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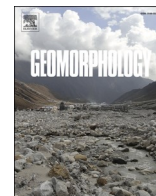
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The long-term dynamics of invasive signal crayfish forcing of fluvial sediment supply via riverbank burrowing

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ABSTRACT

Animals are important drivers of sediment dynamics. Invasive signal crayfish (*Pacifastacus leniusculus*) have been shown to supply sediment to rivers by burrowing into riverbanks. Burrowing directly transfers excavated sediment into the river and also has an additional indirect affect by promoting riverbank failure. While previous research has isolated burrow densities at a point in time, rates of burrow construction and of burrow loss due to erosion are unknown, which introduces uncertainty into estimates of how much sediment burrows contribute to rivers. Here we report results from a 5-year study that evaluated the temporal dynamics of crayfish populations, rates of burrow loss due to erosion, and the mass of sediment directly supplied to rivers by burrow excavation. At ten reaches across five lowland streams in England, we estimated the mass of sediment displaced by 1861 new and previously constructed burrows. Both crayfish and burrow densities were variable over time, suggesting that burrows contribute temporally variable amounts of fine sediment to riverine systems. 42 % of observed burrows were constructed within the previous 365 days, and individual burrows lasted on average 461 days. Applying this to comparable historical data, an average of $2.0 \text{ t km}^{-1} \text{ a}^{-1}$ of sediment was excavated to construct burrows in the study reaches, which is eight times more than estimated in previous studies. Whilst total burrow densities in each year were not consistently correlated with contemporary crayfish densities, the mass of sediment excavated over the prior year was strongly correlated with contemporary crayfish densities. Current fine sediment management practices are largely aimed at controlling fine sediment delivery, predominately from agricultural activities, but biotic burrowing into riverbanks may represent an important and overlooked source of fine sediment supply. Incorporation of biotic processes in sediment dynamics would improve the accuracy of fluvial sediment budgets and enhance the knowledge base underpinning effective fine-sediment management practices.

1. Introduction

Animals are important drivers of sediment dynamics in rivers (termed ‘zoogeomorphology’ or ‘biogeomorphology’; Viles, 1988; Butler, 1995; Statzner, 2012; Rice et al., 2019; Mason and Sanders, 2021). Whilst many animals redistribute sediment stored in channels (e.g., salmonid spawning, Hassan et al., 2008; crayfish bioturbation, Harvey et al., 2014; benthic fish feeding, Rice et al., 2019; caddisfly larvae case building, Mason et al., 2022), animals can also enhance the supply of floodplain sediments to river channels, both directly through burrowing (Guan, 1994; Fallor et al., 2016), and indirectly by promoting accelerated riverbank erosion and retreat (Harvey et al., 2019; Sanders et al., 2021; Fig. 1). Animals that enhance the supply of fine sediment to lotic systems are particularly important geomorphic agents, as this biotic

recruitment of sediment can occur at times when hydraulic energy is low and insufficient to erode cohesive sediments (Mason and Sanders, 2021).

One such example of an animal that supplies fine sediment to rivers is the signal crayfish (*Pacifastacus leniusculus* (Dana 1852), Astacidae). Signal crayfish are one of the most widely distributed invasive species in Europe (Kouba et al., 2014) and have been documented to construct burrows in the banks of rivers that they invade in the UK (e.g., Guan, 1994; Harvey et al., 2011; Harvey et al., 2014; Sanders, 2020). Signal crayfish burrows can contribute substantial quantities of fine sediment to catchment sediment budgets; for example, in the River Bain, UK, signal crayfish burrowing recruited at least $25.4 \text{ t km}^{-1} \text{ a}^{-1}$ of floodplain sediments to the river channel through accelerated bank retreat, comprising at least 12.2 % of the annual reach scale sediment recruitment (Sanders et al., 2021). Excessive delivery and storage of fine

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sediment in lotic systems can have deleterious effects for water chemistry (Bai and Lung, 2005), all trophic levels of the food web (see reviews by Wood and Armitage, 1997; Kemp et al., 2011; Jones et al., 2012), disrupt predator-prey dynamics (Mathers et al., 2020) and can be associated with increased flood risk (Lisle and Church, 2002; Sidorchuk and Golosov, 2003; Lane et al., 2007). The zoogeomorphic potential of invasive species is of particular importance, as their establishment within an ecosystem may disrupt and/or modify geomorphological equilibria (and therefore sediment fluxes and landforms) that have developed within the ecosystem (Pejchar and Mooney, 2009; Funk et al., 2014; Mason and Sanders, 2021; Sanders et al., 2022).

Research on sediment dynamics associated with crayfish burrowing has focused on documenting sediment supply over short time periods based on single burrow surveys (Faller et al., 2016; Rice et al., 2016; Sanders et al., 2021), but the rate of burrow excavation, burrow longevity, and rate of burrow decay, and thus the rate of overall sediment delivery derived from burrowing remains unknown. Signal crayfish burrow densities are unlikely to be stable through time. First, crayfish burrows accelerate riverbank retreat (Harvey et al., 2019; Sanders et al., 2021), and therefore it is likely that some burrows will be eroded away entirely over time and may promote periods of new burrow construction. Second, as crayfish population densities vary, or other drivers of burrowing change (e.g., availability of riverbed refugia), new crayfish burrows may be constructed, and old burrows may be

reoccupied via renewed excavation. Therefore, the longevity of individual burrows and the rate of new burrow construction are vital controls on the long-term generation of fine sediment by crayfish in invaded streams. Whilst many studies have reported signal crayfish burrow densities (e.g., Guan, 1994; Stanton, 2004; Faller et al., 2016; Sanders, 2020), only one study to our knowledge (Rice et al., 2016), has attempted to understand the potential rate of sediment delivery through the construction of crayfish burrows over time. However, this was quantified by dividing the total burrow volume present from a single survey by the time since initial crayfish invasion and was not fully quantified by temporal field observations. The total mass of sediment annually excavated by crayfish, accounting for burrow loss, maintenance, and reconstruction, and the variability of such sediment inputs over time are therefore currently unknown.

