varying signal from the stream.

Water samples for the determination of sediment concentration were obtained using an ISCO 3700 automated water sampler fitted with a stage-activated trigger that drew water from an inlet hose located immediately adjacent to the turbidity sensor. A total of 174, 700ml samples were collected during six storm events and by periodic sampling over 12 days on several occasions. To extend the range of this calibration data an additional 16 samples were obtained while the bed 5-10m upstream of the intake was artificially disturbed. This was achieved by lightly scuffing the bed surface with a booted foot. Disturbance generated clouds of suspended sediment that had mixed through the water depth upon reaching the intake, at which point a water sample was collected and turbidity measurements made. The single point measurements of T and C were assumed representative of the average cross-section values based on the small size of the stream and our visual observations of excellent mixing across a range of flows. Samples were filtered using Whatman 0.7 µm glass microfiber filters and loss on ignition was used to determine total organic and mineral mass. *Bilotta and Brazier* [2008], amongst others, have highlighted the need to be cautious when using continuous turbidity measurements as a surrogate of suspended sediment concentration because turbidity measurements are sensitive to the characteristics of suspended mineral grains and the presence of other suspended materials, including organic detritus. The average organic component in our samples was 18.6% (standard deviation = 4.4%) so the majority of the suspended material affecting measured turbidity was mineral and C was calculated using only the mineral mass. A site-specific calibration was constructed using a LOESS model that best described the non-linear relation between T and C (Figure 2). This model was used to estimate C for all values of T in the annual time series.

Discharge was measured using the velocity-area method [*Herschy*, 1993] on seven occasions at a cross section two metres upstream of the sonde. Velocity measurements were made with a Valeport electromagnetic current meter. The correlation between Q and water depth, Y is significant ($p < 0.001$) and a power model with $R^2 = 0.93$ was fitted using least squares linear regression: $Q = 0.78\ Y^{1.17}$. This model was then used to estimate discharge for the time series of Y. Discharge measured at an Environment Agency gauge located at Brixworth approximately 3.9 km downstream of the monitoring site (SP737708) provides a means of evaluating the quality of the derived time series from Hanging Houghton. The time series are closely matched and cross-correlation yields a peak value of 0.97 at a lag of 1.5 hours, which is consistent with the distance and average water velocity between the two sites. Moreover, at this lag, the discharge measured at the gauge is, on average, 2.4 times larger than at Hanging Houghton, which is consistent with a 2.4 times increase in drainage area between the two sites. We conclude that the estimated discharges are reliable and they were used with the corresponding estimates of C to calculate sediment fluxes Qs_t (mg s^{-1}) for each five-minute interval. For a desired time period, suspended sediment load G (kg) was calculated as:

$$G = 10^6 \cdot \left(\sum_{t=0}^{n} \Delta \cdot Qs_t\right) \qquad [1]$$

where Δ is measurement interval = 300 s and n is the number of intervals in the period of interest.

2.4 Isolation of abiotic and biotic components of sediment load

For the purposes of analysis, it is useful to consider

$$G_{total} = G_{bf} + G_{fl} \qquad [2]$$

in which the subscripts refer to the total, baseflow and flood sediment yields, respectively. Flood and baseflow periods were identified from stage data; baseflow as periods of steady, low, customary discharge and flood flows by unsteady, higher, discharges with clear rising and falling limbs associated with storm-flow runoff. Separate calculations of G_{bf} and G_{fl} were completed using equation 1.

During baseflow periods there is a strong potential for crayfish impact and G_{bf} was decomposed into abiotic (G_{bfA}) and biotic (G_{bfB}) components:

$$G_{bf} = G_{bfA} + G_{bfB} \qquad [3]$$

The two components were isolated by assuming that, in the absence of crayfish bioturbation, turbidity would reach a maximum abiotic value T_A (NTU), which was lower than the bioturbation-enhanced daily average. Time series of T_A were constructed according to the criteria described below and used in the LOESS model to derive Qs_A and thus sediment load in the absence of bioturbation, G_{bfA}. The estimated biotic component, G_{bfB} was calculated as the difference G_{bf} - G_{bfA}.

The key uncertainty in this method is the value of T_A and two values that bracket a reasonable range of likely values were therefore used to provide maximum and minimum estimates of G_{bfB}: (a) T_{min} equal to the minimum measured value of T on each day; and (b) T_0 = 0 NTU, equivalent to clear-water flows. T_{min} represents an empirical estimate of the turbidity in the absence of bioturbation; that is ambient baseflow sediment suspension. However, these values may be elevated by the residual effects of the previous night's bioturbation, in which case T_{min} yields a liberal estimate of the abiotic effect and a minimum estimate of the biotic load G_{bfB}. In the absence of bioturbation, it is feasible that turbidity would approach zero, the limiting case, such that (b) represents a minimum estimate of the abiotic effect and provides a maximum theoretical estimate of G_{bfB}.

In contrast to the treatment of baseflow periods, no attempt was made to partition total flood load G_{fl} into biotic and abiotic components because, as explained above, we do not anticipate a substantial crayfish impact on direct entrainment during flood events and assume it is negligible.

3. RESULTS AND INTERPRETATION

3.1 Turbidity sensor performance

Turbidity measurements were not affected by incident light or ambient temperature cycles. As expected, the turbidity time series from the sensor in clean water inside the Perspex box did not show any fluctuations in turbidity, whereas the sensor located in the stream recorded the anticipated diel pattern (Figure 3). Because they were co-located, they experienced the same light conditions between day and night and the same degree of shading during daylight hours. Water temperature measurements inside and outside the box confirmed that water temperature fluctuations were the same. This result demonstrated that the stream sensors recorded real, unadulterated turbidity variations.

3.2 Crayfish activity and local turbidity

Periodograms for time-series of turbidity and crayfish movement both exhibit peaks in power at a period of 1 day (Figure 4a, b). Thirteen flood days were removed from these analyses because their random temporal distribution added uninteresting low-frequency noise to the turbidity plot. There is a strong temporal association between the two series, with night-time turbidity peaks coincident with nocturnal increases in crayfish activity (Figure 4c).

Spearman rank correlation coefficients for hourly turbidity and crayfish movements were calculated for each 24-hour period during baseflow conditions (90 days in total). Thirteen flood days were removed to exclude hydraulic forcing as a confounding factor. The coefficients are predominantly positive (Figure 4d) and 46 of 48 significant correlations ($p < 0.10$) are positive, indicating that increased activity was typically associated with increased turbidity. Individual insignificant, coefficients ($p > 0.10$) indicate that sampling chance cannot reasonably be ignored as a possible explanation, but the preponderance of positive values is collectively instructive, because in the absence of any association between activity and turbidity one would anticipate an even distribution of insignificant values about zero, which is not the case here. There is a general weakening of the relation between increased activity and increased turbidity between late August and mid-September, corresponding with the crayfish mating season, when activity levels increased and became less strongly nocturnal.

These are the first concurrent field measurements of crayfish activity and turbidity. The strong temporal association between the two time series provides new evidence, to add to that reviewed in the introduction, which supports the argument that crayfish can drive diel turbidity in infested streams [*Rice et al.*, 2014; *Harvey et al.*, 2014]. The correlation analysis (Figure 4d) adds further weight to this conclusion, because it yields evidence of a generally positive association between activity and turbidity on an hourly basis. However, the presence of numerous days when the correlation was insignificant and the fact that the magnitude (rather than timing) of peaks in the time series are not strongly associated, indicates that this relation is not straightforward. We think this reflects, at least in part, imperfections in our measurements of both turbidity and activity: the former because a single turbidity sensor was monitoring a 20m channel length and may easily have missed some crayfish-related entrainment events; and the latter because not all active crayfish were tagged.

3.3 Analysis of turbidity time series

Extended periods of high flow dominated the hydrograph between October 2013 and February 2014 (Figure 5). Periods of baseflow, when crayfish bioturbation might be expected to have directly affected suspended sediment flux, mainly occurred in the spring and summer months and constituted 57% of the study period. Diel variations in turbidity, with higher night time values, are characteristic of these low-flow periods (Figure 5).

For 20 out of 23 low-flow turbidity time series that lasted more than two days, periodograms have a dominant peak at 1-day (Figure 6), confirming the prevalence of a diel pattern. The three time series that do not show this peak (one in October 2013 and two in May 2014) have a secondary peak at 1 day. The strength of the diel variation weakened in the winter months when water temperatures were relatively low and flow depths were relatively high (Figure 7). Crayfish are generally less active during the winter and this decline in activity has previously been associated with lower water temperatures and higher flows [*Bubb et al.*, 2004; *Johnson et al.*, 2014]. Weakening of the diel variation during the winter months is therefore consistent with the argument that crayfish bioturbation is responsible for the diel cycle.

In addition, there is no plausible hydraulic explanation for the observed diel patterns. Variations in water depth are small during the baseflow periods (on the order of 0.10 m) and diel turbidity is present even though the corresponding depth trace is flat or declining slowly, in which case the diel pattern may be superimposed on a declining flood-driven turbidity trend (Figure 5). For example, during the low flow period in March 2014, when water depth steadily declined at a rate of approximately 0.006 m day^{-1}, a clear diel turbidity trend persisted without any significant decline over the same period (Figure 8a). Because stage change is a useful index of change in hydraulic parameters relevant to sediment entrainment (bed shear stress, shear velocity, turbulence intensity), the independence of diel turbidity suggests that hydraulic forcing was not responsible for the diel turbidity cycle.

