The influence of signal crayfish on fine sediment dynamics and macroinvertebrate communities in lowland rivers

by

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A Doctoral thesis submitted in partial fulfillment of the requirements
for the award of
Doctor of Philosophy of Loughborough University

(January 2017)

Abstract

The spread of non-native species is a global threat and the rate at which biological invasions occur is likely to increase in the future. This thesis examines the implications of the invasive signal crayfish, *Pacifastacus leniusculus* (Dana), for instream communities and abiotic processes within lowland rivers in England. The potential effects on lotic macroinvertebrate communities and fine sediment dynamics are investigated at a range of spatial and temporal scales, from the examination of national long-term datasets through to short-term detailed mesocosm experiments. Interrogation of macroinvertebrate community data from three English regions was undertaken to understand the temporal and spatial extent of signal crayfish effects. Invasive crayfish had significant long-term and persistent effects on resident macroinvertebrate communities regardless of the lithology or other environmental characteristics of the region. The resultant modifications to community composition had repercussions for several widely employed freshwater biomonitoring tools which employ faunal abundance in their derivation. A reach-scale field study was undertaken at two sites, one invaded by crayfish and one which did not support populations of crayfish (control), to assess the potential contribution of signal crayfish for fine sediment dynamics (ingress, fluxes and ultimately the overall implications for sediment budgets). Reach-scale field experiments examining the effect of crayfish invasion on resident macroinvertebrate communities over a 126-day period indicated that once crayfish populations are well-established their effects are persistent. However, separating the effects of crayfish from wider macroinvertebrate community dynamics and life-history characteristics of the invader and resident taxa means that attributing the effects is far from clear. The thesis presents the results of a series of novel mesocosm experiments which examined the dynamic and two-way interactions of predator-prey relationships and potential zoogeomorphological effects of signal crayfish and the freshwater shrimp, *Gammarus pulex*. Signal crayfish had a significant effect on the mass of fine sediment infiltrating into the gravel matrix associated with foraging and predatory activity; however this was strongly controlled by prey availability. Finally, through the development of conceptual models, the thesis illustrates the need for greater integration of ecological and geomorphological theories, at relevant environmental scales (temporal and spatial) to achieve truly interdisciplinary research.

Acknowledgements

This thesis is the culmination of three years' work which has only been made possible through the help and support of many people. First and foremost, my thanks go to my two supervisors. To Professor Stephen Rice, for providing this opportunity for which I have enjoyed so much and whose invaluable knowledge, experience and belief in my capabilities have made me such a well-rounded researcher. To Professor Paul Wood, who provided that initial spark all those years ago which ignited my desire to pursue a PhD, who went above and beyond on many occasions and whose continued friendship and support over the years has kept me sane during the highs and lows.

I have been very lucky to have worked with a number of individuals at the Environment Agency whose inputs have been greatly appreciated throughout. Special thanks go to Richard Chadd, whose knowledge of macroinvertebrates is unequivocal, to Jake Reeds, who provided technical and valuable on the ground support, to Mike Dunbar for statistical advice, and to Chris Extence for initiating and ultimately getting the project off the ground. I would also like to thank Joni Cook and the Department of Geography laboratory staff of Stuart Ashby, Fengjuan Xiao and Rebecca McKenzie for making the many hours spent in the research laboratories tolerable. Special thanks go to Richard Harland for his help and assistance in turning many of the requests for whacky scientific creations into a reality. Lord Glendonbrook is gratefully acknowledged for the provision of the studentship to fund this research and thanks go to all the members of the Department of Geography who have made my time at the University so enjoyable.

Given the large amount of fieldwork undertaken over the years I am also indebted to all those who helped me out in the cold, wet and at times labour intensive conditions. These are just too numerous to mention but particular thanks go to the long term stalwarts who I could rely on through thick and thin; Andy Pledger, James Smith and Matt Hill. I would also like to acknowledge those who I have shared an office with and who have made the PhD such a fun and memorable experience in addition to those above, namely; Dan Green; Jonathon Duckett, Tom Mockford and Natalie Tebbett. Finally, I would like thank to my family and friends, for their support and encouragement throughout and for putting up with my long term student status!

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Chapter 1 – Introduction

1.1 Research context and development of research theme

Invasive species are rapidly spreading across the globe (Early et al., 2016). The effects of such taxa are far reaching, associated with direct ecological implications (e.g. predation) and augmented through modifications to the physical environment that enhance their chances of success (e.g. reduced water clarity). The two-way interaction between biota and the physical environment has long been of interest (e.g. Darwin, 1881; Reudemann and Schoonmaker, 1938), however it was not until the 1980s and 1990s that the linkages and feedbacks between biotic and abiotic systems became more widely recognised and investigated. Several research frameworks, such as zoogeomorphology, ecosystem engineering, biogeomorphology and eco-hydromorphology have emerged to address these interdisciplinary topics, and acted as stimuli for further research (Wright and Jones, 2006). Such is the acknowledged importance of the interactions between abiotic and biotic systems, that quantifying and understanding the two-way feedbacks of interacting abiotic and biotic components is now recognised as a key contemporary research challenge (Reinhardt et al., 2010; Wharton et al., 2011; Harvey and Bertoldi, 2015).

It is widely acknowledged that flora and fauna modify the environment in which they live (see Statzner, 2012 for a comprehensive review of lotic fauna). However, scientists have traditionally studied the effect of a species within an ecosystem from different viewpoints dependent on their disciplinary background. Ecologists typically study the environmental changes that occur as a direct consequence of the animal itself in order to understand the effect on biota and the ecosystem. In this respect, an *ecosystem engineer* is an organism that ‘alters the physical environment, thereby modifying or creating habitats, in addition to influencing the flow of resources within the ecosystem’ (Jones et al., 1994; 1997). In contrast, geomorphologists analyse the geomorphic work of organisms in order to understand the effect they can have on the landscape, landforms and sediment budgets; a concept termed *zoogeomorphology* (Butler, 1995). *Geomorphic work* pertains to the modification of landscape features, through the erosion or formation of such features, and the amount of material transported (Wolman and Miller, 1960). Understanding the relative amount of work performed within rivers can be measured in part by comparing the quantity of fine sediment displaced and transported associated with biotic and abiotic processes.

Although ecosystem engineering and zoogeomorphology share common ground, research in the fields have run in parallel (rather than complimentary) with ecologists looking at research questions from one perspective and geomorphologists from another, with little cross integration (Hannah et al., 2004; Butler and Sawyer, 2012; Rice et al., 2010; 2012a). The different terminology used by ecologists and geomorphologists highlights the differences rather than the overlap between disciplines, and in many instances the creation of new sub-disciplines (or terms) does not develop the study field, but arguably leads to the 'reinvention of the wheel' in parallel disciplines (Hannah et al., 2004). It is increasingly apparent that many critical research questions cannot be addressed fully without the integration of both disciplinary approaches and direct collaboration (Palmer and Bernhardt, 2006; Coombes, 2016). The key challenge is to determine which organisms engineer habitats with important outcomes for ecosystem functioning and geomorphic processes, and to establish how these effects are context dependant (Crain and Bertness, 2006). Many species are classified as ecosystem engineers, but their effects are often highly localised (Moore, 2006). This challenge is pressing, in particular associated with the increasing spread of invasive taxa. These taxa represent novel engineers in that they modify ecosystems in a way that may not occur normally in the ecosystem, potentially triggering imbalances in the natural functioning of the ecosystem (Harvey et al., 2011).

Despite research at the interface of ecology and geomorphology having a long tradition, there is a clear need for work which investigates the biotic agent in geomorphological systems and the subsequent feedbacks to the ecological system in synergy. Ultimately the aim of such research is to understand how components at the ecology-geomorphology-hydrology interface interact (Urban and Daniels, 2006; Vaughan et al., 2009). Such interdisciplinary research is widely acknowledged as having the potential to yield substantial benefits (Naylor et al., 2002; Vaughan et al., 2009), but interdisciplinary research remains relatively rare (Hannah et al., 2004; 2007; Nestler et al., 2016).

This research project therefore aims to bridge the gap between the disciplines of ecology and geomorphology and considers the effect and interaction of invasive signal crayfish (*Pacifastacus leniusculus*) with the physical environment (in this instance fluvial fine sediment dynamics) and macroinvertebrate communities. This research has added impetus because signal crayfish, one of the most prevalent non-native species in Europe (Kouba et al., 2014), represent a significant threat to aquatic ecosystems and it is therefore imperative to understand the severity and nature of their invasion effects.

1.2 Aims and research objectives

The principal aim of this thesis is to examine and quantify the biotic and abiotic implications of signal crayfish in lowland rivers in the UK. The effect(s) and interaction(s) of signal crayfish with fine sediment dynamics (suspended and deposited) and in-stream invertebrate communities (through direct predation and indirect habitat modifications) will be examined via a series of *in-situ* field studies and *ex-situ* mesocosm experiments. Specifically, the thesis aims to address the following objectives:

1. To quantify the long term and spatial extent of signal crayfish effects on instream macroinvertebrate communities (Chapters 3 and 5).
2. To examine the potential effect of invasive signal crayfish on commonly employed biomonitoring tools (Chapter 3).
3. To quantify the role of signal crayfish on fine sediment dynamics within lotic ecosystems (Chapters 4 and 6).
4. To experimentally examine the predator-prey interactions of signal crayfish and macroinvertebrates in association with fine sediment loading (Chapter 6).

1.3 Thesis Structure

The structure of the research is outlined in Figure 1.1. Chapter 2 presents a detailed review of the existing literature on freshwater crayfish, the ecosystem engineering activities of crayfish and the interactions of lotic organisms, specifically fish, crayfish and macroinvertebrates, with the physical environment. The specific aims and objectives of the thesis are explored in four primary results chapters (Chapters 3,4,5 and 6). Chapter 3 will address the long term and spatial extent of signal crayfish implications for macroinvertebrate communities and biomonitoring tools across

England. The analysis is based upon long term data obtained from the Environment Agency of England and utilizes a Before – After – Control - Invaded approach. Alterations to macroinvertebrate community composition and individual taxon abundances associated with crayfish invasion are examined in addition to the effects on a selection of commonly employed freshwater biomonitoring tools. The work from this chapter has resulted in two publications, in *Science of the Total Environment* and *Ecological Indicators* (Mathers et al., 2016a,b; Appendix 5 and 6). Chapter 4 addresses the interaction of crayfish with fine sediment dynamics through field surveys of suspended sediment concentrations, fine sediment deposition rates, hydrological conditions and crayfish population dynamics within a control and invaded river. Chapter 5 considers the interactive and potential additive effects of crayfish presence and fine sediment loading for macroinvertebrate communities at the reach scale. The effects of manipulated interstitial sediment concentrations, and crayfish presence / absence for resident macroinvertebrate communities are examined through *in-situ* experiments. Chapter 6 addresses the interaction between predator-prey relationships and the physical environment, in this instance fine sediment loading. The chapter examines the zoogeomorphic activity of crayfish on fine sediment infiltration rates and considers the two-way feedback process between predator-prey relationships (freshwater shrimp and signal crayfish) and geomorphic activity, utilizing an *ex-situ* mesocosm approach. Chapter 7 provides a summary and synthesis of the key findings, considers wider themes arising throughout the thesis and concludes with suggestions for future research.

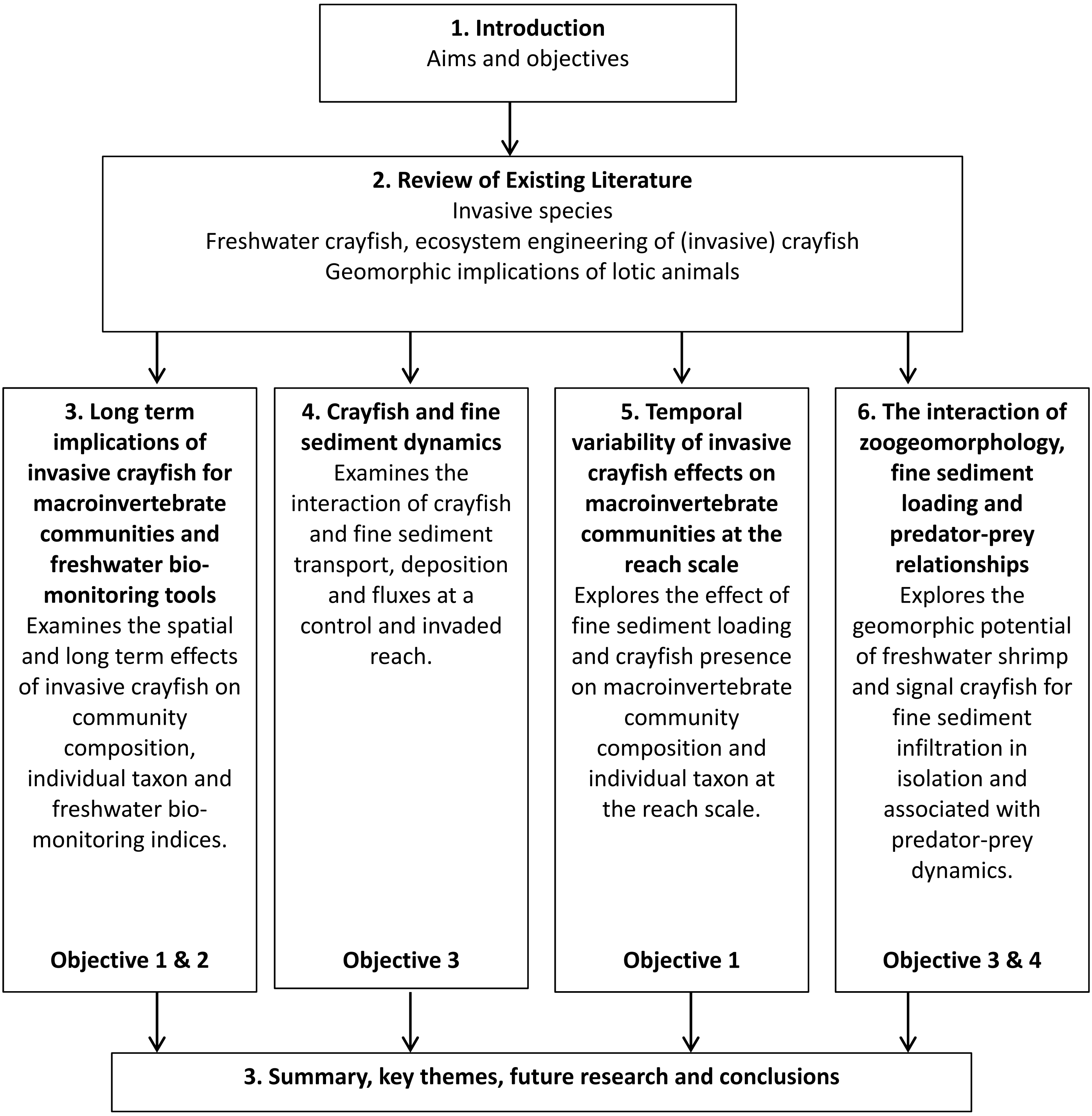

Figure 1.1 Thesis structure. Objectives addressed relate to thesis objectives listed in Chapter 1.1.

Chapter 2 - Invasive crayfish as ecosystem engineers and zoogeomorphic agents

2.1 Invasive Species

2.1.1 Background

The spread of non-native taxa (a species introduced outside of its natural range) represent one of the most significant threats to global biodiversity, economic development and human health, and is an imperative challenge for the management and conservation of natural resources (Sala et al., 2000; Simberloff et al., 2013; Early et al., 2016). Indeed, the consequences are so profound that some biologists have suggested that communities are becoming homogenised by the global redistribution of species (Corlett, 2015). The establishment of an invasive species (a non-native taxa which has the ability to cause damage to the environment or economy) within an ecosystem can severely disrupt the organisation of native communities through the direct displacement of native species and predation, but also via indirect changes in local habitat conditions or through the decoupling of food chains and webs (Nyström et al., 1996; Strayer, 2010; Gutierrez et al, 2014). Direct ecological consequences of invasive taxa can vary as defined under the trophic position hypothesis (Thomsen et al., 2014), in which distinct changes in ecosystems are triggered but differ depending on their position in the food web. If invasive species are introduced at the top of the food web, ‘top down’ control of lower trophic levels is achieved, whilst alterations to primary producers’ dictates ‘bottom up’ control of trophic levels (Heath et al., 2014). Ecological impacts can be further augmented through habitat changes mediated by ecosystem engineering (Gallardo et al., 2016). Consequently, the influence of invasive taxa are often far reaching, with impacts ranging from the replacement of individual species through to the modification of ecosystem processes (Riccardi, 2007; Jackson et al., 2014).

The ability of an invading species to establish populations within a community is dependent on its ability to utilize resources more efficiently or out-compete resident species for available resources (Dodd et al., 2014). Consequently, the influence of invasive species is often far reaching, with changes that range from the replacement of individual species through to the modification of ecosystem processes (Riccardi, 2007; Jackson et al., 2014). Species invasions occur in a range of ecosystems across the Earth, however freshwater ecosystems are some of the most vulnerable in the world (Martinuzzi et al., 2014). Declines in biodiversity in aquatic ecosystems are substantially greater than their terrestrial counterparts (Dudgeon et al., 2006) and aquatic animals represent some of the most destructive agents associated with this decline (GB INNS strategy, 2015).

Invasive species are a significant and growing problem globally; however, the implications for UK biodiversity are only just beginning to be realised. Each year, 10-12 new non-native species become established within the UK and of these, 10-15% are associated with significant deleterious effects (GB INNS strategy, 2015). Within the UK, it has been estimated that invasive species cost the economy up to £1.7 billion per year in terms of physical damage and management costs (Roy et al., 2012), with signal crayfish costs thought to be in excess of £2.6 million per annum (Williams et al., 2010). Predicting the ecological implications of newly emerging invaders is challenging (Dick et al., 2013) but is vital for the long term management and conservation of freshwater ecosystems. In order to effectively tackle the threat of invasive species systematically, detailed information regarding the potential implications of invaders is required to help identify priority mitigation strategies.

2.1.2 Crayfish as invasive species

Crayfish represent some of the most successful and widely distributed aquatic invasive species worldwide, following either intentional introductions for aquaculture or accidental translocation (Holdich et al., 2014; Hudina et al., 2015). There are over 650 species of freshwater crayfish, 28 of which have been translocated outside of their native range and 7 of which are identified as having invasive potential (Crandall and Buhay, 2008; Gheradi, 2010). Within Europe, at least 10 non-native crayfish are known to have invaded waterways (Kouba et al., 2015). These introductions have mainly been associated with aquaculture or the aquaria trade and typically result from the escape or deliberate release of individuals into aquatic ecosystems (Chucholl, 2013).

Genetic evolution within non-native crayfish populations can contribute to their success and the severity of harmful impacts upon the receiving ecosystem. Invasive traits of enhanced growth rates and increased survival have been documented as evolving in invasive populations of the rusty crayfish (*Orconectes rusticus*; Pintor and

Sih, 2009; Sargent and Lodge, 2014). In addition, despite many ‘introduced’ crayfish replacing a native species and thus occupying a similar ecological niche, invader effects are often still strong if the invaders reach greater densities and sizes than that of the native species (Strayer, 2010, Gheradi et al. 2011), especially if this is associated with reduced predation pressure or if invaders are able to exploit a wider range of resources

2.2 Freshwater Crayfish

2.2.1 Background

Crayfish are one of the largest freshwater invertebrates, typically dominating the biomass of benthic organisms where they occur (Momot, 1995; Sousa et al., 2013). They are widely considered to be keystone species in both lotic and lentic habitats due to the size of individuals, population densities and functional role in the ecosystem (Lodge and Hill, 1994; Stenroth and Nyström, 2003; Holdich et al., 2014). Consequently, their introduction or ‘eradication’ can have significant biological effects on the wider ecosystem. Recently, increasing attention has been paid to the role of crayfish as ‘ecosystem engineers’, capable of modifying the mobilisation of fine sediments and other elements of their habitats (Rice et al., 2016; Albertson and Daniels, 2016a; Faller et al., 2016).

Diversity is greatest in North America and Australia (Holdich, 2002; Crandall and Buhay, 2008), whilst other parts of the world are species poor, including Europe, where no more than ten recognised native species have been recorded (Petrusek, 2015). Britain has only one native crayfish species, the white-clawed crayfish, *Austropotamobius pallipes* (Lerebollet)***.*** This species has recently experienced substantial population declines associated with the introduction of the non-indigenous signal crayfish, *Pacifastacus leniusculus* (Dana)*,* and is now regarded as endangered (Füreder et al., 2016). Endemic to North America, the signal crayfish was introduced for the purpose of aquaculture to over 20 countries in Europe in 1959 and is now considered to be the most prevalent non-indigenous crayfish species in Europe (Kouba et al., 2014; Holdich et al., 2014).

2.2.2 Crayfish morphology

Crayfish are representatives of the decapod crustaceans (order Decapoda) and are distinguished by ten prominent walking legs (five pairs of walking legs, periopods, including the large claw on the first pair; Gledhill et al., 1993). The crayfish body is divided into two main parts; cephalothorax and the abdomen (Figure 2.1). The cephalothorax is formed of 13 body segments. The upper and lateral sides of the cephalothorax are covered by a compact shield termed the carapace. The carapace between the eyes runs into a frontal spine called the rostrum. The shape of the rostrum is often a key distinguishing factor between crayfish species. The mouthparts consist of one pair of mandibles and two pairs of maxillae which hold and divide food before ingesting. On one side of the mandibles is a sharp incisor edge whilst the other consists of a molar ridge which helps to crush and tear food. The maxillae are flat appendages which are covered in setae and serve the purpose of holding food for the mandibles (Ďuriŝ et al., 2015a).

In contrast to the cephalothorax, the abdomen is distinctly segmented and is approximately the same length and width as the cephalothorax. The first five true abdominal segments (excluding the telson) possess small appendages termed pleopods (swimmerets). These appendages help to transfer freshwater to the bronchial chambers when at rest or in burrows, but are predominantly used by females to attach egg clusters. When in motion these appendages provide oxygenated water to the eggs and later, juvenile crayfish (Ďuriŝ et al., 2015a).

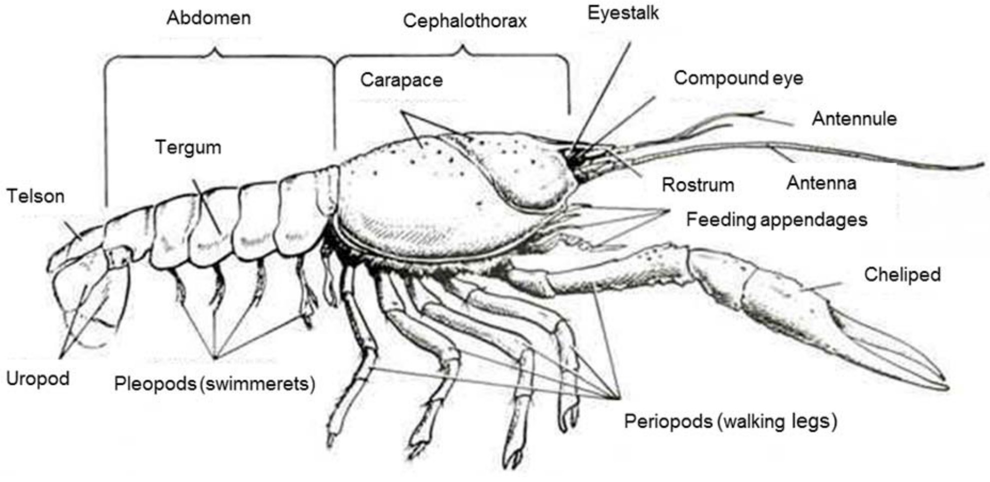

Figure 2.1 Main body parts of freshwater crayfish (Adapted from www.biologyjunction.com).

