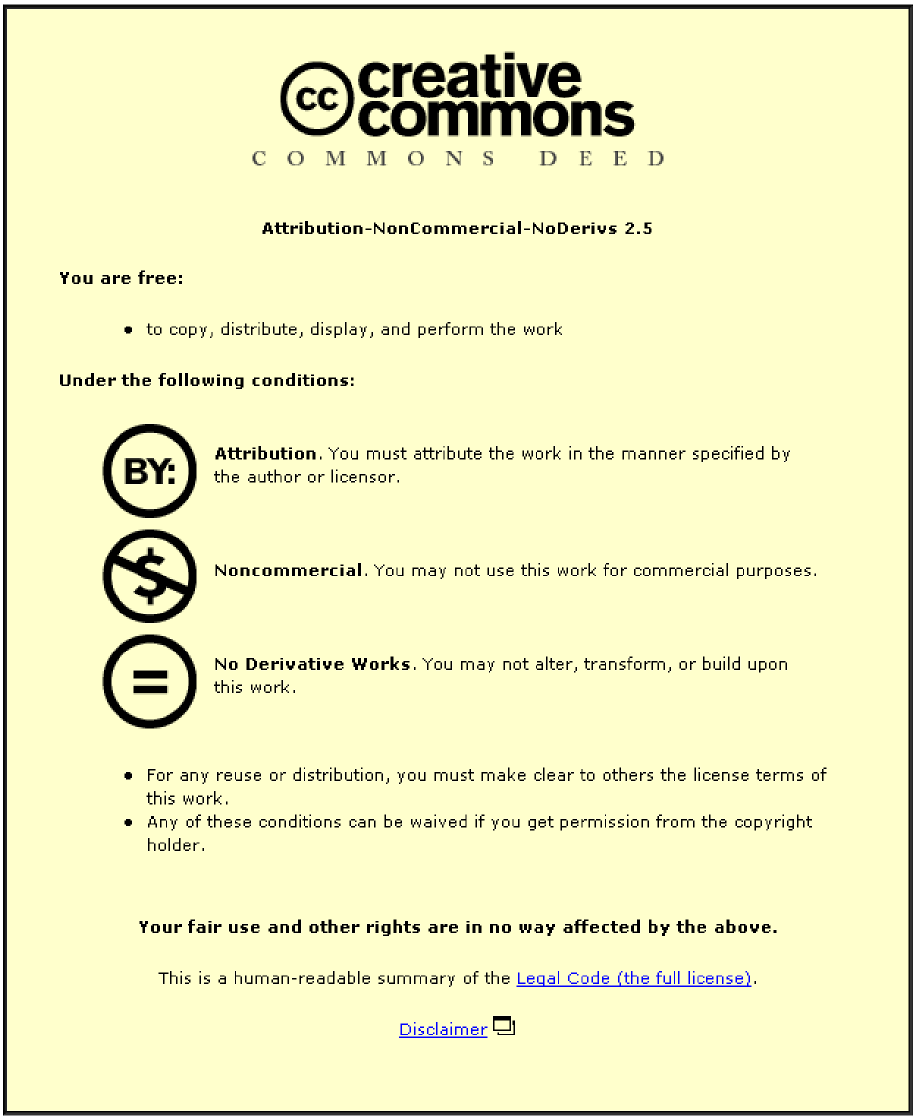

The disturbance of fluvial gravel substrates by signal crayfish (*Pacifastacus leniusculus*) and the implications for coarse sediment transport in gravel-bed rivers.

by
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Abstract

Signal crayfish are an internationally widespread invasive species that can have important detrimental ecological impacts. This thesis aims to determine whether signal crayfish have the potential to also impact the physical environment in rivers. A series of experiments were undertaken in purpose-built still-water aquaria using a laser scanner to obtain Digital Elevation Models (DEMs) of narrowly-graded gravel surfaces before and after exposure to crayfish. The difference between DEMs was used to quantify volumetric changes in surface topography due to crayfish activity. Two distinct types of topographic change were identified. The first was the construction of pits and mounds which resulted in an increase in surface roughness and grain exposure. The second was the rearrangement of surface material caused by crayfish brushing past grains when walking and foraging, reorientating grains and altering friction angles. A series of 80 flume runs were undertaken to quantify alterations made by crayfish to water-worked, as well as loose, gravel substrates at low velocity flows. Crayfish significantly altered the structure of water-worked substrates, reversing the imbrication of surface grains to a more random arrangement. Surfaces were entrained at a relatively high velocity flow subsequent to crayfish activity in order to directly link topographic and structural alterations to substrate stability. Nearly twice as many grains were mobilised from surfaces which had been disturbed by crayfish in comparison to control surfaces that were not exposed to crayfish. A field investigation aimed to determine the potential significance of the geomorphic impact of crayfish in rivers. Signal crayfish were tracked through a 20 m reach of a small, lowland alluvial river for 150 days using a Passive Integrated Transponder (PIT) system. Crayfish were active throughout the channel, although their activity became limited as water temperature dropped and flow stage increased. Substrate was not an important determinant of crayfish activity at this scale. Instead, crayfish tended to be found along the inner bank of a meander bend where there was a substantial cover of macrophytes. Consequently, signal crayfish were active for extended periods on substrates of a similar size to those that they could disturb in flume experiments. These results suggest that signal crayfish could have important geomorphic effects in rivers, disturbing bed structures and increasing the mobility of coarse material. This may have important implications for both the management of some rivers and benthic organisms that reside on the river bed.

Keywords: Biogeomorphology, bioturbation, ecosystem engineering, crayfish, gravel-bed rivers, radiotelemetry, laser scanner, bedload transport, surface analysis.

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Chapter 1

Introduction and Context

1.1. Introduction

Rivers drain rain- and melt-water from topographic highs to topographic lows, usually discharging into ocean basins, and are an important amenity as a water source; in providing a transport network and hydroelectric power; as a food source, particularly in providing sources of protein to continental interiors; and in fertilising marginal land for food production. They can also be extremely destructive where constructions are built close to river channels, particularly on flood plains. Because of this importance, rivers are well studied and many are highly managed, particularly where they occur in densely populated areas. Rivers are diverse in their morphology and flow regimes, both between rivers and with distance downstream from the source. They can have multiple channels or a single channel, be lowland, sand-bedded channels to steep, upland boulder-bedded streams. They can have permanent flow or be ephemeral and the flow regime can change dramatically with time due to floods. Consequently, identifying universal laws or processes that are applicable to all rivers is difficult and, as a result, rivers are often split into types based on their planform, bed material size, flow regime and the climatic area within which they occur. This study focuses on gravel-bed rivers which can range in size greatly but are generally relatively shallow in comparison to the bed material and occur at intermediate areas of the river profile, between upland, step-pool, boulder-bed channels and large, lowland sand-bed channels which eventually drain to the sea.

The majority of material transported in rivers is suspended in the water column but bedload transport is disproportionately important due to its influence as a channel forming process and to the conveyance of water through the system, thereby influencing flood regime, channel navigability, the sedimentation of reservoirs and lateral erosion (Leopold, 1992; Sear *et al.*, 1995). As a result, bedload transport has been studied intensively for over 100 years (Du Buoys, 1879; Gilbert, 1914; Buffington and Montgomery, 1997). Whilst previous research provides us with a substantial knowledge of transport processes, our ability to predict and understand the temporal and spatial variability in transport is still limited (section 1.2). This is because of the large range of grain sizes which typically constitute a gravel bed, which can cover many orders of magnitude. Adequately characterising this grain-size distribution is difficult, yet it is also a prerequisite for studying bedload transport. Many bedload transport formula use a single grain diameter to represent the grain size distribution of the bed. This is often the median grain size (D_{50}). In unimodal sediments there is evidence that this may be suitable in some situations (Parker and Klingeman, 1982; Wilcock and McArdell, 1993); however, for bimodal sediments this is often not representative of the bed (Wilcock, 1992) and will result in modelled results deviating from field results. Characterising heterogeneous substrates into a convenient value or set of values is currently still an issue.

Another difficulty in predicting bedload transport is accounting for the multitude of factors that play a role in determining the stability of a grain and its entrainment. These include the protrusion of grains into the flow, the angle of particle repose, grain size and density, and the grain shape (Fenton and Abbott, 1977; Komar and Li, 1986; Carling *et al*., 1992; section 1.2.1). It is not only the characteristics of the transported grains that are important but the characteristics and geometric arrangement of all the surrounding grains as well (Brayshaw, 1985). Factors such as packing density and imbrication will have a large influence on entrainment, and the continued transport of particles over the substrate (Allen, 1983; Carling *et al*., 1992). The combination of these parameters, which describe the bed structure, will have a controlling impact on the entrainment of substrate material (section 1.2.2).

In addition to the important social and financial implications of bedload transport, the transport of bed material has important repercussions for the many benthic organisms that live on the river bed as substrate stability is an important determinant of habitat suitability (Lancaster and Hildrew, 1993; Death, 1995). Gravel-bed rivers tend to have a high species richness due to the large variety of flow and substrate types and the abundance of organic matter. Despite the high abundance of plants and animals that live within and on gravel-bed substrates, bedload transport (and other fluvial processes) is usually studied in isolation from ecological processes. This also disregards the increasing acknowledgement of organisms as important geomorphic agents in a range of environments (Viles, 1988; Butler, 1995; section 1.3). Plants are known to have a controlling impact on the planform of river channels (Murray and Paola, 2003) and submerged macrophytes have an important impact on the hydraulic environment within channels. Large woody debris is known to have significant impacts on river channel processes and channel change (Abbe and Montgomery, 1996; Gurnell *et al*., 2002; Curran and Wohl, 2003) and many species of invertebrate and fish can modify the sedimentological conditions of river beds (Butler, 1995; Moore, 2006; section 1.4).

It is assumed, based on the results of previous experiments (sections 1.4.3; 1.4.4), that invertebrates will not directly transport material distances comparable to that transported by the flow. However, by moving substrate material, benthic organisms may disturb the structure of gravel beds, impacting on their stability. River beds consolidate and structure at low-to-moderate flows, increasing the stability of substrates. Mobile organisms may oppose this process when foraging and burrowing, decreasing the stability of the bed, increasing the sediment in transport during subsequent high flows. This project aims to determine whether the activity of the invasive signal crayfish (*Pacifastacus leniusculus;* section 1.5) results in alterations to the micromorphology of gravel substrates, with implications for stability and bedload transport.

1.2. Structure and mobility of fluvial gravel substrates

1.2.1. Grain characteristics and geometry

Fluvial gravel beds are characterised as having a heterogeneous mixture of grain sizes, ranging over five orders of magnitude from sands (0.06 mm) to boulders (> 4000 mm) (Rice and Church, 1998; Bunte and Abt, 2001). The size of a grain is usually defined by its intermediate axis (*b* axis) length. Grains in fluvial systems also have heterogeneous shapes. As a result, grains with the same *b*-axis, and consequently considered the same size class, can be substantially different in actual mass. The shape and orientation of a grain will partially determine the area exposed to drag and lift forces and are, consequently, important in predictions of grain mobility (Carling *et al*., 1992). Grains tend to be grouped into four distinct shape classes; compact, platy, bladed and elongated (Zingg, 1935) based on the ratio between the longest (*a*-axis), intermediate (*b*-axis) and shortest (*c*-axis) perpendicular axis, known as the principal axes. Grains can be further divided into numerous sub-classes based on the degree of difference between the principal axes (Sneed and Folk, 1958). As well as the shape of a grain, its roundness is also important in determining the ease with which it can roll over the substrate (Krumbein, 1941).

The great range of grain sizes and shapes which make up the bed material in gravel-bed rivers, result in some grains protruding higher into the flow than others. The protrusion of grains has a significant effect on grain stability as grains protruding high into the flow are exposed to greater flow forces than those sheltering between coarse grains or near to the substrate surface where the flow force will be reduced due to frictional drag (Fenton and Abbot, 1977). Consequently, grains that protrude into the flow are entrained at relatively low shear stresses. The mixing of grains of varying shapes and sizes results in grains having a range of friction angles, also known as pivot angles or angles of repose. This is defined as the angle which much be overcome for a grain to roll over the grains that are partly below and partly downstream of it (Komar and Li, 1986; Kirchner *et al*., 1990; Buffington *et al*., 1992). Therefore, despite the relative coarseness of substrates in gravel-bed rivers, comparatively small alterations of grain-to-grain geometry (often referred to as bed-material fabric) has a substantial impact on bed stability during flood flows (Frostick *et al*., 1984; Reid *et al*., 1985; Lamarre and Roy, 2008). For example, Oldmeadow and Church (2006) found that transport rates were 32% greater in reaches of Harris Creek, British Columbia, where the surface structure had been disturbed in comparison to untouched reaches.

1.2.2. Structure and roughness of fluvial substrates

Gravel-bed rivers tend to have a bimodal grain-size distribution. This has resulted in the division of substrates into framework and matrix material. The framework consists of coarse grains, the pore spaces between which are filled with finer matrix material. If matrix material contributes approximately 30% of the total sediment then the substrate is likely to be ‘matrix supported’ and framework grains are unlikely to touch. If the total sediment is less than 30% matrix then the substrate is said to be framework supported (Church *et al*., 1987). The ingress of fine sediments into the pore spaces with gravel frameworks has a stabilising impact by increasing grain interlock (Frostick *et al*., 1984), resulting in substrates consolidating at low flows, increasing the stresses required to move bed material (Reid and Frostick, 1984). When fines are winnowed from the surface of gravel substrates by marginally competent flows, the surface can coarsen, forming an armour layer that protects the underlying material from entrainment (Carling and Reader, 1982; Dietrich *et al.* 1989; Lisle and Madej, 1992). This results in coarse grains being present on the bed surface in greater proportions relative to the subsurface. Gravel frameworks with a lack of fine matrix material, termed open framework gravels, are important because of their exceptionally high permeability, providing prime spawning sites for salmonid fish (Lunt and Bridge, 2007).

The continuous, unidirectional action of the flow modifies the geometry and location of grains, moving grains from vulnerable positions until they come to rest in locations that are less vulnerable. Consequently, with time, river beds become organised by the flow into resistant structures, particularly due to the interlock of surface grains. A particularly characteristic structure is imbrication which describes when grains interlock with the *a*-axis parallel to the flow, *b*-axis perpendicular to the flow and *c*-axis orthogonal to flow and the *a* – *b* plane dipping upstream with grains stacked against the downstream grains (Marion *et al*., 2003; Aberle and Nikora, 2006; Millane *et al*., 2006). Imbrication imparts stability to grains through grain-to-grain interlock and by producing large friction angles which increase the flow forces required to move grains (Komar and Li, 1986; Kirchner *et al*., 1990). When grains imbricate against a large, stable obstacle clast it can result in the formation of cluster bedforms which are resistant to entrainment, usually termed pebble clusters (Brayshaw *et al*., 1984; Reid and Frostick, 1984; Hassan and Reid, 1990; Church *et al*., 1998; Oldmeadow and Church, 2006; Lamarre and Roy, 2008).

Microforms have a considerable impact on the entrainment and continued transport of bed material locked in the cluster, as well as the whole river bed through altering the surface roughness, influencing the frictional drag on the flow (Hassan and Reid, 1990). The characteristics of the substrate surface, which dictate the bed roughness, significantly impact the hydraulic conditions of the flow, particularly the region directly above the bed, termed the roughness layer (Nikora, 2007). It is within the near-bed hydraulic environment that benthic organisms reside and flow in this region will dictate the entrainment and subsequent transport of bed material (Schvidchenko and Pender, 2001). The flow within this region is dominated by frictional forces as the microtopography of the substrate exerts a significant frictional drag on the flow (Wiberg and Smith, 1991; Dinehart, 1992), particularly in gravel-bed rivers which tend to be shallow relative to the roughness of the bed (Hardy *et al*., 2007). Flow resistance can be characterised at different scales (Robert, 1990). Individual grains can create frictional drag depending on their orientation, shape and spacing (section 1.2.1). The interaction of several grains, potentially forming cluster bedforms, can exert a significant influence on the flow resistance through form drag as can larger reach-scale bedforms, such as pools and riffles (Robert, 1990; 1997; Clifford, 1992; Lawless and Robert, 2001). As the concentration of protruding bed elements, such as pebble clusters, increases, the flow resistance increases; however, at high concentrations the flow resistance can start to decrease as ‘skimming’ flow develops (Hassan and Reid, 1990). There is evidence of an equilibrium spacing of pebble clusters above and below which transport rates are amplified and cluster instability increased (Hassan and Reid, 1990) which corresponds to maximum flow resistance (Reid *et al.*, 1992). Consequently, there is a complex two-way interaction between the bed morphology and the hydraulic environment which has a controlling impact on the entrainment and continued transport of bed material.

1.2.3. Entrainment of bed material from fluvial substrates

The bedload is transported in contact with the substrate, predominately by rolling or sliding in a stepped movement with intermittent rest periods (Andrews, 1983). Due to the applied importance of mobile bed material, it is desirable to have a simple, single parameter describing the initiation of motion. Attempts usually relate transport to boundary shear stress, a widely used example being the Shields parameter (θ) which estimates the dimensionless shear stress at incipient motion (Shields, 1936). A uniform θ of 0.045 has been found to be suitable for bed material when situated in a planar bed (Miller *et al.*, 1977; Buffington and Montgomery, 1997); however, when grains sit proud on the surface values of θ can be as low as 0.01 (Fenton and Abbott, 1977). Alternatively, continuous measures of bedload transport from Turkey Brook, UK have recorded values higher than 0.06 due to the impact of bed structuring (Reid and Frostick, 1984). This variability in entrainment is associated with the impact of differing grain shapes and positions (section 1.2.1), as well as the structuring of the substrate (section 1.2.2) and stochastic fluctuations in flow intensity associated with turbulent bursts (Grass, 1971; Paintal, 1971; Lavelle and Mojfeld, 1987), which mask any simple relationship between grain weight and flow force. As a result, the shears stress required to move a grain is characterised by a probability distribution rather than a single threshold value, above which transport begins and below which it ceases (Kirchner *et al.*, 1990; Wilcock and McArdell, 1993). Consequently, bedload transport equations are generally poor at predicting transport (Gomez and Church, 1989).

It has been suggested that differences in grain geometry equalise differences in the onset of transport for grains of different size (Parker *et al.*, 1982; Parker and Klingeman, 1982; Andrews and Parker, 1987). Finer grains will shelter in the lee of larger grains or in interstices between grains and will, as a result, only be entrained when the surrounding coarser material has also been mobilised. Consequently, all grain sizes on the bed are hypothesised to move at the same flow stage. However, in bimodal mixtures typical of gravel-bed rivers, the concept of ‘equal mobility’ does not hold true. Instead, finer fractions are transported over coarse material at critical shear stresses considerably lower than those of the framework material (Church *et al*., 1991; Wilcock, 1992; Lisle, 1995). This phenomenon has been termed 'partial transport' (Wilcock, 1992; Wilcock and McArdell 1993, 1997).

Wilcock and McArdell (1993) define an initial motion threshold which is associated with the first movement of grains on the bed. Above this they also define a second threshold for fully mobilised transport, when all grain sizes on the bed are in motion, which has also been demonstrated in the field for semi-arid rivers (Powell *et al*., 2001). Between these two thresholds is a region governed by partial transport where the transport of fine fractions is greater than for coarser fractions by amounts that are proportional to grain size. As the shear stress increases in this region, an increasing proportion of the grain-size distribution becomes mobilised so that the transport rates approach full mobility (Wilcock and McArdell, 1997). As stated above, within a size fraction, grains will be entrained over a range of flows due to variability in grain shape and relative location (section 1.3.1). Therefore, partial transport also occurs within individual grain-size fractions (Wilcock and McArdell, 1993). Consequently, if an organism was capable of altering the topography and structural characteristics of substrates, it could potentially have a substantial impact on the entrainment of bed material.

1.3. Interactions between organisms and physical environment

1.3.1. Overview

There is a need to gain a better understanding of the dynamic interaction between biota and physical processes, not just to assess the creation and maintenance of suitable habitats but to understand the importance of the role of organisms in promoting physical processes. The overlap between biological and Earth sciences has led to much recent work towards the development of unified frameworks for study of inter-disciplinary interactions and processes (Naiman *et al*., 2000; Paola *et al*., 2006; Stallins, 2006; Vaughn *et al*., 2009; Reinhardt *et al*., 2010; Rice *et al*., 2010). The two-way interaction between organisms and habitats has long been known and is well studied. For instance, plants are known to alter physical conditions through plant succession (Clements, 1916) and the importance of organisms for soil formation and sediment mixing has been known for over 100 years (Darwin, 1881; section 1.2.2). Organisms and physical processes are known to interact at the largest spatial and temporal scales (Sterelny, 2005; Dietrich and Perron, 2006; Corenblit *et al*., 2007). Despite the long history of research and acknowledged importance of such interactions, it is only relatively recently that frameworks such as zoogeomorphology, ecosystem engineering, geobiology and ecohydraulics have been proposed. These new terms have acted as a stimulus for this area of research (Stallins, 2006; Wright and Jones, 2006).

1.3.2. Bioturbation

The mixing of substrates by organisms has been termed bioturbation (Murray *et al*., 2002; Meysman *et al*., 2006). The importance of bioturbation was reported by Charles Darwin through his examination of the significance of worms in the formation of soil (Darwin, 1881; Feller *et al*., 2006). Bioturbation has since been acknowledged as a fundamental process operating in marine, lacustrine and terrestrial sediments (Fager, 1964; Rhoads and Young, 1971; Murray *et al*., 2002; Gabet *et al*., 2003; Svensson and Leonardson, 2003; Lindström and Sandberg-Kilpi, 2008; de Gilbert and Buatois, 2009).

The vertical mixing of marine substrates results in the oxygenation of sediments and the cycling of nutrients, essential to benthic organisms. Bioturbation can result in either the destabilisation of sediments by altering grain exposure and altering hydraulic conditions, or the stabilisation of sediments by increasing surface roughness and the production of adhesive and cohesive mucus (Jumars and Nowell, 1984). Bioturbation is not only considered an important current process, but fundamental to the evolution of the marine biome (Thayer, 1979; Canfield and Farquhar, 2009). Fossil evidence suggests that the evolution of burrowing organisms at the Precambrian-Cambrian transition, approximately 542 million years ago, led to the reworking and oxygenation of the ocean floor (Thayer, 1979; Crimes and Drosser, 1992; Seilacher *et al*., 2005), enabling the evolution of many of the major groups of marine animals which today constitute the largest biomass of any environment on Earth (Bottjer *et al*., 2000).

1.3.3. Ecosystem engineering

Traditionally in ecology, the interaction between organisms has been studied in terms of trophic and competitive interactions. However, organisms can also impact each other through environmental modifications, for instance, by modifying the flux of resources. This non-trophic, non-competitive interaction is termed ‘ecosystem engineering’ (Jones *et al*., 1994, 1997). Ecosystem engineers can be broadly split into two groups; ‘autogenic engineers’, which change an environment with their own physical structure, such as terrestrial and aquatic plants, corals and mussel beds; and ‘allogenic engineers’, which modify the environment through mechanical means including trampling and wallowing or the construction of nests, burrows and mounds (Jones *et al*., 1994). Even animal footprints can provide habitat for other organisms. Consequently, most, if not all, organisms can be classed as ‘ecosystem engineers’ at some scale (Wright and Jones, 2006) which has led some to challenge the usefulness of the term (Power 1997; Reichman and Seabloom, 2002a; b).

Many species which can be classed as “engineers” have only small, localised impacts. However, there are some organisms which can be defined as both ecosystem engineers and ‘keystone species’, i.e. a species of disproportionate and fundamental importance to the wider community (Power *et al*., 1996). Many keystone species are also ecosystem engineers. However, it should be noted that many large scale environmental modifications are achieved by multiple species, such as the numerous species that constitute a forest or coral ecosystem (Wright and Jones, 2006). Despite this, it is apparent that individuals, and communities of organisms can have a fundamental control on the presence of other organisms through the modification of habitats and the flux of resources. A current challenge for ecologists is to incorporate engineering interactions into the traditional models of trophic and competitive interactions, both in studies of organism ecology (Jones *et al*., 1994; Wilby *et al*., 2001) and evolution (Dawkins, 1982; Lewontin, 1983; Odling-Smee *et al*., 2003; Sterenly, 2005).

1.3.4. Biogeomorphology and zoogeomorphology

Ecosystem engineering focuses on how habitat modification affects other organisms, but the modification of physical processes is also important in understanding Earth surface processes. The importance of organisms to geomorphic processes has been described as ‘biogeomorphology’ (Viles, 1988). Although much of our knowledge of geomorphology has been obtained in isolation from the organisms, examples of biogeomorphology are common and well studied (Viles 1988; Butler, 1995), for instance, the role of plants in instigating bedforms, such as nebkhas in arid environments. The geomorphic impact of animals has been termed ‘zoogeomorphology’, defined as the net loss or gain of material (i.e. erosion or deposition) as a result of the action of an animal (Butler, 1995). An appreciation of ecological interactions has led to an increased understanding of the functioning of dynamic landscapes. For example, the extirpation of gray wolves (*Canis lupus*) from river basins in northwestern USA, led to an increase in grazing of bank-side vegetation by Elk (*Cervis elaphus*), resulting in lateral and vertical incision of fluvial channels which, in turn, led to disconnectivity with the floodplain, increasing the return period of bankfull discharge from 3.1 to 32.4 years (Beschta and Ripple, 2006; 2008).

In fluvial environments, the direct reworking of gravelly substrates by organisms has not been studied to the same extent as it has in sedimentary environments characterised by finer clastic material. Notable exceptions do exist, for instance, the reworking of substrates by spawning salmonid fish which alter the topography and structure of gravel substrates, and can increase bedload transport during high flows (Hassan *et al*., 2008; section 1.4.2). This relative lack of work counters the fact that gravel-bed rivers often support a large diversity and abundance of organisms.

1.4. The reworking of fluvial substrates by organisms

1.4.1. The impact of organisms on the fluvial environment

Organisms can have a significant impact on the planform, hydraulics and transport of material in rivers (Gurnell, 1998; Westbrook *et al*., 2010). Beavers build dams which trap millions of tonnes of sediment in the USA each year, as well as altering the hydraulic conditions both upstream and downstream of the dam (Wright *et al*., 2003; Butler and Malanson 2005). Some amphibian species construct nests in fluvial substrates as well as digging channels and pools in banks (Lutz, 1960; Kok *et al*., 1989) and, when tadpoles, can reduce the accrual of fine sediment (Flecker *et al*., 1990; Ranvestel *et al*., 2004). Reptile species, such as crocodilians, can trample substrates as well as constructing nests, slides, wallows and dens in and on river banks, and mix the water column of stagnant fluvial pools (Greer, 1970; Joanen and McNease, 1989; Kofron, 1989; Naiman and Rogers, 1997). Livestock and large mammals trample substrates and river banks, influencing the planform and also destabilising the banks and bed of rivers (Trimble and Mendel, 1995; Naiman and Rogers, 1997; Gereta and Wolanski, 1998).

Animals also consume and remove algae and higher plant species which can otherwise stabilise the bed and banks of rivers. The presence of plant root systems are an important control on river channel planform (Murray and Paola, 2003; Tal and Paola, 2007; Murray *et al*., 2008; Davies and Gibling, 2010). For instance, it has been suggested that the Permian-Triassic extinction event, which resulted in a mass loss of vegetation, led to a widespread change from meandering channels to braided fluvial systems (Ward *et al*., 2000). In-channel macrophytes have substantial impacts on the hydraulics in rivers, increasing frictional drag on the flow which can instigate deposition in some areas and induce erosion in others by constraining the flow (Cotton *et al*., 2006). Plant debris can also have an important impact on the geomorphology of rivers, particularly large woody debris which can block channels, altering river channel patterns (Abbe and Montgomery, 1996; Gurnell *et al*., 2002; Curran and Wohl, 2003; Jeffries *et al*., 2003).

1.4.2. Geomorphic impacts of fish

The majority of research into the direct reworking of fluvial substrates has been associated with salmonids (salmon and trout) which disturb gravel substrates when nesting. Many salmonid fish migrate from the ocean into rivers, travelling upstream in order to spawn in shallow gravel beds. Moore *et al*. (2004) observed that just the swimming action of sockeye salmon (*Oncorhynchus nerka*) in small creeks and over shallow beaches in lakes within the Wood River drainage basin in southwestern Alaksa, resulted in substantial disturbance of fine sediment and benthos. The construction of nests, termed redds, causes the greatest disturbance. The female constructs redds by turning on her side and rapidly undulating her tail and body (Montgomery *et al.*, 1996; Soulsby *et al.*, 2001). This action excavates a pit into the gravel substrate and sweeps fine particles into the water column which increases the permeability and porosity of the substrate (Field-Dodgson, 1987; Kondolf *et al*., 1993; Montgomery *et al.*, 1996). Moore *et al.* (2004) found there was a five-fold increase in fine sediment accumulation in areas of Alaskan salmon-spawning rivers where salmon were excluded. The removal of interstitial fines, combined with the loosening of the substrate, ensures that eggs and embryos which remain in the redd, are oxygenated by surface water permeating through the substrate (Grieg *et al*., 2007). The disturbance of the bed during spawning has significant impacts on the macroinvertebrate community, biofilm and algal growth, and nutrient concentrations (Moore *et al*., 2004; Moore and Schindler, 2008; Tiegs *et al*., 2009).

Redds form a distinctive topography which persists until high winter flows (Montgomery *et al.,* 1996). The size and density of redds is dependent on the salmonid species. Spawning sockeye salmon can dig nests that cover between 2.1 – 4.1 m^2 and are on average 0.2 m deep (Moore *et al*., 2004) and during redd construction can move more sediment and bury sediment deeper than many flood events (Gottesfeld *et al*., 2004). Sockeye can attain densities in Alaskan creeks of at least 1500 km^{-2} (Peterson and Foote, 2000) from which

Moore (2006) estimates that salmon have consistently disturbed more than 5000 m^2 of the substrate surface every summer over the last 50 years, roughly 30% of the available stream bed.

By displacing fine sediments the substrate surface coarsens (Kondolf *et al.*, 1993; Peterson and Foote, 2000; Moore *et al*., 2004), for instance, Montgomery *et al.* (1996) found that spawning activity caused a 33 to 39% increase in median surface grain size (D_{50}) in Kennedy Creek and a 56 to 57% increase in Montana Creek, USA. The loosening of the bed and removal of fines reduces the consolidation and structuring of the substrate during low flows, with excavated gravels sitting unrestrained and proud on the surface and, therefore subject to significantly higher rates of entrainment (Montgomery *et al*., 1996; Rennie and Millar, 2000; Gottesfeld *et al*., 2004; Hassan *et al*., 2008). Salmon can have considerable topographic impacts in gravel-bed rivers, creating parallel lines of linear riffles perpendicular to the banks and gravel dunes (Field-Dodgson, 1987; Gottesfeld *et al*., 2008; Hassan *et al*., 2008).

Most of the research on disturbance by salmonids is based on Pacific salmon species which are larger and spawn in higher densities than European counterparts, such as brown trout (*Salmo trutta*). The cumulative effects of these other species could still be of importance, as could the activity of other, non-salmonid fish. Biological studies have identified many non-salmonid fish species that construct nests by moving gravels, including species of bream (Pierce 1987; Thorp, 1988), chub (Lachner, 1952), lamprey (Stone, 2006), bass (Winemiller and Taylor, 1982) and stickleback (Rushbrook and Barber, 2008). The foraging activity of fish also results in the disturbance of the bed (Pringle and Hamazaki, 1998). A number of species of detrivorous, tropical fish have been found to significantly decrease fine sediment accrual, as well as impacting the composition of algal and invertebrate assemblages (Flecker, 1992; Flecker, 1996; Flecker, 1997; Flecker and Taylor, 2004). Power (1990) demonstrated that armoured catfish (Loricariidae) could clear sediment from bedrock in the Rio Frijoles, Panama. Statzner *et al*., (2003b) found in experimental channels that barbel (*Barbus barbus*) and gudgeon (*Gobio gobio*) could decrease the accumulation of fine sediment on gravel substrates, as well as modifying the bed elevation which was interpreted as indicating a change in substrate structure and topography. Carp (*Cyprinus carpio*) have also been found to resuspend sediments when foraging (Breukelaar *et al*. 1994; Parkos *et al*. 2003; Chumchal *et al*., 2005; Miller and Crowl, 2006; Roozen *et al*. 2007; Matsuzaki *et al*. 2009), as have bream

(*Abramis brama*), tench (*Tinca tinca*) and ruffe (*Gymnocephalus cernus*) (Persson and Svensson; 2006a, b), although the geomorphic consequences of this disturbance is unknown.

1.4.3. Geomorphic impacts of insect larvae and shrimp

There is growing evidence that the diverse array of benthic invertebrates in fluvial environments, which can occur in densities of many thousands per square metre in temperate and tropical streams, can also influence substrate characteristics. Invertebrates consume small particles and excrete larger faecal material, transforming inorganic and organic particles in rivers (Wallace *et al*., 1993; Wotton *et al*., 1998). In a study in Northern Sweden the transport rate of faecal pellets in the lower reaches of the Vindel River was estimated to peak at 429 Mg dry mass d^{-1} (Malmqvist *et al*., 2001). Chironomid larvae build tubes from sand grains which they glue together with mucus (Brennan and McLachlan, 1979; Pringle *et al*., 1985) and caddisfly larvae build cases from organic and inorganic material within which they pupate; some species carrying cases on their back for protection during their larval phase (Wiggins, 2004). Hydropsychid caddisfly larvae can stabilise material in rivers by binding grains together with silk that is spun to construct filter nets and retreats within which they shelter (Statzner *et al*., 1999; Cardinale *et al*., 2004). Silk threads have been found to increase by 38% the shear stress required to entrain gravels of 4 - 6 mm (Johnson *et al*., 2009), which may facilitate the presence of other invertebrates by reducing the risk of entrainment along with bed material and dislodgement by mobile bed material.

It has been found that shrimps can winnow fine material from interstitial spaces between coarse grains when foraging (Pringle and Blake, 1994; March *et al*., 2002; Visoni and Moulton, 2003; Moulton *et al*., 2004; De Souza and Moulton, 2005). For instance, shrimp were able to reduce the fine sediment covering experimental tiles by 40% in a two week period in a montane stream in Puerto Rico (Pringle *et al*., 1993). Insect larvae have also been found to winnow fine material from between coarse grains, with hunger levels significantly increasing the disturbance (Statzner *et al*., 1996: Zanetell and Peckarsky, 1996). Some macro-invertebrate species have been observed to act like “tiny bulldozers” as they redistribute fine sediment within the substrate, between coarse grains (Boulton, 2000, pg. 56). In fluvial substrates dominated by matrix material, the reworking of sediments by burrowing organisms, and the creation of tunnels in the substrate, can significantly increase the permeability and porosity of the substrate, increasing the transfer of water, oxygen and nutrients between the sub-surface and surface flows (Mermillod-Blondin *et al*., 2002; 2003; 2004; Mermollid-Blondin and Rosenberg, 2006; Nogoro *et al*., 2006).

1.4.4. The geomorphic impact of crayfish

Crayfish, a large freshwater crustacean, have been found to disturb fluvial substrates. Some species of crayfish, including signal crayfish, can burrow extensively into bank and bed material (Holdich, 2002a; Barbaresi *et al*., 2004) which can destabilise river banks (Guan, 1994) and increase turbidity (Angeler *et al*., 2001). Some crayfish species live in terrestrial floodplains and burrow to the water-table, creating complex burrow systems with surface 'chimneys' (Hobbs, 1981). These burrows can have substantial impacts on soil erosion and the cycling of nutrients, as well as the hydrology of the flood plain (Stone, 1993; Butler, 2002; Nordt and Dreise, 2009a; b).

Many studies into the breakdown of organic matter by crayfish have also noted that crayfish activity resulted in the winnowing of fine sediments from gravelly substrates (Parkyn *et al*., 1997; Creed and Reed, 2004; Usio and Townsend, 2004; Helms and Creed. 2005), although the influence is seasonal and its effects have not been observed in winter (Fortino, 2006). Mobilisation of fine sediment is associated with the movement of legs and contact between the substrate and abdomens when walking, which imparts momentum to particles (Usio and Townsend, 2004). Statzner *et al*. (2000) suggest fine sediment is mobilised, at least in part, because crayfish reduce algal cover, which can stabilise fine sediments. In a series of experiments in small artificial channels (0.2 m wide, 1.25 m^2 area), it was found that more material was eroded from an unstructured gravel substrate with a sand covering when the crayfish *Orconectes limosus* was present in comparison to control substrates without crayfish (Statzner *et al*., 2000; 2003a). The critical shear stress of sand was reduced by between 50 and 75% in the presence of crayfish. The impact of abiotic and biotic variables on sediment mobilisation by crayfish has also been explored (Statzner and Peltret, 2006; Statzner and Sagnes, 2008) and 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. Statzner *et al*. (2003) also reported that the presence of crayfish (*O. limnosus*) altered the topography of gravel-sand substrates in their experimental channels. A measured increase in mean bed elevation was interpreted as indicating that gravel consolidation was reduced by crayfish (Statzner *et al*., 2003).The present study aims to extend this previous work on the disturbance of gravel substrates by crayfish.

1.4.5. Synthesis of biogeomorphic research in rivers

Biological and ecological studies have identified large numbers of organisms that are able to modify fluvial environments and processes (sections 1.4.2 to 1.4.4). However, research into the geomorphic effects of such organisms in rivers is dominated by the study of relatively few species, in particular, salmonid fish, beavers and in-channel macrophytes. Alterations to physical environments can be attributed to a range of activities, as well as a range of organisms. Trees and plants can change hydraulic processes through their presence by increasing frictional drag on the flow and stabilising channel banks and beds with their root systems. Some organisms alter the environment as an incidental consequence of an activity, such as caddisfly larvae that can stabilise fine gravel grains with silk that is spun with the purpose of trapping organic material from the flow. Other organisms directly alter environments for their benefit, such as beavers damming channels to create ponded sections of river that offer a more favourable environment. The presence and activity of organisms in rivers can have an influence on the fluvial environment at a complete range of scales, from trees altering channel planform across entire catchments to insect larvae that winnow fine sediment from between coarse grains (table 1.1). In fact, all organisms in rivers will impact the environment at some scale because their presence in the channel will alter the hydraulic environment. However, determining which organisms have an impact at a scale that is of relevance to understanding fluvial processes is an important, interdisciplinary, research question that remains largely unanswered.

Table 1.1. *A synthesis of organisms that are known or suspected to alter fluvial processes and environments, including an indication of the scale of impact.*

Organism		**Activity**	**Impact**	**Scale**
Terrestrial Plants		Root growth	Planform control , bank stabilisation	Catchment
		Large Woody Debris	Planform/channel change, alterations to bed morphology and hydraulics.	Reach
In-channel macrophytes			Alterations to bed morphology and hydraulics. Sedimentation.	Reach
Algae and biofilms			Stabilisation of fine sediments	Patch
Livestock and large mammals, i.e. hippopotamus, wildebeest		Trampling, wallowing.	Bank and bed instability, fine sediment inputs, channel creation	Reach
Beavers		Building dams	Hydraulic alteration, planform change.	Catchment
Crocodilians		Nesting, trampling Wallowing	Bank stability, fine sediment inputs	Reach?
Amphibians	Adult frogs and toads	Nesting	Burrowing, digging nests and constructing channels in river banks	Patch?
	Tadpoles	Foraging	Winnowing of fines	Patch?
Fish	Salmon, trout	Nesting	Gravel structure and stability, hydraulics, winnowing of fines	Reach
	Bream, chub, lamprey, bass, stickleback	Nesting	Gravel structure and stability, hydraulics, winnowing of fines	Reach?
	Gudgeon, barbel, carp	Foraging	Gravel structure and stability, winnowing of fines?	Reach?
Invertebrates	Insect larvae	Faecal matter production	Increased turbidity	Catchment
	Caddisfly larvae, chironomids	Silk and mucus production	Stabilisation of gravels and sands	Patch?
	Shrimp, mayfly and stonefly larvae, crayfish	Foraging	Winnowing of fines	Patch?
	Worms	Burrowing	Alterations to substrate porosity and permeability	Patch?
	Crayfish	Burrowing	Bank and bed instability, increased turbidity, winnowing of fines	Reach?

1.5. Crayfish ecology

1.5.1. Crayfish taxa and distribution

There are over 500 species of crayfish, with representation on every continent, with the exception of Antarctica. Not only are crayfish present on a large spatial scale, they are believed to have evolved from marine lobsters 300 million years ago at the Permian–Triassic boundary (Martin *et al*., 2008). Trace fossils of crayfish burrow systems imply that the burrowing instincts of crayfish have been present for at least 250 million years (Hasiotis and Mitchell, 1993; Berbatau *et al*., 2008). This study focuses on the signal crayfish (*Pacifastacus leniusculus*) which is a large, hardy species that prefers cool, temperate areas. They are native to north-western USA but their size and rapid growth makes them an ideal aquacultural species. Consequently, they have been widely introduced and are now present as an invasive species along the western coast of the USA, Japan and in approximately 20 European nations, including the UK where they were introduced in the 1960s (Holdich, 2002b; Machino and Holdich, 2005).

1.5.2. Crayfish life history and functional role in ecosystems

Signal crayfish typically attain a maximum carapace length (measured from tip of rostrum to end of carapace) of 50 – 70 mm, although individuals up to 95 mm have been recorded in the UK (Holdich, 2002a; Lewis, 2002). It is estimated that signal crayfish can live between 16 and 20 years, but it is unlikely that crayfish in the wild will live to such ages. Survival to age two years is estimated to range from 10 to 52%, depending on abiotic and biotic factors (Lewis, 2002). Signal crayfish usually reach maturity at 2 to 3 years of age. Mating and egg laying occur during October in the vast majority of signal crayfish populations and hatching occurs from March to the end of July, depending on latitude and temperature (Lewis, 2002). Eggs are carried by females on their pleopods, and incubation of eggs lasts from 166 to 280 days. Eggs hatch into miniature crayfish that stay with the mother. Juveniles undergo as many as 11 moults during their first year. By age 3, this is reduced to two moults per year, and by age 4 onwards, one moult a year (Lewis, 2002).

Signal crayfish are considered nocturnal, with maximum activity occurring during dusk-like conditions (Hazlett *et al*., 1974; Hamrin, 1987; Guan and Wiles, 1998). They are omnivorous and exploit a large variety of food sources. They can also alter their diet depending on the availability of food sources (Alcorlo *et al*., 2004). Gut contents analysis of signal crayfish in the River Great Ouse, England, found 22 food groups, the top five being vascular plant detritus, filamentous green algae (*Cladophora*), crayfish fragments, Chironomidae (non-biting midge larvae) and Ephemeroptera (mayfly larvae; Guan and Wiles, 1998). There is suggestion that adult crayfish consume more plant and detrital material than juveniles (Momot *et al.*, 1978; Guan and Wiles, 1998; Parkyn *et al.* 2001; Lewis, 2002), but there is increasing evidence that the importance of detritus and plant material in terms of nutritional requirements has been overemphasised (Ilhéu and Bernardo, 1993; Momot, 1995; Parkyn 2001; Bondar *et al.*, 2006). It is likely that feeding behaviour of crayfish is at least partially reliant on hunting efficiency. Crayfish are known to be predators of slower moving invertebrates such as snails, leeches and mussels and have been shown to have significant effects on the behaviour of snails (Crowl and Covich, 1990; Alexander and Covich, 1991). Although they will attempt to catch the fastest moving prey (Rubin and Svensson, 1993; Guan and Wiles, 1997), capture of mobile animals like fish is challenging (D'Abramo and Robinson, 1989) and this may explain why crayfish prefer detritus and slower moving species.

Crayfish play an important and complex functional role in ecosystems, due to their omnivory (Momot, 1995). Crayfish influence the presence of other organisms through predation, the shredding of organic matter, detrital processing and collecting and grazing plant material which influences its abundance, as well as the habitat heterogeneity (Feminella and Resh, 1989; Weber and Lodge, 1990; Creed, 1994; Usio and Townsend, 2001). In particular, crayfish play a major role in the breakdown of leaves and other organic matter into fine particulate organic matter (FPOM) (Momot, 1995; Parkyn *et al.*, 1997; Schofield *et al.*, 2001). Usio and Townsend (2001) found that crayfish in a headwater stream in New Zealand dominated the shredder functional feeding group, comprising an average of 99% of the total biomass of shredder invertebrates. Where crayfish occur as invasive species they can have substantial negative impacts on the ecological community. In particular, they have significant detrimental impacts on juvenile fish, native crayfish and other invertebrate species which they predate and out-compete for resources, such as shelter (Guan and Wiles, 1997; Holdich *et al.*, 1999; Vorburger and Ribi, 1999; Usio *et al.*, 2001; Stenroth and Nyström, 2003; Crawford *et al.*, 2006). They can also significantly reduce macrophyte and algal cover, removing sources of food and shelter (Creed, 1994; Lodge *et al.*, 1994; Nyström *et al.*, 1996).

1.5.3. Inter- and intra-species interactions

Crayfish are aggressive invertebrates, competing for resources such as food, shelter and mates (Vorburger and Ribi, 1999; Bergman *et al*., 2003). To minimise aggressive encounters between individuals (agnostic interactions), crayfish interact according to a hierarchical system, whereby the dominant individual gets control of contested resources. However, crayfish will still form dominance hierarchies when no resource other than space is being contested (Bovbjerg, 1953; Lowe, 1956). An aggressive encounter between two crayfish escalates through several stages of increasing fight intensity, initiated with threat displays, and followed progressively by ritualised aggression, restrained use of the claws and, finally, brief periods of unrestrained combat (Huber and Delago, 1998; Goessmann *et al*., 2000). Fighting continues until one opponent retreats, either by crawling or backward swimming away from the opponent (Harrison *et al*., 2006). Physical attributes such as body size (Bovbjerg, 1970; Rubenstein and Hazlett, 1974; Pavey and Fielder, 1996) and chelae size (Garvey and Stein, 1993; Rutherford *et al*., 1995) are good predictors of crayfish dominance.

Crayfish are competitive and can have detrimental impacts on other species of crayfish, as well as some fish species (Guan and Wiles, 1997; Rubin and Svensson, 1993). In particular, signal crayfish are known to aggressively defend shelters and will often prevent juvenile fish from sheltering, making them susceptible to predation and entrainment (Griffiths *et al*., 2004). Juvenile crayfish are vulnerable to aquatic predators because of their small size and more frequent moults which result in them being soft and unprotected for extended periods (Lodge and Hill, 1994). Adult crayfish are less susceptible but are still at risk from terrestrial predators, including wading birds. In response to a predator, a crayfish can escape through 'backward swimming' which involves using repeated tail-flips to propel itself rapidly off the substrate and away from a dangerous situation (Webb, 1979; Cooke and McMillan, 1985). Alternatively, a crayfish can alter its behaviour such as increasing its use of shelters or attempting to deter predators with chelae displays (Stein and Magnuson, 1976; Shave *et al*., 1994). Where signal crayfish are invasive they will alter their behaviour in response to non-predatory fish, reducing their foraging behaviour and spending more time in shelters at night (Nyström, 2005).

1.5.4. Movement and habitat preference of signal crayfish

Signal crayfish occupy a range of habitats from small streams to large rivers and lakes. They are tolerant of brackish water and high temperatures but do not occur in waters with a pH lower than 6.0 (Nakata *et al.*, 2002). Signal crayfish are thought to prefer either cohesive substrates within which they can burrow or coarse substrates where they can shelter under large rocks (Parkyn *et al.*, 1997; Lewis, 2002). Burrows into cohesive material can be abundant (5.6 per metre of bank), and can cause destabilisation and bank collapse (Guan, 1994). Signal crayfish populations are distinctly spatially size-sorted in streams. Juvenile crayfish are restricted to shallow, riffle areas, whereas adults tend to be found inhabiting deeper pools (Guan and Wiles, 1996; Englund and Krupa, 2000; Harrison *et al.*, 2006). Therefore, it is likely that larger adult crayfish displace smaller crayfish from pools until juveniles become large enough to successfully compete for resources and shelter (Edsman and Jonsson, 1996; Harrison *et al.*, 2006). The preference of pools by crayfish may be due to the large body size of adults making movement more difficult in shallow, high velocity flows, or deeper water may provide better physical and visual cover from terrestrial predators (Power, 1984).

It has been suggested that water depth is the over-riding hydraulic habitat variable for the crayfish species *Orconectes propinquus*, with large crayfish found to avoid shallow habitats regardless of current velocity (Creed, 1994). There is evidence that high flows can displace and cause mortality of several crayfish species (Momot, 1966; Robinson *et al.*, 2000; Royo *et al.*, 2002). Jowett *et al.* (2008) found, in a large-scale habitat study, that the crayfish *Paranephrops planifron* was present in river reaches with velocities between 0 – 0.4 m s^{-1}, which is consistent with laboratory studies which have found a number of crayfish species begin to lose footing in flows greater than 0.4 m s^{-1} (Maude and Williams, 1983; Clark *et al.*, 2008). Despite this evidence, Bubb *et al.* (2002a, 2004) found that signal crayfish were not entrained by high flows, maybe because crayfish shelter in burrows or flow refugia during flood flows. Consequently, high flows have a significant influence on the activity of signal crayfish as, during high flows, their activity is reduced whilst they remain in refuges.
Signal crayfish have been found to migrate long distances (> 500 m) in upstream and downstream directions (Bubb *et al.*, 2004), as well as moving overland to avoid obstacles. Whilst crayfish can move on land, their movement is far quicker and smoother when submerged, probably because the body weight of crayfish is between 400 – 600% greater on land than under water (Pond, 1975). Crayfish can walk forwards, backwards and sideways

and are agile climbers of vegetation (Pond, 1975). There is evidence to suggest that the upstream movement of signal crayfish is dictated by river gradient. Guan and Wiles (1999) found that signal crayfish movement was only weakly biased in a downstream direction in the River Great Ouse (gradient 0.00118), whereas Bubb *et al.* (2004) found a much stronger bias in the upland River Wharfe (0.00370) and River Ure (0.00233). The reduced upstream movement in steeper rivers may be due to higher flow velocities through the channel, the steepness of the bed, the presence of bedforms such as steps or riffles which may act as barriers to movement, or be a function of a correlated parameter such as flow depth or grain-size (Bubb *et al.*, 2004; Light, 2003).

1.6. Thesis aims and structure

1.6.1. Aims

Previous research has shown that crayfish can winnow fine material from gravel substrates and increase the mobility of substrates after crayfish activity. Whilst these studies have identified that crayfish can modify substrates, they have not determined the activity of crayfish responsible for this disturbance or quantified the impact of this substrate reworking. Nor have they determined the physical limits of crayfish disturbance, i.e. grain-sizes that can be moved. Also, previous experiments have predominately focused on the disturbance of fine sediment by crayfish rather than their impact on the framework grains. An exception is the work of Statzner *et al.* (2000) who noted that crayfish had altered the crest of small gravel riffles.

This project aims to build on this previous work by first examining in detail the potential impact of crayfish on gravel substrates and identifying the limits to crayfish disturbance in terms of grain-sizes that can be moved and the period of time over which crayfish have an impact (Aim 1). The project also aims to determine whether the disturbance of water-worked sediments by crayfish can alter the stability of grains through structural and topographic modifications made to the substrate (Aim 2). Finally, the project aims to link these experimental results to a field environment, a stage which is rarely undertaken in studies which are predominately undertaken in the laboratory. It is necessary to give environmental and ecological context to experimental results in order to determine their significance (Aim 3). Individual objectives within these three broad aims are discussed in relevant chapters.

1.6.2. Thesis structure

The following three chapters are each based on an individual, self-contained, yet interlinked series of experiments. Chapter 2 details a series of experiments conducted in still-water aquaria concerned with Aim 1. Chapter 3 explains a series of flume experiments which were undertaken subsequent to the still-water experiments, described in chapter 2. These were focused on exploring Aim 2. Chapter 4 details a field experiment which involved tracking crayfish using radiotelemetry and relating their location to known substrate facies. This information was used to relate laboratory experiments to a field environment in response to Aim 3. Each of these three chapters contains a brief introduction and review of literature specific to the experiments detailed in that chapter. Each chapter also contains a methods section and a results section. Following presentation of the results within each chapter is a brief discussion of the experimental results specific to, and limited to, the experiments described in that chapter. A broader discussion of the results, linking all three experimental sections together, and a discussion of the significance of crayfish as geomorphic agents in rivers is included in chapter 5. Concluding remarks are included as chapter 6.

Chapter 2

Impact of crayfish on substrate topography.

2.1. Introduction

Due to their importance, as well as their relatively large size and long life, crayfish species are considered to be some of the most notorious invasive organisms in freshwater environments (Lodge *et al*., 2000), resulting in substantial negative impacts on many native species. Previous studies have shown that crayfish impact the physical environment by burrowing into banks and by winnowing fine sediment from substrates. These physical impacts can be added to the key ecological impacts crayfish have on the wider community through trophic and competitive interactions, including by shredding coarse organic matter into finer pieces. The experiments described in this chapter aim to determine whether signal crayfish, a species invasive to the UK, can alter the microtopography of gravel substrates with implications for gravel stability.

2.2. Aims

Previous studies have examined how disturbance by crayfish is influenced by abiotic and biotic interactions (Statzner *et al*., 2000, 2003; Statzner and Peltret, 2006; Statzner and Sagnes, 2008). However, without a detailed understanding of how and the extent to which crayfish move material, it is difficult to draw conclusions about their potential impact on physical processes such as sediment transport.

