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RESEARCH ARTICLE

Influence of invasive crayfish on fine sediment transport, ingress and bed storage in lowland rivers

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Abstract

Historically it has been assumed that abiotic forces dominate fluvial sediment dynamics. However, a growing body of work indicates that biological energy can also exert a significant control over sediment dynamics. The role that invasive species may play in altering fine sediment dynamics is particularly pertinent given that any influence may disrupt the natural equilibrium of the ecosystem. Here we investigated the effect of invasive signal crayfish (*Pacisfastcus leniusculus*) on the transport and storage of fine sediment in a densely populated river compared with a nearby control river without crayfish, over an 18-week period. We observed clear evidence of diurnal fluctuations in turbidity associated with crayfish presence including periodograms with power peaks at a period of 1 day. Fine sediment fluxes indicated that crayfish contributed on average 18.5% extra to baseflow loads than would be likely under abiotic forcing alone. Temporal variations in suspended sediment concentrations were also observed at the control site but these were different in character and exhibited no clear temporal pattern or consistency as confirmed by periodogram analysis. Crayfish did not have an effect on sediment ingress rates relative to the control site and, at the crayfish site, the reach scale sediment budget was in net equilibrium during the sampling period. Our results provide further evidence that biological energy alters riverine fine sediment dynamics and warrants consideration in sediment dynamic models.

KEYWORDS
biogeomorphology, ecosystem engineers, ingress, non-native, sediment budget, sediment fluxes, signal crayfish, zoogeomorphology

1 | INTRODUCTION

Disruptions to fluvial fine sediment dynamics because of anthropogenic activities are a global problem and can have significant implications for ecosystem health (Burdon, McIntosh, & Harding, 2013; Ramezani, Rennebeck, Closs, & Matthaei, 2014; Wood & Armitage, 1997) and channel hydromorphology (del Tánago, Bejarano, de Jalón, & Schmidt, 2015; Grabowski & Gurnell, 2016). Implementation of successful management strategies therefore relies heavily on understanding the processes and mechanisms at work within the fine sediment cascade (Grove, Bilotta, Woockman, & Schwartz, 2015; Owens et al., 2005; Wilkes et al., 2019). Much of our knowledge base underpinning such strategies is focussed on the assumption that abiotic forces dominate sediment dynamics. However, there is growing

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evidence suggesting fauna may have important and significant contributions to fine sediment dynamics, from source through to transportation pathways and storage (Albertson & Allen, 2015; Bétard, 2021; Mason, Rice, Wood, & Johnson, 2019; Statzner, 2012). Despite several early papers that identified the potential importance of organisms as geomorphic agents (e.g., Darwin, 1881; Davison, 1891; Reudemann & Schoonmaker, 1938) the number of studies which have examined these interactions remains limited.

Organisms can have significant and far-reaching implications for the ecosystems that they inhabit. Many act as geomorphic agents, modifying the physical environment and influencing abiotic processes (Bylak & Kukuła, 2020; Jones, 2012; Mason & Sanders, 2021; Rice, Johnson, & Reid, 2012; Viles, 2020). Organisms may also act as 'ecosystem engineers', altering the flow and distribution of resources. This could be through zoogeomorphological effects such as reduced water clarity or enhanced fine sediment availability, or through strong direct ecological consequences such as predation or modifications to biogeochemical cycling (Jones, Lawton, & Shachak, 1994; Mathers et al., 2020; Wilkes et al., 2019; Wright & Jones, 2006). Numerous organisms are recognised as ecosystem engineers, but despite this no conceptual framework exists that enables understanding of when and where they have important influences on abiotic and biotic processes (Moore, 2006; Rice, 2021).

Invasive species are of particular importance when considering the implications of flora and fauna on an ecosystem because successful colonisation and establishment of a non-indigenous population may disrupt the natural equilibrium and dynamics of the system (Fei, Phillips, & Shouse, 2014; Vitousek, 1990). Furthermore, many invasive species represent novel ecosystem engineers modifying the systems they colonise in a manner that would not occur in their absence (Greenwood & Kuhn, 2014; Harvey et al., 2011). Successful colonisation of ecosystems often results in high population densities of invaders due to natural population constraints being absent (e.g., predators or competitors; Mack et al., 2000); a vital attribute in the promotion of high levels of zoogeomorphic activity (Moore, 2006). As such, invasive species provide unique opportunities to understand the potential importance that biota may have on an ecosystem.

One such invasive species is signal crayfish, *Pacisfastcus leniusculus*, one of the most widespread invaders in Europe (Kouba, Petrusek, & Kozák, 2014). Previous research has suggested that signal crayfish are significant biogeomorphic agents, altering the bed topography and roughness of gravel frameworks (Johnson, Rice, & Reid, 2010; Statzner, Fievet, Champagne, Morel, & Herouin, 2000) and enhancing coarse sediment transport (Johnson, Rice, & Reid, 2011; Statzner & Sagnes, 2008; Statzner, Sagnes, Champagne, & Viboud, 2003). Signal crayfish have also been documented as mobilising large quantities of fine sediment on a diel basis associated with their nocturnal foraging behaviour (Cooper, Outram, & Hiscock, 2016; Harvey et al., 2014; Rice, Johnson, Extence, Reeds, & Longstaff, 2014; Rice, Johnson, Mathers, Reeds, & Extence, 2016) and may enhance the delivery of fine sediment through the direct displacement of bank material as a result of burrow excavation and accelerated bank erosion (Faller et al., 2016; Guan, 1994; Rice et al., 2016; Sanders, Rice, & Wood, 2021).

Research has also considered the role of bioturbation by a number of other crayfish species, on sediment accrual and interstitial sediment concentrations. Several studies have reported that both interstitial and benthic accumulation of fine sediment was lower where crayfish were present (Albertson & Daniels, 2016; Helms & Creed, 2005; Parkyn, Rabeni, & Collier, 1997; Statzner et al., 2000) or that ingress increased under experimental conditions (Mathers, Rice, & Wood, 2019). However, the former studies have been largely confined to North American rivers and all have used in situ enclosures or flume experiments predominantly in clean gravel-bed rivers. River reaches characterised by fine bed and bank material, such as lowland rivers, may respond differently and there is a need to investigate processes at local scales in order to determine the wider effects and inform catchment level sediment management (Harvey et al., 2014).

Attempts to quantify the contributions of biotic and abiotic components to sediment transport are rare (Rice et al., 2016) and linkages to subsequent sediment deposition rates are absent. Ex situ experiments have estimated the role of biota in sediment fluxes relative to abiotic controls (Pledger, Rice, & Millett, 2014, 2016; Statzner, Arens, Champagne, Morel, & Herouin, 1999), however very few studies have isolated the role of biota in the field at temporal and spatial scales sufficient to make robust estimations. Hassan et al.'s (2008) study on the contribution of salmonid spawning to baseflow bedload transport and Rice et al.'s (2016) study on the contribution of signal crayfish to baseflow fine sediment fluxes provide two rare exceptions. In both instances, the role of biota induced sediment transport was significant (and at times dominant) during baseflow conditions. As baseflow conditions are times when it is assumed that sediment transport rates are low (as determined by hydraulic conditions), alterations to fine sediment dynamics and the remobilisation and subsequent deposition potentially have significant implications for the health of aquatic communities that would not normally be exposed to elevated fine sediment fluxes at this time. This is particularly true where this is the result of an abundant invasive species (Harvey et al., 2011).

