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Progress in Physical Geography
35(4) 517–533

DOI: 10.1177/0309133311409092
ppg.sagepub.com

Evaluating the role of invasive aquatic species as drivers of fine sediment-related river management problems: The case of the signal crayfish (*Pacifastacus leniusculus*)

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Abstract

Sediment quantity and quality are key considerations in the sustainable management of fluvial systems. Increasing attention is being paid to the role of aquatic biota as geomorphic agents, capable of altering the composition, mobilization and transport of fluvial sediments at various spatiotemporal scales. In this paper invasive species are presented as a special case since: (1) populations may not be constrained by factors characteristic of their native habitats; and (2) they represent a *disturbance* to which the system may not be resilient. Discussion is centred on the signal crayfish which has rapidly colonized catchments in Europe

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and Japan, but the hypotheses and models presented provide a framework applicable to other invasive species. This paper explores the mechanisms by which signal crayfish may influence sediment dynamics from the patch scale to the catchment scale. There is potential for signal crayfish to impact significantly on river sediments and morphology as a function of their interactions with river bed and bank material, and with other aquatic organisms, combined with their large body size and aggressive nature, their presence in very high densities, and the lack of effective mitigation strategies. Potential catchment-scale management issues arising from these factors include habitat degradation, mobilization of sediment-associated nutrients and contaminants, and sediment-related flood risks. Further interdisciplinary research is required at the interface between freshwater ecology, fluvial geomorphology and hydraulics, in order to quantify the significance and extent of these impacts. The paper points to the key research agendas that may now emerge.

Keywords
biogeomorphology, ecosystem engineer, habitat quality, invasive species, river management, sediment dynamics, signal crayfish

I Introduction

Increasing attention has been paid in recent years to the sustainable management of catchment sediment systems, including the quality as well as the quantity of sediment stored and transferred (Owens, 2008). In particular, it is increasingly acknowledged that changes to sediment delivery and dynamics can represent a significant management problem (Owens et al., 2005; Thorne et al., 2010; Walling and Collins, 2008). For instance, increased suspended sediment loads can affect water temperature and light penetration through the water column (Bilotta et al., 2007; Owens et al., 2005), clog aquatic vegetation (Wood and Armitage, 1997, 1999), affect the health and reproductive capabilities of fish and invertebrates (Newcombe and MacDonald, 1991; Petticrew and Rex, 2006), and play an important role as carriers in the transfer of nutrients (e.g. phosphorus) and contaminants (e.g. pathogens, metals, radionuclides, pesticides) that can reduce water quality (Förstner, 1987; Heathwaite and Dils, 2000; Heathwaite et al., 2005; Kretzschmar et al., 1999; Kronvang, 1990). Furthermore, elevated rates of sediment delivery to sensitive reaches can reduce the conveyance capacity of river channels through aggradation, thus increasing flood risk and restricting navigation (Lane et al., 2007; Stover and Montgomery, 2001; Verstraeten and Poesen, 2000) as well as posing a risk to public water supply (Butcher et al., 1993), and smothering aquatic habitats such as gravel beds that are used by fish for spawning (Newcombe and Jenson, 1996; Ryan, 1991; Soulsby et al., 2001).

While the importance of sediment dynamics and sediment management has received increasing recognition, the complexity of the catchment sediment system continues to present difficulties for the accurate representation of key processes (Trimble, 1983; Walling, 1983). Furthermore, future management of catchment sediment dynamics must address a combination of climate-induced changes in sediment delivery (Evans et al., 2004a, 2004b; Lane and Thorne, 2007) and, in Europe, an evolving legislative framework which requires the reconciliation of flood risk management goals with improvements to the ecological status of water bodies (e.g. European Parliament and the Council of the European Union, 2000, 2007). Further research is therefore required across a range of scales from the sediment patch to whole-system modelling (Naden, 2010), with emphasis placed on the reciprocal interactions between the biotic and abiotic components of the fluvial environment (Corenblit et al., 2007, 2008; Moore, 2006).