2.2.3 Life history

Pacifastacus leniusculus

The successful spread of signal crayfish, and the detrimental impacts to aquatic ecosystems associated with their introduction, can be related to their life history strategies. *P. leniusculus* display r-selected characteristics reaching maturity rapidly (by year two, but can be as early as year 1), exhibiting high fecundity and typically reach larger sizes than native crayfish (Kouba et al., 2015). Typically, *P. leniusculus* attain a maximum carapace length of 50-70mm, but individuals up to 95mm have been recorded in British waters (Holdich, 2002; Lewis, 2002). Signal crayfish can live for up to 16 years, although the average maximum age for most populations in the wild ranges from 4-8 years (Belchier et al., 1998; Lewis, 2002). Survivorship through to the age of 2 is estimated to be 10-52% dependant on abiotic and biotic factors (Flint, 1975).

Spawning of the majority of populations occurs during October with the incubation period for eggs primarily being controlled by water temperature. Incubation periods vary from 166 to 280 days (Lewis, 2002) with egg hatching occurring from late March through to the end of July depending on water temperatures (Abrahamsson and Goldman, 1970; McGriff, 1983). The average egg count ranges from 100 eggs to 200 eggs but some females can carry more than 500 eggs (Abrahamsson and Goldman, 1970; McGriff, 1983; Kouba et al., 2015). In the first year, juveniles can undergo as many as 11 moults, which decreases to one moult per year by the fourth year (Lewis, 2002).

Austropotamobius pallipes

In contrast, *A. pallipes* demonstrate K-selected characteristics with slower maturation, lower fecundity and smaller sizes than that of *P. leniusculus.* In Europe, *A. pallipes,* is the second smallest and slowest growing European crayfish species (Kouba et al., 2015). Within the UK, *A. pallipes* have been recorded to reach maximum carapace lengths of only 60mm (Laurent, 1988) with a maximum age of thirteen years being recorded (Pratten, 1980). Survivorship during winter months is low, with mortality rates capable of reducing population sizes between 40-60% (Ibbotson and Furse, 1995). Maturity is typically reached in the third year, but can be as late as the fifth or sixth year (Brewis and Bowler, 1985). The average pleopod egg count is 64 (Carral et al., 1994) with population expansion occurring slowly (Peay, 2002). Growth is seasonal, regulated by water temperatures and the moulting process has been reported to be absent in first year juveniles when temperatures are below 10^{o}C. No significant differences in growth rates have been detected when water temperatures are between 15-20^{o}C with the optimum temperature for growth reported to be 21.4^{o}C (Firkins and Holdich, 1993). *A. pallipes* is highly sensitive to the crayfish plague (*Aphanomyces astaci*) which is commonly transmitted by the largely resistant *P. leniusculus.* The effect of the crayfish plague in combination with the competitive ability of the signal crayfish is largely thought to be responsible for the decline of the native *A. pallipes* within the UK (Kozubiková et al, 2010).

2.2.4 Movement and habitat preference

Signal crayfish occupy a range of habitats including small streams, large lakes and even brackish waters along the coast, and demonstrate tolerance of extreme temperatures, large ranges of pH and pollution (Lewis, 2002; Kouba et al., 2015). Lotic signal crayfish populations are spatially size-sorted. Juvenile crayfish are often restricted to shallow riffles that contain abundant shelters, whilst adult crayfish are typically found in deeper pools (Rabeni, 1985; Guan and Wiles, 1997; Clark et al., 2013). These size and depth preferences can have strong effects on lower trophic levels, with grazing by large crayfish documented to restrict the distribution of algae to shallow waters (Creed, 1994). Heterogeneous habitats, which contain boulders and cobbles, provide shelter for crayfish, reducing predation of juveniles and minimising the risk of cannibalism during moulting amongst adult crayfish (Nyström, 2002; Clark et al., 2013). In contrast, areas with low habitat complexity increase the chance of competition for food and shelter, which can result in reduced recruitment of juvenile crayfish (Olsson and Nyström, 2009).

Signal crayfish are large invertebrates that are capable of moving considerable distances both instream (>500m) and overland and have greater dispersal rates than *A. pallipes* (Claussen et al., 2000; Bubb et al., 2004; 2006). Signal crayfish typically remain in the same location for days to weeks, followed by sporadic movement to a new location associated with suitable refuge (Bubb et al., 2004; Johnson et al., 2014). Instream movements can be triggered or impeded by environmental factors, such as temperature or water levels, with crayfish activity increasing with rising temperatures (Gheradi et al., 1998; Johnson et al., 2014). Water depth has been suggested to be the over-riding hydraulic habitat variable for other crayfish species, with large northern clearwater crayfish, *Orconectes propinquus,* avoiding shallow habitats regardless of the flow (Creed, 1994).

Few studies have considered the role of abiotic disturbance on the establishment, spread and impact of invasive crayfish despite their prevalence in a range of environments that experience both natural and anthropogenic disturbances (Larson et al., 2009). The environmental context is likely to play an important role in determining the implications of signal crayfish on aquatic ecosystem structure and functioning (Cardinale et al., 2000). Densities of crayfish have been documented to decline following significant intense wet season spates, predominantly through the loss of juveniles which are more prone to displacement during periods of high flow (Robinson, 2000; Light, 2003). In contrast, the response of lotic crayfish to stream bed drying is variable but still remains poorly understood. Crayfish can survive periods of drying through burrowing into the hyporheic zone or migration to persistent pools (Jones and Bergey, 2007; Distefano et al., 2009; Magoulick, 2014). High densities of crayfish have been reported in the hyporheic zone during streambed drying indicating the potential for substantial alteration to the structure of substrate (Distefano et al., 2009). The ability of crayfish to survive streambed drying is also enhanced through their ability to walk overland in order to find remaining surface waterbodies (Claussen et al., 2000).

2.2.5 Competition

A. pallipes and *P. leniusculus* are ecological homologues and therefore are competitors for the same resources (Holdich, 1988). The advantageous life history strategy of signal crayfish means that they typically dominate where the species co-occur (Dunn et al., 2009). Consequently, despite *A pallipes* and *P. leniusculus* occupying similar ecological niches, signal crayfish can establish large populations and it is likely that at these high densities, their feeding behaviour may have significant negative impacts on aquatic ecosystems and their associated biota (Bubb et al., 2004; Crawford et al., 2006).

P. leniusculus is a highly aggressive crayfish and through competition for resources and shelter can have a detrimental effect on other species of crayfish as well as some fish species (Rubin and Svensson, 1993; Guan and Wiles, 1997). Intra-specific aggression of signal crayfish in core populations of high densities has been documented as being an important component in invasion dynamics, often leading to successful range expansions (Hudina et al., 2015). To minimize aggressive interactions between individuals, crayfish interact based upon a hierarchical system with the dominant individual gaining control of contested resources (Goessmann et al., 2000). Adult crayfish have been documented to outcompete juvenile fish for shelters / refugia, leaving them susceptible to entrainment and direct predation from crayfish or piscivorous fish (Griffiths et al., 2004; Degerman et al., 2007). In addition, aggressive behaviour has been documented as causing damage to fish fins, and in some cases mortality (Bubb et al., 2009). Evidence is also growing that the presence of signal crayfish can lead to reduced recruitment of salmonid fish in the UK (Peay et al., 2009; Findlay et al., 2015).

Juvenile crayfish are vulnerable to aquatic predators due to their small size, and the frequency of moulting which can leave unprotected fleshy parts of the body exposed for periods of time (Ďuriŝ et al., 2015b). Adult crayfish are less susceptible but are still at risk from the largest individuals. Where signal crayfish are invasive, alterations to their behaviour may occur in response to non-predatory fish, with reductions in foraging behaviour and more time spent in refuges during the night (Nyström, 2005). However, these observations were based on short term responses and therefore longer exposure times may lead to behavioural adaptations where signal crayfish live in environments with consumers that do not pose a direct threat.

2.2.6 Feeding ecology

Signal crayfish are considered to be nocturnal feeders, with maximum foraging typically occurring during 17:00 and 01:00 h in all seasons (Guan and Wiles, 1998). However, one study found that juvenile signal crayfish foraged throughout the 24-hour period with only a slight preference for night (Rundquist and Goldamn, 1983). Similarly, Lozan (2000) demonstrated that the mean level of activity per 12-hour period was 187 minutes during the night and 98 minutes during the day, suggesting that signal crayfish are not exclusively nocturnal and in the absence of natural predators may become active throughout the day. Such flexibility enables populations of non-native crayfish to enhance their foraging behaviour compared to other taxa, which may limit native populations from effectively utilizing remaining resources even when conditions are generally less favourable (Ďuriŝ et al., 2015b).

Crayfish display opportunistic polytrophic feeding habits consuming algae, macrophytes, detritus, zoobenthos, fish and other crayfish (Momot et al., 1978). There have been suggestions that the composition of diet and feeding behaviour varies with age and season (Goddard, 1988; Guan and Wiles, 1998), although there is increasing evidence that the importance of detritus and plant materials has been overemphasised in terms of nutritional requirements (Bondar et al., 2006). Juvenile crayfish are capable of filter feeding and scraping algae through the use of the first macilliped and maxillae, a behaviour which reduces the risk of predation as foraging is not required (Budd, et al., 1978). Adaptions as they grow enable crayfish to consume robust macrophytes and process detritus (Momot et al., 1978; Parkyn et al., 1997). Typically, adult crayfish diets consist of a high proportion of detritus and plants, whilst juveniles feed predominantly on invertebrates (Guan and Wiles, 1998; Rosewarne et al., 2013). This may be due to the ability of the more active juveniles to catch mobile invertebrate prey (Abrahamsson, 1966).

However, the ontogenetic shifts described in the literature may not be ubiquitous for all crayfish species. Studies of juvenile *P. leniusculus* in their native environment document conditioned woody debris as the primary food base (Bondar et al., 2005), in contrast to the aquatic invertebrates reported by other authors (Usio et al., 2006). The feeding behaviour of signal crayfish may therefore differ dependent on their habitat; lentic or lotic and the geographical location. One potential reason for the differences in foraging behaviour is the risk of predation. Within the UK, there are fewer natural predators than typically found in their native habitats and consequently feeding behaviour is most likely to be associated with nutritional requirements through selective consumption and foraging efficiency. Context specific research on the ecological consequences of invasive crayfish for ecosystems is therefore imperative.

2.2.7 Ecological effects of (invasive) crayfish

Crayfish are considered to be keystone species associated with their flexible feeding habits, and therefore have the potential to have deleterious effects on native flora and fauna and ultimately ecosystem functioning where they invade (Nyström et al., 1996; Ďuriš et al., 2015). Keystone species represent organisms which are crucial in maintaining organisation and diversity of a community and which have exceptional importance relative to the rest of the community (Mills et al., 1993). Crayfish can act as ecosystem engineers through the alteration of detrital processing rates (Usio, 2000; Creed and Reed, 2004; Carvalho et al., 2016) and by changing the dominant algal cover on substrate (Creed, 1994). Studies documenting the effect of signal crayfish in stream ecosystems have reported substantial negative effects on the biomass and richness of aquatic macrophytes (Creed, 1994; Lodge et al. 1994; Nyström et al., 2001), and macroinvertebrates (Crawford et al., 2006; Stenroth and Nyström, 2003).

There is a limited body of evidence to suggest that invasive crayfish have a negative impact on fish recruitment through the predation of eggs with larger individuals posing the greatest threat (Findlay et al., 2015). Invading signal crayfish have been found to negatively affect the abundance of brown trout in English streams (Guan and Wiles, 1997; Peay et al., 2010), Arctic Charr in Sweden (Setzer et al., 2011) and North American field studies and lab experiments have demonstrated that *Orconecte*s sp. are effective predators of lake trout eggs (Fitzsimons et al., 2002; Jonas et al., 2005). In contrast, Degerman et al. (2007) reported no negative effects on fish abundances associated with signal crayfish in Swedish streams.

Invasive crayfish may also have variable effects on fish dependent on the life stage, with Wood et al., (2017) documenting reduced growth rates of chub up to 2 years, whilst growth rates of older chub (5 to 6 years +) were typically higher in the presence of crayfish. Invasive crayfish have been associated with reduced growth of small benthic fishes through interspecific competition and predation (Guan and Wiles, 1997; Light, 2005) whilst other studies have documented no effect for juvenile fish survival (Stenroth and Nyström, 2003). However, when abundances are high invasive crayfish can represent novel resources for native fish species such as barbel, which results in modifications to food web structure (Ellis et al., 2011; Baŝić et al., 2015).

The species composition of macroinvertebrate populations has been reported to shift towards more mobile invertebrates adapted to life in strong currents at the expense of slower moving invertebrates such as molluscs and cased Trichoptera following invasions (Parkyn et al., 1997; Keller and Ruman, 1998). Studies have documented that the presence of crayfish can significantly alter the behaviour of gastropods and amphipods (Crowl and Covich, 1990; Alexander and Covich, 1991a; Haddaway et al., 2014). The removal of macrophyte and algal cover may also indirectly affect invertebrate populations through the loss of food sources and shelter (Lodge et al., 1994; Nyström et al., 1996). Selective consumption of trophic resources may lead to skewed communities, thereby reducing the effectiveness of commonly employed invertebrate biomonitoring indices. For a more detailed overview of invasive crayfish interactions with benthic macroinvertebrates see Chapter 3.1.

Despite the widely acknowledged threat that invasive crayfish pose, much of the research to date has been focused on lentic ecosystems and with a strong geographical bias towards North America. Moreover, there has been an emphasis on small scale experiments or short term sampling, such that the impact on stream communities has been poorly quantified in many regions (Stenroth and Nyström, 20003; Pysek et al., 2008; Lodge et al., 2012). There is a real need for enhanced understanding of the effects that invasive taxa pose for the receiving ecosystem in order to fully ascertain the threat to biodiversity and ecosystem functioning (Jeschke et al., 2014; Havel et al., 2015).

The ecological effects of signal crayfish for macroinvertebrates, macrophytes and periphyton are summarised in Table 2.1 and other notable crayfish species in Table 2.2. Detailed descriptions of the individual studies including study type, geographical location, ecosystem and crayfish species can be found in Appendix 1.

Table 2.1 Ecosystem effects of *Pacifastacus leniusculus* on detrital processing, algae, macrophytes, macroinvertebrates and fish. Studies include *in-situ* and *ex-situ* experiments, field surveys and gut analysis from both lentic and lotic systems globally.

Study finding	Author
Detrital processing	
Reductions in organic content of sediment.	Nyström et al., 1996
Identification of ontogenetic diet- adults consumed more detritus and the occurrence of Cladophora was increased in the winter.	Guan & Wiles, 1998
Common in diet.	Stenroth & Nyström, 2003
No ontogenetic diet documented - both juveniles and adults found to have large proportions of detrital matter.	Bondar et al., 2005
Signal crayfish altered decomposition rates via leaf litter breakdown directly along with red swamp crayfish.	Jackson et al., 2014
Algae	
Periphyton biomass was not related to the presence of crayfish.	Nyström et al., 1996
Periphyton biomass increased - most likely as result of reduced grazing from gastropods.	Nyström et al., 2001
Epiphytic algal biomass was not related to crayfish density whilst biomass of epilithic algae was enhanced by the presence of crayfish.	Stenroth & Nyström, 2003
Physical bioturbation of sediments and benthic algae.	Usio et al., 2006
No clear interaction with periphyton.	Ruokonen et al., 2014
Macrophytes	
Macrophyte biomass, cover and species richness declined with increasing crayfish density.	Nyström et al., 1996
Preference of submerged macrophytes to floating-leaved and emergent species. Stronger effects on seedlings than established plants. Damage to macrophytes via consumption and fragmentation.	Nyström & Strand, 1996
Macrophyte coverage reduced through consumption and fragmentation.	Nyström et al., 2001
Mechanical destruction of macrophytes.	Usio et al., 2006

Table 2.1 continued.

Study finding	**Author**
Macroinvertebrates	
Total biomass of invertebrates and herbivores / detritivores declined. Relative biomass of Gastropoda and Odonata declined. Community dominated by Chironomidae and *Sialis* sp.	Nyström et al., 1996
Size selection of gastropods - preference for smaller snails with thinner shells and lower handling times.	Nystom & Perez, 1998
Ephemeroptera were increasingly consumed with size whilst Coleoptera were consumed by juveniles. Seasonal diet was also evident with adults consuming more Chironomidae in spring whilst more Trichoptera were consumed in the summer. Coleoptera consumed more in spring by juveniles.	Guan & Wiles, 1998
Reductions in the biomass of gastropods. Weak direct effects on predatory invertebrates.	Nyström et al., 2001
Declines in slow-moving taxa such as Hirudinea, Odonata, Bivalvia, and Trichoptera observed whereas mobile prey such as Chironomidae and Plecoptera were less affected. Total invertebrate biomass and taxon richness reduced.	Stenroth & Nyström, 2003
Reduction in invertebrate abundance by 60%. Reduced species numbers of Plecoptera, Chironomidae, Diptera and Hirudinea and reduced densities of Plecoptera, Hirudinea, Tricladida and Hydracarina. Community diversity and richness reduced. No evidence of reduced invertebrate biomass or invertebrate size.	Crawford et al., 2006
Emigration of invertebrates due to removal of macrophytes and direct predation on invertebrates. Invertebrate taxa richness halved in the presence of crayfish.	Usio et al., 2006
Crayfish presence significantly reduced invertebrate shredder densities. Total invertebrate density was not affected but species-specific effects were felt for Limnephilidae.	Lagrue et al., 2014
No effect on macroinvertebrate density. Taxa richness was significantly reduced and community composition altered at stony sites. Gastropods were the main species affected with lower overall density and taxon richness and assemblages were dominated by hard shelled spherical species. Indicators of crayfish absence include the presence of predatory taxa such as Hirudinea and Odonata (less prey availability of Gastropoda reduces their abundance in the presence of crayfish). Elmidae may be excluded in the presence of crayfish. Lower Trichopteran abundance. No effect at vegetated sites- less populated or less ability to predate?	Ruokonen et al., 2014
Signal crayfish significantly altered the structure of sub-littoral macroinvertebrate communities with reduced benthic densities and taxon richness. Densities of Trichoptera and Ephemeroptera were lower in addition to lower density and species richness of Chironomidae.	Ercoli et al., 2015a

Table 2.1 continued.

Study finding	Author
Signal crayfish significantly altered the structure of sub-littoral macroinvertebrate communities with reduced benthic densities and taxon richness. Densities of Trichoptera and Ephemeroptera were lower in addition to lower density and species richness of Chironomidae.	Ercoli et al., 2015a
Abundance of macroinvertebrates did not vary but species richness was significantly reduced. Mollusca were particularly affected and overall community composition differed.	Ercoli et al., 2015b
Crayfish had temporally consistent effects on lake macroinvertebrate communities. Gastropoda and Coleoptera were particularly affected.	Ruokonen et al., 2016
Fish	
Cannibalism and predation of fish mainly occurred in summer and increased with size	Guan & Wiles, 1998
General feeding behaviour	
Overall top five main diets for all sizes of crayfish were the same in all four seasons; vascular detritus, filamentous green algae, *Cladophora*, crayfish fragments, Chironomidae, and Ephemeroptera. Nocturnal feeder.	Guan & Wiles, 1998
Feeding plasticity of juveniles based on presence of predators (fish and adult con-specifics).	Bondar et al., 2006
Effects of larger crayfish were more pronounced on macrophytes, isopods, Trichoptera and predatory invertebrates. Magnitude and rate of impacts intensified with increasing crayfish size.	Usio et al., 2006

Table 2.2 Ecosystem effects of wider crayfish species (excluding *Pacifastacus leniusculus)* on detrital processing, algae, macrophytes, macroinvertebrates and fish. Studies include *in-situ* and *ex-situ* experiments, field surveys and gut analysis from both lentic and lotic systems globally.

Study finding	**Author**
Detrital processing	
No leaf material left in high density channels of crayfish presence, 92% lost in medium density and 77% lost in control channels.	Parkyn et al., 1997
Leaf processing rates enhanced.	Usio, 2000
Leaf processing rates not affected	Usio & Townsend, 2004
Leaf breakdown significantly faster.	Creed & Reed, 2004
Consumer exclusion increased sediment organic matter content 2.3x.	Ludlam & Magoulick, 2009
Adults showed greater reliance on detritus.	Rosewarne et al., 2013
Primary productivity increased with invasive crayfish.	James et al., 2015
Decomposition rates were increased fourfold in presence of invasive crayfish.	Jackson et al., 2016a
Algae	
Crayfish had a positive indirect effect on periphyton biomasss (through reduction in grazers).	Weber & Lodge, 1990
Periphyton chlorophyll *a* total amount and quality per unit surface area increased in crayfish enclosures, but due to reductions in macrophytes the total amount declined.	Lodge et al., 1994
Periphyton chlorophyll increased by 48-70%. Periphyton productivity increased by 4-7 times most likely due to crayfish associated reductions in grazer densities.	Charlebois & Lamberti, 1996
50% reduction in phytoplankton	Keller & Ruman, 1998
Reduction in chlorophyll *a* concentrations by large crayfish	Flinders & Magoulick, 2007
Consumer exclusion increased algal chlorophyll *a* 1.5x	Ludlam & Magoulick, 2009
Reduction of periphyton by 50-62%	Dorn, 2013
No consistent effect on algal biomass.	Twardochleb et al., 2013
Macrophytes	
Reduction in macrophyte biomass.	Feminella & Resh, 1989
Crayfish reduced biomass and survival of macrophyte species.	Van der Wal., 2013
Reduction in aquatic macrophytes with invasive crayfish.	Twardochleb et al., 2013
Plant biomass was reduced in presence of crayfish.	James et al., 2015

Table 2.2 continued.

Study finding	Author
Macroinverterbates	
Growth rates of *Physella virgata* enhanced and reproduction delayed in the presence of a chemical cue released by crayfish foraging.	Crowl & Covich, 1990
Crayfish predation reduced gastropod abundances.	Weber & Lodge, 1990
Gastropods crawled to the waterline for several hours to avoid predation before returning to the water. All size classes exhibited avoidance behaviour for *Physella virgata*, whilst only small *Physella trivolvi* exhibited avoidance behaviour.	Alexander & Covich, 1991b
Taxa richness and invertebrate biomass reduced. Reduced abundances of gastropods and cased Trichoptera larvae in the presence of crayfish either through predation or dislodgement as a result of foraging activity. Oligochaeta, Chironomidae, other Diptera, Elmidae and Leptophlebiidae densities were unaffected by the presence of crayfish.	Parkyn et al., 1997
Reductions in native gastropod abundances and richness.	Lodge et al., 1998
Invertebrate densities reduced by 55-72% relative to exclosures	Keller & Ruman, 1998
Reductions in invertebrate densities.	Usio, 2000
Ephemeroptera positively correlated to crayfish most likely due to reductions in predatory taxa or by increase in food resources through leaf decomposition.	Usio & Townsend, 2004
Invertebrate biomass reduced in the presence of crayfish	Flinders & Magoulick, 2007
Reduction of Chironomidae and copepods.	Creed & Reed, 2004
Total invertebrate density reduced. Negative correlations with Diptera, Ephemeroptera and Odonata, as well as some families of Trichoptera.	McCarthy et al., 2006
Macroinvertebrate abundance was greater in enclosures with crayfish. Community dynamics were affected, with 14 taxa from multiple feeding groups increasing in abundance primarily due to alterations in the quantity of fine sediment.	Brown & Lawson, 2010
Benthic invertebrate abundance negatively correlated with crayfish presence.	Nilsson et al., 2012
Larger negative effect on invertebrates than native crayfish. Reduction in invertebrate abundances.	Twardochleb et al., 2013
gastropod density by >95%. Physids reduced by >99% and planorbids by 90%. Physids eggs eliminated. Large planorbids survived through refuge but no recruitment occurred.	Dorn, 2013
All life stages reduced shredder and grazer abundances, particularly thin-shelled *Lymnaea* snails. The small snail *Physa fontinalis* was preferentially consumed by juveniles which may reflect different prey handling ability.	Rosewarne et al., 2013
Native and invasive crayfish presence significantly reduced invertebrate density, diversity and biomass.	James et al., 2015
Benthic invertebrate densities were halved in the presence of invasive crayfish.	Jackson et al., 2016a
Macroinvertebrate density increased in presence of crayfish. No differences in species richness.	Albertson & Daniels, 2016a

Table 2.2 continued.