Crayfish densities are likely a primary control on the rate of sediment recruited through burrowing because burrowing occurs when crayfish population densities exceed the availability of other shelters (Sanders, 2020). Previous field observations have reported that crayfish population density does not correlate with (Guan, 1994), or is a weak predictor (Sanders, 2020) of, burrow density. However, this is most probably because single observations of crayfish densities do not accurately represent temporal variations in crayfish populations (which are expected to correlate with burrowing activity), because of intra- and inter-annual variations in crayfish densities associated with the invasion

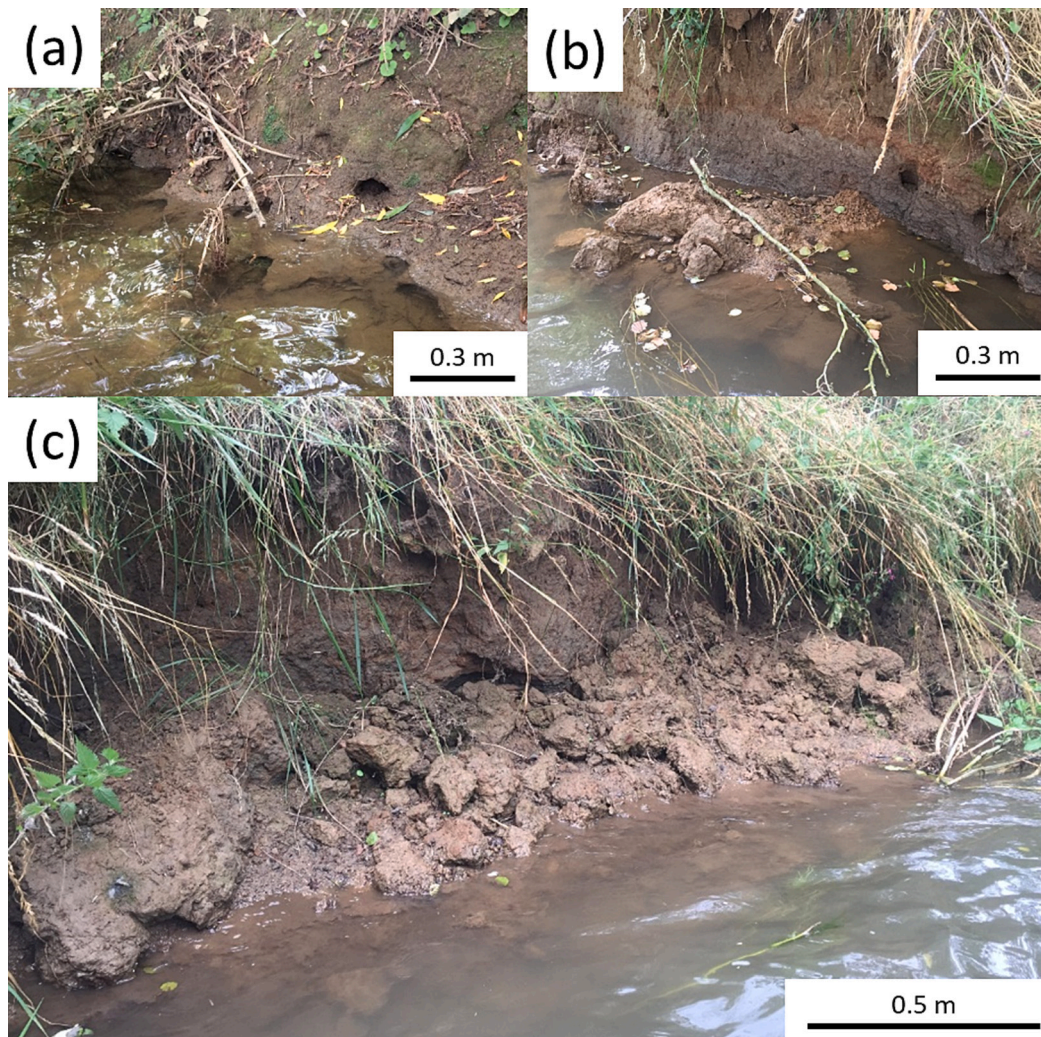


Fig. 1. Signal crayfish zoogeomorphology. (a) Crayfish burrows in a riverbank in Gaddesby Brook, Leicestershire, UK, and riverbank collapses promoted by crayfish burrows at (b) Gaddesby Brook, and (c) the River Bain, Lincolnshire, UK. Scale is approximate.

process (Hansen et al., 2013; Sandström et al., 2014; Larson et al., 2019) and environmental conditions such as discharge regimes (Light, 2003; Mathers et al., 2020). In the case of invasive species, rapid and unsteady increases and decreases in population density (boom and bust cycles) can occur in association with invasion dynamics (e.g., Elton, 1958; Simberloff and Gibbons, 2004; Strayer and Malcom, 2006; Matthews and Marsh-Matthews, 2011; Strayer et al., 2017). Indeed, rapid collapses and fluctuations in invasive crayfish populations have been recorded (Hansen et al., 2013; Sandström et al., 2014; Larson et al., 2019). Such boom-and-bust invasion dynamics may drive important but unquantified variations in sediment excavation on both spatial (e.g., geographical expansions) and temporal (e.g., changes in population densities over time) scales.

Here we present the results from a crayfish burrow monitoring programme (over five years), where repeated burrow and crayfish population surveys were undertaken at ten reaches on five lowland rivers in England to investigate the temporal dynamics of crayfish burrows and their role as a sediment source. Specifically, we addressed the following four research questions:

1. Are there temporal variations in crayfish burrow densities among sites?
2. Do temporal variations in burrow densities correlate with temporal variations in crayfish population densities?
3. On average, what is the temporal longevity of individual burrows before being removed by erosion?
4. How much sediment does crayfish burrowing actively recruit to rivers over time?

2. Methods

2.1. Study reach selection

Ten reaches across five rivers in Leicestershire, Northamptonshire, and Rutland (England) were selected for study (Fig. 2). These reaches are representative of morphologically and geographically similar lowland streams; the stream typology where signal crayfish are most common and abundant in the UK (e.g., Guan and Wiles, 1997; Guan and Wiles, 1999; Harvey et al., 2014; Rice et al., 2014, 2016; Cooper et al., 2016). In addition, these reaches are at different stages of the invasion

