Articles

The importance of biotic entrainment for base flow fluvial sediment transport

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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 fluxes 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 base flow periods, biotic fluxes were isolated because nocturnal crayfish activity drives diel turbidity cycles, such that nighttime increases above daytime lows are attributable to sediment suspension by crayfish. On average, crayfish bioturbation contributed at least 32% (474 kg) to monthly base flow suspended sediment loads; this biotic surcharge added between 5.1 and 16.1 t (0.21 to 0.66 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 0.46 and 1.46% 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 base flow periods, bioturbation can entrain significant quantities of fine sediment into suspension with implications for the aquatic ecosystem and base flow sediment fluxes. Energy from life rather than from elevation can make significant contributions to sediment fluxes.

1. 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], and 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 [National Research Council, 2010] pointed out the need for such research, because understanding of Earth surface geophysical processes is severely constrained without a fuller appreciation of interactions with biota.

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 among 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; De Visscher et al., 2014], and fossorial mammals [e.g., Hall et al., 1999; Eriksson and Eldridge, 2014]. Other studies have benchmarked 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; Zanett and Peckarsky, 1996; Statzner et al., 1996; Pringle and Hamazaki, 1998; Mermillod-Blondin et al., 2003; Usio and Townsend, 2004; Helms and Creed, 2005; Fortino, 2006; Cross et al., 2008; Statzner and Sagnes, 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 4 week data set 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, Pacifastacus 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 nighttime 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 nighttime 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 nighttime 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 favor 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 4-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 mobilized via their sediment recruitment role, but we anticipate direct entrainment by bioturbation to be a factor that affects fine sediment fluxes predominantly during base flow, 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 nighttime increase in suspended sediment flux that we associated with crayfish activity. This was because floods sustained higher average suspended sediment concentrations (hundreds of mg L$^{-1}$ versus tens of mg L$^{-1}$) for longer periods (days versus 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 base flow 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 lognormal 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

Figure 1. Location of the study site on the Brampton Branch of the river Nene, Northamptonshire, UK.
Suspended sediment flux \( Q_s \) (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 min period between 19 July 2013 and 18 July 2014. \( C \) was estimated from a high-resolution time series of turbidity \( T \), nephelometric turbidity unit (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 5 min intervals using a Measurement Specialities, Eureka 2 Manta sonde fitted with a self-wiping turbidity sensor (International Organization for Standardization (ISO) 7027: 0 to 3000 NTU, quoted error \( \pm 1\% \)) and a vented pressure transducer (0–10 m, quoted error \( \pm 0.03\% \)). 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 measured turbidity were not associated with daily variations in incident radiation and temperature. Incident
model was used to estimate constructed using a LOESS model that best described the nonlinear relation between discharge and water depth upon reaching the intake, at which point a water sample was collected and turbidity measured. The single point measurements of 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. Samples were filtered using Whatman 0.7 μm glass microfiber filters, and loss on ignition was used to determine total organic and mineral mass. A site-specific calibration was constructed using a LOESS model that best described the nonlinear relation between turbidity and suspended sediment concentration at the main site, Hanging Houghton.

A total of 174,700 mL 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 5–10 m 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 bed 5 times larger than at Hanging Houghton, which is consistent with a 2.4 times increase in drainage area. 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 (mg s⁻¹) for each 5 min interval. For a desired time period, suspended sediment load G (kg) was calculated as

\[
G = 10^6 \left( \sum_{t=0}^{n} \Delta Q_s \right)
\]

where \(\Delta\) 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

\[ G_{\text{total}} = G_{\text{bf}} + G_{\text{fl}} \]  

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

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

\[ G_{\text{bf}} = G_{\text{bfA}} + G_{\text{bfB}} \]  

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 \( Q_{\text{bfA}} \) and thus sediment load in the absence of bioturbation, \( G_{\text{bfA}} \). The estimated biotic component, \( G_{\text{bfB}} \), was calculated as the difference \( G_{\text{bf}} \) / \( C_0 \) \( G_{\text{bfA}} \).