A key current research focus is the concept of aquatic organisms as ‘geomorphic agents’ or ‘ecosystem engineers’ capable of modifying the surrounding physical environment and the availability of resources for other organisms (Corenblit et al., 2007; Newton, 2010; Statzner et al., 2003). This builds on a long history of interest in the interactions between organisms and geomorphological processes (e.g. Darwin, 1881), underpinned by newer frameworks including ecosystem engineering (Jones et al., 1994), biogeomorphology (Viles, 1988) and zoogeomorphology, which focuses specifically on the impact of animals on geomorphic processes (Butler, 1995). For instance, both living and dead aquatic and riparian vegetation has been shown to be an important control on river hydraulics, morphology and habitats from local-scale modification of velocity patterns and sediment deposition (Gurnell et al., 2006) to larger-scale influences on the structure and connectivity of landform elements such as depositional barforms and floodplain surfaces (Bertoldi et al., 2009). A vast literature describes the influence of a range of lotic organisms, including bacteria, algae, aquatic invertebrates, fish and mammals, on the composition, mobilization and transport of fluvial sediments through feeding, movement, habitat construction and interactions with other aquatic biota. Such influences include organic matter processing and biodeposition of faeces (Vaughn and Hakenkamp, 2001; Wharton et al., 2006); removal of sediments from benthic substrata (Flecker, 1996; Pringle et al., 1993; Zanetell and Peckarsky, 1996); reworking of sediments at the water-sediment interface through bioturbation (Mermillod-Blondin and Rosenberg, 2006; Nogoro et al., 2006); alterations to bed topography, fabric arrangement, and entrainment thresholds (Field-Dodgson, 1987; Gottesfeld et al., 2008; Johnson et al., 2009, 2010; Statzner et al., 2003); bank erosion (Holdich et al., 1999; Meentemeyer et al., 1998); and alterations to hydraulics and sediment transport associated with habitat construction (Gurnell, 1998). Influences may also be indirect, or joint, associated with biotic interactions among aquatic organisms (Beschta and Ripple, 2006, 2008; Naiman et al., 2000; Statzner and Sagnes, 2008). Perhaps the best studied example of animals effecting riverine processes are salmonid fish that modify substrate characteristics when spawning by constructing redds resulting in the loosening of the bed, the winnowing of fine sediment and alterations to surface topography and near-bed hydraulics (Hassan et al., 2008; Montgomery et al., 1996). Rice et al. (forthcoming) review the impact of salmonids, other fish and invertebrates on coarse bed material engineering and its implications for gravel transport in rivers.

In considering the influence of aquatic organisms as geomorphic agents, invasive species may represent a special case, since they have often been released from the suite of factors that would limit their vigour and abundance in their native habitats (Wolff, 2002) and, hence, may be present in very high densities. Furthermore, the presence of an invasive species represents a *disturbance* to the natural functioning of the system to which they have been translocated, with the implication that there may be reduced system resilience to their impacts (Vitousek, 1990). Examples of invasive species that have also been identified as having the potential to alter freshwater environments include zebra mussels (*Dreissena polymorpha*) and some other crayfish species (i.e. *Orconectes* sp.) which have been introduced to Europe, and species of salmon (*Salmo* sp.) introduced to New Zealand. This paper hypothesizes that, as a consequence of these extraordinary characteristics, invasive species can have a disproportionately large influence on fluvial sediment dynamics and may, therefore, lead to a series of sediment-related management issues in impacted river systems. This is one arena, of many in river science, where there is substantial potential for fruitful interdisciplinary progress at the interface of geomorphology, ecology and hydrology (Palmer and Bernhardt, 2006; Rice et al., 2010; Vaughan et al., 2009).

The following discussion is centred around the potential impacts of signal crayfish (*Pacifastacus leniusculus*, Dana) on fluvial sediment dynamics, with emphasis on the supply and routing of fine, suspendable materials, outlining the ways in which their impact as a geomorphic agent at local scales within river systems may create sediment-related management problems at the catchment scale. The paper does not consider coarse sediment, surface engineering by organisms except as a potential mechanism that affects the availability of fine sediments stored within the subsurface matrix. While the discussion relates primarily to the regions in which the signal crayfish represents an invasive species and a potentially significant management problem at present, the hypotheses and models provide a framework which may be transferable to the consideration of altered sediment dynamics and sediment-related management problems associated with other invasive species.

II The signal crayfish

Signal crayfish exhibit several physical and behavioural characteristics which are of significance when examining impacts on the physical environment: an ability to persist in a range of river types; an ability to travel large distances and rapidly colonize river catchments; the potential for severe impacts on other aquatic organisms; and their large body size and aggressive nature. This section, therefore, describes the spread of the signal crayfish as an invasive species and identifies some of the biological characteristics that enhance its potential as a driver of sediment-related management problems in river catchments.