In ten baseflow periods during the summer months, from mid-June to mid-September, depth variations showed a weak daily fluctuation, with depth decreasing by between 0.005 and 0.010 m between mid-afternoon and midnight (e.g. Figure 8b). It is likely that these fluctuations reflect summertime variations in evapotranspiration during periods of soil moisture deficit [*Burt,* 1979; *Bond et al.*, 2002, *Gribovski et al.*, 2010]. Whatever their cause, there is no evidence linking them to the diel turbidity pattern. If depth variations were responsible for the turbidity signal, a positive correlation would be expected between water depth and turbidity, but no associations were evident: taking the ten-day period in June 2014 (Figure 8b) as an example, there is no correlation at lag = 0 for either the 5-minute data (Pearson correlation coefficient $R = 0.03$, $p = 0.11$, n = 2808) or for the time series of 1-hour averages ($R = 0.07$, $p = 0.29$, $n = 234$). A weak, but significant, correlation at a lag of approximately 13 hours in the smoothed time series ($R = 0.23$, $p = 0.00065$, $n = 234$) highlights the phase shift between the depth and turbidity signals, but there is no straightforward physical explanation for this shift, which is therefore interpreted as further evidence of the independence of the depth and turbidity.

To summarize, during baseflow periods turbidity varied on a diel cycle and we believe this reflected nocturnal increases in crayfish bioturbation, because: (1) there is no adequate hydraulic explanation to account for the turbidity pattern (Figure 8, Figure 5); (2) PIT tag data reveal a strong temporal association between crayfish activity levels and turbidity (Figures 4 and 5); and (3) the strength of the diel turbidity signal weakens at those times of year when crayfish are expected to be less active (Figure 7). It is therefore reasonable to apply the technique proposed above (equations 1 to 3) in order to establish biotic and abiotic components of the sediment flux.

3.4 Biotic and abiotic contributions to suspended sediment load

Biotic and abiotic contributions to baseflow suspended sediment load (G_{bf}) and total suspended sediment load (G) are illustrated in Figure 9. Results are presented for the 11 whole months during the study period and, in Table 1, for the annual total load (19 July 2013 to 18 July 2014) as well.

Liberal estimates (using T_0 to calculate G_{bfA}) suggest that crayfish added as much as 13538.3 kg to the annual sediment flux during baseflow periods. Even conservative estimates (using T_{min} in calculations of G_{bfA}) found that biotic contributions were present during all baseflow periods and collectively contributed at least 34.4% (4650.7 kg) to the annual baseflow load G_{bf}. Minimum estimates of the monthly, baseflow bioturbation component G_{bfB} (using T_{min} in calculations of G_{bfA}) ranged between 126.1 and 1142.7 kg with a mean of 430.3 kg; equivalent to percentage contributions of 19.4 to 45.9% with a mean of 35.6% (standard error, SE = 2.6%; Figure 9a). Maximum estimates of G_{bfB} (using T_0 to calculate G_{bfA}) ranged between 403.0 and 3101.6 kg with a mean of 1257.7 kg, equivalent to biotic contributions of 100%.

Almost all (98.8%) of the total annual suspended sediment load (109.1 t), moved during floods. When flood flows are included in the component estimates, the annual bioturbation contribution shrinks to a minimum value of 0.43% (using T_{min} in calculations of G_{bfA}) and a maximum value of 1.24% (using T_0 to calculate G_{bfA}). The monthly figures are highly variable, mainly as a function of the number of flood days per month (Figure 9b). Minimum estimates of the monthly biotic contribution range from 0 to 27% with a mean of 7.2 (SE = 3.1%) and maximum estimates range from 0 to 71.8%, with a mean of 17.9% (SE = 7.7%). In months when floods were rare and total sediment load was therefore low, the estimated bioturbation contribution was relatively high. For example, in April 2014, the bioturbation component is estimated to be between 25.9 and 71.8% of the monthly total, depending on the value used for G_{bfA}. In contrast, in months where flooding dominated, as in January 2014 when there were no days of baseflow, the biotic contribution was estimated as 0%.

4. DISCUSSION

On average, crayfish bioturbation directly added a minimum of 430 kg month^{-1} and a maximum of 1258 kg month^{-1} to the baseflow sediment flux at Hanging Houghton. The minimum estimate is equivalent to 36% of monthly baseflow sediment yield, which means that during baseflow periods crayfish directly mobilized at least 56% more suspended sediment than would have moved in their absence. The largest monthly contribution occurred in March 2014 (minimum estimate 1143 kg and maximum estimate 3103 kg) and the annual cumulative surcharge was between at least 4.7 t and may have been as high as 13.5 t. These data demonstrate that during baseflow periods, bioturbation entrains significant quantities of sediment into suspension.

Between July 2013 and July 2014, the direct contribution of crayfish bioturbation to the total annual sediment flux was small (0.43 to 1.24%), which reflects the dominant effect of flood flows in transporting fine sediment. This might be interpreted as indicating that the biotic contribution to total sediment flux is geomorphologically inconsequential, but two arguments suggest that such a conclusion would be premature. First, during the winter of 2013-14 large areas of the UK, including the Nene catchment, experienced exceptionally high rainfall, groundwater levels and runoff, with sustained, above-average discharge from December to February [*Huntingford et al.*, 2014] and the most sever storminess for 143 years [*Matthews et al.*, 2014]. It is possible that unusually high flows during the measurement period elevated the 2013-14 abiotic contribution and depressed estimates of the baseflow bioturbation effect relative to the long term average. UK Met Office data for the Midlands Region show that 2013-2014 winter rainfall was second highest on record (since 1910) and that spring 2014 rainfall was in the upper quartile. Data from the St Andrews gauge reveal that between 1 August 2013 and 31 July 2014, cumulative water yield was the eleventh highest in the 68-year record. There is no reliable means of evaluating whether these wet conditions depressed biotic effects, but a first-order proxy for the biotic contribution is the number of non-flood days. Using peaks over threshold (POT = 9.95 $m^3 s^{-1}$) at the St Andrews gauge as an index of total flood days, it is clear that nine POT events in 2013-14 was unusual: only three August to July periods in 73 years recorded more than this and the average was 3.7 events yr^{-1}. It therefore is reasonable to hypothesize that the biotic contribution measured in 2013-14 sits at the lower end of the likely range of annual values.

Second, in addition to their mobilization of fine bed sediments via bioturbation, signal crayfish have another impact on fluvial fine sediment dynamics that has not been considered here: the recruitment of large quantities of mobile fine sediment into the river system as a result of burrow construction [*Harvey et al.*, 2011, *Harvey et al.*, 2014]. While burrowing activities lead to the direct entrainment of some fines, burrowing also contributes to the mass of available sediment that is stored on or in the river bed and that is subsequently available for transport during high flows. Recent measurements by us at 13 sites on six rivers in Central England demonstrate that burrow construction contributes 0.25 to 0.50 t km^{-1} a^{-1} to infested rivers. In addition, because burrows can reach very high densities (up to 14 m^{-1}; *Holdich et al.*, 2014], can extend more than 1 metre into the bank and often become interconnected, river banks can be undermined, reducing their integrity and leading to collapse [*Guan* 1994; *Arce and Dieguez-Uribeondo*, 2015]. This accelerated bank erosion contributes further sediment to the river system. It is reasonable to propose that crayfish activity on the Brampton Branch is responsible for a large proportion of the total sediment yield not accounted for by bioturbation; that is, it is likely that a substantial proportion of the sediment that was moved by the main floods (approximately 847 t between December 2013 and February 2014) was available for transport because of long term crayfish infestation. Confirmation of this hypothesis requires measurements of the volume of sediment displaced by crayfish burrowing and longer-term estimates of associated bank failure volumes.

It is appropriate to consider the representativeness and broader relevance of the estimates we have made of biotic contributions to fluvial sediment flux. Many locations across Great Britain have established populations of signal crayfish [*James et al.*, 2014] and show evidence of physical impacts (e.g. burrowing), but the measurements made at Hanging Houghton have not yet been repeated at other invaded sites. Recalling that estimates for the Brampton Branch are between 3.3 to 9.6 adults per trap day, equivalent figures for other UK rivers are between 4.0 and 8.5 adults per trap day [*Peay et al.*, 2009; *Moorhouse et al.*, 2011], with one additional UK river study finding 9 to 28 adults per trap day [*Guan*, 2000]. Elsewhere in Europe, where signals have invaded rivers, typical CPUE ranges are 4 to 6 adults per trap day [e.g. *Hudina et al.*, 2009; *Wutz et al.*, 2013]. Therefore, the density of crayfish and burrows at Hanging Houghton is not exceptional, and it is reasonable to suggest that this site provides a first estimate of crayfish impact that is unlikely to be either excessively high or excessively low in comparison with other locations. The spatial extent and magnitude of crayfish impacts, probably depend upon a combination of biotic (e.g. population density) and abiotic factors (substrate types, in-stream habitat, bank materials and lithology).