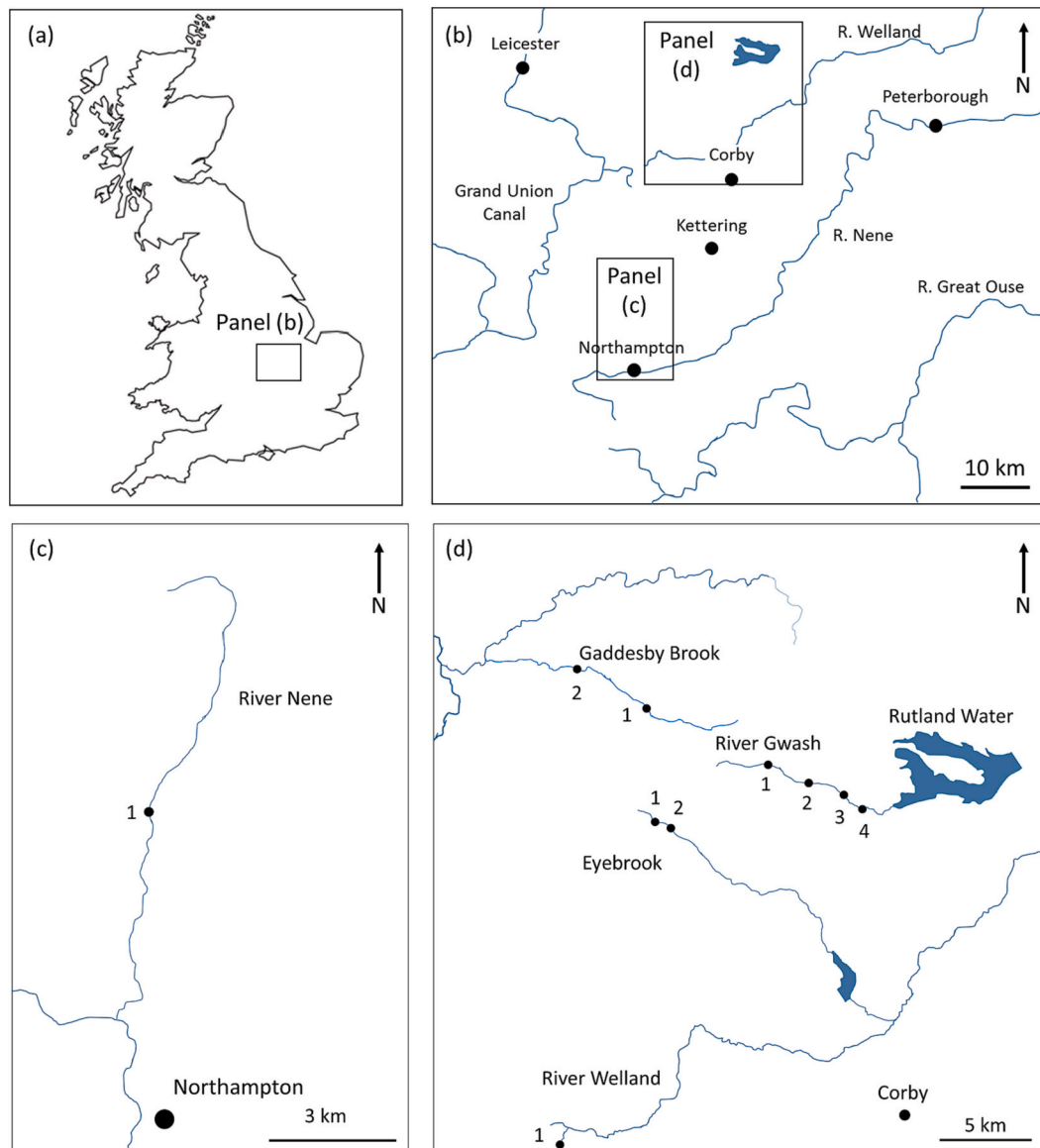


Fig. 2. Reaches where repeated surveys of crayfish burrows were undertaken: River Nene, Gaddesby Brook, River Gwash, Eyebrook, and River Welland (England). Multiple study reaches on the same river are denoted numerically, with '1' referring to the most upstream studied reach.

process, ranging from historically established signal crayfish populations (invasion in 1991) to more recently invaded reaches (invasion in 2013), allowing for the effect of crayfish density as a driver of crayfish burrow density to be examined between reaches. Reaches were also selected because of their accessibility, rather than because of being known activity ‘hotspots’, and therefore they are more likely to represent reach-average, rather than extreme burrow densities. Each monitoring reach consisted of two consecutive riffles and pools. 1861 burrows were recorded across surveys in 2014, 2017, and 2018 (1443 individual burrows, of which 418 were reidentified in subsequent surveys) and crayfish populations were monitored in 2014 and 2018 across all ten sites.

2.2. Crayfish sampling

Relative crayfish population densities were determined using baited Swedish ‘trappy’ traps. Three traps were set for a minimum of one night (three nights for 2014), and the mean catch per unit effort (CPUE) of all traps used as a surrogate measure of population density in 2014 (C_{2014}) and 2018 (C_{2018}). Whilst trapping does not sample juvenile crayfish (< 35 mm carapace length; Chadwick et al., 2021), it is the most common technique used in crayfish research (Parkyn, 2015) and facilitates quantitative comparison between sampling periods and reaches. Crayfish surveys were conducted in British summer (June–August) when crayfish are most active. Signal crayfish invasion dates were identified by previous research undertaken on the reaches (Holdich and Reeve, 1991; Belchier et al., 1998; Sibley, 2000; Peay, 2001; Stanton, 2004; Mathers et al., 2016; Sanders, 2020) supplemented by local knowledge and freshwater invertebrate surveys conducted by the local environmental regulator (Environment Agency personnel, pers. comm.).

2.3. Crayfish burrow surveys

Signal crayfish activity reduces in the autumn (Johnson et al., 2014), and sampling was undertaken after the burrowing season to capture the complete period of burrowing activity. At each reach, crayfish burrow surveys were undertaken on three occasions (September 2014, October 2017, and January 2019 burrowing season). Burrows were identified by their distinctive flattened ‘D’ shape, where the floor of the burrow is flat, and is absent of latrines or feeding platforms that are present in the burrows of rodents. Burrow depths, widths, and the height of entrances were measured to the nearest 5 mm. Burrow depths were measured using a meter rule at the centre of the opening to account for a sloping bank face. The location of each burrow in the reach was recorded to allow for re-identification in subsequent sampling surveys.

2.4. Data analysis

A mathematical modelling approach was undertaken to address each of the research questions, using key population metrics, rates of burrow creation, and rates of burrow decay, in a similar fashion to previous biogeomorphological work that has sought to upscale temporal and spatial observations (sensu Jones, 2012; Coombes and Viles, 2015; Fallor et al., 2016; Sanders et al., 2021).