The signal crayfish is endemic to western North America, but has been introduced into Japan and over 20 countries in Europe since the 1960s (Lewis, 2002; Light, 2003). Signal crayfish were introduced to Britain in 1976 and had colonized more than 250 British waters by 1988 (Lowery and Holdich, 1988). They frequently carry crayfish plague (*Aphanomyces astaci*), a fungal infection to which they are highly resistant (Alderman et al., 1990) but which is lethal for many native European species, such as the British white-clawed crayfish (*Austropotamobius pallipes*). The British population of white-clawed crayfish has been devastated by the arrival of signal crayfish, mainly due to the effects of crayfish plague (Holdich and Rogers, 1997; Lozan, 2000). In the absence of crayfish plague, the displacement of white-clawed crayfish takes place over several years (Bubb et al., 2005), probably via aggressive interspecific competition for in-stream refuges from predation, such as large cobbles and boulders (Bubb et al., 2006). No measure for the effective control of signal crayfish has yet been discovered (Peay, 2001) and signal crayfish can be present in extremely high densities: measurements in US and British habitats range from 0.9 to 20 individuals per square metre (Abrahamsson and Goldman, 1970; Bubb et al., 2004; Goldman and Rundquist, 1977) and, where present, they typically dominate the invertebrate biomass (Momot, 1995). Invasive crayfish have great potential to disrupt the freshwater ecosystems into which they are translocated, by negatively affecting both freshwater biological communities (Gherardi et al., 2001) and the physical environment (Horwitz, 1990).

Most crayfish species, including signal crayfish, are highly mobile and capable of substantial active movements against flowing water (Bubb et al., 2004). In a radio-tracking study of signal crayfish on the UK River Wharfe, Bubb et al. (2004) found that crayfish would usually remain in the same location for days to weeks, followed by movement to a new location associated with a refuge. In that study, the median distance moved (per two days) in an upstream direction was 7.5 m and 7.0 m in a downstream direction (range 0–790 m). In the River Bain, Lincolnshire, radio-tagged signal crayfish were found to remain in a 20 m reach for an average of 11 days, after which they made a long distance movement out of the reach (Johnson, 2010). Within this short river reach, crayfish were highly active, and particularly concentrated along the inner bank of a meander bend where flow velocities were low and macrophyte stands provided cover. Crayfish did not remain in open areas of the channel for extended periods but did make regular nocturnal movements across the channel between banks (Johnson, 2010). Most species of crayfish are nocturnal (Gherardi et al., 2001; Hill and Lodge, 1994; Lozan, 2000), spending daylight hours in refuges from predation such as in burrows or beneath cobbles (Hill and Lodge, 1994). Signal crayfish feed mainly between dusk and dawn (Flint, 1977; Guan and Wiles, 1998), with the length of activity periods directly related to the duration of darkness over 24 hours (Flint, 1977). Styrishave et al. (2007) established that heart rate, locomotor activity and oxygen consumption of signal crayfish increased at night but remained relatively high during daylight hours, compared to those of a more strictly nocturnal species, *Astacus astacus*. Similarly Lozan (2000) demonstrated that the mean length of activity for signal crayfish per 12-hour period was 187 minutes (± 12 minutes) during the night and 98 minutes (± 8 minutes) during the day, indicating that the movements of signal crayfish are primarily, but not exclusively, nocturnal, whereas other species (e.g. *A. astacus*) are exclusively nocturnal. Crayfish activity is highly affected by water temperature: Lozan (2000) showed that the activity of four species of crayfish (including signal crayfish; measured in minutes per day), was highest at 20°C. At 4°C, while all four species were still active, their activity levels were up to 80% lower than at the peak. This is corroborated by signal crayfish activity in the River Bain, which was found to be highest in summer months (temperature 12–18°C) and steadily declined with water temperature and increasing flow stage (Johnson, 2010). Therefore, seasonality in temperate habitats will affect crayfish activity through a combination of affecting night length and water temperature, although the effects of temperature are likely to be more profound than those of day length on signal crayfish.

III Impacts of the signal crayfish on sediment dynamics

Research to date on the impacts of signal crayfish on sediment dynamics has primarily been developed on experimental streams (e.g. Parkyn et al., 1997; Statzner et al., 2000, 2003) and for gravel-bed streams, often in upland environments (e.g. Creed and Reed, 2004). In contrast, there is a dearth of studies within lowland, low-energy systems, despite a potential for significant impacts on sediment dynamics in intermediate-zone reaches where sediments are fine-grained and, hence, potentially more readily mobilized and transported, and where agricultural and industrial contaminants may be bound to sediment particles. Nevertheless, a substantial body of literature suggests that crayfish activities can have negative impacts on the physical environment of river systems (Horwitz, 1990) and hence have the potential to influence sediment dynamics throughout catchments. This evidence base has been used to develop a conceptual model of the impacts of signal crayfish on fluvial sediment dynamics from the micro scale to the catchment scale (Figure 1). The following two sections, supported by Figure 1, examine the two main ways in which signal crayfish may modify sediment dynamics at local scales in river systems: (1) via feeding activities; and (2) via non-feeding activities such as burrowing, walking or fighting.