Study finding	Author
Fish	
Fish benthivory stayed constant (crayfish act as source of food instead of reduced invertebrate densities).	Nilsson et al., 2012
General feeding behaviour	
Foraging profitability (crayfish growth) was greater for smaller crayfish in shallow habitats in addition to invertebrate biomass also being greater and reduced predation risk from large crayfish.	Flinders & Magoulick, 2007

2.2.8 Management approaches to invasive crayfish

The successful management of signal crayfish and the associated ecological and geomorphological implications requires a thorough understanding of the biology, population size and structure, habitat requirements and the ecological niche occupied (Hogger, 1988). The life history and population characteristics of *P. leniusculus* most likely differ significantly between environments, and therefore management should be based upon biological characteristics of the population for which it is intended (Freeman et al., 2010).

A variety of control methods have been tested in lakes and rivers. The most widely employed approach to controlling crayfish is through mechanical removal via baited traps. Application of this method demonstrates size bias towards larger individuals, although it is possible that the addition of fine mesh may increase the proportion of small crayfish captured (Rabeni et al., 1997; Moorhouse and Mcdonald, 2011a). It has been hypothesised that removal of large crayfish may reduce the detrimental effects on aquatic ecosystems (Usio et al., 2009; Moorhouse et al., 2014), but some studies suggest that this may be counteracted by increased growth of the remaining stock, greater juvenile survival and increased immigration rates of large crayfish (Frutiger et al., 1999; Moorhouse et al., 2011a, b and c). Sustained trapping efforts may reduce population densities in the short term but trapping is manually intensive and must be maintained indefinitely and is therefore not sustainable (Freeman et al., 2010; Moorhouse and Mcdonald, 2011a).

Physical construction of barriers has been suggested as a means to prevent the spread of invasive crayfish; however these often prove to be ineffective (Frings et al., 2013). Drainage of ponds may be used to control confined populations of invasive crayfish but it should be noted that dewatering may stimulate the search for new habitat, potentially enhancing the spread to previously uninhabited watercourses (Peay and Dunn, 2014). Other physical intervention methods include the destruction of refuges which is considered impractical in rivers and has been shown to be ineffective in small ponds (Peay and Hiley, 2001). More recently, electric shocking has been tested as a method to control invasive signal crayfish in localised populations of invasive crayfish of small watercourses with some successes (Peay et al., 2015). Complete eradication was however not achieved with individuals surviving in refugia, predominantly within river banks. Other methods of management include chemical treatments and biological control (Freeman et al., 2010). However, these techniques are associated with potential deleterious effects to other non-target flora and fauna. The overall consensus is that there is no straightforward means of eradicating or controlling invasive signal crayfish populations, with most attempts being met with only limited successes (Gheradi et al., 2011). At the present time it is unfeasible to eradicate signal crayfish completely from locations where they have been identified. It is therefore imperative that the ecological and geomorphic consequences of signal crayfish invasion for the receiving ecosystem are fully understood to enable effective mitigation strategies to be implemented.

2.3 Geomorphic implications of lotic animals

2.3.1 Background

In the last 25 years, interest in the interactions between organisms and the physical environment has grown and diversified to include the direct and indirect influences of micro-organisms, plants, animals and humans on earth surface processes (Coombes, 2016). Yet the appreciation of such interactions is not new, with seminal works by Darwin (1881), Shaler (1892) and Cowles (1899) in the late 19th century. Despite a growing appreciation of the multitude of geophysical and ecological processes that organisms influence, integration within mechanistic geophysical models remains limited (Corenblit et al., 2011) and there is an absence of conceptual frameworks which would facilitate such attempts (Moore, 2006). Few studies consider the contribution of biological activity on sediment transport and this remains a significant knowledge gap if we are to fully comprehend the dynamic and complex nature of ecosystem functioning (Rice et al., 2012b; Statzner, 2012; Allen et al., 2014; Albertson and Allen, 2015). Even more pressing is the need to understand how invasive species alter physical and ecological processes and how these modifications may augment the invasion effects for the receiving ecosystem. Successful colonisation by non-native species has the potential to disrupt the natural equilibrium of the invaded ecosystem, resulting in complex and interlinked feedbacks to ecosystem functioning (Harvey et al., 2011; Fei et al., 2014).

The following section provides a review of the geomorphic impact of lotic animals, focusing predominately on the role of fish, macroinvertebrates and crayfish in directly altering substrate and sediment transport. It is worth mentioning however the large array of terrestrial and aquatic geomorphic agents which have been extensively studied and which produce considerable impact in the lotic environment.

The most studied zoogeomorphic agents in rivers are the North American and, to a lesser extent, European beaver (*Castor canadensis* and *Castor fiber*). Dam building has the potential to transform lotic to lentic ecosystems and terrestrial to wetland habitats, thereby altering sediment retention patterns (Butler and Malanson, 2005), soil nutrient recycling (Johnston et al., 1995), organic matter and nutrient deposition (Naiman and Melillo, 1984) and vegetation succession (Westbrook et al., 2011). Beavers are capable of influencing up to 30-50% of the total length of 5th order and smaller streams (Naiman and Melillo, 1984). Moreover, potential initial aggradation of rivers can be as high as 0.47m yr^{-1} which may stabilise to approximately 0.075m yr^{-1} after year six as sediment accumulates on terraces (Pollock et al., 2007). Entrapment of such large amounts of sediment has profound impacts on riverine hydrology, geomorphology, ecology and stream restoration strategies (Pollack et al., 2007; Westbrook et al., 2011; Giriat et al., 2016; Law et al., 2016).

There are also large bodies of research which consider the feedback of terrestrial zoogeomorphic agents for fluvial processes and instream modifications. A number of studies have investigated the effect of unmanaged grazing on rates of bank erosion, sediment production and channel widening (Trimble and Mendel, 1995; Laubel et al., 2003; Wright et al., 2006), in addition to the presence of riparian vegetation influencing bank hydrology and flow hydraulics (Hupp and Osterkamp, 1996; Abernethy and Rutherford, 2000). Research has also considered the potential impact of alterations to food webs that often result in trophic cascades. One such example is the intensified riparian herbivory of Elk (*Cervus elaphus*) following the extirpation of grey wolves in USA, which can lead to the incision of river channels and reduced connectivity of the floodplain (Beschta and Ripple, 2006; 2008).

Plants also play a significant role in the development and maintenance of the physical environment. In particular, the seasonal growth of macrophytes can interact with the flow of water, with large stands of plants creating areas of low velocity and shear stress which encourages sediment deposition (Cotton et al., 2006; Gurnell et al., 2006). The presence of plants can cause local variations in velocity leading to a mosaic of erosional and depositional areas which may alter channel bed topography and grain size distribution with plants typically increasing the retention of fine sediment (O'Hare et al., 2011; Jones et al., 2011). However, the most well studied environment- organism interaction is associated with fish, which will be the discussed in the below section.

2.3.2 Geomorphic impacts of fish

The majority of work associated with reworking of fluvial substrates is primarily associated with salmonids (salmon and trout) during redd construction (nesting). Many salmonid fish are anadromous, migrating from the ocean to freshwater in order to spawn. This act of spawning for most salmonid species occurs in riverine environments (DeVries, 2012). During upstream migration, high densities of adult fish may disturb the bed topography through their swimming action, particularly during passage through shallow riffle areas, which can result in the mobilisation of fine sediments (Moore et al., 2004). However, the most considerable geomorphic effects of salmonids are associated with redd construction.

Salmonids construct redds by digging progressively into the substrate, turning on their sides and rapidly undulating the tail and body to excavate sediments (Montgomery et al., 1996). As the female cuts (excavates) her redd, fine material is released from the interstitial spaces which is transported downstream, resulting in increased bed permeability / porosity (Field-Dodgson, 1987; Kondolf et al., 1993; Kondolf, 2000). The aggregate effect of fine sediment flushing can be substantial with one study documenting a five-fold increase in fine sediment accumulation in areas of Alaskan rivers where salmon were excluded (Moore et al., 2004).

The winnowing of fine sediment typically results in the coarsening of the surface material and partial sorting of the substrate, with disturbed gravel typically having a different size distribution to adjacent gravel. A pit is formed in which the eggs are deposited ready for fertilization. After spawning, the embryos are then covered with excavated material from upstream the pit forming a mound (tailspill) downstream (Kondolf et al., 1993; Quinn, 2005). This distinctive topography often persists until high winter flows (Montgomery et al., 1996). Studies documented a 33-39% increase in median grain size in one Washington stream and a 56-57% increase in another Alaskan stream (Montgomery et al., 1996).

The size and density of salmonid redds is dependent on the species and population size. Chinook salmon mean redd area and disturbance depth has been reported to be 13.6m^2 and 0.34m^2 respectively, equating to a mean disturbance of 4.6m^3 per redd (Moore et al., 2004). In contrast, the total volume excavated by sockeye salmon was approximately 0.3m^3 per redd with a mean area and disturbance depth of 2.1-4.2m^2 and 0.2cm^2 respectively (Steen and Quinn, 1999; Gottesfeld et al., 2004). Assuming one redd per female and no superimposition, it is estimated that salmon have disturbed more than 5000m^3 of stream bed material every summer in two Alaskan streams over the last 50 years, which corresponds to 30% of the available surface area (Moore, 2006). Similarly, in smaller streams up to 2km in length, Field-Dodgson (1987) documented disturbance levels of 50-60% of total stream length. Depending on the density and proximity of redds, alterations to channel bathymetry as a consequence of the distinctive hummocky bed topography may be striking. Concentrations of redds in parallel lines may produce a series of channel spanning ridges or dunes (Field-Dodgson, 1987; Gottesfeld et al., 2008; Hassan et al., 2008). Further redd building may lead to the erosion of channel bars and banks, leading to the creation of uniform bed morphology (Gottesfeld et al., 2008).

Loosening of the substrate through redd building has been hypothesised to reduce the critical entrainment threshold for gravels, thereby promoting sediment entrainment (Montgomery et al., 1996; Buffington and Montgomery, 1997; Hassan et al., 2008; 2015). However, the imbrication of smaller particles from upstream redd building activities and from bedload transport during initial stages of floods, may counteract this effect, resulting in reduced levels of substrate mobility (Montgomery et al., 1996). Despite individual fish only moving substrate downstream that is an order of magnitude shorter than floods, the cumulative volume moved may be substantial dependent on spawning densities (Gottesfeld et al., 2004; DeVries, 2012), and opens up the distinct possibility that the cumulative effects of all lotic animals may be vast.

Most of the research on bed disturbance by fish is based on Pacific salmon species; however, the effect of other fish species may also be as significant. Foraging behaviour can lead to disturbance of bed sediments, resulting in the bioturbation of fines (Pringle and Hamazaki, 1998). Barbel (*Barbus barbus*) and gudgeon (*Gobio gobio*) have been documented to reduce fine sediment accumulation on gravel substrates, in addition to modifying mean bed elevation, substrate stability and subsequent bedload transport (Statzner et al., 2003a; Pledger et al., 2014; 2016). Carp (*Cyprinus carpio*), bream *(Abramis brama)* and tench (*Tinca tinca)* have also all been found to re-suspend sediment during feeding activities (Persson and Svensoon, 2006; Matsuzaki et al., 2009; Huser et al., 2016).

2.3.3 Geomorphic impact of aquatic macroinvertebrates

Despite their relatively small size, there is growing evidence that aquatic macroinvertebrates can have significant impacts on their physical environment. Hydropsychidae caddisflies are one of the most abundant and diverse families of lotic insects worldwide, often accounting for as much as 80% of invertebrate biomass in some streams (Wallace and Merrit, 1980). Hydropsychids construct filtration nets from silk which they use to filter particulate organic matter from the water (Cardinale et al., 2004). This process has been documented to result in increased benthic substrate stability through the binding of individual grains together (Statzner et al., 1999; Cardinale et al., 2004; Johnson et al., 2009; Albertson et al., 2014a). Initial velocity required to entrain sediments has been documented to increase by 10-30% in the presence of hydropschids dependent on population densities and grain size characteristics (Cardinale et al., 2004; Johnson et al., 2009). Consequently, caddisflies may play an important role in creating spatial refuges from disturbance events such as floods. At velocities sufficient to erode 87% of particles from control channels, 57-100% of particles remained stable in channels colonised by hydropsyche, thereby increasing the recurrence interval of bed scouring floods (Cardinale et al., 2004).

Similar results have been documented for other species within Hydropsychidae with mono-specific populations of *Ceratopsyche oslari* and *Arctopsyche californica* resulting in a 21% increase in critical shear stress required for entrainment, which was increased to 26% in mixed species populations (Albertson et al., 2014b). These silk structures are resistant to short lived disturbances of elevated suspended sediment loads and streambed drying and thereby represent important ecosystem engineering tools (Albertson and Daniels, 2016b).

Aquatic invertebrates can also alter the accumulation and distribution of fine sediment. Invertebrate communities have been documented as winnowing fine sediment (organic and inorganic) from interstitial spaces during foraging activities (Wallace et al., 1993), with studies reporting a reduction in sediment accrual in substrates colonised by freshwater shrimps (Pringle and Blake, 1994; March et al., 2002; Visoni and Moulton, 2003), Plecoptera (Zanetell and Peckarsky, 1996; Statzner et al., 1996) and Ephemeroptera (Soluk and Craig, 1990). The stonefly species *Dinocras cephalotes* has been hypothesised to have an erosion potential of about 200-400kg sand m^{-2} yr^{-1} under favourable conditions at natural population densities (Statzner et al., 1996), with hunger levels significantly increasing disturbance levels (Zanetell and Peckarsky, 1996; Statzner et al., 1996). The reduction in fine sediment content associated with aquatic invertebrates is likely to be a combination of direct ingestion and bioturbation (De Souza and Moulton, 2005). In addition, high leaf litter processing rates of invertebrate communities can reduce the standing crop of leaf litter, which most likely diminishes particle retention and thereby positively influences sediment export rates (Wallace et al., 1993).

Invertebrate bioturbation has also been documented to reduce the clogging of bed sediments. High densities of tubificids or Chironomidae can maintain or re-establish vertical hydraulic connectivity in a river bed clogged with fine sediment, influencing the flow of resources and physiochemical conditions (Mermillod-Blondin et al. 2002; 2003; 2004; 2006; Nogaro et al., 2006; 2009). The influence of the invertebrate on sediment clogging is heavily linked to the functional mode of bioturbation of each group. Tubificid worms produce dense networks of galleries in the sediment, which creates pathways for water and reduces clogging of hyporheic sediments. In contrast, chironomids produce u-shaped tubes which are restricted to the superficial layer of sediment, and thus do not influence hydraulic conductivity (Nogaro et al., 2006).

2.3.4 Geomorphic implications of signal crayfish

Studies which focus on the impacts of signal crayfish on sediment dynamics are primarily based around gravelly streams or within experimental flume set ups (e.g. Creed and Reed, 2004; Johnson et al., 2010a). There is an absence of research in lowland rivers, which are dominated by readily mobilised fine sediment grains, and may therefore potentially influence sediment dynamics at the catchment scale. Within these systems there is also the potential for agricultural and industrial contaminants to be bound to the sediment which may impact upon water quality (Harvey et al., 2011).

Signal crayfish have the potential to modify fine sediment dynamics in two main ways; i) feeding or foraging activities; and ii) non feeding activities such as fighting, burrowing and walking (Harvey et al., 2011). The omnivorous diet of signal crayfish can significantly influence the availability of coarse particulate organic matter (CPOM) both directly and indirectly. The direct role in CPOM conversion can be substantial with crayfish dominating the shredder functional feeding group, comprising an average of 99% of the total invertebrate shredder biomass in one study (Usio and Townsend, 2001). Signal crayfish can also indirectly alter the rates of conversion of fine particulate organic matter (FPOM) through their negative influence on aquatic invertebrate shredder populations (Usio, 2000), whilst collector-gathers are most likely to benefit from the increased availability of detritus (Huryn and Wallace, 1987, Creed and Reed, 2004).

Additional impacts on the instream environment through the consumption of macrophytes can also influence fine sediment dynamics. Macrophytes are key elements of roughness in lowland rivers (Petryk and Bosmajian, 1975) and can influence flow behaviour, creating a mosaic of depositional and erosional areas, which in turn determines the distribution of sediments (Malard et al., 2002). In addition, macrophytes and biofilms have been suggested as stabilising fine sediment deposits (Statzner et al., 2003b; Vignaga et al., 2013; Fox et al., 2014). Thus the alteration of near bed hydraulics and local bed material composition through macrophyte removal has the potential to influence the availability of fines.

Signal crayfish are typically considered to be a non-burrowing species in their native habitat range (Shimizu and Goldman, 1983; Lewis, 2002). However, within the UK, extensive burrows in banks and bed material have been observed (Guan, 1994; Rice et al., 2016; Faller et al., 2016) which is leading to significant habitat degradation. Most burrows are simple with just one opening below the water level, however the amalgamation of numerous burrows or changes in soil type may lead to a change in direction, resulting in complex burrows. Despite the simple nature of burrows, high burrow density can cause substantial damage to river banks, increasing instream fine sediment delivery (Angeler et al., 2001; Rice et al., 2016), and ultimately leading to bank collapse (Guan, 1994).

Other studies have documented that crayfish activities can result in the winnowing of fine sediments from gravelly substrates (Usio and Townsend, 2004; Helms and Creed, 2005). In the presence of crayfish, the critical shear stress for sand sized particles was reduced by 50-75% (Statzner et al., 2000; 2003b). Mobilisation of fine sediment is associated with the movement of walking, swimming or foraging for food. Given their large size, high mobility and dense populations, crayfish have the ability to play a major role in sediment distribution through the bioturbation of benthic sediments and may contribute significantly to suspended sediment loads (Rice et al., 2014; 2016). A number of studies have reported diurnal increases in suspended sediment levels associated with crayfish activity (Harvey et al., 2014; Cooper et al., 2016) with the winnowing of fines most likely being seasonally variable, correlating with a decline of crayfish activity in cold temperatures (Fortino, 2006).

Studies have reported that both interstitial and benthic accumulation of fine sediment was lower in experimental channels / enclosures where crayfish were present (Parkyn et al., 1997; Statzner et al., 2000; Creed and Reed, 2004; Albertson and Daniels, 2016b). This bioturbation of sediment is likely to significantly alter the diversity and distribution of macrophytes and aquatic invertebrates (Usio and Townsend, 2004) and may be important for the recovery of stream habitat following silt deposition events (Parkyn et al., 1997). However, high densities of burrows and associated sediment inputs may counteract the sediment mobilisation by bioturbation. Thus crayfish are potentially important at a local scale for both sediment recruitment and outputs, but the balance between these two processes and therefore the net effect on fine sediment dynamics is not currently understood.

Signal crayfish have also been documented to alter the topography of gravel substrates. Measured increases in mean bed elevation in experimental channels have been determined, indicating that gravel consolidation was reduced by the presence of crayfish (Statzner et al., 2003b). Johnson et al. (2010a) documented that signal crayfish alter the grain- to-grain arrangement of particles when walking, in addition to increasing grain protrusion through the construction of shallow pits used for refuge. These alterations to near bed hydraulics and grain scale structure, reduce the stability of gravel beds, with double the amount of gravel sized grains entrained from crayfish- disturbed surfaces than control, water-worked surfaces (Johnson, 2010a). Signal crayfish were also found to move gravel material up to 38 mm in diameter, equivalent to six times the weight of the individuals used in the experiments (Johnson et al., 2010b). A summary of crayfish sediment- interactions within lotic systems is shown in Table 2.3.

Table 2.3 Geomorphic implications of lotic crayfish

Species	Study type	Habitat	Season	Geographical location	Mechanism	Impact	Author
Pacifastacus leniusculus	*In-situ* observations, artificial bank experiments	Riffles and Pools	Winter and Summer	Buckinghamshire (UK)	Burrowing	Construction of burrows in banks, 90% simple linear and 10% complex. 60% of crayfish dug burrows in winter and 67% in summer. Bank collapse in areas of high burrow density.	Guan, 1994
Pacifastacus leniusculus	*Ex-situ* flume	Run	N/S	Loughborough (UK)	Construction of pits, moving	Double the amount of grains mobilised, alterations to gravel geometry.	Johnson et al., 2010a
Pacifastacus leniusculus	*Ex-situ* flume	Run	N/S	Loughborough (UK)	Construction of pits, moving	Displacement of 450cm^3 of sediment over an area of 2400cm^2 which is the equivalent of 1.7kg m^{-2}. Displacement of material up to 38mm in diameter which had a submerged weight of six times that of the individual, alteration of grain geometry.	Johnson et al., 2010b
Pacifastacus leniusculus	*In-situ* sampling & ex-situ mesocosm	N/S	Summer	Oxfordshire (UK)	Burrowing, moving, digging of pits	Observation of pulsed sediment suspension events. Higher total number of pulse events determined for bank experiments compared to just bed substrate. Notable increase in bank collapse occurrence. No clear nocturnal pattern determined but majority of pulses between 0:00-03:00 for laboratory experiments. Clear nocturnal trend determined in field experiments with enhanced ambient turbidity levels.	Harvey et al., 2014

Table 2.3 continued.

Species	Study type	Habitat	Season	Geographical location	Mechanism	Impact	Author
Pacifastacus leniusculus	In-situ sampling, Ex-situ experiment	Riffles and Pools	Summer	Northamptonshire (UK)	Bioturbation, fighting, foraging, digging of pits	Crayfish activity contributed at least 20% of the suspended sediment load over a 28-day period (increased to 47% when flood periods not included). Increased magnitude and number of turbidity spikes at night. Clear increase in turbidity levels during aquaria experiment with crayfish present (6 and 3.5 times higher). Levels declined but did not reach ambient pre-crayfish concentrations when removed. Two crayfish had most notable effect on levels associated with fighting activities.	Rice et al., 2014
Pacifastacus leniusculus	Field surveys	N/S	N/S	London (UK)	Burrow construction	Burrows present on majority of reaches but were patchy in distribution, concentrated in <10% of reaches. Burrow distribution was explained better by local biophysical properties than reach-scale. Factors included cohesive bank material, steeper bank slopes and burrow construction contributed a total of 3 t km^{-1} of fine sediment to invaded rivers surveyed (n = 103).	Faller et al., 2016
Pacifastacus leniusculus	In-situ sampling	Pool	Winter and Spring	Norfolk (UK)	Bioturbation	Diurnal increase in turbidity between 21:00 – 04:00 with values increasing by on average 10 NTU. Lowest readings were recorded 10:00-14:00. Suspended sediment concentrations were 76% larger at night with increases in suspended sediment loads of 30%. Diel turbidity was less prominent during winter.	Cooper et al., 2016

Table 2.3 continued.

Species	Study type	Habitat	Season	Geographical location	Mechanism	Impact	Author
Pacifastacus leniusculus	In-situ sampling and field surveys	Riffles and Pools	Annual	Northamptonshire (+ Rutland & Leicestershire, UK)	Burrow construction, bioturbation	Crayfish bioturbation contributed on average 32% (474kg) to monthly baseflow suspended sediment loads. The biotic surcharge was between 5.1 and 16.1 t (0.21 to 0.66 t km^{-2} yr^{-1}; maximum and minimum estimates). Crayfish contributions were considerable during baseflow periods but hydraulic forcing transported the majority of sediment during flood periods. Measurements at 13 sites indicated crayfish burrow construction contributed 0.25 – 0.5 t $km^{-1}a^{-1}$	Rice et al., 2016
Other species							
Cambarus bartonii bartonii	*In-situ* enclosure / exclosure	Pool	Mid-Summer-early Autumn	Maryland (USA)	Detrital processing, bioturbation	Reduction in FPM.	Creed & Reed, 2004
Orconectes cristavarius, Cambarus chasmodactylus	*In-situ* enclosure / exclosure	Pool	Mid-Summer-early Autumn	North Carolina (USA)	Direct ingestion of sediment and detritus, bioturbation	Decrease of fine sediments from 222mL in control to 95.5mL in enclosures. Majority of crayfish gut contents contained sediment (50-100%).	Helms & Creed, 2005
Cambarus chasmodactylus & *Orconectes cristavarius*	*In-situ* enclosure / exclosure	Pool	Winter	North Carolina (USA)	Bioturbation	No effect on sediment accrual during winter months (inference of seasonal winnowing).	Fortino, 2006

Table 2.3 continued.