The aim in this chapter is to quantify the impact of crayfish bioturbation on the topography of gravel substrates. In contrast to previous experiments, the impact of individual crayfish has been assessed whilst keeping all other factors constant. There are three specific objectives:

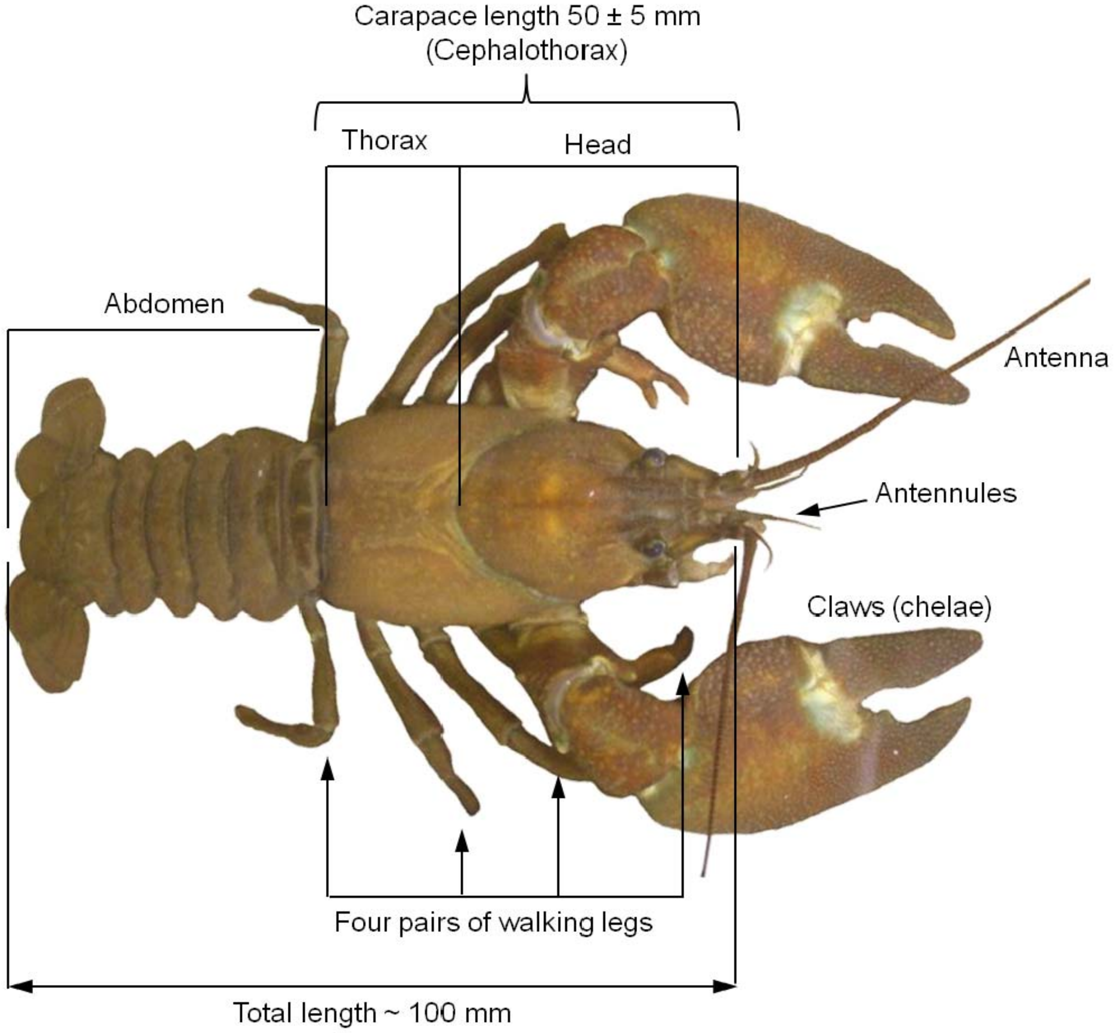
(i) to determine whether crayfish can alter the microtopography of gravel substrates
(ii) to quantify the mechanisms of disturbance
(iii) to determine the influence of grain size on crayfish impacts;
(iii) to determine how reworking of gravel substrates by crayfish is influenced by the length of time crayfish are present on a substrate.

2.3. Methods

2.3.1. Crayfish aquaculture

The crayfish used in this set of experiments were caught with baited crayfish traps in Wood Brook, near Loughborough, UK (1°13’41’’ W., 52°45’24’’ N.) and transported to the laboratory under licence from the Environment Agency of England and Wales and the Department for Environment, Food and Rural Affairs (DEFRA). To limit the variability of impact that might be associated with differing size and age, only individuals with a carapace length of 50 ± 5 mm (approximately 100 mm total length) and having a sub-aerial weight of 55 ± 10 g were selected (figure 2.1). Signal crayfish typically attain a maximum carapace length of 50 – 70 mm, although individuals up to 95 mm have been recorded in the UK (Holdich, 2002a). Selected individuals were also without obvious injury (such as the loss of legs, claws, or antennae) as this affects their exploratory behaviour (Basil and Sandeman, 2000; Koch *et al*., 2006). De-selection also included crayfish with small claws relative to their body size as this indicates previous loss of a claw that is in the process of growing back. The sex of the crayfish was recorded. However, both males and females exhibit no significant differences in activity (Guan, 1994), so the influence of this was not considered in the experiments.

Figure 2.1. *Photograph of a signal crayfish with the measurement criteria for carapace length.*

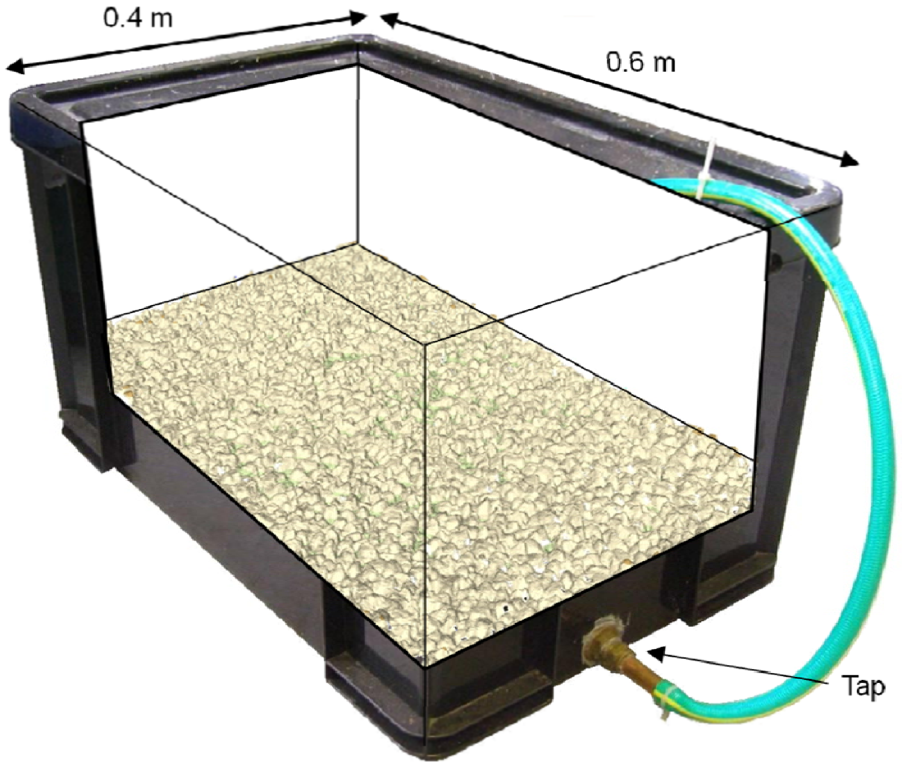


The animals were housed individually, each in anaquarium (figure 2.2a, b) constructed from a plastic box (0.6 x 0.4 x 0.4 m) that had black, opaque sides, as it is known that crayfish survival increases in dark environments (Lewis, 2002) and darkness avoided the experimental complications associated with shadows or movements within the laboratory. Each aquarium had a secure lid with a central opening of 480 x 240 mm that was covered in wire mesh to prevent escape. Ten aquaria were used simultaneously. The aquaria design is similar to ecological studies that have also housed crayfish in still-water aquaria with opaque sides (Figler *et al*., 1999; Issa *at el*., 1999; Basil and Sandeman, 2000; Herberholz *et al*., 2003;

Savolainen *et al.*, 2003; Patullo and Macmillan, 2006; Song *et al.*, 2006). Water temperature was not controlled in this study, but it was monitored and remained consistent between the 10 aquaria, staying between 15 and 21°C for the duration of the experiments. This is well within the temperature range of signal crayfish (Nakata *et al.*, 2002) and is similar to recorded temperatures in other laboratory studies (Crawshaw, 1974; Mundahl and Benton, 1990; Basil and Sandeman, 2000). Each aquarium had a filter pump that circulated water through the tank, removing waste and aerating the water. No shelter was provided for the crayfish whilst experiments were running in order to encourage activity. Pellet fish food had been provided before the start of each experiment and every other day when individuals were not involved in experiments.

Figure 2.2. a) *The internal dimensions of experimental aquaria used in these experiments. The green hose is connected to a tap in the base used to drain aquaria before laser-scanning the surface topography. b) The ten aquaria housing crayfish in the hydraulics laboratory.*

a)



b)

Intra-specific interactions were not studied in experiments as the interaction between crayfish can be highly variable. As such, it would incorporate variability into the results making it difficult to identify trends between crayfish activity and abiotic conditions. Also, biotic variables rarely act in isolation. For instance, two crayfish may interact differently in the presence of a predator or be more aggressive to each other if food or shelter is limited. Therefore, without a detailed understanding of the phenomenon being studied it is difficult to incorporate such complex, dynamic interactions into experiments. These experiments, however, provide this important background information, providing a knowledge base upon which complex and dynamic biotic and abiotic variables can be incorporated effectively.

2.3.2. Experimental procedure

The gravel surface in each aquarium was screeded flat to form a 0.1 m deep, planar substrate, sufficiently deep for crayfish to burrow without reaching the base of the aquarium. A digital elevation model (DEM) of the initial surface was interpolated from a laser scan obtained using a Konica Minolta tripod-mounted laser scanner (section 2.3.4). The tank was filled to a depth of 0.2 m above the gravel surface by slowly introducing water through a hose placed against the side wall of the aquaria with great care to avoid rearrangement of substrate grains.

The filter pump was activated and a single crayfish was released approximately 50 mm above the gravel surface, allowing it to drift slowly onto the bed. Each crayfish was left on a prepared gravel surface in the aquarium for a predetermined period, after which it was removed by hand and the water drained slowly through a tap in the base so as not to disturb the gravel. Once drained, the gravel surface was scanned for a second time. The difference between these two scans, termed a DEM of Difference (DoD) was calculated to quantify a volumetric measure of disturbance by crayfish (section 2.3.4).

In order to estimate the number of grains that were displaced by the crayfish on each substrate, half of the total volume change was divided by the average grain volume of each grain size fraction, after allowing for a porosity of 0.3 (Bunte and Abt, 2001). Half of the total change was used because the DoDs reflect a volume change associated with the new location of a transported grain as well as the void it has left. Grain volume was approximated by assuming an ellipsoid and using average values of the principal axes measured on a subsample of grains from each grain size fraction. A measure of porosity was incorporated to account for the fraction of the total volume difference between surfaces which would unavoidably be associated with voids between grains. This would otherwise be erroneously included in the volume of material moved by crayfish.

2.3.3. Experimental variables

Three series of experiments were conducted, all following the procedure described above. The first (*series 1*) examined how gravel disturbance changed with the length of time that a crayfish was left on a substrate. Screened, 8 – 11 mm (3 – 3.5 φ) marine gravel was used. It consists mainly of chert and the grain density approximates 2650 kg m^{-3}. Clasts were predominantly compact-bladed (Sneed and Folk, 1958) and rounded (0.6 particle roundness; Krumbein, 1941). Crayfish were left on this substrate for either 6, 24, 48, 72, or 96 hours, with 10 replications for each period.

A second series of experiments (*series 2*) also investigated the influence of the period of potential substrate reworking. In this case, shorter intervals of animal occupance were used to obtain a higher resolution data set, but without replication of each time period. A single crayfish was again left on a screeded, 8 – 11 mm (3 – 3.5 φ), gravel bed for a set period. These periods increased in length by 30 minutes up to 24 hours and then by 60 minutes up to 96 hours. An accumulating increase in volume change was not attempted. Instead, ten crayfish were used with each left for a different period of time on a planar surface. In each case, DEMs were obtained at the beginning and end of the set period, giving a total volume of disturbance for that period. After the second DEM was obtained, the substrate was re-set to a planar surface by screeding and a different crayfish was left on this new surface for a new set period. Consequently, rather than giving an accumulating increase in volume change, a total volume change for a range of periods was obtained. An accumulating increase could not be measured as it was necessary to drain aquaria before laser scanning. As crayfish would have to be removed during draining, their re-introduction could instigate re-exploration of the surface as if it was a new environment.

The third series of experiments (*series 3*) aimed to determine what grain sizes could be moved. To establish this limit, individuals were left on one of six narrowly graded and screeded grain sizes (table 2.1). These grain size fractions were determined after considering the *b*-axis diameter and particle weight and allow for an incidental consideration of the influence of grain shape through comparison with *series 1*, as well as size, on substrate reworking by crayfish. The gravel used in this series was obtained from the River Lune, England, consists mainly of limestone with minor contributions of sandstone and has a grain density of approximately 2650 kg m^{-3} (Graham *et al.*, 2005; table 2.1). It was predominately bladed (Sneed and Folk, 1958) and well rounded (0.8 particle roundness, Krumbein, 1941), allowing for a consideration of the influence of grain shape, as well as size, on bioturbation by crayfish. Crayfish were left on each screeded substrate for 24 hours, with 10 replications for each grain size.

Table 2.1: *Characteristics of gravels. The submerged weight was measured from a 100 grain sub-sample of material from each grain size fraction.*

Grain size (b-axis, mm)	Average clast volume (cm^3)	Average clast submerged weight (g)	Average clast submerged density
8 – 11	0.6	0.97	1.62
11 – 16	1.7	3.4	1.65
16 – 22	4.7	7.5	1.6
22 – 32	14.2	21.4	1.58
32 – 38	32.1	53.7	1.62
38 – 45	76.2	121.9	1.6

2.3.4. Creation and analysis of Digital Elevation Models (DEMs)

A Konica Minolta Non-Contact 3D Digitizer Vivid 910/VI-910 laser scanner was used to measure gravel surfaces in these experiments. Three-dimensional spot-height data were obtained from a single laser scan in each case, the axis of the scanner being perpendicular to the gravel surface, yielding approximately 240 000 irregularly spaced x, y and z coordinates with an average xy spacing of 1 mm. These surfaces were broadly cropped to remove outlying material and orientated in the software associated with the laser scanner (Polygon Editing Tool). Laser scanned surfaces were also georectified relative to other laser scans using the Polygon Editing Tool software which matches common points on scans which, in this case, were fixed reference points. Scans of the same surface before and after exposure to crayfish were rectified relative to each other by picking identical points on both surfaces. The identical points used were reference points attached to the side wall of aquaria. At this stage, *z*-values represented the distance from the surface to the scanner. This was converted in the program Rapidform so *z*-values represented height from a user-defined zero plane. Surfaces were saved as ASCII point files.

Before analysis, ASCII files had to be converted to digital elevation models (DEMs) which was undertaken in ArcGIS 9.2. A DEM can be represented as a TIN (triangular irregular network) or as a raster (a grid of squares). TINs can have irregular point spacing and density and create surfaces by triangulating a set of vertices which are connected by a series of edges, forming a network of triangles. Consequently, the resolution of the surface is greater in areas where there is a greater density of points. TINs were used to visualise scans as they better represent surfaces than gridded data but were not used for analysis. Instead, TIN surfaces were gridded to form raster DEMs with a 1 mm cell spacing using a kriging interpolation in ArcGIS. Whereas vector surfaces, such as TINs, present elevations as nodes with vertices connecting points, raster surfaces are a regular grid of rectangular cells with each cell having a value that, in this case, was elevation. Raster data is less spatially accurate than vector data as a point height is generalised across an entire rectangular cell. The incorporation of artefacts into a model can be minimised providing the grid resolution is relatively small such as in this study where cells were 1 mm^2 across a 240 000 mm^2 surface (Brasington *et al.* 2000).

Before analysis, surfaces were detrended and cropped using the mask tool. As it is the grain scale morphology that is of interest, it is important to remove larger trends in elevation such as bed slope which will influence the *z*-values across surfaces, potentially influencing grain-scale trends if not accounted for. To detrend surfaces, the raster DEM was interpolated using a third order polynomial with the 'trend' function (3D Analyst Tools → Raster Interpolation). This produces a new raster surface which represents the large scale trends of the data-set. This surface was subtracted from the original DEM using the 'raster calculator' (Spatial Analyst) with the resultant surface representing a detrended surface with large scale (3rd order polynomial) trends removed. The detrended raster was then cropped to 400 x 600 mm using the mask function (Spatial Analyst Tools → Extraction → Extract by Mask) so that all surfaces had the same dimensions.

All surface manipulation was undertaken in ArcGIS using 3D Analyst Tools and Spatial Analyst Tools. The topographic difference due to crayfish was calculated as the difference between raster surfaces before and after exposure to crayfish. The *z*-values (which represent elevation) of cells on one surface were subtracted from the *z*-values of the corresponding cells on the other surface to create a new raster surface where *z*-values represent the elevation difference. This was achieved using the 'raster calculator' (Spatial Analyst). This DEM of difference (DoD), had a zero plane that represented no topographic change. Volume and surface area associated with the change between surfaces was calculated using the 'area and volume' tool (3D Analyst → Surface Analyst). The roughness of surfaces was parameterized and compared using the standard deviation of elevations across entire surfaces from the raster models (Nikora *et al.*, 1998; Aberle and Smart, 2003).

2.3.5. Error analysis

An analysis was undertaken of the error associated with measurements derived from DoDs. The general experimental procedure described above was repeated 10 times with 8 – 11 mm (3 – 3.5 φ) gravel, but without adding crayfish. Consequently, the two DEMs obtained for each of the 10 experiments should be identical, and the DoDs should be flat surfaces on the zero plane. The results showed that errors ranged between -0.96 and 0.79 mm, with a mean value of -0.05 mm. The distribution of errors was leptokurtic and, as a result, significantly non-normal (Kolmogorov–Smirnov $p < 0.001$), indicating that a relatively small proportion of the distribution was associated with its tails. The distribution of error was not biased towards particular regions of the DoD surface; and the laser scanner does not produce systematic distortions, such as those associated with conventional photography, so no corrections are required. The measured error is associated partly with the measurement error of the laser scanner (quoted by the manufacturer as 0.4 mm in the z-axis) and partly with the experimental procedure, including small-scale dilation or consolidation of the substrate when submerged and subsequently drained. The interpolation of height values between measured points during DEM construction may also introduce small errors to the overall analysis, but because of the density of data in this study (1 point per mm over a surface of 600 x 400 mm), this source of error is likely to be negligible. The measurement error was taken into account in the analysis of results by using ± 1 mm as the minimum discernable difference. Consequently, differences $\leq \pm 1$ mm were considered to indicate no topographic change and, consequently, not included in volumetric measures.

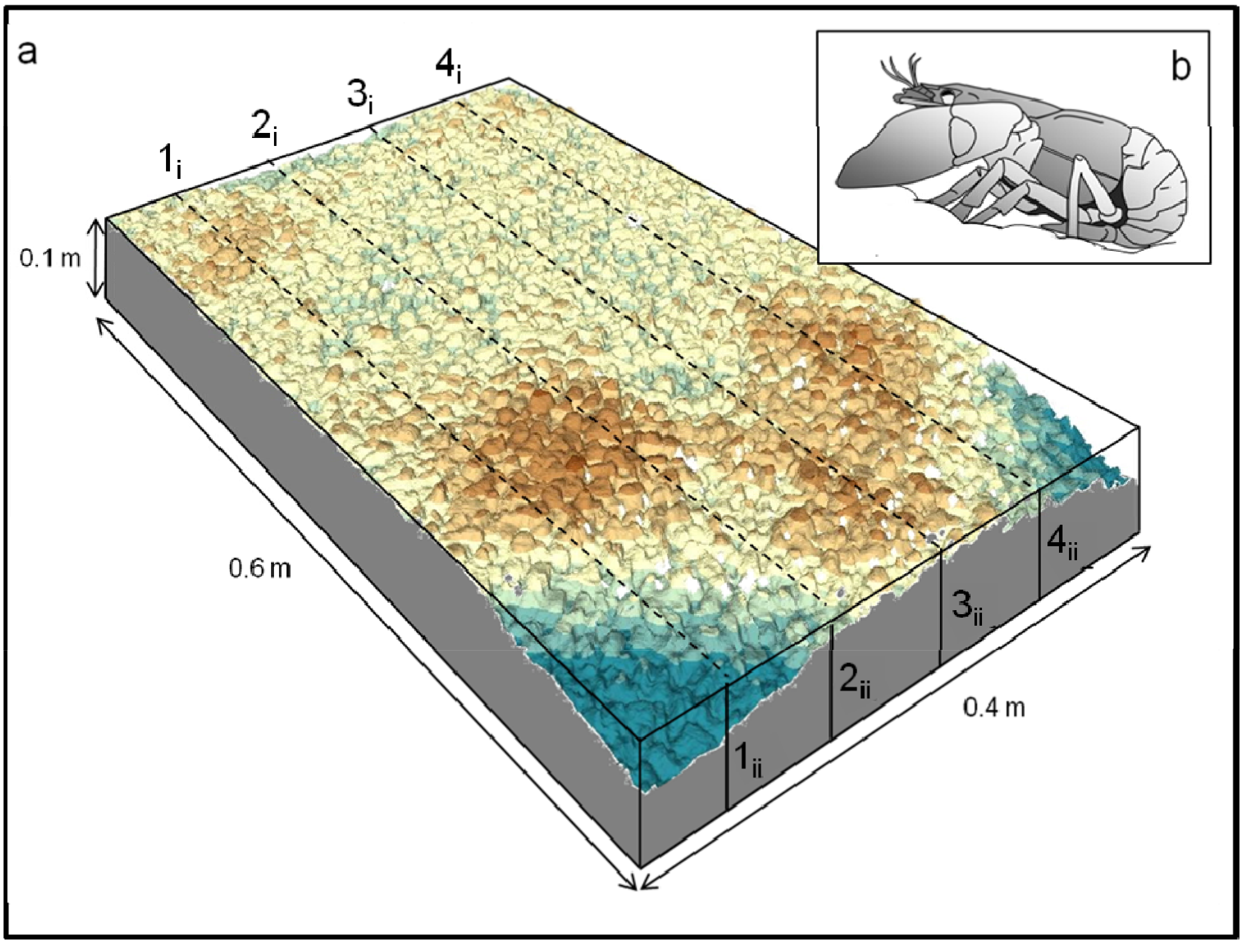
2.4. Results

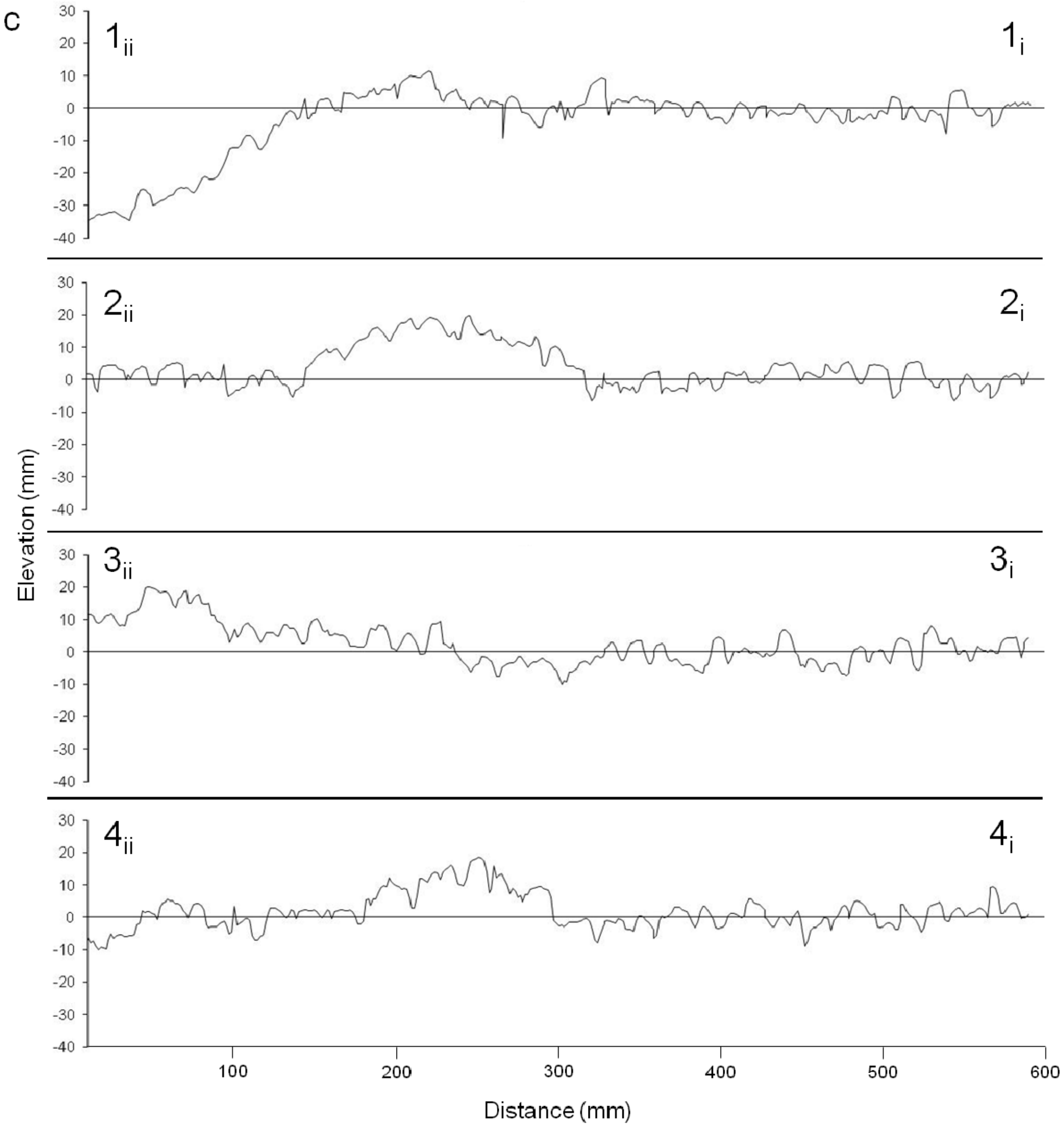
2.4.1. Methods of bed sediment disturbance by crayfish

Crayfish were observed to disturb the substrate in two distinct ways. The first was a rearrangement of surface grains that resulted in subtle adjustments of grain fabric. This was associated with walking and foraging for food by probing the bed with the front pairs of walking legs. The second was visually more dramatic and was associated with the construction of pits and mounds for shelter (figure 2.3). These two types of disturbance have been quantified by partitioning the topographic change of the initial planar surface. Fabric adjustment — the rearrangement of surface grains — has been defined as the volume of topographic change in those areas beyond pits and mounds where change in surface height exceeded the minimum discernable difference of ±1 mm, but was $\leq \pm 1$ median grain diameter (D_{50}). For areas where elevation changes were $\geq \pm 1$ D_{50}, calculated volumes have been attributed to pit digging and mound building. Whilst the incorporation of some mound material and pit excavation in the fabric adjustment volume is possible, the adoption of 1 D_{50} as the height change discriminator has ensured that this is minimized, given that all grains were narrowly graded and superimposition of a single grain on the screeded surface or removal of a single grain from the pit precinct would, on average, produce a height change > 1 D_{50}.

Pits were generally larger in volume than associated mounds (paired *t*-test; $p < 0.001$), but only because excavated material tended to be spread fairly widely across the substrate surface and, using the definitions given above, part has been unavoidably incorporated within the measure of fabric adjustment. The spreading of material was a combination of effort to push gravel away from pits to avoid slumping and an incidental result of activity associated with the brushing of grains when walking during forays. After 24 hours on 8 – 11 mm gravel, pits were, on average, 21 mm (2.2 D_{50}) deep, increasing to 29 mm (3.1 D_{50}) after 96 hours. Conversely, mounds were 16 mm high after 24 hours and 17 mm high after 96 hours, an increase of only 1 mm despite the same lapse of time. This is because crayfish aim at rapidly deepening pits for shelter, but derive no benefit from increasing the height of mounds. Indeed, distributing mound material widely, even if some or most of this is inadvertent, reduces its height and may ensure that both predators and competitors are seen earlier.

Figure 2.3. *a) DEM of an 11 – 16 mm gravel surface after 72 hours of exposure to signal crayfish with four transects (1 – 4) shown. Note the two large pits in the bottom corners of the surface that are surrounded by shallow mounds. b) Cartoon of the posture of a crayfish when sitting in a pit. c) Elevation data for the four transects (1 – 4) marked on the DEM with dashed lines.*




c
1ii
1i
2ii
2i
3ii
3i
4ii
4i
30
20
10
0
-10
-20
-30
-40
Elevation (mm)
100
200
300
400
500
600
Distance (mm)

2.4.2. Substrate reworking and length of exposure

Crayfish were able to move substantial volumes of 8 – 11 mm gravel within 6 hours of being introduced to the substrate (*series 1*; figure 2.4). Length of time of activity was significant for both fabric adjustment (ANOVA; $p = 0.047$) and pit and mound construction (ANOVA; $p = 0.041$). However, Tukey post-hoc tests do not extract which time period is significantly different due to the discrepancy in statistical power between the two tests (table 2.2). Figure 2.4 shows that the majority of grain displacements occurred in the first 6 hours. It also shows a stepped increase in volume change at 48 hours for both fabric adjustment and pit and mound construction. Of interest is that pit and mound construction accounts for a relatively small proportion of the volume change, by comparison with fabric rearrangement. Indeed, in this series of experiments on 8 – 11 mm substrates, an average of 22% (range: 4 – 56%) of the material that was moved was associated with the excavation of pits and the construction of mounds, the remainder being associated with fabric adjustments.

Table 2.2: *Tukey post-hoc p levels of differences in the volume change in gravel surfaces exposed to crayfish for one of five time periods: 6, 24, 48, 72 and 96 hours. The length of time present is statistically significant (ANOVA; p = 0.047) but Tukey post-hoc does not determine which variables are significantly different, hence all p values > 0.05.*

	6	**24**	**48**	**72**	**96**
6					
24	1.000				
48	0.360	0.297			
72	0.142	0.110	0.985		
96	0.090	0.068	0.946	0.999	

Figure 2.4. *Mean (and two standard errors, n = 10) of surface volume change arising from the introduction of a single crayfish on a screeded, planar, 8 – 11 mm gravel surface (600 x 400 mm) for each of five intervals (6, 24, 48, 72, 96 hours) (series 1 experiments). For each time period, unshaded bars indicate fabric adjustment and grey bars indicate pit and mound construction.*

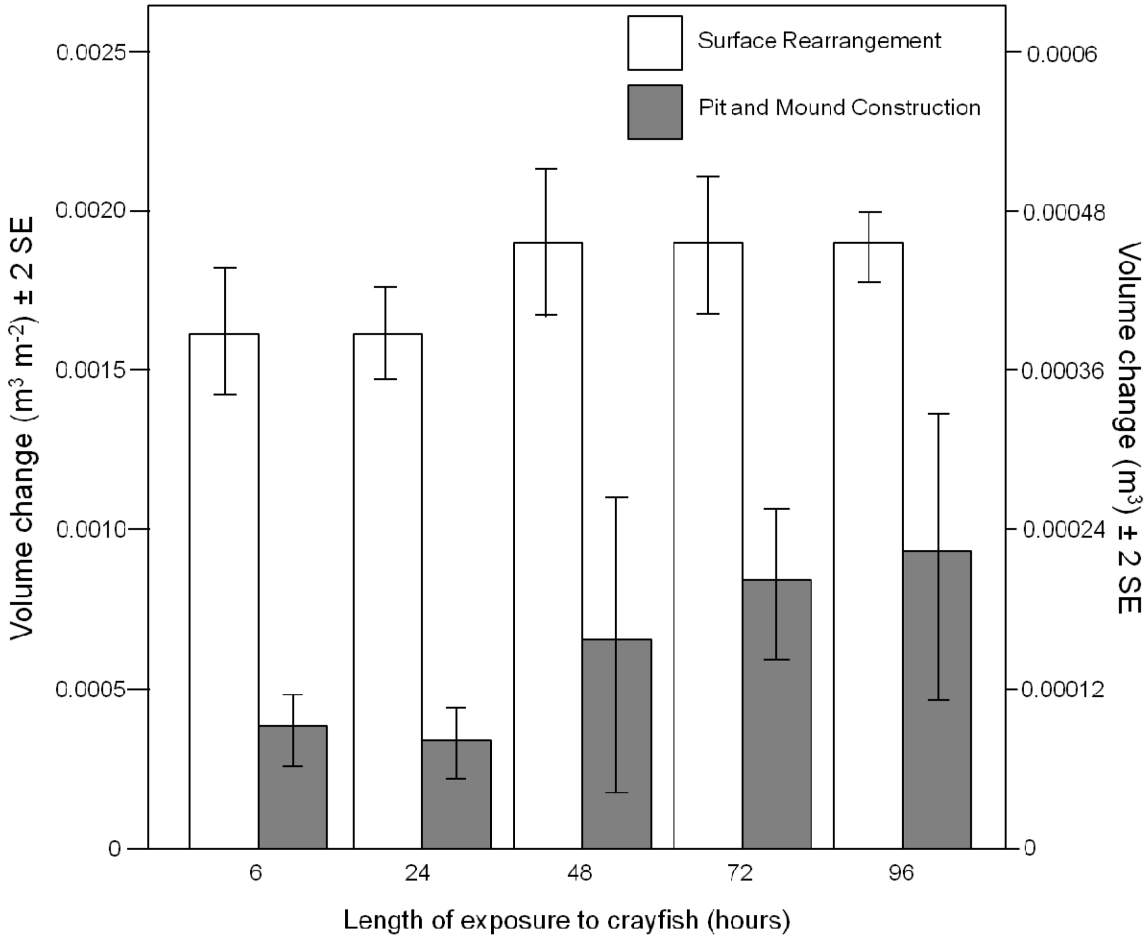
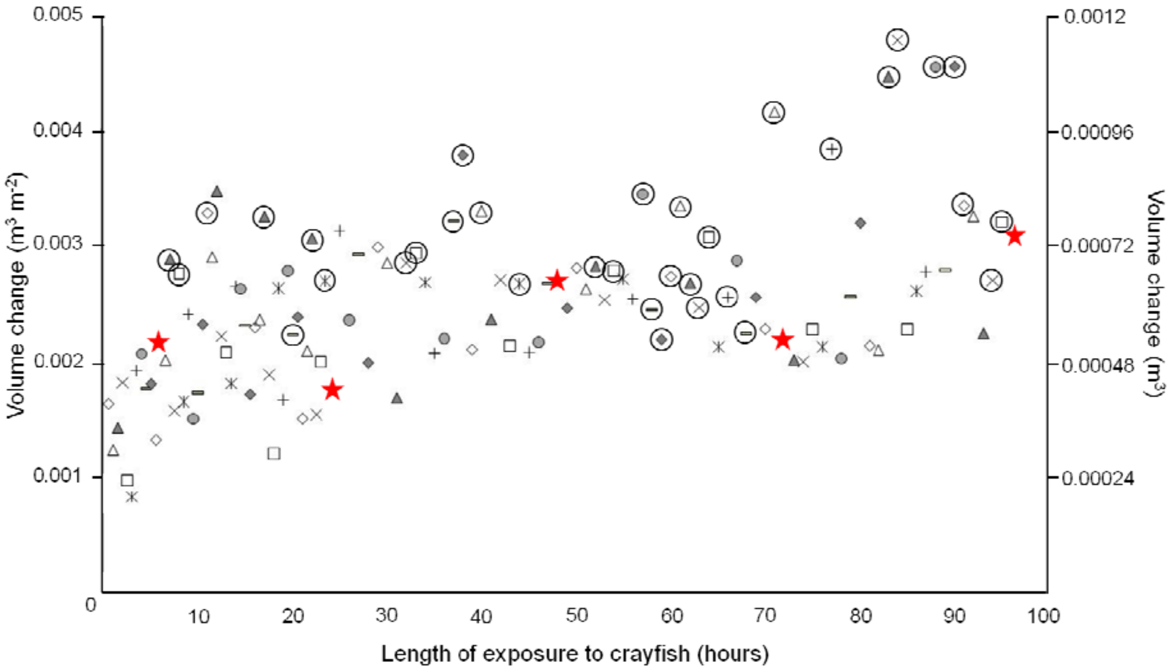


Figure 2.5 shows the volume of material moved by crayfish over periods ranging from 0.5 to 96 hours (*series 2*). Each data point represents a single surface, with volume changes from an individual crayfish plotted against the length of time of exposure. Ten crayfish were used in these experiments, and the impact of each is indicated by a different symbol. The results show an initial period of disturbance followed by a prolonged period when the total volume of material moved did not significantly increase further. The greatest rate of activity was in the first 3 – 5 hours and the majority of bed disturbance occurred within the first 10 – 15 hours of crayfish presence. Beyond about 15 hours, the total volume change was generally

indiscernible, except in those few cases where significant proportions (> 10%) of the surface were associated with late-stage pit and mound construction.

Figure 2.5. *The total surface volume change arising from the introduction of a single crayfish on screeded, planar, 8 – 11 mm gravel surfaces (600 x 400 mm) for a predetermined period of time. Ten crayfish (identified by a specific symbol) were left on substrates for periods ranging from 0.5 to 96 hours (*series 2 *experiments) after which they were removed and the substrates reset by screeding. Red stars represent the mean volume change derived from series 1 experiments (figure 2.4). Those surfaces with ≥ 10% of the surface area associated with pit and mound construction are circled.*



2.4.3. Grain size and the movement of gravel

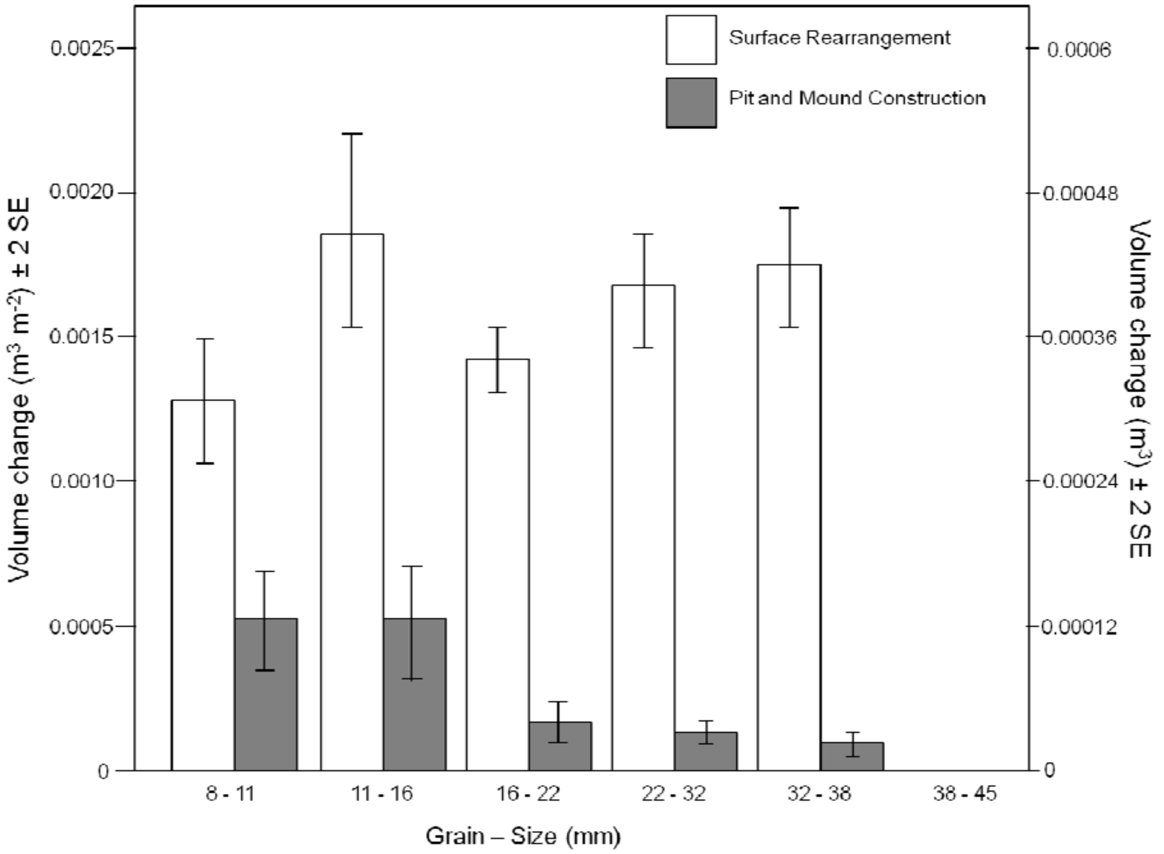
Crayfish moved a wide range of grain sizes, but did not move grains coarser than 38 mm in diameter (*series 3*; figure 2.6a). These 38 mm grains had a mean submerged weight of 54 g, corresponding to six times the mean submerged weight of the crayfish. Of interest is that pit and mound construction became less prevalent as grain size increased (figure 2.6a). Indeed, it became indiscernible where the gravel exceeded 22 mm, at least for the size of crayfish used in these experiments (figure 2.6b).

The volume change differs between grain size fractions for both fabric adjustment (ANOVA; $p = 0.003$) and pit and mound construction (ANOVA; $p < 0.001$; figure 2.6a). Whilst the only significant difference indentified by post-hoc tests for fabric adjustment was that between 8 – 11 mm and 32 – 38 mm substrates (Tamhane T2; $p = 0.48$), figure 2.6 suggests a greater volume of 11 – 16 mm material has been moved than is the case with fractions both finer and coarser. As this cannot be explained by particle weight alone, it is suggested that it is a function of the relation between grain weight and volume (table 4.1). The 8 – 11 mm grains were light enough for crayfish to cause widespread disturbance, but were each of such small volume (0.6 cm^3) that the cumulative volumetric impact was limited. The 16 – 22 mm grains were heavy enough to limit crayfish disturbance, but each had a large volume (4.7 cm^3) so that only a few grains needed be disturbed to match the volume of displaced 8 – 11 mm material. In contrast, the 11 – 16 mm grains are both light enough for crayfish to move easily whilst also having a large enough volume (1.7 cm^3) to account cumulatively for the large volume of moved material.

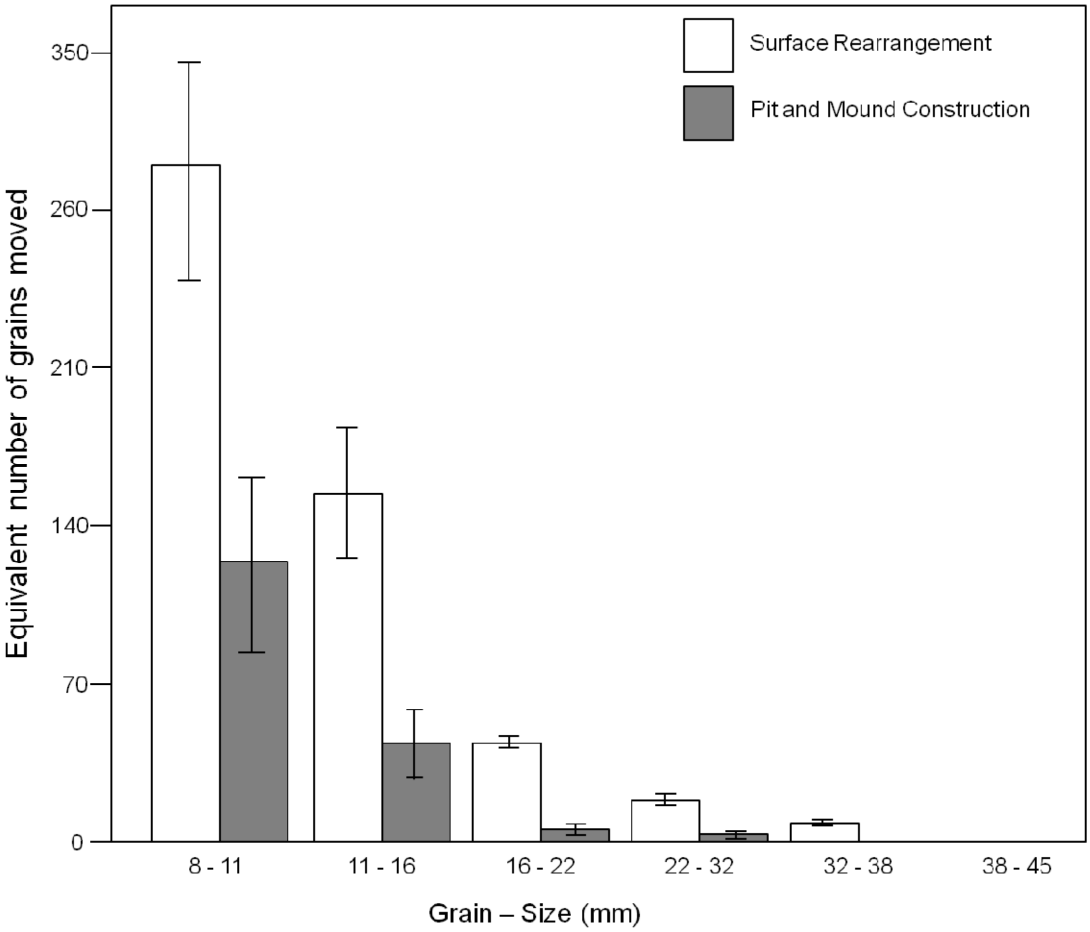
Estimates of the number of grains displaced by the crayfish on each substrate are presented in figure 2.6b, where the inverse exponential relation between mobilized grain numbers and grain diameter reflects the direct relation between individual grain weight and the cube of its radius, size-fraction by size-fraction. A grain-size of 16 mm appears to be a break-point, with considerably fewer equivalent grain volumes moved from surfaces composed of larger and, therefore, heavier grains. Also to be noted is the small number of grains that were moved as pit and mound construction in substrates where grain-size lies between 16 – 32 mm. Furthermore, notice should be taken of the fact that no disturbance at all was recorded where grain submerged weight exceeded 54 g (i.e. > 38 mm), not even minor amounts of fabric adjustment.

Figure 2.6. *a*) *Mean (± 2 SE, n = 10) of surface volume change arising from the introduction of single crayfish on screeded, graded, planar, gravel surfaces (600 x 400 mm), each for 24 hours (*series 3 *experiments). b) Mean (± 2 SE, n = 10) of the equivalent number of grains moved arising from the introduction of single crayfish on screeded, graded, planar, gravel surfaces (600 x 400 mm), each for 24 hours (*series 3 *experiments). For each gravel grade, unshaded bars indicate fabric adjustment and grey bars indicate pit and mound construction.*

a)



b)



2.4.4. Changes to surface roughness

The surface roughness of gravel, parameterised as the standard deviation of bed elevations from DEMs, increased with the length of time crayfish were present (figure 2.7). However, only those surfaces that had had at least 72 hours of exposure to crayfish activity were significantly different from control surfaces (which are shown at time equals zero in figure 2.7; Tamhane T2, $p = 0.011$). The increase in microtopographic roughness associated with crayfish is due to the construction of pits and mounds, which increase in volume through time (figure 2.4). Thus, a strong correlation exists between the microtopographic roughness of the surface and the total fractional area occupied by pits and mounds ($r^2 = 0.675$, $p < 0.001$; figure 2.8).

Figure 2.7. *Microtopographic roughness, defined as the standard deviation of spot heights (mm spacing) of 8 – 11 mm gravel surfaces exposed to single crayfish for intervals of 6, 24, 46, 72, 96 hours (*series 1*; n = 10). Time zero shows the roughness of control surfaces before exposure to crayfish. Surfaces with significant pit and mound construction (≥ 10% surface area) are marked as filled circles; those with minimal pit and mound construction (< 10% surface area) are open circles. The dashed line links the means and associated two standard errors.*

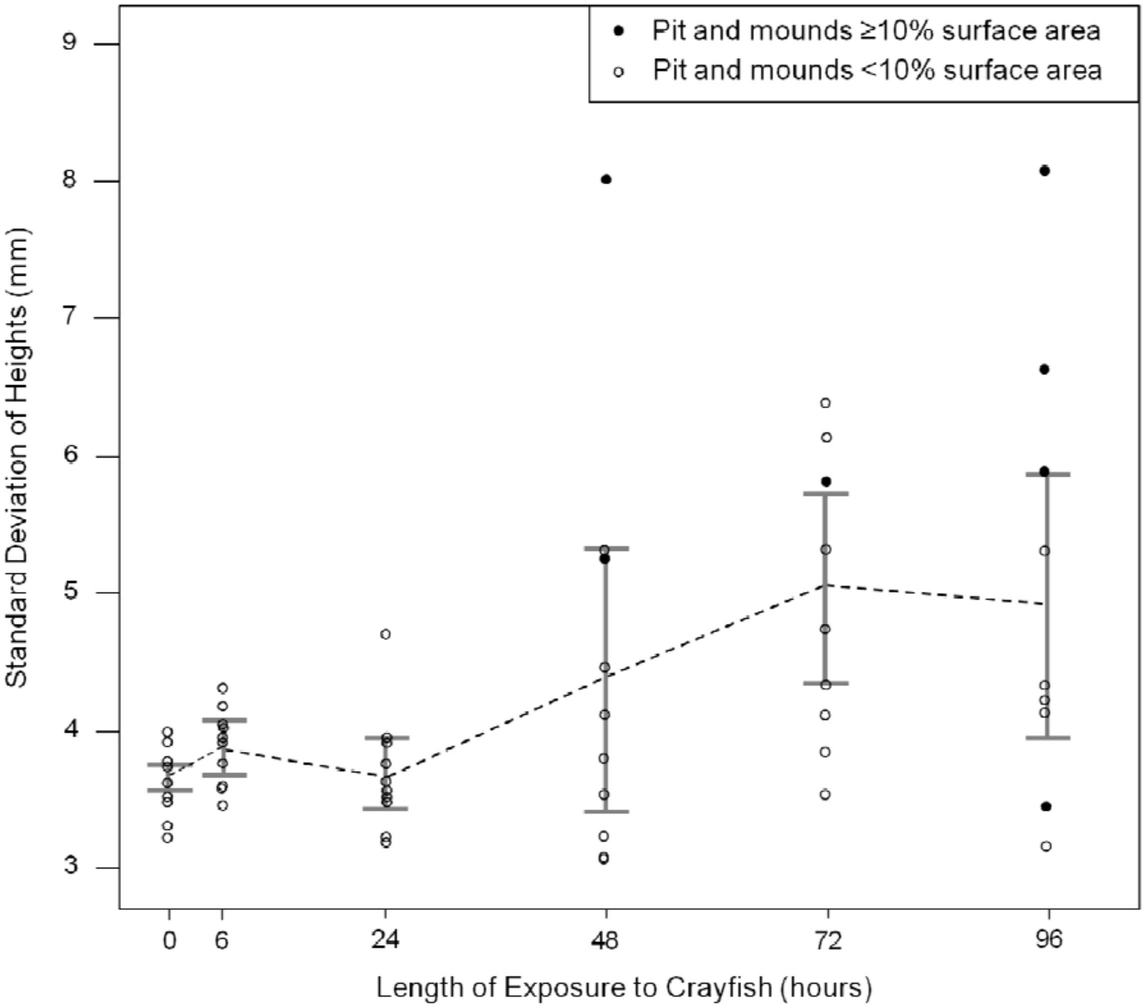
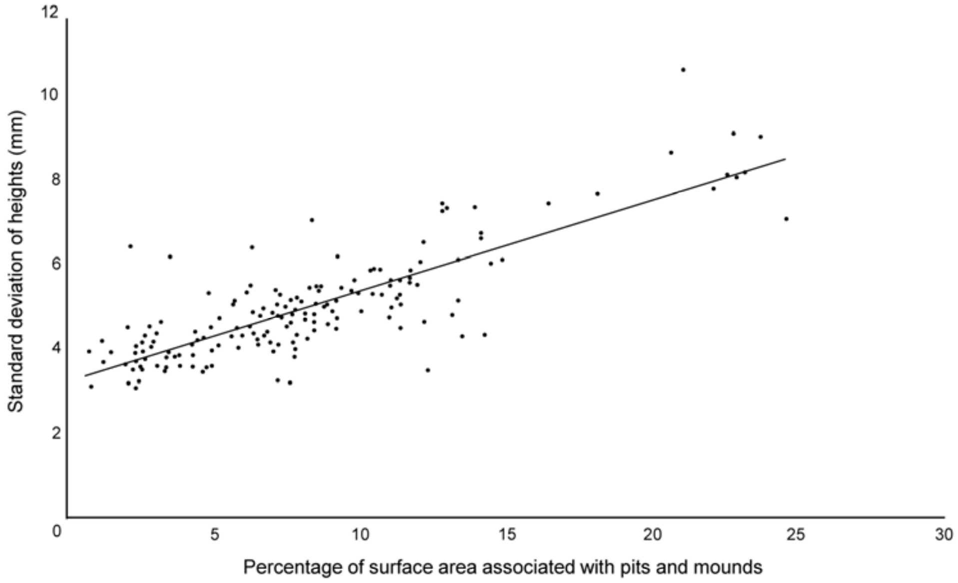


Figure 2.8. *Relation between surface roughness, defined as the standard deviation of spot heights (mm spacing), of initially screeded, planar, 8 – 11 mm gravel surfaces, each exposed to single crayfish for varying intervals up to 96 hours, and the percentage of the surface area associated with pit and mound construction. The linear regression ($y = 0.2119x + 3.1982$) has an r^2 value of 0.675 ($p < 0.001$).*



2.5. Discussion

2.5.1. Linking still-water experimental results to gravel-bed rivers

Crayfish moved grains up to 38 mm in diameter, each weighing approximately six times that of the individuals used in these experiments and reflecting significant amounts of work, especially since much of the displacement involved upslope movements from within a pit. However, it should be noted that, in this study, grains were moved from narrowly graded substrates, and it is possible that similar sized crayfish might be capable of moving coarser grains with ease if these were in a bed of mixed sizes, where coarse clasts would have smaller pivot angles if they were sitting relatively proud on a finer bed. It should also be remembered that these experiments were conducted in still-water aquaria; alteration of gravel microtopography might differ in lotic environments. Crayfish might need to exert a relatively reduced force in streams to mobilise grains in comparison with that required in still-water due to the simultaneous impact of the flow, at least when moving grains in a downstream direction. The opposite would be true if material was being moved in an upstream direction.

Another factor not present in these experiments is inter- and intra-specific interactions. These impact on the activity of crayfish and are, consequently, likely to affect the nature and magnitude of substrate reworking by crayfish. For instance, the presence of a predator might instigate the digging of a shelter. Also, signal crayfish form a hierarchical social structure where dominance increases burrowing and a suppression of burrowing is found in subordinates (Herberholz *et al*., 2003). Therefore, biotic interactions, including social contact between crayfish, are likely to have complex effects on the extent and significance of their geomorphic impact.