Investigations of crayfish zoogeomorphology across gradients of these factors would provide a fuller picture of their cumulative impact at landscape scales. Similarly, there is a need for longer term monitoring to better understand and model the temporal variability of geomorphological crayfish impacts [cf. *Johnson et al.*, 2011, their Figure 8b], which in this case is probably controlled by variations in the number of active individuals, the intensity of their activity and the duration of baseflow periods, which in turn will be influenced by variations in water temperature, seasonal demographics and seasonal changes in behavior, for example associated with mating.

More generally, river bioturbation has received substantially less attention [*Mermillod-Blondin*, 2011] than marine bioturbation [e.g. *Meadows et al.*, 2012], and most work has been motivated by ecological questions concerning the microbiological, biogeochemical and trophic effects of bioturbation at the water-substrate interface [e.g. *Chatarpaul*, 1980; *Stief and de Beer*, 2002; *Nogaro et al.*, 2008, 2009; *Creed et al.*, 2010; *Navel et al.*, 2011] not by geomorphological questions. Consequently, the broad impact of fluvial bioturbation on fluvial sediment transport is simply unknown, although the results presented here and other studies highlight the potential for substantive cumulative impacts [e.g. *Pledger et al.*, 2014].

Looking beyond bioturbation, several recent reviews suggest that other fluvial zoogeomorphic processes, including those that alter bed material stability between entrainment events [e.g. *Johnson et al.*, 2011], are widespread with potentially significant cumulative impacts on large-scale sediment transfer [*Rice et al.*, 2012; *Statzner*, 2012; *Albertson and Allen*, 2015]. Considering several demonstrations that small, but prolific animals can have a significant impact on Earth surface processes [*Darwin*, 1881 et seq.] it certainly seems reasonable to recommend continued investigation of the contribution that fauna make to the movement of sediment across Earth's surface, including in rivers. Such an argument is further supported by *Phillips'* [2009] demonstration that the biosphere provides an energy subsidy that fuels geomorphological work, by growing acceptance that seamless coupling of biotic and abiotic systems properly explains Earth history [*Corenblit et al.*, 2007, 2008; *Davies and Gibling*, 2010; *Steiger & Corenblit*, 2012] and by the underperformance of many purely geophysical models of Earth surface mass transfer [*NRC*, 2009].

Finally, and briefly, it is useful to consider the ecological relevance of the impact of signal crayfish on fine sediment suspension. During baseflow periods, turbidity typically increased by between 10 and 20 NTU, from 10 to 20 NTU during the day up to 20 to 40 NTU at night. Even such small changes in turbidity, can have a detrimental effect on some ecological processes [*Henley et al.*, 2000; *Bilotta and Brazier*, 2008] including reductions in primary productivity [Lloyd et al., 1987] changes in the behavior of visually-orientated fish [e.g. *Van Landeghem et al.*, 2011] and increased macroinvertebrate drift [e.g. *Doeg and Milledge*, 1991]. Of specific interest in the context of signal crayfish invasion, is the potential impact of fine sediment suspension by *P. leniusculus* on the indigenous white-clawed crayfish, *A. pallipes*, which has experienced a substantial population decline and is now considered to be endangered [*Füreder, et al.* 2010; *Almeida et al.*, 2014]. The competitive advantage of the larger more aggressive *P. leniusculus* and their resistance to the fungal crayfish plague (*Aphanomyces astaci*) are generally regarded as key reasons for their success at the expense of *A. pallipes* [*Dunn*, 2009]. However, alterations to suspended sediment concentrations as demonstrated here, may facilitate further advantages over native species because *Rosewarne et al.* [2014] have shown that *A. pallipes* are significantly less tolerant of suspended sediment than signals, suffering greater gill fouling, gill damage and reduced aerobic scope across a range of sediment concentrations. Therefore, the ecosystem engineering activities of *P. leniusculus* may have contributed to their invasive success.

5. CONCLUSION

In this paper, a direct comparison of the biotic and abiotic contributions to fluvial suspended sediment flux during baseflow periods and to the total annual load was made for a single, small catchment. To our knowledge, this is the first published assessment of bioturbation's contribution to fluvial sediment transport in a field setting and adds to a single previous comparison of biotic and abiotic sediment movement of bed material load in rivers affected by salmonid spawning [Hassan *et al.*, 2008]. Nocturnal crayfish bioturbation accounted for at least 36% of monthly suspended sediment load during baseflow periods or an average surcharge of 430 kg per month (based on data from 11 complete calendar months). When flood loads are included, these figures represent an average contribution to total monthly loads of at least 7%. Depending on the use of conservative or liberal estimates of crayfish impacts on daytime fluxes, crayfish bioturbation contributed between 4651 and 13538 kg (0.19 to 0.55 t km^{-2} yr^{-1}) to the annual suspended sediment load. These data demonstrate that, at least at some places, at some times, bioturbation effects are not trivial: energy from life rather than energy from landscape position can make a significant contribution to sediment flux.

As anticipated, the dominant effect of hydraulic forcing during flood events means that the proportionate contribution of crayfish bioturbation to the annual suspended load at Hanging Houghton was relatively small in 2013-14 (between 0.43 and 1.24%). However, this range should be regarded as a conservative estimate, because it is likely that unusually high flows during the study period depressed estimates of the bioturbation effect relative to the norm. Moreover, although bioturbation provides a convenient means of evaluating the relative importance of zoogeomorphic effects, because it involves a direct link between faunal energy expenditure and sediment flux, bioturbation does not capture the complete effect of zoogeomorphic activity. Animals also affect fluvial sediment transport indirectly, for example by enhancing or retarding bed mobility [*Stazner*, 2012; *Rice et al.*, 2012], which alters entrainment probability under geophysical forcing and, as in the case of the crayfish studied here, by augmenting recruitment of new sediment from the landscape via burrow construction and bank erosion.

Because this work has considered one process (bioturbation) associated with a single species (*Pacifasticus leniusculus*), it assesses the geomorphological impact of only a tiny fraction of biotic energy expenditure across the catchment. We have not investigated the role of other plants, animals and microorganisms in driving (or retarding) sediment movement in this catchment and the total biological contribution to sediment flux, here and more widely, is almost certainly greater. The importance of the estimates herein is that they give a clear indication that in an unremarkable stream, biotic energy is significant geomorphologically, which suggests that it is prudent to investigate other cases and endeavor to establish models for estimating biotic impacts on sediment flux.

ACKNOWLEDGMENTS

We would like to thank Holly Longstaff and Andrew Pledger for their help in the field and the National River Flow Archive (Centre for Hydrology and Ecology) for providing flow gauge and rainfall data. Data are available upon request at the discretion of the corresponding author. We are also grateful to Tom Lisle, editor John Buffington and an anonymous reviewer for their extremely helpful comments and suggestions.

REFERENCES

Albertson L.K. and D.C. Allen. (2015), Meta-analysis: abundance, behavior, and hydraulic energy shape biotic effects on sediment transport in streams, Ecology, 96, 1329-1339, doi:10.1890/13-2138.1.

Albertson L.K., L.S. Sklar, P. Pontau, M. Dow, B.J. and Cardinale (2014), A mechanistic model linking insect (Hydropsychidae), silk nets to incipient sediment motion in gravel-bedded streams, Journal of Geophysical Research: Earth Surface 119, 1833–1852, doi:10.1002/2013JF003024.

Almeida D., A. Ellis, J. England and G.H. Copp (2014), Time – series analysis of native and non-native crayfish dynamics in the Thames River Basin (south-eastern England), Aquatic Conservation: Marine and Freshwater Ecosystems, 24, 192-202, doi: 10.1002/aqc.2366.

Arce J.A. and J. Diéguez-Uribeondo (2015), Structural damage caused by the invasive crayfish Procambarus clarkii (Girard, 1852), in rice fields of the Iberian Peninsula: a study case, Fundamental and Applied Limnology, 186, 259-269, doi:10.1127/fal/2015/0715.

Beschta R.J. and W.J. Ripple (2012), The role of large predators in maintaining riparian plant communities and river morphology, Geomorphology, 157, 88-98, doi:10.1016/j.geomorph.2011.04.042.

Bilotta G.S. and R.E. Brazier (2008), Understanding the influence of suspended solids on water quality and aquatic biota, Water Research, 42, 2489-2861, doi:10.1016/j.watres.2008.03.018.

Bond B.J., J.A. Jones, G. Moore, N. Phillips, D. Post, and J.J. McDonell (2002), The zone of vegetation influence on baseflow revealed by diel patterns of streamflow and vegetation water use in a headwater basin, Hydrological Processes, 16, 1671-1677, doi: 10.1002/hyp.5022.

Borsje, B.W., M.B. de Vries, S.M.J.H. Hulscher, and G.J. de Boer (2008), Modelling large scale cohesive sediment transport by including small scale biological influences, Estuarine, Coastal and Shelf Science, 78, 468-480, doi:10.1016/j.ecss.2008.01.009.

Bubb, D.H., M.C. Lucas and T.J. Thom, (2002), Winter movements and activity of signal crayfish Pacifastacus leniusculus in an upland river, determined by radio telemetry, Hydrobiologia, 483: 111–119.

Bubb, D.H., T.J. Thom and M.C. Lucas (2004), Movement and dispersal of the invasive signal crayfish Pacifastacus leniusculus in upland rivers, Freshwater Biology, 49, 357-368, doi: 10.1111/j.1365-2426.2003.01178.x.

Burt, T.P. (1979), Diurnal variations in stream discharge and throughflow during a period of low flow, Journal of Hydrology, 41, 291-301, doi:10.1016/0022-1694(79)90067-2.