Species	**Study type**	**Habitat**	**Season**	**Geographical location**	**Mechanism**	**Impact**	**Author**
Orconectes meeki meeki	*In-situ* enclosure	Pool of intermittent stream	Summer	Arkansas (USA)	Feeding, bioturbation	Decrease of mean epibenthic sediments by up 80% in mass. The effects were negatively related to water depth.	Ludlam & Magoulick, 2009
Paranephrops planifrons	*In-situ* experimental channels	Run	Spring	New Zealand	Organic matter processing, bioturbation	425g dry weight of sediment lost in high density experiments compared to controls and 527g dry weight lost in medium density experiments.	Parkyn et al., 1997
Paranephrops zealandicus	*In-situ* experimental channels	Pool	Autumn	New Zealand	Sediment consumption, bioturbation (walking)	Reduction in sediment accrual.	Usio & Townsend, 2004
Orconectes marchandi	*In-situ* enclosures	Pool and Riffles	Summer-Autumn	Missouri (USA)	Walking, feeding	Reductions in silt dry mass associated with large crayfish. Little effect by small crayfish.	Flinders & Magoulick, 2007
Orconectes limosus	*Ex-situ* flume	Pool and Riffles	Spring-autumn	River Rhone (France)	Walking, swimming	Increase of baseflow sand by up to 2kg m^{-2} d^{-1} and gravel by up 4 kg m^{-2} d^{-1}.	Statzner et al., 2000
Orconectes limosus	*Ex-situ* flume	Pool and Riffles	Spring-autumn	River Rhone (France)	Walking, swimming	Shear stress for gravel reduced by 75%, reduction in sand shear stress by 50% in pools and 75% in riffles.	Statzner et al., 2003b
Orconectes limosus	*Ex-situ* flume	Pool and Riffles	Spring-autumn	River Rhone (France)	Walking, swimming	Increase in baseflow transportation rates.	Statzner & Peltret, 2006

Table 2.3 continued.

Species	Study type	Habitat	Season	Geographical location	Mechanism	Impact	Author
Orconectes limosus	*Ex-situ* flume	Pool and Riffles	Spring-autumn	River Rhone (France)	Walking, swimming	Reduction of surface sand and algal cover, increase in baseflow transport of sand by 0.1kg m^{-2} d^{-1} and gravel by 1.1 kg m^{-2} d^{-1}, reduction of shear stress by up to 40% for gravel.	Statzner & Sagnes, 2008
Orconectes rusticus	*In-situ* enclosures	Riffles	Autumn	Valley Creek (USA)	General activities	Total suspended solids were lower with crayfish present suggesting increased suspension and reduced settling of particles. Pit and depression structures evident in crayfish enclosures with significant more subsurface material exposed.	Albertson & Daniels, 2016a

2.4 Justification of research aims

The majority of work investigating the ecological effects of invasive crayfish is predominantly focussed on lentic ecosystems through short term studies or field manipulations. There is a distinct lack of studies which consider the long term and spatial extent of biological invasions for the receiving ecosystem, particularly with regards to lotic environments. Objective 1 (*quantify the long term and spatial extent of signal crayfish effects on instream macroinvertebrate communities*) will provide results which will address this research gap (Chapters 3 and 5; Figure 1.1). Moreover, despite invasions of ecosystems occurring across the globe at a rapid rate, little attention has been given as to how these ‘new’ taxa and the subsequent modifications to native community composition will affect commonly employed riverine biomonitoring tools. Within freshwater ecosystems, a number of biological metrics based around the native community composition are employed which provide a measure of health relative to external stressors i.e. pollution, flow and fine sediment. Invasion by non-native taxa provides a potential threat to the effectiveness of such biomonitoring tools. Objective 2 (*examine the potential effect of invasive signal crayfish on commonly employed biomonitoring tools*) aims to tackle this research challenge (Chapter 3; Figure 1.1).

The implications of crayfish for sediment transport have been studied through a number of flume experiments and *in-situ* surveys. It is evident that crayfish can have significant implications for both coarse and fine sediment transport, however the direct effect of biota on sediment transport comparative to a control river has not yet been tested. In addition, the net effect of crayfish presence for fine sediment dynamics is not yet understood. Crayfish have the potential to alter fine sediment inputs and outputs but their role in sediment budgets and the process of fine sediment storage has not yet been examined. Objective 3 (*quantify the role of signal crayfish on fine sediment dynamics within lotic ecosystems*) will provide results to address this research gap (Chapters 4 and 6; Figure 1.1).

Finally, signal crayfish clearly have the potential to alter both biotic and abiotic processes in the rivers which they invade. Despite studies focussing on the ecological effects of crayfish and similarly their interactions with the physical environment, work which truly considers the two-way feedback between the ecological and physical components is rare. It is likely that by modifying the physical environment, in this instance fine sediment dynamics, crayfish may enhance their ecological effects for the receiving ecosystem. This thesis aims to provide an overall body of research which tackles this important research gap, with this also being a particular focus of objective 4 (*experimentally examine the predator-prey interactions of signal crayfish and macroinvertebrates in association with fine sediment loading;* Chapter 6; Figure 1.1). Individual research questions associated with these four objectives are outlined in subsequent chapters.

Chapter 3 - The long-term implications of invasive signal crayfish for instream macroinvertebrate communities and commonly employed freshwater biomonitoring tools

3.1 Introduction

Crayfish display opportunistic polytrophic feeding habits, consuming algae, macrophytes, detritus, zoobenthos, fish and other crayfish (Momot et al., 1978; Lagrue et al., 2014; Ercoli et al., 2015b). Invasive crayfish may also act as ecosystem engineers through the alteration of detrital processing rates (Creed and Reed, 2004; Bobeldyk and Lamberti, 2008; Carvalho et al., 2016) and by changing the dominant algal cover on substrates (Creed, 1994; Matsuzaki et al., 2009). Studies documenting the effect of invasive crayfish in stream ecosystems have identified significant reductions in the biomass and richness of aquatic macrophytes (Lodge et al. 1994; Nyström et al., 2001), and macroinvertebrates (Nyström et al., 1999; Stenroth and Nyström, 2003; Crawford et al., 2006; Nilsson et al., 2012; Ercoli et al., 2015a).

Following invasion by crayfish, macroinvertebrate community composition has been reported to shift towards more mobile taxa adapted to high flow velocities (e.g. Ephemeroptera species) at the expense of less mobile taxa such as Mollusca, Hirudinea and case-bearing Trichoptera species (Keller and Ruman, 1998; Parkyn et al., 1997; Dorn, 2013). The mobility of taxa, in addition to prey handling time (time taken for crayfish to consume prey items), has been cited as key characteristics influencing the vulnerability of individual species associated with preferential predation (Ilheu and Bernado, 1993; Nyström and Perez, 1998; Nyström, 1999). However, many taxa display behavioural and life history changes in response to predator pressure through avoidance strategies such as vertical migration or enhanced locomotion (Crowl and Covich, 1990; Alexander and Covich, 1991a; Haddaway et al., 2014; Chapter 6).

Indirect effects may also be evident within the ecosystem with a removal of macrophyte and algae cover affecting invertebrate populations through the loss of trophic resources and habitat availability (Lodge et al., 1994; Nyström et al., 1996).

Similarly, a reduction of sedentary periphyton grazers (such as gastropods) and stimulated productivity through the excretion of nutrients may potentially benefit mobile grazers via the liberation of resources (Flint and Goldman, 1975; Charlebois and Lamberti, 1996). There have been suggestions that the composition of diet and feeding behaviour of crayfish varies with season (Goddard, 1988; Guan and Wiles, 1998), although evidence remains limited. Crayfish activity is seasonally variable being strongly regulated by water temperature (Gheradi et al., 1998; Bubb et al., 2004), as is the availability of macroinvertebrate prey (Worischka et al., 2015).

The spatial and biological implications of invasions are often driven and influenced by natural and anthropogenic environmental change (Lapointe et al., 2012). Anthropogenic modifications to aquatic habitats are altering the structure of many freshwater ecosystems (Friberg, 2014) and biomonitoring programmes that assess the status of freshwater water bodies have become an essential means of monitoring and evaluating such pressures (Buss et al., 2015). Benthic macroinvertebrates are one of the most commonly employed freshwater groups globally (Carter et al., 2006) and in Europe are designated as one of the biological quality elements employed in the implementation of the EU Water Framework Directive (WFD; EU, 2000). The occurrence of indicative aquatic invertebrate taxa and assemblages based upon functional traits and life histories have enabled the development of a multitude of biomonitoring tools used in the identification and quantification of a range of anthropogenic disturbances and stressors (Bonada et al., 2006). Consequently, selective predation by many invasive crayfish species is likely to modify communities (Gheradi and Acquistapace, 2007; Ercoli et al., 2015a,b) and may significantly compromise the use of aquatic macroinvertebrates as bioindicators (MacNeil et al., 2013). This may thereby reduce the ability of commonly employed biomonitoring indices to accurately characterise the pressures they were designed to assess, but to date this has never been evaluated.

As invasive crayfish extend their range, understanding their effects on biodiversity and ecosystem services is therefore becoming increasingly important for informing management strategies (Lodge et al., 2012; Jackson et al., 2014; Moorhouse et al., 2014). Despite the widely acknowledged threat that invasive crayfish pose, much of the research to date has been focused on lentic ecosystems, whilst the impact on stream communities has been poorly quantified in many regions (Stenroth and

Nyström, 2003; Pysek et al., 2008; Lodge et al., 2012). The majority of studies have investigated the short-term effects of invasive crayfish at site or reach scales via small-scale *in-situ* enclosure experiments or through the use of *ex-situ* laboratory mesocosms typically over one season (e.g., Parkyn et al., 1997; Stenroth and Nyström, 2003; Magoulick, 2014; see Twardochleb et al, 2013 for a meta-summary of all published invasive crayfish studies). Other studies have employed *in-situ* sampling over a limited duration (1 -12 months) where invading crayfish populations are already well established (e.g., Crawford et al., 2006). Short term experiments provide mechanistic insights into crayfish – community or individual population interactions. However, it is also necessary to investigate the long-term and large scale effects of invasive crayfish in order to determine whether they are persistent and if the effects vary spatially, temporally or seasonally. Long- term studies also provide the opportunity to quantify the extent of invasion effects that cannot be captured though experimental mesocosm studies (Wilson et al., 2004; McCarthy et al., 2006).

3.2 Research Aims

In this chapter the long-term effects of the invasive signal crayfish, *Pacifastacus leniusculus* (Dana) on macroinvertebrate community composition, individual taxa and biomonitoring metrics was examined within lowland rivers in England (UK) during spring and autumn seasons. Unlike previous studies, the effect of invasive crayfish is investigated using multiple regions and catchments before and after invasion, and in direct comparison with control sites where long-term monitoring has not recorded the presence of *P. leniusculus.*

Specifically the following questions are addressed:

1) Does the invasion of *P. leniusculus* lead to significant changes in benthic macroinvertebrate community composition in lotic ecosystems?
2) Is the effect of *P. leniusculus* invasion on macroinvertebrate community composition spatially extensive (is the effect evident over different bio-geographical ranges of lowland England) and do the effects persist over time (multiple years)?

3) Are the ecological implications of *P. leniusculus* invasion seasonally dependent or are the effects on the macroinvertebrate community composition persistent and evident all year round?
4) Are the observed changes to macroinvertebrate community composition associated with the same groups of lotic taxa identified in previous studies of *P. leniusculus* invasion (e.g. *sensu* Guan and Wiles, 1998; Usio and Townsend, 2004; Crawford et al., 2006)?
5) Does invasion by *P. leniusculus* effect the performance of six commonly employed macroinvertebrate biomonitoring metrics used in the routine ecological assessment and management of freshwaters in the UK?

3.3 Methods

3.3.1 Characterisation of datasets

Following preliminary consultation with staff from a statutory environmental monitoring authority, the Environment Agency of England, macroinvertebrate community data from three English regions were extracted from the Environment Agency 'BIOSYS' database. The database covers sites across England and contains long term biomonitoring (benthic macroinvertebrate) records for over 27 000 sites. To allow comparison between sites invaded by *P. leniusculus* and control sites, those selected for the study shared similar characteristics with the exception of invasion by crayfish. This aimed to minimise the influence of any potential confounding factors on the analysis. All sites selected had to fulfil the following criteria: i) records extended over multiple years with a minimum of 5-years macroinvertebrate community data prior to invasion by *P. leniusculus* or in the case of control sites 5-years before the average date other rivers in the region were invaded; ii) sites did not support a native crayfish population during any of the time series; iii) sites were not subject to other recent invasions and; iv) sites were not significantly impacted by anthropogenic stressors such as water abstraction, flow regulation or impaired water quality. Criterion iii) was relaxed for the non-native gastropod *Potamopyrgus antipodarum* (Gastropoda: Hydrobiidae) because this species is widely distributed across most regions of the UK since its introduction over a century ago (Ponder, 1988) but is not thought to have a significant influence on freshwater invertebrate communities in most European streams (Murria et al., 2008).

Data from three regions formed the basis for the analysis, encompassing natural variability in community composition across England (East, South East and North West England; Figure 3.1). A fourth region, South-West England, was also examined but only family level data were available and therefore analysis of the data is informative but is not directly comparable with data from the other three regions and is presented within Appendix 2. Data from a fifth region, South Wales, was also considered but the control sites were not physically or ecologically comparable to the invaded rivers and only family level macroinvertebrate data was available. Consequently no data is presented from this region within the chapter. The three regions employed were selected to reflect natural biogeographical, geological and hydrological variability across England, thus reflecting the diverse regional variability of lowland river systems. Following screening of the data, a total of 7 ‘invaded’ and 7 ‘control’ lowland rivers were identified (Table 3.1). Rivers were selected to have broadly comparable physical characteristics within the individual regions (channel size, discharge, water chemistry, altitude and geology). Rivers in South-East England were predominately characterised by chalk deposits, those in East England by mudstones and those in the North West by sedimentary sandstone and igneous rocks. The characteristics of the rivers employed by region are shown in Table 3.2. Rivers utilised in the study were not heavily managed or regulated and consequently physical and hydrological characteristics did not change during the study period. In addition, electrofishing surveys conducted by the Environment Agency of England indicate no major changes in fish populations occurred over time at any of the rivers studied.

Table 3.1 Rivers included in the long-term analysis. Control sites were assigned a nominal date to allow comparison with invaded sites (denoted in bold italics) based on the average date of invasion for the respective region (**Note -** control sites were free from crayfish during the entire study period).

River	English Region	Duration of record	Control / Invaded?	Invasion point
Gwash	East	1989-2013	Invaded	1996
Nene	East	1991-2013	Invaded	1998
Chater	East	1990-2013	Control	***1997***
Eyebrook	East	1990-2013	Control	***1997***
Harrop Brook	North West	1990-2013	Invaded	1996
Torkington Brook	North West	1990-2004	Invaded	1998
Glossop Brook	North West	1990-2013	Invaded	1997
Bollin	North West	1990-2013	Control	***1997***
Sett	North West	1986-2013	Control	***1997***
Ver	South East	1990-2013	Invaded	2002
Rib	South East	1975-2013	Invaded	2006
Gade	South East	1983-2013	Control	***2003***
Mimram	South East	1975-2013	Control	***2003***
Ash	South East	1977- 2013	Control	***2003***

Table 3.2 Summary of selected abiotic characteristics (mean values) of rivers employed in analysis by region. The rivers examined in the study were not heavily managed or regulated and consequently physical and hydrological characteristics did not change significantly during the study period.

	North West invaded	North West control	South East invaded	South East control	East invaded	East control
Altitude (m a.o.d)	138	199	59	73	86	63
Depth (m)	0.13	0.11	0.25	0.16	0.22	0.1
Width (m)	3.67	3	7.5	4.67	3.33	4.5
Annual discharge (m^3 / sec)	0.62	0.31	0.46	0.31	0.36	0.46
Alkalinity mg L^{-1}	79	47	265	262	212	201

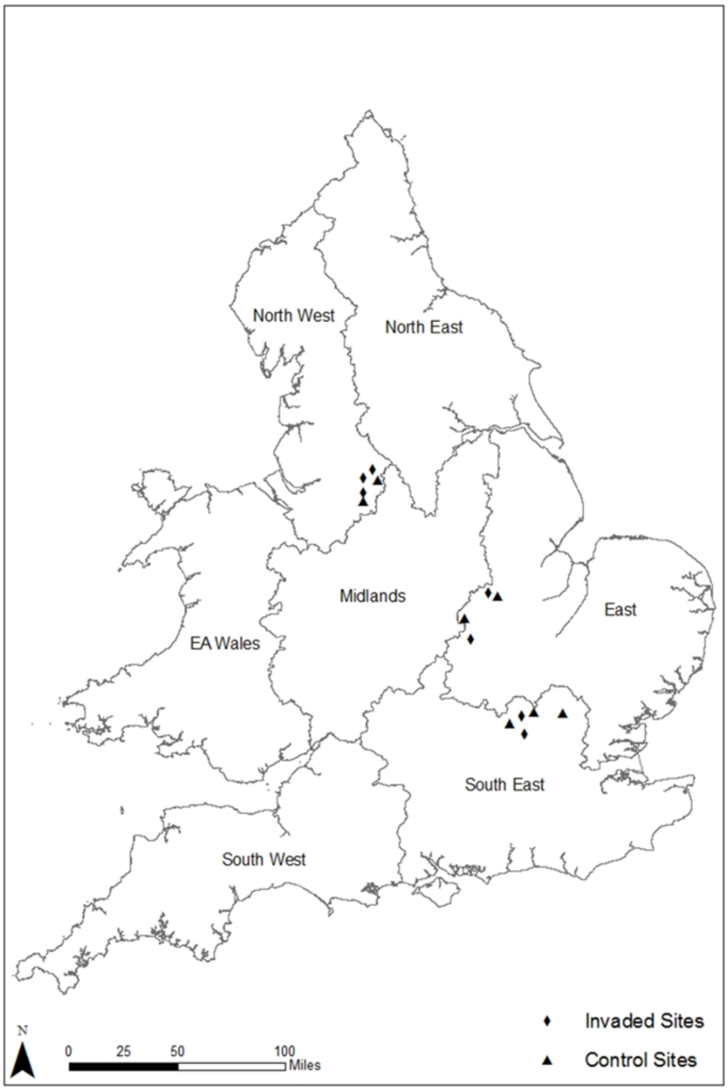

Figure 3.1 Site locations of the long term macroinvertebrate biomonitoring records employed from the South East, North West and East regions of England.

All benthic invertebrate samples were collected using the Environment Agency's standard sampling protocol comprising a 3-minute 'kick-sample', which encompasses all available habitats, and an additional 1-minute, detailed hand search (Murray-Bligh, 1999). This sampling strategy has provided an effective means of detecting temporal changes in invertebrate communities of English and Welsh rivers previously (Monk et al., 2008; Durance and Ormerod, 2009). Each site has a season specific record of community composition; Spring (March –May, df 300), Summer (June-August, df 119), Autumn (September – November, df 352) and Winter, (December – February, df 75). Data were initially analysed on an annual basis (incorporating all seasons) and then subsequently divided on a seasonal basis

(Spring, March-May and Autumn, September – November) to examine whether trends were seasonally consistent. Within the seasonal analysis, duplicate samples (i.e. 2 samples within a season) and replicate sites were removed to provide a single record for each river for each season. However, all samples were retained in the long-term biomonitoring analyses as the Environment Agency sample on an ad hoc basis and typically sample to assess / quantify specific pressures. The final seasonal data-set comprised a total of 530 samples (255 and 275 from invaded and control samples respectively) with the majority of samples collected between 1990 and 2013 (three sites had data series extending back to the 1970s and an additional three further sites had data from the mid 1980s).

Given the length of macroinvertebrate community records many of the faunal lists comprised mixed taxonomic levels of identification. As a result the lowest possible taxonomic level available across the three regions was used. In the majority of instances this meant genus level data were utilised, although species level data were available for a number of taxa. Diptera larvae were resolved to family level and Hydracarina to order level throughout the series. Due to variations in the way in which abundance data were recorded over time, reflecting a shift from abundance classes on a 33rd percentile logarithmic scale to abundances on standard logarithmic scales (and real counts for single digit abundances), abundance data were standardised into ordinal classes (Durance and Ormerod, 2009) to enable comparison over the whole series (1 = ≤ 9, 2 = 10 – 32, 3 = 33 – 99, 4 = 100 – 332, 5 = 333 – 999, 6 = ≥1000). In total, 596 taxa were recorded.

3.3.2 Data analysis

Data were categorised into four groups: i) control - before invasion, ii) control - after invasion, iii) invaded - before invasion and; iv) invaded - after invasion. For invaded sites the approximate date of invasion was determined by the first occurrence of *P. leniusculus* in the historical faunal series. No crayfish density data was available for the sites because routine sampling of crayfish populations is not a standard biomonitoring practice following invasion. Detecting signal crayfish is difficult due to their high mobility (Gladman et al., 2010) and there are currently no methods of determining crayfish populations below a density of 0.2m^{-2} (Peay, 2003). For the kick-net samples utilised in this study, it is likely that the detection limit is higher, probably approaching a density of 1.0m^{-2}. Consequently for all sites employed in this study, crayfish densities would be significant, although some variation by sites and through time is likely. In addition, it is important to acknowledge that signal crayfish may have been present at the study sites for a several years prior to formal detection, albeit most likely at low densities in such cases.

Control sites were divided into two periods (before invasion and after invasion) based on the mean date of invasion for the invaded rivers in the respective region (1997 for East; 1997 for North West; and 2003 for South East). The assignment of a nominal date allowed a direct comparison between the control and invaded sites over the same time-period and also provided a means of assessing whether there were temporal shifts in invertebrate community composition not associated with crayfish invasion. This approach was taken because previous long-term analyses of UK data sets have revealed changes in community composition associated with drought (Monk et al., 2008), modification of channel morphology (Dunbar et al., 2010) and improvements in water quality (Durance and Ormerod, 2009).

3.3.3 Community composition

Changes to macroinvertebrate community composition were examined via non-metric multidimensional scaling (NMDS) using Bray-Curtis similarity coefficients. NMDS is an ordination technique used to visually represent the degree of dis(similarity) among sample communities within a dataset (Clarke, 1993). Sites with similar ecological communities are plotted closer together on the ordination axes and those which are dissimilar further apart. This process is iterative, which is based upon rank similarity matrices of the samples and the distance in ordination space. The iterative procedure (in this study 999 iterations were applied) refines the relative position of the sites on the ordination axes to minimize the degree of ‘stress’ as much as possible. Stress represents the lack of fit or distortion between the similarity matrix and the ordination space (Kruskal, 1964). A stress level of ≤0.2 is widely accepted as an appropriate fit and can provide an accurate visualisation of (dis)similarity although it is widely regarded that increasing numbers of samples typically increase stress levels (Clarke, 1993).

A One way ANOSIM (Analysis of Similarities) was used to examine differences in the communities amongst the control and invaded rivers before and after ‘invasion’.

ANOSIM compares the ranked significance of similarity between sites with that which would be generated by chance (Clarke and Gorley, 2006). For each sample 999 random permutations were tested. Both P and R ANOSIM values were examined, with R values >0.75 indicating strong separation amongst groups, R = 0.75–0.25 indicating separate groups with overlapping values and R <0.25 as barely distinguishable groups (Clarke and Gorley, 2006). Preliminary NMDS analysis indicated strong differences among regions (Figure 3.2) for macroinvertebrate community composition. ANOSIM indicated significant differences for all pairwise comparisons of regions in both seasons; all P values <0.001 and R values > 0.75 and as a result subsequent analyses were conducted on a regional basis.