2.5.2. The impact of crayfish on the microtopography of substrates

It has been shown that the impact of crayfish on the microtopography of gravel substrates occurs in two ways. First, pits and mounds were found on the majority of surfaces where grain size was finer than 16 mm and, despite representing a relatively small proportion of the overall volume of disturbance, they produced the most obvious topographic change. Pits are dug to provide shelter by either piling up grains using the first two pairs of walking legs and then pushing the body into the pile, "bulldozing" these grains forward, or pushing the large claws (chelae) into the gravel and levering or pushing grains out from the bed. While burrowing by crayfish into cohesive sediments has been widely reported (Guan, 1994; Barbaresi *et al*., 2004), the excavation of non-cohesive bed material has not been examined in detail, despite having been observed in both the field and laboratory (Stein and Magnusson, 1976; Itagaki and Thorp, 1981; Parkyn *et al*., 1997; Herberholz *et al*., 2003). In the experiments reported here, the majority of pits were situated in the corners of the aquaria, but some were dug in central regions. However, while crayfish were in holding tanks between experiments, we also observed them excavating gravel (8 – 11 mm) from between coarse clasts in order to increase the suitability of such crevices as shelters. This is consistent with field observations of the species *Paranephrops planifrons* in New Zealand (Parkyn *et al*., 1997). It implies that heterogeneous substrates, which are characteristic of many gravel-bed rivers, may provide different opportunities for digging.

It is hypothesised that pits excavated in the current experiments are makeshift shelters that are constructed when more appropriate retreats, such as macrophyte stands or burrows in cohesive banks, are not available. This implies that more bed material will be excavated by crayfish when these other shelters are not available. In support of this, Statzner *et al*. (2000) found that the total erosion of material from small artificial channels where crayfish were provided with shelters was 2.8 kg m^{-2}, whereas this increased to 4 kg m^{-2} when shelters were removed. They interpreted this as being due to an increase in aggression associated with lack of shelter. However, the results of the present study suggest that the cause of the increased bedload flux observed by Statzner *et al*. (2000) might be due, at least in part, to increased excavation and destabilization of the substrate by crayfish constructing shelters.

The importance of the second type of disturbance by crayfish became evident only after the DoDs were analysed. This was associated with the more subtle rearrangement of surface grains as the crayfish brushed past them when walking and foraging. Grains that protruded on the substrate surface were particularly susceptible to being displaced. Fabric adjustment accounted for the majority of the volume change in gravels finer than 38 mm. The majority of this adjustment involved *in situ* movement of grains, such as changes in orientation and friction angle. Previous studies have also suggested that body contact by crayfish is important in promoting sediment transport, particularly for fine material (Statzner *et al*., 2000; Usio and Townsend, 2004) but crayfish were also observed to rearrange surface gravels by probing the bed pushing the small claws on their first and second pairs of walking legs into interstitial spaces. In addition, they would occasionally pick up grains finer than 16 mm with their first pair of legs and rotate them in front of their mouth before dropping them back onto the substrate. This is likely to be a foraging behaviour and is similar to that observed in *P. planifrons* which "lift and jostle small stones" with walking legs when looking for food (Parkyn *et al*., 1997, p. 689). All of these actions caused a reorientation and displacement of grains finer than 16 mm by distances of generally <1 D_{50}. As the grain size increased (*series 3*), the disturbance caused by probing was reduced because crayfish could fit their legs into interstitial spaces with less, or no, disturbance of the surrounding grains.

2.5.3. The impact of grain size and length of exposure on topographic alterations by crayfish

By expressing the movement of material in terms of the equivalent number of grains, it is apparent that disturbance involved many more grains in substrates finer than 16 mm (figure 2.7). This is not surprising, given the submerged weight of individual clasts in each of the graded beds. In addition, there appeared to be an abandonment of any attempt at pit and mound construction in substrates coarser than 16 mm. This is almost certainly because larger grains are much more difficult to dislodge. However, in addition to weighing more, larger grains also require the simultaneous dislodgement of similar-sized neighbours because of restraint by grain-grain interlock. It is not surprising, therefore, that there is a limit to the size of material that can be moved (figure 2.6). As a result, grains coarser than 16 mm were rarely displaced, whereas grains finer than 16 mm were regularly displaced through distances of multiple D_{50}. This implies that the extent of reworking by signal crayfish will be greater on gravels finer than 16 mm, at least for animals of the size used here, despite their ability to move coarser grains.

A substantial volume of gravel was moved within 6 hours of the introduction of crayfish to a surface. Little extra material was moved after further exposure except where significant pit and mound construction took place later (figure 2.5). Crayfish initially explored the aquaria by walking along the edges of the substrate and then crossing into the central area. This initial exploration led to a rapid alteration of the surface grain fabric and is consistent with observations made by others (Basil and Sandeman, 2000; Patullo and Macmillan, 2005). After a few hours, individuals selected a location, normally a corner, where they remained at rest, sometimes for an extended period. During this phase, crayfish often excavated a pit, within which they sheltered. From this shelter, crayfish continued to venture periodically, exploring the aquarium, usually returning to the pit after a period of several minutes. After approximately 38 hours, there was often a noticeable amount of renewed activity that was sometimes associated with substantial expansion of a pit. This lapse might reflect the period of time it took crayfish to acclimatize to the substrate and it is this renewed activity, coupled with pit and mound construction, which accounts for the increase in volume change at 48 hours and beyond in the experimental runs of *series 1* (figure 2.4) and the late-stage outliers in *series 2* (figure 2.5).

The total volume of topographic change between initial and crayfish disturbed surfaces during a 24 hour period (*series 3*) was consistent for all grain sizes except 11 – 16 mm, with an overall mean of 450 cm^3 (S.D. = 123 cm^3) from surfaces, each of 2400 cm^2. Interestingly, this volume change is consistent with the time-series experiments of *series 1*, where an average change of 469 cm^3 (S.D. = 89 cm^3) was recorded for the same period. As different shaped gravels were used in these two series, the similarity of the quantity of material moved suggests that the work performed was not affected by grain shape. Crayfish would have had to move only 225 cm^3 of gravel to create an average, 24 hour, volume change of 450 cm^3. Given a bulk density of 1830 kg m^{-3}, this equates to a disturbance of 1.7 kg m^{-2} d^{-1}. We can compare and contrast this with the results of Statzner *et al.* (2000), who found that the activity of 10 crayfish in a small flow channel resulted in maximum transport of a sand-gravel mixture of 4 kg m^{-2} d^{-1}. In this context, these still-water experiments, each run involving a single animal, suggest that the actions of the crayfish in either directly displacing or preparing material for movement by the flow could be of considerable significance.

2.5.4. Potential impact of topographic changes by crayfish on sediment transport

The changes in surface roughness from pit and mound construction undoubtedly influence the local near-bed hydraulic environment. Protuberances on the bed have a significant influence on flow resistance through form drag (Brayshaw *et al.*, 1983; Hassan and Reid, 1990; Robert, 1990, 1997; Lawless and Robert, 2001) and also induce a complex and variable hydraulic environment, including local reversal of the boundary shear stress vector (Buffin-Bélanger *et al.*, 2006; Garcia *et al.*, 2007). A heterogeneous near-bed hydraulic environment has a significant impact on the presence and behaviour of benthic organisms that reside on the substrate (Carling, 1992; Lancaster *et al.*, 2006; Rice *et al.*, 2008) and on the entrainment of bed material (Schvidchenko and Pender, 2001). Pit and mound construction results in changes to the local bed slope, which has an impact on gravel entrainment through an increase or decrease in friction angle (Hardisty and Whitehouse, 1988). Pits and mounds also alter the degree of protrusion or “hiding” of grains. Fenton and Abbott (1977) found that changes in grain protrusion of less than 1 D_{50} in an otherwise planar bed alters the critical shear stress by an order of magnitude. Here, in 8 – 11 mm material, mounds were, on average, 1.8 D_{50} high and pits were 2.7 D_{50} deep, which would, in flowing water, entail significant alterations to the stresses exerted on protruding or “hiding” grains.

Although less material was moved through distances ≥1 D_{50} in substrates coarser than 16 mm, the ability of crayfish to dislodge larger grains might be of significance in preparing the river bed for sediment transport, given the limited entrainment of coarse, framework grains by marginally competent flows, the majority of which transport only fine material over and between the more stable framework (Church *et al.*, 1991; Lisle and Madej, 1992; Wilcock and McArdell, 1997). In the Allt Dubhaig, Scotland which has a surface D_{50} of 32 – 45 mm, Wathen *et al.* (1995) found that material coarser than 16 mm rarely moved except in the largest flood events and that it made up < 50% of the bedload even when shear stress exceeded 30 N m^{-2}. Church and Hassan (2002) similarly found that 16 – 45 mm grains in Harris Creek, British Columbia, were mobilized only when boundary shear stress exceeded 27 N m^{-2}. These examples remind us that coarse bed material in the range that crayfish can displace is only infrequently moved by the flow and, consequently, this leads us to speculate that crayfish may be an important force acting on material coarser than 16 mm, especially during extended periods of low to modest flow that typically occur between flood events or flood seasons. While such disturbance will not in itself result in downstream displacement, it might act to reduce the integrity of surface structure, thereby enhancing the potential for subsequent displacement of coarser grains as part of the bedload by reducing critical entrainment stresses. Disturbance of these coarse grains might then promote the mobilisation of finer clasts which had formerly been sheltering in sub- and adjacent positions beneath and between the displaced coarser clasts.

Because they alter grain fabric and protrusion, and because they are not limited to movement in a downstream direction, crayfish might significantly counter the structuring and consolidation of gravels by the flow. So, where active, they might oppose abiotic factors that have been identified as accounting for differences in entrainment mechanics at the start and finish of bedload transport, such as grain clustering, matrix development and the length of time for granular consolidation between bed-disturbing flows (Reid and Frostick, 1984; Reid *et al.*, 1985; Reid and Hassan, 1992). They might also reduce the impact of other biotic factors that add strength to the bed, such as the production of silk bonds by caddis larvae (Johnson *et al.*, 2009) and the growth of algal films (Gerbersdorf *et al.*, 2008). The consolidation and structuring of gravel substrates occurs during extended periods of low flow, and it is during these periods that crayfish will be most active (Light, 2003). So, extended periods of minimal hydraulic disturbance will allow the cumulative impact of crayfish to increase. It is known that crayfish can significantly reduce the accumulation of fines in gravel substrates by winnowing sand grains (Parkyn *et al.*, 1997; Statzner *et al.*, 2000, 2003; Creed and Reed, 2004; Usio and Townsend, 2004) and the present study has found that crayfish can modify the protrusion, orientation, and friction angle of surface framework grains. It follows, therefore, that crayfish may have substantial impact in preparing bed material for entrainment during subsequent floods.

Chapter 3

The impact on gravel structure and stability of exposure to crayfish.

3.1. Introduction

In still-water, signal crayfish significantly altered the topography of gravel substrates. Gravels up to 38 mm in diameter (*b* axis) were moved from narrowly-graded substrates but disturbance was greatest in materials finer than 16 mm. Two distinct types of disturbance were apparent. The first was a geometric change associated with the construction of ecological bedforms creating topographic pits and mounds across surfaces. The second was the reworking of substrate fabric. Whilst pits and mounds were important in increasing the roughness of gravel surfaces, changes to the substrate fabric were the dominant form of surface alteration by crayfish. Both hydraulic roughness and bed material fabric, particularly structural arrangement, are of critical importance for the stability of bed materials. Therefore, these results raise the question of whether crayfish can alter the stability of river bed gravels.

3.2. Structuring of gravel substrates

3.2.1. Quantifying fluvial substrate structure

Despite the known importance of gravel structure, predictions of surface roughness and transport processes usually characterise a substrate with a single statistical measure of the grain-size distribution (e.g. D_{50}) (Meyer-Peter and Mueller, 1948; Parker, 1990; Wilcock and Crowe, 2003). This is, in part, due to the difficulty of quantifying the *in situ* roughness and structure of the bed using traditional techniques, such as grain sieving and Wolman (1954) sampling. More appropriate quantification of substrate structure can be achieved by creating a Digital Elevation Model (DEM) of a substrate surface. This allows the bed to be described as a series of elevations (x, y, z coordinates) from which statistical roughness and structural parameters can be derived in a non-destructive way (Smart *et al*., 2004; Aberle and Nikora, 2006). Whilst this approach has been used in the past (Furbish, 1987; Robert, 1988, 1990, 1991; Clifford *et al*., 1992), it has recently become more prevalent due to technological advances in photographic and laser scanning methods (Nikora *et al*., 1998; Goring *et al*., 1999; Butler *et al*., 2001; Aberle and Smart, 2003; Marion *et al*., 2003; Nikora and Walsh, 2004; Smart *et al*., 2004; Hodge *et al*. 2009).

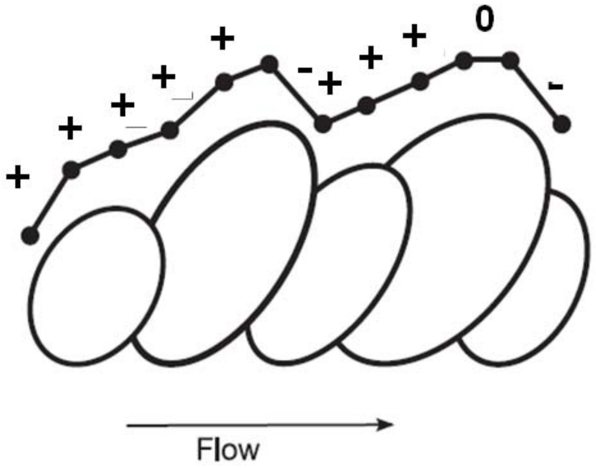
The surface structure of a substrate can be studied by quantifying trends in the surface elevations measured from DEMs of surfaces. Such a technique can be used to obtain measures of roughness, such as those described previously (section 2.2.5) and to obtain information on the protrusion of grains from a substrate. Patterns of surface elevations can also be studied using structure functions where pairs of elevations on a surface are correlated and grouped based on their distance apart (lag) and direction. The use of structure functions in surface analysis is usually associated with semivariograms which present the averages of point correlations across a surface (Robert, 1988; 1991; Nikora *et al*., 1998; Butler *et al.*, 2001; Marion *et al*., 2003; Smart *et al*., 2004; Aberle and Nikora, 2006; Hodge *et al*., 2009). Therefore, semivariograms give a measure of the level of structuring across an entire surface. Deciphering the nature and direction of this structuring is more difficult without using more specific indices.

Inclination is the slope between points at a predetermined distance (Smart *et al.*, 2004). Imbricated surfaces are expected to have an asymmetric distribution of inclinations in a direction stream-wise to the flow. There should be more positive inclinations than negative inclinations in a flow parallel direction and an equal number in a cross-stream direction (figure 3.1). Smart *et al.* (2004) defined an inclination index (I_l) which describes the difference between the number of positive and negative inclinations across a surface:

$$I_l = \frac{p_l - n_l}{p_l + n_l + z_l} \tag{3.1}$$

Where l is the lag distance, p is the number of positive inclinations, n is the number of negative inclinations and z is the number of pairs of points which define a zero slope (i.e. are of the same elevation). Consequently, an equal number of positive and negative inclinations will give a result of zero and, as asymmetry increases, I_l will increase to the maximum values of ± 1 (Smart *et al*., 2004; Millane *et al*., 2006).

Figure 3.1: *Illustration of the asymmetric distribution of slopes across an imbricated surface. Modified from Hodge et al. (2009).*



The magnitude and aspect of cell slopes across a surface has also been suggested to provide useful information regarding the structuring of substrates (Hodge *et al*., 2009). The aspect shows the orientation at which cells are facing. For imbricated surfaces it is expected that proportionally more cells will have upstream facing slopes and relatively few cells will have slopes orientated downstream (figure 3.1). Cells with upstream aspects should exhibit a predominance of low slope values whereas downstream facing slopes will have a greater proportion of steep slopes. These expectations can be used to provide an index of imbrication.

3.2.2. Importance of fluvial structure to substrate stability

The structure of gravel substrates can be considered a representation of the processes which formed that surface (Nikora and Walsh, 2004). As a result, surfaces that have been formed by flowing water should be distinct from those formed by other forces such as gravity (Nikora *et al*., 1998; Nikora and Walsh, 2004). The structuring of substrates by flowing water can increase their stability (section 1.2) and, consequently, the stability of a surface is partially determined by the history of flows over it. This was demonstrated quantitatively by Reid *et al*. (1985) with continual bedload recording in Turkey Brook, UK. It was found that sediment entrainment during floods which followed extended periods of relatively low flows required greater critical flow stresses to mobilise the bed than floods which followed closely together. This was hypothesised to be because of the structuring of substrates at low flows including grain interlock and the proportion of fine matrix material in the bed which has been found to be dependent on flood history (Frostick *et al.*, 1984). This result was corroborated by Oldmeadow and Church (2006) who found that river reaches where the surface structure had been destroyed had bedload transport rates 32% higher than untouched reaches. They also found that over the course of three flood events the bed mobility decreased in disturbed reaches to approach that of undisturbed reaches due to surface restructuring (Oldmeadow and Church, 2006). Lamarre and Roy (2008) obtained similar results in Moras Creek, Québec, where sediment structures quickly developed over the course of two bedload transport events at low magnitude discharge after they had been disturbed.

The importance of flow history on the structure and stability of substrates has also been quantified in flume studies. Stress history was found to increase the critical shear stress of sand grain-size fractions by 27% under certain antecedent conditions (Paphitis and Collins, 2005). Similarly, Haynes and Pender (2007) found that the magnitude and length of antecedent flows had a significant influence on the entrainment of gravel bed material. Typically, rates of bedload transport were reduced by an order of magnitude within the first 150 minutes of flow subsequent to antecedent shear stresses of 53% or 77% of the critical shear stress (Haynes and Pender, 2007). This reduction in transport was due to the structuring of the bed with progressive arrangement of grains into more flow resistant positions (Paphitis and Collins, 2005).

3.3. Aims

Crayfish had a substantial impact on loose, unstructured gravels in still-water experiments (chapter 2). This chapter aims to determine whether the rearrangement of surface grains by crayfish results in a structural alteration of substrate surfaces that affects bed stability because, in nature, fluvial substrates are structured by the flow into arrangements that tend to be more resistant to entrainment and, perhaps, more resistant to modification by crayfish. Therefore, it is important to determine whether crayfish have an impact on loose and also on water-worked gravels. To achieve these aims there are four specific objectives:

i) To quantify the behaviour of crayfish on gravel substrates and link this to the magnitude and nature of substrate reworking.

ii) To quantify the impact of crayfish activity on the topography and fabric of water-worked and loose gravels under flowing water.

iii) To determine whether modifications to the fabric of gravels by crayfish result in a structural change to the substrate surface.

iv) To determine whether sediment reworking by crayfish has a significant impact on the stability of gravels during high flows.

3.4. Methods

3.4.1. Experimental overview

In order to study the impact of crayfish on the topography and structure of gravel substrates, a series of experiments were undertaken in a laboratory flume. Narrowly-graded gravel was placed in an experimental section of the flume and screeded flat. In half of the experiments, surfaces were left as loose, random arrangements of gravel (*series 1*) and, in the other half, surfaces were water-worked in the flume prior to the introduction of crayfish (*series 2*). Water-working of gravels in these experiments is described in full in section 3.4.4. Crayfish were left on these substrates at a low velocity flow (average velocity [v] = 0.1 m s^{-1}; shear stress [τ] = 0.19 Nm^{-2}; Shield parameter [θ] = 0.001) for six hours and their behaviour in the flume was continuously recorded. Laser scans of the gravel surfaces before and after water-working, as well as before and after crayfish activity, were obtained and compared in terms of both topographic and structural alterations. The patches of gravel were then entrained in the flume at a high velocity flow (v = 0.9 m s^{-1}; τ = 12.75 Nm^{-2}; θ = 0.05) and the mobility of the gravels was quantified from digital video recordings. The mobility of gravels from surfaces which had been disturbed by crayfish were compared to control runs where no crayfish were present on the gravel surfaces.

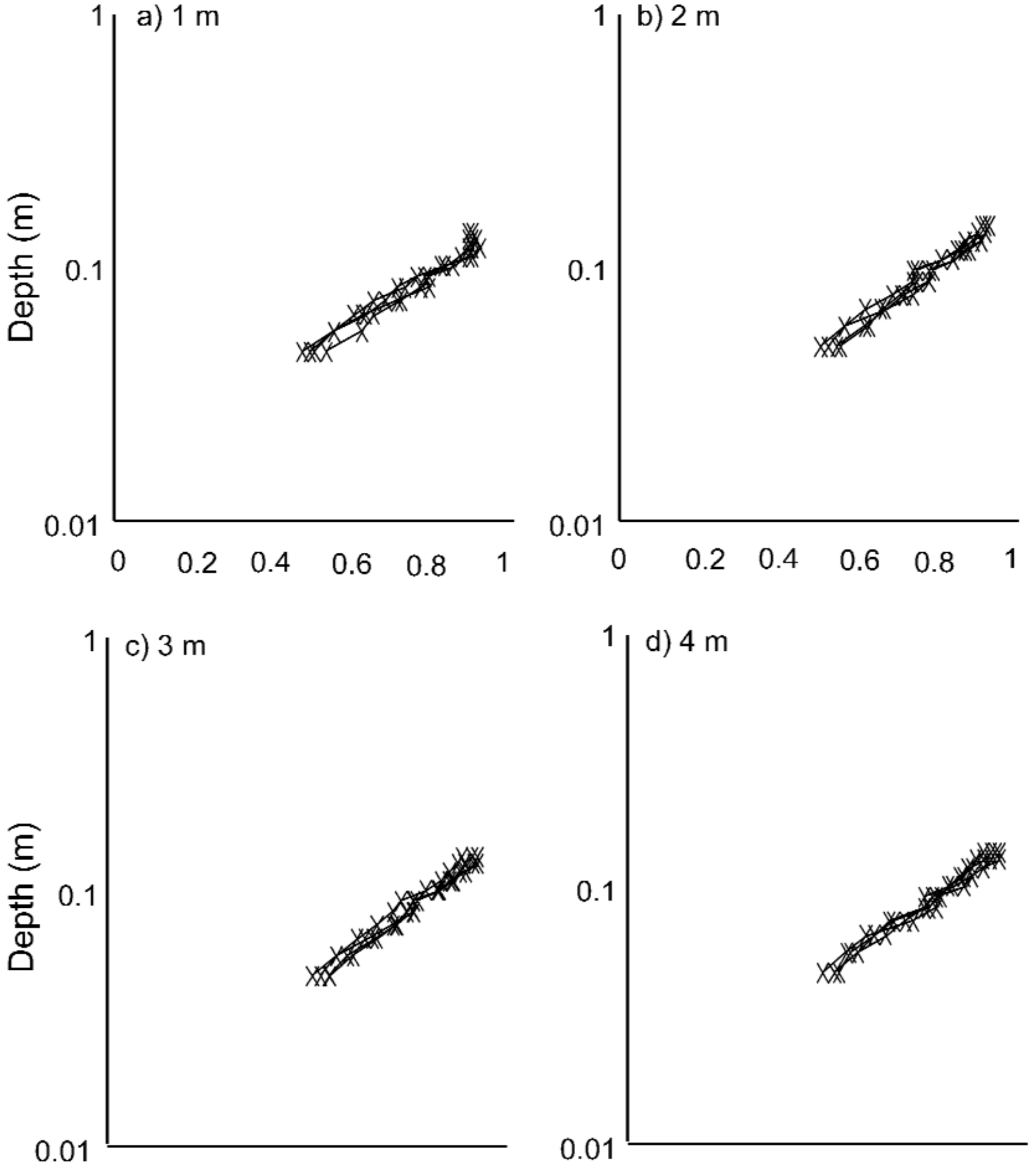
3.4.2. Experimental set-up of flume channel and experimental area

These experiments were undertaken in a large, indoor, tilting laboratory flume. It has a 5 m long, 0.6 m wide working section with 0.5 m high glass walls. An experimental area, which is 0.8 m long and 0.6 m wide, was located 2.5 m from the flume inflow and 1.7 m from the flume outflow. For the entire length of the channel, both upstream and downstream of the experimental section, a 0.1 m deep substrate of 25 – 35 mm material was used to provide a rough surface to generate frictional drag on the flow, resulting in the development of a logarithmic velocity profile analogous to that associated with rivers. Development of this boundary layer was aided by use of flow-training tubes at the channel inlet and was measured with ADV measurements at 1 cm depth intervals at four distances from the flume inflow.

These measurements indicate that the velocity profile was logarithmic for the entire length of the flume channel although a slight deviation does occur near the water surface 1 m from the flume inflow (figure 3.2). Over the experimental patch (figure 3.2c) the flow is logarithmic and descriptions of specific flows over the test patch follow in section 3.4.4. Digital video cameras were mounted in the flume channel, one facing upstream and the other downstream to get a complete coverage of the experimental area. A laser scanner was mounted above the flume on a frame to generate each DEM and was rotated to get two scans from two vertical directions relative to the experimental area (figure 3.3).

The experimental area was filled to a depth of 0.1 m with one of two narrowly-graded grain-size fractions; 11 – 16 mm and 16 – 22 mm. These two sizes were selected based on the results of still-water experiments (chapter 2), where it was found that a distinct change in the nature and magnitude of disturbance was present at 16 mm. By using these sizes this distinction could be further studied. The gravel used was the same as described in section 2.3.3; derived from the River Lune, predominately bladed (Sneed and Folk, 1958) and well rounded (0.8, Krumbein, 1941) and with a grain density of approximately 2650 kg m^{-3} (Graham *et al*., 2005). In the flume, loose, unstructured gravels were screeded flat to form a planar bed. Between each run the surface was thoroughly mixed to ensure that any structuring of the bed from previous runs was destroyed and did not influence the replicability of the substrate conditions.

Figure 3.2: *Log-depth velocity profiles. Distance from inflow was a) 1 m; b) 2 m; c) 3 m and d) 4 m. Profiles c were over the experimental area. Five replications were made for each.*



Crayfish were kept in the experimental area using a cage constructed from 0.7 mm diameter wire. The cage was 0.6 m long, 0.4 m wide and 0.3 m high with a regular, 10 mm square hole, mesh. The cage was only placed in the flume at low velocity flows when crayfish were in the channel. It was not in the flume during structuring or entrainment stages of the experiments. The cage was placed between four fixed reference points to ensure that it, and consequently the area of crayfish activity, was in the same location for all flume runs. These reference points were also used to rectify laser scans (section 3.4.8). The location of the cage resulted in a 0.1 m boundary between the edge of the experimental area and the area of crayfish activity (figure 3.3a, b). This ensured crayfish were not affected by side-wall drag.

Figure 3.3a. *Photograph of the flume set-up showing the position of underwater cameras, the laser scanner and cage for when crayfish were in the flume. The flume was covered in a tarpaulin when crayfish were in the channel.*

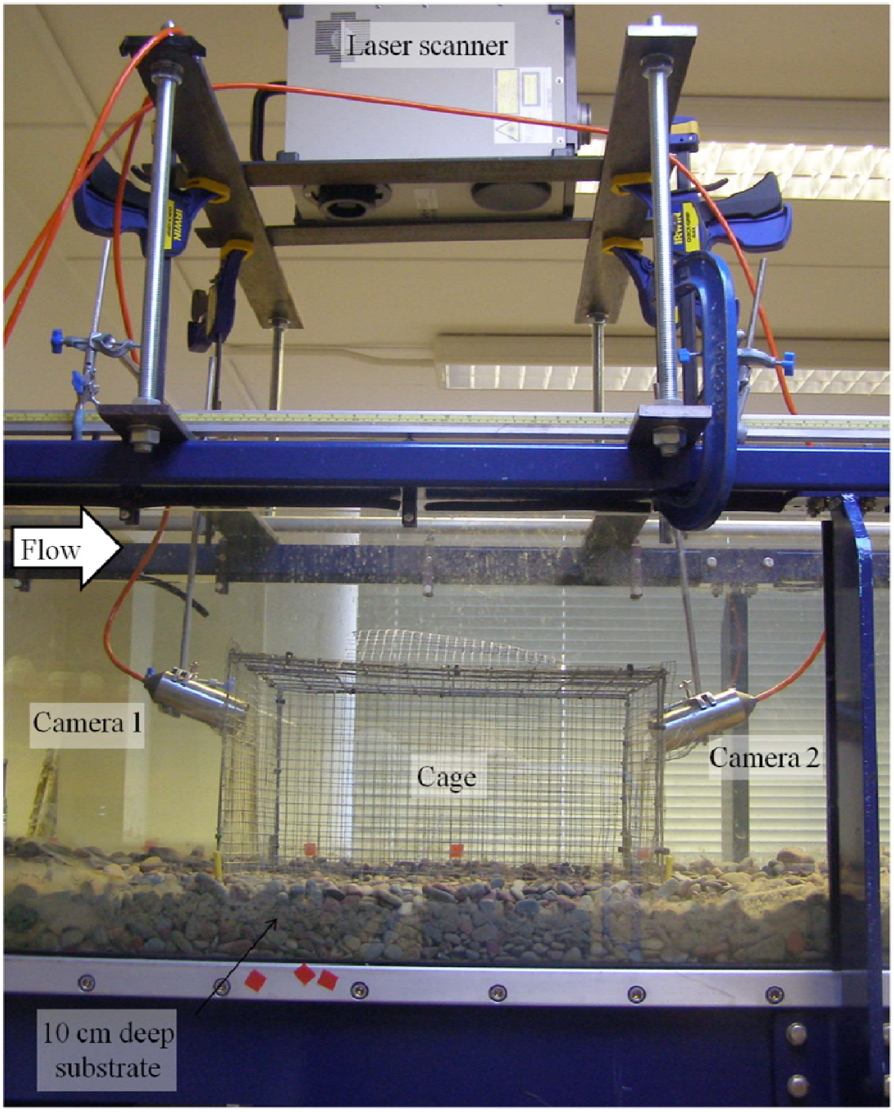
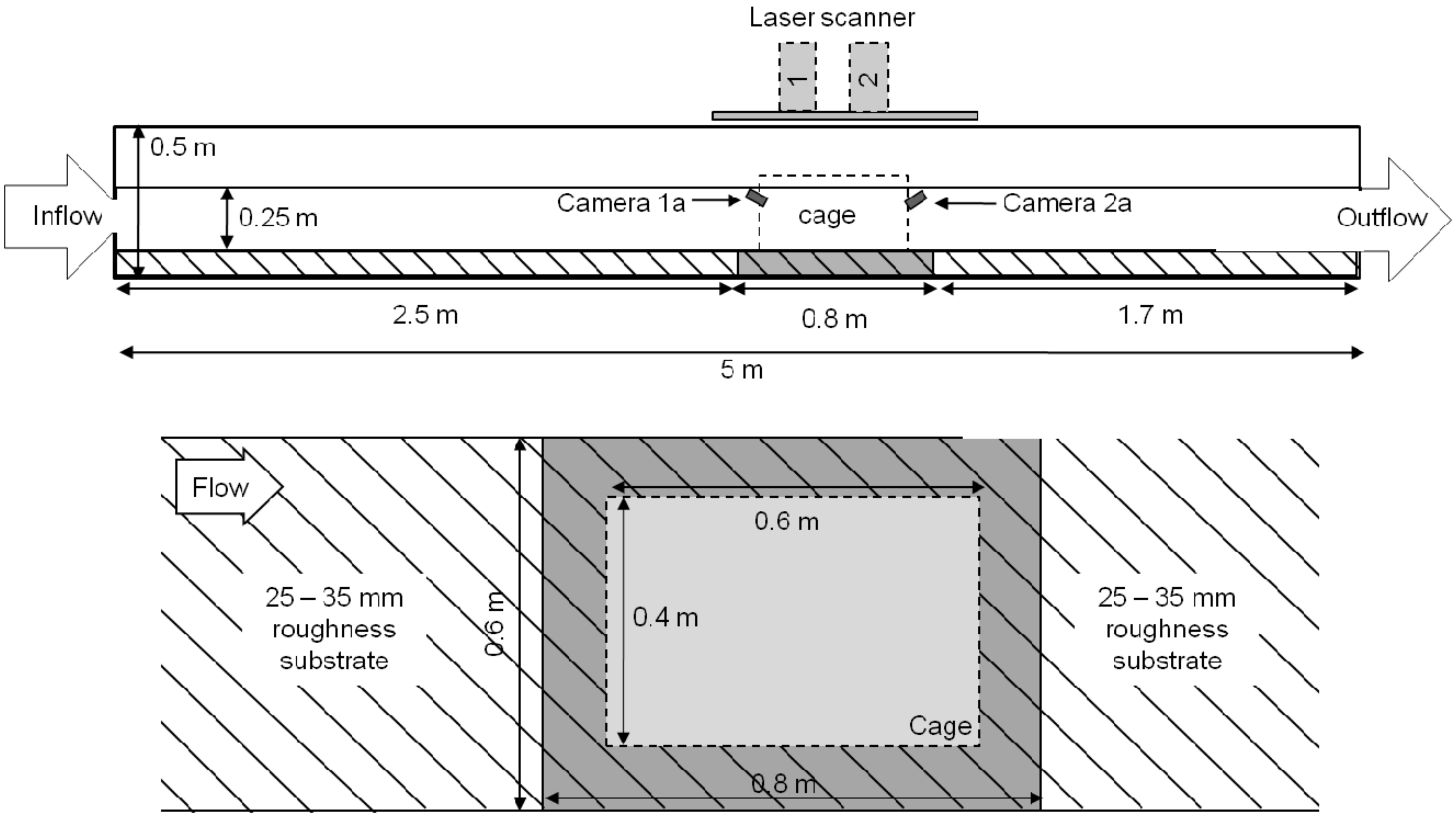


Figure 3.3b: *Diagram of the experimental set-up whilst crayfish were in the flume a) a side view of the dimensions and set-up of the flume channel. b) a plan view of the dimensions and set-up of the experimental area of the flume.*



3.4.3. Experimental procedure

Initially, the experimental area was filled with one of the grain-size fractions to a depth of 0.1 m and gently screeded approximately flat. This substrate was then laser scanned (described in more detail in section 2.3.4) and the data used to create a digital elevation model (DEM) of the surface. To water-work substrates in *series 2* experiments, the flume channel was slowly filled with water making sure that surface grains were not disturbed. Once filled, the tail weir and pump were slowly altered to gradually generate a flow of 0.06 $m^3 s^{-1}$ (average velocity [v] = 0.4 m s^{-1}, depth [d] = 0.25 m; $\tau = 2.88$ N^{-2}; Shields [θ] = 0.01), described in more detail below (section 3.4.4). The discharge was approximately 50% of that used for the entrainment flow and the shear stress was approximately 20%. The flume was left running at this discharge for two hours to structure the surface, after which the pump discharge was gradually reduced and the flume channel was slowly drained. During the two hours, gravel was fed into the patch at a similar rate to its transport out of the experimental patch. The water-worked surfaces were then laser scanned again. After scanning the initial loose (*series 1*) or water-worked surfaces (*series 2*), the cage was placed over the experimental area, between reference points.

Once the cage was in place, the flume was slowly filled with water and a flow of 0.016 $m^3 s^{-1}$ (v = 0.1 m s^{-1}, d = 0.25 m; $\tau = 0.19$ Nm^{-2}; $\theta = 0.001$) was generated (section 3.4.4). This flow was not sufficient to disturb the surface gravels or limit the movement of crayfish. Once this flow was established, a single crayfish was placed by hand onto the substrate surface through an opening in the top of the cage. Crayfish were released approximately 0.05 m from the substrate surface and allowed to drift down to the surface slowly. The capture, selection and aquaculture of crayfish used in these experiments is described in section 2.3.1. A total of 20 crayfish were used in the 40 flume runs that involved crayfish, with each animal used twice. While crayfish were in the flume, the channel was covered by a tarpaulin to create a dark environment because crayfish are nocturnal and this avoids complications associated with shadows in the flume laboratory. A large water cooler (Teco Tr120 Chiller Unit) was used to control water temperature in the channel as this could affect the activity of crayfish. The water temperature in the channel was monitored throughout the runs and was maintained between 15°C and 20°C during all experiments. It never increased by more than 2°C during the period when a crayfish was in the flume channel. The crayfish were left in this constant flow for six hours after which they were removed by hand and the flume was slowly drained. During the six hours that each surface was exposed to crayfish, the area within the cage was continuously monitored with two digital video cameras. Once the flume had been drained, the cage was removed and the surface was laser scanned again.

Finally, the flume was filled again and a high velocity flow was generated of approximately 0.11 m^3 s^{-1} (v = 0.8 m s^{-1}, d = 0.2 m; τ = 12.75; θ = 0.05; section 3.4.4). The entrainment flow lasted for two hours, during which the experimental area was continuously monitored with video cameras (section 3.4.7). No sediment feed took place during this period. After entrainment, another laser scan was obtained of the surface. This four-stage experimental procedure was replicated 10 times for the four substrate types (loose and water-worked for both grain sizes) with crayfish. To provide control runs, the procedure was also replicated a further ten times for each substrate type without crayfish. Therefore, a total of 80 flume runs were undertaken (table 3.1). During control runs, the cage was placed in the flume and left for six hours of low velocity flow but, in each case, no crayfish were released into the flume.

Table 3.1: *Diagrammatic representation of the 80 flume runs undertaken in this study.*

Grain-size (mm)	Substrate Type	Crayfish	Replications
11 – 16	Loose	With crayfish	10
		Without crayfish	10
	Water-worked	With crayfish	10
		Without crayfish	10
16 – 22	Loose	With crayfish	10
		Without crayfish	10
	Water-worked	With crayfish	10
		Without crayfish	10
		Total	80

3.4.4. Hydraulic environments and measurements

Three different flow conditions were used in the flume during these runs. All flows were turbulent and sub-critical, with a water surface parallel to the substrate surface and a logarithmic velocity profile with depth. During each run, flow measurements were taken with an ADV positioned at 0.6d, 0.1 m downstream of the experimental area. Five velocity profiles were measured for each of the three flows in order to quantify the hydraulic environment and test the replicability of the flow conditions. Velocity profiles were also used to estimate the bed shear stress (τ_i) according to the law of the wall as:

$$\tau_i \ = \rho \, v^{*2} \tag{3.2}$$

where ρ is water density (= 1000 kg m^{-3}) and v* is shear velocity. Shear velocity was estimated from:

$$v^* \ = \frac{b}{c} \tag{3.3}$$

where *c* = 2.5 and is the reciprocal of the von Karman constant for clear water flows, κ = 0.41, and the parameter *b* is the slope of a linear least-squares regression of velocity (m s^{-1}) on the logarithm of depth (m) in the measured profile (r^2 values ranging from 0.953 – 0.997). To enable a direct comparison between the shear stresses for both grain sizes used in these experiment, the dimensionless Shields parameter (θ_i) was calculated as:

$$\theta_i \ = \frac{\tau_i}{(\rho_s - \rho) g \mathrm{D}_i} \tag{3.4}$$

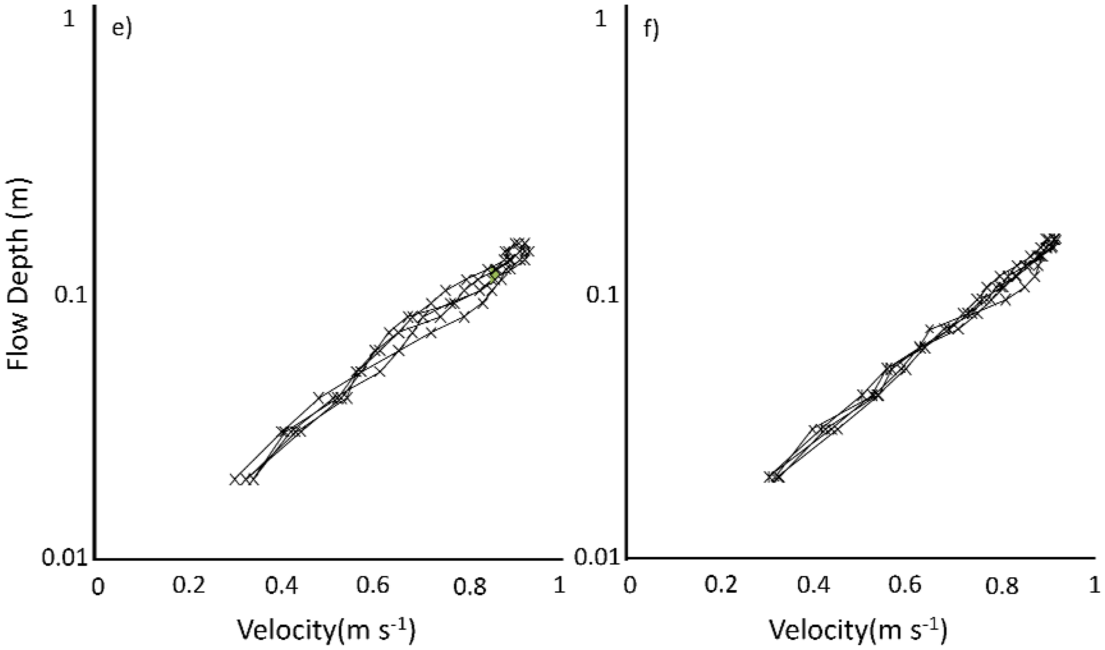
where τ_i is the shear stress at each flow over grain size D_i, *g* is the acceleration due to gravity (= 9.81 m s^{-2}) and ρ_s is sediment density (approximated as 2650 kg m^{-3}).

The flow used to water-work substrates in *series 2* experiments generated a similar bed shear stress on both substrate sizes (ANOVA; p = 0.632) and resulted in a similar magnitude of structuring across both grain-sizes (section 3.7.1). Consequently, the same water-working flow was used for both sizes of substrate. The shear stress generated by the entrainment flow was also similar for both substrate sizes (ANOVA; p = 0.692) and was therefore also used for both grain sizes when entraining bed material.

Table 3.2: *Flow parameters measured during water-working, crayfish and entrainment flows .Pump discharge and water depth were set at the beginning of each run. Mean velocity was measured at 0.4 depth. Bed shear stress was estimated from the law of the wall from measured velocity profiles presented in figure 3.4.*

Grain size (mm)	Discharge ($m^3 s^{-1}$)	Depth (m)	Bed slope	Mean velocity ($m s^{-1}$)		Reynolds Number		Froude Number		Shear stress ($N m^{-2}$)		Shields parameter (θ)	
Water-working flow													
11 – 16	0.06	0.25	0	0.39	0.01	53634	2948	0.357	0.02	2.69	0.72	0.012	0.003
16 – 22										3.06	0.61	0.010	0.002
Crayfish flow													
11 – 16	0.016	0.25	0	0.1	0.01	16295	549	0.109	0.004	0.19	0.05	0.0009	0.0002
16 - 22										0.19	0.07	0.001	0.0002
Entrainment flow													
11 – 16	0.11	0.2	0.005	0.88	0.02	134461	2370	0.896	0.016	12.21	2.09	0.052	0.009
16 - 22										13.30	1.02	0.043	0.003

Figure 3.4: *Log-depth velocity profiles measured above the test patch during the water-working flow (a and b), crayfish flow (c and d), and entrainment flows (e and f). Five replications were made for each flow type across both 11 – 16 mm (a, c, e) and 16 – 22 mm (b, d, f) substrates.*



3.4.5. Entrainment procedure

The observation of entrainment thresholds is inherently subjective (Neill and Yalin, 1969) and as a result there have been numerous definitions of incipient motion and threshold transport (Lavelle and Mojfeld, 1987; Buffington and Montgomery, 1997). Any linear relationship between time-averaged flow stress and the physical size of grains is obscured by the influence of the surface geometry and stochastic fluctuations in stress intensity due to turbulence (Grass, 1971). Consequently, a particular grain could be entrained over a range of flows rather than at a single discrete threshold (Wilcock and McArdell, 1993; 1997). As a result, it has been argued that entrainment is inherently stochastic and grains can be entrained at a wide range of time-averaged flows due to local variations in instantaneous stress intensity associated with turbulence (Paintal, 1971; Lavelle and Mofjeld, 1987). For this reason, rather than trying to determine a single entrainment threshold, the movement of grains was counted over a two hour period of relatively high shear flow (section 3.4.4). This flow was designed to be the lowest flow which was sufficient to induce bedload transport over the entire substrate patch (i.e. more than a few isolated grains). Although more grains were entrained from 11 – 16 mm surfaces than 16 – 22 mm material, it was decided that this entrainment flow was suitable for both fine and coarse material as lower flows did not regularly or frequently entrain bed material and higher flows induced deep scour in the bed for both sizes.

The entrainment flow was generated consistently by following three steps: 1) the flume channel was slowly filled at a zero slope to produce a discharge of 0.03 $m^3 s^{-1}$ (v = 0.2 m s^{-1}, d = 0.25 m); 2) the flume slope was increased to 0.005; 3) the flume was left for 10 minutes, after which the flow depth was lowered to 0.2 m and the discharge was slowly increased to 0.11 $m^3 s^{-1}$ generating the entrainment flow described in detail above (section 3.4.4). Video recordings showed no grain movement during the filling of the flume.

3.4.6. Camera set-up and analysis of crayfish behaviour

In order to quantify the link between crayfish behaviour and substrate reworking (objective 3) and to ascertain whether crayfish activity in the flume was analogous to that in nature, the activity of crayfish was continuously monitored with two digital underwater video cameras. The cameras were 12 cm long and had a diameter of 5 cm. To record crayfish activity, one camera was positioned upstream of the experimental patch and the other positioned downstream at heights 0.18 m above the bed surface. Both were directed towards the experimental patch giving a complete coverage of its surface from two directions (figure 3.3).

Video recordings of crayfish activity were analysed by a single operator (MFJ) by recording when, and for how long, crayfish spent undertaking each of six predefined activities described in table 3.3. The use of behavioural classifications has been previously undertaken in ecological studies of crayfish activity (Stein and Magnuson, 1976; Breithaupt and Eger, 2002; Herberholz *et al.*, 2003; Harrison *et al.*, 2006). The behavioural classifications used in this study were partly based on those of Stein and Magnuson (1976) and could be used to divide up all six hours of crayfish activity in the flume into discrete classes. A well documented behaviour of crayfish which is not included in this classification is ‘backwards swimming’ where crayfish launch themselves off the substrate into the water column when disturbed. This was not observed during any experimental run because disturbance to crayfish was minimised. Consequently, it was not included in the division of crayfish activity. The direction crayfish were facing when walking and stationary was recorded by assigning the orientation of crayfish into one of eight directions in relation to the flow direction. These were the four directions parallel and perpendicular to the flow as well as the four intermediate diagonals. The location of crayfish in the experimental section was recorded by assigning their position into one of three classes. Crayfish were recorded as being at the edge of the experimental patch if they were within one body width of the cage. If within one body width of two cage edges, crayfish were recorded as in the corner of the patch. If crayfish were more than one body width from the cage edge they were considered to be in a central location.

Table 3.3: *Classifications of crayfish behaviour used to analyse video of crayfish activity when in the flume channel.*

Activity	Description
Walking	Locomotion using walking legs.
Stationary	Locomotion had ceased and walking legs were not being used to probe the substrate or groom.
Climbing	Walking legs were used to climb the cage walls. Climbing began when all walking legs were off the experimental area.
Grooming	Locomotion had ceased and walking legs were being used for grooming
Digging	Walking legs and chelae were being actively used to dislodge and displace grains creating voids in the substrate
Foraging	Crayfish were actively pushing their legs into the substrate

Whilst the determination of all crayfish activity, orientation and location measures were subjective, they were all made by the same operator (MFJ) and, as such, any small errors should be consistent between runs. To test this, error analysis was undertaken by analysing the activity of crayfish over the same 60 minute period five times. The 60 minute period was the first hour of presence in the experimental area, which was the period when crayfish were most active. It was found that assignment of an activity did not differ by more than five seconds for each individual period of an activity across the five replications. This error was entirely associated with determining exactly when an activity started and stopped. There was no error in defining the nature of the activity. Therefore, the cumulative error is dependent on the number of individual occasions an activity is undertaken and will be larger if crayfish spend short periods of time undertaking many different activities rather than relatively few extended periods of activity. The total cumulative amount of walking over the 60 minute period differed by a maximum of 2 minutes 20 seconds (mean = 1 minute 38 seconds, σ = 54 seconds) over the five replications. For the other activities which were not as frequently undertaken as walking, the cumulative average difference ranged from ten seconds to one minute. As a result the maximum error associated with the analysis of behaviour from the video is not believed to be greater than 2% of the total and is subsequently ignored.

3.4.7. Camera set-up and video analysis for grain entrainment

Video cameras were not used underwater during the entrainment run as they would have altered the hydraulic environment in the channel due to the shallow depth at which they would necessarily have been placed. Instead, cameras were set up to record through the glass side-wall of the flume. This gave a continuous, oblique view of the transport of material from the experimental area within the flume channel. The number of mobile grains was then counted by a single operator (MFJ) and binned into discrete time periods. For the first ten minutes of video, the number of grains which moved over ten second intervals was recorded. After ten minutes, the number of grains which moved every minute was recorded. In later analysis, the number of grains moved was sometimes grouped into larger time intervals. All mobile grains were counted from the two hour videos. A grain was defined as being mobile if it was displaced a distance greater than a single grain diameter from its original location. Consequently, this gives a gross measure of the stability of the surface and does not take into consideration the length of grain movement.

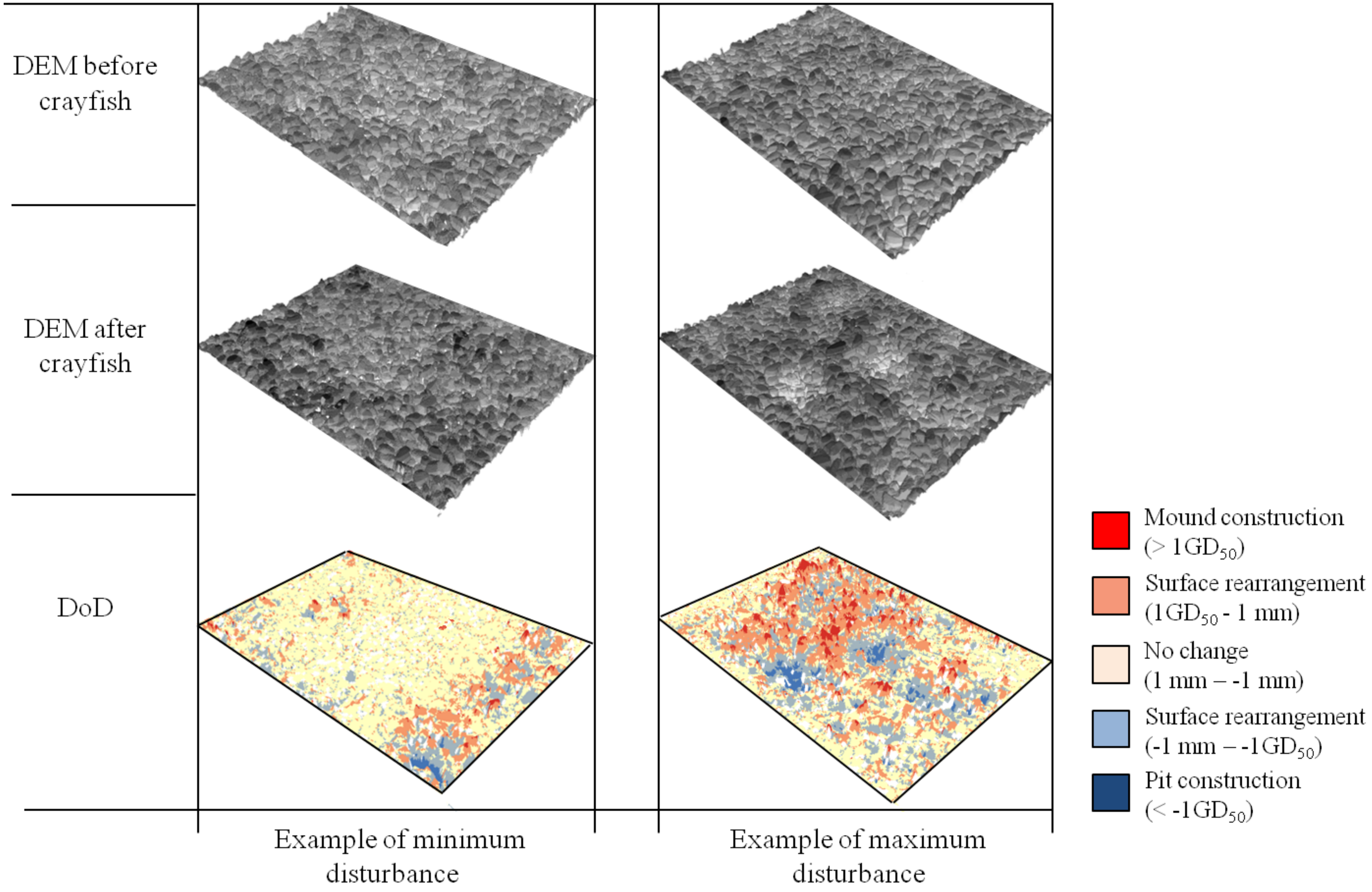
As a single operator analysed all video, the results are expected to be consistent between flume runs. This was tested by analysing the same 120 minute entrainment video five times. The surface used was 11 – 16 mm loose gravels, as this was the most mobile, and was consequently the most difficult to analyse. The majority of transport occurred within the first 20 minutes of the run and this period of video was analysed at half speed and, for the first five minutes, frame by frame. Between 20 minutes and 120 minutes, the video was watched at twice normal speed and slowed down to normal speed (or slower) when a grain was observed to move. This was because grains tended to move in groups at the same moment and, when speeded up, it was difficult to determine the number of grains that moved within a cluster.

Nearly all error was associated with the first 20 minutes of entrainment. Between 20 minutes and 120 minutes there was a maximum error of four grains between the five replications. Error recorded in the first 20 minutes of video was associated with the large numbers of grains moving at the same time, making it difficult to count them all, even when played back frame-by-frame. After 20 minutes, bedload was associated with individual grains moving infrequently, either in isolation or in groups of two or three which were relatively easy to count. It was found that the total cumulative number of grains which moved differed by a maximum of 24 grains (mean = 16; σ = 5). This is 5% of the total number of grains moved over the entire 120 minute video (average total 465 grains moved). As with the crayfish video, this 5% error was found to be insufficient to modify the mean-based trends associated with crayfish activity and, therefore, is not mentioned further.

3.4.8. Laser scanner and GIS procedure

Surface models were obtained from two laser scans, both perpendicular to the bed (figure 3.3). Two scans were used here because the distance between the laser scanner and the substrate surface was limited by the ceiling height and, therefore, required two scans for complete coverage despite being the same size area as the surfaces in still-water experiments. These surfaces were stitched together in the operational software for the laser scanner (Polygon Editing Tool) and merged to form a single surface. This was achieved by matching up common points (reference points) between the two scans to be stitched together. Surfaces were then cropped, orientated and rectified in Polygon Editing Tool software following the same procedure as in the still-water experiments (section 2.3.4). Surfaces were imported into ArcGIS as ASCII files and interpolated into raster DEMs where they were subsequently detrended following the same procedure as described in section 2.3.4. DEMs were then cropped to include only the experimental area (600 x 400 mm) using the mask tool (Spatial Analyst Tools → Extraction → Extract by Mask) so that all DEMs were of a consistent size. Topographic change due to exposure to crayfish was calculated by subtracting the *z*-value of each cell on one surface from the corresponding *z*-values on the other scan. The resultant surface had *z*-values which represent the topographic difference between scans. This was achieved using the raster calculator, explained in more detail in section 2.3.4.