Butler, D.R. (1995), Zoogeomorphology: Animals as Geomorphic Agents. Cambridge University Press, Cambridge.

Butler D.R. and C.F. Sawyer (2012), Introduction to the special issue—zoogeomorphology and ecosystem engineering, Geomorphology, 157-158, 1-5, doi:10.1016/j.geomorph.2012.02.027.

Butler D.R., and G.P. Malanson (2005), The geomorphic influences of beaver dams and failures of beaver dams, Geomorphology, 71, 48-60, doi:10.1016/j.geomorph.2004.08.016.

Chatarpaul L., J.B. Robinson and N.K. Kaushik (1980), Effects of tubificid worms on denitrification and nitrification in stream sediment, Canadian Journal of Fisheries and Aquatic Sciences, 37, 656-663, doi: 10.1139/f80-082.

Corenblit D., J. Steiger, A. Gurnell and E.Tabacchi (2007), Darwinian origin of landforms, Earth Surface Processes and Landforms, 32, 2070-2073, doi:10.1002/esp.1536.

Corenblit D., A.M. Gurnell, J. Steiger, and E. Tabacchi (2008), Reciprocal adjustments between landforms and living organisms: extended geomorphic evolutionary insights, Catena 73, 261-273, doi:10.1016/j.catena.2007.11.002.

Creed R.P., A. Taylor, and J.R. Plfaum (2010), Bioturbation by a dominant detritivore in a headwater stream: litter excavation and effects on community structure, OIKOS, 119, 1870-1876, doi:10.1111/j.1600-0706.2010.18432.x.

Cross W.F., A. Ramírez, A. Santana, and L. Silvestrini Santiago (2008), Toward quantifying the relative importance of invertebrate consumption and bioturbation in Puerto Rican streams, Biotropica 40, 477-484, doi:0.1111/j.1744-7429.2007.00388.x.

Darwin C.R. (1881), The Formation of Vegetable Mould, through the action of worms, with observations on their habitat. John Murray, London.

Davies N.S., M.R. Gibling and M.C. Rygel (2011), Alluvial facies evolution during the Palaeozoic greening of the continents: Case studies, conceptual models and modern analogues, Sedimentology 58, 220-258, doi:10.1111/j.1365-3091.2010.01215.x.

Davison C. (1891), On the amount of sand brought up by lobworms, Geological Magazine 8, 489-493.

De Backer A., F. Van Coillee, F. Montserrat, P. Provoost, C. Van Colen, M. Vincx, and S. Degraer (2011), Bioturbation effects of Corophium volutator: Importance of density and behavioural activity, Estuarine, Coastal and Shelf Science, 91, 306-313, doi:10.1016/j.ecss.2010.10.031.

Demers, A., and J.D. Reynolds, (2002), A survey of the white-clawed crayfish, Austropotamobius pallipes (Lereboullet) and of water quality in two catchments of Eastern Ireland. Bulletin Français de la Pêche et de la Pisciculture, 367, 729-740.Doeg T. J., and G.A. Milledge, (1991), Effect of experimentally increasing concentration of suspended sediment on macroinvertebrate drift, Marine and Freshwater Research, 42, 519-526, doi: doi:10.1071/MF9910519

Dorn N.J., R. Urgelles and J.C.Trexler, (2005), Evaluating active and passive sampling methods to quantify crayfish density in a freshwater wetland. Journal of the North American Benthological Society, 24, 346–356, doi: 10.1899/04-037.1.

Dunn J.C., E. McClymont, M. Christmas and A.M. Dunn. (2009), Competition and parasitism in the native White Clawed Crayfish Austropotamobius pallipes and the invasive Signal Crayfish Pacifastacus leniusculus in the UK, Biological Invasions, 11, 315-324, doi:10.1007/s10530-008-9249-7.

Eriksson B. and D.J. Eldridge (2014), Surface destabilisation by the invasive burrowing engineer Mus musculus on a sub-Antarctic island, Geomorphology, 223, 61-66, doi:10.1016/j.geomorph.2014.06.026.

Flecker A.S. (1997), Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength, Journal of the North American Benthological Society, 16, 286-295, DOI: 10.2307/1468258.

Fortino K. (2006), Effect of season on the impact of ecosystem engineers in the New River, NC, Hydrobiologia, 559, 463-466, DOI 10.1007/s10750-005-5325-5.

Fuller R.M., Smith G.M., Sanderson J.M., Hill R.A., Thomson A.G. (2002), The UK Land Cover Map 2000: construction of a parcel-based vector map from satellite images, *Cartographic Journal*, 39, 15-25.

Füreder, L., F. Gherardi, D. Holdich, J. Reynolds, P. Sibley, P. & C Souty-Grosset, (2010). Austropotamobius pallipes. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Last accessed 23 January 2016.

Gillain, S. (2005), Diel turbidity fluctuations in streams in Gwinnett County, Georgia. In Proceedings of the 2005 Georgia Water Resources Conference, K.J. Hatcher (ed.),, April 25–27, 2005. The University of Georgia, Athens, Georgia, USA.

Gribovski, Z., J. Zsilágyi and P. Kalicz (2010), Diurnal fluctuations in shallow groundwater levels and streamflow rates and their interpretation – A review, Journal of Hydrology, 385, 371-383, doi:10.1016/j.jhydrol.2010.02.001.

Guan, R-Z. (1994), Burrowing behaviour of signal crayfish, Pacifastacus leniusculus (Dana), in the River Great Ouse, England, Freshwater Forum 4, 155-168

Guan, R-Z. (2000), Abundance and production of the introduced signal crayfish in a British lowland river. Aquaculture International, 8, 59-76. doi: 10.1023/A:1009272916339

Guan, R.-Z. & P. R. Wiles, (1998). Feeding ecology of the signal crayfish Pacifastacus leniusculus in a British lowland river, Aquaculture, 169, 177–193.

Hall K. and N. Lamont (2003), Zoogeomorphology in the Alpine: some observations on abiotic-biotic interactions, Geomorphology, 55, 219-234, doi:10.1016/S0169-555X(03)00141-7.

Hall K., J. Boelhouwers and K. Driscoll (1999), Animals as erosion agents in the alpine zone: Some data and observations from Canada, Lesotho, and Tibet, Arctic Antarctic and Alpine Research, 31, 436-446, doi: 10.2307/1552592. 10.2307/1552592.

Harvey G., A. Henshaw, T. Moorhouse, N. Clifford, H. Holah, J. Grey and D. Macdonald (2014), Invasive crayfish as drivers of fine sediment dynamics in rivers: field and laboratory evidence, Earth Surface Processes and Landforms, 39, 259-271, doi:10.1002/esp.3486.

Harvey, G., T.P. Moorhouse, N.J. Clifford, A. Henshaw, M.F. Johnson, D.W. MacDonald, I. Reid, and S.P. Rice (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, doi:10.1177/0309133311409092.

Hassan M.A., A.S. Gottesfeld, D.R. Montgomery, J.F. Tunnicliffe, G.K.C. Clarke, G. Wynn, H. Jones-Cox, R. Poirier, E. MacIsaac, H. Herunter and S.J. Macdonald (2008), Salmon-driven bedload transport and bed morphology in mountain streams, Geophysical Research Letters, 35, L0440 doi:10.1029/2007GL032997

Helms B.S, and R.P. Creed (2005), The effects of 2 coexisting crayfish on an Appalachian river community, Journal of the North American Benthological Society, 24, 113–122, doi:10.1899/0887-3593, doi:10.1899/0887-3593(2005)024<0113:TEOCCO>2.0.CO;2.

Henley W.F., M.A. Patterson, R.J. Neves and A.D. Lemley (2000), Effects of Sedimentation and Turbidity on Lotic Food Webs: A Concise Review for Natural Resource Managers, Reviews in Fisheries Science, 8, 125-139, doi: 10.1080/10641260091129198.

Herschy, R. (1993), The velocity-area method, Flow Measurement and Instrumentation, 4, 7-10, doi:10.1016/0955-5986(93)90004-3.

Hiley P.D. (2003), The slow quiet invasion of signal crayfish (Pacifastacus leniusculus), in England – prospects for the white-clawed crayfish (Austropotamobius pallipes),. In Holdich, DM and Sibley PJ (eds), Management and Conservation of Crayfish: Proceedings of a conference held on 7th November 2002 at the Nottingham Forest Football Club, Nottingham, UK. Environment Agency, Bristol, 127-138.

Holdich D.M., J. James, C. Jackson and S. Peay S (2014), The North American signal crayfish, with particular reference to its success as an invasive species in Great Britain, Ethology Ecology and Evolution, 26, 232-262, doi:10.1080/03949370.2014.903380.

Holtmeier F-K. 2015. Animals' influence on the landscape and ecological importance: Natives, newcomers and homecomers, Springer, Dordrecht.

Hudina S., M. Faller, A. Lucić, G. Klobučar and I. Maguire (2009), Distribution and dispersal of two invasive crayfish species in the Drava River basin, Croatia. Knowledge and management of aquatic ecosystems, 9, 394-395, doi:org/10.1051/kmae/2009023

Huntingford C., T. Marsh, A.A. Scaife, E.J. Kendon, J. Hannaford, A.L. Kay, M. Lockwood, C. Prudhomme, N.S. Reynard, S. Parry, J.A. Lowe, J.A. Screen, H.C. Ward, M. Roberts, P.A. Stott, V.A. Bell, M. Bailey, A. Jenkins, T. Legg, F.E.L. Otto, N. Massey, N. Schaller, J. Slingo, and M.R. Allen (2014), Potential influences on the United Kingdom's floods of winter 2013/14, Nature Climate Change, 4, 769-777, doi:10.1038/NCLIMATE2314.