The volume and mass of sediment excavated from each burrow, and each reach, were calculated following Fallor et al. (2016) and Sanders et al. (2021). The volume of sediment excavated from each burrow was calculated by treating the burrow shape as an elliptical cylinder:

$$B_V = L \pi (A/2 B/2) \quad (1)$$

where B_V is burrow volume (m^3), L is the depth of the burrow (m), A is the entrance width (m), and B is the entrance height (m). The total and mean values of burrow volume were calculated for all burrows present in each reach and converted to fine sediment mass B_M (kg) using a bulk density $\delta = 1500 \text{ kg m}^{-3}$:

$$B_M = \delta B_V \quad (2)$$

Reach-scale burrow density (B_{RL} , burrows m^{-1} river channel) and the total mass of sediment displaced by burrows normalised for reach length (M_{RL} , $t \text{ km}^{-1}$) were calculated as:

$$B_{RL} = B RL^{-1} \quad (3)$$

$$M_{RL} = \sum B_M RL^{-1} \quad (4)$$

where B is the number of burrows recorded in the reach, RL is the reach length (km) and $\sum B_M$ is the sum of the mass of sediment displaced by all burrows in the reach (t).

2.4.1. Temporal variations in burrow densities

Burrow density and the mass of sediment excavated were reported for each timestep. The change in burrow density, mass of sediment excavated and crayfish population density over time was reported for all reaches.

2.4.2. Burrow longevity

Burrows that were present in multiple surveys were identified by: (a) their location, and (b) having the same entrance height and entrance width ($\pm 0.02 \text{ m}$ to account for burrow maintenance). Burrow depths were expected to change, both shortening through bank retreat and mass failure, and extending through continued construction.

A half-life theorem approach was used to calculate burrow decay rates, based on previous studies examining the decomposition rate of biogeomorphic features (e.g., Gunzburger and Guyer, 1998; Travers and Eldridge, 2016). Using the proportion of burrows that were recorded as present in subsequent years across the reaches, the half-life of burrows ($t_{1/2}$, the time over which half of the burrows were lost) was calculated as:

$$t_{1/2} = t / (\log_{1/2}(N(t)/N_0)) \quad (5)$$

where t is the time in days between surveys, $N(t)$ is the number of crayfish burrows remaining, and N_0 is the initial number of burrows at the time of the first survey.

Calculating the half-life of crayfish burrows assumes that they are lost in a logarithmic fashion. Crayfish burrow loss is likely to be caused through bank retreat, and in particular mass failure. These processes affect different sections of burrowed riverbank independently (Sanders et al., 2021), and it can be expected that burrows will be lost through erosion, slumping, and mass failure events stochastically, meaning that the half-life theorem is an applicable way to infer their decay. Half-life values were reported for each river. Mean values were calculated across all ten rivers for both survey periods to report overall burrow half-life. Outlier values (defined as values $>1.5 \times$ interquartile range above the 3rd quartile or below the 1st quartile) from individual timesteps were excluded from the calculation of overall burrow half-life. Reported means for the full length of study were weighted 75:25 % towards the 2014–2017 data compared to the 2017–2018 data to account for the three years between monitoring in 2014 and 2017, compared to one year between 2017 and 2018.

Variability in burrowing rates was observed across the study, and to increase the applicability of the results beyond the immediate study sites and time periods examined, calculating the proportion of burrows that would collapse in a given year, where the same number of burrows are required to be present every year, was required (Sanders et al., 2021). Therefore, burrow half-life was used to calculate burrow decay rates, and thus the proportion of burrows that would collapse in a given year (365 days), where the same number of burrows are required to be present every year from a known half-life:

$$A_{(t)} = A_0 e^{kt} \quad (6)$$

where $A_{(t)}$ is the number of burrows remaining after a given length of time t , A_0 is the initial number of burrows, e is Euler's constant (2.718), k is the decay rate (calculated as $\ln(1/2)/t$, where t is determined half-life), and t is the given time period over which the decay occurs (here, 365 days).

The proportion of burrows calculated to remain after the period of one year (365 days) was reported for each study site.

2.4.3. Temporal crayfish burrow sediment recruitment to river systems

To estimate the mass of sediment recruited directly from the construction of new burrows each year M_A , the mass of burrow-displaced sediment from persistent burrows (identified in repeat surveys) was subtracted from the total mass of burrowed sediment and normalised for reach length, and for the time since the previous survey:

$$M_A = \left(\sum B_M - B_E \right) RL^{-1} T^{-1} \quad (7)$$

where M_A is newly burrowed sediment per kilometre of river per annum ($t \text{ km}^{-1} \text{ a}^{-1}$), B_E is the mass of sediment attributed to re-identified burrows (t), RL is reach length (km), and T is the time in years since the previous survey. It should be noted that M_A is specifically applicable to the density of burrows and sediment measured, and upscaling beyond directly measured study reaches should be done with appropriate caution and field validation.

The proportion of all excavated sediment ($\sum B_M$) accounted for by new excavations (M_A) was calculated as:

$$\%M_A = M_A / \sum M_{RL} * 100 \quad (8)$$

where $\%M_A$ is the proportion of observed sediment that has been excavated over a period of year (%).

M_A and $\%M_A$ were calculated for the two subsequent time steps (2017 and 2018) and reported for each reach. Means are presented for each study period and for the full length of study. The reported means for the full length of study were weighted 75:25 towards the 2014–2017 data compared to the 2017–2018 data.

To increase the wider applicability of the results, the mass of sediment excavated to rivers from burrows in a steady-state equilibrium system per year (BE_A) was calculated by combining the results of Eq. (6) with the mass of sediment excavated across the reach length (M_{RL}):

$$BE_A = (100 - A_{(t)}) M_{RL} \quad (9)$$

The mass of sediment excavated from burrows in a steady-state equilibrium system per year (BE_A) was calculated for each studied river.

2.4.4. Association between changing burrow densities and crayfish populations

Correlation analyses were undertaken between crayfish population densities measured in the 2014 and 2018 surveys (C_{2014} and C_{2018} , CPUE) and the normalised mass of excavated sediment ($M_{RL, 2014}$ and $M_{RL, 2018}$), following previous analyses (e.g., Guan, 1994; Sanders, 2020). In addition, to examine the effects of inter-annual variability, correlation analyses between C_{2014} and C_{2018} and the mass of sediment excavated per annum (M_A) were investigated to understand if there was an association between crayfish population density and the mass of sediment actively excavated to the channel. Variables were normally distributed (Shapiro-Wilk; $p > 0.1$) and as such Pearson's correlation coefficients (r) were calculated.

To examine if crayfish population variability was important for understanding the observed long-term sediment dynamics, we also investigated the association between change in crayfish population density (C_C , change in CPUE a^{-1}) and change in the reach-normalised mass of excavated sediment (M_C , $t \text{ km}^{-1} \text{ a}^{-1}$):

$$C_C = (C_{2018} - C_{2014}) / 4 \quad (10)$$

$$M_C = (M_{RL, 2018} - M_{RL, 2014}) / 4 \quad (11)$$

where the year subscripts indicate values in that particular year.