Here we examined the effect of signal crayfish on fine sediment dynamics (suspension, transportation and deposition) at the reach scale within a lowland river in England, UK, over an 18-week period. In contrast to previous studies that have focussed solely on crayfish infested rivers, we consider these results alongside a control river and consider the implications for reach-scale fine sediment budgets. This research sought to address the following three research questions:

1. Are nocturnal increases in turbidity evident in a river colonised by non-native crayfish (sensu Cooper et al., 2016; Harvey et al., 2014; Rice et al., 2014, 2016) and how does the turbidity time series compare to an adjacent site free from crayfish?
2. What effect does the presence of signal crayfish have on suspended sediment budgets and what is the relative contribution of signal crayfish to sediment fluxes?
3. Do signal crayfish alter the bed material storage of fine sediment (ingress rates) compared to the site free from crayfish?

Research questions 1 and 3 will be investigated through direct comparison of sediment data collected at a site with and without crayfish whilst research question 2 will focus on detailed suspended sediment data collected within a crayfish reach.

2 | METHODS

2.1 | Field locations

Field sampling took place between May 21 and September 24, 2015 comprising nine 14-day sampling sets (see Table 1 for sampling details). The application of 14-day sampling sets was both pragmatic and purposeful. We wanted time periods that were long enough to ensure sediment ingress measurements were appropriate but also sufficiently numerous to capture variations in turbidity and ingress that we anticipated associated with crayfish lifecycle attributes. It was expected that the first few 14-day periods would capture low crayfish activity (as water temperatures remained low), most 14-day periods would capture high diurnal crayfish activity and the last few 14-day periods would capture the mating season (where activity is more constant and less diurnal). The study took place on two small lowland rivers in Rutland, UK; the River Gwash (invaded by crayfish) and the River Chater (no crayfish), both tributaries of the River Welland (Figure 1). The River Gwash drains ca. 24.5 km^2 of well-developed floodplains across a total relief of 127 m before flowing into Rutland Water reservoir (surface area 10.86 km^2). Dominant land uses are grassland (50%) and arable farming (36%; Fuller, Smith, Sanderson, Hill, & Thomson, 2002). Close to the catchment outlet, mean flow is 0.18 m^3 s^{-1} and Q10 (90th percentile) flow is 0.449 m^3 s^{-1} (NRFA ID 31025). Monitoring on this river focussed on a headwater reach approximately 450 m in length near the village of Brooke (52°38′41″ N 00°44′42″ W) where the catchment area is 19.46 km^2. The Chater drains approximately 68.9 km^2 across a total relief of 190 m. Dominant land uses are arable farming (51%) and grassland (32%; Fuller et al., 2002). Close to the catchment outlet, mean flow is 0.52 m^3 s^{-1} and Q10 (90th percentile) flow is 1.16 m^3 s^{-1} (NRFA ID 31010). Monitoring on this river focussed on a headwater reach approximately 200 m in length near the village of Ridlington (52°37′26″ N, 00°42′36″ W) where the catchment area is 32.22 km^2.

Sites were selected to be as broadly comparable in physical characteristics (channel size, water chemistry, altitude and geology) as possible and were located 2.6 km apart (Figure 1) and therefore experienced similar hydroclimatological regimes. Catchment geology is dominated by Jurassic mudstones and sandstones (British Geological Survey, 2008). Bankfull widths were 4.3–6.5 m at Ridlington and 2.9–5.3 m at Brooke. Sampling of the surface material (400 pebble count from two pools and riffles – 200 at each [Wolman, 1954]) indicated that Ridlington contained a larger proportion of coarser material (Table S1). Subsurface bed material (based on four pooled individual McNeil samples from two pools/riffles per site, average sample weight 20.01 kg [McNeil & Ahnell, 1964]) indicated similar framework composition with Ridlington containing greater quantities of fine sediment (Table S1). At both sites, significant quantities of fine sediment (<2 mm) were available for transport (ca. 20–30% of total sampled bed material based on McNeil bulk samples; Table S1).

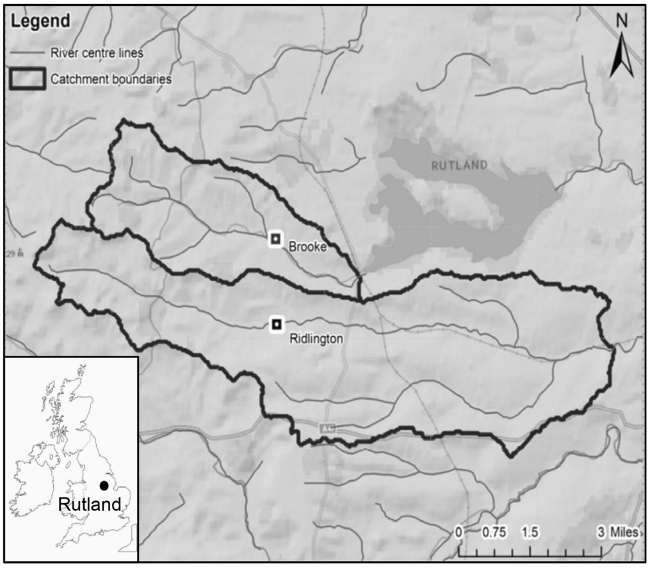

FIGURE 1 Location of the lowland study sites on the river Chater (Ridlington, no crayfish) and river Gwash (Brooke, Invaded), Rutland, UK

TABLE 1 Summary of datasets collected for this study at the Brooke (invaded) and Ridlington (no crayfish) sites

		Brooke				Ridlington	
Sample set	Dates covered (noon to noon)	Sediment traps	Turbidity data U/S	Turbidity data D/S	Crayfish trapping locations	Sediment traps	Turbidity data
1	21/05/15–04/06/15	$n = 11$	−	−	−	$n = 3$	−
2	04/06/15–18/06/15	$n = 12$	+	Partial	$n = 1$	$n = 3$	−
3	18/06/15–02/07/15	$n = 12$	+	+	$n = 1$	$n = 4$	Partial
4	02/07/15–15/07/15	$n = 12$	+	+	$n = 1$	$n = 8$	Partial
5	15/07/15–30/07/15	$n = 11$	+	+	$n = 2$	$n = 8$	+
6	30/07/15–13/08/15	$n = 12$	+	+	$n = 1$	$n = 7$	+
7	13/08/15–27/08/15	$n = 12$	+	+	$n = 2$	$n = 8$	+
8	27/08/15–10/09/15	$n = 11$	Partial	Partial	$n = 3$	$n = 8$	Partial
9	10/09/15–24/09/15	$n = 12$	−	Partial	$n = 3$	$n = 8$	+

Note: + data collected and − no data.

Invasive signal crayfish, *P. leniusculus*, are present in high abundances throughout the river Gwash. However, historic routine sampling by the Environment Agency of England (EA) and contemporary sampling during the study period by the authors has not recorded any individuals in the river Chater. Routine macroinvertebrate biomonitoring sampling on the river Gwash by the EA first recorded *P. leniusculus* in 1996 at a site 2 km downstream of the field site. Density estimates obtained using baited trapping by the authors in 2014 and 2015 (represented by Catch Per Unit Efforts [CPUE]) revealed abundances between 1.5 and 10.3 (mean 4.7, $n = 20$) adults per trap day at Brooke. Electrofishing indicated that the fish populations present are not large enough, individually or collectively, to act as significant geomorphic agents in the study rivers, with 16 bullheads (*Cottus gobio*) and 6 stone loach (*Barbatula barbatula*) sampled at Ridlington and 26 three-spined sticklebacks (*Gasterosteus aculeatus*) recorded at Brooke.