Figure 3.5: *DEMs of 11 – 16 mm gravel surfaces (0.4 x 0.6 m) before and after 6 hours of crayfish activity in a low velocity flow (0.1 m s^{-1}) with resultant DoDs shaded according to the magnitude of topographic change. a) an example of the minimum disturbance by crayfish and b) an example showing the maximum disturbance by crayfish.*



Geostatistical analysis of the surface structure was also performed in ArcGIS. The surface roughness was paramaterised as the standard deviation of elevation measurements (*z* values) across the surface (Aberle and Smart, 2003). The structure of the surface was characterised using two techniques. The first involved the inclination of slopes in a stream-wise and cross-stream direction using the inclination index (I_l) derived by Smart *et al.* (2004), discussed above (section 3.2.1) with a lag distance *l* set to 2 mm to ensure each pair of points was on the same grain (Smart *et al.*, 2004; Millane *et al.*, 2006). To determine the number of positive and negative slopes, a raster DEM of a surface was copied and shifted (ArcToolbox → Data Management Tools → Projections and Transformations → Raster) by the lag distance (2 mm) in a direction parallel to the flow. For a cross-stream direction, the surface was shifted by 2 mm in a direction perpendicular to the flow. The original DEM was then subtracted from the shifted DEM to create a new surface where *z*-values indicated the magnitude of slopes and whether they were positive or negative. The proportion of the surface associated with positive and negative slopes was determined as a surface area using the 'area and volume' function in the spatial analyst toolbox (3D Analyst → Spatial Analyst).

The second method of quantifying surface structure used the frequency distributions of the magnitude and aspect of slopes across surfaces. This was achieved using spatial analyst tools in ArcGIS. The 'aspect' tool (ArcToolbox → Spatial Analyst Tools → Surface) was used to create a new raster where *z*-values indicate the aspect of slopes across the surface. The aspect is derived by identifying the downstream direction of the maximum rate of change in value from each cell to its neighbour using a 3 x 3 moving window. A 'slope' map was then created of the same DEM (ArcToolbox → Spatial Analyst Tools → Surface), again, using a 3 x 3 moving window to determine the maximum rate of change in value from the cell in question to its eight neighbouring cells. The *z*-values which represent slope and aspect in these surfaces were then reclassified into a numeric label identifying each group (ArcToolbox → Spatial Analyst → Reclass), shown in table 3.4.

Table 3.4: *Original and Reclassified z-values for aspect and slope maps.*

	Original Values	**Numeric label**
Aspect	337.5° – 22.5°	1
	22.5° – 67.5°	2
	67.5° - 112.5°	3
	112.5° - 157.5°	4
	157.5° - 202.5°	5
	202.5° - 247.5°	6
	247.5° - 292.5°	7
	295.5° - 337.5°	8
Slope	≤ 20°	10
	20° – 40°	20
	40° – 60°	30
	≥ 60°	40

The reclassified aspect and reclassified slope maps were then combined using the 'Single Output Map Algebra tool' (ArcToolbox → Spatial Analyst Tools → Map Algebra) by adding the *z*-values of one surface to the other. As a result, a new surface was created were *z*-values between 11 and 18 indicate slopes ≤ 20° and *z*-values in the twenties indicate slopes between 20° and 40°. The *z*-values ending in a 1 (i.e. 11, 21, 31 and 41) indicate an aspect of 337.5° - 22.5° and values ending in 2 indicate aspects of 22.5° - 67.5°, and so on. The proportion of the surface associated with each of the 32 categories was recorded and used to corroborate the results of the inclination index.

3.4.9. Statistical analysis

All statistical analysis was undertaken in SPSS 14.0. Volumetric measurements were analysed by comparison of means between data grouped into substrate types using an Analysis of Variance (ANOVA). ANOVA was also used in analysis of entrainment data and crayfish activity. If an ANOVA test was statistically significant, post-hoc Tukey tests were used to determine which variables were significantly different when the variance was homogenous. If the Levene's test for the homogeneity of variance was not met, a Tamhane post-hoc test was used instead of the Tukey. ANOVA is only appropriate for use if substrate categories are independent and, consequently, could only be used when comparing *between* flume runs. ANOVA could not be used on geostatistical data because comparisons were made *within* substrate groups (i.e. before and after crayfish on the same surface) and, therefore, the groupings are dependent. As a result, geostatistical data was analysed using paired *t*-tests.

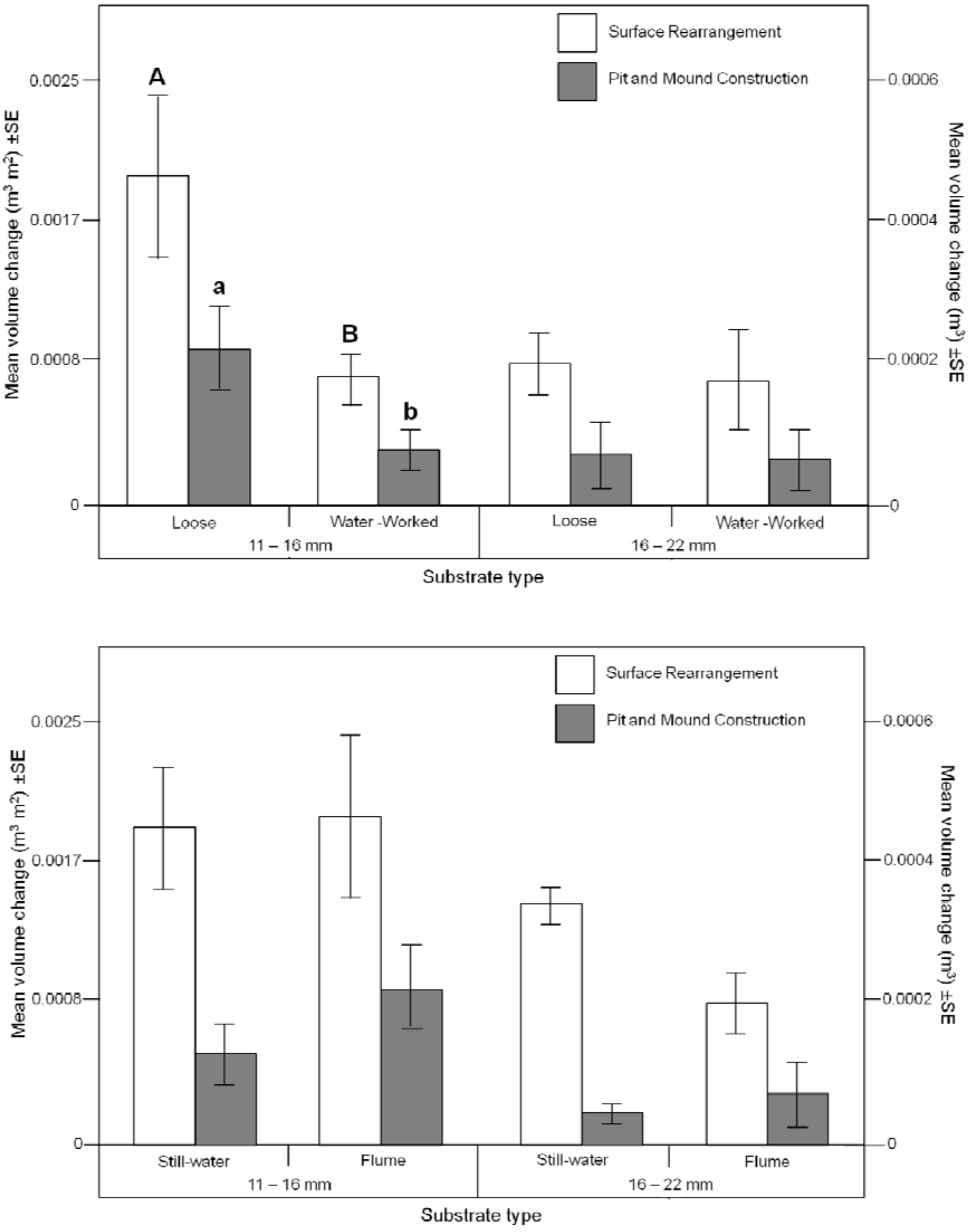
3.5. Topographic alterations

3.5.1. Topographic alterations to gravel substrates by signal crayfish

The difference in the impact of crayfish on loose (*series 1*) and water-worked surfaces (*series 2*) in a low velocity flow was highly significant for 11 – 16 mm ($p = 0.002$) material. Both pit and mound construction and fabric rearrangement were substantially reduced by water-working 11 – 16 mm material (figure 3.5a). However, in 16 – 22 mm, there was no statistically significant difference in topographic change between loose and water-worked surfaces ($p = 0.823$). Interestingly, water-working of 11 – 16 mm surfaces reduced the volume of material moved by crayfish to a level which was not significantly different from 16 – 22 mm material ($p = 1.000$). Therefore, a similar volume of material was moved in both 11 – 16 and 16 – 22 mm water-worked surfaces.

A comparison was made between the impact of crayfish on loose, unstructured surfaces in flume and still-water environments (chapter 2) to determine the impact of low velocity flow on topographic alterations made by crayfish. The total volumetric impact of crayfish was similar in both environments for both grain sizes (ANOVA; 11 – 16 mm $p = 0.460$; 16 – 22 mm $p = 0.114$). Consistent with the findings of the still-water experiments, more material was moved in 11 – 16 mm than 16 – 22 mm surfaces and the rearrangement of surface grains was the dominant method of bioturbation by signal crayfish (figure 3.5b). This dominance was reduced in the flume with approximately 39% of the total volume change associated with pit and mound construction in flume experiments in comparison to only 22% in still-water experiments (figure 3.5b). The increase in volume associated with pits and mounds was due to a greater number of pits being dug rather than an increase in the depth of pits.

Figure 3.6: *The mean (± 2 SE, n = 10) volume change between surfaces. Grey bars indicate fabric rearrangement and white bars indicate pit and mound construction. a) before and after crayfish activity for loose (series 1) and water-worked (series 2) surfaces. Significant differences occur between columns A and B (p < 0.001) and a and b (p = 0.002).b) loose surfaces in still-water and low velocity flow (flume) environments. Grey bars indicate fabric rearrangement and white bars indicate pit and mound construction.*

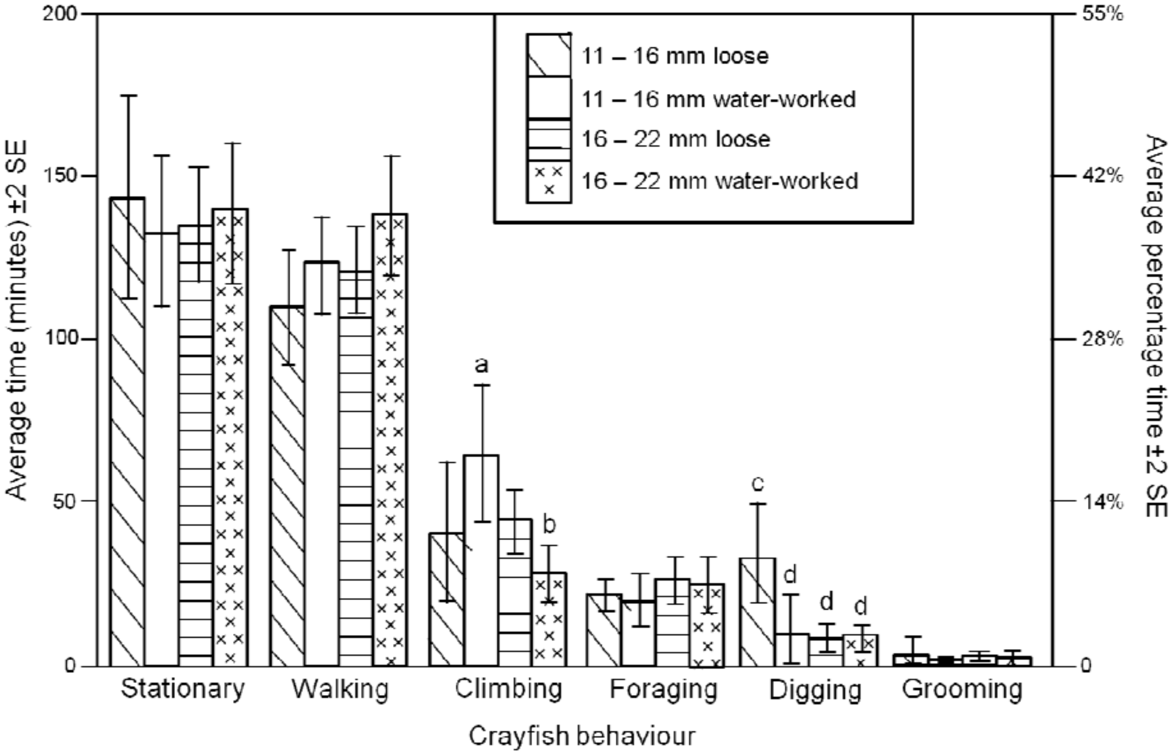


3.6. Crayfish activity

3.6.1. Cumulative activity of crayfish and substrate type

It was found that crayfish spent, on average, approximately 40% ($\sigma = 10\%$) of the six hour period they were in the flume stationary and this varied little between the four substrate types (figure 3.6). The majority of the time spent active was associated with walking and, again, this did not vary greatly between the four substrate types. Between the four substrate types there were no significant differences between the activity of crayfish with the exception of the proportion of time crayfish spent climbing and digging (figure 3.6). Crayfish are agile climbers and, in rivers, will climb vegetation and river banks. Climbing on cages is a function of the cage design but was unavoidable. Time spent climbing was not removed from future analysis as it represents a significant proportion of the time crayfish spent active in the flume (11%). Crayfish spent significantly longer climbing on the cage when present on 11 – 16 mm water-worked surfaces in comparison to 16 – 22 mm water-worked surfaces, however, the reasons for this difference are currently unknown. Crayfish also spent significantly longer digging in 11 – 16 mm loose surfaces than on all other surfaces. This is consistent with volumetric results which show that the volume associated with pits and mounds in 11 – 16 mm loose surfaces was substantially higher than all others. The finer grain-size and lack of surface structuring in this substrate may result in it being easier to dig into and, consequently, crayfish may be more prepared to spend extended periods digging shelters, discussed in greater detailed below (section 3.6.2).

Figure 3.7: *The mean (± 2 SE; n = 10) length of time crayfish exhibited six distinct behaviours during six hours in the flume, for each substrate type shown in the key. Significant differences (ANOVA; Tamhane post-hoc test) are indicated by letters a and b (p = 0.046) and c and d (p = 0.002).*

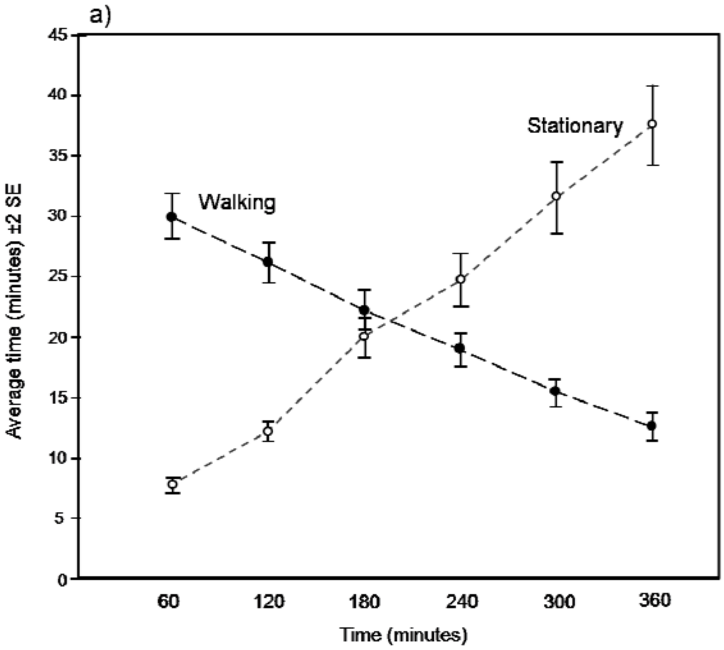


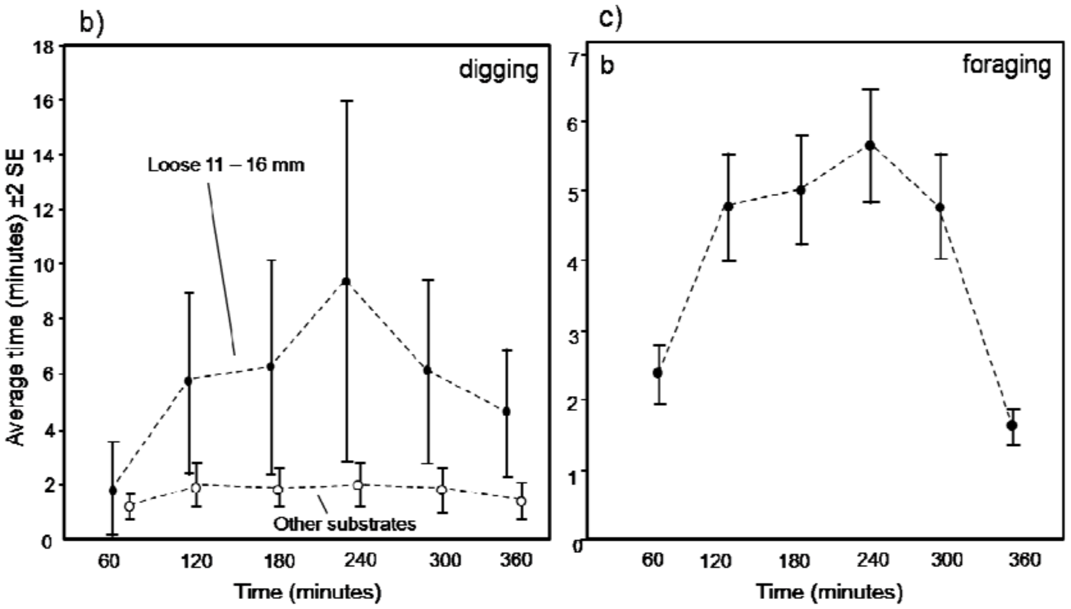
3.6.2. Temporal changes in crayfish behaviour

Crayfish spent significantly different periods of time walking ($p < 0.001$) and stationary ($p < 0.001$) with time in the flume (figure 3.7a). The cumulative proportion of time crayfish spent walking and stationary in the flume was consistent between different substrate types, hence why all substrate types were grouped in this analysis. Crayfish spent more time walking in the first hour of introduction to the surface than subsequent hours in the flume, with a linear decline in time spent walking over the six hour period. An opposite linear trend is present for stationary behaviour, with crayfish spending increasingly more time stationary on the experimental area as exposure time increases to six hours (figure 3.7a).

It was shown in figure 3.7 that significantly more time was spent digging on 11 – 16 mm loose surfaces than for other surfaces over the six hour period. Despite this, crayfish spent a similar length of time digging for each hour in the flume channel ($p = 0.538$) (figure 3.7b) which indicates that crayfish do not give up attempting to dig entirely, despite their limited impact in water-worked and 16 – 22 mm surfaces. Instead, after starting to dig, crayfish rapidly stop, with an average unbroken period of digging lasting 1 minute 11 seconds on loose, 11 – 16 mm surfaces, but only 32 seconds on the other surfaces. This suggests that crayfish regularly attempt to dig into substrates but only keep digging for extended periods where it is relatively easy to excavate grains. Alternatively, crayfish spent similar cumulative lengths of time foraging on all surfaces (*p* = 0.456) but the intensity of foraging varied significantly (*p* < 0.001) over a six hour period (figure 3.7c).

Figure 3.8: *The mean (± 2 SE, n = 40) number of minutes crayfish spent active during each hour of the six hour flume runs. a) minutes spent walking (filled circles, n = 40) and stationary (open circles, n = 40) grouped for all substrates. b) minutes spent digging for loose 11 – 16 mm surfaces (black circles, n = 10) and other surfaces (open circles, n = 30) c) minutes spent foraging on all substrate types (n = 40).*

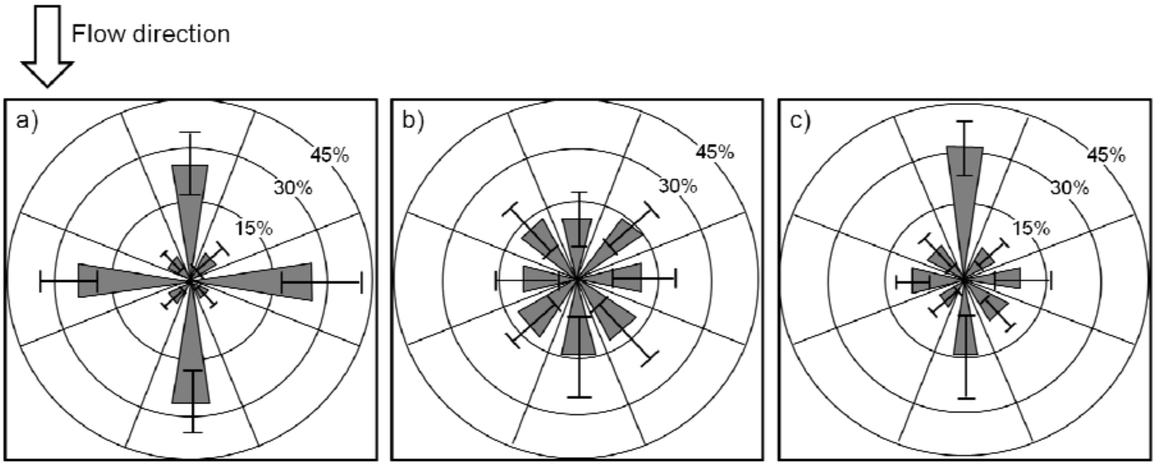




3.6.3. The location and orientation of crayfish in the flume

There were no significant differences in the orientation of crayfish (p = 0.452) or their location relative to cage edges (p = 0.748) between the four substrate types. Therefore, all surfaces were grouped together in this analysis. When stationary, crayfish spent 81% of the time in the corners or edges of the experimental patch and 19% of the time in central areas, consistent with observations in still-water experiments where crayfish avoided central areas (section 2.5.3). Crayfish orientation was dominated by both stream-wise and cross-stream directions with limited diagonal walking paths (figure 3.8a). This bias is an artefact of the experimental set-up as crayfish tend to walk along the edges of the environment, in this case the edges of the cage, as part of their exploratory behaviour. This is also reflected in the fact that 66% of walking by crayfish was located along the edges and corners of the aquaria in comparison to 34% in central areas. If the edges of the aquaria are removed from the analysis there is no bias in the direction of movement by crayfish which confirms that the initial bias is due to exploratory behaviour and not a hydraulic effect (figure 3.8b). When stationary, crayfish predominantly orientated themselves so they were facing in an upstream direction (figure 3.8c).

Figure 3.9: *Rose diagrams showing the mean (± 2 SE, n = 40) percentage time crayfish spent in each of eight orientations, grouped for all substrate types. a) Orientation of walking by crayfish over the entire patch. b) Orientation of walking by crayfish in central regions. c) Orientation of crayfish when stationary.*



3.7. Structural impacts of crayfish activity

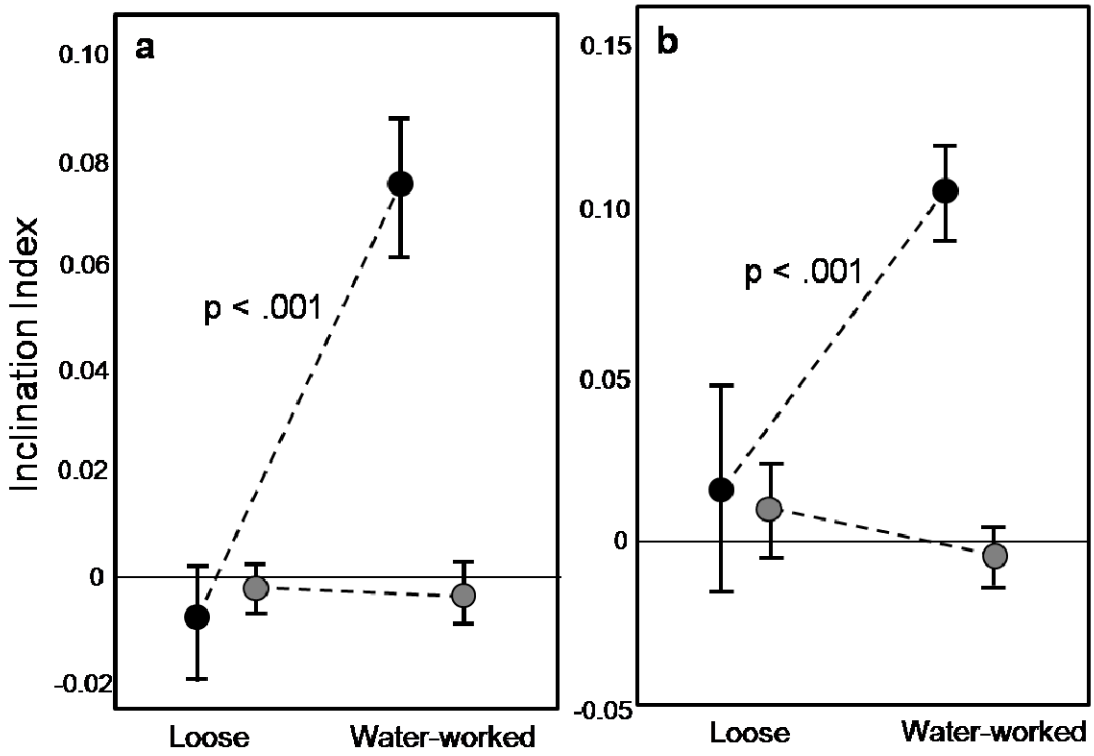
3.7.1. Confirmation and quantification of structuring due to water-working

The structural difference between surfaces before and after two hours of structuring flow was quantified using geostatistical analysis of substrate surfaces. Loose surfaces had no asymmetry in inclination in both stream-wise and cross-stream directions indicating that the surface was unstructured. Water-worked beds had a strong asymmetry in surface inclinations in a stream-wise direction but no asymmetry in a cross-stream direction indicating a structuring of the substrate by the flow (figure 3.9). The difference in inclination index between loose and water-worked surfaces was found to be statistically significant in stream-wise directions but not in cross-stream directions (table 3.5). These results indicate that the antecedent flow conditions successfully structured substrate surfaces. The values of the inclination index here (I_I = 0.07 - 0.1) are consistent with those of other studies which have used the index and found inclination to be between 0.03 – 0.18 in gravel-bedded rivers (Millane *et al*., 2006).

Table 3.5: *Significance levels (p-values) derived from paired t-tests for the inclination index in both stream-wise and cross-stream directions before and after water-working (WW).*

		11 – 16 mm			16 – 22 mm		
		Mean	**St.dev**	***p*-value**	**Mean**	**St.dev**	***p*-value**
Stream-wise	Loose	-0.0134	0.0213	< 0.001	-0.0022	0.0128	< 0.001
	WW	0.0743	0.0131		0.0963	0.00314	
Cross-stream	Loose	-0.0032	0.0108	0.473	0.0041	0.0187	0.258
	WW	-0.0004	0.0010		-0.0019	0.0184	

Figure 3.10: *Mean (±2 SE; n = 10) difference in the inclination index between loose and water-worked surfaces in both a stream-wise direction (black circles) and a cross-stream direction (open circles). Significance levels are derived from paired t-tests. a) 11 – 16 mm. b) 16 – 22 mm.*



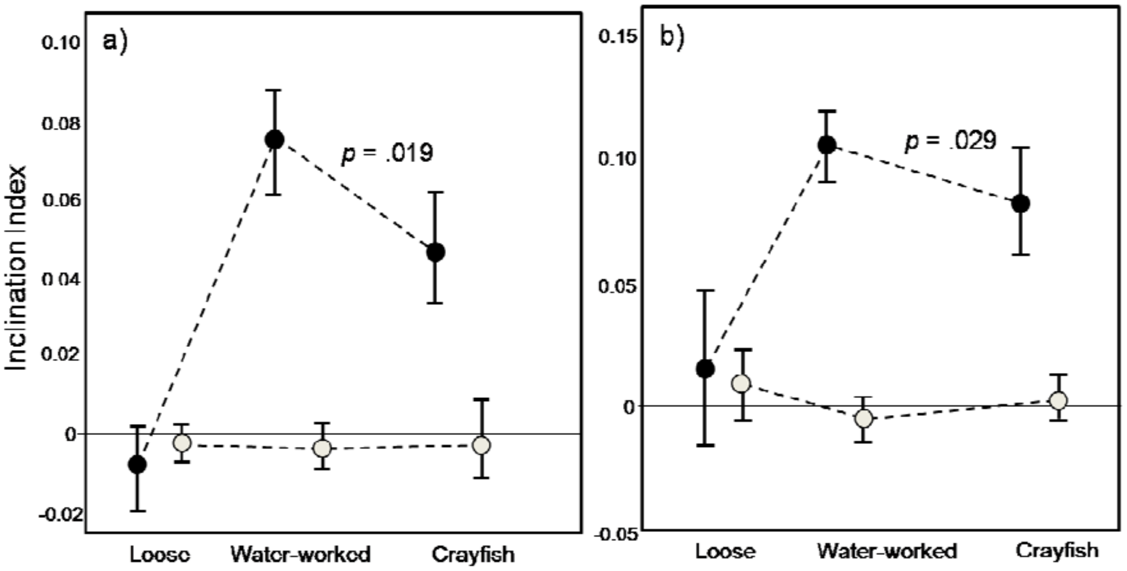
3.7.2. The impacts of crayfish on gravel structure

Six hours of crayfish presence on water-worked surfaces (*series 2*) had a statistically significant impact on the stream-wise inclination index (table 3.6). In 11 – 16 mm gravels, the inclination index, representing stream-wise slope asymmetry, was reduced by 37% and by 20% in 16 – 22 mm substrates (figure 3.10). There was no alteration in the distribution of inclinations in a cross-stream direction. When crayfish were placed on an initially loose surface (*series 1*) they altered the inclination index but had no statistically significant impact. This indicates that they disturbed the substrate surface, altering the distribution of both stream-wise and cross-stream slopes, but, unlike water-working, they did not structure the surface into an organised arrangement of grains. These results indicate that crayfish have the potential to oppose the structuring of substrates by the flow by partially randomising surface inclinations. However, crayfish activity does not structure loose surfaces or surfaces in a cross-stream direction. The reduction in the level of structuring of water-worked surfaces in a stream-wise direction by crayfish was not sufficient to return the surface to an unstructured state, like that of loose surfaces (*series 1*; figure 3.10). This can be proven because initially water-worked surfaces which were disturbed by crayfish had a significant asymmetry in inclinations compared to initial loose surfaces (paired *t*-test; 11 – 16 mm $p = 0.001$; 16 – 22 mm $p < 0.001$), indicating that the crayfish-disturbed surfaces were still structured in a stream-wise direction.

Table 3.6: *Significance levels (*p *values) from paired t-tests for structural parameters between initially water-worked surfaces before and after crayfish activity.*

		11 – 16 mm			**16 – 22 mm**		
		Mean	**St.dev**	***p*-value**	**Mean**	**St.dev**	***p*-value**
Stream-wise I_l	Before	0.074	0.021	0.019	0.106	-0.013	0.029
	After	0.046	0.023		0.083	0.034	
Cross-stream I_l	Before	-0.008	-0.009	0.812	-0.013	0.015	0.534
	After	-0.010	0.016		0.004	0.014	

Figure 3.11: *Mean (±2 SE; n = 10) alterations to the inclination index between substrates before and after water-working and after crayfish activity in both stream-wise (black circles) and cross-stream (open circles) directions. Significance levels are derived from paired t-tests. a) 11 – 16 mm. b) 16 – 22 mm.*



To further explore the impact of crayfish, and to corroborate results from the inclination index, trends in the aspect and magnitude of slopes were investigated. Water-worked surfaces are characterised by having significantly more slopes in an upstream facing aspect than in a downstream facing aspect and this can be seen in figure 3.11. However, after six hours of crayfish activity this asymmetry was consistently reduced for both 11 – 16 mm surfaces and 16 – 22 mm gravels (figure 3.11). Although this was not statistically significant and after crayfish activity there still remained a dominance of upstream facing slopes, this corroborates the results from the inclination index and indicates that six hours of crayfish activity reduced the structuring of the surface, even if only slightly.

The distribution of slope magnitudes within upstream and downstream aspects was also modified by crayfish for both 11 – 16 mm and 16 – 22 mm surfaces (figure 3.12). Water-worked surfaces had fewer steep slopes in upstream facing directions and an increased number of shallow slopes (<40°) which represent the upstream face of imbricated grains. Alternatively, there were significantly more steep slopes (> 60°) in downstream facing aspects which represent the steep downstream edge of imbricated grains. Crayfish reduced both of these inequalities in the distribution of slope magnitudes, increasing the number of steep slopes in upstream facing aspects and decreasing steep slopes in downstream facing aspects. This indicates that crayfish reduced the imbrication of surface grains but, the effect was not statistically significant, except for 11 – 16 mm downstream aspects, where crayfish significantly reduced the number of slopes steeper than 60° (figure 3.12). These results, in combination, indicate that crayfish reduced the level of imbrication across water-worked surfaces for both grain sizes.

Figure 3.12: *The mean (± 2 SE, n = 10) percentage of slopes falling within each aspect category for water-worked (red) and crayfish disturbed (black) surfaces. a) 11 – 16 mm surfaces and b) 16 – 22 mm surfaces*

Figure 3.13: *The mean (± 2 SE, n = 10) percentage of slopes in each magnitude category in an upstream and downstream direction for water-worked (red) and crayfish disturbed (black) surfaces. a) 11 – 16 mm surfaces and b) 16 – 22 mm surfaces. * indicates a significance level derived from a paired t-test* $p < 0.001$.

3.7.3. Roughness alterations between loose and water-worked surfaces before and after crayfish activity

Water-worked beds had a lower surface roughness, defined as the standard deviation of surface elevations, than loose surfaces, which was statistically significant for both grain sizes (table 3.7). This is likely to be due to the imbrication of the water-worked surface and the movement of grains protruding into the flow. This result is consistent with the results of Cooper and Tait (2009) who found that water-worked, fed beds with a heterogeneous substrate had a smaller range of bed elevations than unworked surfaces.

Six hours of exposure to signal crayfish increased the surface roughness, but this was not statistically significant for initially loose (*series 1*) or initially water-worked surfaces (*series 2*; table 3.7). Unlike still-water experiments, there was no significant correlation between the proportion of pit and mound construction and surface roughness. This is likely to be due to the limited time crayfish were exposed to a surface in the flume and the lack of solid side-walls to reduce slumping of material into pits, allowing for pits to be dug deeper in still-water aquaria than in the flume.

Table 3.7. *Significance levels (p-values) derived from paired t-tests for the difference in surface roughness, parameterised as the standard deviation of surface elevations, between surfaces before and after water-working and before and after crayfish activity.*

	11 – 16 m p-value	16 – 22 mm p-value
Loose – WW	< 0.001	< 0.001
Loose - crayfish	0.214	0.701
WW - crayfish	0.135	0.534

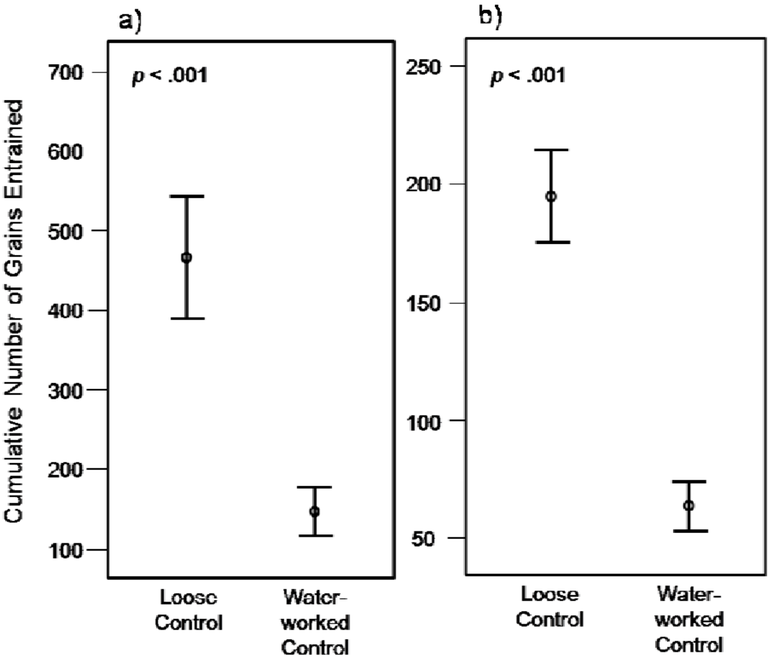
3.8. Entrainment

3.8.1. Differences in mobility between loose and water-worked substrates without crayfish

During the water-working, grains were observed to restructure over the two hour period. The majority of grains which were entrained during the water-working were entrained in the first 20 minutes of the flume run. These tended to be grains sitting proud on the surface. Grains were observed to rotate on an axis and to vibrate *in situ*, consistent with observations made by Carling *et al*. (1992). Grains with high friction angles were also observed to rock back and forth in the substrate pocket where they were located. The rocking and reorientation of grains was most prevalent in the first hour of the imbrication run but continued to a lesser degree throughout the two hours.

As anticipated, during the entrainment tests at the higher velocity flow, water-worked surfaces were considerably more stable than loose surfaces. In 11 – 16 mm substrates, on average, three times more grains were moved from loose surfaces than water-worked surfaces (figure 3.13). The nature of entrainment from surfaces is described in more detail in section 3.8.3.

Figure 3.14: *The mean (± 2 SE; n = 10) number of grains moved over a 2 hour period from a 2400 cm^2 surface for a) 11 – 16 mm and b) 16 – 22 mm loose and water-worked control surfaces. Significance levels were derived from paired t-tests.*



3.8.2. Impact of crayfish on the number of grains entrained

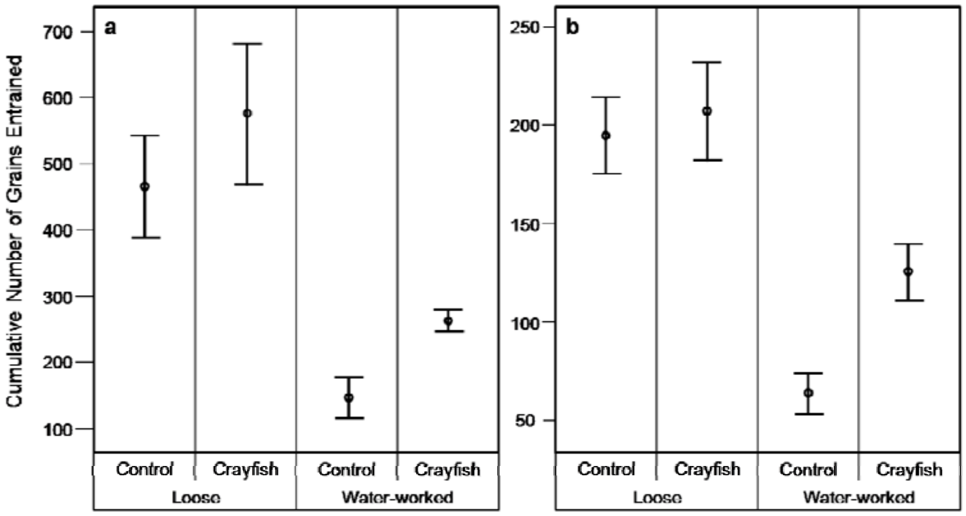
Six hours of exposure to crayfish had a substantial impact on the stability of gravel patches with significantly more grains moved from crayfish disturbed surfaces than control surfaces (table 3.8). On average, 1.8 times more material was moved from crayfish-disturbed surfaces than water-worked control surfaces. Whilst the magnitude of the change appears to be similar for both loose (*series 1*) and water-worked surfaces (*series 2*), this was only statistically significant for water-worked surfaces due to the variability in the number of grains entrained from loose surfaces, indicated in figure 3.14.

There was a significantly greater variance for initially loose surfaces (*series 1*) than those that were initially water-worked (*series 2*) for both 11 – 16 mm and 16 – 22 mm surfaces (table 3.8). This indicates that there was a great range in the number of grains entrained between the ten replications of loose surfaces for each grain size but only a relatively small difference between the ten replications of water-worked surfaces. This was expected as water-worked surfaces had been structured under the same conditions and, therefore, had a similar surface structure between replications. Conversely, loose surfaces had very different structures as they were random distributions of grains resulting in the great range of entrainment counts. The activity of crayfish did not alter significantly the variance of entrainment counts within any substrate type despite increasing the total average number of grains entrained (table 3.8). Had crayfish completely reversed the imbrication of water-worked surfaces then it would be expected that the variance in entrainment data would have increased, as well as the total number of grains entrained. As such, this result may indicate that crayfish had only limited structural impact as entrainment rates from water-worked surfaces remained similar between flume runs even after crayfish activity.

Table 3.8: *The mean and standard deviation of the number of entrained grains for the four substrate types between control and crayfish disturbed surfaces. Significance levels (p-values) in the mean number of grains moved between control and crayfish disturbed surfaces, derived from an ANOVA (tukey post-hoc test) are presented. Significance levels between the variance in the number of grains mobilised was derived from a Levene's test.*

		Control		**Crayfish**		**Means**	**Variance**
		Mean	**St.dev**	**Mean**	**St.dev**	***p*-value**	***p*-value**
Loose	**11 – 16 mm**	465	124	576	165	0.107	0.327
	16 – 22 mm	195	31	207	39	0.464	0.455
Water-worked	**11 – 16 mm**	147	50	264	30	< 0.001	0.359
	16 – 22 mm	64	15	125	22	< 0.001	0.498

Figure 3.15: *The mean (± 2 SE, n = 10) number of grains moved during a two hour entrainment period across a 2400 cm^2 area for loose and water-worked surfaces after six hours of low velocity flow with crayfish (crayfish) and without crayfish (control). a) 11 – 16 mm surfaces and b) 16 – 22 mm surfaces.*



3.8.3. Cumulative effects on entrainment

At the start of experimental runs, the number of grains mobilised from loose surfaces rose rapidly before levelling off. The initial steep rise was associated with the entrainment of particularly susceptible grains which were relatively common on loose, unstructured gravel. These vulnerable grains were entrained and transported out of the patch or into less vulnerable positions within the patch. As a result, the number of grains entrained declined as the substrate became structured. Not surprisingly, the water-worked control surface had substantially fewer grains entrained during the initial part of the flume run because grains in vulnerable positions or orientations had already been moved to more stable positions by the structuring flow (figure 3.15).

By dividing the entrainment run into three periods; 0 – 3 minutes, 3 – 40 minutes and 40 – 120 minutes, subtle differences between treatments which cannot be identified on figure 3.15 could be explored. Figure 3.16a shows the first three minutes of entrainment, with mobile grains counted over 10 second intervals and highlights the significance of the first 20 minutes of entrainment, with a substantial increase in the number of grains entrained from crayfish-disturbed surfaces, as described above (section 3.8.2; figure 3.15). Figure 3.16b shows entrainment data between 3 and 40 minutes. The number of grains mobilised was grouped into one minute intervals to highlight differences in transport rates between surfaces. Hence, the number of grains moved appears similar to that of 0 – 3 minutes (figure 3.16a) but in fact bedload transport rates are only a fraction of those of earlier time periods. Whilst differences between surfaces are relatively small and variable, the crayfish disturbed surfaces consistently lie above the control surfaces. This indicates that the activity of crayfish still had an impact on bedload transport up to 40 minutes after the entrainment run began.

Figure 3.19c shows the bedload transport from 40 minutes until the end of the run at 120 minutes. The number of grains moved has been grouped into 10 minute intervals to indicate better the differences in transport between surfaces. If grouped into 10 second intervals, as in the 0 to 3 minute data (figure 3.16a), an average of less than one mobile grain would be recorded and data variability would be so great as to obscure any trends in the data. The crayfish disturbed surfaces lie consistently above control surfaces indicating that substrate reworking by crayfish still influences bedload transport after an hour of entrainment flow, despite the fact that the majority of the impact of crayfish occurs during the first few minutes. These results demonstrate that crayfish disturbance has an impact for the entirety of the entrainment period (120 minutes).

Figure 3.16: *The cumulative number of grains moved with time. Lines indicate the mean, shaded regions are ± 2 SE of the mean (n = 10) a) 11 – 16 mm b) 16 – 22 mm. Lines were constructed from 10 second grain counts for the first 10 minutes and one minute counts for the following 110 minutes.*

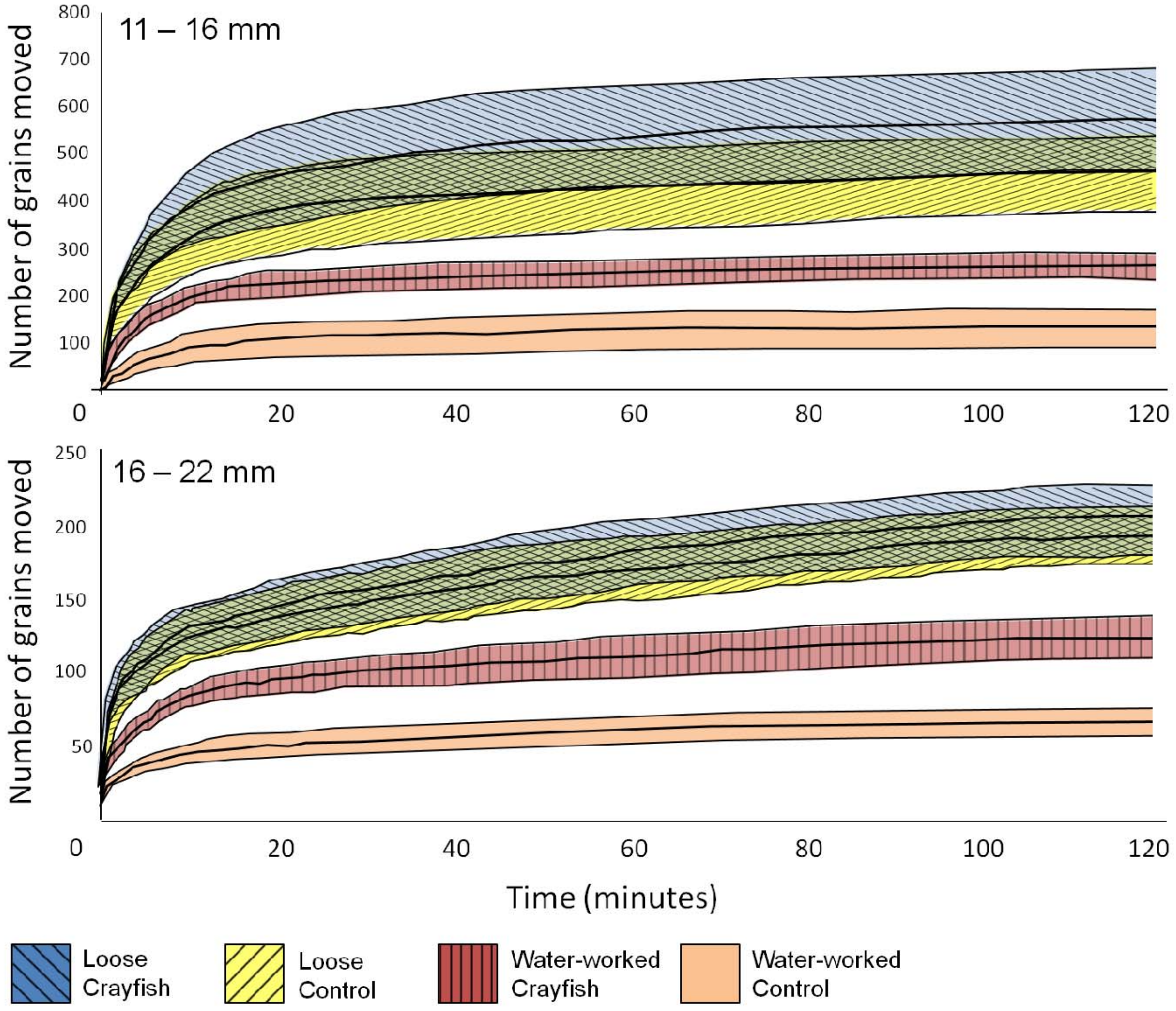
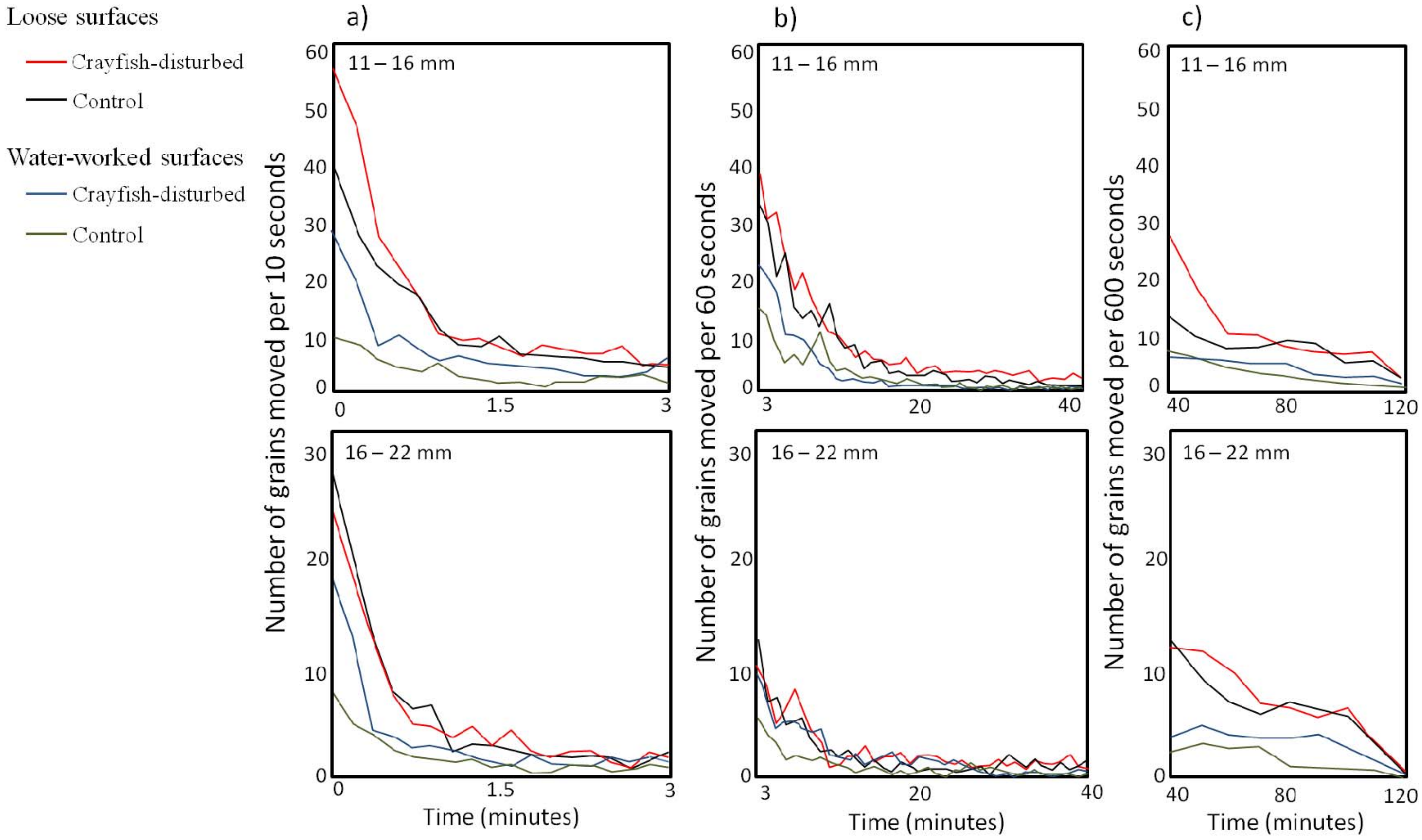


Figure 3.17: *The mean number of grains (n = 10 for each case entrained from substrates a) over the first 3 minutes (grouped into 10 second intervals), b) between 3 and 40 minutes (grouped into 60 second intervals) and c) between 40 and 120 minutes (grouped into 600 second intervals). Black lines indicate loose control surfaces; red lines indicate loose crayfish-disturbed; green lines are water-worked controls and blue lines a water-worked, crayfish disturbed surfaces.*



3.9. Discussion

3.9.1. Potential impact of crayfish on the consolidation of gravel substrates

The modification of substrate topography and structure by crayfish could act to oppose the consolidation of gravel-bed rivers. This was suggested based on results from still-water experiments (section 2.6.4) and is supported by the results of flume experiments where exposure to crayfish substantially altered the mobility of grains from water-worked substrates. Because the water-worked surfaces used in these experiments were narrowly-graded, they cannot be taken as representative of naturally heterogeneous bed materials. How the homogenous nature of the substrates used would impact physical disturbance by crayfish is currently unknown but several lines of evidence suggest that crayfish would still have an impact. It is known that crayfish burrow against coarse grains (Parkyn *et al*., 1997) suggesting that a heterogeneous sediment mixture may encourage more digging. A heterogeneous sediment mixture may also make it easier for crayfish to dislodge grains, as similar-sized grains do not necessarily need to be moved in order to dislodge a grain and crayfish may get more leverage on a grain which projects from the surface.

Another difference between water-worked beds in the flume and a natural fluvial substrate is structuring of the subsurface. Cooper and Tait (2009) found that the subsurface of a gravel bed was also structured by the flow, particularly due to the ingress of fines and imbrication. Water-worked surfaces in these experiments are assumed to have only surficial structuring as only surface grains were mobilised during the water-working phases. There was also no fine sediment included in substrates which are known to reduce the friction angle of surface grains as well as tightening the packing of the bed. The reorientation of surface grains during structuring disturbs fines which then settle back onto the substrate, further consolidating the bed into a tighter packing arrangement (Frostick *et al.*, 1984). Therefore, water-worked substrates in these experiments are likely to only partially mimic natural river beds.