1 Feeding activities

Crayfish are benthic omnivorous and detritivorous feeders, feeding on a variety of items including amphibian eggs and larvae (Axelsson et al., 1997; Gamradt and Kats, 1996), macroinvertebrates (Guan and Wiles, 1998; Hanson et al., 1990; McCarthy et al., 2006), algae (Creed, 1994; Hanson et al., 1990), macrophytes

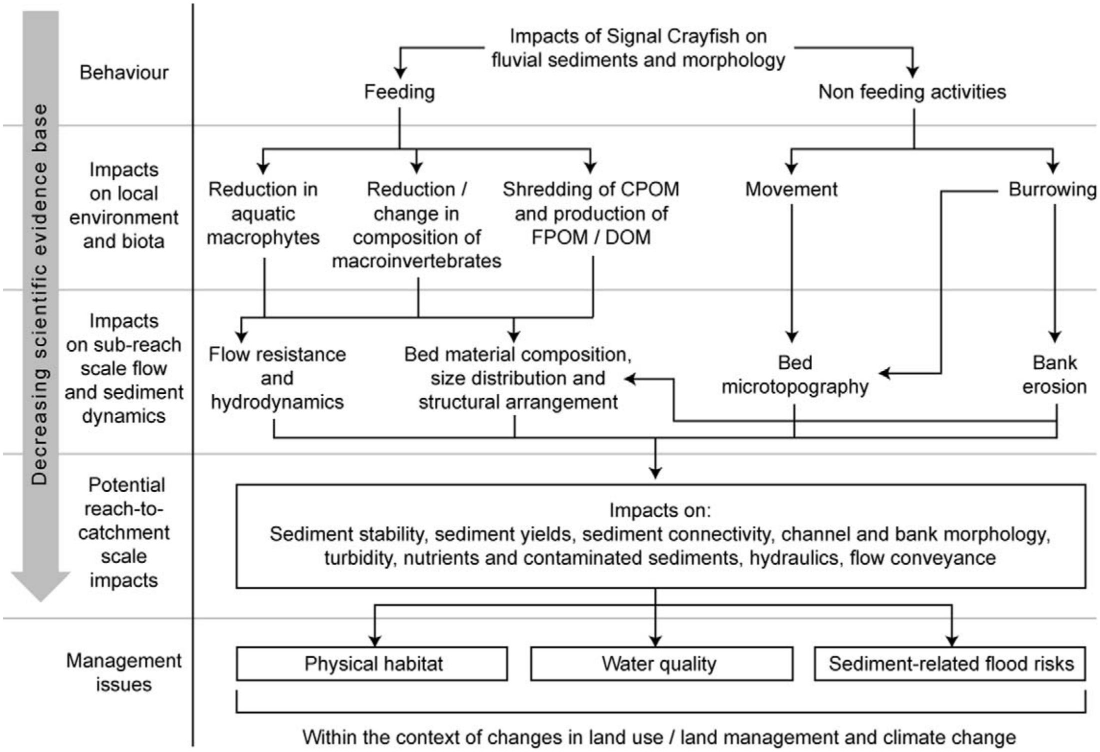

Figure 1. Conceptual model of the impacts of crayfish on the physical structure of river systems from the micro scale to the catchment scale. See text for detailed explanation of linkages.

(Lodge et al., 1994; Nyström and Strand, 1996), fish and their eggs and larvae (Guan and Wiles, 1998, 1999) and dead leaves (Usio, 2000). High densities of invasive crayfish may, therefore, lead to severe negative impacts on a range of native flora and fauna (Holdich et al., 1999). Fish species may be affected by direct predation (as above), but also through competition for food and shelter (especially benthic fish such as bullhead, *Cottis gobio* and stone loach, *Noemacheilus barbatulus*; Guan and Wiles, 1997) and by destroying breeding sites through, for example, macrophyte reduction (Guan and Wiles, 1998). High crayfish densities also typically cause a shift in macroinvertebrate composition towards relatively fast-moving and sediment-burrowing taxa (Crawford et al., 2006; Hanson et al., 1990; Lodge et al., 1994).