2.2 | Field and laboratory sampling methods

2.2.1 | Crayfish activity

Crayfish trapping data was used as a surrogate for crayfish activity. Periodically ($n = 14$; Table 1), baited 'trappy' traps (50 × 20 cm with an opening of 5 cm and mesh size 3 cm) were deployed at Brooke overnight in three pool locations ($n = 2$ per location) throughout the reach (upstream, middle and downstream). The number of locations trapped on each occasion varied due to trap availability associated with a wider investigation on crayfish induced sediment fluxes. For each trapped individual, carapace length (tip of rostrum to end of carapace), sex and evidence of damage was recorded. Catch Per Unit Estimates (CPUE) were calculated from the total number of individuals caught at each location for each sampling set and employed as an abundance index. It should be noted that on all but one occasion a minimum of one adult was caught at Brooke during this study period and that juveniles were consistently recorded within bed sediment infiltration pots used to measure fine sedimentation (see sediment traps below and Mathers, Rice, & Wood, 2018). Trapping was conducted on four occasions at Ridlington on the river Chater to confirm the absence of crayfish during the sampling period. Sediment infiltration pots on the Chater never recorded any juvenile crayfish and there was no evidence of crayfish burrowing in the riverbed or banks. Importantly, historic (dating back to 1990) and contemporary routine bi-annual macroinvertebrate sampling of the Chater by the Environment Agency has never recorded a signal crayfish (Mathers et al., 2016). As such we are confident that crayfish were not present in the Chater during this study.

2.2.2 | Turbidity measurements

Turbidity (Nephelometric Turbidity Unit [NTU]), stage and water temperature were measured at both the upstream (U/S) and downstream (D/S) end of the reach at Brooke and at one location at the upstream boundary of Ridlington. Details of the equipment employed can be found in Appendix S1. Recording problems during the study were intermittent. Where a single measurement was missed, records were interpolated using a local average of the previous and subsequent measurement, but where large sections were missing this remained as gaps in the time series. Ridlington datasets ran from June 17 to October 31 (136 days) with 12.0 days being removed as a result of biofouling problems. Upstream (U/S) measurements at Brooke ran from June 8 to October 31 (145 days) with 18.1 days missing due to recording problems. Brooke downstream (D/S) records ran from June 8 to October 12, 2015 (126 days) and include 7.32 days of missing data. To ensure measurements were not adversely affected by local environmental conditions such as daily fluctuations in incident radiation and temperature (Rice et al., 2016), the performance of the turbidity sensors were independently tested (see Appendix S2 for details and results of these tests – Figure S1).

2.2.3 | Suspended sediment concentrations

At each site, 500 ml water samples were collected using a ISCO 3700 automated water sampler fitted with a stage-activated trigger to enable the determination of suspended sediment concentration (SSC). Six storms and four occasions of periodic sampling over 12-days (samples were collected at midday and midnight) were undertaken at Brooke and three storms and two occasions of periodic 12-day sampling at Ridlington. Following, rigorous data screening, 75 samples had to be discarded from Ridlington and 34 from Brooke as turbidity values in the series indicated that material may have built up on the sensor, or that recordings were affected by technical issues. This resulted in a total of 93 and 206 samples, respectively, from Ridlington and Brooke. Collection of periodic samples every 12-hr enabled visual corroboration of diurnal variability in SSC as inferred from turbidity measurements. Storm samples over a range of flows provided a large range of SSC values to enable a more accurate calibration model to be constructed. The single point measurements of turbidity and sediment concentration were assumed to be representative of the average cross-section values based on the small size of the streams (Rice et al., 2016).

Samples were filtered using Whatman 0.7 μm glass microfiber filters in the laboratory and routinely analysed for organic matter and mineral mass (Dean, 1974). Using continuous measurements of turbidity as a surrogate of SSC should be undertaken with caution since turbidity measurements are sensitive to the physical characteristics of the material including the presence of organic detritus (Bilotta & Brazier, 2008; J. Lewis, 2003). The average organic component of samples at Brooke was 21.5% ($SD = 5.4\%$) and 26.3% at Ridlington ($SD = 7.8\%$) and as a result SSC was calculated using only the mineral mass. Site-specific calibrations were constructed using a LOESS model fitted with an alpha smoothing value of 0.4 (Hicks, Gomez, & Trustrum, 2000; Gray, Pasternack, Watson, Warrick, & Goñi, 2015; Rice et al., 2016; Figure S2). For both the U/S and D/S sites at Brooke LOESS models utilised one set of SSC values extracted from water samples at the D/S location, but LOESS models were independently fitted to corresponding local turbidity measurements at each location (U/S or D/S).

2.2.4 | Sediment ingress rates

At both Brooke and Ridlington, sediment traps were installed to measure fine sediment ingress rates. Each trap comprised a PVC cylinder (diameter 65 mm, height 200 mm) perforated with 12 horizontal holes (diameter 6 mm) to permit both horizontal and vertical exchange of flow and fine sediments (Mathers & Wood, 2016). All cylinders were filled with a prewashed gravel framework collected from each of the respective sample sites (truncated at 8 mm), enclosed in a net bag (7 mm aperture). Application of a local gravel framework negates the potential influence that differing framework matrices have on ingress rates (Petticrew, Krein, & Walling, 2007).

Cylinders were inserted flush in the riverbed to a depth of 200 mm with surrounding stream bed remaining unchanged. Cylinders were left in situ for the entire sampling campaign, but every 14 days the gravel netting bag was removed and replaced, providing a constant record of sediment accumulation at a 14-day resolution. At the end of each 14-day sampling period, the net bag (containing the gravel clasts) was carefully lifted out and a clean gravel bag inserted into the cylinder. Sediment traps were installed 21st May–24th September providing a record of 126 days (9 sample sets; Table 1).

Three riffle sites were examined at Brooke and two at Ridlington (initially one until July 2) at Ridlington. At each riffle four cylinders were installed providing a total of 12 replicates at Brooke and 8 at Ridlington (4 initially for 3 sample sets). Samples were evenly spaced across the riffle unit (head through to tail) as fine sediment accumulation can vary due to longitudinal vertical hydrological gradients (Mathers & Wood, 2016). In total 105 and 57 ingress samples were examined from Brooke and Ridlington, respectively (3 cylinders were lost at both sites during the campaign). In the laboratory, the contents of the cylinder samples were passed through 4 and 2 mm sieves to remove the artificial substrate. Fine sediment samples (<2 mm) were oven dried at 60°C until a constant weight was recorded. Samples were gently disaggregated, passed through a sieve nest (1,000 and 125 μm) and each fraction weighed to determine the grain size distribution. Grain sizes were examined because the rate of fine sediment ingress is inherently associated with the ratio of pore filling/infiltrating particles to the framework matrix (Frings, Kleinhans, & Vollmer, 2008).