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 \( G_{\text{bfB}} \): (a) \( T_{\text{min}} \) equal to the minimum measured value of \( T \) on each day and (b) \( T_0 = 0 \) NTU, equivalent to clear-water flows. \( T_{\text{min}} \) represents an empirical estimate of the turbidity in the absence of bioturbation, which is ambient base flow sediment suspension. However, these values may be elevated by the residual effects of the previous night’s bioturbation, in which case \( T_{\text{min}} \) yields a liberal estimate of the abiotic effect and a minimum estimate of the biotic load \( G_{\text{bfB}} \). 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 \( G_{\text{bfB}} \).

In contrast to the treatment of base flow periods, no attempt was made to partition total flood load \( G_{\text{fl}} \) 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 that 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 colocated, 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 (Figures 4a and 4b). 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 nighttime 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 h period during base flow 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
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 26 August overtopped the box, filling it with stream water.

Figure 4. Periodograms of (a) turbidity and (b) crayfish movements for base flow periods between 1 June and 30 September 2013. The peaks in movements and turbidity at 0.5 day are harmonics reflecting the nonsinusoidal 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’s rank correlation coefficients for the association between hourly averaged turbidity and crayfish movements per hour during each 24 h period, 1 June to 30 September 2013. Solid circles are significant correlations ($\alpha = 0.10$). 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.
with increased turbidity. Individual insignificant coefficients ($p > 0.10$) indicate that sampling chance cannot reasonably be ignored as a possible explanation, but the predominance 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 section 1, 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 is not strongly associated indicates that this relation is not straightforward. We think that 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 20 m 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 base flow, 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 nighttime values, are characteristic of these low-flow periods (Figure 5).

For 20 out of 23 low-flow turbidity time series that lasted more than 2 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 base flow 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 d$^{-1}$, 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, and turbulence intensity), the independence of diel turbidity suggests that hydraulic forcing was not responsible for the diel turbidity cycle.

In 10 base flow 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 10 day period in June 2014 (Figure 8b) as an example, there is no correlation at lag = 0 for either the 5 min data (Pearson correlation coefficient $R = 0.03$, $p = 0.11$, $n = 2808$) or for the time series of 1 h averages ($R = 0.07$, $p = 0.29$, $n = 234$). A weak, but significant, correlation at a lag of approximately 13 h in the smoothed time series ($R = 0.23$, $p = 0.00065$, $n = 234$) highlights the phase
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, 7 days apart. The light grey line is 5 min turbidity data, the red line is 1 h average turbidity, and the blue line is 1 h 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 labeled month.
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 base flow 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 (Figures 8 and 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 base flow 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.

![Figure 7](https://example.com/figure7.png)

**Figure 7.** Differences between nighttime and daytime turbidity during 23 low-flow periods at Hanging Houghton, July 2013 to July 2014 (solid black circles). Average nighttime and daytime 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 4 h 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 nighttime 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](https://example.com/figure8.png)

**Figure 8.** Examples of depth and turbidity signals for 10 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 min turbidity data, the red line is 1 h average turbidity, and the blue line is 1 h average water depth. Five minute depth data are not plotted because variations about the average are too small to resolve.
Liberal estimates (using $T_0$ to calculate $G_{bfA}$) suggest that crayfish added as much as 16,092.6 kg to the annual sediment flux during base flow periods. Even conservative estimates (using $T_{min}$ in calculations of $G_{bfA}$) found that biotic contributions were present during all base flow periods and collectively contributed at least 31.8% (5,118.1 kg) to the annual base flow load $G_{bf}$. Minimum estimates of the monthly, base flow bioturbation component $G_{bfB}$ (using $T_{min}$ in calculations of $G_{bfA}$) ranged between 143.8 and 1,278.0 kg with a mean of 474.2 kg; equivalent to percentage contributions of 18.2 to 41.8% with a mean of 32.4% (standard error, SE = 2.3%; Figure 9a). Maximum estimates of $G_{bfB}$ (using $T_0$ to calculate $G_{bfA}$) ranged between 522.9 and 3,707.2 kg with a mean of 1,497.8 kg, equivalent to biotic contributions of 100%.