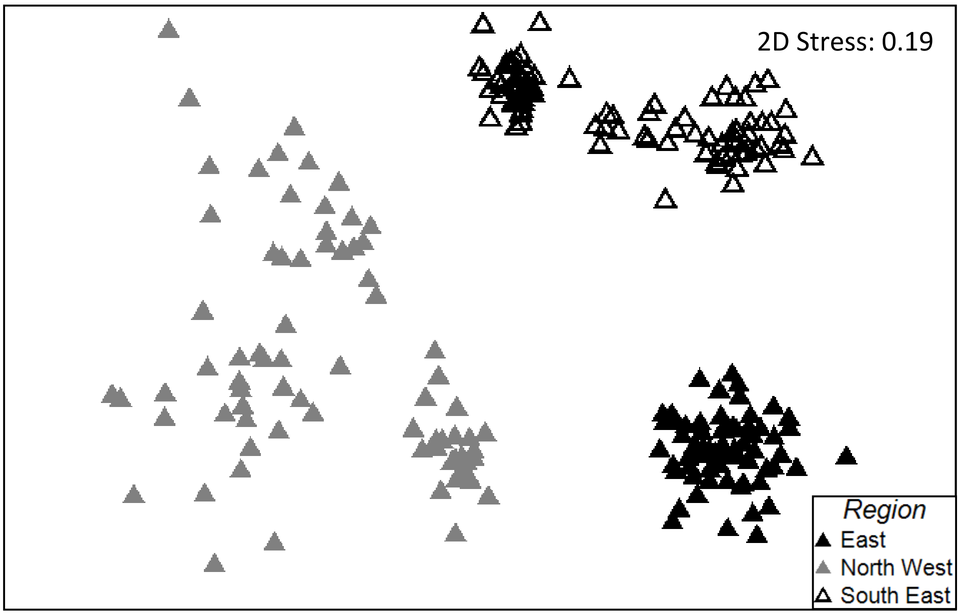

Figure 3.2 Preliminary NMDS ordinations of benthic macroinvertebrate community data for all three English regions (East, North West and South-East England) using the Bray-Curtis similarity coefficients for spring samples.

To assess temporal changes in community composition and determine if macroinvertebrate communities demonstrated recovery following invasion, temporal trajectories of changes in assemblage composition were plotted for each river and season. Taxa contributing to the differentiation of communities within individual regions and for a river group (control and invaded) were identified through the application of the similarity percentage (SIMPER) with a selection of taxa examined in further analysis according to criteria described below. SIMPER ranks the contribution of each taxon to the observed similarity within a group and the dissimilarity between all pairwise factor groups based on Bray-Curtis similarity coefficients (Clarke and Gorley, 2006). All ordination analyses were performed in PRIMER Version 6.1.16 (PRIMER-E Ltd, Plymouth, UK).

3.3.4 Taxon specific changes

To assess changes in individual taxa associated with crayfish invasion, taxon occurrence (presence or absence) amongst the control and invaded rivers both before and after invasion were examined. Nine taxa (3 Mollusca, 2 Ephemeroptera, 2 Hirudinea, 1 Trichoptera and 1 Crustacean) were selected for further analysis on the basis of the following criteria: i) taxa identified as driving community differentiation in a number of regions through application of SIMPER in analyses outlined above and / or ii) taxa widely cited in previous studies of invasive crayfish effects in lotic systems (e.g. Keller and Ruman, 1998; Haddaway et al., 2014; Moorhouse et al., 2014) and; iii) taxa abundant in all regions and sites during the study period.

Generalised linear mixed models (GLMMs) were fitted to each taxon for each season (Spring and Autumn) using a binomial error distribution. GLMMs combine the properties of two statistical model frameworks, linear mixed models (which incorporate random factors) and generalised linear models (which handle non normal data by using link functions and exponential family distributions). Generalised linear models contain a flexible covariate structure which allows for unbalanced data and for the application of longitudinal repeated measures data whereby there is likely to be a underlying relationship between at least one of the predictor variables and the observations of the individuals (Lindstrom and Bates, 1990; Cudeck, 1996). GLMMs are therefore regarded as the best tool to analyse non-normal data which involve random factors (Bolker et al., 2009; Nakagawa and Schielzeth, 2013).

Models were fitted to presence / absence data using the glmmADMB version 0.8.1 package (Fournier et al. 2012, Skaug et al., 2014) in R version 3.1.2 (R development Core Team, 2014). The final model was built using region, treatment (control or invaded) and time period (before or after invasion) as terms. Monitoring site was specified as a random effect to reflect that taxon occurrence through time at individual sites will be correlated. To assess the effect of crayfish on the occurrence of specific taxa, the significance of the interaction term (time period x treatment) was examined. This enabled determination of whether taxa changes over time occurred in both invaded and control rivers or if the effects size was different to those where *P. leniusculus* occurred. Results were visualised by predicting probabilities of occurrence for each Before - After - Control - Invaded combination calculated from the GLMM on the linear predictor scale and transformed to the response scale using the inverse-logit function to enable the direction and trends of change to be ascertained. Standard errors for predictions were calculated on the linear predictor scale by multiplying the model matrix for each Before –After- Control - Invaded combination by the variance-covariance matrix for the fixed-effect parameter estimates. These were converted to confidence intervals (+/- 2 SE) on the same scale and similarly back-transformed. Visual predictions of the Before – After – Control – Invaded relationship are based upon an ‘average’ site as a function of the global GLMM.

3.3.5 Biomonitoring indices

Six standard biomonitoring indices of ecological and hydrological quality were also derived for each sample. Three of these indicators are routinely used to characterise water quality by the Environment Agency: the Biological Monitoring Working Party Score (BMWP; Chesters, 1980), the Number of BMWP-scoring families present (NTAXA) and the Average Score Per-Taxon (a derivative of BMWP). The Lotic Invertebrate index for Flow Evaluation (LIFE; Extence et al., 1999) which quantifies river flow pressures (e.g. low flows during drought, abstraction or impoundment pressures), and the Proportion of Sediment-sensitive Invertebrates (PSI; Extence et al., 2013) , which provides a measure of community sensitivity to fine sediment were also calculated for each sample. For some samples PSI scores were unclassified reducing the sample number from 846 to 745. All five of the above indices are widely employed by the Environment Agency to provide a measure of ecosystem health within lotic ecosystems. The final index employed was the richness of aquatic insect larvae within the orders Ephemeroptera, Plecoptera and Trichoptera (EPT richness) and is widely used internationally (e.g. Ligeiro et al., 2013; Tonkin et al., 2015). All indices were standardized by site (Z-scores) to control for natural variability associated with individual rivers.

To assess the potential influence of crayfish invasion on the biomonitoring indices, Generalised Linear Models (GLMs) were fitted to each metric with waterbody included as a random effect. To enable a GLM to be fitted to the data, Z-scores were normalised to positive values prior to analysis. This standardised the indices, making them comparable with each other, without modifying the variance or trends within the series. Models were fitted using the glm function in R Version 3.1.2 (R development Core Team, 2014). Inspection of the Akaike's Information Criteria (AIC) indicated that a Gaussian error distribution and identity link was the most suitable structure. Only significant terms were included in the final model and were examined using the drop function. For each index, a GLM was fitted which encompassed all available data. To assess the effect of crayfish on indices, the significance of the interaction term (time x treatment) was examined. To determine any seasonal effects GLMs were fitted to indices based on Spring and Autumn samples (df 300, and 352 respectively – 265 and 321 for PSI). Changes in index scores associated with invasion were visualised and inspected via error plots in IBM SPSS Statistics (version 21, IBM Corporation, New York). Index scores were visualised on a river, region and global basis to identify and confirm the consistency of the trends.

3.4 Results

3.4.1 Community composition

Non-metric Multi-Dimensional Scaling (NMDS) ordination diagrams for the three regions where predominately genus and species level data were available (South East, North West and East England) indicated distinct clusters of macroinvertebrate communities following crayfish invasion for the global dataset (all seasons; Figure 3.3) and for Spring and Autumn seasons (Figure 3.4). In most instances, each of the regional diagrams indicated similar community composition between control and invaded sites prior to crayfish colonisation. Following colonisation, the invaded and control sites formed distinct groups, indicating a change in community composition at both control and invaded sites compared to the period preceding crayfish invasion.

The degree of separation between the groups using Analysis of Similarity (ANOSIM) on the seasonal plots indicated highly significant differences for all pairwise comparisons of groups for South East England (all $P < 0.02$), North West (all P <

0.002) and East England (all P < 0.001). R values indicate that before colonisation, control and invaded groups were barely distinguishable in the South East (R_s = 0.116 and R_a = 0.16 for spring and autumn respectively) and in the East during spring months (R_s = 0.130). During autumn months for East England (R_a = 0.280) and for both seasons in North West England (R_s =0.636 and R_a = 0.344) the degree of similarity between invaded and control sites before invasion was less strong but was still evident. Following colonisation by crayfish, invaded and control groups demonstrated a higher degree of separation in all three regions and were strongly separated in the North West (R_s = 0.886 and R_a = 0.861) and were separated but overlapping within the South East (R_s = 0.512 and R_a = 0.421) and East (R_s = 0.457 and R_a = 0.609). ANOSIM values for the annual analysis (all seasons) are presented in Table 3.4.

Table 3.4 Results of ANOSIM analysis on the annual long term benthic macroinvertebrate data. Note: CB = control before; IB = invaded before; CA = control after and; IA = invaded after.

Region	CB & IB	CA & IA	*p* values
South East	0.14	0.40	<0.001
North West	0.38	0.86	<0.001
East	0.10	0.26	0.005

N.B. p values provided are for all the pairwise comparisons of groups

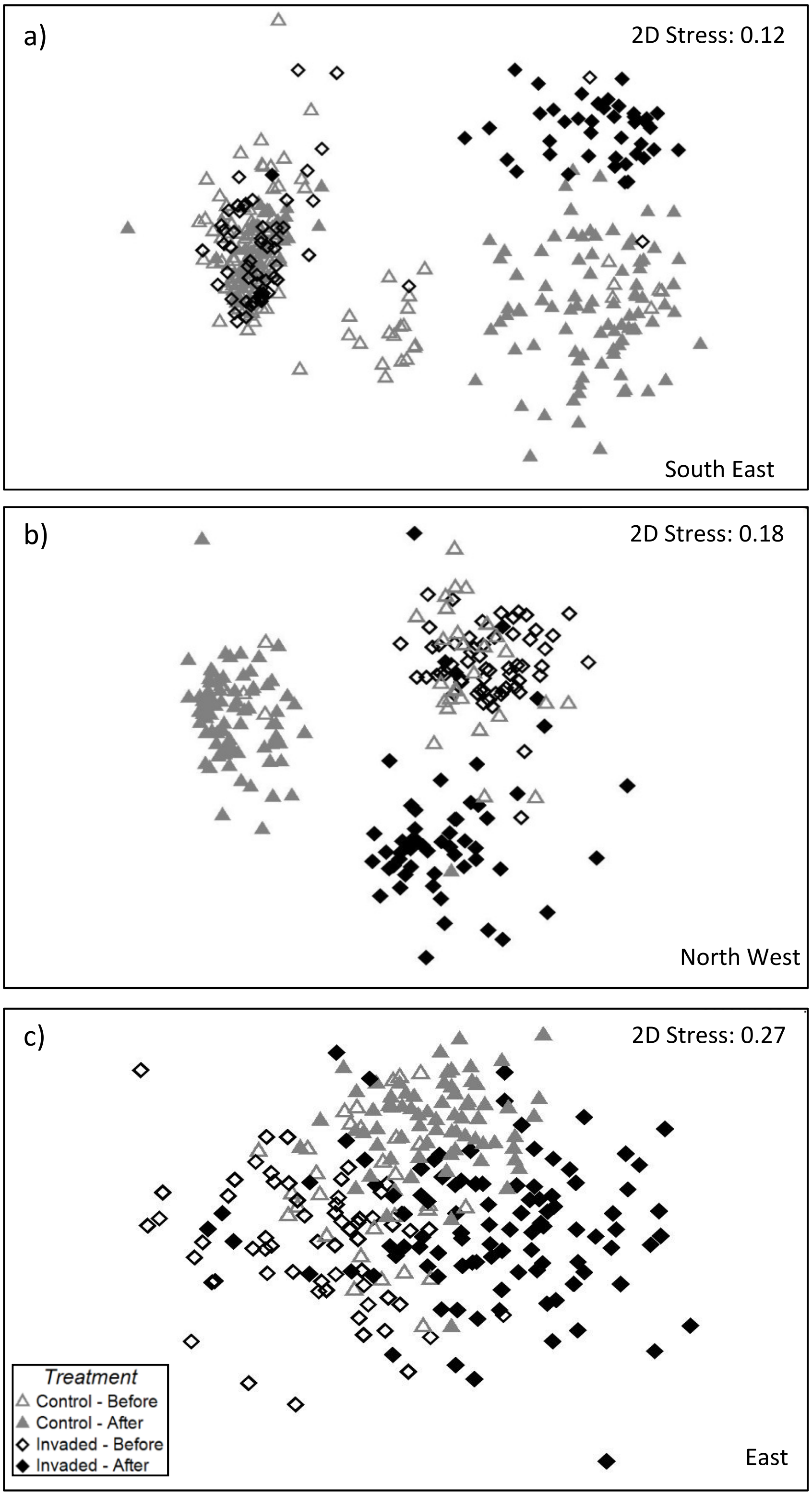

Figure 3.3 NMDS ordinations of macroinvertebrate community data using the Bray-Curtis similarity coefficients for all seasons for: a) South East; b) North West and; c) East England. Data was subsequently spilt into spring and autumn for further analysis.

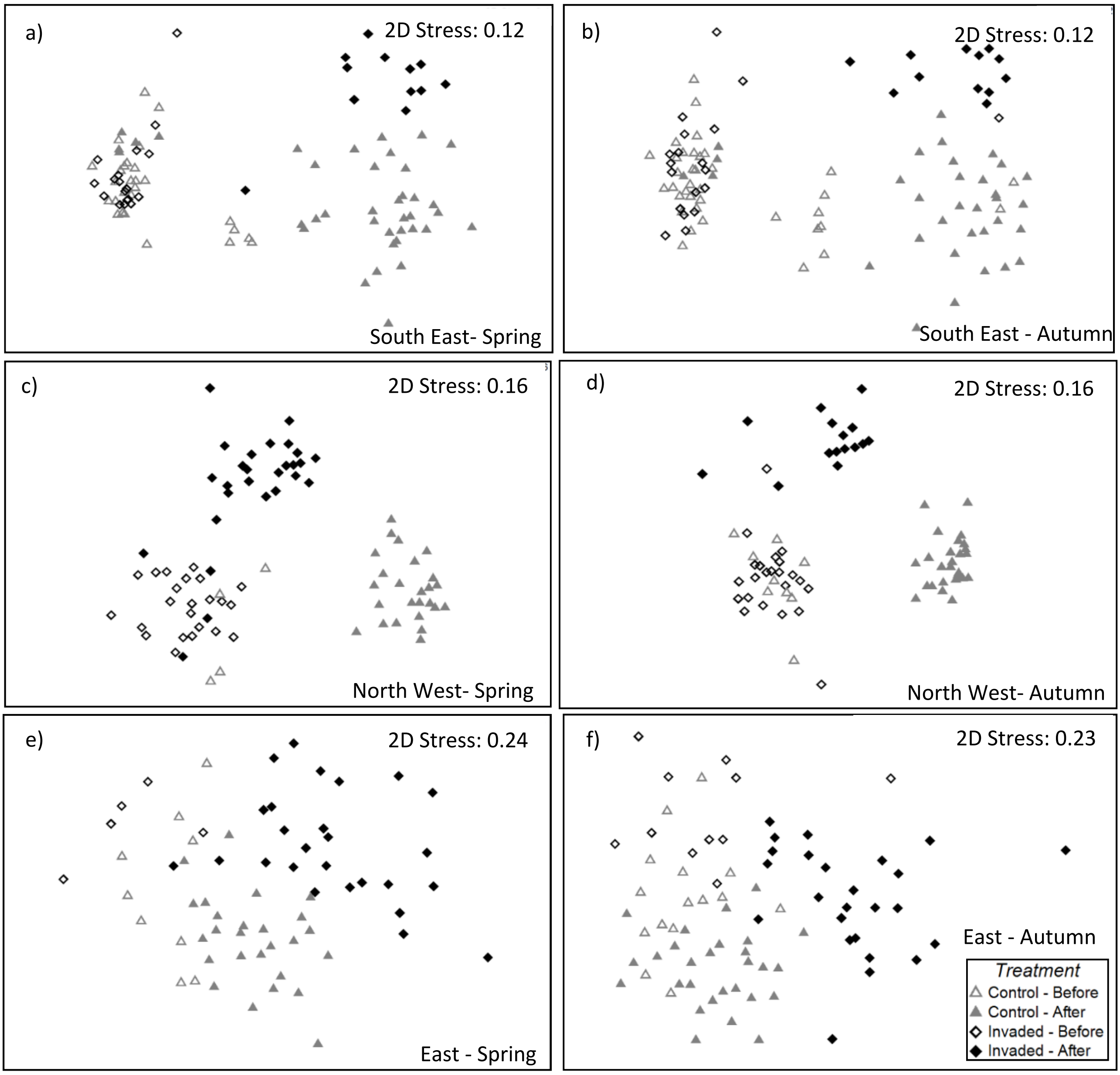

Figure 3.4 NMDS seasonal ordinations of benthic macroinvertebrate community data using the Bray-Curtis similarity coefficients for spring and autumn for: a) & b) South East; c) & d) North West and; e) & f) East England.

Temporal trajectories of macroinvertebrate community change were observed for both invaded and control rivers (Figure 3.5). Within invaded rivers, the community demonstrated clear changes in structure directly after invasion. Community changes were also evident in control rivers over the time period but these were different to those recorded for invaded sites and very little overlap was evident after the invasion point (IP on Figure 3.5). Prior to invasion, control and invaded river trajectories demonstrated considerable overlap with pathways intersecting on a number of occasions. Following the invasion point, trajectories of change for both control and invaded rivers remained discrete, with no similarities apparent or marked reversals in trajectory paths (to indicate recovery) evident for invaded sites.

The taxa primarily responsible for community composition changes within invaded rivers (before vs after), as identified by the similarity percentage (SIMPER), differed regionally as a function of natural biogeographic differences in community composition, although several taxa were common to two or more regions: 3 regions - *Gammarus pulex*, *Hydropsyche* spp., *Potamopyrgus antipodarum, Baetis* spp. and Hydracarina and; 2 regions – Sphaeriidae, Simuliidae and Elmidae (Table 3.5). Where several species were identified by SIMPER from the same genus within or between regions, these were combined to enable analysis of the most ubiquitous taxa across regions through application of the GLMM (e.g. *Hydropsyche* spp., *Baetis* spp., *Caenis* spp. and *Radix* spp. contained several species identified by SIMPER). Regions also displayed some seasonal differences in the taxa driving changes, with some taxa identified to be driving community dissimilarity in one season but not the other (e.g. Planorbidae, *Asellus aquaticus*, Heptageniidae). Taxa identified to be driving changes in control river communities over time are presented in Table 3.6.

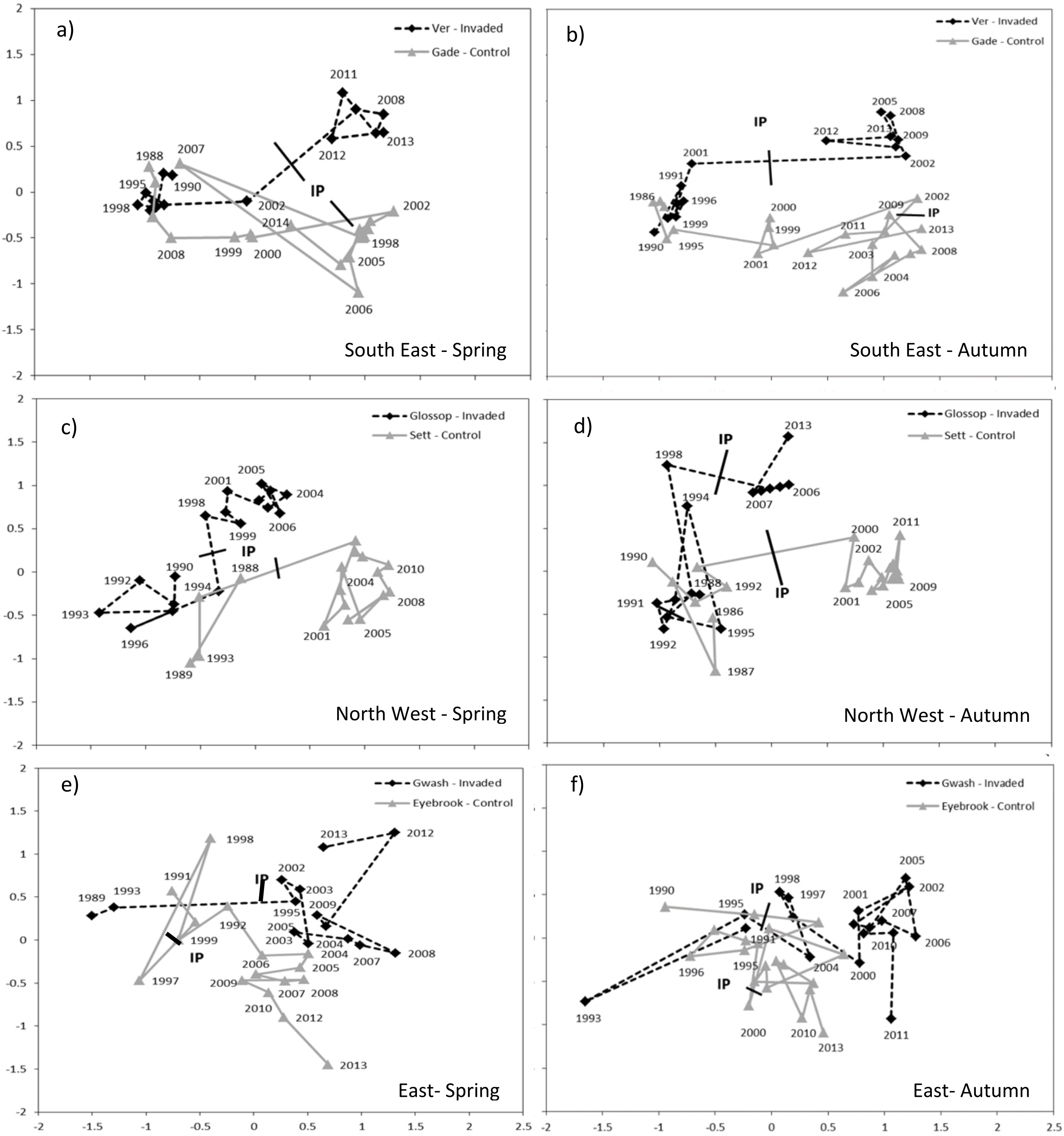

Figure 3.5 NMDS temporal ordinations of benthic macroinvertebrate community data. Individual rivers are linked by temporal trajectories of change during the sampling period. Plots represent pairwise comparisons of invaded river(s) and control river(s) by region and season for: a) & b) South East rivers Ver and Gade; c) & d) North West rivers Glossop and Sett and; e) & f) East England rivers Gwash and Eyebrook. The invasion date for both invaded and control rivers are denoted using the abbreviation IP (Invasion Point). Control rivers are symbolised by a solid grey line and invaded rivers by a black dashed line.