Stream invertebrates play a key role in the breakdown of leaf material in streams (Webster and Benfield, 1982) and, in both laboratory studies and stream manipulations, shredding invertebrates have been shown to increase the conversion of coarse particulate organic matter (CPOM, particles typically >1 mm in diameter; Wallace and Webster, 1996) to fine particulate organic matter (FPOM, particles typically 0.45 μm to 1 mm in diameter; Cuffney et al., 1990) and dissolved organic matter (see review in Wallace and Webster, 1996). Through their feeding activities, crayfish directly and indirectly influence rates of CPOM conversion (Momot, 1995; Parkyn et al., 1997; Schofield et al., 2001; Usio et al., 2006). Their direct role in breaking down CPOM can be substantial: in a headwater stream in New Zealand, Usio and Townsend (2004) found that crayfish dominated the shredder functional feeding group, comprising an average of 99% of the total biomass of shredder invertebrates. Crayfish also have indirect effects on FPOM production through their various functional ecosystem roles (Creed, 1994; Feminella and Resh, 1989; Weber and Lodge, 1990; Usio and Townsend, 2004), not least their potential influence on the abundance of other organisms and especially macroinvertebrate shredders (Usio, 2000). Crayfish impacts on CPOM:FPOM ratios are not, therefore, straightforward but, by affecting organic particle size distributions, crayfish are expected to influence organic particulate resuspension rates, downstream transport of FPOM and the fine organic component of the bed sediment composition.

An additional indirect impact on the instream environment associated with feeding activities is the destruction of aquatic macrophytes, which also are a food source for signal crayfish (Flint and Goldman, 1975; Guan and Wiles, 1998). Flint and Goldman (1975), working on signal crayfish, demonstrated that the standing crop of *Myriophyllum* sp. increased in experimental cages containing no, or low, crayfish biomass (0.17 g m^{-1}), but decreased in response to crayfish biomasses of greater than 69 g m^{-1} to a maximum decrease of 1.9 g m^{-1} per day in high crayfish biomass treatments (200 g m^{-1}). Similarly, Chambers et al. (1990), working on the crayfish *Orconectes virilis*, demonstrated that crayfish biomasses of 5–10 g m^{-1} decreased biomass of three species of aquatic macrophyte by approximately 50%. Aquatic macrophytes are a key roughness element in lowland rivers (Haslam, 1978; Petryk and Bosmajian, 1975) and have been shown to influence flow velocity behaviour at both the reach and channel cross-section scales, localized patterns of fine sediment deposition, bank erosion and aggradation (Cotton et al., 2006; Gregg and Rose, 1982; Gurnell et al., 2006; Naden et al., 2006; Wharton et al., 2006). Thus, signal crayfish feeding activities have the potential to alter local bed material composition and hydraulics by directly modifying CPOM conversion rates, and through impacts on invertebrate and macrophyte communities (Figure 1).

2 Non-feeding activities

Crayfish directly modify river bed and bank sediments through non-feeding activities such as movement and fighting (Parkyn et al., 1997; Statzner et al., 2003; Usio and Townsend, 2004) and by burrowing into the banks (Holdich et al., 1999; Lewis, 2002; Figure 1) and river bed (see below). Signal crayfish dig extensive burrows into soft river banks (up to 10–20 m^{-2}; Figure 2). Bank burrows have been observed to accelerate bank erosion (Guan, 1994; Holdich et al., 1999) and increase the delivery of fine, suspendable sediments to streams (Angeler et al., 2001). While studies seeking causal relationships between crayfish burrowing and bank erosion are few, it can be hypothesized that burrowing activity may contribute to bank erosion in a number of ways. Localized erosion may be associated with the action of tunnelling into the bank and displacing sediment from burrow entrances. Dense networks of burrows may increase the susceptibility of banks to erosion by other agents (fluvial and subaerial) as a result of increasing the area of the bank surface that is subject to erosive forces. Burrowing is also likely to increase the probability of bank collapse via mass failure processes. The exact mechanism of failure is likely to be influenced by the variability of burrow density in the vertical dimension; burrow geometry; and the properties of the bank itself, including sediment calibre and composition, bank angle and riparian vegetation cover (Lawler et al., 1997).

A widely reported impact of mobile crayfish on bed sediment composition is the winnowing, from the substrate, of fine inorganic sediment (Creed and Reed, 2004; Helms and Creed, 2005; Matsuzaki et al., 2009; Parkyn et al., 1997; Usio and Townsend, 2004). Statzner et al. (2000, 2003), working in small artificial channels (0.2 m wide, 1.25 m^2 total area), found that more sediment was eroded from an unstructured, sand-gravel substrate when the crayfish *Orconectes limosus* was present, than from control substrates without crayfish. The critical shear stress for sand-sized particles was reduced by 50–75% in the presence of the animals. In the