Table 1. Estimates of Biotic and Abiotic Contributions to Base Flow and Total Suspended Sediment Load

|               | Biotic Load, $G_{bfB}$ (kg) | Abiotic Load, $G_{bfA}$ (kg) | Biotic Contribution (%) | Abiotic Load, $G_{bf} + G_{bfA}$ (kg) | Biotic Contribution (%) |
|---------------|-----------------------------|-------------------------------|-------------------------|----------------------------------------|-------------------------|
|               | Minimum                     | Maximum                       | Minimum                 | Maximum                                | Minimum                 |
| Jul 13 (partial) | 137.3                       | 383.4                         | 0.0                     | 246.1                                 | 35.8                    | 100.0                                | 6,575.3                   | 6,821.4               | 2.0                     | 5.5                   |
| Aug 13        | 393.7                       | 995.5                         | 0.0                     | 601.8                                 | 39.6                    | 100.0                                | 1,987.0                   | 2,588.8               | 13.2                    | 33.4                  |
| Sep 13        | 242.3                       | 729.7                         | 0.0                     | 487.4                                 | 33.2                    | 100.0                                | 275.3                     | 762.7                 | 24.1                    | 72.6                  |
| Oct 13        | 202.2                       | 771.3                         | 0.0                     | 569.2                                 | 26.2                    | 100.0                                | 83,866.3                  | 84,435.5              | 0.2                     | 0.9                   |
| Nov 13        | 251.0                       | 643.2                         | 0.0                     | 392.2                                 | 39.0                    | 100.0                                | 7,075.3                   | 7,467.5               | 3.3                     | 8.3                   |
| Dec 13        | 143.8                       | 522.9                         | 0.0                     | 379.0                                 | 27.5                    | 100.0                                | 233,558.7                 | 233,937.8             | 0.1                     | 0.2                   |
| Jan 14        |                             |                               |                         |                                       |                         |                                      | 334,333.1                 | 334,333.1             | 0.0                     | 0.0                   |
| Feb 14        | 522.9                       | 2,871.3                       | 0.0                     | 2,348.4                               | 18.2                    | 100.0                                | 282,624.4                 | 284,972.8             | 0.2                     | 1.0                   |
| Mar 14        | 1,278.0                     | 3,707.2                       | 0.0                     | 2,429.1                               | 34.5                    | 100.0                                | 77,158.8                  | 79,588.0              | 1.6                     | 4.6                   |
| Apr 14        | 691.9                       | 1,655.6                       | 0.0                     | 963.7                                 | 41.8                    | 100.0                                | 1,050.1                   | 2,013.7               | 25.6                    | 61.2                  |
| May 14        | 251.3                       | 840.1                         | 0.0                     | 588.8                                 | 29.9                    | 100.0                                | 50,943.3                  | 51,532.1              | 0.5                     | 1.6                   |
| Jun 14        | 765.2                       | 2,241.4                       | 0.0                     | 1,476.2                               | 34.1                    | 100.0                                | 7,475.4                   | 8,951.6               | 7.9                     | 23.1                  |
| Jul 14 (partial) | 238.3                       | 730.9                         | 0.0                     | 492.6                                 | 32.6                    | 100.0                                | 1,066.4                   | 1,559.0               | 13.3                    | 40.7                  |
| Whole month avg | 474.2                       | 1,497.8                       | 0.0                     | 1,023.6                               | 32.4                    | 100.0                                | 98,213.4                  | 99,143.9              | 7.0                     | 18.8                  |
| Whole month SD | 353.3                       | 1,096.9                       | 0.0                     | 789.8                                 | 7.2                     | 0.0                                  | 124,817.3                 | 124,842.5             | 9.8                     | 26.2                  |
| Whole month SE | 111.7                       | 346.9                         | 0.0                     | 249.8                                 | 2.3                     | 0.0                                  | 37,633.8                  | 37,641.4              | 2.9                     | 7.9                   |
| Annual total  | 5,118.1                     | 16,092.6                      | 0.0                     | 10,974.5                              | 31.8                    | 100.0                                | 1,087,989.3               | 1,098,963.8           | 0.46                    | 1.46                  |
Almost all (98.5%) of the total annual suspended sediment load (110.4 t) moved during floods. When flood flows are included in the component estimates, the annual bioturbation contribution shrinks to a minimum value of 0.46% (using $T_{\text{min}}$ in calculations of $G_{\text{BTA}}$) and a maximum value of 1.46% (using $T_0$ to calculate $G_{\text{BTA}}$). 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 25.6% with a mean of 7.0 (SE = 2.9%) and maximum estimates range from 0 to 72.6%, with a mean of 18.8% (SE = 7.9%). In months when floods were rare and total sediment load was therefore low, the estimated bioturbation contribution was relatively high. For example, in September 2014, the bioturbation component is estimated to be between 24.1 and 72.6% of the monthly total, depending on the value used for $G_{\text{BTA}}$. In contrast, in months where flooding dominated, as in January 2014 when there were no days of base flow, the biotic contribution was estimated as 0%.