James J., F. Slater and J. Cable (2014), A.L.I.E.N. databases: Addressing the lack in establishment of non-native databases, Crustaceana, 87, 1192-1199, doi:10.1163/15685403-00003329.

Johnson M.F., S.P. Rice and I. Reid (2011), Increase in coarse sediment transport associated with disturbance of gravel river beds by signal crayfish (Pacifastacus leniusculus), Earth Surface Processes and Landforms, 36, 1680-1692, doi:10.1002/esp.2192.

Johnson M.F., S.P. Rice and I. Reid (2014), The activity of signal crayfish (Pacifastacus leniusculus), in relation to thermal and hydraulic dynamics of an alluvial stream, Hydrobiologia, 724, 41-54, doi: 10.1007/s10750-013-1708-1.

Johnson M.F. and Rice S.P. 2014. Macrozoobenthos, hydraulics and sediment dynamics in A Users Guide to Ecohydraulic Experimentation, edited by Frostick L.E. Thomas R.E., Johnson M., Rice S. and McLelland S., CRC Press, Leiden, Netherlands, 117-147.

Jones C.G., J.H. Lawton and M. Shachak (1994), Organisms as ecosystem engineers, Oikos, 69, 373-386, doi:10.2307/3545850.

Jones C.G. (2012), Ecosystem engineers and geomorphological signatures in landscapes, Geomorphology, 157-158, 75-87, doi:10.1016/j.geomorph.2011.04.039.

Jouquet P., T. Henry-des-Tureaux, J. Mathieu, T.D. Thu, T.T. Duc, and D. Orange (2010), Utilization of near infrared reflectance spectroscopy (NIRS), to quantify the impact of earthworms on soil and carbon erosion in steep slope ecosystem: A study case in Northern Vietnam, Catena, 81, 113-116, doi:10.1016/j.catena.2010.01.010.

Lloyd D.S., J.P.Koenings and J.D. Laperriere, (1987), Effects of Turbidity in Fresh Waters of Alaska, North American Journal of Fisheries Management, 7, 18-33, doi: 10.1577/1548-8659(1987)7<18:EOTIFW>2.0.CO;2.

Loperfido J.V., C.L. Just, A.N. Papanicolaou and J.L. Schnoor (2010), In situ sensing to understand diel turbidity cycles, suspended solids, and nutrient transport in Clear Creek, Iowa, Water Resources Research, 46, W06525, doi:10.1029/2009WR008293

Matthews T., C. Murphy, R.L. Wilby and S. Harrigan (2014), Nature Climate Change 4, 738-740, doi:10.1038/nclimate2336

McNeil, W. J. and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. U.S. Fish and Wildlife Service, Special Scientific Report Fisheries 469.

Meadows P.S., A. Meadows and J.M.H. Murray (2012), Biological modifiers of marine benthic seascapes: Their role as ecosystem engineers, Geomorphology, 157–158, 31–48, doi:10.1016/j.geomorph.2011.07.007.

Mermillod-Blondin F., J-P. Gaudet, M. Gérino, G. Desrosiers and M. Creuzé des Chatelliers (2003), Influence of macroinvertebrates on physico-chemical and microbial processes in hyporheic sediments, Hydrological Processes, 17, 779-794, DOI: 10.1002/hyp.1165.

Mermillod-Blondin F. (2011), The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems, Journal of the North American Benthological Society, 30, 770-778, doi:10.1899/10-121.1

Moore J.W. (2006), Animal ecosystem engineers in streams, Bioscience, 56, 237-246, doi:10.1641/0006-3568(2006)056[0237:AEEIS]2.0.CO;2.

Moorhouse T.P. and D.W. Macdonald (2011), The effect of removal by trapping on body condition in populations of signal crayfish, Biological Conservation 144, 1826-1831, doi:10.1016/j.biocon.2011.03.017

Naiman R.J., S.R. Elliott, J.M. Helfield and T.C. O'Keefe (2000), Biophysical interactions and the structure and dynamics of riverine ecosystems: the importance of biotic feedbacks, Hydrobiologia, 410, 79-86, doi:10.1023/A:1003768102188.

National Research Council (2009), Landscapes on the edge: new horizons for research on Earth's surface. National Academies Press, Washington, D.C., USA.

Navel S., F. Mermillod-Blondin and B. Montuelle (2011), Water-sediment exchanges control microbial processes associated with leaf litter degradation in the hyporheic zone: a microcosm study, Microbial Ecology, 61, 968-979, doi: 10.1007/s00248-010-9774-7.

Nogaro G., F. Mermillod-Blondin, B. Montuelle, J-C. Boisson and J. Gibert (2008), Chironomid larvae stimulate biogeochemical and microbial processes in a riverbed covered with fine sediment, Aquatic Science, 70, 156-168, doi:10.1007/s00027-007-7032-y.

Nogaro G., F. Mermillod-Blondin, M.H. Valett, F. Francois-Carcaillet, J-P. Gaudet, M. Lafont M and J. Gibert (2009), Ecosystem engineering at the sediment–water interface: bioturbation and consumer-substrate interaction, Oecologia, 161, 125–138, doi:10.1007/s00442-009-1365-2.

Peay S. (2003), Monitoring the White-clawed Crayfish, Austropotamobius pallipes. Conserving Natura 2000 Rivers, Monitoring Series No. 1. English Nature, Peterborough.

Peay S., N. Guthrie, J. Spees, E. Nilsson and P. Bradley (2009), The impact of signal crayfish (Pacifastacus leniusculus) on the recruitment of salmonid fish in a headwater stream in Yorkshire, England, Knowledge and Management of Aquatic Ecosystems, 12, 394-395.

Phillips J.D. (2009), Biological energy in landscape evolution, American Journal of Science, 309, 271-289, doi:10.2475/04.2009.01.

Pledger A.G., S.P. Rice and J. Millet (2014), Reduced bed material stability and increased bedload transport caused by foraging fish: a flume study with juvenile Barbel (Barbus barbus), Earth Surface Processes and Landforms, 39, 1500-1513, doi:10.1002/esp.3592.

Power M.E. (1990), Resource enhancement by indirect effects of grazers: armored catfish, algae and sediment, Ecology, 71, 897-904, doi: 10.2307/1937361.

Pringle C.M. and T. Hamazaki (1998), The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects, Ecology, 79: 269-280, doi:10.1890/0012-9658(1998)079[0269:TROOIA]2.0.CO;2.

Rice S.P., M.F. Johnson, J. Reeds, C. Extence and H. Longstaff (2014), Diel patterns of suspended sediment flux and the zoogeomorphic agency of invasive crayfish, Cuadernos de Investigación Geográfica, 40, 7-27, doi:10.18172/cig.2508.

Rice S.P., M.F. Johnson and I. Reid (2012), Animals and the Geomorphology of Gravel-bed Rivers, in Gravel-bed rivers: processes, tools, environments, edited by M. Church, P. Biron, A.G. Roy, 225-241, John Wiley and Sons, Chichester.

Richardson D.C., L.A. Kaplan, J.D. Newbold and A.K. Aufdenkampe (2009), Temporal dynamics of seston: A recurring nighttime peak and seasonal shifts in composition in a stream ecosystem, Limnology and Oceanography, 54, 344-354, doi:10.4319/lo.2009.54.1.0344.

Rosewarne P.J., J.C. Svensden, R.J.G. Mortimer and A.M Dunn (2014), Muddied waters: suspended sediment impacts on gill structure and aerobic scope in an endangered native and an invasive freshwater crayfish, Hydrobiologia, 722, 61–74, DOI 10.1007/s10750-013-1675-6.

Souty-Grosset C., D.M. Holdich, P.Y. Noël, J.D. Reynolds, P. Haffner (Eds), (2006), Atlas of crayfish in Europe. Collection Patrimoines Naturels, 64, Muséum National d’Histoire Naturelle, Paris.

Statzner B. and P. Sagnes (2008), Crayfish and fish as bioturbators of streambed sediments: assessing the joint effects of species with different mechanistic abilities, Geomorphology 93, 267-287, doi:10.1016/j.geomorph.2007.02.019.

Statzner B., U. Fuchs and L.W.G. Higler (1996), Sand erosion by mobile predaceous stream insects: implications for ecology and hydrology, Water Resources Research, 32, 2279-2287, doi:10.1029/96WR00977.

Statzner B., M.F. Arens, J-Y. Champagne, R. Morel and E. Herouin (1999), Silk producing stream insects and gravel erosion: significant biological effects on critical shear stress, Water Resources Research, 35, 3495-3506, doi:10.1029/1999WR900196.

Statzner, B. (2012), Geomorphological implications of engineering bed sediments by lotic animals, Geomorphology,157-158, 49-65, doi:10.1016/j.geomorph.2011.03.022.