All data were analysed in MS Excel and SPSS Statistics Version 28 (IBM, 2021).

3. Results

3.1. Temporal variations in burrow densities and crayfish densities

Burrow density (B_{RL}) and the mass of excavated sediment (M_{RL}) changed through time at each of the ten studied reaches (Fig. 3). In nine reaches, B_{RL} decreased from 2014 to 2018 by an average of 63.0 % (range = 23.3–88.0 %; SD = 20.0 %), but in one reach (Eyebrook 2) an increase of 180.0 % was observed. M_{RL} displayed similar patterns to B_{RL} with a mean reduction of 86.3 % (range = 68.8–95.6 %; SD = 7.7 %) across the nine reaches, whilst an increase of 159.1 % was observed at Eyebrook 2. Excluding the anomalous Eyebrook 2 data, this equated to a mean annual reduction across all reaches of 15.8 % in B_{RL} (range = 22.0 % to 5.8 % reduction; outlier = 45.0 % increase; SD = 5.0 %) and 21.6 % in M_{RL} (range = 23.9 % to 17.2 % reduction; outlier = 39.8 % increase; SD = 1.9 %). Despite reductions in B_{RL} and M_{RL} at nine of the ten studied reaches across the full study period, this trend was not linear with increases also observed between some surveys. Crayfish population density was largely consistent across the survey (Fig. 3c), with a mean change of 0.0 CPUE (SD = 0.77).

3.2. Burrow longevity

Burrow half-life varied between reaches and survey periods (Table 1), from 200.8 days at R. Gwash 4 (2014–2017) to 946.2 days at the R. Welland (2017–2018). The mean half-life was 564.4 days for 2014–2017, and 285.2 days for 2017–2018. Considering all 17 surveys, mean burrow half-life was 461.1 days or approximately one year and three months. Over a given year (365 days), using the average half-life value of 461 days, 57.8 % of burrows present one year previously will persist ($A_{(t)}$), and 42.2 % of burrows will have been eroded. Thus, in a stable system, where the same number of burrows are required to be present in subsequent years, an estimated 42 % of observed burrows are likely to have been constructed within the previous year.

3.3. Temporal crayfish burrow sediment recruitment into river systems

Mean newly excavated sediment M_A ($t \text{ km}^{-1} \text{ a}^{-1}$) across all ten reaches over the full study period (2014–2018) was $0.25 t \text{ km}^{-1} \text{ a}^{-1}$, ranging between $0.14 t \text{ km}^{-1} \text{ a}^{-1}$ at R. Gwash 2 to $0.44 t \text{ km}^{-1} \text{ a}^{-1}$ at Gaddesby Brook 1 (Table II). As a proportion of total cumulative sediment delivery ($\%M_A$) the overall mean was 16.6 % and ranged from 5.3 % at R. Gwash 2 to 85.7 % at R. Gwash 1 (Table II).

In a steady-state equilibrium, where the same density of crayfish burrows is required every year, a mean of $1.0 t \text{ km}^{-1} \text{ a}^{-1}$ of sediment ($+/- 1.3 t \text{ km}^{-1} \text{ a}^{-1}$), up to a maximum of $4.2 t \text{ km}^{-1} \text{ a}^{-1}$ at the River Gwash 4 was estimated to be annually excavated by signal crayfish burrowing (Table III).

3.4. Association between changing burrow densities and crayfish populations

Crayfish population density in 2014 (C_{2014}) was strongly positively correlated with the total mass of excavated sediment recorded from all burrows ($M_{RL, 2014}$; $r = 0.727$, $p = 0.017$; Fig. 4a), but C_{2018} was not correlated with $M_{RL, 2018}$ ($r = 0.456$, $p = 0.254$; Fig. 4b). Changes to the mass of sediment excavated by burrowing over the full study period (M_C) were not significantly correlated with changes in crayfish population density (C_C ; $r = -0.563$, $p = 0.147$; Fig. 4c) or with historical

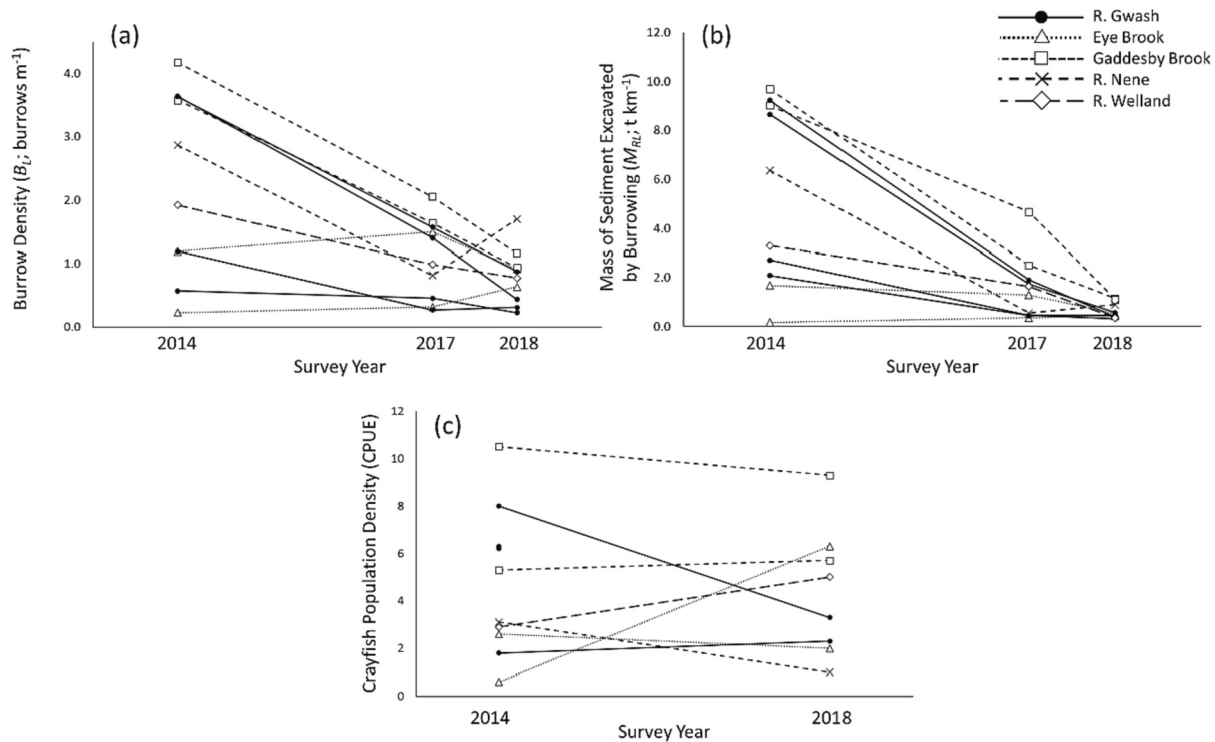


Fig. 3. Change in (a) crayfish burrow density (B_L ; burrows m^{-1}) and (b) mass of sediment excavated by crayfish burrowing (M_{RL} ; $t km^{-1}$) at the ten surveyed reaches. Multiple lines represent different study reaches on the same river.