4. Discussion

On average, crayfish bioturbation directly added a minimum of 474 kg month$^{-1}$ and a maximum of 1498 kg month$^{-1}$ to the base flow sediment flux at Hanging Houghton. The minimum estimate is equivalent to 32% of monthly base flow sediment yield, which means that during base flow periods, crayfish directly mobilized at least 47% more suspended sediment than would have moved in their absence. The largest monthly contribution occurred in March 2014 (minimum estimate 1278 kg and maximum estimate 3707 kg), and the annual cumulative surcharge was at least 5.1 t and may have been as high as 16.1 t. These data demonstrate that during base flow 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 (0.46 to 1.46%), 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 2013–2014 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 severe storminess for 143 years [Matthews et al., 2014]. It is possible that unusually high flows during the measurement period elevated the 2013–2014 bioturbation and depressed estimates of the base flow 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 nonflood 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 2013–2014 was unusual: only three August to July periods in 73 years recorded more than this, and the average was 3.7 events per year. It therefore is reasonable to hypothesize that the biotic contribution measured in 2013–2014 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 m into the bank, and often become interconnected, river banks can be undermined, reducing their integrity and leading to collapse [Guan, 1994; Arce and Diéguez-Urribondo, 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 854 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 and 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 and Macdonald, 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 and Geist, 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 zoogeomorphic processes 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, 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 base flow 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 et al., 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 important 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] and 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 et al., 2011; Steiger and Corenblit, 2012] and by the underperformance of many purely geophysical models of Earth surface mass transfer [NRC, 2010].

Finally, and briefly, it is useful to consider the ecological relevance of the impact of signal crayfish on fine sediment suspension. During base flow 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., VanLandeghem et al., 2011] and increased macroinvertebrate drift [e.g., Doeg and Milleidge, 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 et al., 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 base flow 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. It adds to a single previous comparison of biotic and abiotic contributions to bed load sediment movements in rivers affected by salmonid spawning [Hassan et al., 2008]. Nocturnal crayfish bioturbation accounted for at least 32% of monthly suspended sediment load during base flow periods or an average surcharge of 474 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 5118 and 16093 kg (0.21 to 0.66 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 2013–2014 (between 0.46 and 1.46%). 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 factors, 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 [Statzner, 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 (*Pacifastacus 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.

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