Steiger J. and D. Corenblit (2012), The emergence of an ‘evolutionary geomorphology’?, Central European Journal of Geosciences, 4, 376-382, doi:10.2478/s13533-011-0075-6

Stief P. and D. de Beer (2002), Bioturbation effects of Chironomus riparius on the benthic N-cycle as measured using microsensors and microbiological assays, Aquatic Microbial Ecology, 27, 175-185, doi:10.3354/ame027175.

Tashiro T. and T. Tsujimoto (2006), Numerical analysis of population dynamics of net spinning caddis larvae and substratum adhesion due to their inhabitation in a cobble-bed river with fewer disturbances, Journal of Hydroscience and Hydraulic Engineering, 24, 115-131.

Usio N. and C.R. Townsend (2004), Roles of crayfish: consequences of predation and bioturbation for stream invertebrates, Ecology, 85, 807-822, doi: doi.org/10.1890/02-0618.

VanLandeghem M.M., M.P. Carey and D.H. Wahl, (2011), Turbidity-induced changes in emergent effects of multiple predators with different foraging strategies, Ecology of Freshwater Fish, 20, 279-286, doi: 10.1111/j.1600-0633.2011.00494.x.

Viles H.A. (1988), Biogeomorphology. Blackwell, Oxford

De Visscher M., J. Nyssen, J. Pontzeele, P. Billi and A. Frankl (2014), Spatio-temporal sedimentation patterns in beaver ponds along the Chevral river, Ardennes, Belgium, Hydrological Processes, 28, 1602-1615, 10.1002/hyp.9702.

Wheaton J.M., C. Gibbins, J. Wainwright, L. Larsen, and B. McElroy (2011), Preface: Multiscale Feedbacks in Ecogeomorphology, Geomorphology, 126, 265-268, doi:10.1016/j.geomorph.2011.01.002.

Williams A.M., A.D. Hiday and T.I. Wilch (2011), Assessment of diel cycling in agricultural streams in south-central Michigan – a focus on turbidity. Geological Society of America Abstracts with Programs 43 (5), 118. GSA Annual Meeting, Minneapolis (9–12 October 2011).

Wolman, M.G. (1954), Method of sampling coarse river-bed material, Eos Trans. AGU, 35(6), 951– 956.

Wright J.P. and C.G. Jones (2006), The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges, Bioscience, 56, 203 – 209, doi:10.1641/0006-3568(2006)056[0203:TCOOAE]2.0.CO;2.

Wutz S., and J. Geist (2013), Sex-and size-specific migration patterns and habitat preferences of invasive signal crayfish (Pacifastacus leniusculus Dana). Limnologica-Ecology and Management of Inland Waters, 43, 59-66, doi:10.1016/j.limno.2012.02.002.

Zanetell B.A. and B.L. Peckarsky (1996), Stoneflies as ecological engineers – hungry predators reduce fine sediments in stream beds, Freshwater Biology, 36, 569-577, doi:10.1046/j.1365-2427.1996.00132.x.

Table 1. Estimates of biotic and abiotic contributions to base flow and total suspended sediment load

	Baseflow load, G_{bf} (kg)						**Baseflow and flood flow load, G (kg)**			
	Biotic load, G_{bfB} (kg)		Abiotic load, G_{bfA} (kg)		Biotic contribution (%)		Abiotic load, $G_{fl} + G_{bfA}$ (kg)		Biotic contribution (%)	
	min.	*max.*	*min.*	*max.*	*min.*	*max.*	*min.*	*max.*	*min.*	*max.*
July 13 (partial)	130.4	336.3	0.0	205.9	38.8	100.0	6522.6	6728.5	1.9	4.9
Aug 13	376.9	880.9	0.0	504.0	42.8	100.0	1937.0	2441.0	13.4	31.3
Sept 13	229.9	638.3	0.0	408.4	36.0	100.0	250.9	659.2	25.9	71.8
Oct 13	191.1	662.8	0.0	471.7	28.8	100.0	83260.1	83731.9	0.2	0.8
Nov 13	220.7	483.3	0.0	262.6	45.7	100.0	6262.6	6525.2	3.3	7.2
Dec 13	126.1	403.0	0.0	276.9	31.3	100.0	232355.4	232632.3	0.1	0.2
Jan 14							330921.2	330921.2	0.0	0.0
Feb 14	475.3	2449.4	0.0	1974.0	19.4	100.0	280746.5	282720.6	0.2	0.9
March 14	1142.7	3101.6	0.0	1959.0	36.8	100.0	76548.9	78507.8	1.4	3.9
April 14	619.4	1349.5	0.0	730.1	45.9	100.0	947.2	1677.3	27.0	58.8
May 14	224.7	690.4	0.0	465.7	32.5	100.0	49836.4	50302.1	0.4	1.4
June 14	696.3	1917.4	0.0	1221.1	36.3	100.0	7169.3	8390.4	7.7	21.1
July 14 (partial)	217.3	625.4	0.0	408.2	34.7	100.0	977.4	1385.5	13.6	39.0
Whole month avg	430.3	1257.7	0.0	827.4	35.6	100.0	97294.2	98046.3	7.2	17.9
Whole month SD	315.3	930.7	0.0	659.9	8.1	0.0	123919.3	123951.9	10.4	25.6
Whole month SE	99.7	294.3	0.0	208.7	2.6	0.0	37363.1	37372.9	3.1	7.7
Annual total	4650.7	13538.3	0.0	8887.6	34.4	100.0	1077735.6	1086623.2	0.43	1.24

Notes. Whole month averages refer to the 11 months from August 2013 to June 2014. Annual totals in the final row include additional days (to a total of 365) in July 2013 and July 2014. Minimum estimates are based on calculating sediment load in the absence of bioturbation G_{bfA}, using either conservative ($T_A = T_{min}$) or liberal ($T_A = T_0$) values for turbidity in the absence of crayfish.

FIGURES

Figure 1. Location of the study site on the Brampton Branch of the River Nene, Northamptonshire, UK.

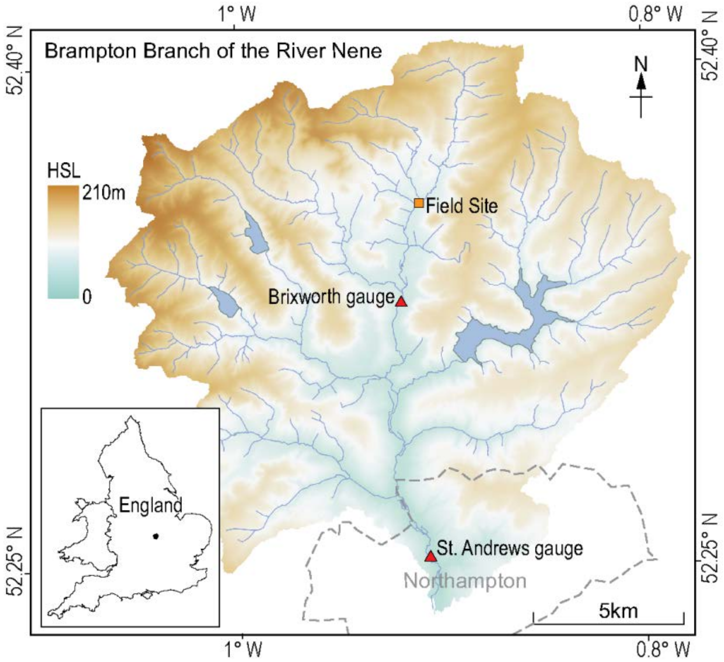

Figure 2. LOESS calibration model (smoothing parameter, α = 0.30) based on 190 concurrent measurements of turbidity and suspended sediment concentration at the main site, Hanging Houghton.

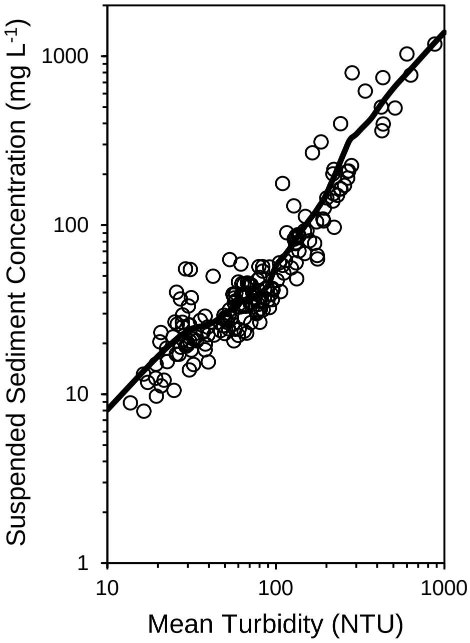

Figure 3. The effect of ambient light and water temperature on sensor performance. The solid black line is for the main sensor located in the open stream and the blue dashed line is for the instrument located adjacent to it, but inside a Perspex box filled with clean water. The initial drop in turbidity inside the box represents settlement of foreign material inadvertently included during field deployment A flood event on August 26th overtopped the box, filling it with stream water.