The impact of crayfish may be reduced by the presence of fines. However, set against this, crayfish have already been found to winnow substantial quantities of fine material. Fine sediment can be mobilised by the movement of legs and contact between the substrate and abdomen when walking (Usio and Townsend, 2004). When frightened, crayfish escape by backwards swimming, which exerts considerable force on the substrate directly below the crayfish and which may disturb fine sediments (Webb, 1979; Cooke and McMillan, 1985).

Studies focusing on the impact of crayfish on invertebrate density and leaf decomposition have also noted that crayfish species can winnow fine material from substrates (Parkyn *et al.*, 1997; Creed and Reed, 2004; Usio and Townsend, 2004). Therefore, it is likely that crayfish will still have an impact on multi-modal gravel-sand sediments more typical of those found in gravel-bed rivers.

3.9.2. Topographic alterations by crayfish of loose and water-worked surfaces

Crayfish modified the topography of all gravel surfaces in the running-water flume experiments. For 11 – 16 mm material, substantially more material was moved by crayfish on loose surfaces (*series 1*) than water-worked surfaces (*series 2*). As might be expected, this implies that the structuring of gravel substrates reduces their vulnerability to disturbance by crayfish. Interestingly, the same pattern is not true of the coarser 16 – 22 mm material where similar volumes of material were moved by crayfish on both loose and water-worked surfaces. It is hypothesised that this is because of a distinction in fabric rearrangement which was observed to occur as either a by-product of walking and foraging, or by active movement of grains when crayfish are foraging and digging pits. The former, accidental rearrangement of grains, is dominant in finer grain sizes where the body weight of a crayfish is sufficient to disturb the orientation and friction angle of gravels. However, in water-worked surfaces, due to the increased stability imparted by grain interlock, grains did not tend to move as obviously as loose surfaces as a result of the brushing past of crayfish. In coarser, 16 – 22 mm gravels, the accidental rearrangement of grains was less dominant due to the increased weight of individual grains relative to that of a crayfish and resulted in significantly lower volumes of moved material. The fabric rearrangement that did occur tended to be as a result of foraging, digging and the probing of the bed on purpose. In this case, water-working did not further limit volume of material crayfish moved implying that grain weight was already an over-riding limiting factor.

Pit and mound construction was also significantly less in 11 – 16 mm, water-worked surfaces than initially loose surfaces. This is likely to be due to the difficulty of dislodging grains from a structured surface where grains are interlocked. This had less impact in coarse material because grain weight already limits the pit and mound construction. It was found that crayfish did not give up digging completely on coarse and water-worked surfaces, but instead dug for significantly shorter periods than on loose 11 – 16 mm surfaces. This suggests that, despite the fact crayfish can dig into 16 – 22 mm material, they limit themselves, perhaps because pit digging is not seen as a good investment of energy in substrates which are difficult to dig into.

To summarise, water-working limited the accidental reorganisation of surface fabrics by walking and foraging crayfish and reduces pit and mound construction by making it more difficult for crayfish to dislodge grains from the surface. This was more pronounced in finer material presumably because crayfish disturbance was already limited by the relative weight of grains coarser than 16 mm.

3.9.3. The activity of crayfish in laboratory experiments

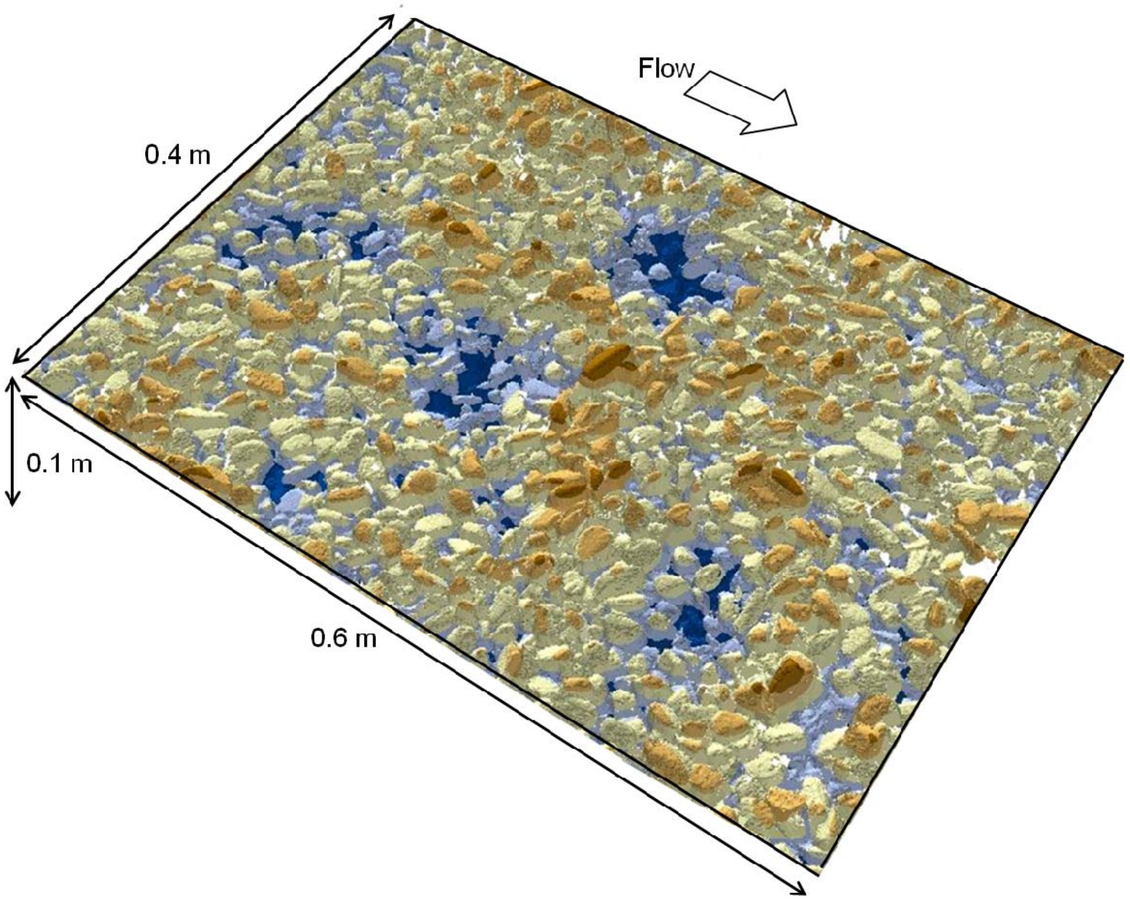
It was important to quantify the activity of crayfish when in the flume to establish whether their activity was consistent with observations made in nature and to aid in determining how and why crayfish rework substrates. The proportion of time spent stationary (40%) and walking (38%) was very similar to the results obtained by Stein and Magnuson (1976) who found that adult crayfish (*Orconectes propinquus*) spent approximately 40% of the time in aquaria stationary and a further 40% walking. Crayfish spent longer foraging between hours 2 – 5, than in the first and sixth hour. The lack of foraging in the first hour is likely to be associated with the dominance of walking associated with crayfish exploring their environment. The lack of foraging in the sixth hour is interesting but appears to be associated with the greater length of time crayfish spent stationary. In the sixth hour crayfish spent 38% of their time stationary and this may reflect a completion of their exploratory behaviour.

Whilst the activity of crayfish in still-water experiments was only qualitatively assessed, there are strong similarities between activity in the flume and in aquaria. Crayfish initially explored along the edges of the environment, eventually crossing into central areas. Also, crayfish tended to pick an area, usually in a corner where they would construct a pit from which they would further explore the aquarium. Crayfish spent increasing amounts of time sheltering after an initial exploration of the substrate. This similarity is interesting because there were some important differences between the environments, not least the flowing water in the flume. Aquaria had solid, black, opaque sides whereas crayfish in the flume were in a cage, through which crayfish could presumably see. Other studies have found that the topographic environment has an important impact on the exploratory behaviour of crayfish (Basil and Sandeman, 2000; Patullo and Macmillan, 2006) and the results of this study would support that, implying that it is the size of the enclosure and the nature of the substrate which is important in the exploratory response of crayfish, at least when the flow is low.

3.9.4. Alterations to pit and mound construction associated with flowing water.

It was found that a greater volume of material from loose surfaces was associated with pit and mound construction in low velocity flow conditions than in still-water conditions described in chapter 2. This volume increase was a result of more pits being dug in the flume environment rather than an increase in pit depth. In the flume environment, pits were shallow dishes with excavated material heaped into shallow mounds around them which tended to form ridges across the surface due to the density of pits (figure 3.17). This differed from pit morphology in still-water environments which tended to be deeper because pits could be dug against aquaria edges which reduced the slumping of material back into pits. The increase in pit construction in the flume suggests that flowing water instigates digging by crayfish. It is known that crayfish prefer slow moving water and are not well adapted physically to withstand moderate flow velocities (Maude and Williams, 1987; Clark *et al*., 2008). However, crayfish are rarely displaced by high flows, suggesting they shelter in flow refuges such as burrows (Bubb *et al*., 2002). The fact that crayfish construct pits at low flows and in still-water would suggest that pits are also associated with factors other than flow conditions, such as protection from predators.

Figure 3.18: *DEM of an 11 – 16 mm surface after six hours of crayfish activity. Note the four distinct areas of pit construction (blue areas) and the ridges of mounded material (brown) which network between pits.*



The hypothesis that pits act as make-shift refugia is supported by the orientation of crayfish when sitting in pits. Crayfish predominant faced upstream. When sheltering in pits in still-water experiments it was recorded that crayfish always sat in a typical posture with their vulnerable tails folded under their bodies and their intimidating claws in front of their heads. This was interpreted as protection from predators. In the flume environment, it was apparent that this typical posture may also be an effective way of stream-lining the crayfish body, reducing the flow forces operating on the crayfish and lowering its relative protrusion. It is known that other species of crayfish can posture to reduce flow stresses over their body at high flows (Maude and Williams, 1987). It was found that stationary crayfish in flows with an average mean velocity of 15 – 25 cm s^{-1} faced upstream, lowered their cephalothorax and abdomen to the substrate and kept their claws in front of their body. Posturing in pits may be an extension of this. By using flow visualisation, Maude and Williams (1987) found that crayfish claws deflected the flow over the top and around the sides of the crayfish, reducing the lift and drag forces acting on the body. Whilst posturing could also be associated with other behaviours such as sensing chemical signals transported from upstream, the similarity of the posture in this study with previous studies makes it seem most likely that crayfish orientation and posture reflects an attempt to lower its relative protrusion and limit the lift forces affecting them, perhaps in preparation for flows capable of entraining them. This may be especially true where shelters, such as burrows into cohesive material, are not available.

3.9.5. Relationship between alterations in substrate fabric and structural alterations to surfaces

Across all surfaces, whether in still-water (chapter 2) or flume experiments, topographic alterations were dominated by fabric rearrangement. It was found that crayfish did not structure loose substrates (*series 1*) through their activity but they could partially reverse the structuring of water-worked surfaces (*series 2*). Consequently, after six hours of crayfish activity the rearrangement of surface grains on a loose surface is unlikely to have a substantial impact on grain stability and this is confirmed by the entrainment data discussed below. The modification of grain protrusion through pit and mound construction is likely to be of more significance to grain stability in loose surfaces.

It was found that two hours of moderate velocity flow (40% discharge of that used to entrain substrates) was sufficient to strongly structure surfaces by creating an asymmetry in the distribution of slopes across gravel surface, typical of grain imbrication. Six hours of crayfish activity reduced this asymmetry over both substrate sizes, reversing the imbrication of the surface by re-randomising the distribution of slope aspect and magnitude across surfaces. Crayfish were not able to reverse surface structuring back to a level comparable to loose surfaces, probably because of the limited period crayfish were left on substrates.

In summary, the magnitude of restructuring by crayfish, whilst statistically significant, is relatively subtle in comparison to structuring by the flow. However, the structuring of substrates by the flow will only occur occasionally when the bed is mobile. Whereas, crayfish will reverse structuring whenever they are active and cumulatively may have a substantial impact, especially where they occur in high densities. Also, the experiments demonstrate that the relatively subtle restructuring by crayfish was responsible for significant alterations in grains stability.

3.9.6. Relative importance of topographic changes to sediment entrainment

The importance of pit and mound construction in the entrainment of material is demonstrable from entrainment data of loose surfaces. Loose surfaces which were exposed to crayfish (*series 1*) had substantially more grains entrained from them than control surfaces. This increase could not have been associated with structural changes because crayfish did not alter the structure of grains across loose surfaces, instead altering them from one random arrangement to a different, but still apparently random structure. Therefore, this increase in entrained material must be associated with pit and mound construction and the modification in grain protrusion and friction angle.

The importance of pit and mound construction is corroborated on water-worked surfaces by the variance of grain entrainment data. Loose surfaces had a significantly greater standard deviation of entrainment counts than water-worked surfaces, which were much more consistent between runs. This is because loose surfaces had a random arrangement of grains creating a random structure (section 3.7.1). Therefore, grains across the surface had a great range of entrainment thresholds despite being of near uniform size. Alternatively, the water-worked surfaces had been structured by the flow, creating a consistency in the structure of surfaces both across individual surfaces and between surfaces. Exposure to signal crayfish did not increase the variability in the total number of grains entrained from water-worked surfaces. Had crayfish completely randomised the structure of the water-worked surface it would be expected that the range of entrainment data would be increased to a comparable level to loose surfaces. In fact, the difference in the standard deviation of entrainment data for 11 – 16 mm loose and water-worked gravels which had been disturbed by crayfish are lower than for control surfaces.

Whilst these points demonstrate the importance of pit and mound construction, it is also apparent that structural changes were an important component in promoting sediment transport. The majority of grains transported from crayfish-disturbed surfaces were entrained in the first 20 minutes of the run, suggesting crayfish increased the number of very vulnerable grains which are likely to be associated with both mound construction and structural changes. However, even after 100 minutes of entrainment crayfish surfaces were still more mobile than control surfaces (figure 3.19). This is more likely to be associated with structural changes than with changes in protrusion which would leave grains sitting proud on the surface and, consequently, likely to be entrained earlier in the flume run. It was observable that after approximately 30 minutes, pit and mound topography was much less apparent due to the mobilisation of the bed in comparison to the beginning of the run. It is also likely that, if crayfish had been left for longer on surfaces, the importance of structural changes would increase relative to protrusional change as crayfish are unlikely to constantly increase the size of pits but, through consistently walking and foraging, the cumulative impacts on the surface structure will continue to build. Therefore, this analysis suggests both pit and mound construction and structural alterations had important impacts on the stability of gravel beds.

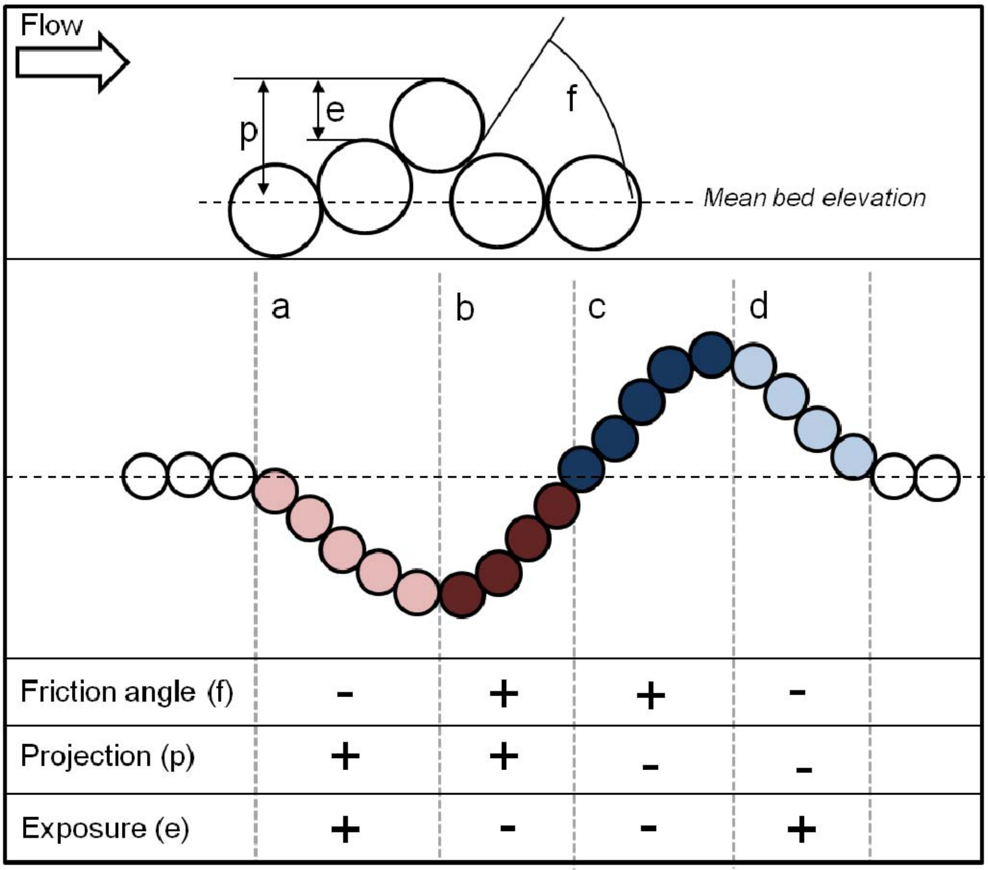
3.9.7. Importance of crayfish to sediment entrainment

Crayfish led to a significantly greater number of grains being entrained from surfaces, discussed relative to other geomorphic processes in chapter 5. This increase has been explained in terms of reductions in frictional angle and increased protrusion of grains due to pit and mounds construction. However, there will be many grains that have an increased friction angle (Figure 3.18a; regions b and c) or that are ‘hidden’ in pits which may act to stabilise grains (a and b). Also, using the terminology of Kirchner *et al*. (1990), it is apparent that many grains in mounds project above the local bed surface but have a low exposure due to the presence of other grains in the mound which also project into the flow (figure 3.18). In fact, all areas in the simple model presented in figure 3.18 that have an increased friction, theoretically imparting stability to the grain, occur in areas of increased exposure, reducing stability and *vice versa*. Consequently, it is difficult to determine the exact impacts of pit and mound topography on transport without more detailed measurements even though the overall impact was shown to reduce the stability of the bed.

The presence of pits and mounds will also have hydraulic impacts. They have already been shown to increase surface roughness in still-water environments (section 2.3.4) although the same was not true of flume experiments where crayfish were left for a shorter periods of time. Mounded material may create areas of recirculating flow, similar to other protruding objects such as pebble clusters (Hassan and Reid, 1990; Buffin-Belanger and Roy, 1998; Lawless and Robert, 2001). These hydraulics impacts will also have impact implications for the entrainment of grains. Montgomery *et al*. (1996) found that the construction of pits and mounds by spawning salmonid fish creates a fluid drag on the flow which reduces bed mobility, counteracting the loosening of the bed through excavation. A similar effect may also be true for the pits and mounds constructed by crayfish, however, without detailed hydraulic measurements it is difficult to ascertain exactly how these features influence the entrainment of individual grains, however, it seems likely that crayfish activity will increase the *range* of stresses required to entrain grains of the same size across a surface, discussed further in chapter 5.

The path length of grains transported from crayfish-disturbed surfaces was also not quantified. A grain on the 'lip' of a pit (figure 3.18) may be considered unstable but is likely to only be moved the short distance into the pit, where it would be in a relatively stable position, sheltered from the flow. Therefore, pits may act as bedload traps. This would result in the topography of the bed quickly becoming planar again with the mounded material eroded and transported into downstream pits. Material that is mounded on the upstream edge of a pit may be simply washed back into the pit, where it was originally excavated by crayfish. If crayfish occur in high density then, when constructing a pit for themselves, they may also push mounded material back into adjacent pits. Interestingly, Gottesfeld *et al.* (2008) found that as the density of Chinook salmon (*Oncorhynchus tshawytscha*) increased, bed morphology changed from dune forms characteristic of salmonid spawning to a more uniform, plane bedform. Consequently, crayfish density may influence the geometry of pits and mounds which would also have a substantial impact on the path length of mobilised material.

Figure 3.19: *Generalised pit and mound topography, split into four units (a – d) based on the friction angle, projection and exposure at each location. A positive symbol indicates an increase in stability whereas a negative symbol indicates a reduction in stability. Schematic diagram is modified from Kirchner et al. (1990).*



	a	b	c	d
Friction angle (f)	-	+	+	-
Projection (p)	+	+	-	-
Exposure (e)	+	-	-	+

Chapter 4

The spatial and temporal distribution of signal crayfish in a lowland British river.

4.1. Introduction

It has been found in still-water and at low velocity flows in a laboratory flume that crayfish can substantially rework gravel substrates. The reworking of substrates by signal crayfish resulted in two important alterations to surfaces. The first was a topographic change due to the construction of pits and mounds associated with digging and foraging. The second was a structural change associated with crayfish brushing past grains when walking and foraging, altering the geometry of surface grains and having the potential to partially reverse grain structuring. The combination of topographic and structural alterations resulted in a substantial increase in the number of grains that were entrained from narrowly-graded substrates. In order to assess the potential significance of these results in rivers, it is necessary to determine whether crayfish occupy substrate sizes that they are known to disturb in laboratory conditions. This was achieved by tracking crayfish across the patchy bed of a lowland British river using radio-telemetry.

4.2. Techniques for quantifying crayfish activity

4.2.1. The use of radio-telemetry to track organisms

Radio-tags have been used for a variety of applications in both ecological and geomorphic studies. A distinction can be made between active and passive radio-tags. An active radio-tag contains an internal power source allowing the tag to send a signal to an antenna array giving a continuous path of movement of the object being tracked (Habersack, 2001). Passive Integrated Transponder (PIT) tags do not contain an internal power source allowing tags to be small (2 mm wide, 10 – 20 mm long) and to be used to track individuals for many years. PIT tags are located using an antenna that generates an electromagnetic field that the tag derives power from so it can transmit information to a tag reader. This information is usually used to ascertain the point location of the tagged individual at a specific time. The range and efficiency of tag detection depends on the electromagnetic field created by the antenna but most systems have a detection range between 0.01 m and 3 m. PIT tags can be fixed onto or placed inside sediment particles and organisms. PIT tags have a very high reliability in tag detection (95 – 100%) and reading accuracy (100%) (Gibbins and Andrews, 2004).

PIT tags were initially used to identify individual animals using handheld tag readers that are held directly over the tags attached to or inserted into the animal, for example in agriculture (Freeland and Fry 1995). Portable detectors have since been developed that are swept across an environment like a metal detector (Roussel *et al*., 2000; Morhardt *et al*., 2000). These tend to consist of a circular antenna mounted on a pole. Portable detectors have been widely used to locate tagged fish (Roussel *et al*., 2000; Zydlewski *et al*., 2001; Hill *et al*., 2006), including fish in ice covered streams (Limnansaari *et al*., 2007). More recently, this technique has been used to identify and trace clasts in marine, hill-slope and fluvial environments (Nichols, 2004; Allen *et al*., 2006; Carré *et al*., 2007). A major benefit of this technique is that organisms only need to be disturbed once to attach the tag, after which, they can be located without further disturbance. The main weakness of using hand-held antennae is that the spatial and temporal extent and resolution of the data obtained is dependent on intensive surveying effort, making it a labour intensive approach.

Rather than sweeping an environment with an antenna, automated detection systems can be used. In this case, one or more antennae are distributed in space (for example, across the river bed) and connected together with a Multi-Point Decoder (MPD) that is connected to a dedicated data logger. If a tag is detected, its identification number, the antenna number and a time and date is logged and recorded. Automated systems are an effective, non-destructive way of monitoring the passage of particles or organisms, or for establishing residence times at points within the sampling frame. The main limitation of using automated systems is that antennae must be placed in locations where the tagged objects will come into range of them. This assumes some knowledge of the future location of tagged particles. Consequently, automated tracking is also particularly well suited to the fluvial environment. Automated systems have been used for a variety of ecological studies. For example, Riley *et al*. (2003; 2006) used an automated system consisting of two MPD connected to 31 antennae placed on the substrate surface to monitor the location of different fish species within a river channel. A grid of 242 buried antenna located throughout a 100 m riffle-pool section of the Ruisseau Xavier, Quebec, is being used to detect the location of tagged fish (Johnston *et al*., 2009).

4.2.2. The use of radio-telemetry to study the activity of crayfish

Both active and passive radio-tags have been used to investigate the movement and activity of crayfish (Schütze *et al.*, 1999; Bohl, 1999; Gherardi and Barbaresi, 2000; Robinson *et al.*, 2000; Bubb *et al.*, 2002a, b, 2004, 2006a, b, 2007). Signal crayfish movement is sporadic with crayfish remaining in one area for days to weeks and occasionally making long distance movements to another area, probably associated with a new refuge (Bubb *et al.*, 2002a, 2004; Light, 2003). This nomadic behaviour has also been observed in other crayfish species (Gherardi *et al.*, 2000; Robinson *et al.*, 2000). Signal crayfish have been found to move at rates of up to 120 m day^{-1} (Bubb *et al.*, 2002a; Light, 2003). The potential for crayfish to make long distance migrations is partly responsible for their rapid spread as an invasive species in environments where they have been introduced. Bubb *et al.* (2002b, 2006b) have successfully used PIT tags to track the long distance movement of signal crayfish through the River Wharfe, UK using a portable, handheld antenna. Bubb *et al.* (2002a, 2004, 2006a) have also used active radio-tags to record the distance moved by signal crayfish in the River Wharfe and the River Ure, UK. Robinson *et al.* (2000) used both active radio-tags and mark-recapture methods to study summer movements of white-clawed crayfish (*Austropotamobius pallipes*). These studies provide great insight into the large scale movements of crayfish in rivers but between long distance movements crayfish are usually characterised as “stationary”. In fact, crayfish are likely to be highly active between long distance movements within their home range, defined as the spatial area used in normal activities such as foraging and mating (Burt, 1943). It is small scale movements within the home range of crayfish that are of interest to this study.

4.3. Aims

It has been found in laboratory experiments that crayfish can rework fluvial gravels up to 38 mm in *b*-axis diameter. This has substantial impacts on the topography, structure and stability of substrates. To identify the significance of this phenomenon it is important to relate experimental studies to a field environment. Consequently, the aim of this chapter is to determine whether signal crayfish were present and active on substrate sizes which they had been found capable of reworking in experimental studies (chapter 2 and 3) in a natural environment. Previous studies by others have quantified the activity of crayfish over relatively long reaches of river. This study has aimed at quantifying the activity and substrate preferences at a smaller-scale within the home range of crayfish. The specific objectives of this study are:

i) To map and quantify the activity of signal crayfish within a river reach.
ii) To determine if crayfish are preferentially located in particular areas of a reach.
iii) To relate areas of preferred crayfish presence to substrate and hydraulic conditions within a reach.
iv) To determine any temporal variation in the spatial location of signal crayfish within a river reach.

4.4. Methods

4.4.1. Overview

The movement and behaviour of signal crayfish were investigated using PIT tags. Their location was tracked using an array of 16 automated antennae installed just below the surface of a river bed. Antennae were buried within discrete geomorphic patches defined by flow and substrate characteristics, as well as macrophyte presence. Every time a tagged crayfish moved within range of an antenna, the time, date, antenna number and tag number were recorded by a data-logger. Antennae were continuously monitored for 150 days from 26th June 2009 to the 22nd November 2009. Water stage and temperature were also continuously recorded during the tracking period and used to relate the presence and activity of signal crayfish to abiotic conditions.

4.4.2. Site location

Signal crayfish were tracked through a 20 m reach of the River Bain, Lincolnshire, UK (0° 09’ 41’’ W, 53° 20’ 15’’ N; figure 4.1). The River Bain is approximately 32 km long from its source to its confluence with the River Witham. The River Bain catchment is 197 km^2, and predominately underlain by chalk. The largest settlement within the catchment is Horncastle (population approximately 6,000 [2001 census]) which is 8 km downstream of the field site used in this study. The River Bain has its source in the Lincolnshire Wolds at Luford and has shallow valley sides along its course.

A 20 m reach at Biscathorpe was selected for use in this study (figure 4.2). The reach is situated within a 200 m length of the river with an average width of approximately 3 m located upstream of a road ford (figure 4.2). This gently meandering reach was selected because it contains a number of discrete substrate facies and flow patches that are representative along the length of the river over some considerable distance. These patches are discussed in section 4.4.6 but, in general, the substrate is non-cohesive and gravelly and the flow is relative shallow (approximately 0.4 m deep) with a flow velocity generally less than 0.5 ms^{-1} at 0.6*d*. At the time of study, the riparian area was cattle-grazed grassland with isolated trees. Downstream of the ford the river is wider (4 – 6 m). This reach of the River Bain is notable because it is known to have a large, stable and long established population of signal crayfish. In the mid-1980s, crayfish were introduced to a pond within the catchment but quickly colonised the river by moving down the first-order tributary shown in figure 4.2. They then rapidly spread both upstream and downstream along the main river channel and have been reported to occur in densities in excess of 10 m^{-2} (Holdich *et al*., 1995).

Figure 4.1. *A map of the River Witham catchment. The River Bain, a tributary of the River Witham, is shown in light blue. The approximate location of the field site is shown with a red square and the location of Goulcby Bridge gauging station shown with a white circle.*

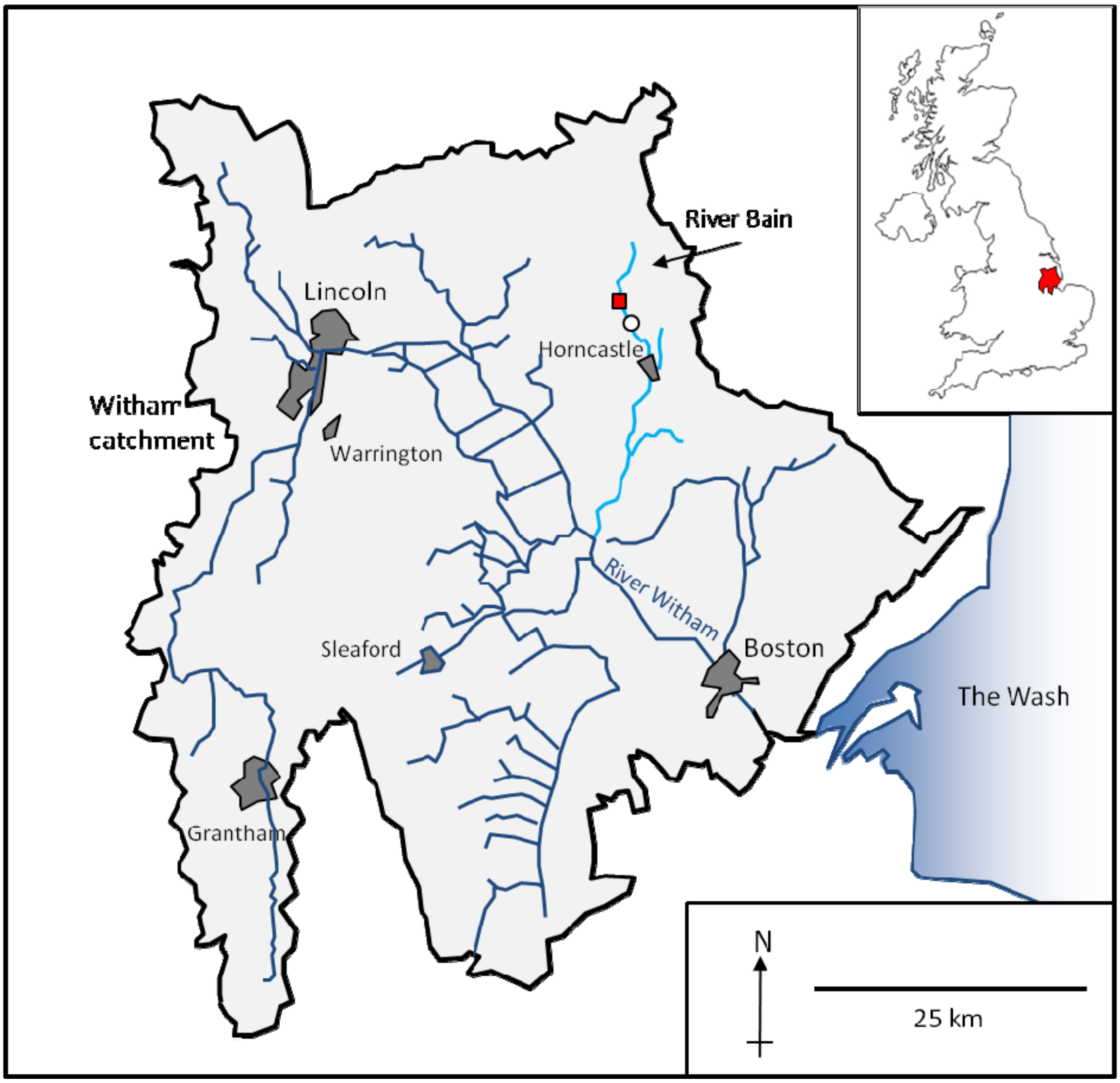
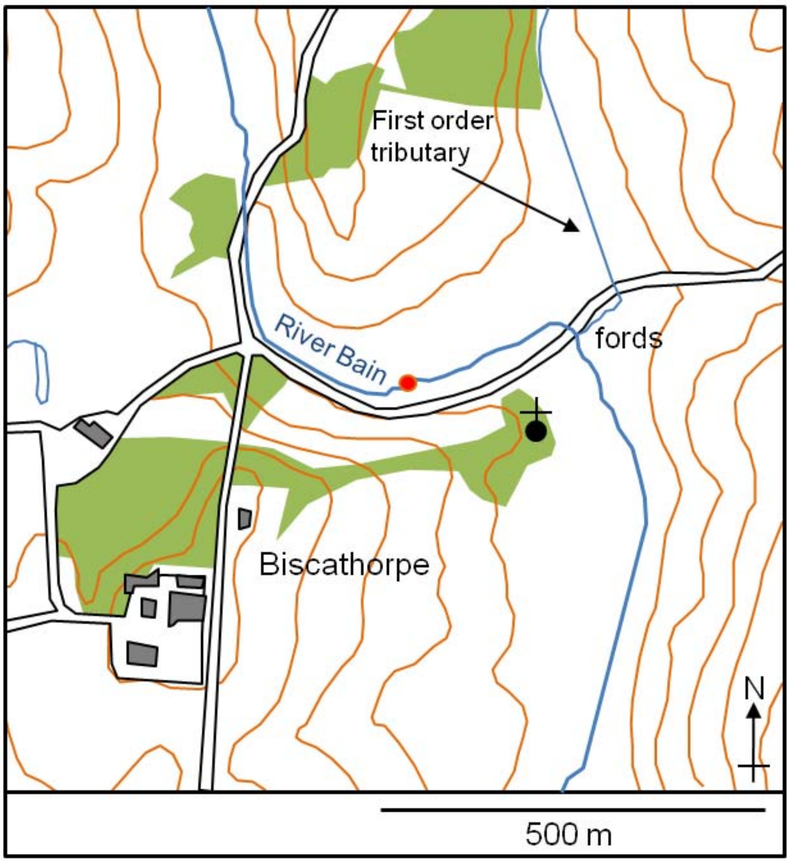


Figure 4.2. *Map of a section of the River Bain (0° 09' 41'' W, 53° 20' 15'' N) with the 20 m reach used in this study marked with a red circle.*



4.4.3. Historic hydraulic conditions within the River Bain

The River Bain is gauged at Goulceby Bridge, approximately 5 km downstream from the study reach. The catchment upstream of the gauging station is 62.5 km^2 and there are no significant tributaries between the tracking reach and gauging station. The station is a Crump weir with a 4.877 m crest length and has been recording daily-averaged discharge since 1972. During this 38 year period, the mean annual flow has been 0.35 m^3 s^{-1} with a 95% exceedance (Q_{95}) of 0.068 m^3 s^{-1} and a 10% exceedance (Q_{10}) of 0.729 m^3 s^{-1} (figure 4.3). Gauged flow data used in this study were obtained from both the National River Flow Archive (NRFA) and directly from the Environment Agency, which operates the gauging station.

In general, the long-term record reveals that the flow remains low from July to October and rises through October to December, remaining relatively high until spring. The discharge drops gradually and relatively consistently from March to June. In most years, there are isolated high flow events in the summer and autumn but these rarely exceed 2 m^3 s^{-1}. The flow regime is dominated by ground-water flow with super imposed rainfall-driven high flows giving the hydrograph spikes. Prior to the tagging campaign, during 2007 and 2008, flow was unusually high and contained three of the largest five flow events of the last 38 years, the other two being on the 25th April 1981 which had maximum discharge of 10.43 m^3 s^{-1} and the 11th October 1993 which reached 6.09 m^3 s^{-1}. In 2006, winter floods in January and February were substantially higher than the Q_{10} of the river. The summer of 2007 also had two extremely high flow events (figure 4.4). It was believed that these extreme flows had washed signal crayfish from the River Bain, but the population quickly recovered, demonstrating their resilience to high flow events.

Figure 4.3. *Rating curve for the River Bain gauging station at Goulceby Bridge, 6 km downstream from the site used in this study (data obtained from the NRFA).*

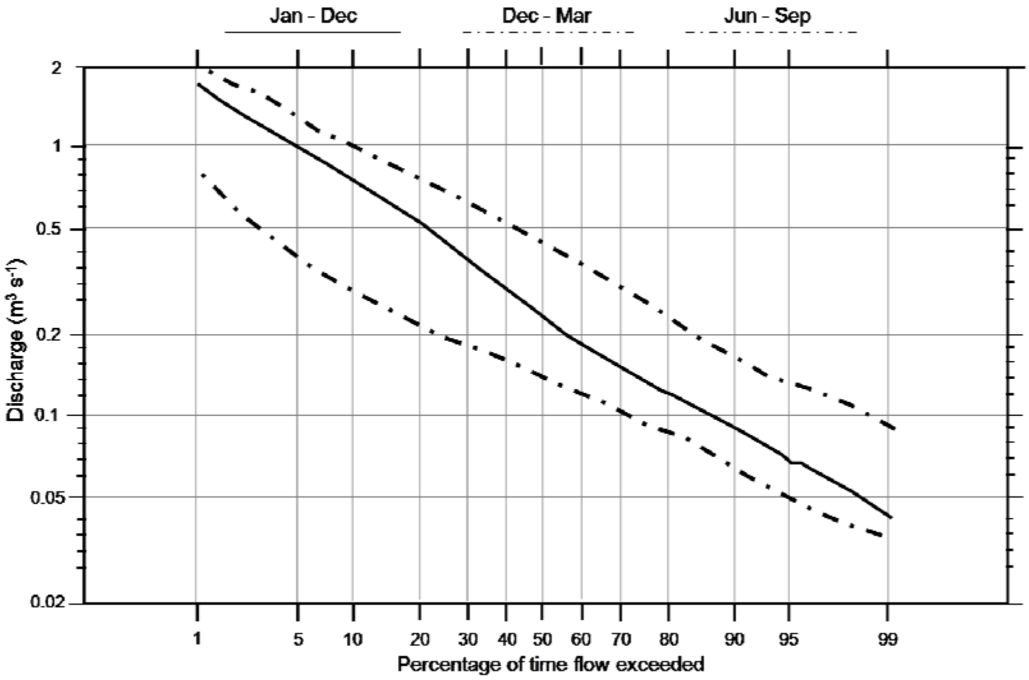
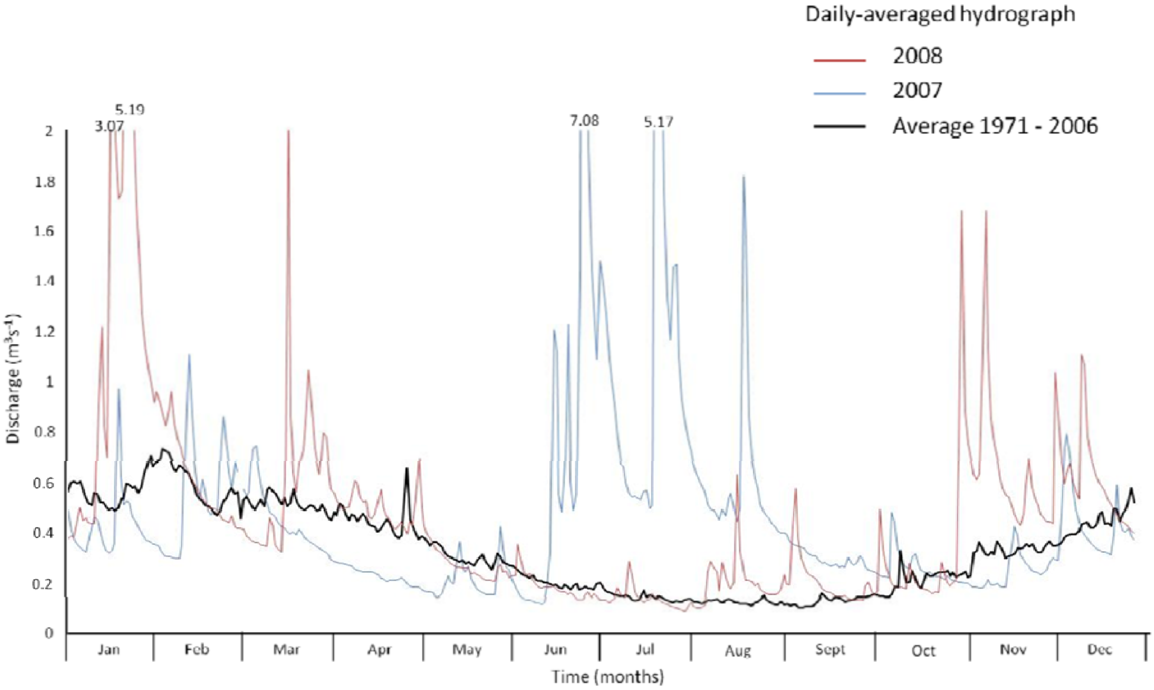


Figure 4.4. *An averaged 35 year daily-averaged hydrograph for the River Bain gauged at Goulceby Bridge from 1971 to 2006 (black line). The daily-averaged hydrograph for 2007 (blue line) and 2008 (red line) are also presented (data obtained from the NRFA).*



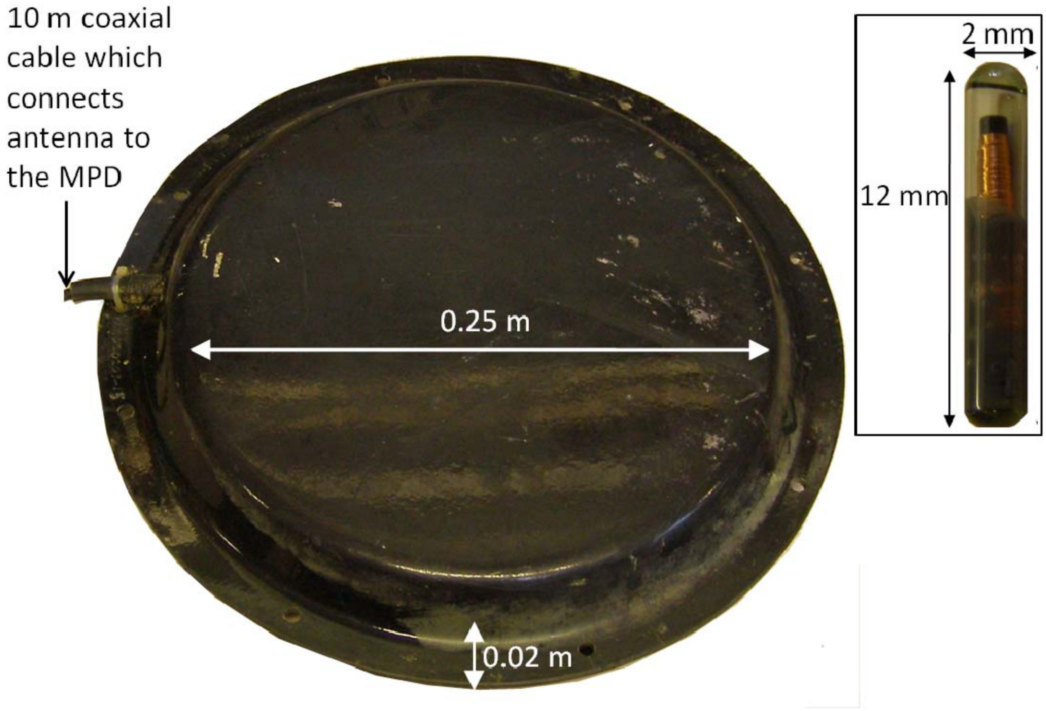
4.4.4. Radio-telemetry equipment

Signal crayfish were tracked using PIT tags which were 2 mm wide and 12 mm long. Tagged crayfish were located using 0.25 m diameter, circular antennae. Antennae were constructed from coils of wire cemented in resin with a vacuum formed black plastic cover and flange around the edge to peg antennae into the substrate (figure 4.5a). Each antenna had a 10 m long coaxial cable which connected it to a Multi-Point Decoder (MPD) (figure 4.5b). The detection range of an antenna was approximately 0.1 m above the antenna and 0.02 m around the antenna edge. This meant that when a tag was recorded it was within a 0.29 m diameter circle centred on the antenna. When powered, a tag sent its unique identification code to the MPD which also acted as a data-logger. The 16 antennae were interrogated in turn in a three-second cycle. This rapid interrogation removed potential issues of multiple tags being recorded at the same time which can lead to incorrect readings, and interference between antennae positioned close together. It was not seen as a limitation due to the relatively slow movement of crayfish over the substrate making it unlikely any crayfish could cross an antenna within three seconds. All equipment was purchased from Wyremicrodesign Ltd, UK.

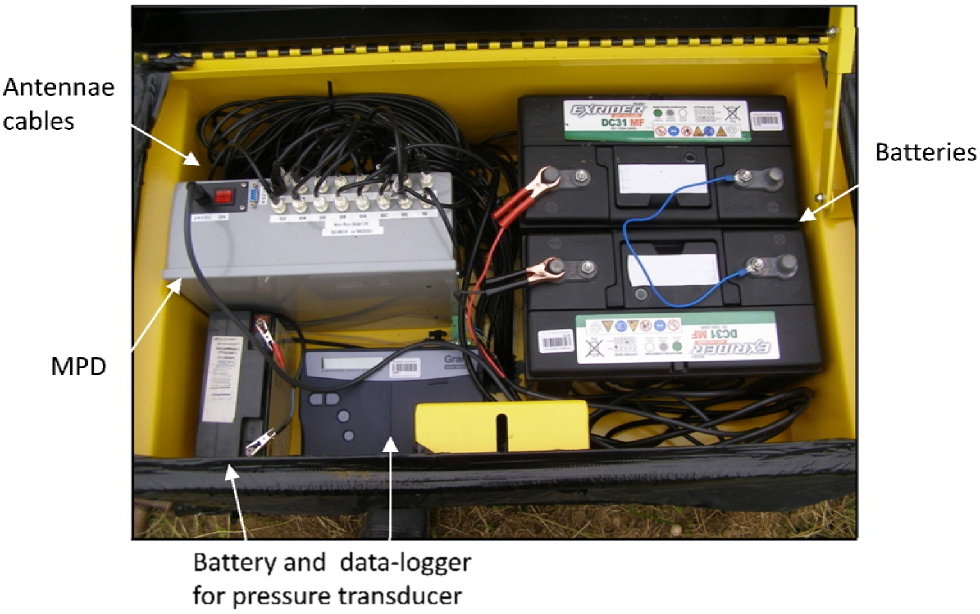
Two rechargeable 12 V batteries powered the MPD and antennae array for 8 – 10 days after which they were replaced by fully charged batteries. The MPD and batteries were housed in a black metal box positioned on the river bank (figure 4.5c).

Figure 4.5 a) *An image of an antenna used to power Passive Integrated Transponder (PIT) tags (inset) and transmit information used to locate the tag in both time and space.* **b)** *An image of the control box. The Multi-Point Decoder (MPD) was connected to the 16 antennae and also acted as a data-logger for PIT tag information. The MPD and antennae were powered by two 12 V batteries. The data-logger and additional battery were used with a submerged, vented pressure transducer to record water depth in the channel. Study reach of the River Bain which is instrumented with the control box situated on the meander bend. Flow is from left to right.*

a)



b)

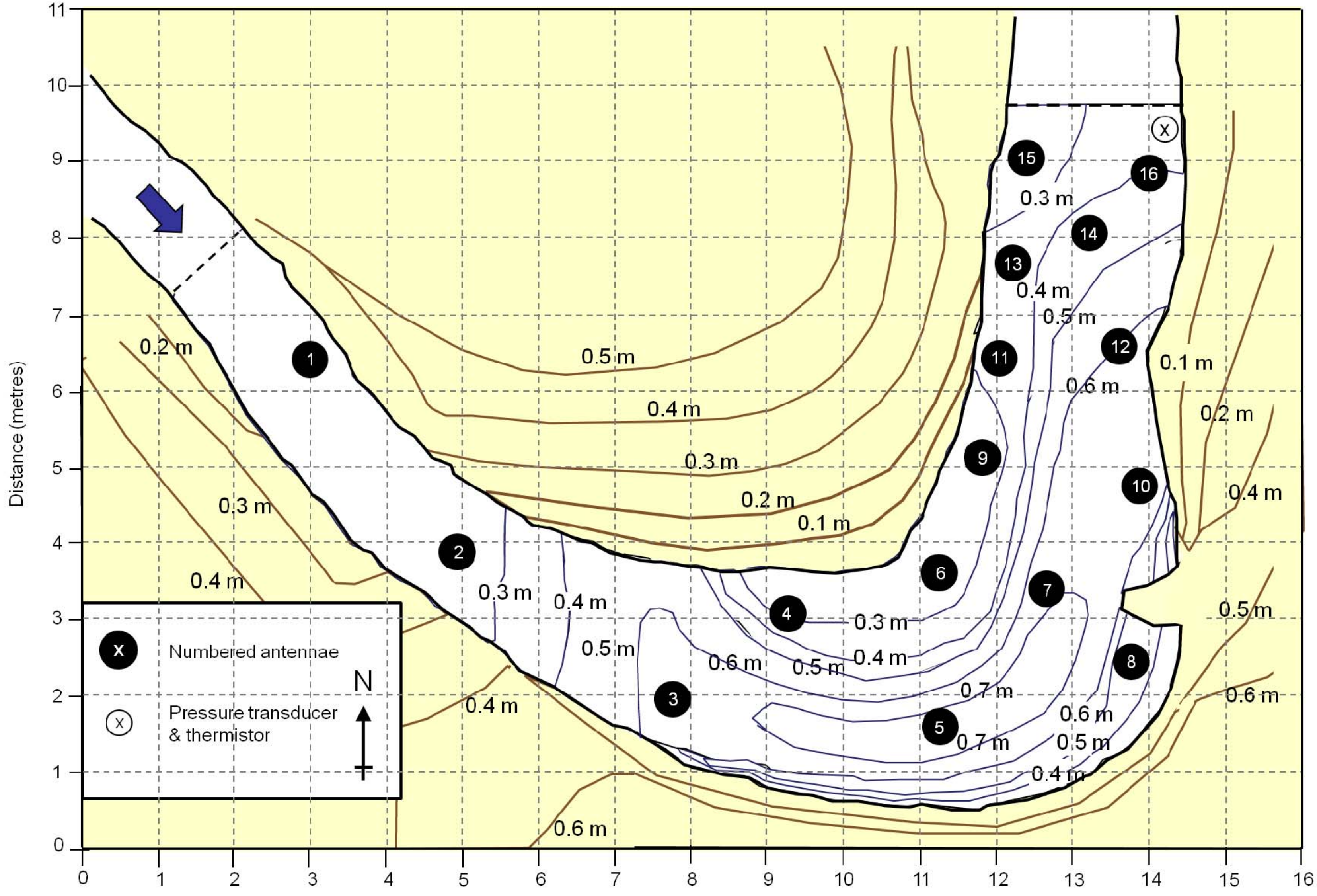

Antennae cables
Batteries
MPD
Battery and data-logger for pressure transducer

c)

4.4.5. The dimensions of the reach and positioning of antennae

The morphology of the study reach is typical of that of a meander bend in a small alluvial river. A comparatively steep, straight, coarse-grained glide flows into a leftward swinging meander bend with deep thalweg closer to the right bank. This outside bank is characterised by complex, steep topography due to the slumping of cohesive bank material. On the inner-bank is a fine-grained point bar which grades into an open-framework gravel riffle which crosses the channel and is succeeded by a rightwards swinging meander, immediately downstream of the study reach. The antennae were strategically placed in discrete units which were defined by the substrate facies, macrophyte presence and flow conditions. The topography of the reach was mapped using a dumpy level and the location of antennae is shown in figure 4.6. In addition to the 16 antennae, a thermistor and a pressure transducer were also positioned in the channel to continuously record water temperature and flow stage, respectively. Water stage was recorded every 10 minutes and the water temperature was recorded every hour. The location of the thermistor and pressure transducer is shown on figure 4.6. The water depth and flow velocity over each antenna was recorded every 8 – 10 days. Flow velocity was measured using an impeller flow meter as an electromagnetic flow meter may have interfered with antennae signals. Measurements were made at 0.6*d* over each antenna and immediately adjacent to the pressure transducer on 17 occasions throughout the tracking period.