2.3 | Statistical analysis

2.3.1 | Turbidity measurements

Time series of turbidity measurements were analysed to determine the presence of a diurnal bioturbation signal as a result of crayfish presence and activity. Dominant periodicities in the turbidity measurements were examined by calculating periodograms of the time series using the software PAST version 3.12. Periodograms enable the investigation of periodic components (or frequencies) of a time series to determine the presence of statistically significant oscillations (Hernandez, 1999). Prior to analysis, data was despiked by replacing individual data records that were greater than 1 *SD* from the monthly average with the local average (of the previous and subsequent 5-min record; following Rice et al., 2016). Periodograms were then calculated to provide a graphical representation of the measure of relative importance of all frequency values that may describe the oscillation pattern within the data; thereby enabling the dominant frequencies in the series to be identified (Stoica & Moses, 2005). If diurnal signals in the turbidity data are present (following Rice et al., 2016) then a peak periodicity of 24-hr should be returned in the time series whilst the control site will return other non-consistent peaks. Periodograms were calculated using the Discrete Fourier Transform.

2.3.2 | Sediment flux estimation associated with crayfish presence

Due to an absence of a local gauging station providing discharge data, continuous stage measurements at 15-min resolution were collected at the upstream location in association with discharge measurements via the velocity-area method on 10 occasions. The correlation between measured water depth values and estimated discharge was significant and first order polynomial regression models were fitted to provide a means of estimating discharge at the site. Discharge was assumed to be similar at the U/S and D/S reach locations due to the spatial proximity and small nature of the streams. Discharge measured at a gauging station (NRFA ID 31025) ca. 3.2 km downstream was closely matched with our discharge estimates yielding a correlation of 0.95 at a lag time of 1.5 hr. At this lag rate, the discharge is on average 1.4 times smaller which is consistent with a 1.3 increase in discharge area. Discharge values are therefore reliable and were used with corresponding estimates of SSC to calculate sediment fluxes SF (mg s^{-1}) for each 5-min interval at Brooke (both U/S and D/S). For a desired time period, the suspended sediment load SL (kg) was calculated as:

$$L = 10^6 \left(\sum_{t=0}^{n} \Delta SF \right), \tag{1}$$

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

2.3.3 | Isolation of abiotic and biotic components of sediment load associated with crayfish presence

Suspended sediment loads can be deconstructed into two flow components which constitute the total sediment load, baseflow (SLbf) and flood periods (SLf). Flood and baseflow periods were identified from the stage data, with baseflows defined as periods of steady and low discharge, and flood flows by unsteady, higher than average discharge with clear rising and falling limbs associated with stormflow runoff. Using Equation (1) separate calculations were conducted for SLbf and SLf. During baseflow periods there is a strong potential for crayfish activity to have an impact on sediment fluxes and therefore SLbf was decomposed into biotic (SLbfB) and abiotic (SLbfA) elements following the procedure outlined by Rice et al. (2016) at Brooke:

$$\mathrm{SLbf} = \mathrm{SLbfB} + \mathrm{SLbfA}. \tag{2}$$

The two components were isolated on the assumption that turbidity values would record a lower maximum abiotic value than the bioturbation enhanced daily averages that were measured. Time series of abiotic turbidity values were constructed according to the criteria below and used in the LOESS model to derive sediment fluxes in the absence of bioturbation (SLbfA). The estimated biotic component was calculated as the difference between SLbf and SLbfA.

There is one significant uncertainty in this method in that the abiotic value of turbidity is not known. A minimum estimate was employed which constituted the minimum measured value of turbidity each day (see Figure 2 for example plot decomposing the turbidity data into biotic and abiotic components). However, minimum turbidity values are likely to be elevated by the residual effects of the previous night's bioturbation and as result it is possible that in the absence of such activity, turbidity levels could reach lower values resulting in load estimates being smaller than in reality. No efforts were made to decompose flood periods as it is not anticipated that bioturbation would have a significant effect on entrainment during high flow events (Albertson & Allen, 2015; Moore, 2006).

2.3.4 | Sediment balance at Brooke

To determine the influence of crayfish on sediment storage, a sediment budget structured around the amount of suspended material entering and leaving the reach was constructed as per the following continuity equation:

$$\mathrm{I} - \mathrm{O} = \Delta \mathrm{S}, \tag{3}$$

where I is the sediment input, O is the sediment output and ΔS is the change in sediment storage. This was possible due to load estimates being measured at both ends of the invaded reach providing I and O values for any given time period.

2.3.5 | Sediment ingress rates associated with crayfish presence

Prior to analysis sediment weights for each grain size were converted to deposition rates (kg m^{-2} day^{-1}). To satisfy model assumptions values of the 1,000–2,000 μm fraction were square root transformed and all other fractions were log transformed. A linear mixed effects (LME) model was employed to examine grain size differences with regards to site (Brooke or Ridlington). Models were fitted using the lme function in the 'nlme' package in the R environment (R development Core Team, 2020). The model was fitted with the fixed interacting factors of site (to assess the implications of crayfish presence) and time (to assess if there were differences over time if not overall) and riffle identity was included as a random factor to account for autocorrelation in space and time.

3 | RESULTS

3.1 | Signal crayfish demographics

Catch per unit effort (CPUE) numbers exhibited variability during the sampling period, with spatial and temporal differences in individuals trapped (average 3.9 adults, range 9.7–1.5 adults per trap night; Figure 3). There was little variation in the size of adults trapped spatially or over time (average 34.8 mm, range 28.6–40.6 mm). Populations were dominated by females (average 69.4%) with 21.44% exhibiting some form of damage. CPUE estimates during the sampling period (Brooke set 2–9) exhibited moderate negative correlation with water temperature ($r = -0.5$, $p > .05$). No crayfish were caught on the four sampling occasions at Ridlington.

3.2 | Crayfish presence and turbidity time series

Examination of the turbidity series at Brooke indicated that the patterns recorded at the U/S and D/S sites were similar (Figures S3–S5) and therefore as the most complete timeseries only Brooke D/S is presented to avoid duplication. The turbidity time series at Brooke D/S is variable in nature, however there is clear evidence of diurnal

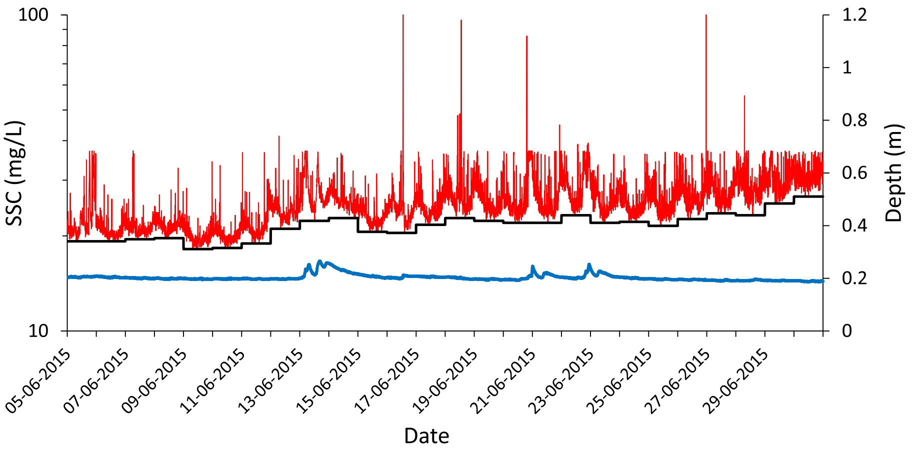

FIGURE 2 Example plot decomposing the turbidity data into biotic and abiotic components. The red line is 5-min turbidity data, the blue line is 5 min stage data and the black line indicates the minimum turbidity value used as a surrogate for the abiotic fine sediment load (SLbfA). The area above the black line and below the red is assumed to represent enhanced fine sediment fluxes associated with biota (SLbfB) [Color figure can be viewed at wileyonlinelibrary.com]