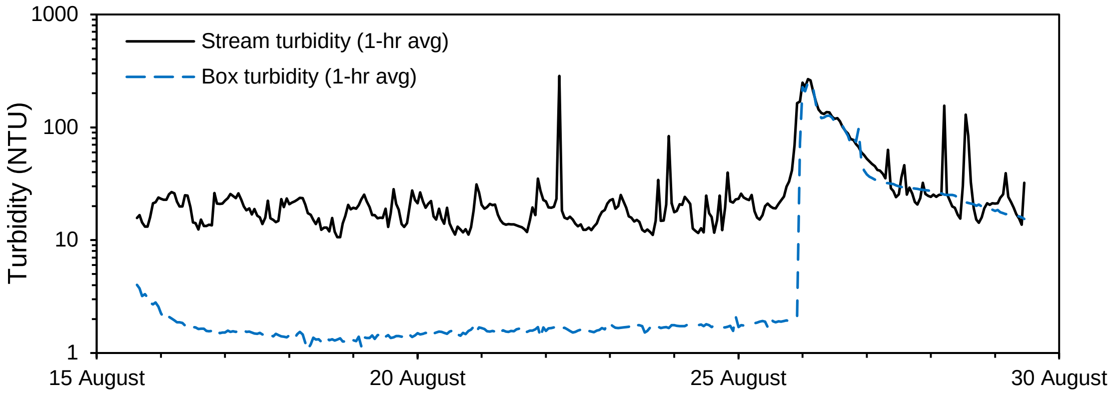

Figure 4. Periodograms of (a) turbidity and (b) crayfish movements for baseflow periods between 1 June and 30 September 2013. The peaks in movements and turbidity at 0.5 day are harmonics reflecting the non-sinusoidal nature of the daily variation. (c) Temporal association between crayfish activity (solid red bars) and turbidity (continuous black line) in July 2013. Gaps correspond to high-flow periods and vertical grey lines mark midnight. The two blue bars correspond to two flood events. (d) Spearman rank correlation coefficients for the association between hourly averaged turbidity and crayfish movements per hour during each 24-hour period, 1 June to 30 September 2013. Solid circles are significant correlations (α = 0.10). Open circles are insignificant correlations. Positive correlations indicate that on a particular day increases in crayfish activity were associated with increases in turbidity. Data from flood days and days when the sensor was clogged by floating debris are excluded.

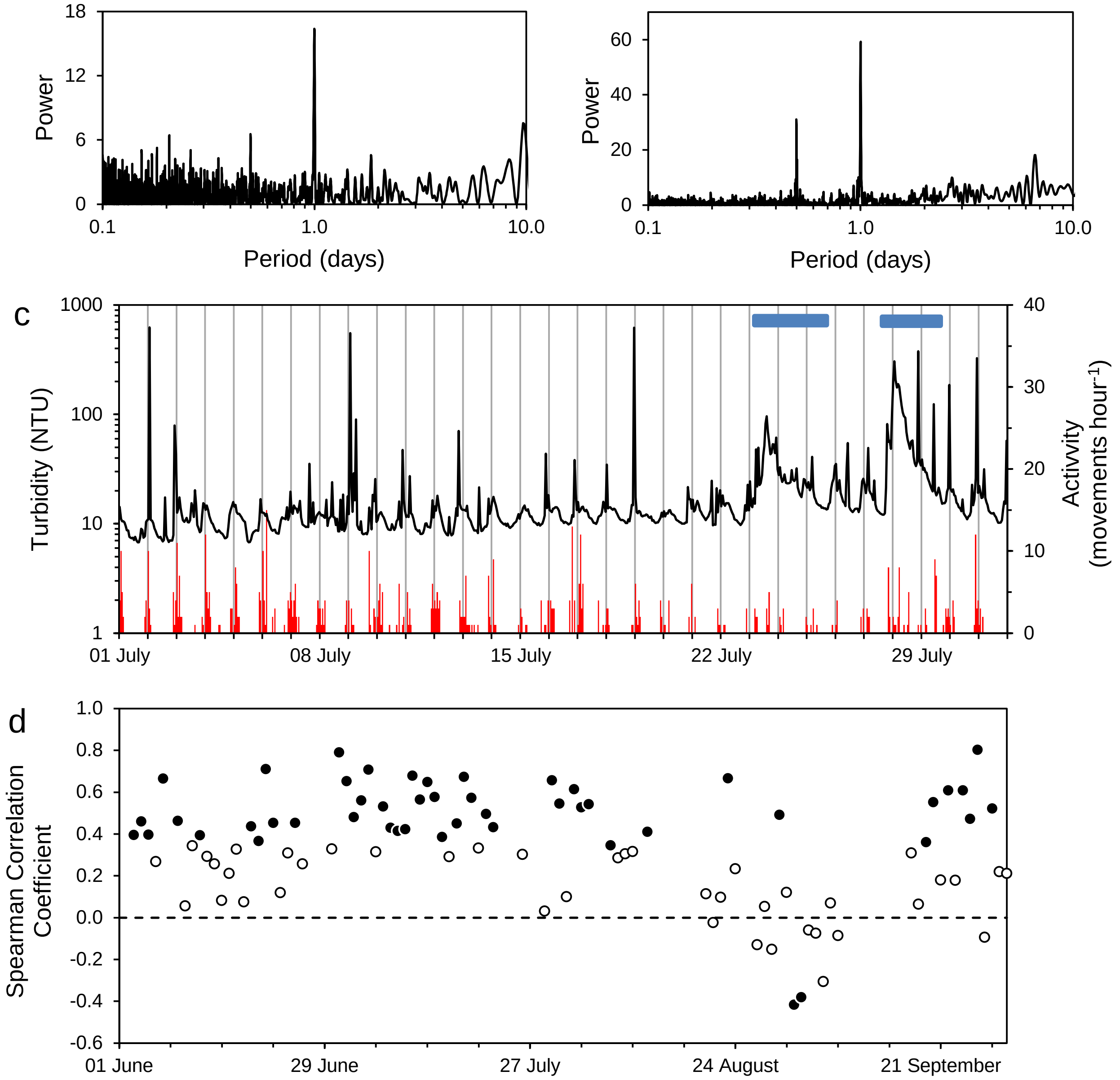

Figure 5. Turbidity and water depth at the main monitoring site at Hanging Houghton between 1 August 2013 and 18 July 2014. The first few days of the record (late July 2013) are not shown. Tick marks are at midnight, seven days apart. The light grey line is 5-minute turbidity data, the red line is 1-hr average turbidity and the blue line is 1-hr average water depth.

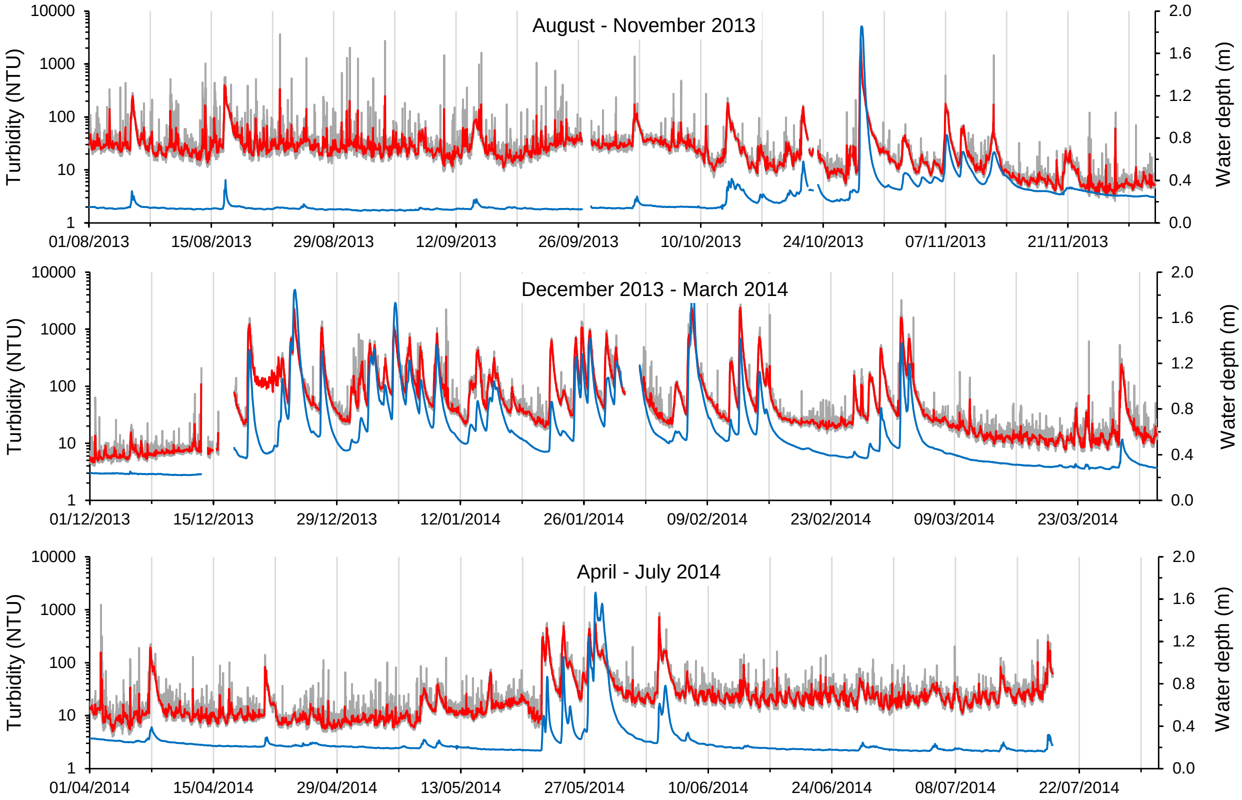

Figure 6. Periodograms of turbidity time series during 23 low-flow periods July 2013 to July 2014. Data that were more than one standard deviation from the mean were replaced with a local average and second order polynomial models were used to remove trends. Power is normalized by the maximum value for the respective time series. The main peaks are significant ($p<0.01$) in all cases. The different line styles on individual plots are periodograms for different low-flow periods in the labelled month.