Figure 2. Crayfish burrows in the banks of the River Windrush, Oxfordshire, UK

North River, North Carolina, USA, Fortino (2006) noted that crayfish-related winnowing of fine sediment was not observed in winter due to a decline of crayfish activity in cold temperatures. Mobilization of fine inorganic sediment is associated with the movement of legs and contact between the substrate and abdomens of walking crayfish (Usio and Townsend, 2004). Statzner et al. (2000) also suggest that increased mobility of fine sediments may reflect grazing by crayfish of algal cover that might otherwise stabilize fine sediments. The impact of abiotic and biotic variables on substrate reworking by crayfish has also been explored (Statzner and Peltret, 2006; Statzner and Sagnes, 2008). They found that the presence of fish (gudgeon, *Gobio gobio*) and crayfish, both of which have been shown to rework substrates in isolation, did not have an additive effect on substrate disturbance when combined, indicating the potentially complex effects of communities of organisms on sediment reworking.

Statzner et al. (2003) also reported that the presence of the crayfish (*O. limnosus*) altered the topography of the gravel-sand substrates in their small experimental channels. A measured increase in mean bed elevation was interpreted as indicating that gravel consolidation was reduced by crayfish (Statzner et al., 2003). In a series of experiments, Johnson et al. (2010) found that signal crayfish can move gravels up to 38 mm in diameter, with a submerged weight on average six times greater than that of the crayfish used in the experiments. Importantly, signal crayfish altered the grain-to-grain geometry of substrates by brushing past grains when moving around. Analysis of laser-scanned digital elevation models revealed that crayfish movements

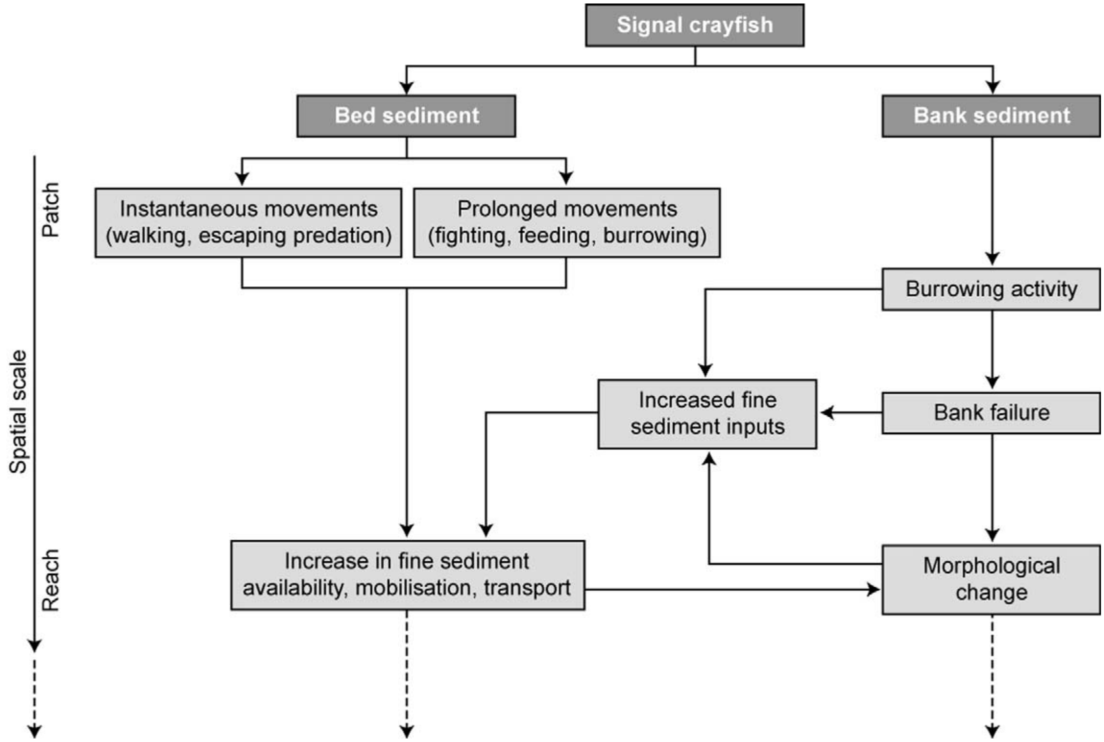

Figure 3. Key processes associated with bed and bank sediment disturbance by signal crayfish, and potential implications for reach-scale morphology and fine sediment dynamics. Dotted lines signify the potential for impacts beyond the reach scale.

disturbed imbricate grain structures that form naturally under low-intensity flows in gravel-bed rivers and which are associated with imparting significant stability to coarse, water-worked substrates (Johnson, 2010). Crayfish also constructed pits and mounds across gravel surfaces that resulted in substantial changes to grain protrusion (Johnson et al., 2010) and near-bed hydraulics. These impacts, coupled with the grain-scale structural changes, were found to reduce significantly the stability of gravel substrates when exposed to high flows: almost double the number of gravel grains were entrained from crayfish-disturbed surfaces than from water-worked control surfaces, unaffected by crayfish (Johnson, 2010).