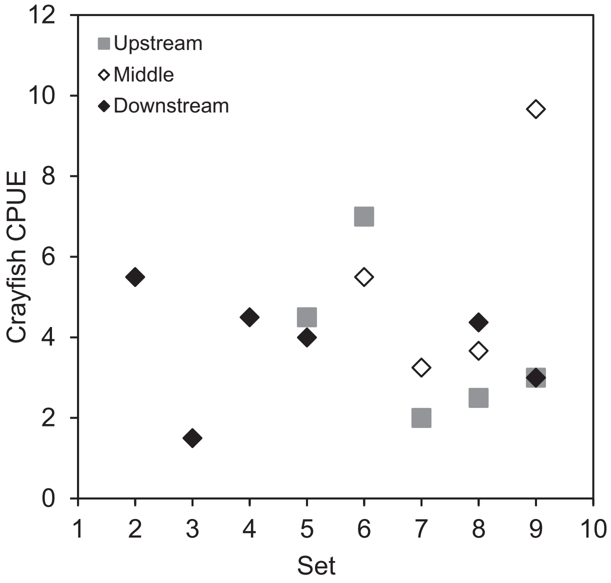

FIGURE 3 Signal crayfish catch per unit effort (CPUE) for each sample set at Brooke (June 21–September 24, 2015)

fluctuations (see e.g., Figure 5 plot and full time series in Figure S5). Periodograms for the turbidity time series at Brooke D/S exhibit peaks in power predominately at the period of 1 day in all (Sets 3–8) but one instance (Set 9; Figure 4). For set 9, data was analysed in two parts due to missing data, with the first half of the set (10th–14th September) indicating a peak in power at 1 day but the latter half (17th–24th September) at 0.5 days (Figure 4). There is no obvious hydraulic explanation for the observed diel patterns with water depth remaining consistent during baseflow periods (Figures 4 and S5).

Turbidity at Ridlington demonstrated considerable variability with the series being characterised by intermittent spikes (Figure S6). Periodograms for the time series indicate an absence of a regular dominant frequency with all sampling sets providing differing peak frequencies (average 6.02 days, range 1–11.63 days; Figure 4). Only one sampling set indicated a periodic peak at 1 day (set 6) which is evident in the turbidity series (Figure S6). This diurnal pattern is very spiky in comparison with the gradual rising and falling limbs evident at Brooke and in other crayfish zoogeomorphic studies (Figure 5; Harvey et al., 2014; Rice et al., 2014, 2016). This pattern also coincides with minor diurnal fluctuations in stage (0.1–0.2 m) between mid-afternoon and midnight evident in Figure S6. During flood events, turbidity responded as expected with corresponding peaks at both Brooke and Ridlington suggesting the presence of widespread sediment availability at both sites. Average SSC over the sampling period were 32.2 mg L^{-1} at Ridlington and 38.0 mg L^{-1} at Brooke.

3.3 | Biotic and abiotic contributions to suspended sediment load associated with crayfish presence

Biotic and abiotic contributions to baseflow suspended sediment load (SLbf) and total suspended sediment load (SL) are presented in Table 2a. Conservative estimates (using minimum daily turbidity values) of biotic contributions to sediment fluxes indicate that crayfish added on average 18.5% (standard error = 1.4%) to baseflow loads during the sampling period. Estimates range from 8.5 kg day^{-1} through to 30.7 kg day^{-1} (equivalent to 9.3–23.5%). Biotic contributions during baseflow conditions vary as a function of time and space. On average, the contribution of bioturbation was greater at the D/S site (average 21.0%, range 17.5–24.6%) compared to the U/S site (average 18.5%, range 9.3–22.1%). 86.3% of total suspended sediment was transported as a result of abiotic processes when high flow periods were included in calculations. That is, when flood spates are included, bioturbation contributions were reduced to an average of 13.7% (note that 2 sample sets did not include any flood periods, Sets 4 and 6) and ranged 5.8–23.5%; 9.5–31.6 kg day^{-1} (Table 2b). The monthly figures are highly variable, mainly as a function of the number of flood days and the magnitude of such flows (Figure S7).

3.4 | Sediment flux and budget estimation associated with crayfish presence

Sediment fluxes during the sampling period varied considerably with an overall net loss of fine material (2,485 kg). For five out of the seven sampling sets (Sets 4–7) the sediment budget remained in equilibrium with a negligible net gain of 25 kg 14 day^{-1} (Figure 6). Sediment fluxes during this period remained consistent (average 132.6 kg day^{-1}, range 105.4–146.2 kg day^{-1}). Fluxes during set 2 and 3 resulted in an overall net loss of material from the reach (−95.7 and −111 kg day^{-1}) associated with three storm flows entraining greater amounts of fine sediment at the downstream end of the reach (Figure S5). In addition, a number of turbidity spikes occurred between 16th June and 20th June at the downstream end of the reach which contributed large quantities of fines to the suspended sediment load (Figure S5).

3.5 | Fine sediment ingress associated with crayfish presence

Ingress rates demonstrated no consistent site effect over time but demonstrated significant temporal variability (Figures 7 and S8). There were no statistical differences in ingress rates between Brooke and Ridlington for any of the size fractions ($p > .05$, LME) when overall differences or individual size fractions were considered. Furthermore, there was no significant interaction between site and time for any of the size fractions or <2 mm overall ($p > .05$, LME).

4 | DISCUSSION

4.1 | Crayfish presence and local turbidity records

The results presented here provide the first direct comparison of a turbidity series at paired sites where signal crayfish are present in high numbers at one site and absent at the other. A number of other