Table I

Calculated half-lives of crayfish burrows at the ten reaches for the two study periods. Means were weighted 75:25 to 2014–2017 to reflect the length of study. Starred outliers (*; defined as values $>1.5 *$ interquartile range above the 3rd quartile or below the 1st quartile) were excluded from mean calculations.

| | Calculated half-life (d) | | | Proportion of burrows remaining after one year ($A_{(t)}$) |
|------------------|--------------------------|-----------|--------|--|
| | | | Mean | |
| | 2014–2017 | 2017–2018 | | |
| Eyebrook 1 | 840.3 | 355.9 | 719.2 | 70.3 |
| Eyebrook 2 | 3578.4* | 268.3 | 268.3* | 39.0 |
| Gaddesby Brook 1 | 585.0 | 225.4 | 495.1 | 60.0 |
| Gaddesby Brook 2 | 527.7 | 284.0 | 466.8 | 58.2 |
| R. Gwash 1 | 256.1 | 342.7 | 277.8 | 40.2 |
| R. Gwash 2 | 471.9 | 760.9* | 471.9 | 58.5 |
| R. Gwash 3 | 514.3 | 327.3 | 467.6 | 58.2 |
| R. Gwash 4 | 491.8 | 200.8 | 419.0 | 54.7 |
| R. Nene | 446.2 | 1020.3* | 446.2 | 56.7 |
| R. Welland | 946.2 | 277.1 | 778.9* | 72.3 |
| Mean | 564.4 | 285.2 | 461.1 | 57.8 |

invasion dates ($r = 0.594$, $p = 0.070$; Fig. 4d). However, both 2014 and 2018 crayfish population densities (C_{2014} and C_{2018}) were strongly positively correlated with the mean mass of new sediment annually excavated across the full study period (M_A ; $r = 0.685$, $p = 0.029$; $r = 0.846$, $p = 0.008$; Fig. 4e and f).

4. Discussion

Previous studies investigating the zoogeomorphic potential of crayfish burrows have done so at a single point in time, but this study demonstrates the importance of considering the temporal dynamics of crayfish burrows to enable accurate estimations of biotically eroded material. Crayfish burrow densities (B_{RL}) and the mass of sediment

Table II

Sediment recruited directly through crayfish burrowing per year and the proportion of total cumulative sediment delivery accounted for by the annual amount. Starred (*) values are considered to be outliers and were excluded from mean calculations.

| | Mass of sediment recruited from burrows per year | | | | | |
|------------------|--|-------------------|--------------------------|-------------------|--------------------------|-------------------|
| | 2014–2017 | | 2017–2018 | | Weighted mean | |
| | MA (t $km^{-1} a^{-1}$) | %MA (% a^{-1}) | MA (t $km^{-1} a^{-1}$) | %MA (% a^{-1}) | MA (t $km^{-1} a^{-1}$) | %MA (% a^{-1}) |
| Eyebrook 1 | 0.28 | 16.9 | 0.17 | 13.2 | 0.25 | 15.9 |
| Eyebrook 2 | 0.07 | 37.7* | 0.30 | 85.7 | 0.12 | 85.7* |
| Gaddesby Brook 1 | 1.07* | 11.9 | 0.44 | 9.4 | 0.91* | 11.3 |
| Gaddesby Brook 2 | 0.38 | 3.9 | 0.47 | 18.8 | 0.40 | 7.6 |
| R. Gwash 1 | 0.14 | 6.7 | 0.17 | 37.6 | 0.15 | 14.4 |
| R. Gwash 2 | 0.03 | 1.1 | 0.26 | 57.6 | 0.09 | 15.2 |
| R. Gwash 3 | 0.27 | 3.2 | 0.16 | 9.0 | 0.24 | 4.6 |
| R. Gwash 4 | 0.39 | 4.2 | 0.17 | 8.8 | 0.33 | 5.4 |
| R. Nene | 0.07 | 1.1 | 0.46 | 84.0 | 0.17 | 21.9 |
| R. Welland | 0.24 | 7.3 | 0.05 | 3.2 | 0.19 | 6.3 |
| Mean | 0.21 | 6.3 | 0.26 | 32.7 | 0.22 | 11.4 |

excavated (M_{RL}) were not consistent through time, with temporal variation at each reach studied. In 90 % of the studied reaches, there was a general decline in the numbers of burrows recorded over time. The reasons for this are unknown and the finding unexpected, given the stable population densities observed across the study, and the lack of correlation between changes in crayfish population densities and burrow densities. One hypothesis for this could be the reoccupation of burrows. Signal crayfish may display an increased propensity to burrow early in an invasion cycle as the population expands, followed by a reduced propensity following population stabilisation (Sanders et al., 2023). Burrowing is an energy expensive process (Meysman et al., 2006), and thus burrows are often readily reoccupied and reused by

Table III

Estimated sediment recruited directly through crayfish burrowing per year in a steady-state equilibrium via application of calculated half-lives and burrow decay rates for each studied river.

| | Mass of sediment estimated to be recruited from burrows per year in a steady-state equilibrium ($\text{t km}^{-1} \text{a}^{-1}$) | | |
|------------------|---|------|------|
| | 2014 | 2017 | 2018 |
| Eyebrook 1 | 0.50 | 0.38 | 0.16 |
| Eyebrook 2 | 0.11 | 0.22 | 0.27 |
| Gaddesby Brook 1 | 3.61 | 1.87 | 0.44 |
| Gaddesby Brook 2 | 4.06 | 1.04 | 0.48 |
| R. Gwash 1 | 1.25 | 0.27 | 0.19 |
| R. Gwash 2 | 1.12 | 0.19 | 0.19 |
| R. Gwash 3 | 3.62 | 0.72 | 0.24 |
| R. Gwash 4 | 4.18 | 0.86 | 0.18 |
| R. Nene | 2.75 | 0.24 | 0.39 |
| R. Welland | 0.91 | 0.45 | 0.10 |

organisms across the animal kingdom (e.g., burrowing owls (*Athene cunicularia*), Holmes et al., 2003; European bee-eater (*Merops apiaster*), Brust et al., 2015; European badger (*Meles meles*), Fischer and Dunand, 2016), including crayfish (virile crayfish (*Faxonius virilis*), Bovbjerg, 1953). It may be that following high initial crayfish burrowing activity an increased proportion of burrows are reused, rather than new burrows being constructed. Despite a reduction in active burrow construction rate, the collapse and reconstruction of burrows actively supplies sediment to the river, and so the negative trend represents a reduction in new sediment supplied to the channel. Should crayfish populations reach stable lower densities, this would still equate to a surplus of floodplain sediment supplied to the river than would otherwise be supplied by hydraulic erosion in the absence of crayfish burrowing activity.