In addition to their impacts on the composition, structural arrangement and mobility thresholds of river bed materials, crayfish also appear to affect the availability and mobilization of suspended sediments. Figure 3 summarizes the ways in which crayfish disturbance to the bed material and banks, through different activities (such as movement on the river bed and bank burrowing), may influence fine sediment dynamics from the patch to the reach scale. It is possible that crayfish directly accomplish the suspension of sediments when walking or back-swimming across patches of surface fines. Furthermore, topographic or textural alterations made by crayfish to the bed are likely to alter local near-bed hydraulics pertinent to sediment suspension and may, therefore, indirectly affect the mobility of fine surficial material. In addition to affecting fine sediment mobilization, crayfish may also increase the availability of fine inorganic sediment: their interaction with coarser surface grains that hide or protect finer sediments may alter the supply of fines to the surface and their exposure to incident turbulent stresses; and, by reducing the stability of coarse-grained surface layers, crayfish may encourage surface layer breakup, thereby increasing the availability of fines from the subsurface sediment mixture. Preliminary research conducted on a lowland, low-energy UK river dominated by fine substrates complements these hypotheses: nocturnal increases in crayfish activity were reflected by an increase in the frequency of intermittent high-magnitude sediment suspension (turbidity) events, which have a cumulative impact on 'ambient' turbidity levels within a reach colonized by signal crayfish (Harvey et al., forthcoming). In addition, bank burrowing activity may cause increases in fine sediment supply associated with creation, maintenance and occupation of burrows, and, over time, further impacts may be associated with the destabilization and subsequent failure of river banks following exceedance of a burrow network density threshold, leading to changes in channel morphology and fine sediment inputs.

IV Up-scaling the impacts of signal crayfish on sediment dynamics: A call for research

The foregoing discussion suggests that there is great potential for the signal crayfish to impact significantly on sediments and morphology at the patch scale of river systems, as a function of a combination of factors: (1) their interaction with bed material, river banks and other aquatic organisms; (2) their large body size and aggressive nature; and (3) the potential for invasive signal crayfish to be present in very high densities. However, given that short timescale and small spatial-scale processes are known to be capable of influencing system behaviour over longer timescales and larger space-scales (Lane and Richards, 1997), it is also highly plausible that signal crayfish impacts could extend beyond the scale of the immediate surroundings of the habitat patch within which individuals interact at a particular point in time/space (cf. Sousa et al., 2009). As indicated in Figure 1, key knowledge gaps remain regarding the ways in which signal crayfish activities at patch scales may cumulatively influence sediment dynamics at reach to catchment scales and, thus, instigate or enhance sediment-related river management problems. However, there are strong physically based arguments that support this hypothesis and these are outlined in the following section.

Changes in the character and composition of sediment in river channels resulting from signal crayfish activities can increase the *availability* of sediment for entrainment and transport, and reduce the *stability* of this sediment over broad areas (Johnson et al., 2010; Sousa et al., 2009; Statzner et al., 2003). Thus, in addition to the direct bioturbation that occurs when they move, signal crayfish are likely to increase the amount of sediment mobilized during competent transport events. Signal crayfish are also likely to enhance the potential for this material to be transported over greater distances than would otherwise occur by increasing the degree of *connectivity* between reaches (cf. Fryirs et al., 2007; Hooke, 2003). The destruction of aquatic macrophytes, alterations to bed microtopography and changes in channel morphology are all likely to modify reach-scale hydraulics (cf. Ashworth and Ferguson, 1986; Clifford et al., 1992a, 1992b; Gurnell et al., 2006; Lane and Richards, 1997; Naden et al., 2006; Simon and Senturk, 1992), thereby potentially reducing opportunities for sediment retention and enhancing throughput to areas further downstream. In combination, these effects have the potential to destabilize sediment dynamics across large sections of river networks and even in downstream areas where signal crayfish are absent.