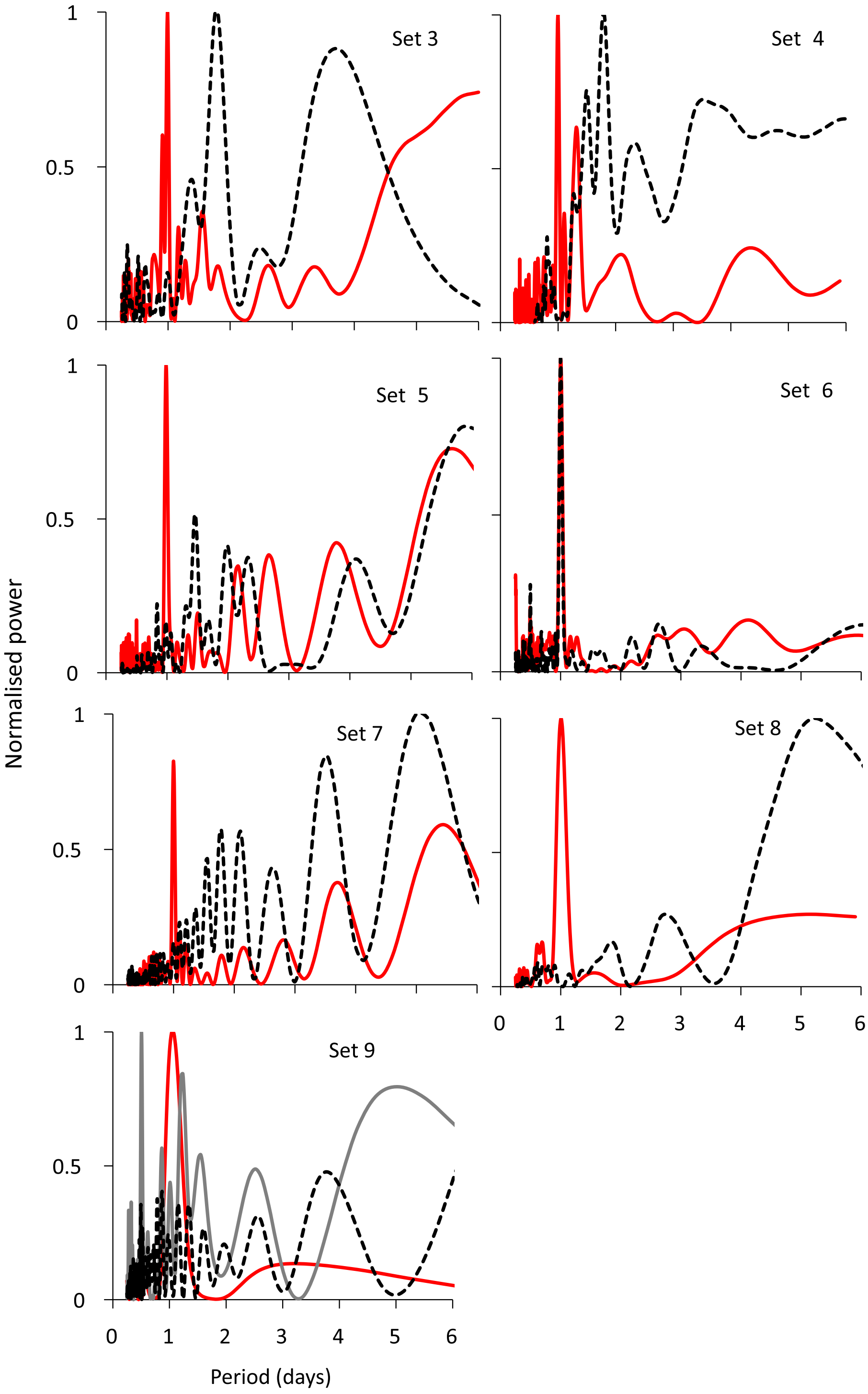

FIGURE 4 Periodograms of turbidity time series from June–September 2015 from two lowland UK rivers. Red (and grey in set 9) solid lines represent Brooke D/S (crayfish) and black dashed Ridlington (no crayfish). Data that were more than one standard deviation from the monthly mean were replaced with a local average. Power is normalised by the maximum value for the respective time series. Note no turbidity or water data was collected during the first set (June 21–July 4, 2015) due to equipment problems and set 2 is missing data at the start of the record (June 4–June 8, 2015). The main peaks are significant in all instances ($p < .05$). Periodogram indicates the periodic signal of timeseries data to identify if there is a dominant cyclical peak [Color figure can be viewed at wileyonlinelibrary.com]

studies have documented the presence of diurnal fluxes in fine sediment at sites where crayfish are present which cannot be associated with hydraulics. Our data recorded during a 16-week period over the course of a summer provides further evidence to support observations made by Harvey et al. (2014), Rice et al. (2014, 2016) and Cooper et al. (2016). The turbidity signal has a clear and distinctive signature, demonstrating a gradual increase in ambient sediment concentrations of between 10 and 20 NTU, presumably associated with the additive effects of fine sediment mobilisation as the number of crayfish and the level of activity increased over the course of the night. Turbidity levels subsequently remain elevated for a few hours before gradually declining over the course of early morning as crayfish activity declined. Signal crayfish activity is predominantly nocturnal (Bubb, Lucas, Thom, & Rycroft, 2002; Johnson, Rice, & Reid, 2014) and it is therefore reasonable to assume that any effect on fine sediment dynamics would be most likely during these hours. Crayfish are significant bioturbators and can alter bed sediment resuspension through foraging, pit construction, walking, tail flipping and fighting

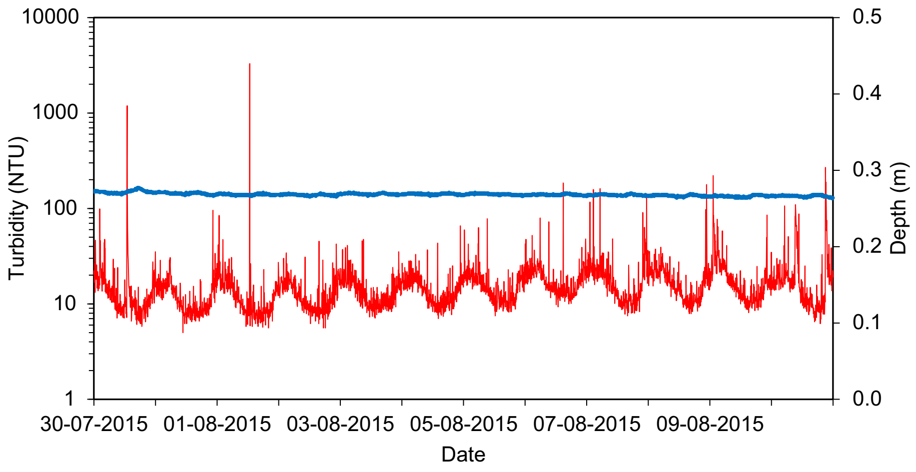

FIGURE 5 Example of turbidity and depth series for a 10 day period in August 2015 at Brooke D/S (crayfish) demonstrating the diurnal ambient increases in turbidity at night. Tick marks are at midnight. The red line is 5 min turbidity data and the blue is 5 min stage data [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Estimates of biotic and abiotic contributions to (a) base flow and (b) total suspended sediment load at Brooke

(a)

	Upstream				Downstream			
Sample set	Abiotic load, SL_{bfA} (kg)	Biotic load, SL_{bfB} (kg)	Biotic contribution (%)	Days missing[a]	Abiotic load, SL_{bfA} (kg)	Biotic load, SL_{bfB} (kg)	Biotic contribution (%)	Days missing[a]
2	775.01	93.01	12.00	2.99	983.51	211.88	21.54	3.02
3	925.57	94.97	9.31	3.75	895.40	292.83	24.64	3.65
4	1,646.30	372.40	22.62	0.00	1,561.52	331.24	21.21	0.00
5	1,506.90	395.02	26.21	2.42	1,310.15	327.08	24.96	3.44
6	1,365.32	387.72	28.40	0.00	1,405.03	430.41	30.63	0.00
7	1,215.77	180.56	14.85	3.93	948.00	273.62	28.86	5.51
8								
9					516.29	137.86	26.70	5.33

(b)

	Upstream		Downstream	
Sample set	Abiotic load, SL_{bfA} (kg)	Biotic contribution (%)	Abiotic load, SL_{bfA} (kg)	Biotic contribution (%)
2	1,257.01	7.40	2,213.55	9.57
3	1,556.92	6.10	3,110.49	9.41
4	**1,646.30**	**22.62**	**1,561.52**	**21.21**
5	1984.21	19.91	1966.58	16.63
6	**1,365.32**	**28.40**	**1,405.03**	**30.63**
7	1902.47	9.49	1852.45	14.77
8				
9			841.96	16.37

Note: Bold denotes that these sample periods contained no flood flows.