There is also likely to be some variability in the temporal longevity of burrows following construction associated with context specificity. For example, should crayfish abundances decline, burrows may erode quickly in some rivers, whereas they may persist for multiple years in others dependent on the discharge regime and bank properties. Indeed, the mass of sediment recruitment per annum (M_A) was significantly associated with contemporary crayfish population densities (C_{2018}), demonstrating an important association between crayfish and burrow densities not previously observed.

Previous studies have employed historical records of crayfish presence (Faller et al., 2016) and trapping from a single point in time (Sanders, 2020) to understand the drivers of crayfish burrow presence. This research however reveals that repeated burrow surveys, that enable the calculation of annual amounts of sediment excavated, are required to develop a greater understanding of the ecological drivers of burrowing and its implications for instream sediment delivery. In particular, this research has highlighted why previous studies may not have recorded (Guan, 1994) or observed a weak (Sanders, 2020) association between crayfish population densities and burrow densities. Both crayfish population densities and burrow densities were unstable over time, and so the strength of associations observed would be reduced by the legacy of prior burrows excavated by historic crayfish populations. Indeed, whilst crayfish population densities and the total mass of excavated sediment in 2014 were significantly associated, this association was not observed in 2018. Therefore, repeated monitoring of organisms and their geomorphological implications are required to fully understand the strength of their effects on the ecosystems, particularly where populations vary temporally, and especially those experiencing boom and bust dynamics following invasion (e.g., Strayer and Malcom, 2006; Matthews and Marsh-Matthews, 2011).

Despite the reduction in burrow density over time, a substantial quantity of sediment was still actively supplied to the river channels, with a mean of $0.27 \text{ t km}^{-1} \text{a}^{-1}$ recorded across all reaches during the full study period, with a maximum of $>0.5 \text{ t km}^{-1} \text{a}^{-1}$ recorded at

Gaddesby Brook 2. There were also extreme values of $>1 \text{ t km}^{-1} \text{a}^{-1}$ recorded at Gaddesby Brook 1. This indicates that crayfish burrows directly recruit substantially more sediment to river systems than previously recognised. The application of burrow half-life values to estimate annual sediment yields indicated values an order of magnitude greater than measured, with a mean of $1.0 \text{ t km}^{-1} \text{a}^{-1}$ of sediment estimated to be annually excavated across colonised reaches in a stable scenario. Calculations using data from the 2014 burrow surveys estimated a mean of $2.0 \text{ t km}^{-1} \text{a}^{-1}$ of sediment across all the studied reaches, which is eight times more than Rice et al. (2016)'s estimates of 0.25 to $0.5 \text{ t km}^{-1} \text{a}^{-1}$, based on 2014 measurements for these same reaches. Further, the calculations presented here are likely to produce conservative estimates for two reasons. First, some burrows will have been constructed and completely removed by erosion between survey periods. Second, whilst the results presented in this study quantify rates of burrow construction per year, there is likely to be a high variability of burrow construction within the year. Crayfish activity is greatest during the summer months (Bubb et al., 2004; Johnson et al., 2014), meaning that sediment inputs caused by crayfish burrowing are likely to be greater during the summer months, resulting in higher short-term rates than the annual rates given here.

Understanding the rates of animal burrow erosion has a broader importance and application beyond crayfish burrowing and freshwater environments. Whilst much biogeomorphological research has been conducted into an array of burrowing species, particularly mammals (e.g., see Haussmann, 2017; Coggan et al., 2018; Mallen-Cooper et al., 2019), freshwater and marine crustaceans (e.g., see Schlacher et al., 2016; Mason and Sanders, 2021), and invasive species more broadly (Harvey et al., 2019), studies have typically only observed burrows at one snapshot in time, with very few studies examining inter-annual variability of burrows, or quantifying burrow longevity. Coombes and Viles (2015) observed that population fluctuations in European badgers (*Meles meles*) in a UK woodland was significantly associated with changing rates of soil excavation via sett construction ($n = 64$) across a 17-year period, indicating that burrow construction rates are related to active population densities. However, understanding the rate of burrow loss alongside burrow construction is needed to fully evaluate the mass of sediment mobilised by animals. A small number of studies have examined burrow longevity; Holmes et al. (2003) observed 17 % of 99 burrowing owl (*Athene cunicularia*) burrows in Oregon to be eroded over a three-year period; Sharp et al. (2010) observed 69 % and 81 % of 120 spider burrows in grazing areas in South Australia to be closed over a one-year period; Gunzburger and Guyer (1998) monitored 25 Red Hills salamander (*Phaeognathus hubrichti*) burrows in Alabama for 18 months, and modelled burrow half-life to be 120 days; and Barbaresi et al. (2004) observed that 73 % of 100 red swamp crayfish (*Procambarus clarkii*) burrows collapsed within seven days in rice paddies on the Iberian peninsula. This study substantially extends understanding of burrow longevity by examining interannual and between-site variability. Such methods should be applied to other species and sites in the future to better increase our understanding of animal burrow longevity, and their full contribution to sediment budgets.