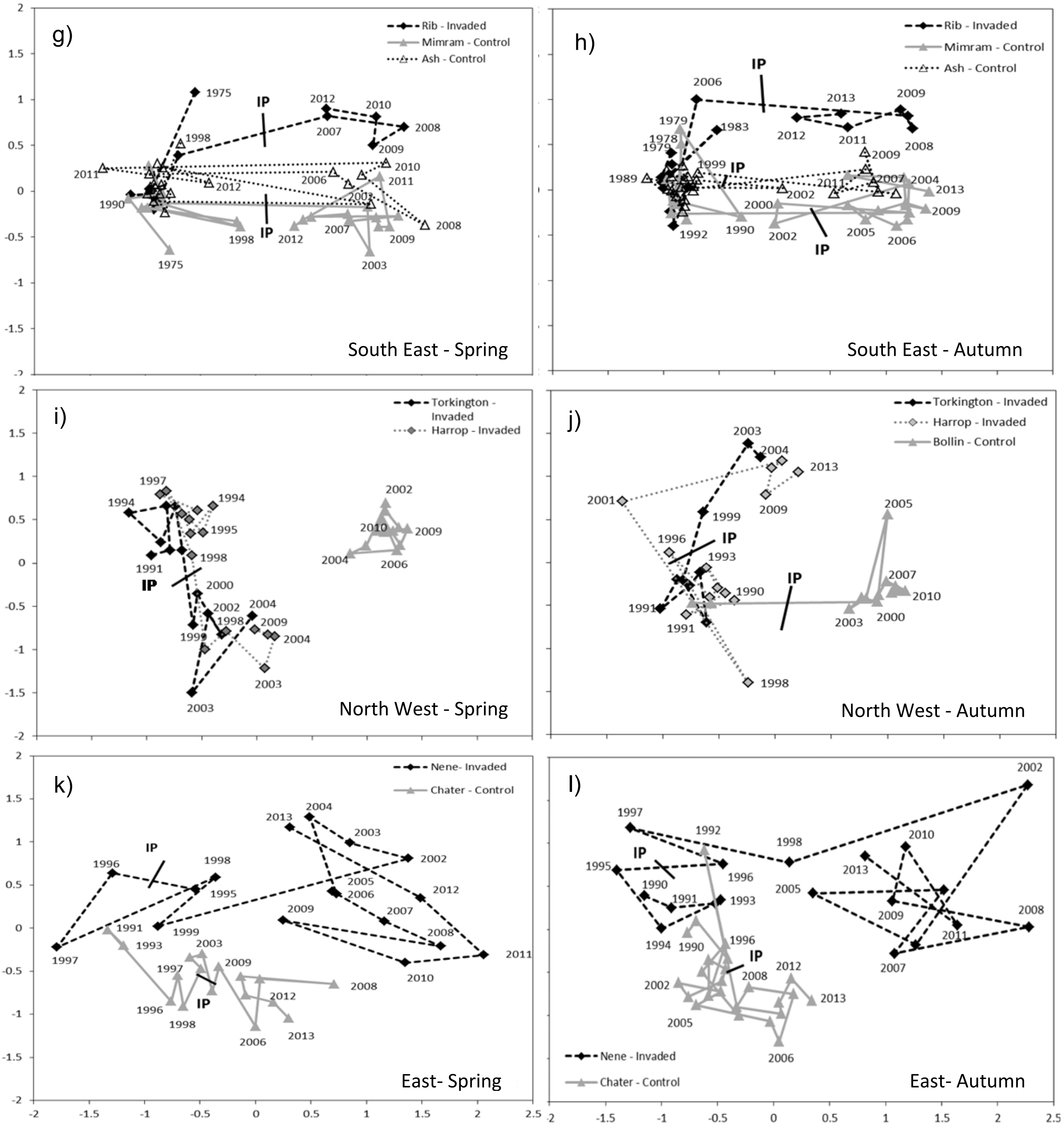

Figure 3.5 continued. NMDS temporal ordinations of benthic macroinvertebrate community data. Individual rivers are linked by temporal trajectories of change during the sampling period. Plots represent pairwise comparisons of invaded river(s) and control river(s) by region and season for: g) & h) South East rivers Rib, Mimram and Ash; i) & j) North West rivers Torkington, Harrop and Bollin and; k) & l) East England rivers Nene and Chater. The invasion date for both invaded and control rivers are denoted using the abbreviation IP (Invasion Point). Control rivers are symbolised by a solid grey line and invaded rivers by a black dashed line.

Table 3.5 For invaded rivers, summary of the top 10 invertebrate taxa (ranked percentage dissimilarity) as identified by SIMPER analysis as most strongly influencing site dissimilarity of community composition before and after crayfish invasion for the different regions and seasons. Total change in abundance following invasion indicated in parentheses (+/-), and season (Spring = S, Autumn = A). Where no letter is provided taxa identified for both seasons.

East	South East	North West
Hydropsyche spp. (-)	*Hydropsyche* spp. (-)	*Hydropsyche* spp. (+)
Glossiphonia complanata (-)	*Baetis* spp. (+)	*Baetis* spp. (+)
Sphaeriidae (-)	Sphaeriidae (-)	*Gammarus pulex* (+)
Gammarus pulex (+)	*Gammarus pulex* (+)	Chironomidae (+)
Caenis spp. (-)	*Valvata piscinalis* (-)	Elmidae (+ A)
Radix spp. (-)	*Potamopyrgus antipodarum* (+)	*Ecdyonurus* spp. (-)
Baetis spp. (+)	Elmidae (-)	Hydracarina (-)
Potamopyrgus antipodarum (- S, +A)	Leptoceridae (-)	Simuliidae (-)
Ancylus fluviatilis (-)	Hydracarina (-)	*Potamopyrgus antipodarum* (-A)
Hydracarina (-)	Simuliidae (- A)	*Asellus aquaticus* (- A)
	Planorbidae (- S)	Heptageniiidae (+S)
		Empididae (+S)

Table 3.6 For control rivers, summary of the top 10 invertebrate taxa as identified by SIMPER analysis (ranked percentage dissimilarity) as most strongly influencing site dissimilarity of community composition within before and after crayfish invasion for the different regions and seasons. Total change in abundance following invasion indicated in parentheses (+/-), and season (Spring = S, Autumn = A). Where no letter is provided taxa identified for both seasons.

East	South East	North West
Hydropsyche spp. (+)	*Gammarus pulex* (+)	*Baetis* spp. (+)
Potamopyrgus antipodarum (+)	*Hydropsyche* spp. (+)	*Hydropsyche* spp. (+)
Gammarus pulex (+)	*Baetis* spp. (+)	*Gammarus pulex* (+)
Sphaeriidae (-)	Planorbidae *(-)*	*Serratella ignita* (+)
Lepidostoma hirtum (+)	Sphaeriidae (-)	Elmidae (+)
Simuliidae (-)	Leptoceridae *(-)*	*Sericostoma personatum (+)*
Baetis spp (+S)	Hydrobiidae (-)	Oligochaeta (+)
Chironomidae (-S)	Elmidae (+S, -A)	*Rhithrogena semicolorata* (+)
Elmidae *(+)*	*Caenis* spp. (-S)	*Potamopyrgus antipodarum* (+)
Hydroptila spp. *(-S)*	Simuliidae (-S)	*Asellus aquaticus* (+)
Ancylus fluviatilis (-A)	Chironomidae (+A)	*Ancylus fluviatilis (+A)*
Theodoxus fluviatilis (+A)	Hydracarina *(-A)*	*Dicranota* spp. (+A)
Hydracarina (+A)		

3.4.2 Taxon-specific responses

Results presented below are for the GLMM model fitted to presence / absence of nine taxa by individual season based upon a global model (all regions). Results indicate if changes in taxa occurrence over time were common across all sites (both control and invaded rivers) or if they were confined to invaded sites and therefore could be attributed to crayfish invasion.

3.4.2.1 Spring

The prevalence of the leech *Glossiphonia complanata* ($Z_{3, 280}$ = -2.26, P = 0. 024) declined significantly following crayfish invasion whilst the occurrence of *Erpobdella octoculata* did not differ significantly compared to control sites ($Z_{3, 280}$ = -1.40, P = 0.161), although a general reduction in its occurrence was evident (Figure 3.6). The occurrence of the bivalve family Sphaeriidae declined following invasion but this was not statistically significant when compared to control sites ($Z_{3, 280}$ = -1.21, P = 0.228). The prosobranch gastropod mollusc *P. antipodarum* ($Z_{3, 280}$ = -0.99, P = 0.320) demonstrated no significant changes in occurrence associated with crayfish invasion whilst the pulmonate gastropod *Radix* spp. declined significantly ($Z_{3, 280}$ = -2.91, P = 0.003; Figure 3.6). Mayflies from the genus *Caenis* displayed reduced prevalence following invasion but this was not significant relative to control sites ($Z_{3, 280}$ = -1.39, P = 0.165). The mayfly *Baetis* spp. and amphipod *G. pulex* displayed no change in prevalence ($Z_{3, 280}$ = 0.12, P = 0.120 and $Z_{3, 280}$ = -1.88, P = 0.060 respectively) following crayfish invasion with their occurrence remaining high (Figure 3.6). The occurrence of the caddisfly nymph, *Hydropsyche* spp., reduced significantly ($Z_{3, 280}$ = -2.55, P = 0.010) following crayfish invasion compared to control sites (Figure 3.6).

3.4.2.2 Autumn

The occurrence of the leech species *G. complanata, E. octoculata,* and the gastropod *Radix* spp. (all P < 0.001) declined significantly following crayfish invasion relative to control sites (Figure 3.7). Both Sphaeriidae and *P. antipodarum* demonstrated no change in occurrence following crayfish invasion ($Z_{3,250}$ = 0.20, P = 0. 84 and $Z_{3,250}$ = 00.73, P = 0.225 respectively; Figure 3.7). Insect larvae within the order Ephemeroptera displayed contrasting responses following crayfish invasion. The prevalence of *Baetis* spp. did not differ significantly over time at either control or invaded sites ($Z_{3,250}$ = -0.38, P = 0.700) whilst *Caenis* spp. were significantly less common following crayfish invasion ($Z_{3,250}$ = -3.61, P= < 0.001; Figure 3.7). The amphipod *G. pulex* ($Z_{3,250}$ = -1.08, P = 0.281) demonstrated no significant changes following invasion, whilst the Trichoptera *Hydropsyche* spp. declined at invaded sites ($Z_{3,250}$ = -2.20, P = 0.028; Figure 3.7). All statistical significance levels and standard error values for the Before-After-Control-Invaded interaction effect for each taxon are shown in Table 3.7.

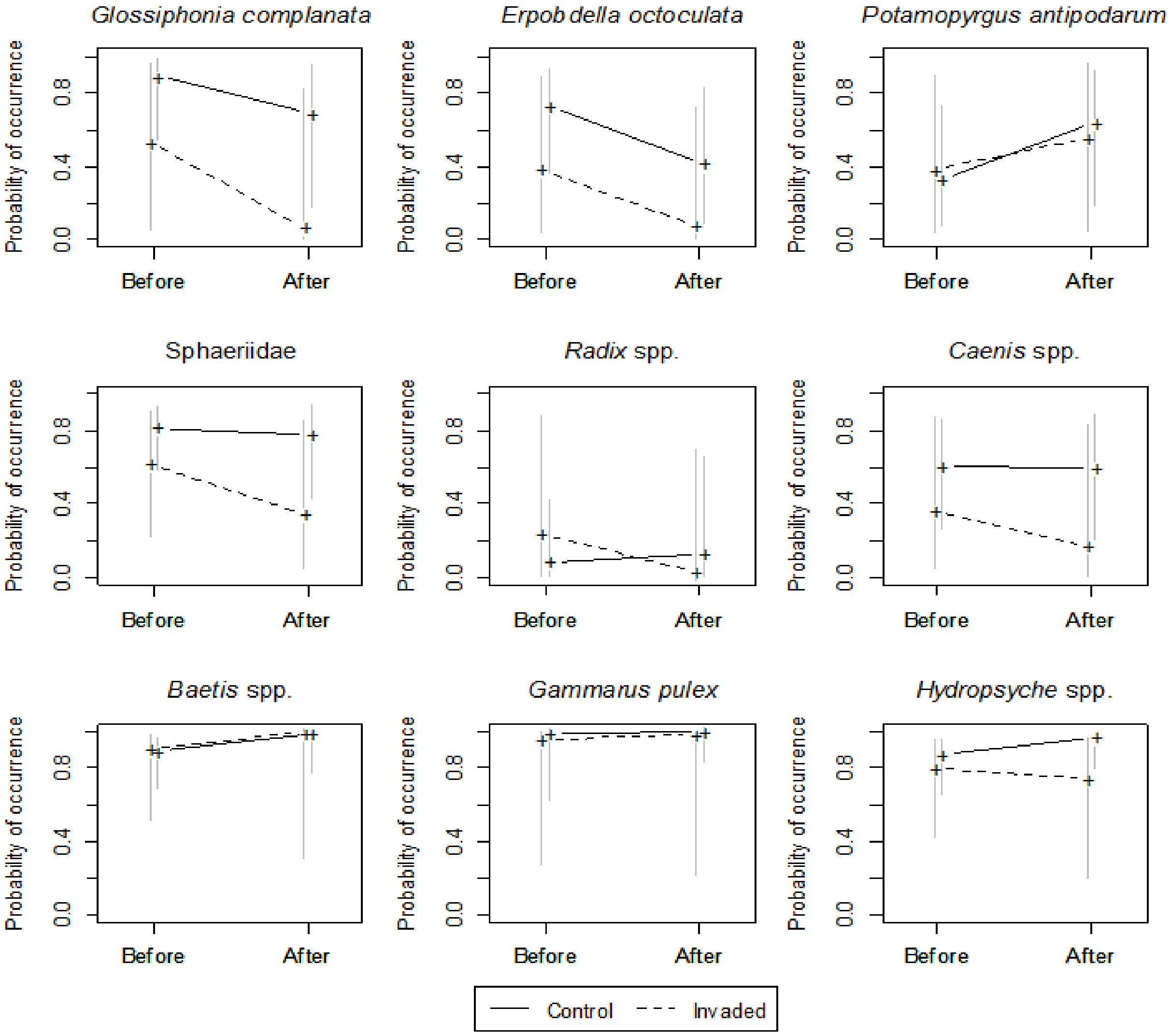

Figure 3.6 Predictions for spring months (March - May) of average probability of occurrence for individual taxa with confidence intervals for each combination of before, after, control and invaded factor. Predictions made for nine selected taxa using the Generalised Linear Mixed Model approach described in the text. Predictions of occurrence for each taxon are made using the global GLMM dataset (all regions) with predictions representing an average of all sites.

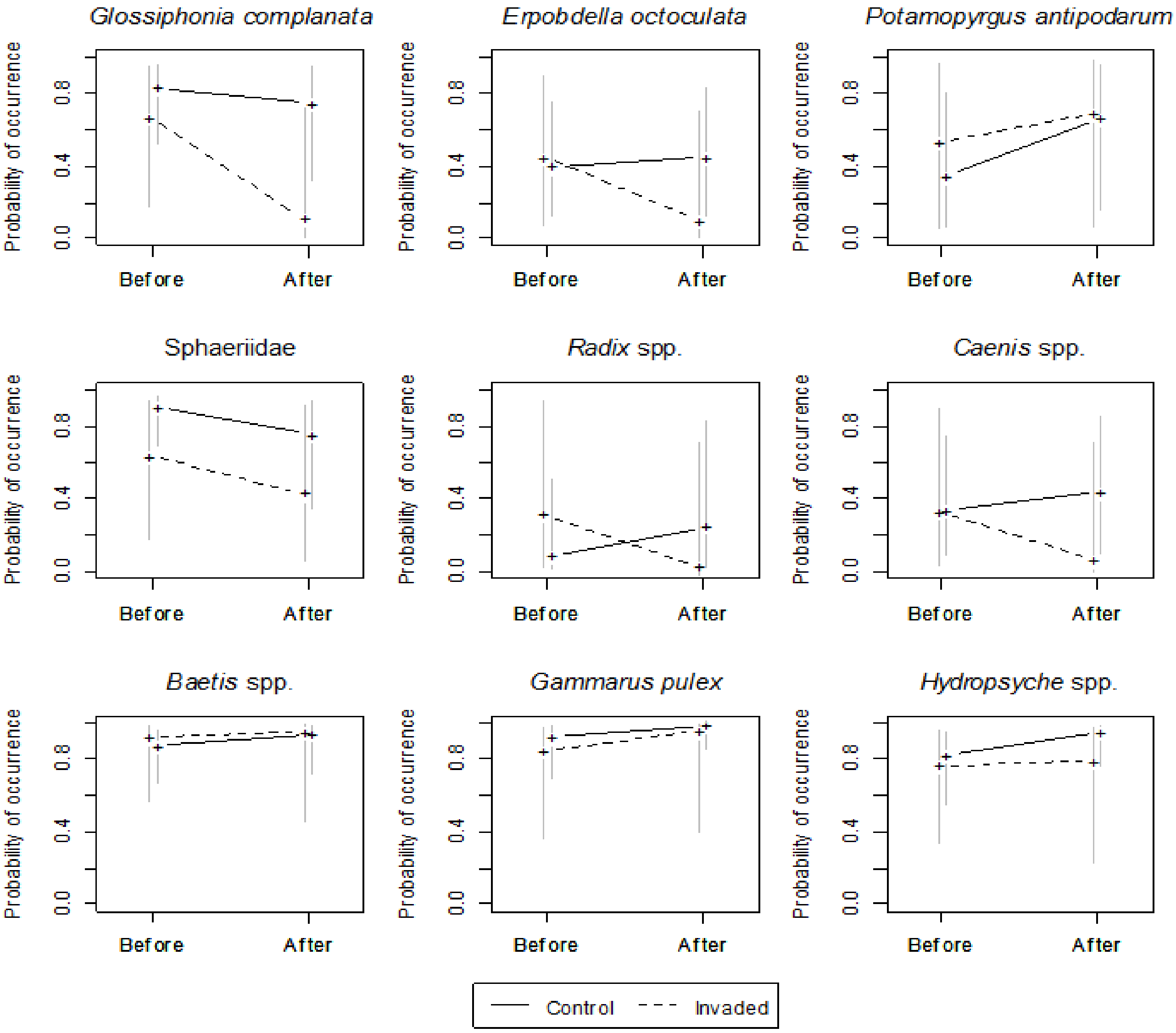

Figure 3.7 Predictions for autumn months (September – November) average probability of occurrence for individual taxa with confidence intervals for each combination of before, after, control and invaded factor based on autumn months. Predictions made for nine selected taxa using the Generalised Linear Mixed Model approach described in the text. Predictions of occurrence for each taxon are made using the global GLMM dataset (all regions) with predictions representing an average of all sites.

Table 3.7 Summary values for the Before-After-Invaded-Control interaction effects from the GLMM predictions for each taxon for spring and autumn. Significant terms are denoted in bold.

Taxon	Spring Standard Error	Spring Z-Value	Spring P Value	Autumn Standard Error	Autumn Z-Value	Autumn P Value
Hirudinea						
Glossiphonia complanata	0.978	-2.26	**0.024**	0.784	-3.57	**<0.001**
Erpobdella octoculata	0.791	-1.40	0.161	0.657	-3.42	**<0.001**
Mollusca						
Potamopyrgus antipodarum	0.765	-0.99	0.320	0.730	-1.21	0.225
Sphaeriidae	0.685	-1.21	0.228	0.692	0.20	0.840
Radix spp.	1.109	-2.91	**0.003**	1.151	-4.65	**<0.001**
Ephemeroptera						
Caenis spp.	0.744	-1.39	0.165	0.774	-3.61	**<0.001**
Baetis spp.	1.518	0.12	0.908	0.903	-0.38	0.700
Trichoptera						
Hydropsyche spp.	0.838	-2.55	**0.01**	0.703	-2.20	**0.028**
Crustacean						
Gammarus pulex	1.557	-1.88	0.06	1.004	-1.08	0.281

3.4.3 Biomonitoring scores

ASPT scores (derived from BMWP) demonstrated no significant changes following crayfish invasion, with both ‘control’ and invaded rivers demonstrating an increase in scores ($T_{3,\,846}$ = -0.183, P > 0.05; Figure 3.8a). BMWP, NTAXA and EPT richness displayed inconsistent responses following crayfish invasion when individual rivers and regions were considered; some rivers and regions displayed a decrease comparative to the ‘control’ rivers whilst others displayed increases (Figures 3.8b, c & d). Both LIFE and PSI displayed a significant elevation of scores following crayfish invasion compared to control sites. For both indices, the overall temporal trend of increasing scores was present in both ‘control’ and invaded streams, however the increases in invaded streams following invasion were determined to be statistically inflated ($T_{3,\,846}$ = 3.905, P < 0.001 and T =$_{3,\,745}$ = 3.905, P < 0.001 respectively; Figures 3.8e & f). When season was considered, LIFE and PSI scores displayed significantly inflated scores within invaded rivers for the autumn season ($T_{3,\,350}$ = 2.906, P <0.005 and T = $_{3,\,321}$ = 4.529, P<0.001 respectively; Figures 3.9a & b). In contrast no significant differences in the temporal trends between invaded and ‘control’ sites were identified for any of the biomonitoring scores for the spring sampling period (P > 0.05). All statistical significance values and measures of standard error for the Before-After-Control-Invaded interaction effect for each index and season (Spring and Autumn) are presented in Table 3.8.

Table 3.8 Summary values for the Before-After-Invaded -Control interaction effects from the GLM for each biomonitoring index

	SE	T-Value	P-Value	Degree of sig
All seasons				
BMWP	0.141	-3.374	<0.001	***
ASPT	0.135	-0.183	0.855	
NTAXA	0.148	-4.188	<0.001	***
EPT richness	0.139	-3.121	0.002	**
LIFE	0.134	3.905	<0.001	***
PSI	0.150	5.239	<0.001	***
Spring				
BMWP	0.253	-0.786	0.433	
ASPT	0.244	-0.008	0.994	
NTAXA	0.248	-0.692	0.489	
EPT richness	0.266	-1.513	0.131	
LIFE	0.233	1.576	0.116	
PSI	0.265	1.626	0.105	
Autumn				
BMWP	0.217	-2.605	0.010	*
ASPT	0.200	0.569	0.570	
NTAXA	0.224	-3.280	0.001	**
EPT richness	0.219	-2.429	0.015	*
LIFE	0.212	2.906	0.004	**
PSI	0.232	4.529	<0.001	***

N.B *** = P ≤ 0.001 , ** = P ≤ 0.005, * = P ≤ 0.05

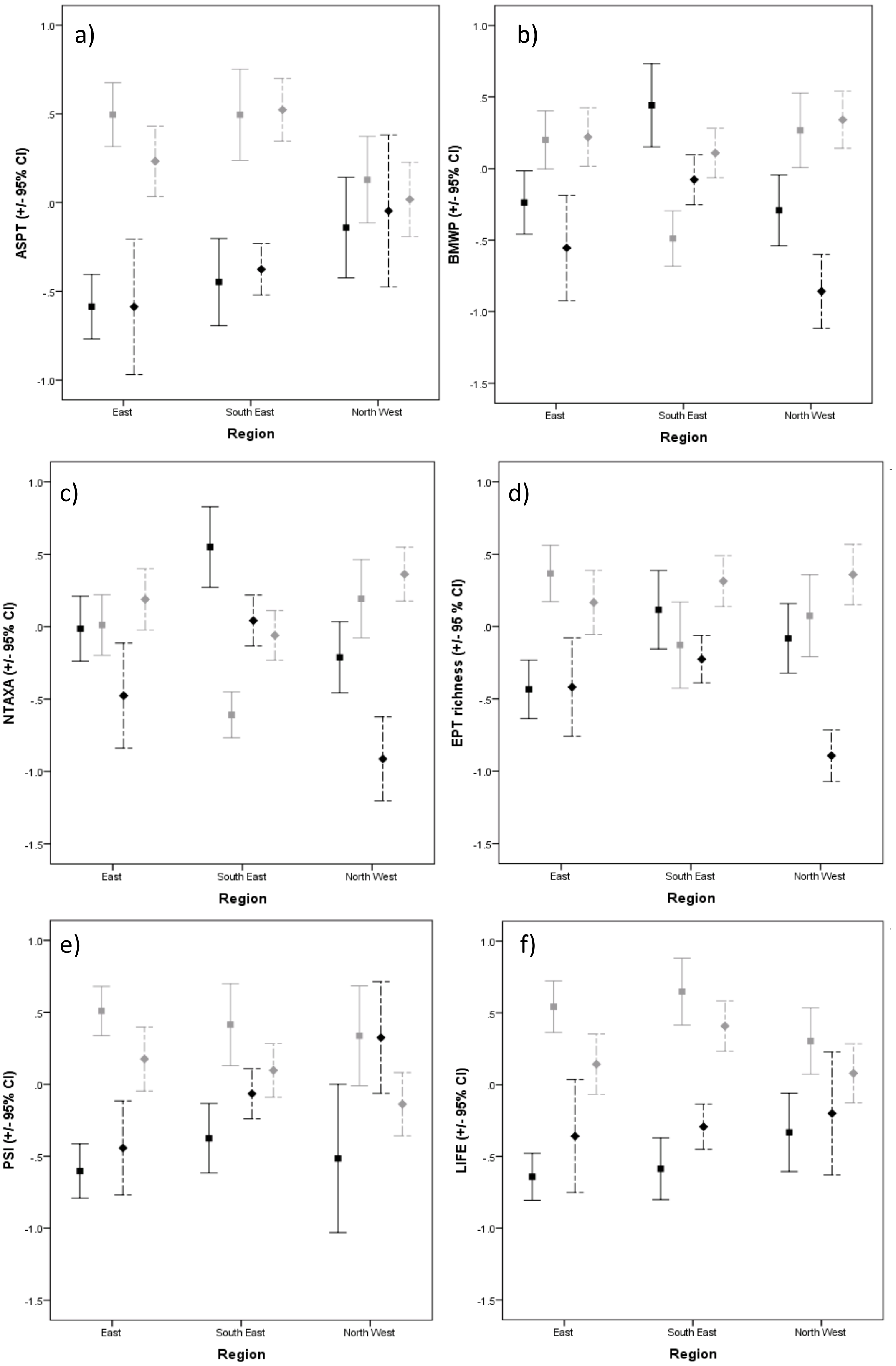

Figure 3.8 Macroinvertebrate biomonitoring indices (mean ± 95% CI) recorded for each before, after, invaded and control factor in East, South East and North West England; a) ASPT; b) BMWP; c) NTAXA ; d) EPT richness; e) PSI and; f) LIFE. Error bars that are black solid = Before Invaded; grey solid = After Invaded; black dashed = Before Control and; grey dashed = After Control. Metrics standardised to Z-scores.