[a] Comprises missing data and flood days, set 2 record is missing data at the start and commences on June 8, 2015. Set 8 turbidity was highly intermittent and so no estimates were calculated.

activities (Albertson & Daniels, 2016; Creed & Reed, 2004; Rice et al., 2014). In addition, burrowing activities by signal crayfish can result in pulses of fine sediment of sufficient magnitude to increase ambient turbidity levels (Harvey et al., 2014). As stage is a useful index of change in hydraulic parameters relevant to sediment entrainment (shear stress and shear velocity), the independence of the diel turbidity fluctuations from stage suggest that hydrological conditions were not responsible for this pattern.

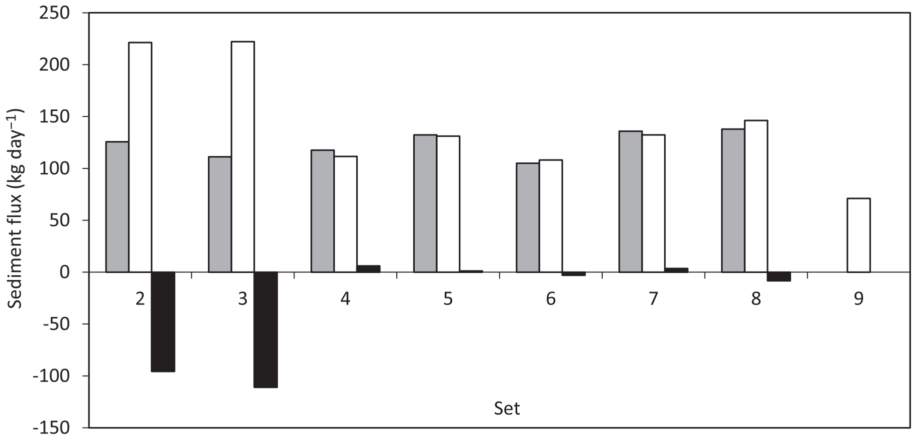

FIGURE 6 Daily sediment fluxes (kg day^{-1}) for each 14-day period of the sampling campaign at Brooke (June 8–September 24, 2015; crayfish). Grey bars = upstream reach; white bars = downstream reach and; black bars = change in storage. No data were collected during the first set (June 21–July 7, 2015) due to equipment problems, set 8 consists of 2.68 missing days and only data from D/S was available for set 9

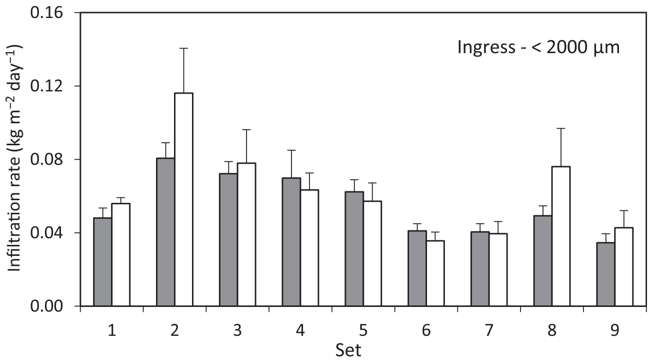

FIGURE 7 Mean (±1 *SE*) infiltration rates (kg m^{-2} day^{-1}) for each period of the sampling campaign (June 21–September 24, 2015) for particles <2,000 µm. Solid grey bars = Brooke (crayfish) and white bars = Ridlington (no crayfish). For corresponding plots by grain size fraction (1,000–2,000, 125–1,000 and <125 µm) see Figure S8

Periodogram analysis further supports these arguments. The dominant peak frequency of turbidity is 1 day for six (of the seven) 14-day sample sets in the river supporting crayfish suggesting a diurnal cyclicity in peak turbidity values. The final sample set (late September) had two dominant frequencies, with the start of the record displaying a dominant periodicity of 1 day, whilst the latter half of the record became noisier with a peak frequency of 0.5 days. The reason for the change could be associated with the reproductive behaviours of crayfish. Spawning behaviour of *P. leniusculus* typically occurs during October in the majority of populations in the UK (S. D. Lewis, 2002) and it is likely that activity levels alter in the lead up to mating season. Visual observations indicated that crayfish were more active in the day during this time period, and Rice et al. (2016) noted a similar pattern with increased activity levels (as determined by passive integrated transponder [PIT] data) and a corresponding weakening in diurnal turbidity fluctuations. Consequently, when investigating the role of biota as zoogeomorphic agents, consideration should be given to behavioural and life cycle attributes which may influence the extent of their geomorphic potential.

In the case of Ridlington (control site), the turbidity series was not as anticipated because in the absence of crayfish acting as geomorphic agents, it was assumed that turbidity levels would maintain a consistent low level. Instead, some diurnal variation was observed in one of the seven 14-day sample sets analysed. However, the nature of this diurnal pattern was quite different from that at Brooke (crayfish site), with the turbidity data lacking the characteristic slow increase in turbidity evident in the presence of crayfish. The turbidity series at Ridlington is spiky in nature with a large number of noisy peaks throughout the day. These peaks represent short time frames where turbidity spikes for an hour and then returns to base levels. It is difficult to attribute what the cause of these turbidity fluxes is, but as the periodograms confirm, these spikes do not demonstrate any pattern but rather appear as 'noise'. Long term monitoring of SSCs or turbidity are rare, with much of the historical monitoring taking place at low resolutions (Duvert, Gratiot, Némery, Burgos, & Navratil, 2011) or being heavily focussed towards hydrological events (i.e., to investigate sediment hysteresis) reflecting the conventional view that energy conditions control the transport of fine sediment (e.g., J. Lewis, 1996; Walling & Collins, 2016). As such it is difficult to compare the observed patterns in this study at Ridlington with baseline data from other locations.

It is possible that the assumption that turbidity remains fairly consistent during baseflows is unfounded and that variations in levels of SSC unrelated to flow are natural (Duvert et al., 2011; J. Lewis, 2003). Grove et al. (2015) suggest that these temporal variations in suspended sediment should be expected given the temporally variable contributions of fine sediment from channel and non-channel sources even under consistent hydraulic conditions as sediment sources naturally connect and disconnect. It may also be associated with differences in the size of material (fine material vs. larger turbidity particles; Bright, Mager, & Horton, 2020), shape of material (Kitchener, Wainwright, & Parsons, 2017) or composition of material (organic vs. inorganic; Davies-Colley, Hughes, Vincent, & Heubeck, 2021) being transported at particular points in the time series, all of which have been shown to affect the turbidity measurements.