Figure 4.6: *Contour map of the instrumented reach of the River Bain showing antennae locations. The datum in this case is the water level at a flow depth of 0.3 m.*



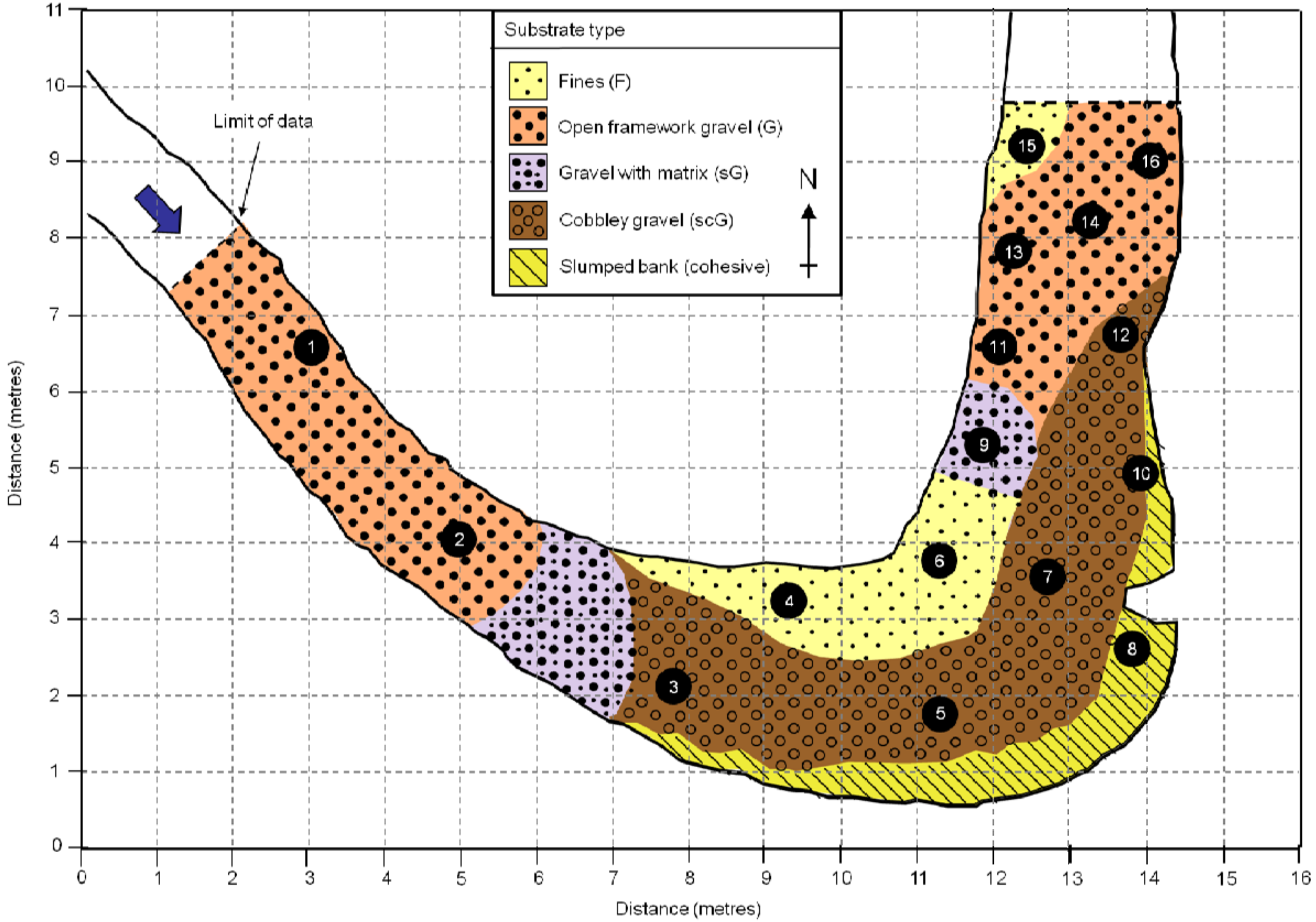
4.4.6. Substrate facies selection and definition

Substrate facies in the reach were defined based on a visual determination of the average and maximum surface grain size within recognisable, homogeneous patches. A visual technique was used due to the destructive nature of physical sampling. Destructive techniques would have been inappropriate for the small substrate patches in this reach (2 – 16 m^2) and would also have disturbed crayfish. The discrete nature of the surface substrate facies increased the suitability of a visual determination technique. The level 1 classification of Buffington and Montgomery (1999) was used, where textural facies are defined based on the relative proportion of sand (0.006 – 2mm), gravel (2 – 64 mm) and cobbles (64 – 256 mm) in the surface. Each facies is then given an abbreviated designation where the dominant category is capitalised. For instance a substrate with sand < gravel < cobble would be abbreviated sgC. The level 2 classification which further defines categories was not undertaken according to Buffington and Montgomery (1999). Five individual textural facies were identified within the 20 m meander bend (table 4.1). Antennae were positioned within each of the facies to determine their usage by crayfish. If one facies unit was substantial enough to cover a gradient of flow depths, then antennae were placed throughout the depth gradient, discussed above (figure 4.7). The presence of macrophytes was also taken into account in the same way. Consequently, areas with similar bed characteristics but a complex flow depth profile or macrophyte growth had more antennae in proportion to areas with a more uniform flow depth and no macrophyte growth. The open-framework gravels (substrate 2) were most similar to the narrowly-graded gravels used in the experimental flume studies (chapter 3). The majority of the substrate material in the river (> 80%) was finer than 38 mm, the largest diameter material crayfish were able to move in still-water experiment (chapter 2).

Table 4.1. *Description of five substrate facies with the designated abbreviation according to the level 1 classification scheme of Buffington and Montgomery (1999) in brackets. Grain sizes are based on the Wentworth scale.*

Facies	Classification used herein	Buffington & Montgomery (1999)	Description	Location	Grain-size (mm)	
					Mode	Maximum
1	Fines	F	Fine, unconsolidated sediment mainly in the sand fraction.	Point bar and in a marginal area downstream.	Coarse to Very Coarse sand	
2	Open-framework gravels	G	Gravel with minimal surface matrix material.	The upstream glide and downstream riffle.	16 – 22	64
3	Gravels with matrix	sG	Framework supported gravels of the same size-range as above but with significant matrix material.	The upstream transition from riffle to deeper water and the downstream transition from point bar to riffle.	16 – 22	64
4	Cobbley-gravels with matrix	csG	Gravel with cobble and substantial matrix material. Some algal growth was present anchored to coarser clasts.	Along the deep thalweg of the meander bend.	22 – 32	128
5	Slump		Cohesive material which had slumped into the channel from the outer bank of the meander bend.	The outer bank of meander.	Silt and clays	

Figure 4.7: *The instrumented reach with the numbered antennae marked on and predetermined substrate facies shown.*



4.4.7. The presence and distribution of macrophytes

Macrophytes (water cress) were present in the channel for much of the tracking period and rapidly increased in size throughout July and August (figure 4.8a). The macrophytes grew from marginal areas into more central areas of the channel (figure 4.8b). From the end of September the size of the macrophyte stands began to reduce and by the end of October they were absent from the channel. The distance macrophytes spread into the channel was measured with a tape measure at 1 m intervals along the bank every 8 – 10 days when batteries were changed and the PIT tag data downloaded. Consequently, the measurements of marginal macrophytes are approximate and do not represent an exact measurement of macrophyte area in the channel. Marginal terrestrial plants, particularly grasses, occasionally hung into the water and, during high flows became submerged.

Figure 4.8a: *Changing area of macrophyte coverage.*

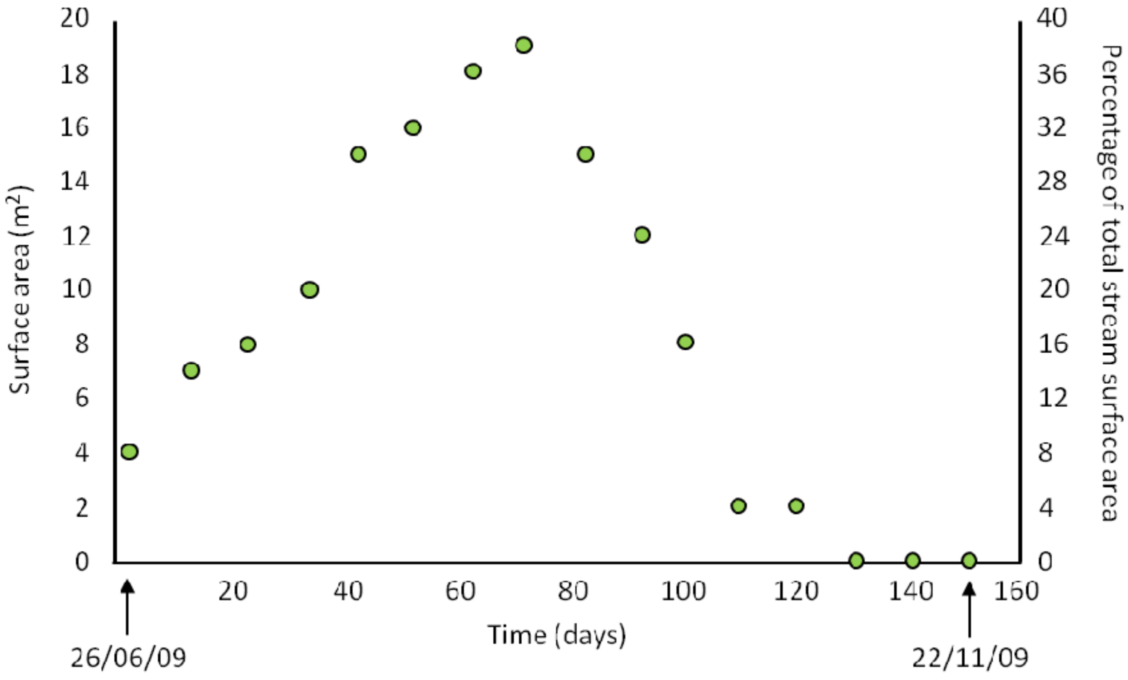
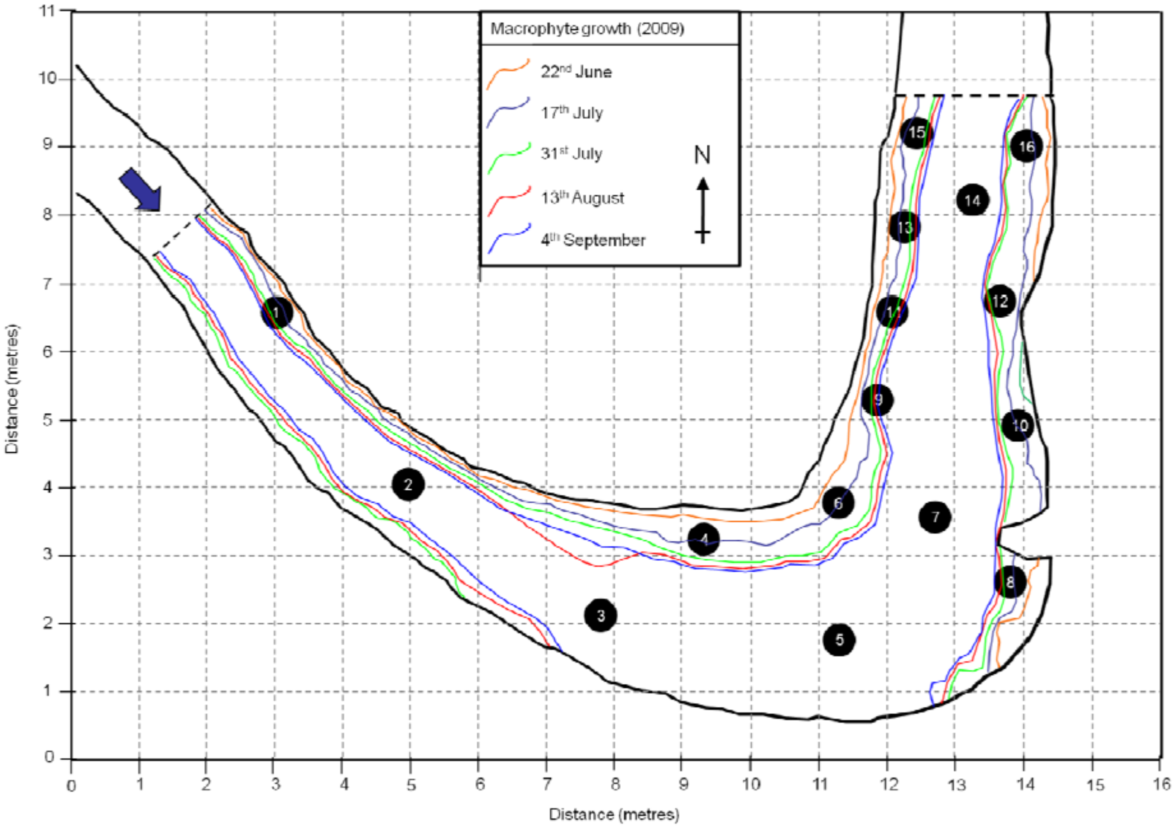


Figure 4.8b. *The changing distribution of in-channel macrophyte coverage within the river reach. Five of the 17 measurements of macrophyte size are presented as coloured lines. The maximum extent of macrophytes was on 4th September 2009 and macrophytes were almost absent from the channel by 24th October 2009.*



4.4.8. PIT tag attachment and data collection procedure

Signal crayfish make sporadic long distance movements so individual animals did not remain within the reach for the entirety of the tracking period. Consequently, signal crayfish were tagged and released throughout the tracking period to maintain between three and five PIT-tagged crayfish in the reach at any time. Permission to catch and track crayfish was given by the land-owner and the Environment Agency. Crayfish were caught by hand in the reach by lifting aquatic marginal vegetation out from the channel and removing sheltering signal crayfish from the mass of stems and roots. Only crayfish with a carapace length of 55 ± 5 mm were selected because a PIT tag may have been a burden to smaller crayfish. Also, juvenile crayfish behave differently to adult crayfish and, consequently, would not relate to flume and still-water experiments. All crayfish were caught within 20 m upstream or 20 m downstream of the experimental reach in an attempt to minimise the number that vacated the instrumented reach once tagged. Both male and female crayfish were caught and tagged as behaviour has been found to be similar between different sexes (Guan and Wiles, 1997; Kirjavainen and Westman, 1999; Bubb *et al.*, 2004). No female crayfish carrying eggs were caught. Tracking ceased on the 22nd November 2009 because no further crayfish could be caught. This may have been due to decreased water temperature, increased flow and/or reduction in macrophyte growth. Other studies have also found it problematic to catch sizeable numbers of crayfish in late autumn to winter (Abrahamsson, 1981; Bubb *et al.*, 2002a).

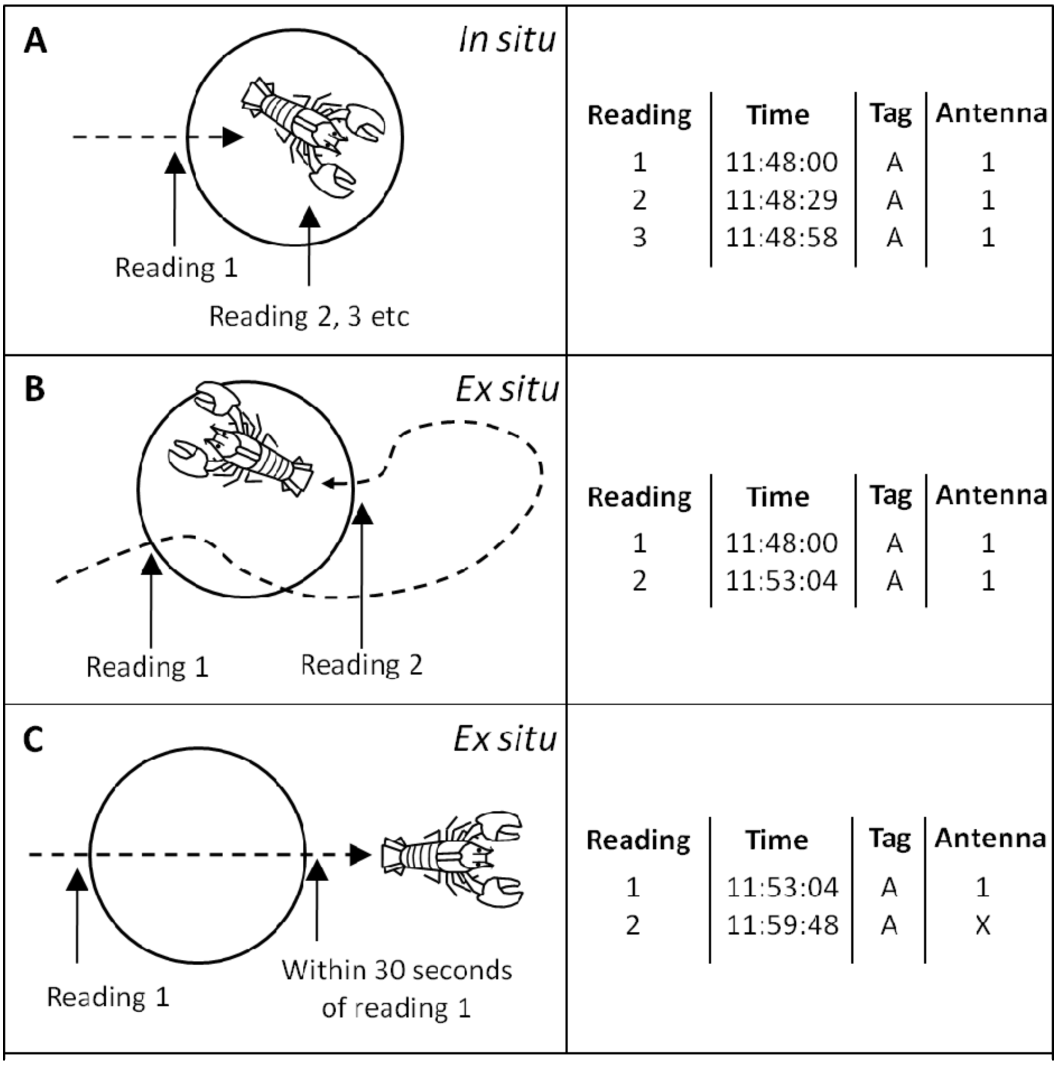
Once caught, crayfish were placed in buckets. PIT tags were attached to the cephalothorax of crayfish (figure 4.9). The cephalothorax was lightly dried using a fabric rag and then a PIT tag was attached using cyanoacrylate adhesive (i.e. superglue). The adhesive was first placed on the crayfish and the tag was then gently placed onto the adhesive patch. The crayfish was left in a bucket for five minutes whilst the glue dried and was then submerged under water and left for a further 15 minutes to ensure that the PIT tag was attached and that the animal had not been adversely affected. Crayfish were then released into the river over antenna 4. This was because of the central position of antenna 4 and the presence of macrophyte cover which prevented tagged crayfish being exposed during daylight. Initially placing them on an antenna also ensured that the tag was recorded at least once on the day of release which made later analysis easier as the exact time of release was recorded to the nearest second.

Figure 4.9. *Photograph of PIT-tagged signal crayfish caught in the River Bain, UK. Note the PIT tag attached to the back (cephalothorax) of the crayfish.*

4.4.9. In situ *and* ex situ *activity readings*

There was a filter algorithm built into the logging system so that, if the same tag was present over the same antennae for extended periods, the tag was only recorded every 29 seconds (± 2 seconds). This reduced the volume of collected data and allowed a distinction to be made between *in situ* and *ex situ* readings, described below. If the same tagged crayfish was recorded on the same antenna for consecutive readings and the time difference between these readings was 29 seconds (± 2 seconds) this indicated that the crayfish had remained over that antenna for 29 seconds (± 2 seconds). This was considered an *in situ* reading (scenario A in figure 4.10). If a consecutive reading of the same tag over the same antenna was recorded but the time difference was < 27 seconds or > 31 seconds this indicated that the crayfish moved off the antenna and back onto it again and was considered an *ex situ* reading (scenario B). If a tagged crayfish was only recorded once on an antenna the time stamp indicated when the crayfish first encountered the antennae. The crayfish will have moved out of range of the antennae within 29 seconds (± 2 seconds) of the initial (and only) recording and is also considered an *ex situ* reading (scenario C). In all above cases, the time when a tagged crayfish left an antenna could only be determined as within 29 seconds (± 2 seconds) of the previous reading. This is because, had crayfish remained on the antennae for a further 29 seconds after the last reading, a subsequent reading would have been obtained. Therefore, the time a crayfish moved into range of antennae was recorded to the nearest second. However, the time when a tagged crayfish left an antenna could only be determined to within 29 seconds (± 2 seconds) of the last reading.

Figure 4.10: *Diagram showing the interpretation of PIT data, in particular, relating the timing of recordings of crayfish activity to when and for how long crayfish remained on antenna.*



Reading	Time	Tag	Antenna
1	11:48:00	A	1
2	11:48:29	A	1
3	11:48:58	A	1

Reading	Time	Tag	Antenna
1	11:48:00	A	1
2	11:53:04	A	1

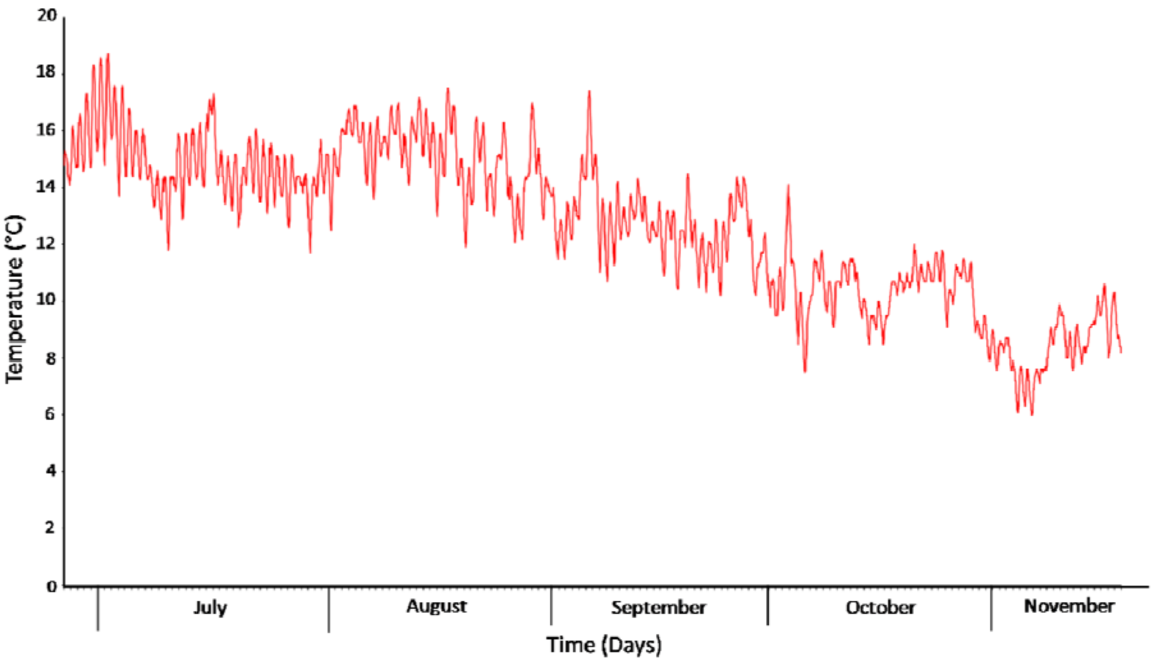
Reading	Time	Tag	Antenna
1	11:53:04	A	1
2	11:59:48	A	X

4.5. Abiotic conditions during the tracking period

4.5.1. Temperature conditions during the tracking period

The daily-averaged water temperature within the reach ranged from 6.8 – 17.1°C between 26th June and the 22nd November 2009. Diurnal variations in the water temperature can clearly be seen on figure 4.11 and were more pronounced in summer than winter, as would be expected. Longer term variations in water temperature were also apparent which were associated with changing weather systems. There was a relatively steady linear decline in water temperature from the 19th August to the 22nd November 2009 ($y = -0.0031x + 14.936$; $r^2 = 0.75$).

Figure 4.11. *Hourly measurements of water temperature in the instrumented reach of the River Bain, UK between 26th June 2009 and 22nd November 2009.*



4.5.2. Hydraulic conditions during the tracking period

Continuous flow stage measurements were recorded for the duration of the 150 day tracking period (figure 4.12). Flow depth during this period was variable with a number of isolated high flow events, three of which were clustered in late July/early August. An extended period of low flow (approximately 0.3 m at the pressure transducer) occurred throughout August and September 2009. In October and November the flow depth increased rapidly and remained high throughout November (figure 4.12). The trends in water depth are consistent with those recorded at the gauging station in Goulceby, described in section 4.4.3. Figure 4.13 shows the daily-averaged discharge measurements for 2009 at Goulceby bridge gauging station alongside the flow stage measurements made with a pressure transducer in the instrumented reach. As would be expected due to the dependent relationship between flow depth and discharge, there was a strong similarity in the magnitude of change between the measurements at the gauging station and the reach used in this study. There was also consistency between the 2009 gauged hydrograph between July and November and the 38 year average which implies that the flow during the tracking period was relatively typical and not anomalous.

Figure 4.12. *The water depth (metres) measured at a ten minute intervals with a pressure transducer in the instrumented reach of the River Bain, UK between 26th June 2009 and the 22nd November 2009.*

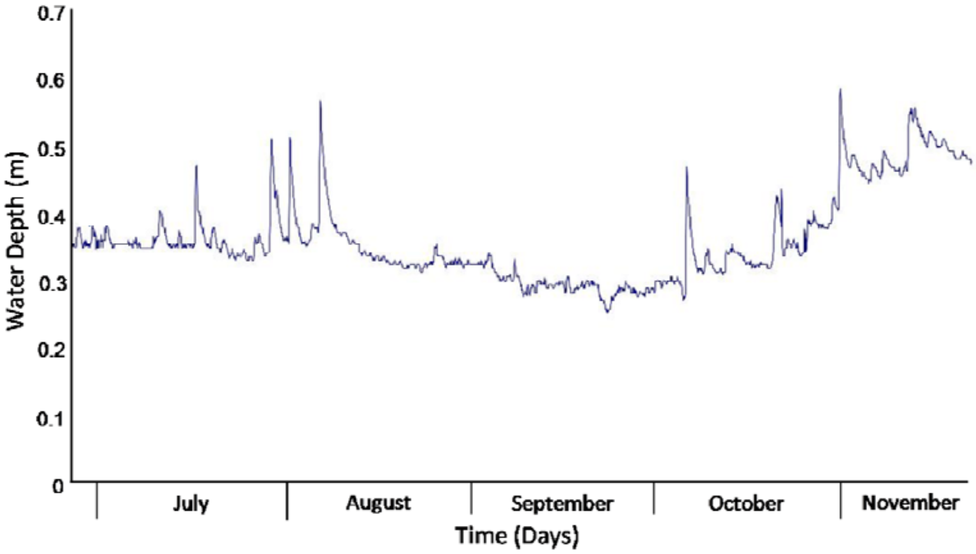
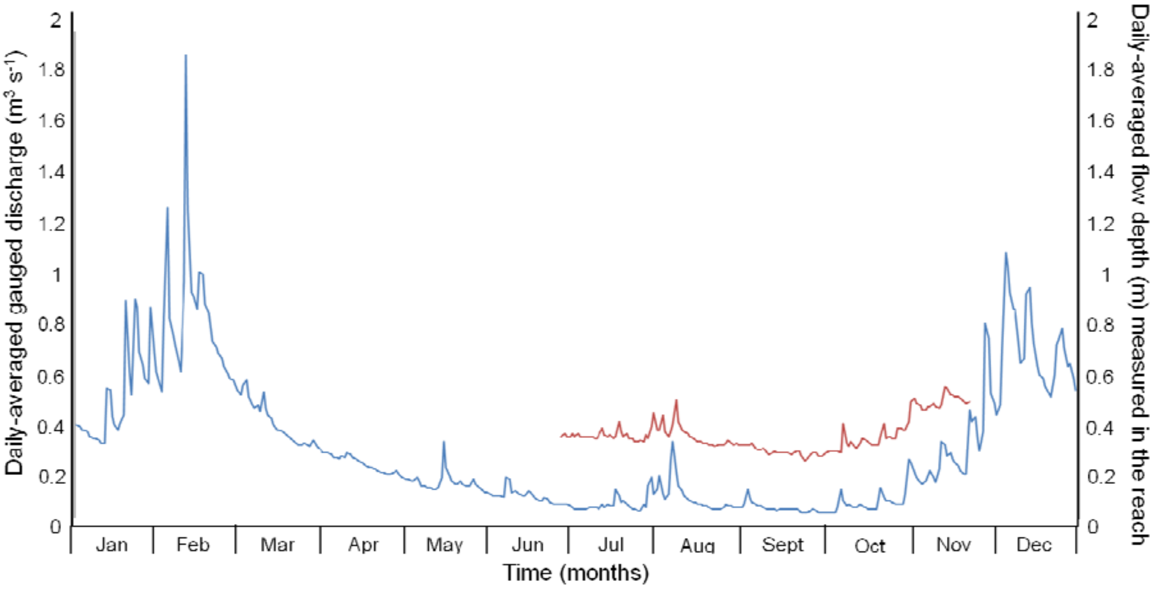


Figure 4.13. *Daily-averaged gauged flow (m^3 s^{-1}) at Goulceby Bridge in 2009 (blue line) obtained from the NRFA and EA. The daily-averaged flow depth measurements using a pressure transducer situated in the experimental reach are presented as a red line.*



4.5.3. Hydraulic conditions over each antenna during the tracking period

The water depth and flow velocity at 0.6 *d* were also measured over each antenna at 17 intervals throughout the tracking period. The water depth over each antenna was correlated with the continuous water depth measurements recorded from the pressure transducer. There were strong positive correlations for all 16 antennae (r^2 ranging from 0.9232 to 0.9911). Therefore, the depth over antennae at any period during the 150 day tracking period could be estimated from the continuous results of the pressure transducer. The shallowest depths were recorded over antennae 6 and 9 and the deepest over antenna 5 which was situated in the thalweg of the channel (figure 14a and b). At the deepest flows through the channel the point bar bank became inundated, slightly increasing the area of the channel.

Figure 4.14a. *Interpolated flow depth at the lowest recorded flow at the pressure transducer (0.26 m).*

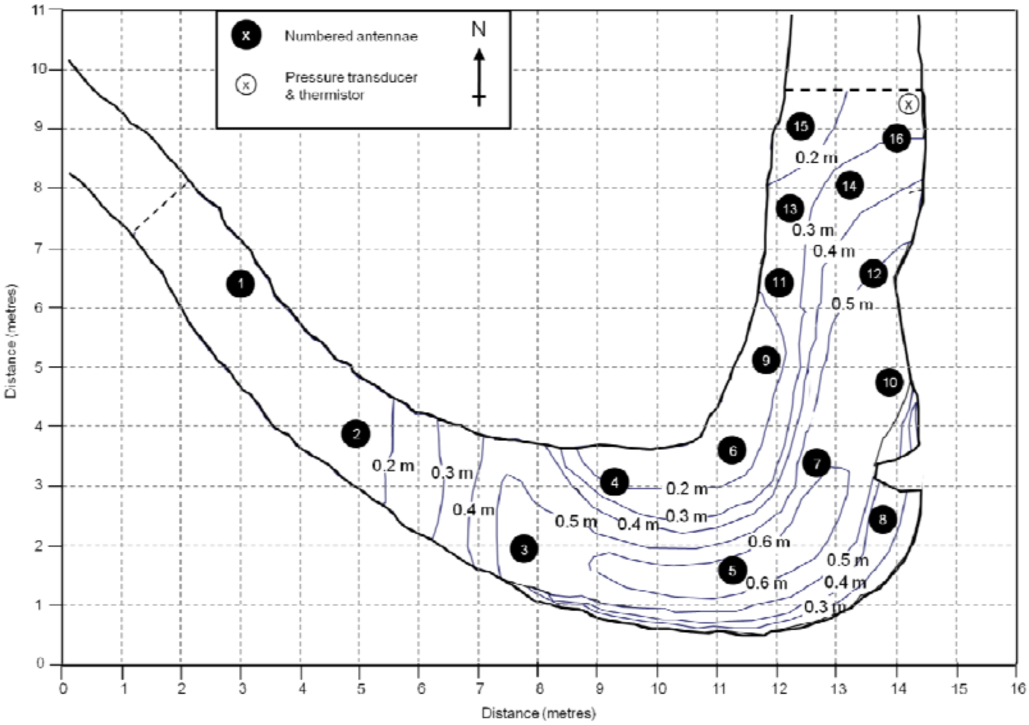
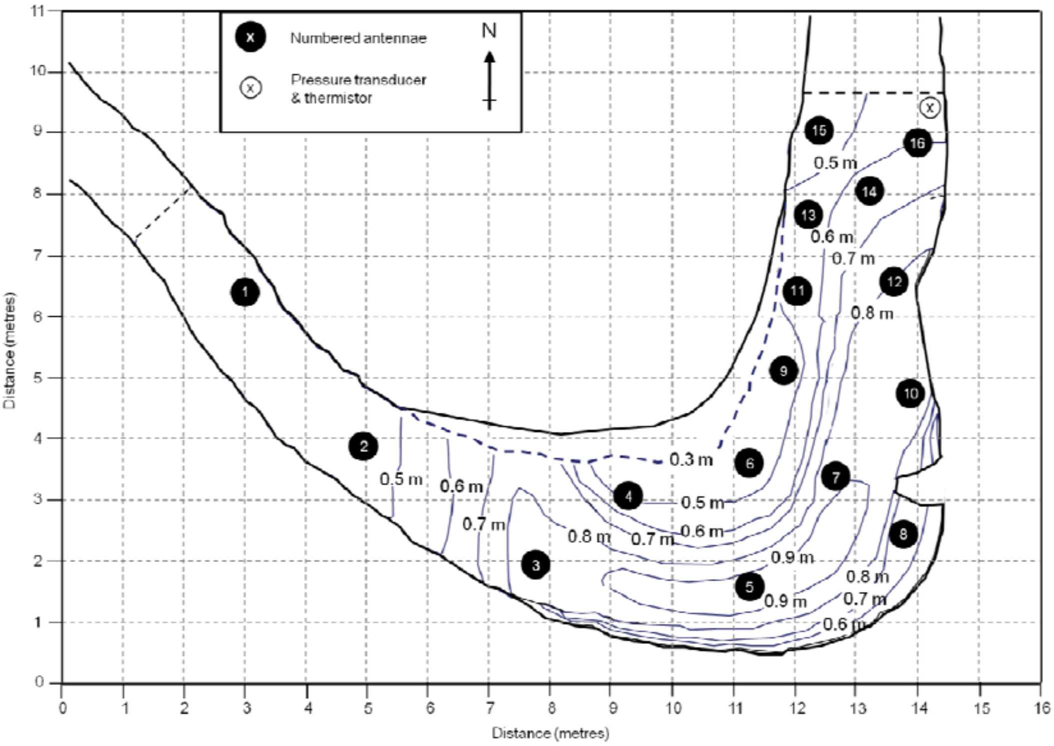


Figure 4.14b. *Interpolated flow depth at the highest recorded flow at the pressure transducer (0.55 m).*



Water depth and flow velocity measured on 17 separate occasions over each antenna were plotted together in order to determine hydraulic groupings (figure 4.15a). Antenna 2 (group A) was situated under flows which were consistently shallower and faster than those over other antennae resulting in the hydraulic environment being distinct from that above all other antennae. Antennae 3, 5, 7 and 10 were located along the deeper thalweg of the channel and were relatively distinct from the other antennae in the reach (group D). The other antennae could broadly be divided into two groups but with some overlap between them. Group B was the largest group and characterised by antennae under shallow, slow flows. These were antennae 1, 4, 6, 9, 11, 13, 15 and 16. All were on the inside bank of the meander bend, with the exception of antenna 16, and had substantial vegetation cover. Group C contained the remaining antennae (8, 12 and 14) which were buried under topographically dissimilar areas of the bed. They were located in marginally deeper and faster flows than group B. However, because of variability in the flow conditions during the 150 day tracking period, group C has substantial overlap with groups B and D. Figure 4.15b shows the locations of these hydraulic groupings within the reach and there spatial similarity can be clearly seen i.e. group B is found along the inside edge of the meander bend and group D is located in the centre of the channel thalweg. Group C were positioned in dissimilar areas including the downstream riffle and in amongst the slumped bank material on the outer-bank of the meander bend.

Figure 4.15a. *The water depth plotted against the flow velocity at 0.6 water depth measured over each antenna at 17 intervals throughout the 150 day period.*

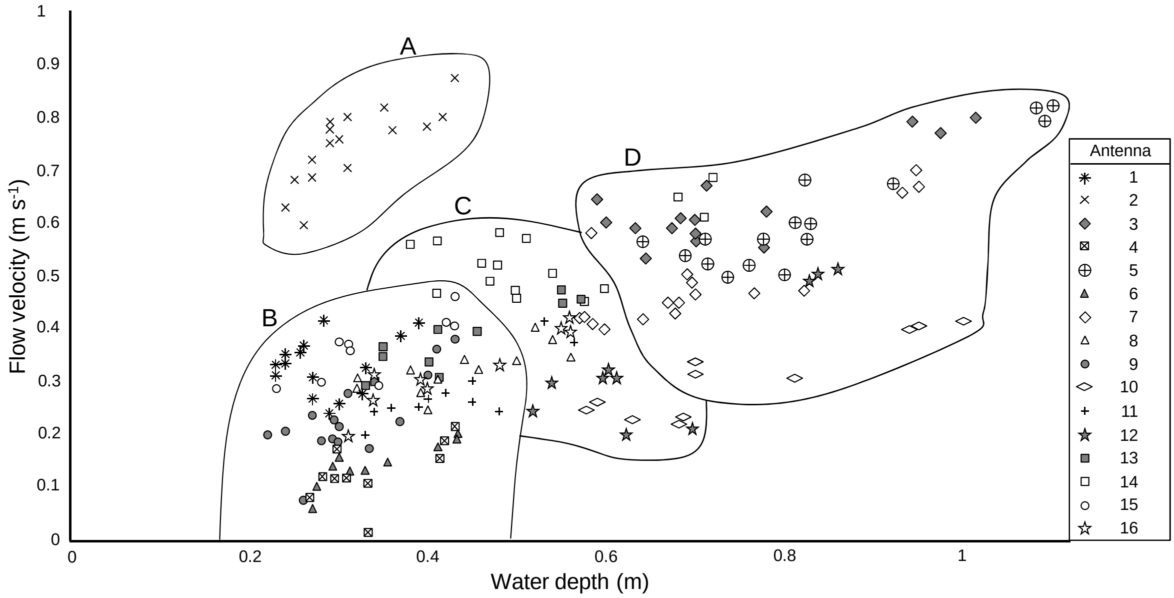
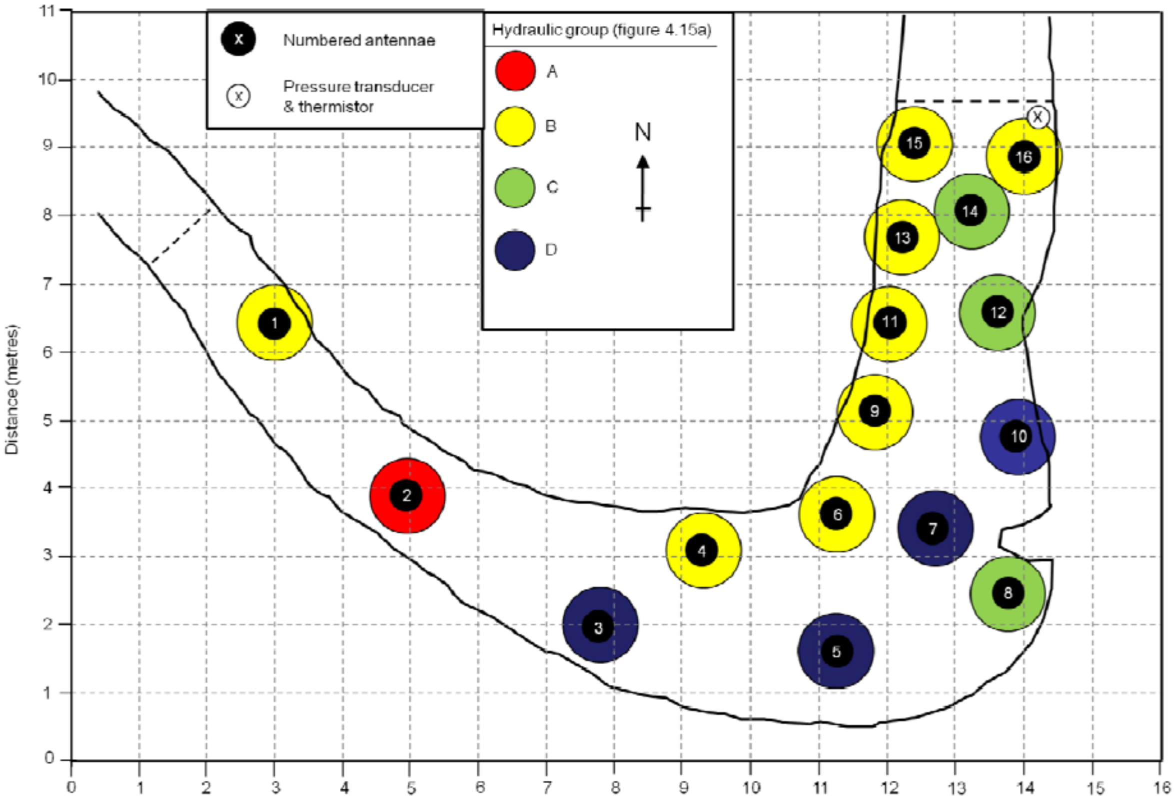


Figure 4.15b. *Map of the reach showing the hydraulic grouping over each antennae.*



4.6. Variation in total crayfish activity within the reach

4.6.1. The temporal and spatial extent of the home range of signal crayfish

The activity of PIT-tagged signal crayfish was highly variable both temporally and spatially. Over the 150 day period, 10,884 point locations were recorded from 65 tagged crayfish. As expected, crayfish remained in the instrumented reach for a limited time period before making a longer distance movement to a different location (figure 4.16). On average five PIT-tagged signal crayfish were tracked in the reach each day (st.dev = 3). There was no apparent difference in the movement of PIT tagged male and female crayfish during the tracking period. Both male and female crayfish had similar rates of activity, defined as the total number of antenna recordings made per day (ANOVA; $p = 0.782$) and had similar antennae site preferences. This is consistent with the results of Bubb *et al*. (2002a; 2002b).

Signal crayfish remained in the instrumented river reach for a mean period of 11 days (st. dev. 9 days) after which they left the reach and rarely returned. This is consistent with the nomadic behaviour previously described for signal crayfish (Bubb *et al*., 2002a; 2004; Light, 2003) and other crayfish species (Gherardi *et al*., 1998; Schütze *et al*. 1999; Gherardi *et al*., 2000; Robinson *et al*., 2000). The number of days crayfish were tracked in the reach was not statistically different between months (ANOVA, $p = 0.468$). After tagging, crayfish were released back into the river during daylight. This obviously resulted in crayfish being recorded during daylight activity when they are predominately nocturnal, suggesting that movement on the first day of release was inconsistent with their natural activity and a direct result of the tagging and release. Consequently, the movement of crayfish on the day of release was removed from the data-set and consequently all future analysis. Robinson *et al*. (2000) described a 'fright response' after release of radio-tagged white-claw crayfish (*Austropotamobius pallipes*) with crayfish moving significantly more in the two days following release. However, Robinson *et al*. (2000) quantified long distance movements and, consequently, any 'fright response' on the scale observed in that study would result in crayfish leaving the instrumented reach in this study. Figure 4.17 shows that 11% (7 out of 65) of crayfish left the reach within one day of being tagged which may indicate that tagging and releasing crayfish promoted a 'fright response' with crayfish moving out of the reach. As substantial effort was made to minimise the disturbance to crayfish during tagging, and 89% of tagged crayfish remained in the reach, the loss of these crayfish is not considered to be a major limitation to the study.

Figure 4.16. *The length of time (days) individual crayfish were tracked in the River Bain, UK, between 26th June 2009 and the 22nd November 2009 (black horizontal lines). Red vertical lines indicate days when new crayfish were tagged and released in the river reach. The blue line represents daily-averaged flow depth at the stage transducer and the red line shows daily-averaged water temperature.*

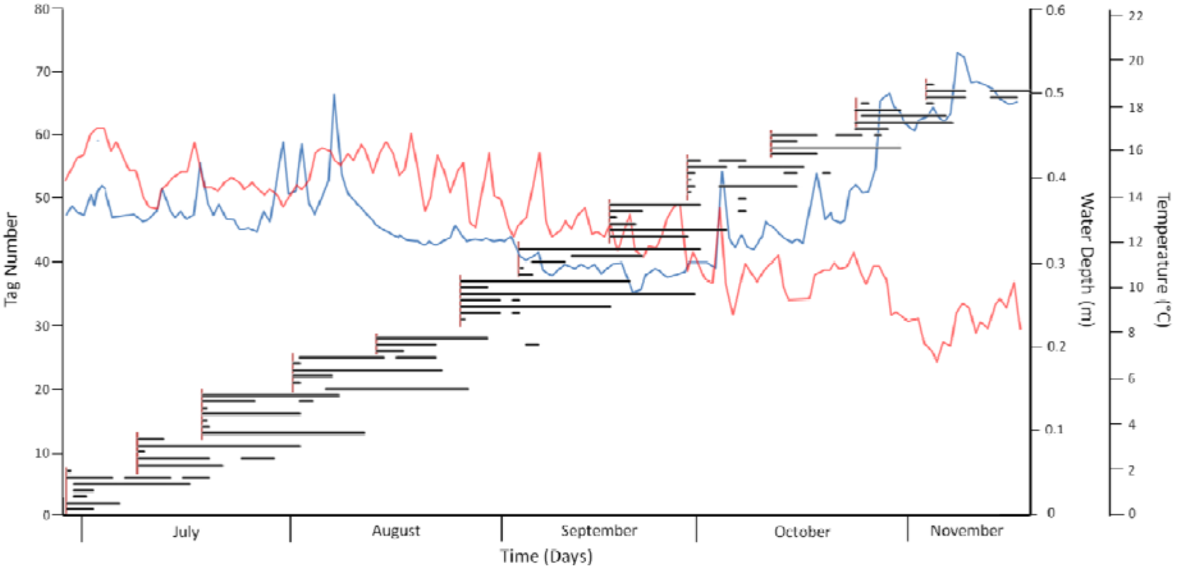
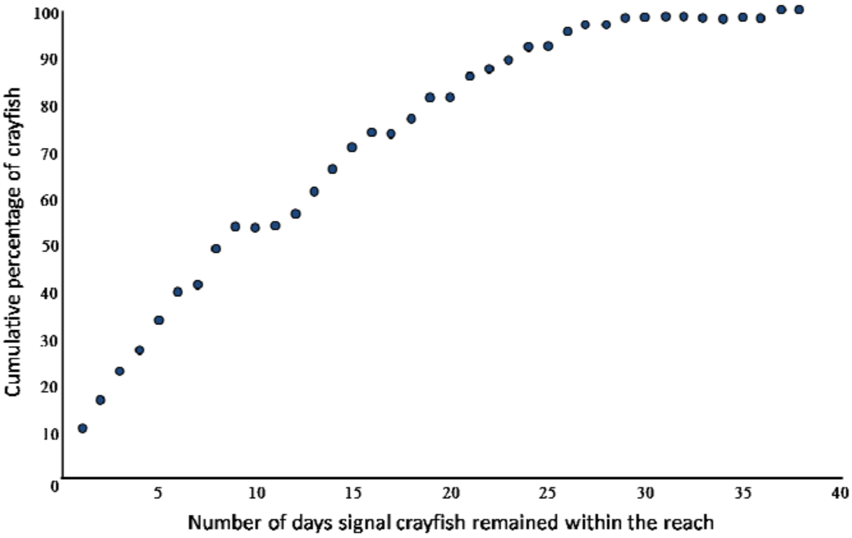


Figure 4.17. *The number of days crayfish were tracked in the tracking reach presented as a cumulative percentage of all tagged crayfish (n = 65).*



4.6.2. Nocturnal behaviour of signal crayfish

As expected, signal crayfish were highly nocturnal with less than 10% of all recorded movements occurring between 07:00 and 20:00 (figure 4.18). The most popular hour for crayfish movement was 22:00 which is consistent with other studies that found crayfish to be most active at dusk (Guan and Wiles, 1998; Nyström, 2005). When the activity of crayfish was divided between months, nocturnal activity was more pronounced in September to November, with more daytime activity in July and August (figure 4.19). In general, crayfish were most active between 22:00 and 02:00 with activity then declining throughout the remainder of the night.

Figure 4.18. *The mean (± 2 SE) percentage of the total number of recordings on all antennae for the 150 day tracking period in the River Bain for PIT-tagged signal crayfish (n = 65).*

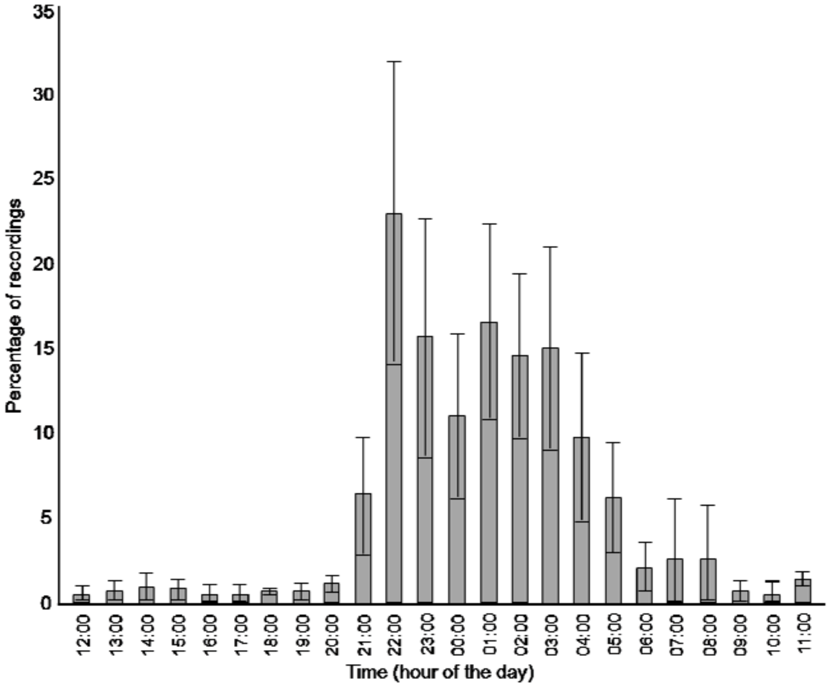
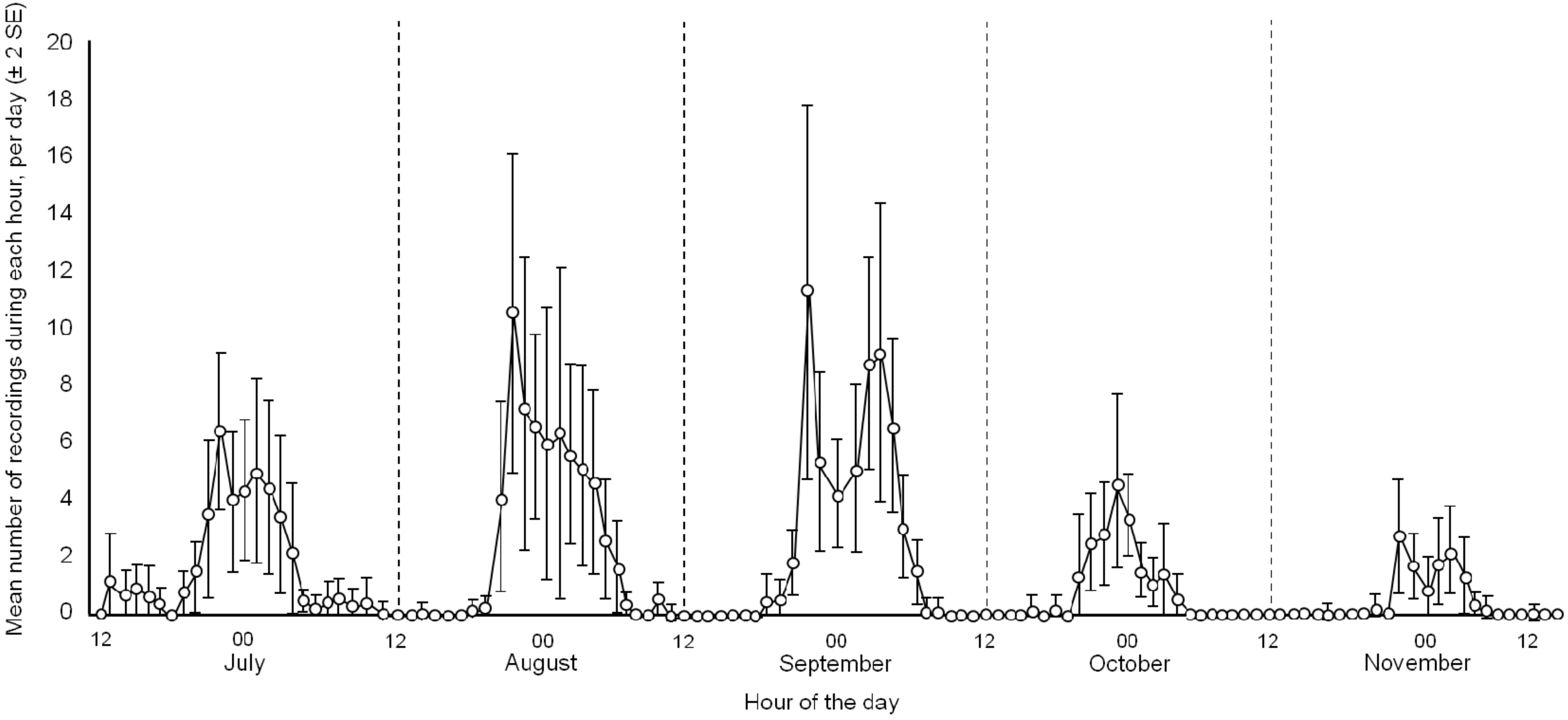


Figure 4.19: The mean (± 2 SE) number of recordings by movement of crayfish across all antennae within each hour of the day, grouped for all days within each month.



4.6.3. Temporal variation in total crayfish activity within the reach

As expected, the activity of crayfish, defined as the total number of recordings across all antennae by all crayfish each day, was very variable across the 150 day tracking period (figure 4.20). Crayfish were most active in July and August but activity was also most variable during these two months. During the low flows of September, crayfish activity was less variable and remained relatively high. The activity of crayfish declined from mid-September through to the end of the tracking period in November. The decline in crayfish activity appears to be predominantly linear and parallels the decline in water temperature. This is interesting because the water temperature does not drop below 6.7°C which is significantly warmer than recorded temperatures at which crayfish activity has been found to cease. For instance, Bubb *et al*. (2002a) found crayfish stopped making long distance movements when the water temperature dropped to an average of 4.2 °C ($\sigma = 1.3$°C). Despite the similarity in declines in daily-averaged crayfish activity and water temperature, the correlation between the two is relatively weak ($r = 0.55$) (figure 4.21a).

There is evidence (figure 4.20) that during peaks in flow depth, the activity of crayfish was reduced. However, there were numerous other troughs in the activity of crayfish which were not directly associated with the water depth. Consequently, the correlation between daily-averaged flow depth and daily-averaged crayfish activity was also weak (figure 4.21b). It may be that activity is controlled by an unknown correlate or one or both of these factors. However, it does appear that instead of a linear correlation between activity and these abiotic variables there is a threshold condition, below which crayfish were active and above which activity ceased (figures 4.21a and b). These thresholds are indicated with dashed lines and suggest that crayfish were strongly influenced by temperature and water depth when it exceeded a particular level but were relatively unaffected below that level. This is not unexpected of ecological data and has been widely found and discussed elsewhere (Lancaster and Downes, 2010).