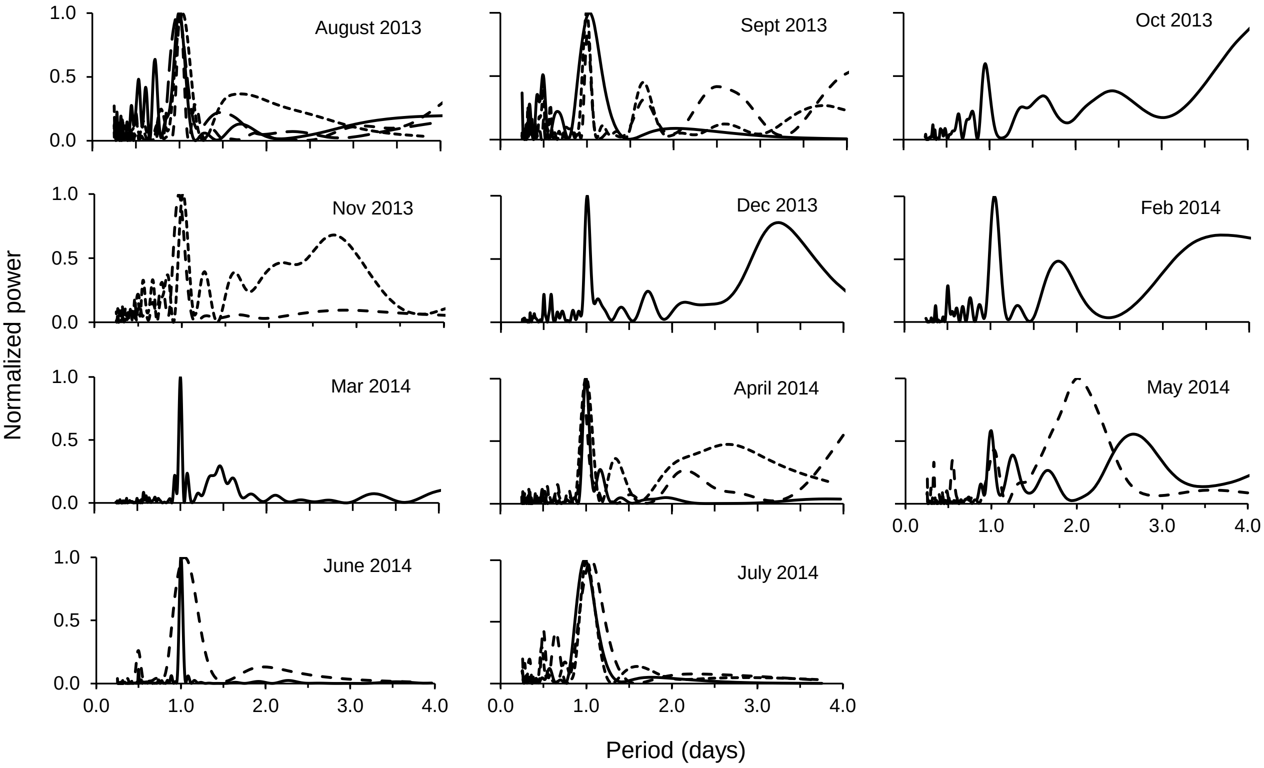

Figure 7. Differences between night time and day time turbidity during 23 low-flow periods at Hanging Houghton, July 2013 to July 2014 (solid black circles). Average night time and day time turbidity was calculated for 23:00 to 03:00 and 11:00 to 15:00, respectively, with the offset around midnight and noon reflecting asymmetry in observed daily patterns. The two four-hour blocks are designed to capture the core periods of crayfish activity and inactivity throughout the study period, irrespective of seasonal changes in daylight hours. Positive values indicate higher night time averages. Error bars are one standard error. Average water depth (blue triangles) and average stream temperature (red, open circles) are also shown for each period. Data points are plotted at the approximate midpoint of each period.

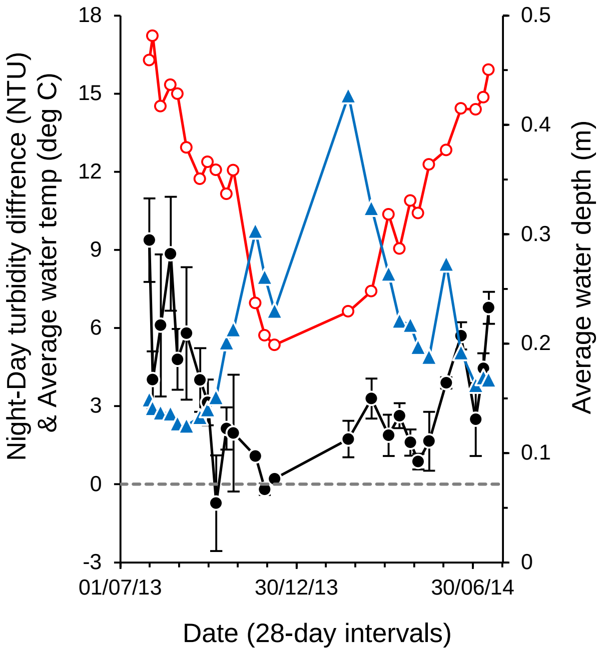

Figure 8. Examples of depth and turbidity signals for ten-day, low-flow periods in (a) March 2014 and (b) June 2014. Tick marks and vertical grey lines are at midnight. The light grey line is 5-minute turbidity data, the red line is 1-hr average turbidity and the blue line is 1-hr average water depth. 5-minute depth data is not plotted because variations about the average are too small to resolve.

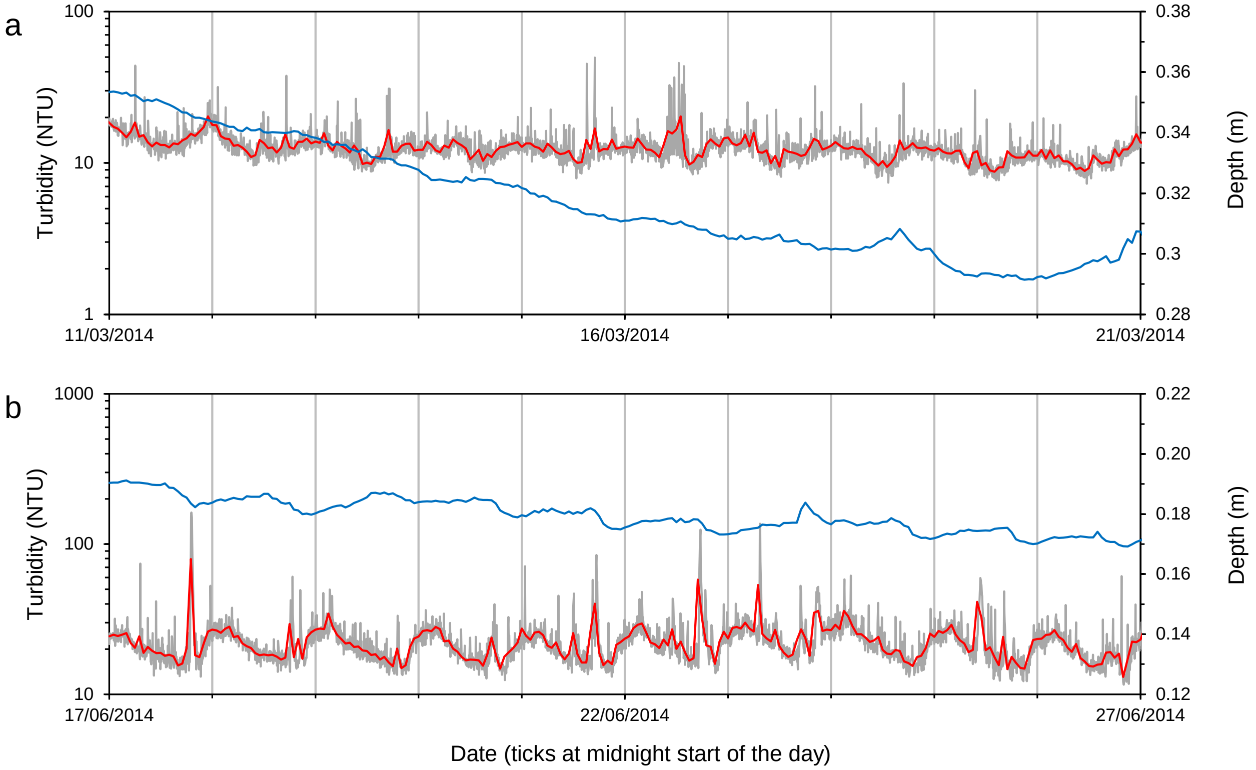

Figure 9. Variations in the contribution of crayfish bioturbation to monthly suspended sediment loads: (a) baseflow load and (b) total load, incorporating flood contributions. Grey bars are minimum estimates and white bars are maximum estimates. (b) also includes the percentage of flood days (solid black line and black dots) in each month, accounting for any hours of missing data.