The possibility that animals may also act to entrain and suspend material again highlights the distinct paucity of studies which consider this process and the possibility that other organisms may be influencing fine sediment dynamics (Bylak & Kukuła, 2020; Mason & Sanders, 2021; Rice, 2021; Rice et al., 2016). These potential geomorphic agents are not limited to aquatic flora and fauna (such as vertebrates, invertebrates and fish) but could also include large semi-aquatic organisms such as birds, otters, mink and water voles, which are capable of having a large impact on fine sediment dynamics when foraging. Domesticated animals including cattle are well known causes of fine sediment mobilisation, but were not present close to the study sites. Whatever the cause, there is a need for improved continuous monitoring of SSC to extend our knowledge of sediment fluxes beyond that tied to discharge and into natural temporal variations (at sufficient resolutions) that may not be associated with hydraulic drivers (J. Lewis, 2003).

4.2 | Crayfish contribution to suspended sediment loads

On average crayfish added 271 kg to 14-day baseflow sediment loads with a maximum of 430 kg added during the first half of August. This estimate is equivalent to 18.5% (maximum of 23.5%) of the sediment load and highlights the potential importance of biotic interactions for fine sediment dynamics during baseflow conditions. If flood periods during the study are incorporated in the calculations this contribution reduces to 13.7%, which still represents a significant contribution to sediment fluxes for a small lowland stream, albeit during the predominantly drier spring and summer months. Rice et al. (2016) documented similar additions at a site invaded by crayfish with an average annual contribution of 31.8% during base flows reduced to 1.5% when winter flood periods were included, during a particularly wet winter. The results of this study provide further support for the growing evidence that biota are significant bioturbators in rivers and that their influence on sediment dynamics needs to be considered if we are to fully understand sediment mobilisation and deposition in fluvial systems (Corenblit et al., 2011; National Research Council, 2010).

Within this study, the contribution of crayfish induced sediment loads demonstrated significant variability both temporally and spatially. Biotic fluxes were on average greater at the D/S reach (26%) compared to the U/S reach (19%). Furthermore, temporal differences in rates were more prominent at the U/S reach with a considerable increase during set 4 (July) from an average of 11% to 26% for the next 6 weeks. The implications of biota on the physical environment are heavily dependent on three biological characteristics; body size, abundance and behaviour (Moore, 2006). Within this study, the body size of individuals did not vary over time or space and is therefore unlikely to have affected the flux rates measured. Behavioural effects on bioturbation associated with reproductive behaviours were evident in the weakening of the diurnal turbidity pattern as discussed above. The CPUE however did demonstrate some variability over time with estimates being highly correlated with temperature (Johnson et al., 2014). For example, there was an absence of clear diurnal trends in turbidity during the first few sample sets (Figure S5), early in the summer, which is likely associated with water temperatures being lower and is known to correspond to reduced crayfish activity (Cooper et al., 2016).

The variability in the contribution of crayfish to sediment fluxes, particularly in the instance of the U/S reach, is most likely associated with spatial differences in crayfish populations throughout the reach (and potentially U/S of the reach). Crayfish typically remain in the same location for days to weeks but then sporadically move to new locations (Bubb et al., 2002). As such these alterations to localised abundances will have repercussions on the extent of biotic interactions with the environment (Albertson & Allen, 2015). Consequently, when considering the role of biota as geomorphic agents' attention should be paid to localised population dynamics and movement patterns rather than just their presence or absence.

Within the study reach, the spatial distribution of crayfish over time had a considerable effect on channel storage and ingress rates. Sediment fluxes demonstrated a net loss of material (2,510 kg) during the first 4 weeks (June) with three high flow events entraining a large amount of material at the D/S end of the reach. However, sediment budgets remained largely in equilibrium during the entire sampling period (18-weeks) with a negligible net gain of 25 kg (average flux of 1,594 kg). It is likely that this estimate reflects the dense population of crayfish throughout the river Gwash. Selection of the river reach was focussed on a riffle-pool structure which supported an abundant population of crayfish. Within the river Gwash the distribution of crayfish remains high throughout, with multiple sites on the river supporting high abundances of crayfish; CPUE estimates based on 3 nights trapping during 2014–6.8 adults at a site 1.7 km U/S and 6.2 at a site 2 km D/S. As a result, the amount of fine sediment entering and leaving the reach is likely to be similar, and therefore, in this river, crayfish do not act as a net source of fine sediment to reaches downstream. However, in a river which may be experiencing crayfish colonisation and is in the early stages of invasion or in one which supports isolated pockets of abundant populations, the implications of crayfish on downstream fluxes may be notable. Sites in which crayfish are present may act as a source of material whilst those D/S may act as a store with the river channel slowly aggrading over time and consequently moving the river out of equilibrium.

4.3 | Fine sediment ingress over time as a function of crayfish presence

Fine sediment ingress rates demonstrated no overall differences when crayfish presence was considered for any of the 14-day time periods. Similar amounts of fine sediment accumulation were present at both Brooke and Ridlington. A number of other studies have documented a reduction in sediment accrual associated with the presence of crayfish (Albertson & Daniels, 2016; Creed & Reed, 2004; Helms & Creed, 2005; Parkyn et al., 1997; Usio & Townsend, 2004) and Mathers et al. (2019) documented an increase in fine sediment infiltration mediated by prey availability in an experimental setting. However, all these studies have significant limitations in that they are conducted under controlled conditions utilising in situ enclosures or through flume/mesocosm studies (in situ experimental channels or ex situ) where crayfish activity was associated with repeated foraging within a small spatial area. In reality, crayfish activity will not be confined to small spatial areas but distributed across multiple foraging patches which likely differ each night. Moreover, the findings of this study consider the cumulative effect of invasive crayfish on fine sediment deposition as a function of inputs (burrowing and fluxes) in addition to outputs (remobilisation via foraging).

As in the case of suspended sediment budgets, the spatial distribution of crayfish populations probably influences the extent to which crayfish affect deposition rates. It is assumed that the rates of sediment inputs into each riffle were similar because of a homogenised crayfish distribution throughout the reach and therefore overall deposition rates did not differ when compared to that of Ridlington. The contribution of crayfish to sediment fluxes therefore most likely mitigates their potential role as fine sediment winnowers in this instance. This effect is most likely emphasized in the lowland reaches studied as a result of their high fine sediment content and clay banks. Results may differ as a function of different geologies and bed sediment composition. In locations in which there is a low fine sediment content, crayfish presence may act to reduce the accrual of fine sediment. Similarly, rivers in which there are isolated pockets of crayfish, or at the invasion front, may produce differing results. Environmental context and spatial and temporal knowledge of biota population dynamics and densities is therefore vital in understanding their effects on the environment.

4.4 | Biotic contributions to fine sediment dynamics

The consequences of biota for fine sediment dynamics are heavily dependent on a number of factors. First, the abundance of biota in time and space (also dependent on the stage of invasion if non-native) which controls the ability of the organism to influence sediment dynamics. Second, life cycle attributes that often alter an organism's behaviour and therefore their interactions with the physical environment (e.g., spawning behaviour). Third, environmental controls such as discharge and temperature which exert an influence over activity levels and the overall contribution of the biota to sediment fluxes. Despite the growing body of literature focussed on the role of organisms as geomorphic agents, studies which examine the implications of their behaviour on the physical environment associated with the above attributes are limited. Further research is therefore imperative to enhance our understanding of biogeomorphic contributions to sediment dynamics across time and space. Invasive species represent particularly important organisms when considering their interactions with the physical environment as these dynamics may otherwise be absent.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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