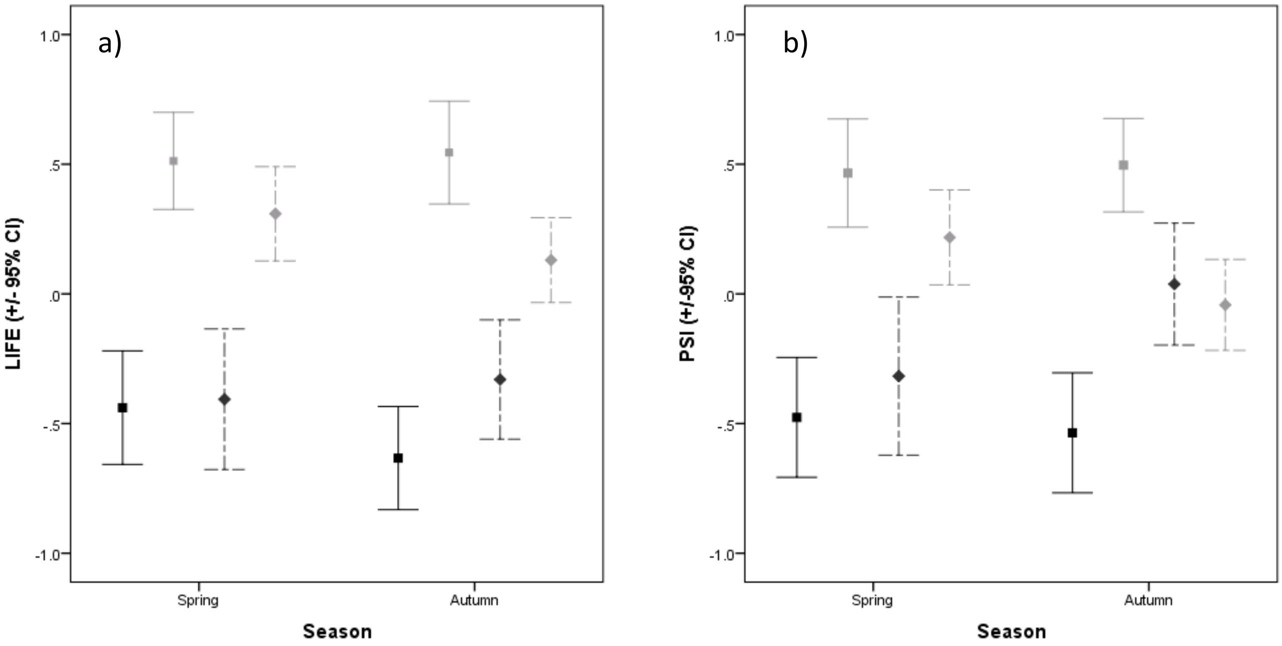

Figure 3.9 Macroinvertebrate biomonitoring indices (mean ± 95% CI) recorded for each before, after, invaded and control factor for spring and Autumn samples from all three regions; a) LIFE and; b) PSI. Error bars which are black solid = Before Invaded; grey solid = After Invaded; black dashed = Before Control and; grey dashed = After Control. Metrics standardised to Z-scores.

3.5 Discussion

3.5.1 Invertebrate community responses to *Pacifastacus leniusculus* invasion

The results from this study provide strong evidence that invasive signal crayfish affect invertebrate community composition in lowland rivers. All three regions examined experienced marked changes in benthic community composition following invasion when compared to both pre-invasion conditions and control sites. The effect on macroinvertebrate communities in all three regions was evident and consistent all year round, being strongest during autumn months, but was also apparent in spring months. Crayfish movement and growth is strongly driven by water temperature, with activity typically peaking during summer months (Sousa et al., 2013; Johnson et al., 2014). Consequently, stronger effects on macroinvertebrate communities during the autumn months were expected, as these samples typically occur at the height or toward the end of crayfish activity (notably directly after the breeding season). Slight differences in the taxa driving the community changes between seasons were also evident, suggesting that seasonal heterogeneity of prey availability, and thus preferential predation, is a key process determining the effects of invaders on macroinverterbrate communities (Xu et al., 2012).

In each of the regions examined, the community composition of control and invaded sites diverged when compared with samples from the pre-invasion period. In addition, control sites displayed a shift in community composition temporally, but these changes were different to those recorded in the invaded rivers, suggesting the presence of a widespread stressor across all sites. During the study period, England experienced highly variable hydro-climatological conditions with a series of high magnitude droughts and prolonged periods of low flows in 1989-1992, 1995-1997 and 2004-2006, with the latter years focussed in the South East of England (Marsh et al., 2007; Hannaford and Buys, 2012). With the exception of one site, the River Ver in South East region, the invasion by *P. leniusculus* occurred during or directly after one of these high magnitude low flow periods known to have resulted in community changes across England (Wright et al., 2004; Monk et al., 2008; Laize et al., 2014; Worrall et al., 2014). These periods are likely to have been associated with the changes to community composition at all of the sites examined and provides evidence to explain the long-term changes observed at control sites in addition to those at sites invaded by *P. leniusculus*. However, it is important to note that the invasion of sites in this study is likely to predate the point in which they were recorded in biomonitoring samples in some instances. As a result, the drought conditions may have facilitated the expansion of non-native crayfish populations. The interaction between flow regime / hydrological variability and invasive taxa requires further detailed examination. Evidence suggests that crayfish populations are not severely affected during high magnitude drought events (Jones and Bergey, 2007; Distefano et al., 2009; Dyer et al., 2015) and consequently invasive crayfish may have strong effects on stream ecosystems irrespective of the occurrence of hydrological stressors (Magoulick, 2014).

3.5.2 Temporal and spatial persistence of crayfish invasion effects

Results from this study indicate that crayfish invasions have long term effects on rivers across a broad biogeographical range with invasion effects not dependent on a specific physical setting. Community impacts were evident and persisted within all of the regions despite being characterised by different lithologies, flow regimes and habitat characteristics. Despite control and invaded rivers representing discrete communities following invasion in all sites, the degree of separation varied between regions. The effect of invasive crayfish is heavily dependent on original community composition as this dictates which species are preferentially predated. Communities which support abundant populations of taxa susceptible to predation will therefore be more severely affected following invasion events. I am aware of only two other studies which have examined the long-term impact of invasive crayfish on benthic communities thus far (Wilson et al., 2004; McCarthy et al., 2006), however both were focussed on lentic systems in North America over limited spatial scales. Both studies reported significant modifications to benthic community composition with dramatic long term and potentially irreversible effects on the ecosystem evident as a whole. Results from the current investigation, provide the first evidence that crayfish invasion effects within rivers are long-standing and persist once the invading population has become established.

Temporal trajectories of community change indicated that shifts occurred directly after invasion in the majority of rivers examined. As the precise date of invasion is not known for these rivers (IP on Figure 3.5 indicates the point they were detected in routine benthic samples), it is likely that densities would have reached significant numbers before being formally detected and explains the immediate shift in community following the identified invasion point. Time lags are typically evident in invasion processes, with the effects on communities often taking several years to appear as densities of the invading organism increase (Saki et al., 2001; McCarthy et al., 2006). The ordination plots of all invaded rivers suggest that no recovery of the communities occurred following the establishment of crayfish populations, with control and invaded rivers displaying distinct trajectories. Changes to the macroinvertebrate community in invaded rivers appear to occur rapidly once crayfish densities are high enough to be detected in kick samples (Hiley, 2003). Consequently it is likely that there is a threshold effect at which impacts on the macroinvertebrate community become significant and potentially irreversible. Early detection of signal crayfish in lotic ecosystems through routine monitoring is therefore imperative in order to manage and potentially limit the implications of crayfish populations on the wider macroinverterbrate community and ecosystem.

3.5.3 Taxa-crayfish interactions

Despite differences in the response of individual taxa following invasion, the occurrence of a number of ubiquitous taxa significantly changed across all regions. The class of Hirudinea is widely cited as being severely affected following crayfish invasion, typically demonstrating significant reductions in abundance (Stenroth and Nyström, 2003; Crawford et al., 2006; Ruokonen et al. 2014). Results from this study provide further evidence to support this with *G. complanata* displaying significant reductions in occurrence following crayfish invasion for both spring and autumn survey periods. The occurrence of *E. octoculata* was reduced considerably during the autumn months but displayed no significant differences during spring months (although reductions were evident). Differences in predation of these two taxa in spring months may be as a result of reproduction characteristics. Glossiphonids are the only leeches to brood and carry their young, whilst Erpobdellids form cocoons on the substrate, which may protect the young from predation during the months of March - July (Elliot and Mann, 1979). A number of reasons have been speculated as potential mechanisms to account for the reduction of Hirudinea taxa following crayfish invasion including the predatory nature of leeches and direct competition for resources. The life history of a number of Hirudinea species is strongly associated with gastropod populations as a function of their ectoparasitic nature (Elliot and

Mann, 1979; Ruokonen et al., 2014), although their low mobility and soft bodies most likely results in preferential predation by *P. leniusculus* (Stenroth and Nyström, 2003).

The most widely cited taxa affected by invasive crayfish colonisation are gastropods and bivalves, with reductions in species richness, abundances and biomass widely reported (Weber and Lodge, 1990; Lodge et al., 1994; Nyström et al., 1996; 2001; Stenroth and Nyström, 2003; Dorn, 2013; Ruokonen et al., 2014). Results from this study indicate a significant effect of crayfish on *Radix* spp. with reductions in occurrence observed during both spring and autumn months. Gastropods have been cited as being particularly vulnerable to crayfish predation because of their limited speed of locomotion (Hanson et al., 1990; Nyström and Perez, 1998; Rosewarne et al., 2013). However, not all mollusc taxa displayed similar responses. Sphaeriidae displayed no change in response to crayfish invasion (although some reductions were evident during spring months), nor did the non-native mud snail, *P. antipodarum.* Some life history characteristics may reduce predation effects and, as a consequence of their high predation risk, many gastropod species display avoidance behaviour by migrating above the waterline for several hours (Alexander and Covich, 1991; Crowl and Covich, 1990; Turner et al., 1999), whilst others demonstrate changes to their life history through enhanced growth rates and lowered reproduction rates (Hoverman et al., 2005). Under experimental conditions *P. antipodarum* has been shown to avoid predation through increased vertical migration in the presence of crayfish (Haddaway et al., 2014). This avoidance mechanism would enable them to evade crayfish predation and may explain why their populations remain largely unchanged in this study despite evidence of selective predation of crayfish on gastropod species based upon handling times (Crowl and Covich, 1990; Nyström and Perez, 1998).

Another taxon which is highly adaptable in their ability to evade predation and which displayed no change in occurrence for either spring or autumn months in this study was the freshwater amphipod *G. pulex*. This taxon has been widely cited as adopting various avoidance strategies in order to evade inter and intra-specific predation, including enhanced drift and locomotion, vertical migration and increased use of refuges (Andersson et al., 1986; McGrath et al., 2007; Haddaway et al., 2014). Consequently, it is likely that this species possesses a repertoire of strategies and defences towards predation, which potentially makes them able to evade crayfish more readily than other taxa. The vertical avoidance behaviour of *G. pulex* in the presence of signal crayfish, and the interaction of this behaviour with fine sediment is specifically considered and investigated in Chapter 6.

Several studies considering the impact of crayfish, have discussed the impact of crayfish on Ephemeroptera as a whole order, rather than individual taxa (Guan and Wiles, 1998; Usio and Townsend, 2004). Results from previous research suggests that the effects on Ephemeroptera are not consistent, with some studies documenting a decrease in abundance (McCarthy et al., 2006) or selective predation by crayfish on individuals with a greater body size (Guan and Wiles, 1998), whilst others have reported an increase in abundance or no change at sites where crayfish have invaded (Keller and Ruman, 1998; Usio and Townsend, 2004; Crawford et al., 2006; Grandjean et al., 2011). Results from the current study indicate that as an order, individual Ephemeroptera taxa may display different responses to crayfish invasion. Within this study, the largely ubiquitous ephemeropteran genus *Baetis* demonstrated no change in occurrence during both spring and autumn months. This most likely reflects their relatively high mobility, thus enhancing their ability to evade crayfish predation (Peckarsky, 1996). However, not all Ephmeroptera taxa displayed positive or benign responses to crayfish invasion, with *Caenis* spp. demonstrating significant reductions in occurrence following crayfish invasion during both spring and autumn. This reduction may reflect habitat preferences of most *Caenis* spp. for fine sediment accumulations which makes them prone to ingestion or physical disturbance by foraging crayfish (Capelli, 1980; Gutierrez- Yurrita et al., 1998; Usio and Townsend, 2004; Helms and Creed, 2005).

The Trichoptera *Hydropsyche* spp., also displayed a significant reduction in occurrence during both spring and autumn months following crayfish invasion. The majority of feeding activity by this taxa is associated with net building during spring and summer months, with net construction typically representing simple open structures to permit filter feeding (eg. Hildrew, 1995). This sedentary activity, in addition to the open nature of the fixed shelter (Mackay and Wiggins, 1979), may make them preferential prey for crayfish, in contrast to other caseless caddisfly larvae which are free living and mobile such as Rhyacophilidae (Elliot, 1968) or those which are much more hidden such as Psychomyiidae in fixed enclosed tunnel like galleries (Christian et al., 2005).

3.5.4 Crayfish influence on biomonitoring metrics

The results of this study clearly indicate that the presence of signal crayfish has not significantly changed the effectiveness of the commonly utilized water quality indices, ASPT, NTAXA or BMWP, employed for EU WFD ecological assessment (Furse et al., 2006). ASPT displayed no significant differences among control or invaded streams, with a similar magnitude of increase in the score over time. BMWP, NTAXA and the biometric of EPT richness all demonstrated no consistent pattern in either control or invaded streams, between regions or between rivers in the same region. However it should be noted that NTAXA demonstrated smaller increases at invaded sites comparative to control sites. All four of these scores are based on records of presence only and do not incorporate any weighting for the abundance of the taxa contributing to the score (recorded at family level). Furthermore, BMWP, NTAXA and EPT richness are additive measures which may be influenced by habitat richness and sampling effort, and are inherently more variable in species composition than their numerical score typically suggests (Clarke et al., 2003). It is likely that should these metrics include abundance weightings in their future derivations (as in the case of the proposed BMWP / NTAXA replacement – the Whalley, Hawkes, Paisley & Trigg metric; WHPT, WFD-UKTAG, 2014), then alterations to scores following invasion may occur and the resulting scores would need to be interpreted with this in mind.

Moreover, the taxonomic resolution used in scoring may play a key role in assessing how and whether crayfish effects are identified, with greater taxonomic level (genus or species level data), making identification of invasion effects more likely. Reduced taxa richness (number of taxa) has been observed in other studies associated with crayfish invasion (Crawford et al., 2006; Ruokonen et al., 2014), although the family level data used to derive the metric NTAXA did not identify any assemblage changes in the current investigation. Family level data may include a number of genus or species and these individuals are likely to display a high degree of variability in traits and responses to stressors. This effect has been highlighted in a number of studies (Marshall et al., 2006; Jones, 2008; Monk et al., 2012) and it is likely that coarser resolution data is unable to detect subtle community changes as a result of crayfish invasion, a factor evident in the South West (Appendix 2) with less clear separation of communities following invasion being apparent.

EPT richness (Ephemeroptera, Plecoptera and Trichoptera orders) demonstrated no response to signal crayfish invasion within this study, however this index is one of the most commonly employed bioindicators internationally (e.g. Ligeiro et al., 2013; Tonkin et al., 2015). The results from this study further highlight that interpretations of order level responses to disturbances associated with invasive crayfish should be undertaken with caution, especially orders supporting highly variable habitat and feeding preferences and life histories. Future studies concerned with inferring the effect of an invasive crayfish should do so using the finest level of taxonomy possible.

LIFE and PSI indices, which incorporate an abundance weighting component of taxa contributing to their score, both displayed significantly inflated scores following crayfish invasion compared to control rivers. The application of LIFE scores enables flow regime variability to be quantified based upon the flow requirements of invertebrate species (Extence et al., 1999). Macroinvertebrate community composition following crayfish invasion is reported to shift towards more mobile taxa adapted to faster flow velocities at the expense of slower, less mobile taxa (Parkyn et al., 1997). A number of studies have reported increasing or unaltered abundances or dominance of highly mobile and velocity sensitive Ephemeroptera larvae at sites where invasive crayfish are present, a shift in taxa which was present in the large scale dataset employed in this study (Usio and Townsend, 2004; Grandjean et al., 2011). The inflated LIFE scores recorded within invaded streams therefore most likely reflects the greater mobility of the remaining flow sensitive taxa, characteristics which are likely to enhance their ability to evade crayfish predation (Peckarsky, 1996). Predator avoidance strategies, including enhanced locomotion and vertical migration to the waterline or into the river bed (Crowl and Covich, 1990; Haddaway et al., 2014), by some taxa could potentially lead to the inflation or depression of biomonitoring scores. The application of biological indicators typically assumes that the impacts of predation and competition within macroinverterbrate assemblages are minor relative to the environmental changes that the index was designed (and employed) to detect. It is likely that native predatory species have little effect on the performance of biomonitoring tools because the community is adapted to the predation pressures. However, the invasion of a non-native ‘alien species’ into a waterbody may disrupt this natural equilibrium leading to changes in the performance of some biomonitoring tools.

The PSI score was designed to identify the effect of fine sediment pressure (primarily deposition) based upon tolerance ranges of individual taxa (Extence et al., 2013). It appears that the inflated PSI and LIFE scores recorded in this study were influenced by the markedly reduced presence of Gastropoda, Bivalvia and Hirudinea taxa. The prevalence of these taxa reduced significantly within this study, with two Hirudinea species (*G. complanata* and *E. octoculata*) and one mollusc (*Radix* spp.) being heavily affected. These taxa are among the most widely documented prey items of crayfish and may be selectively or preferentially predated by crayfish in many lotic ecosystems (Dorn, 2013). Although the prevalence of some prey taxa are likely to decrease in the presence of invasive crayfish, there is limited evidence to suggest that they become locally extinct. Consequently, the inflated PSI and LIFE scores may represent a shift to a community dominated by fine sediment and flow sensitive taxa through predation rather than a shift in flow regime or fine sediment present at a site (although future work is required to test this). Future application and potential modifications to these indices should consider the potential effect of invasive species upon them. The use of these indices in their current form could be used to help identify sites subject to invasive taxa but may also lead to the misinterpretation of the stressors affecting water bodies if not identified.

Given the variety of invertebrate biomonitoring tools available it is recommended that, where feasible, a multi-metric approach is employed in the ecological assessment of freshwater bodies. The application of individual metrics may not indicate pressures associated with the stressor it was designed to quantify, but when used in combination with other metrics derived in different ways (e.g. presence / absence data, total abundance or abundance weighted), may provide evidence to indicate the presence of an ecological stressor(s). Together with knowledge regarding the wider environmental and ecological context, this approach may help inform water resource and river managers of potential threats to the ecological status of freshwater bodies associated with the spread of invasive species.

When individual seasons were considered, no significant differences were recorded between control and invaded sites / rivers for the spring sampling period. As discussed previously (section 2.2.4), crayfish movement and growth is strongly regulated by water temperatures, with activity increasing with rising temperatures (Johnson et al., 2014). Spring samples typically occur when crayfish activity is at its minimum and consequently it is unsurprising that none of the indices were significantly affected at this time of year. In contrast, autumn samples are usually collected at the height or towards the end of crayfish activity (notably directly after the breeding season); with inflated elevation of both the LIFE and PSI scores evident at invaded sites. It is therefore recommended that routine biomonitoring samples collected in autumn need to be interpreted with caution if invasive crayfish are present or if their presence is suspected. Samples collected in spring were not determined to be significantly affected but should still be considered with caution. It is advisable that those applying macroinvertebrate biomonitoring indices to identify environmental stressors or those developing new indices should be conscious of the potential influence that invasive species may have on the effectiveness of such tools, especially if abundance weightings are incorporated in their derivation.

3.6 Summary

Crayfish are considered to be influential organisms within many aquatic ecosystems, interacting with all trophic levels of the food web (Creed, 1994; Momot, 1995). The results of this chapter provide direct evidence to suggest that the implications of crayfish invasion are persistent and result in major changes to benthic invertebrate communities, although the effects on the community are stronger during autumn. Invasion effects are not dependent on the physical and habitat characteristics of the lotic ecosystem, with modifications to macroinvertebrate communities evident across the range of bio-geographical regions typical of lowland rivers in the UK. The specific effects on the invaded ecosystem are however dependent on original community composition. The resulting fauna affected and those which account for the community changes observed may therefore vary between rivers.

The spread of invasive taxa across the globe may also represent a significant challenge to ongoing environmental monitoring programmes. The results of this research clearly suggest that the predation and interaction of an invasive species with the receiving ecosystem can significantly modify aquatic community composition. These community modifications may thereby affect the results of widely utilised biomonitoring indices and as a result care should be taken when interpreting routine biomonitoring data (i.e. water quality, river flow or fine sediment pressures) where non-native / invasive taxa are known to be present (MacNeil et al., 2013). This study highlights the value and need for further multi-scale research to fully understand the wider spatial and temporal implications of historic invasions to complement reach scale and mesocosm studies (Wilson et al., 2004; McCarthy et al., 2006). This fundamental knowledge base is needed to inform and underpin management strategies which are aimed at controlling and mitigating the effects of invasive species (Moorhouse et al., 2014).

The results of this chapter have resulted in two publications:

> **Mathers, K.L.,** Chadd, R.P, Dunbar, M.J, Extence, C.A, Reeds, J., Rice, S.P. and Wood, P.J. (2016) The long-term effects of invasive signal crayfish (*Pacifastacus leniusculus*) on instream macroinvertebrate communities. *Science of the Total Environment*. 556, 207-218.
>
> **Mathers, K.L.,** Chadd, R.P., Extence, C.A., Rice, S.P. and Wood, P.J. (2016) The implications of an invasive species on the reliability of macroinverterbrate biomonitoring tools used in freshwater ecological assessments. *Ecological Indicators*. 63, 23-28.