Figure 4.20. *The activity (i.e. the total number of crayfish recordings in the reach per day) of signal crayfish in the River Bain (black line). Daily-averaged water temperature (red line) and daily-averaged water depth (blue line) are also included.*

Figure 4.21: *a) Correlation between daily-averaged active crayfish readings and daily-averaged water temperature. b) Correlation between hourly-averaged activity and hourly-averaged flow depth. Dashed lines represent hypothesised threshold conditions.*

4.7. Presence and activity of signal crayfish

4.7.1. Overview of spatial PIT-tag readings

Consecutive readings over the same antenna (types A and B; Fig. 4.10) and readings indicating movement between antennae (type C) were split and will be described in this section separately. The average length of time crayfish spent over antennae and the average number of movements made between antennae was calculated. A potentially negative impact of averaging between the 65 crayfish is that crayfish appear to spend relatively little time on or moving between antennae. This is because many crayfish were inactive over particular antennae for the duration of time they were present in the reach. It should also be remembered that 11% of all crayfish left the reach within one day, and thus spent very little time anywhere in the channel.

Crayfish were highly active within the reach and all 16 antennae were triggered at least once. The path of movement crayfish took between antennae was not known but, by knowing the start and end point of movement, the net direction and distance of movement could be established. Figure 4.22 indicates the average number of movements by each crayfish, giving an indication of the network of crayfish movement through the reach. Crayfish most often moved along the inner bank of the meander bend and were substantially less active on the outer bank (figure 4.22). There did not appear to be any relationship between the *ex situ* movement (type C) of crayfish between antennae and the underlying substrate type.

The pattern of movement presented in figure 4.22 was further analysed using spatial network analysis which identifies ‘nodes’ that are connected by ‘edges’. A node is a point in space which is connected to other nodes by edges which can represent transport routes, the flow of information or the spread of diseases between people (Gatrell *et al.* 1996; Urban and Keitt, 2001; Proulx *et al.*, 2005). In this case, the antennae are represented by 16 nodes which are connected by edges that represent the movement of crayfish between pairs of antennae. The edges can be weighted to give more information about the linkages between nodes. In this case, edges are weighted to indicate the average number of times each of the 65 crayfish triggered that pair of antenna in sequence. In this analysis, edges can represent movement by crayfish in either direction, for example, an edge linking antenna 1 and 2 can indicate movement from antenna 1 to antenna 2 or from antenna 2 onto 1. Edges can be split to account for differences in the direction of the link, but in this analysis, the direction of movement relative to the flow was deemed of more interest and is discussed below (section 4.7.3).

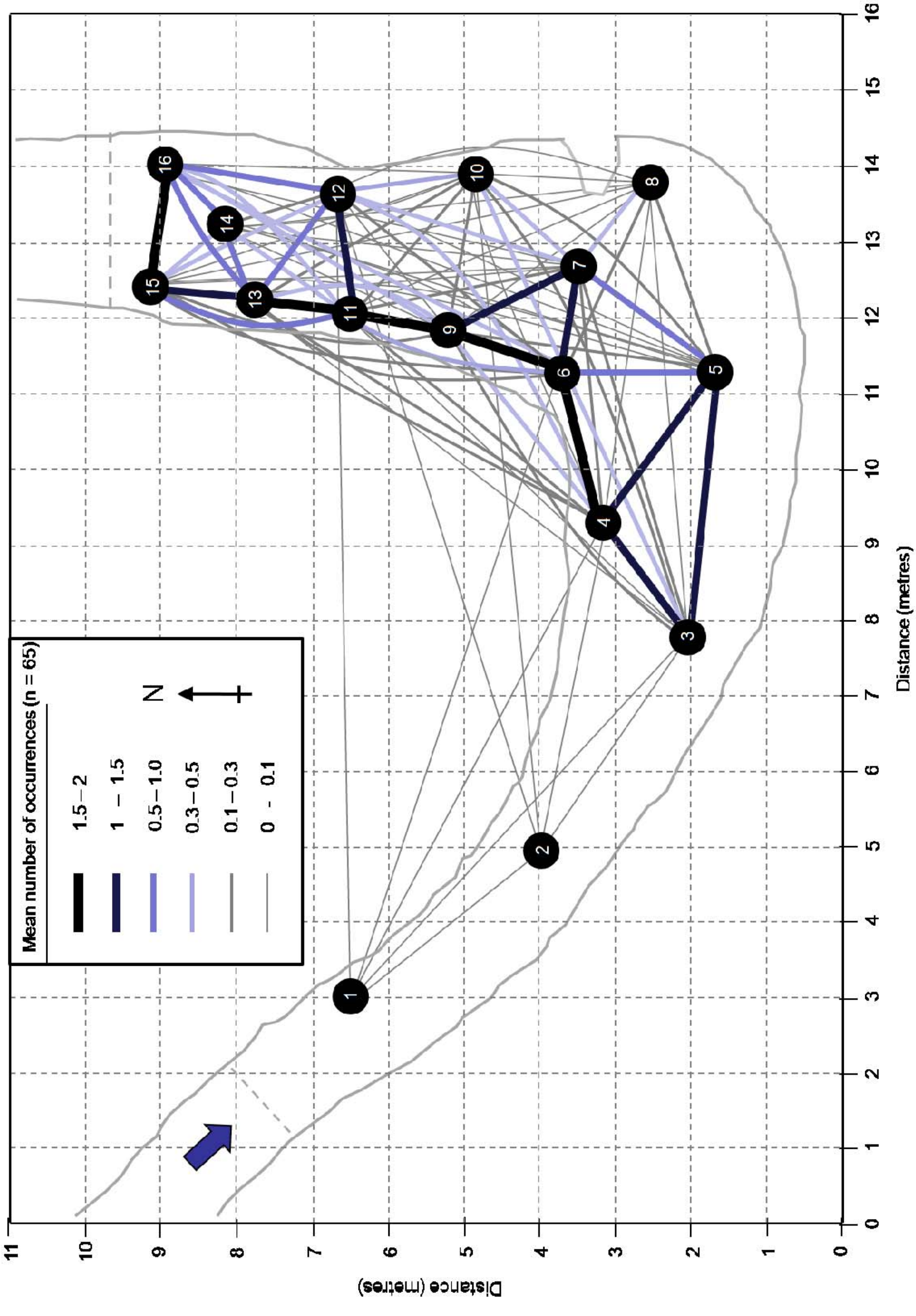
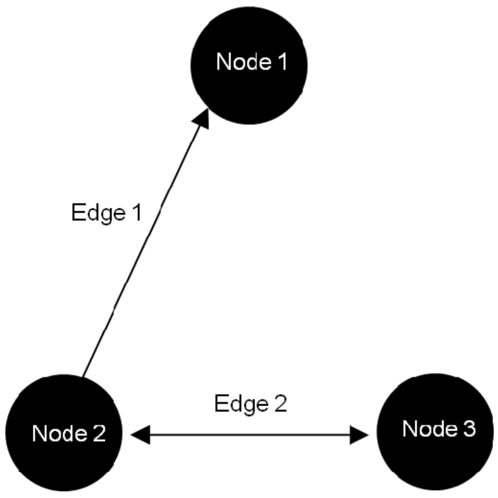


Figure 4.22: *A weighted spatial network graph showing the mean number of movements made by each tagged crayfish between pairs of antennae (n = 65) over 150 days.*

The total number of edges linking nodes, divided by the total possible number, gives a measure of network cohesion, indicating how well connected each point in the network is (Opdam *et al*., 2003; figure 4.23). The network of crayfish movement (figure 4.22) has a cohesion index of 0.4 (99 edges out of a total possible of 240) which indicates that crayfish used many of the available pairs of antennae. This indicates that crayfish were not confined to moving along a few pathways within the reach and utilised a large proportion of the available area of the reach. However, this does not account for the weight of edges and it is apparent, as mentioned above, that crayfish regularly move between a relatively limited selection of antennae pairs but infrequently move between a wide number of other pairs.

Antennae 6, 9 and 11 have the highest total numbers of edges indicating that crayfish travelled to a range of other antennae from these positions (figure 4.24). This was expected as these three antennae were in a central location in the reach and, therefore, crayfish did not have far to move in order to reach any of the other antennae.

Figure 4.23. *An example of a simple network with three nodes and two edges and an explanation of how to calculate the cohesion of a network.*

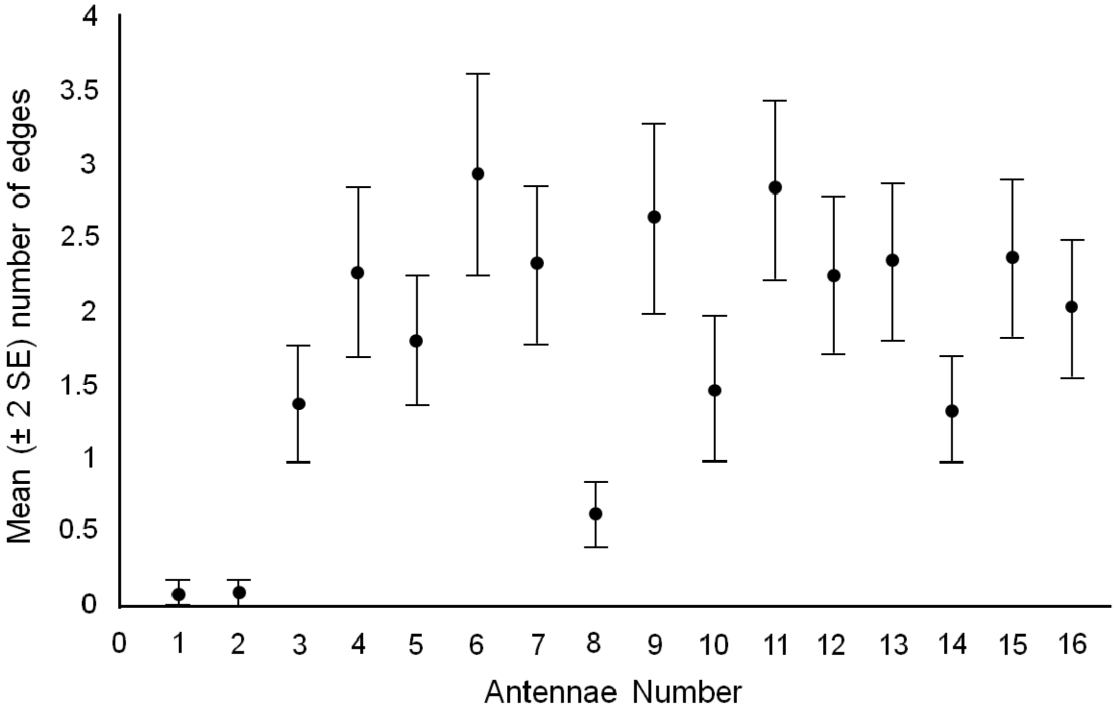


Network parameters

$$\textbf{Cohesion of the network} = \frac{\text{Number of edges}}{\text{Total possible}} = \frac{2}{3}$$

	Edges
Node 1	1
Node 2	2
Node 3	1

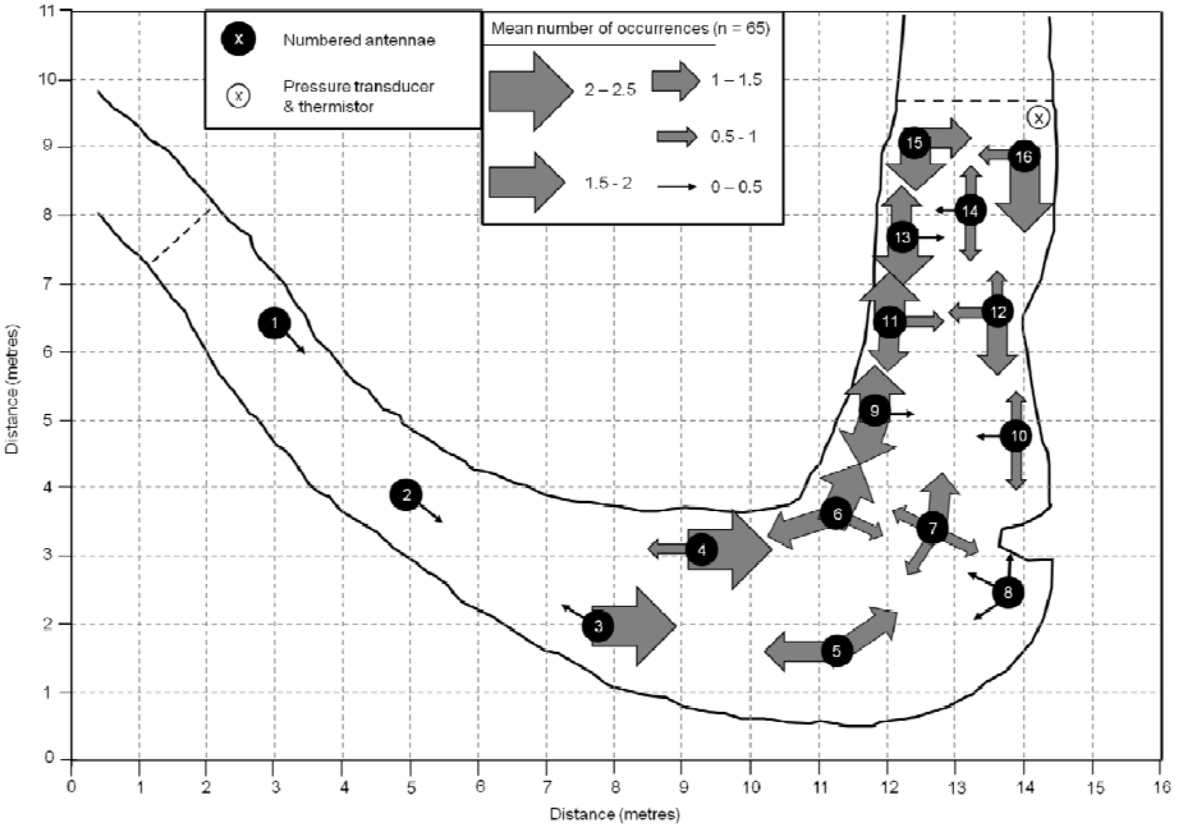
Figure 4.24. *The mean (± 2 SE) number of movements made from or to each antenna over 150 days for each crayfish.*



4.7.2. The direction of crayfish movement in relation to the flow.

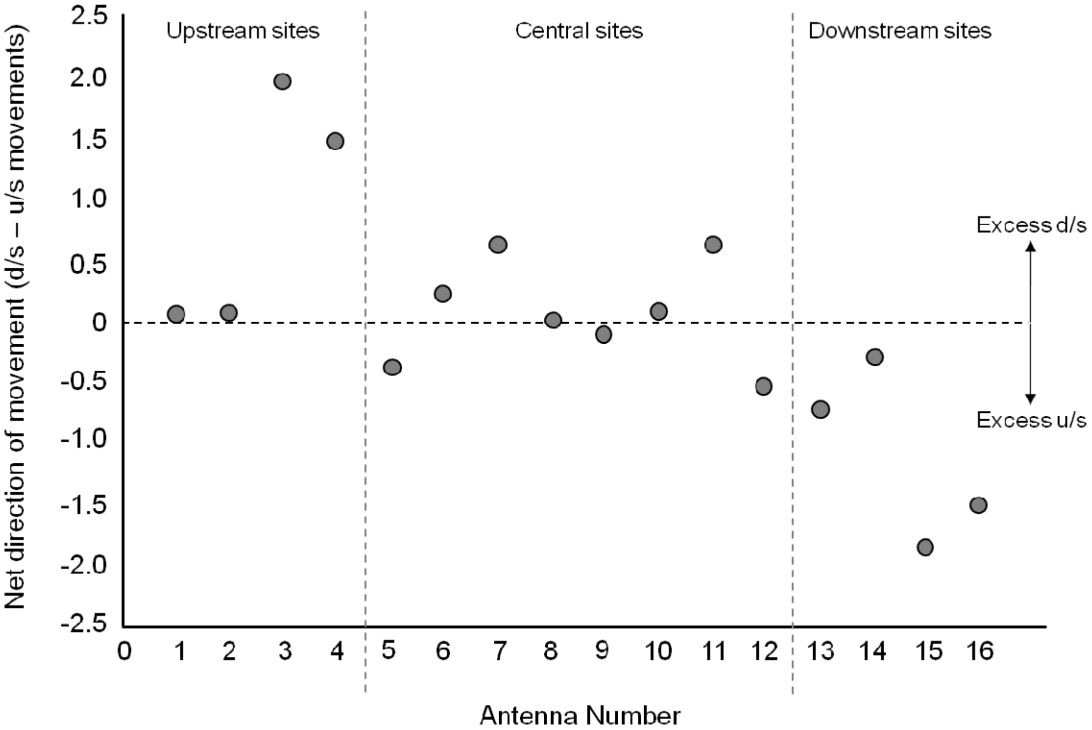
The direction of movement relative to the flow could be determined from movement between antennae (figure 4.25). Signal crayfish moved in both upstream and downstream directions as well as moving across the stream from one bank to the other. Interestingly, over the 150 days crayfish made, in total, more upstream movements (1127) than downstream movements (866). This may be because a large number of downstream movements were not counted as they were made out of the reach from antennae 15 and 16. A corresponding upstream impact was not present from antennae 1 and 2 because crayfish rarely moved onto these antennae. This could potentially be responsible for the imbalance in upstream and downstream movements.

Figure 4.25. *The mean number of upstream, downstream and cross-stream movements made by tagged crayfish (n = 65) over 150 days.*



By subtracting the number of upstream movements made from each antennae from the downstream movements, an index of the net movement direction (termed ‘net status’ in spatial network analysis) of each antenna could be calculated (figure 4.26). It was clear that this index was strongly affected by the relative position of the antennae. This is because an antenna requires another antenna to be positioned upstream of it in order to register an upstream movement. Therefore, the probability of an upstream movement from an antenna increases as the number of upstream antennae increases. This can be clearly seen in figure 4.26 as downstream antennae (13 to 16) have more upstream values and upstream antenna 1 (3 to 4) have many more downstream movements, excluding antennae 1 and 2 which have very few recordings in both directions. Antennae 5 to 12 are located throughout the centre of the reach and plot around zero indicating equal upstream and downstream movements. Slight deviations from this trend can be identified, for instance, antennae 5 had more upstream movements relative to downstream movements than would perhaps be expected in its position. Alternately, antennae 11 had more downstream movements relative to upstream movements than expected. The lack of bias in the gross direction of movement across central antennae is supportive of case that crayfish do not show any preference to move with or against the flow (Bubb *et al.*, 2002a; Bubb *et al.*, 2004).

Figure 4.26. *The net status of each antenna calculated as the mean number of upstream movements subtracted from the mean number of downstream movements made by crayfish.*



4.7.3. Temporal variability in the movement of crayfish within the reach

Substantially fewer movements were made between pairs of antennae by crayfish in October and November than in previous months (table 4.2; shown graphically in Appendix A). The cohesion of the network declined with each month and was very limited by November. This indicates that crayfish moved between fewer pairs of antennae, strongly suggesting that the area of the substrate that was used by crayfish became substantially reduced in later months. The reduction in network cohesion was associated with an increased dominance of movements between antennae situated on the inner bank of the meander bend. The number of edges between antennae was also variable between months (figure 4.27). During July and August, antennae consistently had a higher number of edges than in other months, indicating that crayfish moved between many antennae. The lowest number of edges connecting antennae was recorded in October and November indicating that crayfish moved between fewer antennae in these months, corroborating the results of the network cohesion index.

The net direction of movement was grouped for all antennae to show the proportion of the total number of upstream movements relative to downstream movements between months (table 4.2). More downstream movements than upstream movements were made in October and November which was also the period of highest flow. More upstream movements were made in July and September when the flow was lower. In August the number of upstream and downstream movements was approximately equal. The pattern when looking at the direction of movement for each antenna is more confused with no discernable trends apparent (figure 4.28). The expected trend, described above (section 4.7.2), was present in the data due to the relative locations of the antennae. The only major deviations from this were antennae 5 and 6 in September due to substantially more upstream movements being made relative to downstream movements.

Table 4.2. *Parameters used to characterise the network of crayfish movement for each month of the tracking period. Direction indicates the total number of upstream movements made from antennae subtracted from the number of downstream movements. Consequently, negative values indicate more upstream movements than downstream and* vice versa.

		July	August	September	October	November
Number of movements	**Mean**	69	108	56	33	15
	σ	45	95	42	24	13
Cohesion		90	80	61	59	20
Direction		-1.66	-0.08	-0.57	1.54	0.75

Figure 4.27. *The mean number of edges linking antenna for each month of the year. Note that data points associated with July and August consistently plot above all others and those for November consistently plot below all others.*

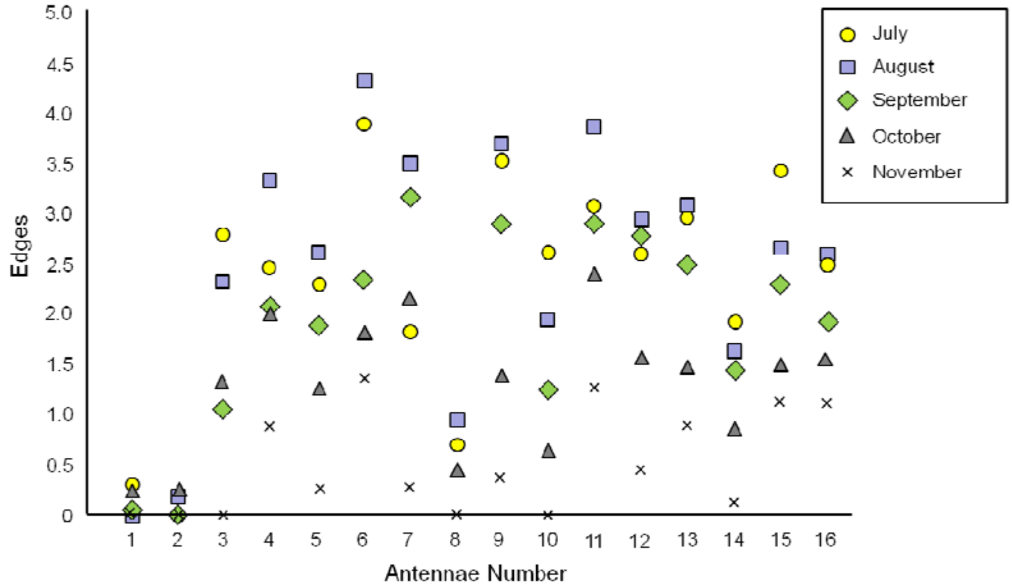
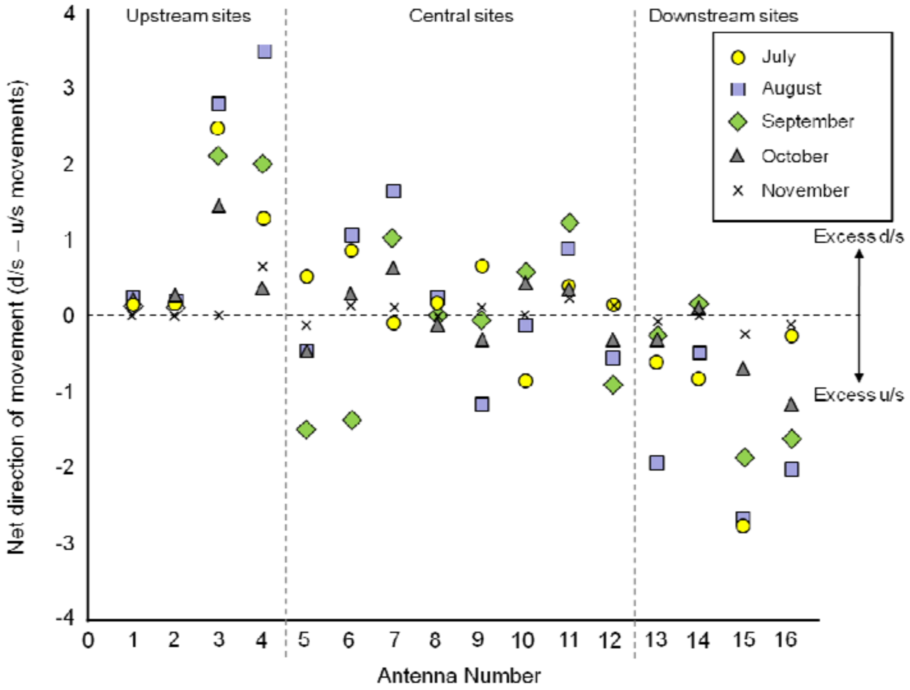


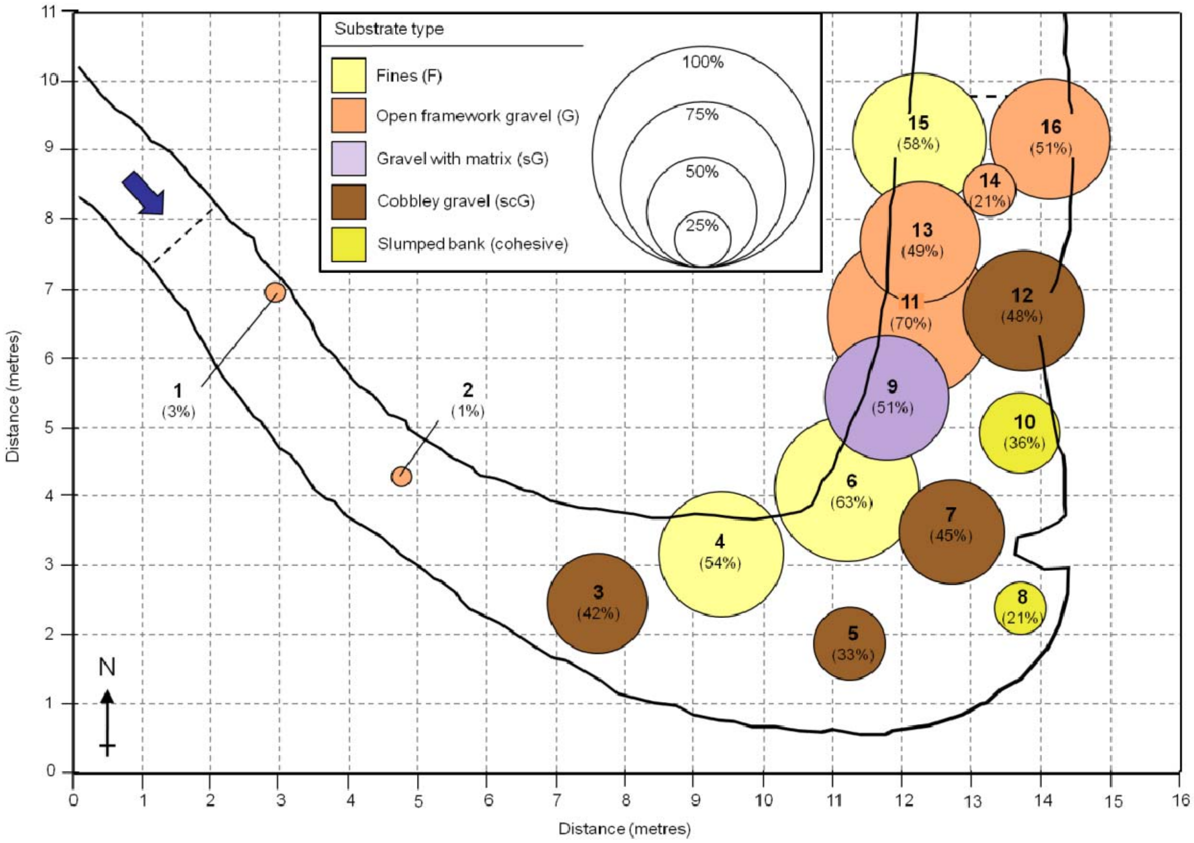
Figure 4.28: *Net direction of movement made from each antenna in each month calculated as the number of upstream movements subtracted from the number of downstream movements.*



4.7.4. The length of time signal crayfish spent over each antenna

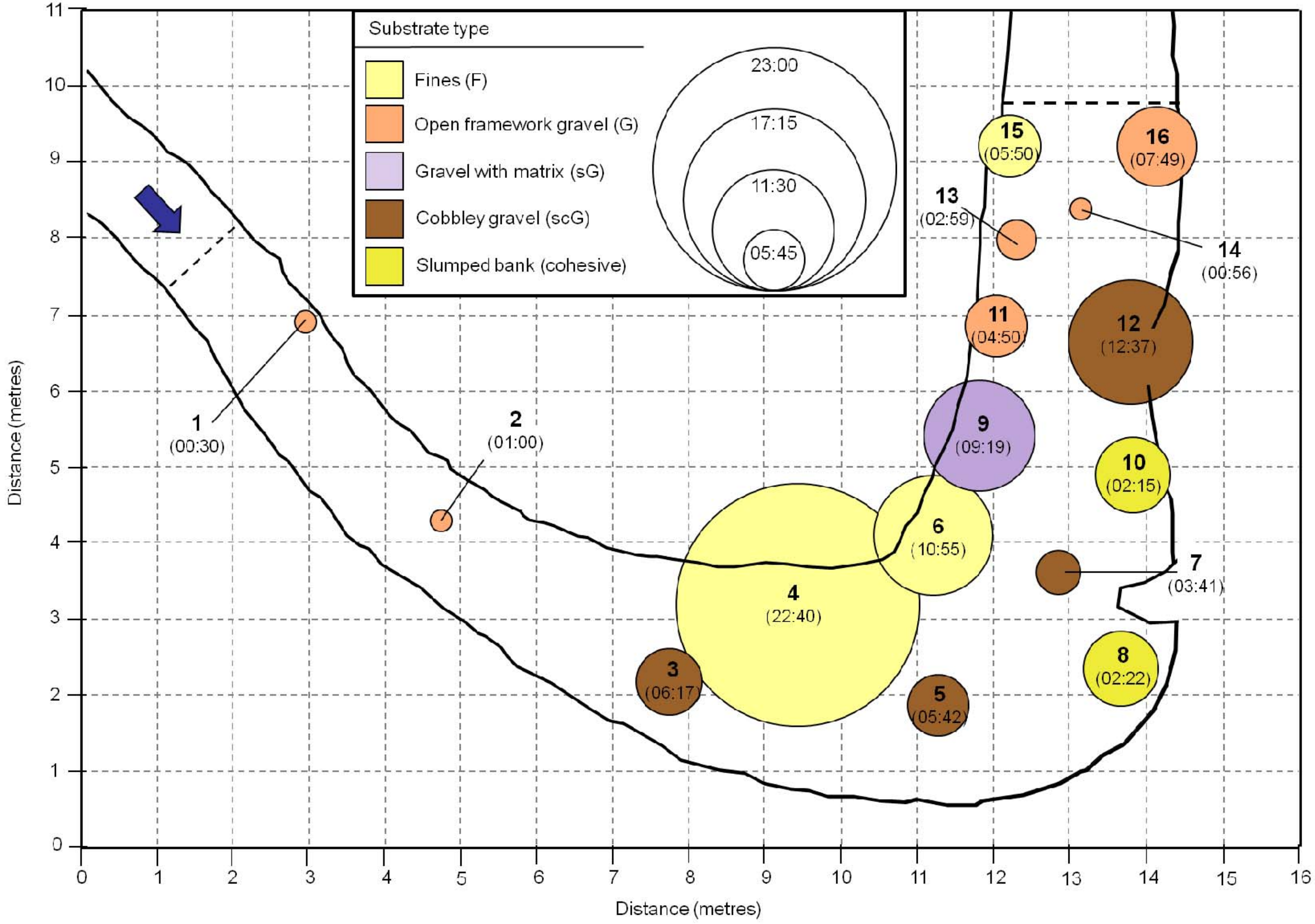
As well as moving between antennae, crayfish also remained active on antennae for extended periods (type A and C). In total, the 65 tagged crayfish spent 90 hours on antennae over the 150 days. However, the average length of time spent over antenna, as presented in the following section, appears to be low due to the great variability in antenna use by tagged crayfish. For instance, only 51% of crayfish recorded an *in situ* reading over antenna 9 during the 150 day tracking period and, consequently, 49% of crayfish will have spent zero hours active on this antenna, lowering the overall average (figure 4.29). It should also be noted that 11% of all tagged crayfish left the reach within one day of tagging and, therefore, spending little time over any antenna and dragging averages down.

Figure 4.29. *Percentage of PIT-tagged crayfish (n = 65) that were recorded by each antenna during the 150 day tracking period. Numbers in bold refer to antenna identification number.*



The location used by the most crayfish (70%) was antenna 11 which was situated just beneath open-framework gravels on the downstream riffle in the reach (section 4.7.1; figure 4.29). However, the average length of time crayfish spent on this antenna during their duration in the reach (av. 11 days) was only 4 minutes 50 seconds, ranking it 7th out of all 16 antennae (figure 4.30). On average, signal crayfish spent the longest period of time on antenna 4 which was positioned under the point bar of the meander bend. Crayfish remained on antennae 4 and 6 for relatively few but extended periods rather than numerous short periods. This may imply that crayfish used these antennae predominately for shelter. The second longest average length of time was recorded from antenna 12 and this was unusual due its location in deep water on the outer bend of the meander. Other deep, cobble areas were not characterised by significant crayfish presence. With the exception of antenna 12, it is the inside bend of the meander, particularly the point bar, where crayfish spent the longest time present over antenna, similar to the analysis of movements between antennae. The average times spent on antennae 1 and 2 are misleading because of the few occasions they were utilised. The total length of time, aggregated for all 65 crayfish over the 150 days, is only 2 minutes for each antenna.

Figure 4.30: *Map of the instrumented reach of the River Bain, UK, where circle area is proportional to the mean amount of time (minutes: seconds) crayfish spent over each antenna. Colours represent the substrate facies unit.*



4.7.5. Temporal variability in patch use by crayfish

There was a great deal of variability in the average length of time crayfish remained over antennae between months in the tracking period (table 4.3; and presented visually in Appendix B). In general, crayfish spent less time over antennae in October and November than in previous months. Antennae 5 and 6 remained two of the most popular in all months whereas antennae 1 and 2 remained unpopular in all months Whereas crayfish used all antennae with the exception of antennae 1 and 2, between July and September, crayfish only used seven antenna in November, all of which were located on the inner bank of the meander bend, with the exception of antenna 15. This is consistent with analysis of the movement of crayfish between pairs of antennae (section 4.7.3) which found the dominance for antenna on the inner-bank of the meander increased in later months. Crayfish consistently spent the longest periods of time over antennae in August and September. Interestingly, in September which was characterised by constant low flows, crayfish remained active over antennae 5 and 7, both in the channel thalweg, for substantially longer periods than in other months.

Table 4.3. *The average (and standard deviation, n = 65) time period tagged crayfish spent active over the same antenna (type A and B; Figure 4.10) and the average number of occasions each crayfish moved between antennae (type C), for both the total 150 day period and during each month.*

		Total	**July**	**Aug**	**Sept**	**Oct**	**Nov**
Type A and B movement (hh:mm)	*Mean*	00:37	00:33	01:04	00:43	00:21	00:13
	St.Dev	00:38	00:32	00:55	00:37	00:16	00:11
Type C movement	*Mean*	26	29	33	31	19	4
	St.Dev	28	27	32	35	18	3

4.8. Discussion

4.8.1. General activity of crayfish within the study reach

Signal crayfish were found to be highly active within their home range, before making long distance movements. The total activity of crayfish was variable during the tracking period and, whilst only weakly correlated to flow or temperature, there was strong evidence of abiotic threshold conditions influencing crayfish activity in the reach. This is a potentially similar result to other studies that have found crayfish activity to be strongly related to water temperature and/or depth (Creed, 1994; Robinson *et al*., 2000; Bubb *et al*., 2002a; Light, 2003). If the tracking period had lasted longer and encompassed a greater range of flows and temperatures, more significant trends may have been identified.

Previous studies have found that high flow can displace and cause mortality of crayfish (Momot, 1966; Parkyn, 2000; Robinson *et al*., 2000; Royo *et al*., 2002) and it is known from laboratory studies that crayfish are entrained at relatively low velocities (0.4 m s^{-1}) (Maude and Williams, 1987; Clark *et al*., 2008). Bubb *et al*. (2002, 2004) found, using radio-telemetry, that signal crayfish were not entrained by high flows (> 80 m^3 s^{-1}) because they sheltered in burrows or in stable areas of substrate. A similar pattern was observed in this study, with crayfish rarely moving during high flows or cold temperatures and always re-emerging in the reach after high flow events. This supports the theory that the impact of flow on crayfish activity is more likely to be accurately expressed as a threshold condition rather than a linear correlation.

Studies of the long-distance movement of crayfish have found that crayfish are weakly biased to move in a downstream direction (Holdich *et al*., 1995; Bubb *et al*., 2002a; Bubb *et al*., 2004). In this study it was found that crayfish were biased to moving in an upstream direction. Although this is likely to be associated with the methodological design as upstream movements from an antenna can only be recorded if there is another antenna upstream, it is clear that crayfish were not biased to movement in a downstream direction during the 150 days. However, in October and November there was a bias for more downstream movements which coincides with when the flow was high. Alternately, when the flow was low in September, more upstream movements were made. This would suggest that the direction of movement by crayfish was influenced by the flow conditions, again supporting the hypothesis that flow does have an important, yet potentially complex and variable, influence on the activity of signal crayfish.

The vast majority of crayfish activity took place at night with peak activity typically occurring around 22:00. This was consistent with other studies, for instance, Nystrom (2005) found that signal crayfish were most active at dusk. Radio-tracked white-clawed crayfish have also been found to be significantly more active at dusk (21:00 – 00:00) than at dawn (03:00 – 06:00) or the morning and afternoon (Robinson *et al.*, 2000). Inconsistent with previous studies is the fact that crayfish in this reach remained active throughout the night. Guan and Wiles (1998) studied the nocturnal foraging of signal crayfish using capture techniques in the River Ouse, UK. They found signal crayfish foraged between 17:00 and 01:00 in all seasons, much less between 01:00 and 09:00 and only occasionally between 09:00 and 17:00. In this study, crayfish were, cumulatively, more active between 01:00 and 09:00 than between 17:00 and 01:00, suggesting that in this small stream, crayfish only had a weak preference for a particular period of night. In July, crayfish were more active during daylight hours than during any other month. This is consistent with the results of Gherardi *et al.* (2000) who found Red Swamp crayfish were nocturnal but made significantly more daylight movements during the spring. Therefore, the increased daylight activity of signal crayfish in July may reflect a season change in the level of nocturnalism.

4.8.2. The location of crayfish activity within the reach

Adult crayfish have been found to prefer pool habitats and avoid shallow riffles where juvenile crayfish tend to remain (Guan and Wiles, 1996; Englund and Krupa, 2000; Harrison *et al.*, 2006). In pools, adults make slow and more diffuse movements and spend more time feeding and grooming than in riffles (Harrison *et al.*, 2006). Pools were also found to be favoured by juveniles, however, they were less habitat specific than adults (Harrison *et al.*, 2006). It is therefore likely that adult crayfish displace smaller crayfish from riffles until they become large enough to successfully compete for resources and shelter (Edman and Jonsson, 1996; Harrison *et al.*, 2006). The preference of pools has been hypothesised to be due to the increased cover from terrestrial predators, difficulty in moving in shallow, fast flows and due to an accumulation of detrital food items in pools.

In this study, instead of a longitudinal distinction in the presence of crayfish, associated with pools and riffles, crayfish presence was organised laterally with crayfish preferentially found in marginal areas of the channel. Jowett *et al*. (1998) also found in their study using 793 quadrats from 30 rivers that presence and numbers of crayfish were positively related to the edge of rivers. Crayfish were particularly found on the inner bank of the meander bend. An exception is the popularity of the deep water, cobble-gravel area situated above antenna 12 which was popular with crayfish. This appears unusual because other, similar areas were not utilised by crayfish to the same degree. This particular area may be popular because between four and seven crayfish burrows were positioned in the adjacent bank which, if used by tagged crayfish, would result in the antennae being regularly triggered. This area will also be characterised by recirculating flow along the meander bend which would trap detrital food, providing a popular foraging area for crayfish and, potentially explaining why crayfish burrows were preferentially found in this area. Tagged crayfish were also highly active on the downstream riffle in the studied reach which was shallow and fast flowing in places.

This discrepancy in the habitat choices made by crayfish between this study and other studies, may be due to the relatively small size of the stream which consequently lacked any deep pool habitat which crayfish are normally associated with. In fact, the size of pools in this river would provide only very limited space for such a high density of crayfish (approaching 10 m^{-2}), which may have resulted in crayfish utilising more of the substrate, including the riffle area. It may also reflect the presence of extensive marginal macrophyte growth which may be valued as a better source of cover than pool habitat. This may be particularly true in the River Bain which was relatively shallow even in its deepest location, never exceeding 1 m deep for the tracking period. Also, in pools crayfish often shelter underneath large clasts. However, the grain-size distribution in pools, whilst containing the coarsest material recorded in the channel, did not contain material coarse enough to provide cover for adult crayfish, hence their preference for marginal areas.

Interestingly, there were discrepancies between the popularity of sites in terms of *ex situ* and *in situ* readings. For instance, the open-framework gravels in which antenna 11, was situated, had one of the highest numbers of *ex situ* readings indicating that crayfish regularly moved across the antenna (section 4.7.1). However, it was only the 7th most popular antenna in terms of how long crayfish remained on top of it (*in situ*). This implies that crayfish within the reach were prepared to move regularly across areas of the channels that they did not deem suitable to remain in for extended periods. Previous experiments, which have predominately used trapped and mark-recapture techniques to study the habitat preference of crayfish, may have, therefore, failed to account for regular nocturnal movements made by crayfish in shallower areas of the bed which are not necessarily suitable for extended periods of inactivity.

4.8.3. The impact of abiotic conditions on the spatial location of crayfish

It seems apparent that the main determinants of the spatial location of crayfish were the hydraulic conditions and macrophyte cover. Crayfish significantly preferred areas of the substrate in hydraulic group B (figure 4.15), characterised by low flow velocities, low to moderate flow depths and substantial macrophyte growth. Jowett *et al*. (2008) modelled the habitat preference of Koura crayfish (*Paranephrops planifrons*) in New Zealand. They found that crayfish presence was positively related to areas with velocities between 0 – 0.4 m s^{-1} which is consistent with the study of Maude and Williams (1987) who found crayfish lost their footing at 0.4 m s^{-1}. PIT-tagged crayfish in this study avoided antennae 1 and 2 which were the least triggered antennae, both in terms of *in situ* and *ex situ* activity of crayfish. This was probably because of the shallow water depth and constant high flow velocities (range 0.6 – 0.9 m s^{-1}) over antenna 2. Antenna 1 had a similar hydraulic environment as antennae 4 and 6 (group B) which were the most triggered antennae in the reach. This implies that the hydraulic conditions over antenna 2 acted as a barrier to crayfish movement, preventing crayfish from reaching antenna 1, although antenna 1 did lack the significant macrophyte cover present in downstream regions. Crayfish regularly used all other antennae although some were more popular than others, particularly in terms of *in situ* readings over antennae. This indicates that the hydraulic environment did not prevent crayfish from utilising any other area of substrate in the reach. Therefore, it appears that threshold hydraulic conditions, which in this reach approached 0.6 m s^{-1} in 0. 25 m deep flow, dictate the spatial location of crayfish as well as the temporal activity of crayfish (discussed above in section 4.8.1).

Jowett *et al*. (1998) found that cover was a more important determinant of crayfish location than both substrate and hydraulic variables. Cover has also been recorded as an important determinant of crayfish presence in other studies (Alderstadt *et al*., 1996; Parkyn and Collier, 2004; Aquiloni *et al*., 2005; Kutka *et al*., 1996; Usio *et al*., 2006). In this study it also appears that cover is the most important variable in determining the spatial location of crayfish. Its significance may also be increased in this stream due to the limited potential for burrowing into cohesive banks, the relatively shallow water depths and lack of coarse bed material potentially increasing the susceptibility of crayfish to predation by terrestrial predators, including wading birds and the invasive mink which were known to predate crayfish in this reach.

4.8.4. Temporal changes in the location of crayfish activity within the reach

The location of crayfish within the reach changed substantially between months, particularly in terms of movements between antennae. In winter months the network of crayfish movement was vastly reduced indicating that crayfish did not move as far, or as often, as in previous months of the year. In July, movements were made throughout the reach with a slight dominance for the inner bank. There were also numerous long distance movements made between antennae which were far apart whereas, in September, these infrequent movements were substantially reduced and in October and November they had ceased altogether. With passing months the dominance for the inner bank increased and by November there were no movements along the outer-bank of the meander bend. This progressive simplification in the network of crayfish movement was likely to be associated with the increasing flow depth and velocity through the reach and decreasing water temperatures (Appendix A). The reduction in macrophyte cover in winter months may also have had an impact on reducing the movement of crayfish.

4.8.5. Substrate preference and implications

Crayfish remained on areas of fine, unconsolidated sediment (facies type 1; section 4.4.6) for longer than other substrate types (figure 4.31). However, this preference was associated with the fact that fine sediment in the reach accumulated in areas of low flow and macrophyte cover (hydraulic group B; section 4.5.3). Disentangling these three parameters is difficult but it consistently appears that substrate was not an important determinant of crayfish activity within the reach. Figure 4.31 illustrates the similarity between *in situ* and *ex situ* movements between substrate patches with the exception of the slumped area of banking (group 5) which had substantially less crayfish activity on it. There were also substantially fewer *ex situ* movements from antenna in gravels with matrix (group 3), but, this is likely to be associated with the fact only one antenna was situated under this facies. Crayfish were mostly present in marginal areas of channel regardless of substrate type (group B). Probably as a result of the hydraulic conditions rather than the substrate type, crayfish did not spend extended periods active on antennae positioned in areas of open-framework gravels (type 2) in comparison to some other areas of the bed. However, this substrate facies was the most used by crayfish with over 80% of tagged crayfish spending time in these bed regions (figure 4.32). As a result, crayfish were highly active on open-framework gravels which are similar in surface grain-size distribution to the flume gravels.

Figure 4.31: *The mean (± 2 SE) number of* ex situ *movements (grey circles) and the mean (± 2 SE) length of* in situ *movements (black circles) from each hydraulic group (a; A – D, section 4.5.3) and substrate facies (b; 1 – 5, section 4.4.6).*

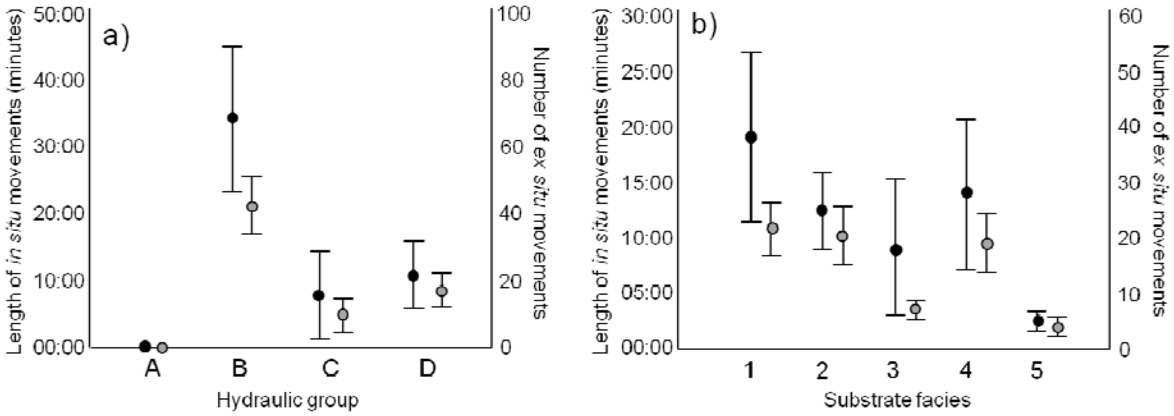
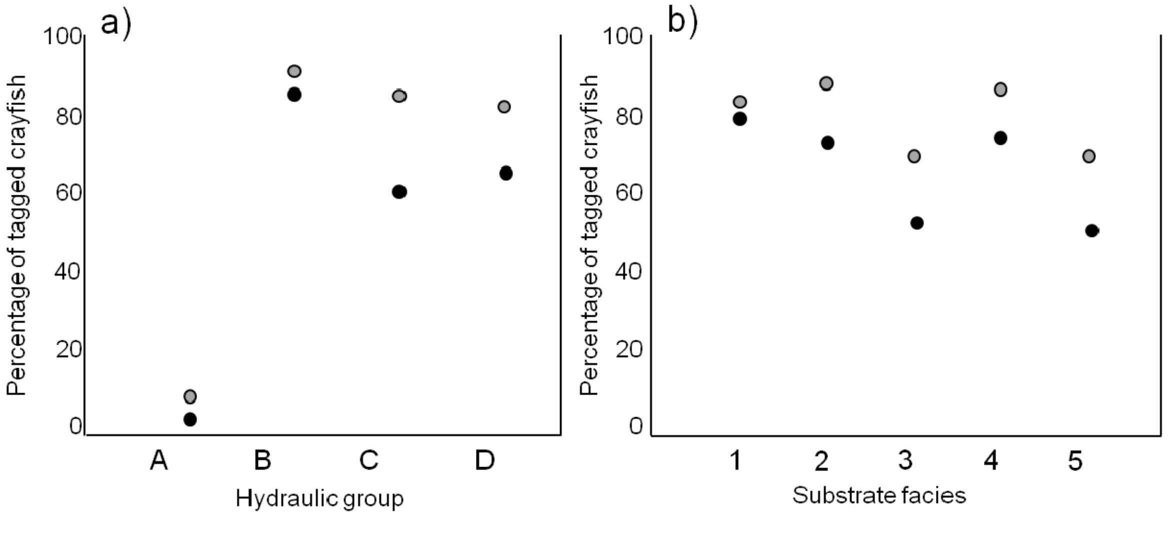


Figure 4.32: *The percentage of tagged crayfish that recorded an* in situ *(grey circle) or* ex situ *(black circle) in each hydraulic group (a; A – D, section 4.5.3) and each substrate facies (b; 1 – 5, section 4.4.6).*



Crayfish have been found to be more active from July to September which would imply that any geomorphic impact associated with crayfish will also occur predominantly between these months. Not only were crayfish less active in winter months, but crayfish spent proportionally less time on unconsolidated gravels during October and November. Instead, crayfish activity was increasingly found in marginal areas of the channel where they could shelter in macrophyte stands. Therefore, disturbance of gravels by crayfish in the River Bain is likely to occur mainly between July and September. This is also expected to be the period of river bed consolidation with the ingress of fines and structuring of the substrate by low flows. Therefore, these results support the hypothesis that signal crayfish could have a substantial impact on the stability of gravel beds in rivers.

Chapter 5

Discussion: Implications of experimental results for river geomorphology and ecology

5.1. Introduction

Signal crayfish have been found to modify the topography (chapter 2) and structure (chapter 3) of fluvial gravel substrates. These substrate modifications have significant impacts on the stability of water-worked gravels (chapter 3). In rivers, crayfish were found to be present for extended periods on the sizes of gravel that they are known to be able to disturb (chapter 4). These findings support the hypothesis that crayfish have a significant impact on the structure and mobility of bed material in gravel-bed rivers, with implications for the geomorphological and ecological environment which are discussed separately below. The fact that signal crayfish are invasive to rivers in the UK adds to the potential significance of these results implying that crayfish not only impact native organisms through ecological interactions, but also alter the habitats within which they live.

5.2. The potential geomorphic impact of signal crayfish

5.2.1. The impact of crayfish on fluvial gravel substrates

When exposed to narrowly-graded substrates signal crayfish were able to move material up to 38 mm in diameter although they moved substantially more material when particles were finer than 16 mm. They had an impact within six hours of introduction to a surface, mostly associated with their exploratory behaviour. Their impact increased with time, particularly in terms of the volume of displaced sediment associated with the construction of pits and mounds. Whilst pits and mounds were more visually apparent, the dominant method of disturbance across all surfaces, in all experiments, was the rearrangement of surface grains associated with brushing past grains when walking and foraging. In flume experiments, it was found that surface rearrangement led to an alteration of the structure of surface grains which suggests that crayfish can, at least partially, undo the imbrication of water-worked gravels. The combined impact of pit and mound construction and surface rearrangement resulted in a substantial increase in the number of grains entrained across loose and water-worked surfaces at high velocity flows. For water-worked surfaces this was statistically significant, with nearly double the number of grains entrained over a two hour period. Crayfish have the potential to have both direct and indirect impacts on geomorphic processes, both of which are discussed below (section 5.2.4 and section 5.2.5 respectively). The combination of these effects could result in signal crayfish having a significant impact on the mobility of gravels in rivers with important implications for both bedload transport and for the substrate as a habitat for other benthic organisms (section 5.2.5).

5.2.2. Implications of the geomorphic impact of signal crayfish

We have a substantial knowledge of bedload transport processes in gravel-bed rivers (section 1.2); however, predictions of bedload transport are still difficult and rarely accurate (Gomez and Church, 1989). Prediction is particularly challenging for incipient motion because of the great variability in the entrainment and continued transport of grains at a given flow. Paintal (1971) states that grains can move at any flow, it is only the likelihood of movement that increases with flow strength. In flume experiments, crayfish nearly doubled the number of grains in transport from control surfaces, thereby increasing the proportion of the grain size fraction in transport by altering the relative position of grains and partially undoing the imbrication of surface grains. Therefore, the action of crayfish increased the probability of grain entrainment (although see section 3.9.7 regarding the potential stabilisation of grains). At very high velocity flows, which are sufficient to mobilise the whole bed i.e. approaching full mobility, crayfish modifications are unlikely to have importance because of the relative significance of the flow force. Crayfish activity is more likely to be of importance at intermediate flows by increasing the proportion of the surface grains in transport. Movement of the bed will also be more frequent as a greater proportion of the hydrograph will exceed the critical shear stress for the weakened bed.

Crayfish were found to increase the proportion of a size fraction in transport in flume experiments but this impact is size-dependent as crayfish were unable to move material coarser than 38 mm and moved substantially more grains from substrates finer than 16 mm. As a result, crayfish disturbance may encourage inequality in bed material transport by promoting the entrainment of finer material (< 16 mm) but having less of an impact on coarser, framework material.

Crayfish will almost certainly also lower the flow required to initiate motion through altering gravel structure and protrusion. Conversely, altering the topography of the bed and increasing the surface roughness, crayfish will also be impacting the hydraulic environment, potentially increasing the drag and decreasing the entrainment of material. Therefore, it may be speculated that crayfish will widen the range of flows over which a grain can be entrained by loosening the bed but simultaneously modifying the hydraulic environment. A similar phenomenon has been observed for salmon which loosen the bed, removing fines and disturbing the armour layer and bed structures when spawning, but the resultant redd topography modifies the hydraulics, reducing the shear stress and potentially decreasing bed material transport (Montgomery *et al*., 1996).