Possible catchment-scale management issues that may result include the adequate provision of physical habitats that are suitable for native aquatic organisms, and hence the ability to meet legislative demands for hydromorphological and ecological quality (e.g. European Parliament and the Council of the European Union, 2000); the potential for upstream impacts on sediments and morphology to undermine river rehabilitation and improvement works further downstream (Brierley and Fryirs, 2005); and increased levels of flood risk resulting from both morphological changes that modify conveyance capacity and the potential for crayfish to undermine certain types of flood defence works (e.g. earth embankments). Widespread increases in ambient water turbidity levels would pose a threat to aquatic biota (Soulsby et al., 2001) and, in catchments affected by intensive agricultural or mining activity, changes in sediment stability and connectivity may facilitate the mobilization and transfer of nutrients and contaminated sediments, with further implications for water and sediment quality (Cappuyns et al., 2006; Dennis et al., 2003; Macklin et al., 2006).

Further research is urgently required to quantify the magnitude of these impacts and improve our understanding of how local-scale signal crayfish impacts are propagated beyond their immediate vicinity. Temporal variation in crayfish activity may be an important factor since, for example, increased activity during summer months may elevate the significance of sediment-related river management problems that result from high-magnitude hydrological events. Significantly though, the spatial distribution of the potential impacts identified is likely to be determined principally by the sensitivity of a particular habitat patch, reach or catchment to impacts, rather than preferential habitat use by signal crayfish: the rapid spread of signal crayfish throughout the UK and Europe illustrates their ability to occupy a range of habitat types. The most sensitive locations may, therefore, be found within lowland reaches or the ‘intermediate zones’ of river systems, which are characterized by fine bed material and, potentially, associated with greater levels of anthropogenic floodplain disturbance (e.g. contamination from industrial and agricultural activity). Efforts should therefore be directed towards the identification of metrics capable of describing sensitivity to crayfish impacts. Research should also be conducted within the context of anticipated future changes in climate and land use which may have the potential to exacerbate current impacts. This is likely to include a combination of direct impacts on population dynamics and activity levels associated with projected future changes in climate (specifically temperature, see above) together with broader changes in spatial patterns and rates of sediment delivery to river systems associated with future climate and land-use change.

V Conclusion

This paper identifies the ways in which an invasive aquatic species, acting as a system disturbance, has the potential to greatly modify fine sediment dynamics within river catchments and, hence, act as a driver of river management problems. A conceptual model outlines the key mechanisms by which the signal crayfish may influence fine sediment dynamics, from the mechanistic impacts of individual crayfish movements and activities on the local physical environment to potential reach- and catchment-scale influences on sediment stability and connectivity, channel and bank morphology, river hydraulics, and the mobilization and transport of nutrients and contaminated sediments. While the wider impacts of signal crayfish have not been explored directly in previous literature, established process knowledge of reach- and catchment-scale sediment dynamics supports the identification of key parameters which may be affected. Outcomes will depend in part on river character and behaviour in combination with interactions between crayfish and other organisms that may also be acting as geomorphic agents. While similar impacts may be expected in association with the activities of other (native) crayfish species, it is argued here that the impacts of signal crayfish may be of particular significance due to their larger body size and more aggressive nature, their presence in catchments in extremely high densities, and the lack of effective removal or mitigation measures. This paper focuses on potential impacts in regions where the signal crayfish represents an invasive species and, hence, a disturbance to which the river system may not be resilient. However, it is possible that similar problems may arise in regions where signal crayfish, or other burrowing crayfish species, are endemic and present in very high densities.

Further directed interdisciplinary research is, therefore, required at the interface between freshwater ecology, fluvial geomorphology and hydraulics at various spatiotemporal scales in order to quantify the significance of different impacts, develop the hypotheses presented in this paper and provide a sound scientific underpinning to the management of signal crayfish impacts on sediment dynamics at a range of spatiotemporal scales. In particular, research should focus on: improved understanding of the mechanistic impacts of signal crayfish on fine sediments; quantification of the significance of modifications to bed and bank sediments and associated sediment mobilization and transport within a range of different river environments; the influence of biological interactions, particularly with other organisms known to act as significant geomorphic agents within rivers; and exploration of the potential for current signal crayfish impacts to exacerbated by future changes in sediment dynamics associated with changes in climate and land-use management. This paper, and the suggested further research, are necessarily interdisciplinary, and provide an illustration of the advantages of coupling various earth, environmental and biological perspectives. To many, this exemplifies interest in increasingly interconnected biophysical phenomena and analyses, but it is also essentially the pursuit and domain of physical geography.

Acknowledgements

Tom Moorhouse was funded by the Esmée Fairbairn Foundation, Alex Henshaw was in receipt of an EPSRC PhD Plus Fellowship (EP/P5011431/1) at the University of Nottingham and Matthew Johnson was in receipt of a Loughborough University Faculty Studentship.

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