The results of this study also have important implications for the management of freshwater streams. Fine sediment pollution is an important stressor in many lowland streams resulting in reductions in biodiversity and impairment of ecosystem functioning (Wood and Armitage, 1997; Jones et al., 2012; Kemp et al., 2011). Current management policies aimed at reducing excessive fine sediment supply typically target floodplain management and agricultural runoff (Pulley and Collins, 2019; Davey et al., 2020; Pulley and Collins, 2021). However, our study and others (Cooper et al., 2016; Rice et al., 2016; Sanders et al., 2021; Mathers et al., 2022) demonstrate the potentially important and currently overlooked contribution of biotic sediment delivery with estimations of $2.0 \text{ t km}^{-1} \text{a}^{-1}$ (sediment supplied into the channel directly from burrowing; this study), 0.21 to $0.66 \text{ t km}^{-1} \text{a}^{-1}$ (contribution to suspended sediment load; Rice et al., 2016), and 25.4 t km^{-1}

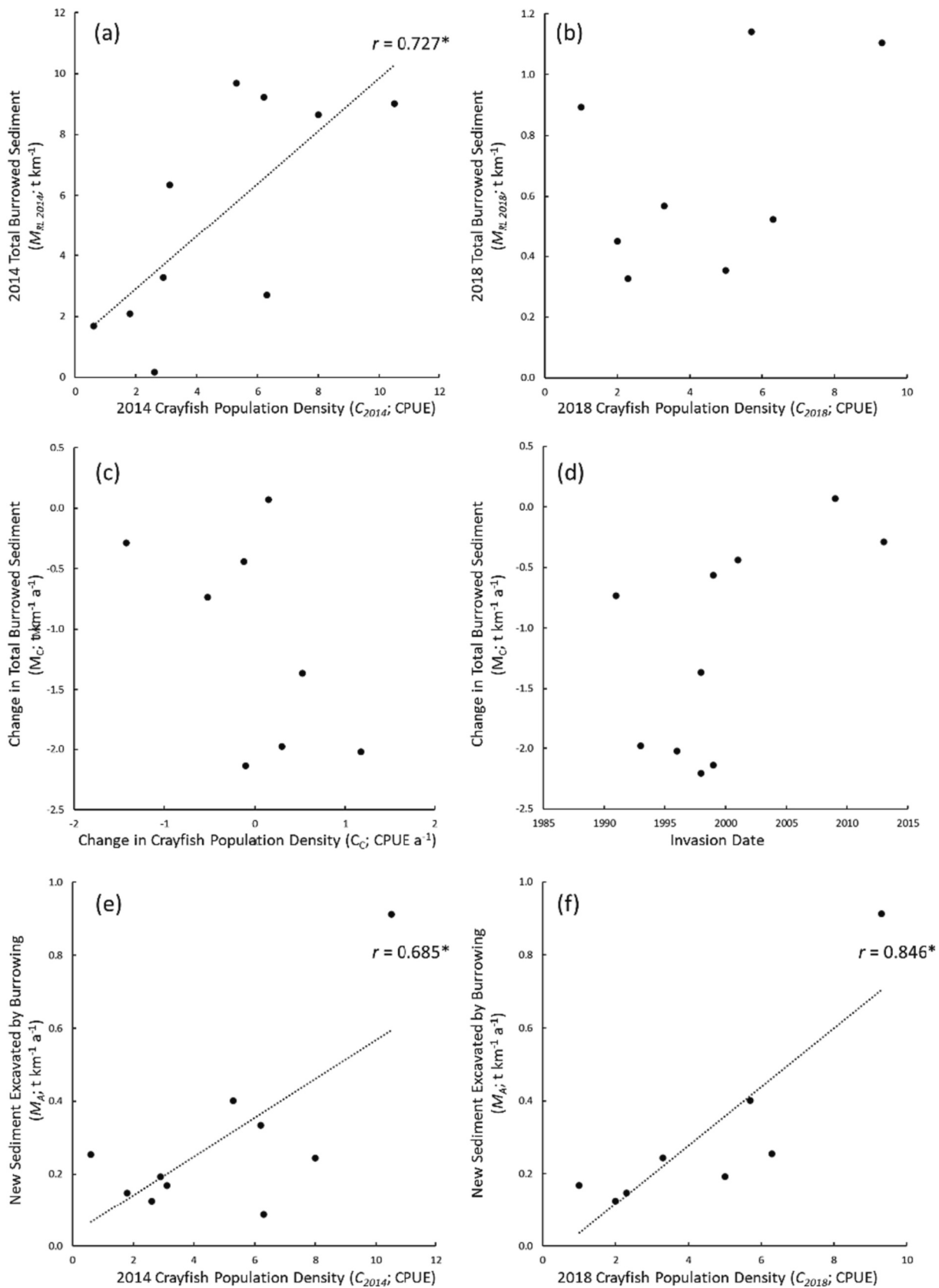


Fig. 4. Scatter plots between excavated sediment from crayfish burrows and crayfish population density (CPUE) considering (a) the mass of sediment measured as excavated in 2014 and crayfish population density in 2014, (b) the mass of sediment measured as excavated in 2018 and crayfish population density in 2018; (c) change in total burrowed sediment and change in crayfish population density, (d) change in total burrowed sediment and crayfish invasion date; (e) the mean mass of new sediment excavated by burrowing per year across the full study period and crayfish population density in 2014, and (f) the mean mass of new sediment excavated by burrowing per year across the full study period and crayfish population density in 2018. Significant correlations are indicated by asterisks ($p < 0.05$).

a^{-1} (accelerated bank retreat; Sanders et al., 2021) per annum. While some sediment transport and stream evolution models (e.g., Castro and Thorne, 2019; Wilkes et al., 2019) are beginning to conceptually incorporate biotic energy, this component is still largely disregarded in existing models (Rice et al., 2019). Not considering biotic energy in fine sediment management plans and sediment budgets risks missing an important component of fine sediment delivery (Sanders et al., 2021; Mathers et al., 2022). This is particularly pertinent to small lowland streams, where the physical energy required to erode cohesive bank material and transport excess in-channel fine sediment is infrequently reached (Naden et al., 2016; Mason and Sanders, 2021). Therefore, we call for further repeated monitoring of burrow dynamics to fully quantify interannual, between-site, and between-species variability such that the biotic contributions can be fully understood and incorporated into fine sediment management policies, and sediment transport and stream evolution models.

5. Conclusion

Animals can be important drivers of sediment dynamics, but understanding of zoogeomorphic impacts, especially their longer-term, spatially distributed effects has been constrained by a focus on short-term, local measurements and experiments. Long-term monitoring of 1861 signal crayfish burrows revealed that crayfish burrowing can supply up to eight times more sediment to river channels than previously recognised, and crayfish densities were a strong driver of contemporary sediment supply in the reaches we studied. Signal crayfish burrows lasted, on average, for 15 months before being lost to erosion, with 58 % of burrows persisting beyond the year in which they were constructed. Understanding the temporal dynamics and longevity of zoogeomorphic features like burrows is vital for understanding the importance of biological energy expenditure in modifying contemporary landscapes and sediment fluxes, and more broadly, for understanding the importance of the geomorphic activity of animals in long-term landscape evolution.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available from the lead author upon reasonable request.

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