The presence of other organisms, known to be geomorphic agents, may also contribute to widening the range of flows over which grains are entrained. For instance, crayfish and benthic fish species which forage by disturbing bed material may loosen the bed whereas other organisms such as hydropschid caddisfly larvae can stabilise grains and prevent the entrainment of grains (2 – 8 mm) at shear velocities 38% greater than unbound grains (Johnson *et al*., 2009; figure 5.3). Consequently, some of the variability in entrainment, leading to inaccurate predictions of transport, may be associated with the benthic activity of a number of organisms present in gravel-bed rivers.

5.2.3. Limitations when scaling experimental results to field environments

River beds are comprised of a range of grain sizes. However, in this study, grains were moved from narrowly-graded substrates in order to ascertain the size limits to material moved by crayfish and to limit the variability in results between substrate replications, particularly in terms of entrainment data. As a result, it is possible that similar sized crayfish might be capable of moving coarser grains or more grains from a bed of mixed sizes, where coarse clasts would have smaller pivot angles if they were sitting relatively proud on a finer bed. It should also be remembered that the time series experiments (section 5.2.1) were conducted in still-water aquaria which may alter both the behaviour of crayfish and their impact on the microtopography. In still-water, crayfish might need to exert an increased force in order to mobilise grains in comparison with that required in flowing water due to the simultaneous impact of the flow, at least when moving grains in a downstream direction. Of course, the opposite pertains when moving grains in an upstream direction. However, the similarity in both the behavioural observations of crayfish and the topographic changes between surfaces in still-water and low velocity flow flume experiments suggest that any differences are minimal.

Pit and mound construction, observed in these experiments, is described as the construction of make-shift shelters because more appropriate shelter was not available. The extent to which crayfish would burrow in a natural environment where there may be more suitable shelter, for instance, macrophyte stands in the River Bain, is unknown. The fact that every crayfish caught during the study dug pits on introduction to gravel substrates suggests that it is a common behaviour and crayfish have also been observed to dig when foraging and to excavate beneath coarse rocks to create shelter in the field (Parkyn *et al*., 1997). Therefore, even in the presence of more recognised shelter, crayfish are likely to still burrow. Another potential issue is that, in laboratory experiments, crayfish were constrained within an area of 0.24 m^2 which may have concentrated their impact, increasing topographic and structural alterations per unit area. In the River Bain, crayfish were found to be active throughout a 60 m^2 area for an average of 11 days before moving further afield and, consequently, their disturbance was spread over a much larger area. Of course, any diffusion of their impact would be counteracted by the fact that multiple crayfish will be active simultaneously (densities > 10 m^{-2} in the River Bain) and are not limited to six hours activity, as in flume experiments.

Another factor not accounted for in these experiments is the impact of inter- and intra-specific interactions on geomorphic impacts. Competition and predation are known to affect the activity of crayfish and are, thus, also likely to affect the nature and magnitude of substrate reworking. For instance, Stein and Magnusson (1976) found crayfish spent longer periods ‘buried’ in aquaria when a fish predator was present than when alone. Despite the obvious importance of such interactions, discussed in detail in section 5.3, they were not considered here because they would have increased the variability in results due to the great range of potential responses. The field component (chapter 4) integrates all abiotic and biotic variables over a 150 day period and found crayfish were regularly present on substrate facies with a size distribution they are known to have the potential to disturb. The fact that the highly significant impacts of crayfish in flume experiments also resulted from general, widely observed crayfish behaviours, such as foraging and walking, supports the hypothesis that signal crayfish are potentially significant geomorphic agents in rivers.

5.2.4. Estimating direct impacts of signal crayfish in a lowland river

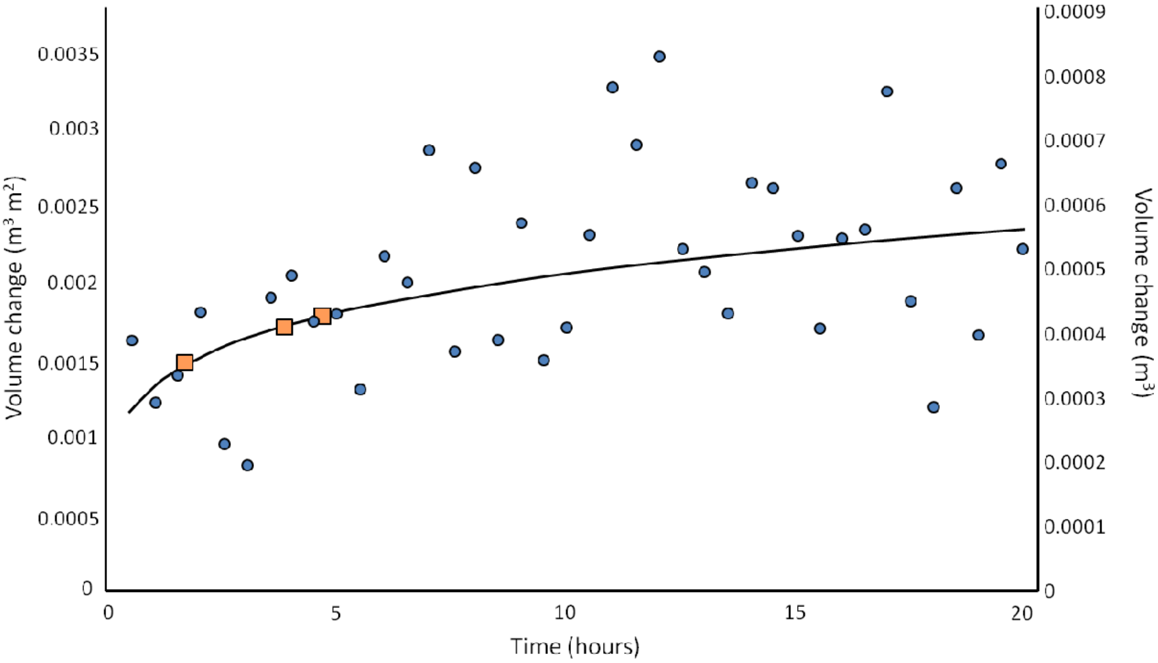
The distribution of crayfish activity through the instrumented reach of the River Bain was primarily related to the hydraulic environment and the presence of macrophyte stands, resulting in crayfish being preferentially active along the base of the river banks (section 4.7). Substrate was not an important determinant of the location of crayfish. Open-framework gravels, mostly found in riffle areas, were the most similar facies to the gravels used in laboratory flume experiments (chapter 3). The length of time crayfish remained active on these gravels has been used to estimate the potential impact that they may have had, using the results of the still-water experiments (chapter 2) as a guide to their impact per unit time. Crayfish remained on open-framework gravels for a total of between 1 hour 38 minutes (antenna 13) and 4 hours 26 minutes (antenna 16) over the 150 day period (table 5.1). However, it should be remembered that crayfish more frequently walked over these antennae (type C activity) rather than remaining stationary on them. Also, crayfish movement was not continuously recorded, but only recorded when crayfish moved within range of antennae which accounted for only an average of 40 minutes (maximum 4 hours 47 minutes) of total recording time for each crayfish whilst in the reach. Consequently, using the time spent active over these three antennae is likely to produce a very conservative estimate of the length of time crayfish actually spent active in areas of open-framework gravel.

The volume of material crayfish would be expected to move if left for these time periods was estimated using results from still-water experiments (chapter 2). A least squares regression was calculated for the volume of material crayfish moved with time, increasing in 30 minute intervals from 30 minutes to 20 hours (*series 2* still-water experiments; section 2.5.2). From this regression analysis it was calculated that the volume of material crayfish may be expected to move if active for the time periods recorded in the field was between 0.0015 m^3 m^{-2} and 0.0018 m^3 m^{-2} (figure 5.1). In flume experiments, it was found that the reworking of approximately 0.0012 m^3 m^{-2} of water-worked gravels was sufficient to increase the number of grains transported by 180% for 11 – 16 mm material and 195% for 16 – 22 mm material. Of course, these estimates of crayfish disturbance are unlikely to reflect the actual movement of material, not least because of the under-estimation of time spent in the relevant areas. Also, abiotic and biotic conditions in the field were variable both spatially and temporally, unlike the controlled conditions in laboratory experiments (section 5.2.3). However, the fact that signal crayfish spent extended periods of time on gravels within the size range they are known to be able to disturb supports the hypothesis that signal crayfish could have an impact on substrate structure and topography in some streams and the conservative estimates made here suggest that the impact on bed material transport may be significant.

Table 5.1. *The volume of material moved by signal crayfish estimated from the length of time crayfish spent over each antenna in the River Bain in field tracking experiments and a regression of still-water results, shown in figure 5.1.*

Antenna Number	Substrate	Total time	Estimate volume moved (cm^3)	Estimated volume per unit area (m^3 m^{-2})
11	Clean gravel	3 hrs 47 mins	414	0.0017
13	Clean gravel	1 hrs 38 mins	352	0.0015
16	Clean gravel	4 hrs 26 mins	428	0.0018

Figure 5.1. *A least-squares regression of the measured volume change in gravel substrates due to the presence of crayfish in still-water aquaria for time periods increasing in 30 minute intervals (blue circles;* $r^2=0.26$*;* $y=0.0013x^{0.188}$*). Orange squares indicate the volume of material crayfish would be expected to move if left for the time periods spent on antennae 11, 13 and 16 in the River Bain.*



This estimation of the volume moved can lead to a more speculative calculation of the transport rate of material moved by crayfish. The volume of material moved by crayfish will include the movement of material in all directions, not just downstream. Therefore, this measure is not directly comparable with the transport rate associated with the flow in determining the movement of material out of the reach but is a useful measure for comparing the relative importance of crayfish in terms of the quantity of material affected per unit area in comparison to the flow. Comparison will be made with Turkey Brook as it is a small lowland river, similar in size to the River Bain and with a comparable bed sediment size to both the River Bain and laboratory experiments (surface D_{50} = 22 mm, sub-surface D_{50} = 16 mm). The transport rate of material directly moved by crayfish can be estimated by calculating:

$$\text{Transport rate (kg m}^{-2}\text{ s}^{-1}) = \frac{\text{volume moved (m}^{3}\text{ m}^{-2}\text{) x bulk density (kg m}^{-2}\text{)}}{\text{time (seconds)}}$$

where the bulk density is 1800 kg m^{-2} and the volume moved is calculated from the regression of still-water results, discussed above (table 5.1; figure 5.1). As a result, the estimated transport rate ranges from 0.0002 kg m^{-2} s^{-1} (antennae 11 and 16) to 0.0004 kg m^{-2} s^{-1} (antenna 13). However, an unknown fraction of this movement will be in a downstream direction which is likely to approximate 50% of the quoted total assuming there is no bias in the direction that crayfish move material. Whilst this is an order of magnitude less than the transport rate associated with the flow at the onset of transport in Turkey Brook (0.001 kg m^{-2} s^{-1}), it illustrates the potential significance of crayfish as a direct component of bedload transport, particularly at low flows. It should also be remembered that this is likely to be a conservative measure, as stated in section 4.2.1, due to the nature of PIT-tag data. This equates to crayfish moving 34.6 kg of material across the 20 m reach (60 m^{2}) of the River Bain each day, indicating that crayfish have the potential to disturb large quantities of material in invaded, fluvial environments. As stated above, an unknown proportion of this material will be moved in a downstream direction and it is unlikely that crayfish will move material a distance comparable to transport by the flow. It is also likely that the flow will mobilise much greater quantities of material than crayfish. However, the relocation of 34.6 kg of material a day represents a substantial disturbance to the surface structure of substrates with implications to the stability of sediments as demonstrated in flume experiments (chapter 3). It should also be remembered that bedload transport only occurs at high flows that represent a relatively small proportion of the hydrograph whereas crayfish could potentially move 34.6 kg of material every day during low to moderate spring-summer flows. Therefore, in rivers with favourable conditions for crayfish disturbance, crayfish could represent the dominant mechanism of substrate mobilisation for much of the year. This supports the hypothesis that crayfish could be an important indirect factor in promoting sediment transport in combination with the flow in rivers.

5.2.5. The significance of crayfish in indirectly promoting sediment transport

Crayfish are unlikely to be of great relative importance in directly moving material because they do not move material a great distance, at least in comparison to the downstream displacement of grains by the flow. However, by altering the position of grains crayfish increase their vulnerability to movement by the flow, nearly doubling the transport rate from water-worked substrates in flume experiments. Turkey Brook, UK, has an armour layer with D_{50} of 22 mm which is well within the range crayfish can disturb. If crayfish activity breached this coarse surface layer it would have significant implications for bedload transport as it would uncover the finer, and more easily eroded, sub-surface material (D_{50} = 16 mm). In Turkey Brook it was found that bedload transport peaked on the receding limb of flood hydrographs when the event followed an extended period of low flow, as the rising limb altered the substrate structure and winnowed fine material from the surface, loosening it before entrainment on the receeding limb (Reid *et al.*, 1985). Alternatively, floods that rapidly followed a previous flood event had a transport peak on the rising limb because the surface was already loosened (Frostick *et al.*, 1984; Reid *et al.*, 1985). Therefore, it has been quantitatively proven that the structuring of the bed in Turkey Brook is of fundamental importance to bedload transport and, consequently, the activity of crayfish in restructuring gravels and winnowing fines would have important implications to the timing of transport during flood events, as well as increasing the quantity of material in transport. Equally, this illustrates the importance of the timing of crayfish activity in relation to river bed consolidation which is discussed further below (section 5.3.3).

5.3. The importance of environmental and ecological context

5.3.1. Determinants of the potential significance of animals in environments

Moore (2006) proposes a framework to assess the potential impact of an ecosystem engineer in a stream environment which, assuming the magnitude of habitat alteration and ecological response are proportional, is also suitable for assessing the significance of the geomorphic impact of an organism. It states that the importance of an organism in an environment is dictated by its body size, density and behaviour, as well as the hydrological regime. For instance, a hippopotamus will have large impacts on an environment without needing to occur in high densities, whereas Moore and Schindler (2008) found that salmon only had an impact on the local benthic community when the spawning density was in excess of 0.1 m^{-2}.

Crayfish are the largest freshwater invertebrate in temperate areas, and in a stream the size of the River Bain, are likely to be the largest animal present. Crayfish can also live to be 20 years old in captivity but are more likely to reach 5 – 6 in the wild, dominating the biomass in some streams, occurring at densities in excess of 10 m^{-2}. In this study, crayfish were found to alter habitats through common-place activities such as walking and foraging and, therefore, they score high on all three criteria proposed by Moore (2006). This implies that their potential for habitat modification is high. Whilst the density of an organism is undoubtedly of importance, the geomorphic impact of an organism does not necessarily increase linearly with density. The impact of crayfish on the ecological community through trophic and competitive interactions has been found to increase with density (Anastacio *et al.*, 2005; Gherardi and Acquistapace, 2007), as has their resuspension of fine sediment (Matsuzkia *et al.*, 2009). However, the resuspension of fine sediment was primarily associated with walking and foraging whereas the disturbance described in this study was also associated with pit digging which, assuming equivalence to burrowing, is known to not increase linearly with density, but to be influenced by the hierarchical social structure of crayfish (Barbaresi *et al.*, 2004). Therefore, the total impact of crayfish may increase with density, but the nature of this disturbance, and its geomorphic significance, may be related to density in more complicated ways.

5.3.2. Importance of intra- and inter-specific competition on the geomorphic impact of crayfish

Predation and competition between crayfish and other species will alter crayfish behaviour and, consequently, their potential to alter geomorphic conditions. These interactions are not simple and can lead to complex, variable responses from habitat modifying organisms. For instance, Statzner and Sagnes (2008) studied the impact of the crayfish *Orconectes limosus* on fine sediment when the predatory gudgeon, which can also mobilise sediment, was added to experimental channels. It was found that the addition of this biological interaction yielded complex results, but with no discernable impact on the quantity of sediment entrained. Similarly, Zhang *et al*. (2004) found both signal crayfish and cutthroat trout (*Oncorhynchus clarki*) significantly reduced the amount of fine organic material that settled in experimental troughs, but, when the two organisms were placed together their impacts did not prove to be additive, having no greater impact than each species individually.

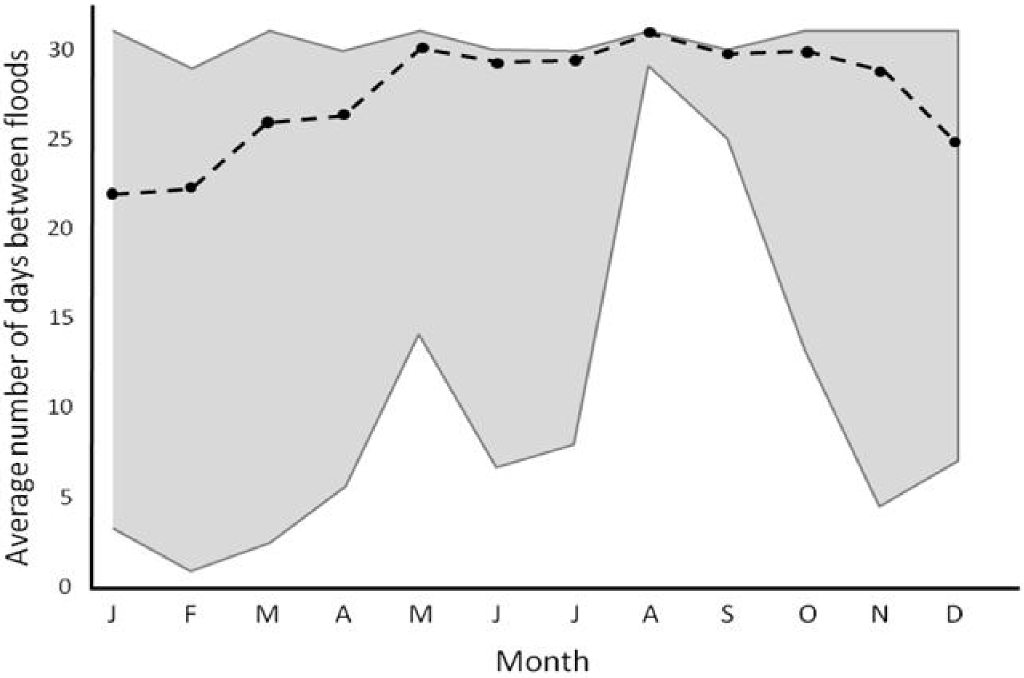
It has been found that red swamp crayfish (*Procambarus clarkii*) and common carp (*Cyprinus carpio*) had additive impacts in enclosure experiments in a shallow eutrophic lake in Japan, probably because carp foraged to a greater depth than crayfish which disturbed the bed mainly through walking, burrowing and feeding activities (Matsuzaki *et al*., 2009). Therefore, additive impacts are possible when the method and nature of disturbance differs. This leads to an interesting question about the impact of whole crayfish populations as it is known that the habitat usage and activity of adult and juvenile crayfish differs. Adults are usually found preferentially in pools, burrowing into bank material and beneath cobbles, whereas juveniles are limited to riffle areas where they live between gravel and cobble grains. Consequently, juvenile crayfish are likely to cause the winnowing of interstitial fines, in the same way as other small crustaceans, including shrimp (Pringle *et al*., 1993) whereas adults are likely to disturb the coarse framework when foraging and digging. Where crayfish populations are organised by age in terms of width-scale bedforms, then the impact of crayfish would be structured in a similar way with interesting spatial implications for bedload transport which may include increased fines sediment transport from riffles, with increased gravel instability in pools.

5.3.3. Importance of environmental conditions on the geomorphic impact of crayfish

In addition to biotic interactions and the life cycle of an organism, Moore (2006) in his review of ecosystem engineering in rivers, highlights the importance of hydrological regime in determining the relative significance of animal impacts. For instance, a river with regular flood events which dominate the disturbance regime will render the disturbance associated with bioturbation of little relative significance. However, it is not just the flow regime that is of importance, but the whole environmental context, in particular, the temperature regime and substrate characteristics in rivers and streams. For instance, in this study it has been shown that crayfish can only disturb substrates up to 38 mm in diameter and move significantly more grains from substrates finer than 16 mm. The influence of environmental factors in limiting or promoting geomorphic impacts will result in some gravelly river beds being more susceptible to crayfish disturbance than others. The importance of environmental context has been shown to be of direct importance to the geomorphic impact of spawning salmonids in a meta-analysis of 37 publications by Janetski *et al*. (2009) who found salmon had substantial impacts on benthic macroinvertebrates, biofilm development and stream biochemistry, but the effect magnitude was dependent on substrate grain size, as well as other physical parameters.

Crayfish did not move gravels long distances or displace them constantly in a downstream direction, but by modifying the gravel fabric and altering the topography and hence near-bed hydraulics, they significantly destabilised water-worked laboratory gravels. As such, the significance of crayfish became manifest at high flows, subsequent to the activity of crayfish. Therefore, for crayfish to have a substantial impact, a period of relatively low flow would be required followed by a high flow event which mobilises destabilised grains. However, if the high flow is sufficient to mobilise the bed without the destabilising impact of crayfish, then the impact of crayfish is rendered insignificant. Consequently, the impact of crayfish is likely to be greatest in a stream with high flow events that follow extended periods of low to moderate flows. The activity of crayfish in the River Bain was mostly related to flow stage, at least at the temporal and spatial scale of this field experiment. The River Bain hydrograph was characterised as having periods of relatively low flows, typically lasting from late- spring to early-autumn followed by periodic, rapid-onset, moderate-to-high flows, associated with rainfall events, predominantly occurring in winter and early spring. It is unusual over the past 38 years of daily gauged flow records in the River Bain for there to be more than one flood event in a single month, leaving extended periods of relatively low flows between them (figure 5.2). Considering crayfish are known to be able to move material of the same calibre as that in the River Bain, and considering that crayfish were found to be highly active during summer and autumn low flows, it would imply that the River Bain is particularly susceptible to bed disturbance by crayfish.

Figure 5.2: *The average number of days between flood events (flows ≥ 1 $m^3 s^{-1}$) during each month (dashed line), averaged for the last 38 years of gauged flow records (described in chapter 4). The grey region indicates the range.*



Studies have found that signal crayfish activity in the UK is seasonal, with crayfish moving less often and less far in cold temperatures (Bubb *et al*. 2004). A similar trend can be seen in the field data from the River Bain with crayfish moving less in autumn months (mean number of recordings per month = 18) than summer months (31). Therefore, it follows that the impact of crayfish on substrates will also be seasonal, resulting in substrate restructuring by crayfish occurring during summer months which is typically characterised by low flows, fine sediment ingress and structuring by the flows. In the New River, a 4th order, gravel-bedded river in North Carolina, USA, Fortino (2006) found that the effect of crayfish on the accumulation of fine sediment in winter was limited, whereas Helms and Creed (2005) found crayfish to have a significant impact in summer using the same experimental set-up, in the same river. The same is likely to be true in the River Bain due to the lack of recorded crayfish activity as water temperature decreased and flow stage increased. As stated above, it is during low flows that gravel beds consolidate and fine sediment ingresses into the framework which has a substantial stabilising impact on the bed (Frostick *et al*., 1984; Reid and Hassan, 1992). This implies that crayfish will be most active during the period of greatest consolidation in the River Bain, further supporting the hypothesis that they could be an important factor in promoting sediment transport.

5.3.4. Implications of disturbance by invasive crayfish to the ecological environment

Geomorphic processes have been modified by humans directly and through the manipulation of animal populations, both by over-exploiting geomorphic agents (Coleman and Williams, 2002; Butler, 2006) and through introducing invasive species (Crooks, 2002; Cuddington and Hastings, 2004; Butler, 2006). Some of the most damaging invasive species can also be classified as ecosystem engineers due to their habitat modification, for instance zebra mussels, rabbits and pigs. This is because they have both biological and physical impacts, resulting in native organisms having to adapt to an altered environment as well as survive increased predation and/or competition (Vitousek, 1990). Invasive species are considered to be one of the largest threats to biodiversity in global freshwater environments because of the relative ease of dispersal in streams and the importance of rivers to humans for commerce and recreation (Lodge *et al*., 1998; Gherardi *et al*., 2006).

Crayfish have been widely introduced to water bodies, with over 20 invasive species now established worldwide (Hobbs *et al*., 1989; Gherardi, 2006). As stated above (section 5.3.1), signal crayfish are large, long-lived, and can occur in high densities, making their environmental modifications of particular significance to the ecological community and, potentially, the geomorphology of the river. In fact, most crayfish species are considered keystone species (Nyström *et al*., 1996) due to their impact on food webs and their importance to the breakdown of organic matter, facilitating the presence of other invertebrate species (Momot, 1995; Parkyn *et al*., 1997; Schofield *et al*., 2001). These factors together make crayfish some of the most notorious invasive organisms in freshwater environments (Lodge *et al*., 2000). In particular, invasive crayfish species have significant detrimental impacts on juvenile fish, native crayfish and other invertebrate species which they predate and out-compete for resources, such as shelter (Guan and Wiles, 1997; Holdich *et al*., 1999; Vorburger and Ribi, 1999; Usio *et al*., 2001; Stenroth and Nyström, 2003; Crawford *et al*., 2006) They can also significantly reduce macrophyte and algal cover, removing sources of food and shelter and countering any stabilising impacts they have on the substrate (Creed, 1994; Lodge *et al*., 1994; Nyström *et al*., 1996).

Chapter 6

Conclusion

This study has shown that signal crayfish can rework substrates and disturb bed structures in such a way as to enhance bedload transport. This indicates that crayfish have the potential to have substantial impacts on the geomorphic environment in gravel-bed rivers, supported by a field study which found signal crayfish were active for extended periods on substrates of a similar grain-size to those disturbed in laboratory studies. This study has built on previous research, particularly that of Statzner *et al*. (2000; 2003), by identifying that crayfish cannot move gravels coarser than 38 mm from uniform substrates and that crayfish can move material within only a few hours of introduction (aim 1). It was found that the impact of crayfish was significant across both loose and water-worked surfaces and that the alterations made to the substrate had a substantial impact on gravel mobility during subsequent high flows which was also significant for water-worked gravels (aim 2). These experimental results were linked back to a field environment by tracking crayfish through a reach of the River Bain with PIT tags. It was found that crayfish were highly active on open framework gravels within the size range that they had been found to move in both still-water and flume experiments (aim 3). The overall results of these three interlinked areas of research strongly suggest that signal crayfish have the potential to be an important geomorphic agent in gravel-bed rivers.

It is unlikely that crayfish are important in directly moving material in rivers relative to the flow as they do not move gravels consistently in a downstream direction, nor do they move grains long distances. Consequently, in comparison to transport by the flow, their impact is likely to be relatively insignificant. However, by disturbing the bed and altering the structure and topography of the bed, crayfish condition the substrate, loosening it between high flows. In the flume, this resulted in the mobilisation of nearly twice the number of grains by a high velocity flow over a two hour period. This has important implications for bedload transport in rivers as it is known that the structuring of river beds at low-moderate flows increases their stability during subsequent high flows events. Consequently, whilst the quantity of material directly moved by crayfish is relatively subtle, it has a disproportionately large impact on the entrainment because it loosens the bed surface material. The full influence of bed disturbance is currently unknown but there is evidence from other studies that crayfish also prevent the accumulation of fines (Parkyn *et al.*, 1997; Usio and Townsend, 2004) and can increase suspended sediment concentrations through burrowing and bed disturbance (Angeler *et al.*, 2006; Harvey *et al.*, in press)

Whilst this research has illustrated the potential for signal crayfish to impact bed structure and mobility, their impact in rivers is likely to be variable and complex. It is apparent that the net impact of crayfish is to loosen the bed, but, by altering the protrusion of grains and the near-bed hydraulic environment, it is possible that crayfish increase the stability of some grains. Research on bed disturbance by spawning salmon has identified similar conflicting impacts which are also dependent on density (Montgomery *et al.*, 1996; Gottesfeld *et al.*, 2008). Consequently, an area of future research would be to determine the impact of crayfish density on their geomorphic impact and to quantify alterations to the hydraulic environment due to the construction of pits and mounds and relate this to bed stability. Both of these factors are part of the much wider area of interest which is concerned with understanding biotic and abiotic interactions in river systems and the geomorphic impact of plants and animals.

Organisms are increasingly acknowledged as having important geomorphic impacts in a range of habitats (Viles, 1988; Butler, 1995). ‘Ecosystem engineering’ is a common-place term that signals the increasing interest in this area of research. However, it is important to gain a process-level understanding of how organisms have an impact, as well as determining what that impact is. This is particularly important when attempting to determine the significance of an organism in an environment. In rivers, research on zoogeomorphology is limited to relatively few species, mainly large salmonid fish which spawn at high densities, particularly in North America. However, there are a large number of other fish, mammal and invertebrate species that are known to alter the physical environment when nesting, foraging or moving across and through the river bed. The significance of most of these impacts for the geomorphology of rivers is currently unknown, as is the cumulative impact of many geomorphologically active species. These may prove to be important questions in understanding sediment dynamics in some rivers and streams.

The vast majority of fluvial research has been undertaken in isolation from ecological processes and organisms. The effect of vegetation in rivers is now well established, but the impacts of animals are less studied. The large diversity of animals that live in rivers and the very high densities that they occur would support the claim that animals can have important impacts on the hydraulic environment and transport of bed material. Signal crayfish are a widespread, internationally important, invasive species, which is known to have detrimental impacts on native plants, fish, and invertebrate populations, including other species of crayfish. This study has shown that they also have potentially significant effects on the streambed physical environment, adding to the catalogue of geomorphic impacts attributed to biota.

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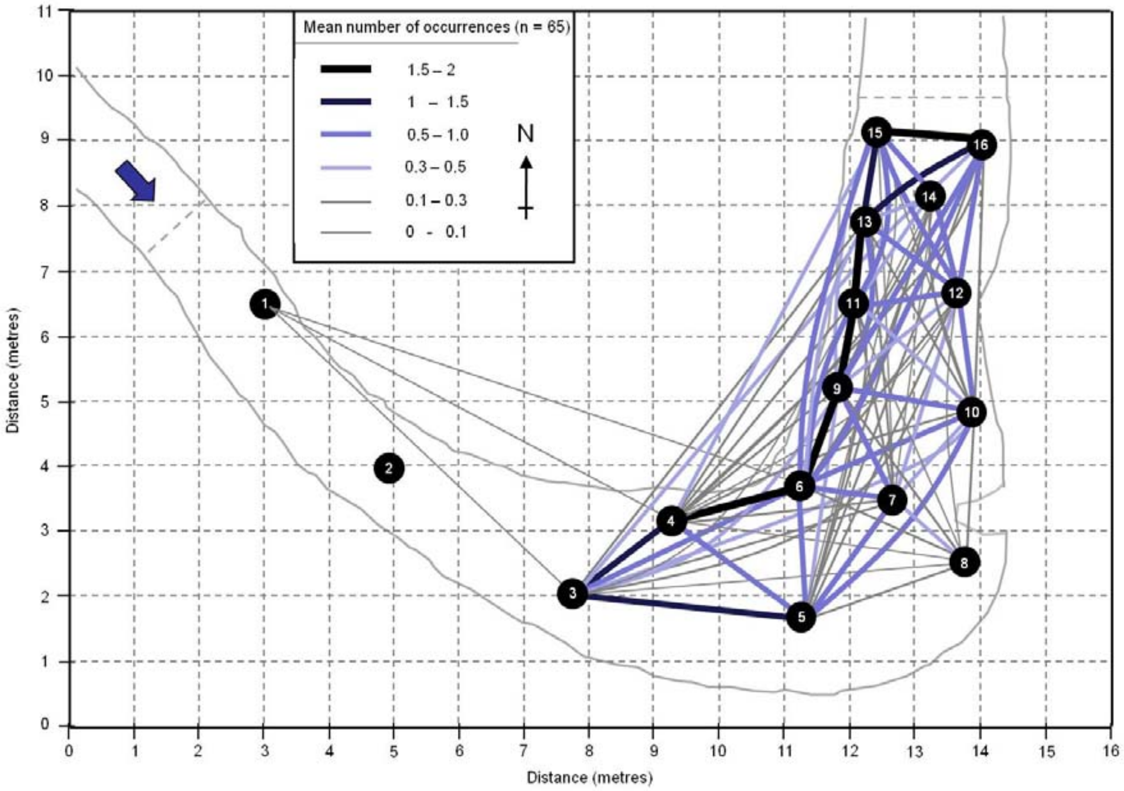
Appendix A

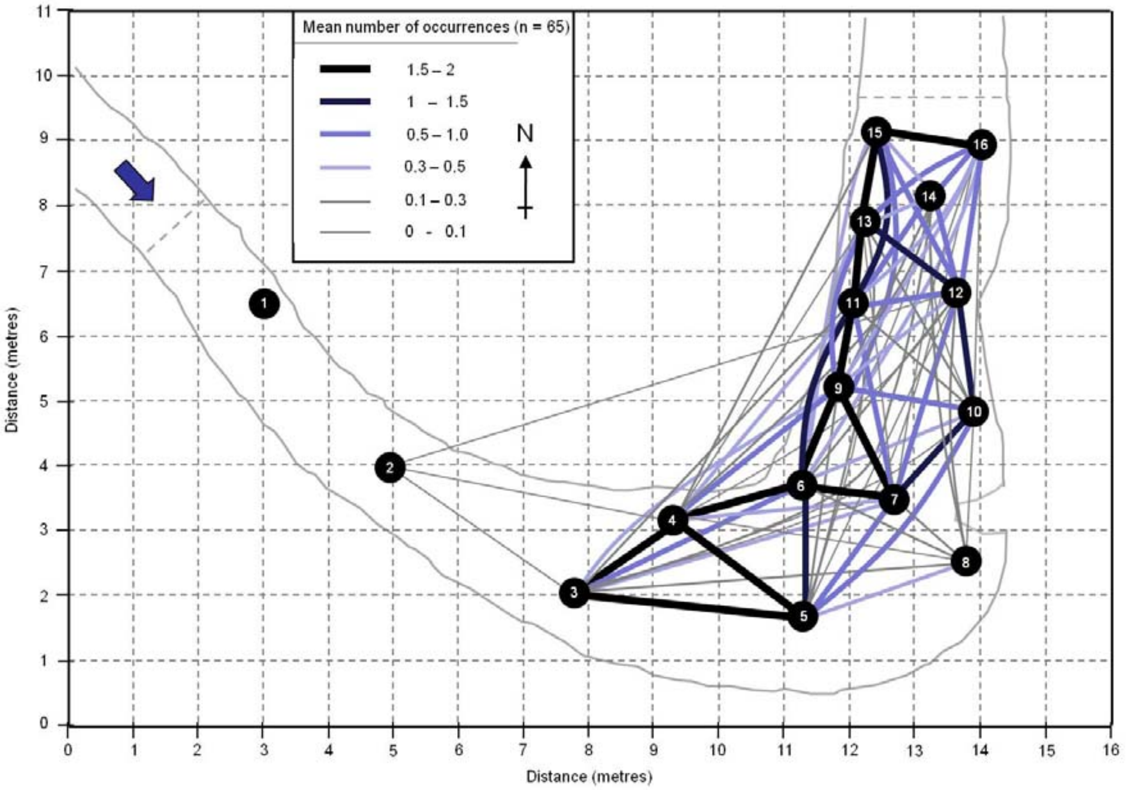
Movements between pairs of antennae each month

The mean number of movements by tagged crayfish between pairs of antennae for each individual month of the tracking period.

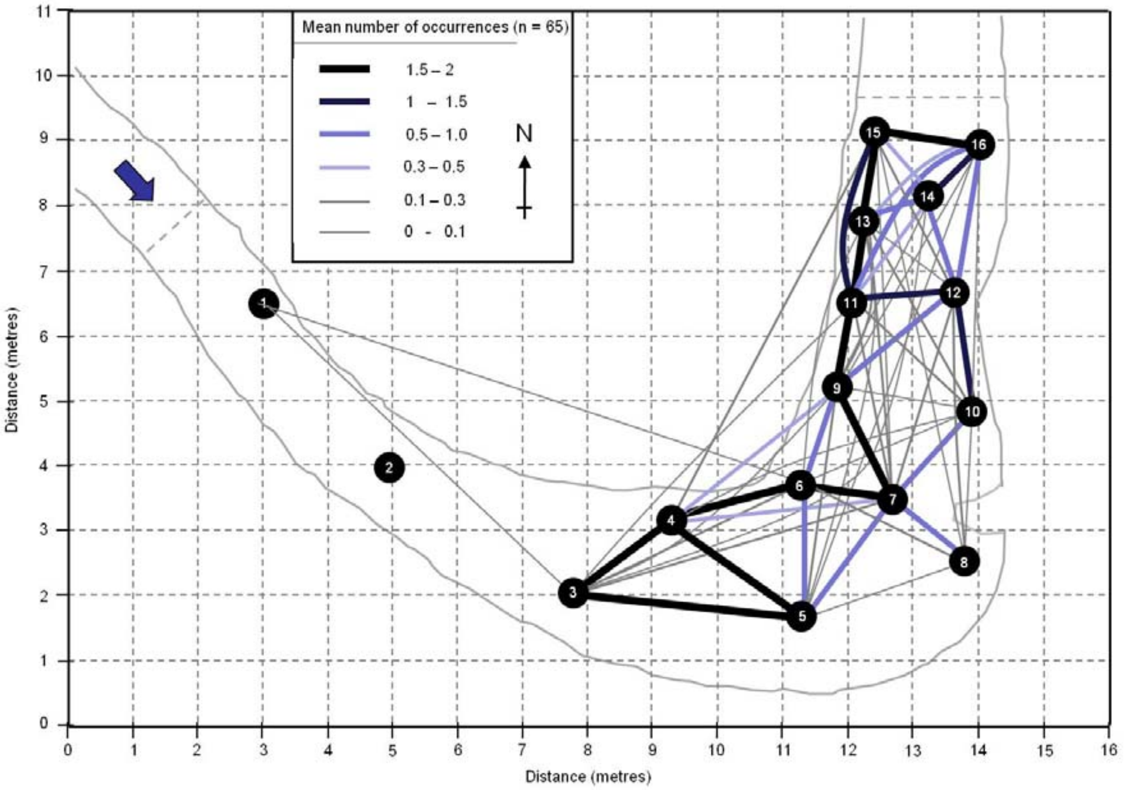
July



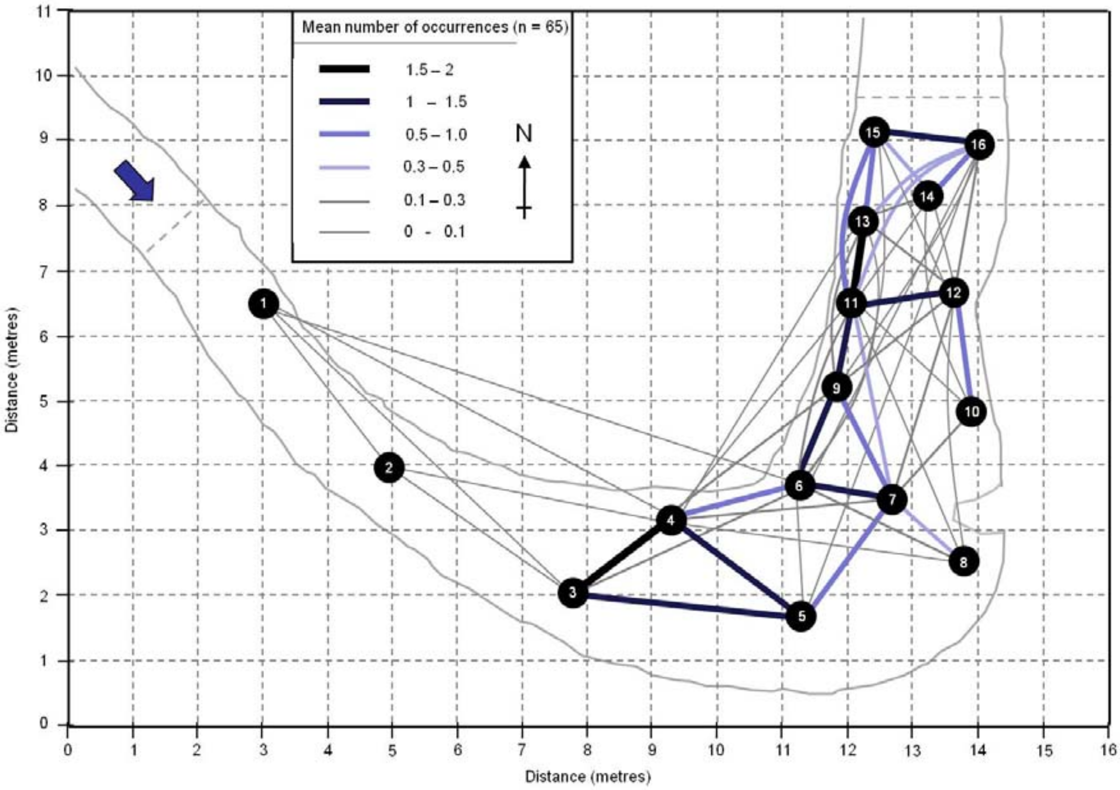
August



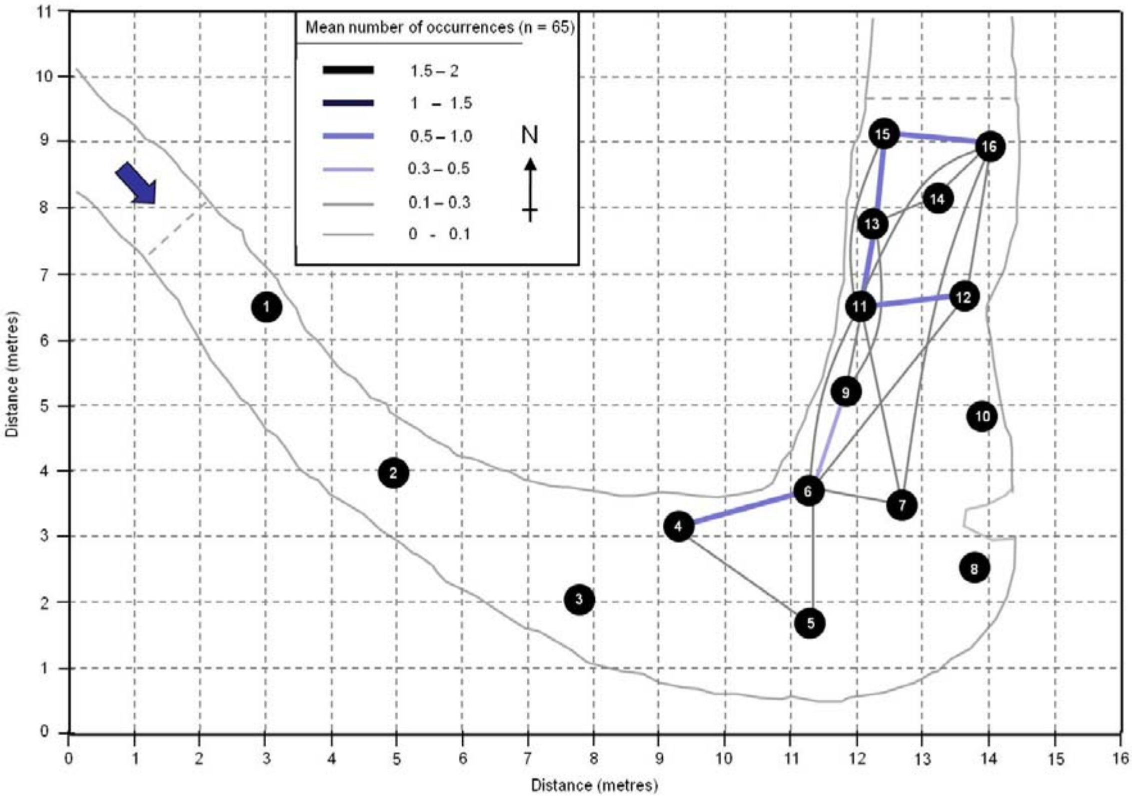
September



October



November

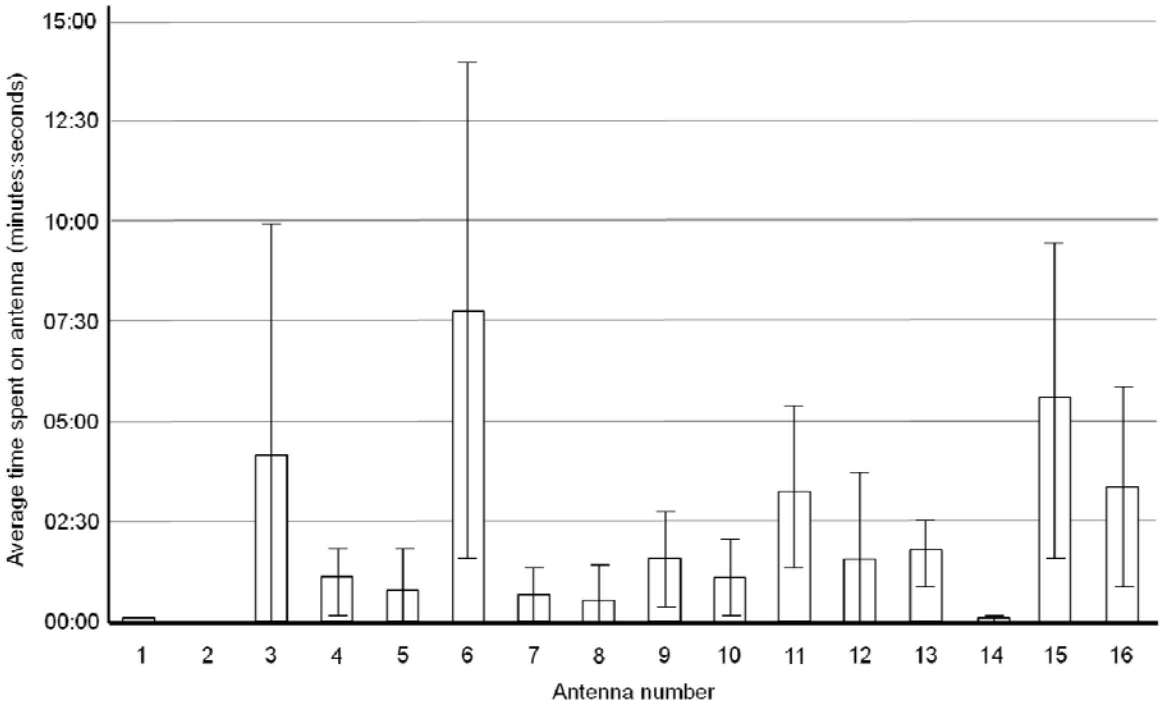


Appendix B

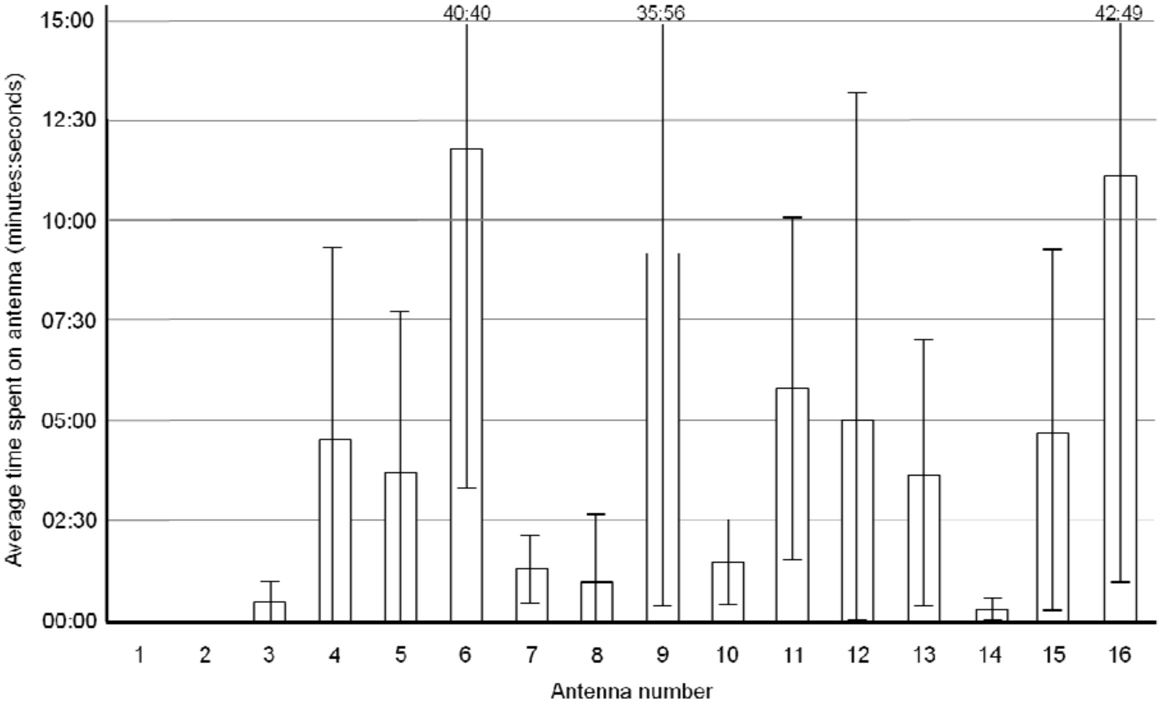
Movement over each antenna

The mean length of time (± 2 SE) tagged crayfish spent over each antenna (i.e. *in situ* activity) for each month of the tracking period.

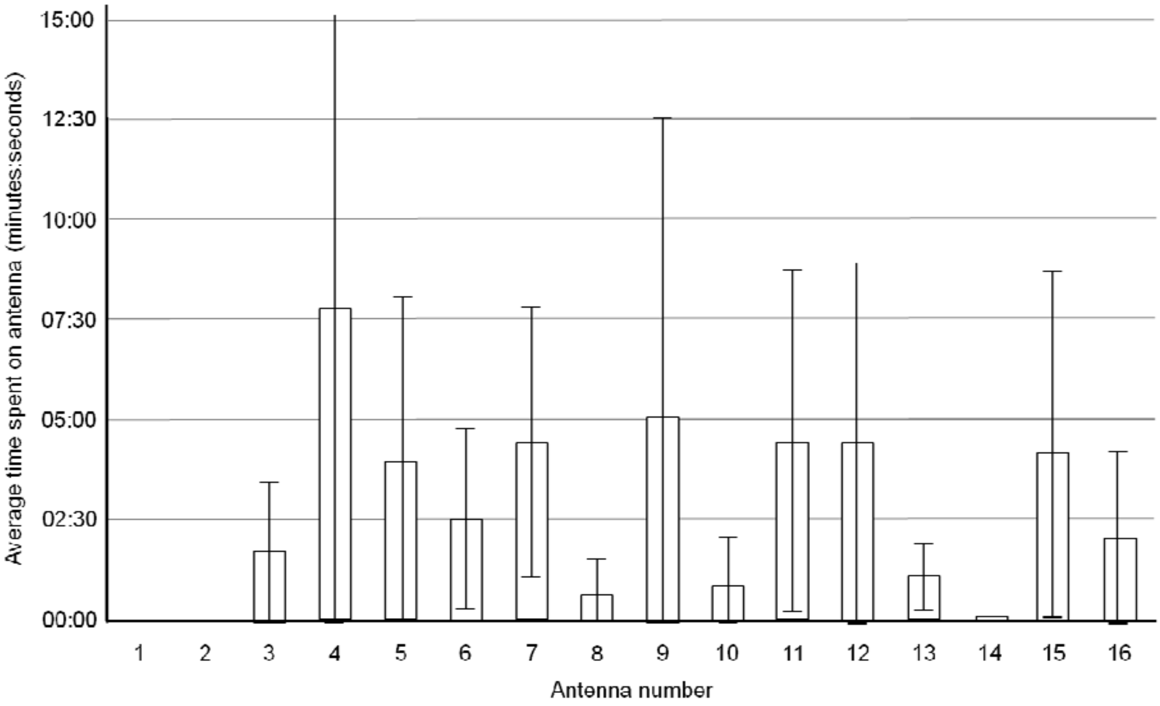
July



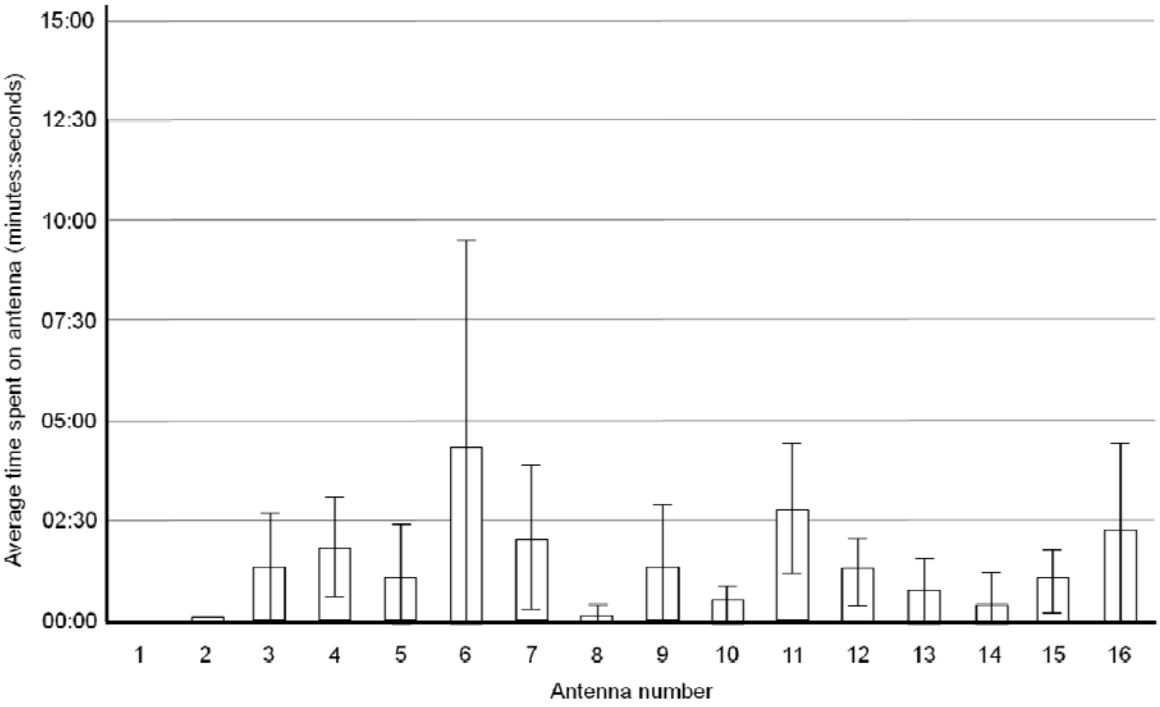
August



September



October



November