Chapter 4 - Crayfish and fine sediment dynamics

4. 1 Introduction

4.1.1 The interaction of zoogeomorphology and fine sediment dynamics

Disruptions to fluvial fine sediment dynamics as a result of anthropogenic activities are a global problem and can have significant implications for ecosystem health (Wood and Armitage, 1997; Burdon et al., 2013; Ramezani et al., 2014) and channel hydromorphology (del Tánago et al., 2015; Grabowski and Gurnell, 2016). Implementation of successful management strategies therefore relies heavily on understanding the processes and mechanisms at work within the fine sediment cascade (Owens et al., 2005; Grove et al., 2015). Much of our knowledge base underpinning such strategies is focussed on the assumption that abiotic forces dominate sediment dynamics. However, there is growing evidence suggesting fauna may have important and significant contributions to fine sediment dynamics, from sources through to transportation pathways and storage (Statzner et al., 2012; Albertson and Allen, 2015). Despite several early papers that identified the potential importance of organisms as geomorphic agents (e.g. Darwin, 1981; Davison, 1891; Reudemann and Schoonmaker, 1938) the number of studies which investigate these linkages remains limited.

Organisms can have significant and far reaching implications for the ecosystems that they inhabit. Many act as geomorphic agents, modifying the physical environment and influencing abiotic processes (Jones, 2012; Rice et al., 2012b). Organisms may also act as ‘ecosystem engineers’, altering the flow and distribution of resources, either through ecogeomorphological effects such as reduced water clarity or enhanced fine sediment availability which feedback into the ecosystem, or through strong direct ecological consequences such as predation or modifications to biogeochemical cycling (Jones et al., 1994; Wright and Jones, 2006; Chapter 3). There are numerous organisms that act as ecosystem engineers, but despite this there is no conceptual framework in place that enables understanding of when and where eco-engineers have important influences and effects for abiotic and biotic processes (Moore, 2006).

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

One such invasive species is the signal crayfish, *Pacisfastcus leniusculus*, which is considered to be one of the most widespread invaders in Europe (Kouba et al., 2014). Previous work has suggested that signal crayfish are significant biogeomorphic agents, altering the bed topography and roughness of gravel frameworks (Statzner et al., 2000; Johnson et al., 2010a) and enhancing coarse sediment transport (Statzner et al., 2003b; Statzner and Sagnes, 2008; Johnson et al., 2011). Signal crayfish have also been documented as mobilising large quantities of fine sediment on a diel basis associated with their nocturnal behaviour (Harvey et al., 2014; Rice et al., 2014; 2016; Cooper et al., 2016) and may enhance the delivery of fine sediment through the direct displacement of bank material as a result of burrow excavations (Guan, 1994; Rice et al., 2016; Faller et al., 2016).

Research has also considered the role of bioturbation, by a number of other crayfish species, on sediment accrual and interstitial sediment concentrations. Several studies have reported that both interstitial and benthic accumulation of fine sediment was lower where crayfish were present (Parkyn et al., 1997; Statzner et al., 2000; Helms and Creed, 2004; Albertson and Daniels, 2016a). However, these studies have been largely confined to North American rivers and have used *in-situ* enclosures or flume experiments such that they are predominantly focussed on coarse gravelly bed material. Reaches characterised by fine bed and bank material may respond differently and there is therefore a need to investigate processes at local scales in order to upscale and inform catchment level sediment management (Harvey et al., 2014).

Attempts to quantify the contributions of biotic and abiotic components to sediment transport are rare (Rice et al., 2016) and linkages to subsequent sediment deposition rates are absent. A number of ex-situ experiments have estimated the role of biota in sediment fluxes relative to abiotic controls (Statzner et al., 1999; Pledger et al., 2014; 2016), however very few studies have isolated the role of biota in the field at temporal and spatial scales sufficient to make robust estimations. Hassan et al's (2008) study on the contribution of salmonid spawning to baseflow bedload transport and Rice et al's (2016) study on the contribution of signal crayfish to baseflow fine sediment fluxes provide the two exemplar exceptions. In both instances, the role of biota induced sediment transport was significant (and at times dominant) during baseflow conditions.

Furthermore, studies which quantify reach-scale sediment storage have largely been overlooked to date, and those which account for biotic effects are scarce. A large variety of benthic dwelling organisms are likely to engineer the temporal and spatial distribution of fine sediment, altering settling and erosion processes (Swanson et al., 1982). One study, conducted on the Wadden Sea, an intertidal zone in the Netherlands, determined a significant seasonal impact of predominantly benthic invertebrates on the sediment budget at the scale of whole tidal basins (De Vries and Borsje, 2008); although, this study remains the exception. There is a clear need for further research to extend these observations and provide additional evidence that corroborates the overlooked geomorphic work that organisms may have on sediment dynamics in lotic ecosystems. As baseflow conditions are times when it is assumed that sediment transport rates are low (as determined by hydraulic conditions), alterations to fine sediment dynamics and the remobilisation and subsequent deposition will likely have significant implications for the health of aquatic communities. This is particularly true where this alteration is as a result of invasive taxa (Harvey et al., 2011).

4.1.2 The fine sediment problem and physical processes influencing fine sediment deposition

Excessive sedimentation pressures within aquatic ecosystems are of global concern and can have detrimental consequences for all aspects of ecosystem health (Heppell et al., 2009; Relyea et al., 2012; Naden et al., 2016). The deleterious effects of fine sediment on biota are well documented and it is clear from this evidence that the implications of fine material are predominantly associated with deposited rather than the suspended solids component (Kemp et al., 2011; Jones et al., 2012a, b; 2014). Consequently, effective management of fine sediment loading requires knowledge of the relationship between fine sediment deposition as a function of sediment supply and discharge (Diplas and Parker, 1992). Infiltration rates within a gravel framework are highly complex and dynamic, relating to a number of controlling factors including sediment supply (Petts, 1988), local hydraulics (Buffington and Montgomery, 1999), vertical and lateral interstitial hydrological exchange (Mathers and Wood, 2016), ratio of filtrating and framework particles (Gibson et al., 2009a), and stream capacity (Naden et al., 2016).

A number of studies utilizing controlled water releases from impoundments have examined the factors influencing infiltration rates of sediment, with fine sediment availability being a key determinant (Petts, 1984; Sear et al., 1993). Experiments conducted under laboratory conditions typically corroborate the importance of suspended sediment concentrations (Beschta and Jackson, 1979; Carling, 1984; Carling and McCahon, 1987). In general infiltration rates are highest during flood events when sediment transport rates are at maximum and sediments are scoured from pools and intergravel deposits (Beschta et al., 1981; Sear, 1993; Petticrew et al., 2007). There is however a need for studies which investigate the relationship of ingress under natural conditions (Franssen et al, 2014), and indeed whether biotic activities modify the rates of deposition.

Moreover, there is an apparent absence of studies which simultaneously investigate the relationship between flow (stream capacity), sediment supply (turbidity) and deposition at a sufficiently high resolution to assess the potential explanatory power of different facets of these regimes (Wohl et al., 2015). Direct data on sediment transport is severely limited relative to discharge and there is a need for more high resolution and long term suspended sediment concentration data in order to characterise the magnitude, frequency, duration, timing and rate of change in suspended sediment levels (*sensu* Poff et al., 1997). Greater understanding of the components of flow and sediment which are geomorphically important for infiltration could significantly enhance the knowledge base guiding management strategies.

Local hydraulic forces such as shear stress, flow velocity and the Froude number have been significantly associated with elevated fine sediment accumulation, but studies often disagree regarding the gross influence of hydraulic parameters (Petticrew et al., 2007). Beschta and Jackson (1979) found that the Froude number was positively associated with ingress, whilst Einstein (1968) and Carling (1984) found no relationship with flow parameters. Indeed, it is likely that the local hydraulic influences differ as a function of the dominant hydrological process. In slack waters, infiltration rates are higher because deposition rates are enhanced (Wood and Armitage, 1999), whereas in high velocity areas sediment supply is accentuated enhancing the availability of fine sediment for subsequent infiltration (Frostick et al., 1984). As such, the availability of fines (as regulated by supply, transport capacity and, potentially, biotic interactions) dominates the rate of infiltration irrespective of local hydraulics and framework size (Carling and McCahon, 1987; Sear, 1993). However, despite enhanced understanding of the small scale processes which control fine sediment infiltration at minute timescales, there is a distinct lack of studies that consider ingress over longer time frames (weeks- months) associated with broad scale process such as variable suspended sediment loads and discharge.

4.1.3 Integration of suspended sediment regimes and ‘geomorphological flows’ for fine sediment deposition assessments: lessons from ecohydrology

There is a growing need to set water management targets that maintain a healthy rate of fine sediment deposition globally (Collins et al., 2011) and gaining an understanding of the factors that influence fine sediment ingress at intermediate scales relevant to management strategies is vital (e.g. Naden et al., 2016). Despite the complexities arising from nonlinear interactions between water and sediment dynamics, in many cases the fine sediment regime can be managed through consideration of the flow-sediment balance (Wohl et al., 2015). In this regard, lessons can be learned from the large body of literature within the discipline of ecohydrology which utilizes a novel ‘redundancy’ methodological approach to associate time series hydrological data with spot measurements of ecology (Richter et al., 1996; Olden and Poff, 2003). These studies aim to determine the ecologically relevant components or ‘facets’ of flow (duration, timing, frequency, magnitude, rate of change in flow events; Poff et al., 1997) which support biologically healthy rivers, thereby enabling the setting of ‘environmental flows’ across the globe (Monk et al., 2007; Wharfe et al., 2014; Mustonen et al., 2016). However, it should be noted that data redundancy approaches should be applied with caution as they may reject variables of importance which are not principal drivers of statistical variability (Monk et al., 2007).

Increasingly studies have also adapted the facets framework in order to establish associations between stream temperature variability and instream communities (Jackson et al., 2007; Olden and Naiman, 2010; White et al., 2017). Using the ‘Range of Variability Approach’, annual river management targets can be identified using a comprehensive statistical characterisation of relevant regime characteristics (Richter et al., 1997). In a similar vein to environmental flow / temperature assessments for instream ecology, the implementation of management strategies that maintain a healthy level of fine sediment storage and transport within the ecosystem are likely to be highly dependent on determining the geomorphologically relevant components of flow and suspended sediment regimes; a challenge that has yet to be tested.

4.2 Research Aims

In this chapter the implications of signal crayfish for fine sediment dynamics will be examined at the reach scale within a lowland river in England, UK. In contrast to previous studies, the interactions of crayfish will be considered alongside a control river and will extend the observations into the implications for fine sediment storage and the overall effect for fine sediment budgets. In addition, the chapter seeks to examine the potential relationships between discharge and suspended sediment concentrations and how these regimes control fine sediment ingress within the river bed.

The aims of this study were twofold:

1. Quantify the potential role of signal crayfish on fine sediment dynamics (suspension, transportation and deposition) in association with a 'control' reach (free from crayfish).
2. Examine the relationship between discharge, turbidity and fine sediment ingress rates into the river bed, with and without crayfish.

To address the first aim three research questions were examined:

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

To address the second aim, a novel approach that investigates the relations between ingress and metrics of turbidity and hydrological time series was undertaken. A two stage approach was employed:

- i) Classification of hydrological and turbidity time series into a small subset of indices that effectively characterise dominant components of the series via a redundancy method (*sensu* Olden and Poff, 2003).
- ii) Examination of the dominant processes that influence the mass of sediment ingress using correlation matrices and the development of multiple linear regression models centred around principal components.

4.3 Methods

4.3.1 Field Sites

The study took place on two small lowland rivers in Rutland, UK. The south arm of the River Gwash is a headwater tributary of the River Welland, Leicestershire, UK (Figure 4.1). It drains approximately 24.5 km^2 of well-developed floodplains across a total relief of 127m before flowing into Rutland Water reservoir (surface area 10.86 km^2). Dominant land uses according to UK Land Cover Map 2000 are grassland (50%) and arable farming (36%; Fuller et al., 2002). Close to the catchment outlet, mean flow is 0.18 m^3 s^{-1} and Q_{10} (90th percentile) flow is 0.449 m^3 s^{-1} (Manton gauging station, Ordnance survey grid reference SK874050). Monitoring on this river focussed on a headwater reach approximately 450 m in length near the village of Brooke (SK8497705995) where the catchment area is 19.46 km^2. The second study river, the River Chater is also a small headwater tributary of the River Welland, Leicestershire, UK. It drains approximately 68.9 km^2 across a total relief of 190 m. Dominant land uses are arable farming (51%) and grassland (32%; Fuller et al., 2002). Close to the catchment outlet, mean flow is 0.52 m^3 s^{-1} and Q_{10} (90th percentile) flow is 1.16 m^3 s^{-1} (Fosters Bridge gauging station, Ordnance survey grid reference SK960030). Monitoring on this river focussed on a headwater reach approximately 200 m in length near the village of Ridlington (SK8494303710) where the catchment area is 32.22 km^2.

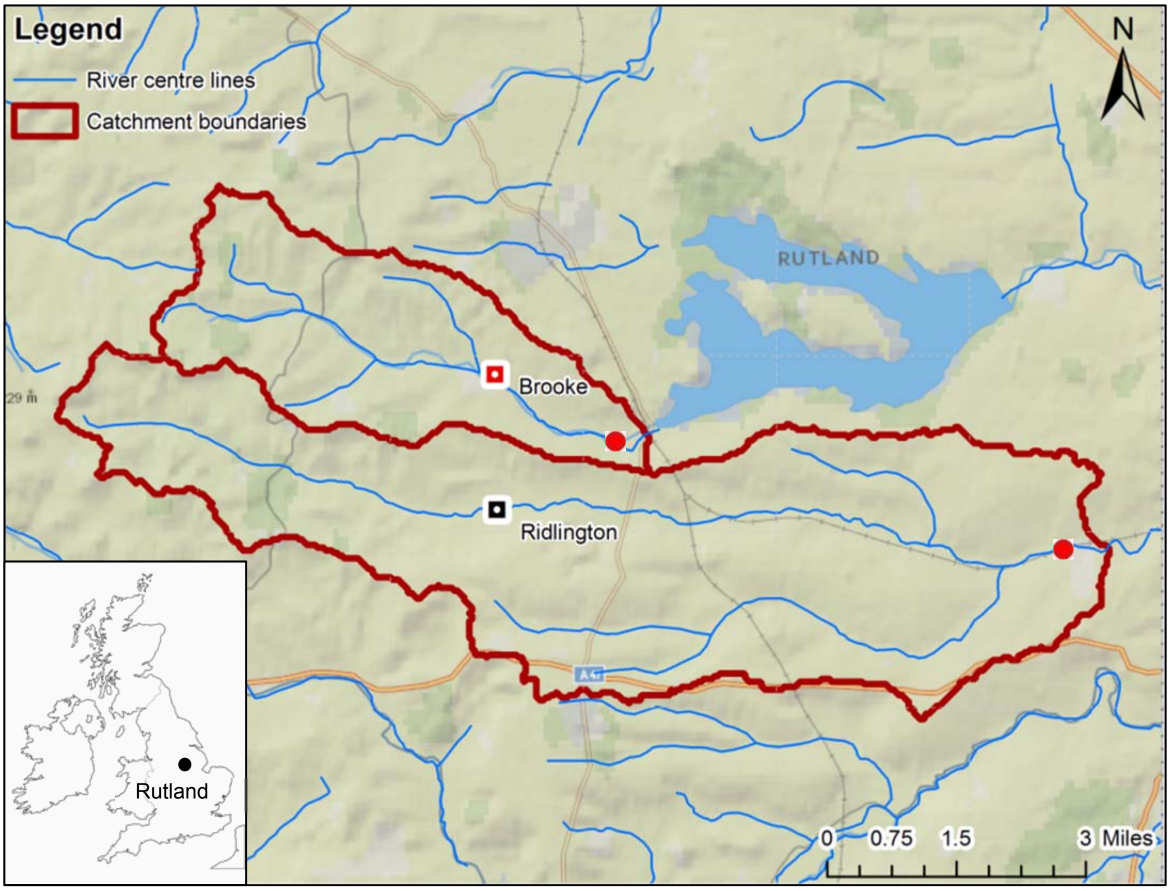

Figure 4.1 Location of study sites on the River Chater (Ridlington, control site) and River Gwash (Brooke, Invaded), Rutland, UK. Red circles indicate the location of the gauging stations for the respective rivers.

Sites were selected to be as broadly comparable in physical characteristics (channel size, water chemistry, altitude and geology) as possible. Sites were located 2.6 km apart and therefore experienced similar hydroclimatological regimes. Land use at both of the sites is predominantly arable farming and there was no grazing stock in the area or upstream of the reaches. Catchment geology is dominated by Jurassic mudstones and sandstones (British Geological Survey, 2008). The channels were characterised by riffle-pool structure and were between 4.3 and 6.5m wide at Ridlington and between 2.9 and 5.3m wide at Brooke (Bankfull width). Sampling of the surface material (400 pebble count from two pools and riffles – 200 at each [Wolman, 1954]) indicated variations in the GSD with Ridlington containing a larger proportion of coarser material in both pools and riffles (Table 4.1, Figure 4.2a). Subsurface bed material (based on four pooled individual McNeil samples from two pools / riffles per site, average sample weight 20.01kg [McNeil and Ahnell, 1964]) indicated similar grain size distributions (GSD) with Ridlington containing greater quantities of fine sediment (Table 4.1, Figure 4.2b). At both sites, significant quantities of fine sediment were available for transport (Figure 4.3). Macrophyte and benthic algae coverage was minimal at both sites (< 5%) and therefore did not influence sedimentation dynamics.

Invasive signal crayfish, *Pacifastacus leniusculus*, are present in high abundances in the River Gwash but historic routine sampling by the Environment Agency of England and contemporary sampling during the study period by the author has not recorded any individuals in the River Chater. Widespread evidence of crayfish at Brooke is present throughout the reach, with significant burrow excavations and subsequent enhanced bank collapse contributing a significant source of fine sediment at this site (Figure 4.4). Routine biomonitoring sampling (benthic macroinvertebrate) on the River Gwash by the Environment Agency first recorded *P. leniusculus* in 1996 at a site 2 km downstream of the field site (Gunthorpe SK8660305165). Signal crayfish are difficult to detect using routine sampling protocols (Gladman et al., 2010) so their presence in routine kick samples indicates a well-established and abundant population likely to be exceeding 1 per m^2. Density estimates obtained using baited trapping in 2014 and 2015 (represented by Catch Per Unit Efforts, CPUE) revealed abundances between 1.5 and 10.3 (mean 4.7, n = 20) adults per trap day at Brooke (Environment Agency Trapper Number EE073-L-487).

Electrofishing during summer 2016, using a back pack electric fishing machine at 108v and 1.5 amps, duty cycle 10%, frequency 50Hz was conducted on a 150 m stretch directly upstream of the water quality instrumentation equipment at both sites to assess the fish populations. Results indicated that the fish populations present at both sites are not large enough, individually or collectively, to act as significant geomorphic agents in the study rivers, with 16 bullheads (*Cottus gobio*) and 6 stone loach (*Barbatula barbatula*) sampled at Ridlington and 26 three-spined sticklebacks (*Gasterosteus aculeatus*) recorded at Brooke. Field sampling took place between 21st May and 24th September 2015 with a number of parameters being recorded during this time period at the two sites (see Table 4.2 for a breakdown of the sampling campaign). These are described in more detail below.

Table 4.1 Summary table of grain size distributions and fine sediment measures for the study reaches.

Grain size characteristic	Brooke Pool	Brooke Riffle	Ridlington Pool	Ridlington Riffle
Surface				
D_{16} (mm)	N/A	4.2	N/A	6.0
D_{50} (mm)	13.9	13.4	29.0	32.0
D_{84} (mm)	30.8	20.6	76.6	64.0
Mass < 4mm (%)	25.0	4.3	23.5	3.9
Subsurface				
D_{16} (mm)	1.3	1.4	0.9	0.8
D_{50} (mm)	8.6	9.1	8.0	7.8
D_{84} (mm)	23.0	24.2	23.5	36.3
Mass < 2mm (%)	19.8	20.0	23.9	28.8

Table 4.2 Summary of datasets collected for this study at Brooke and Ridlington.

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

+ data collected and - no data

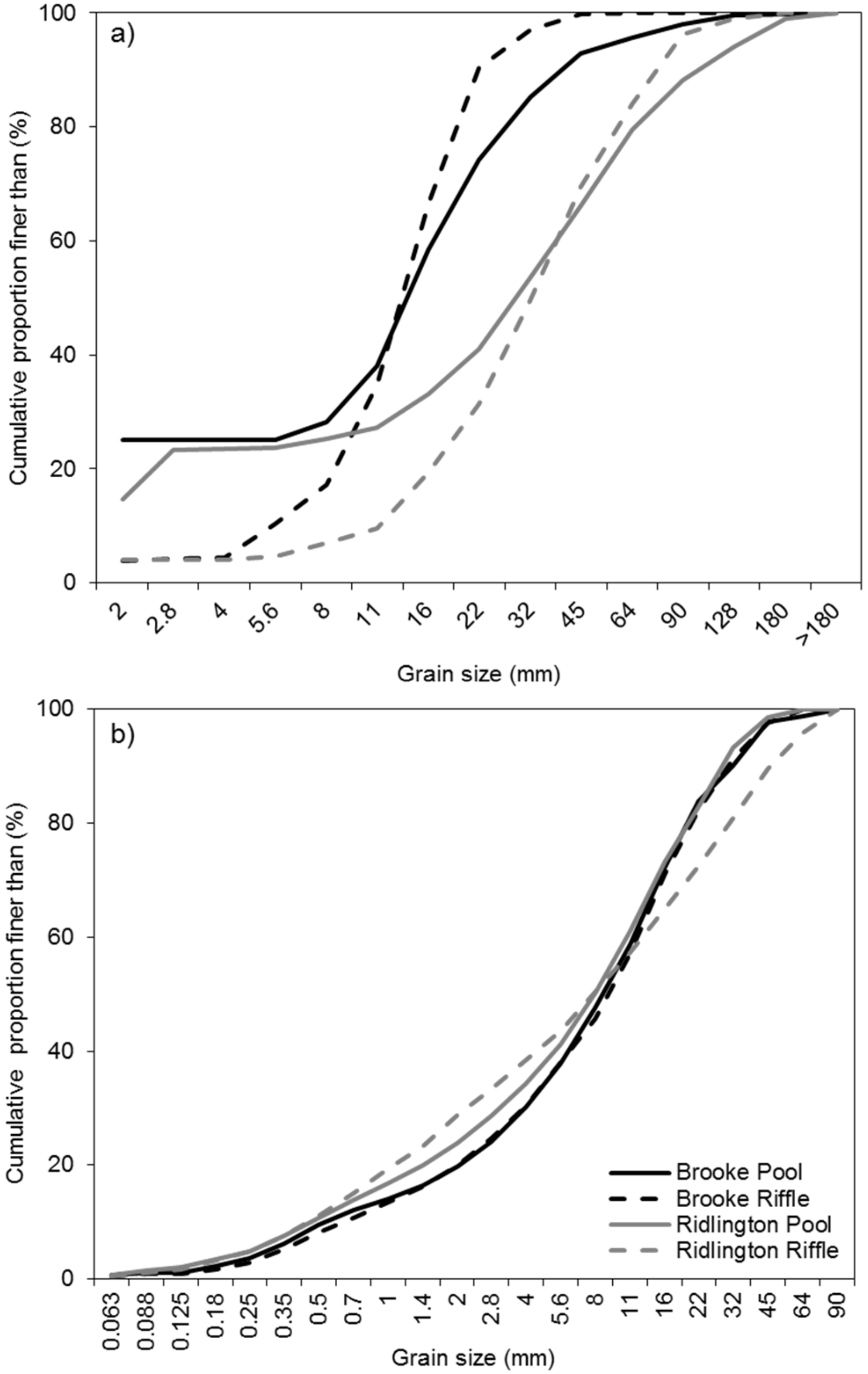

Figure 4.2 Grain size distribution of a) surface and; b) subsurface substrates at Brooke and Ridlington by riffle and pool sub-units.

Figure 4.3 Typical bed sediment composition of a) Ridlington and; b) Brooke showing abundant available fine sediment at both sites.

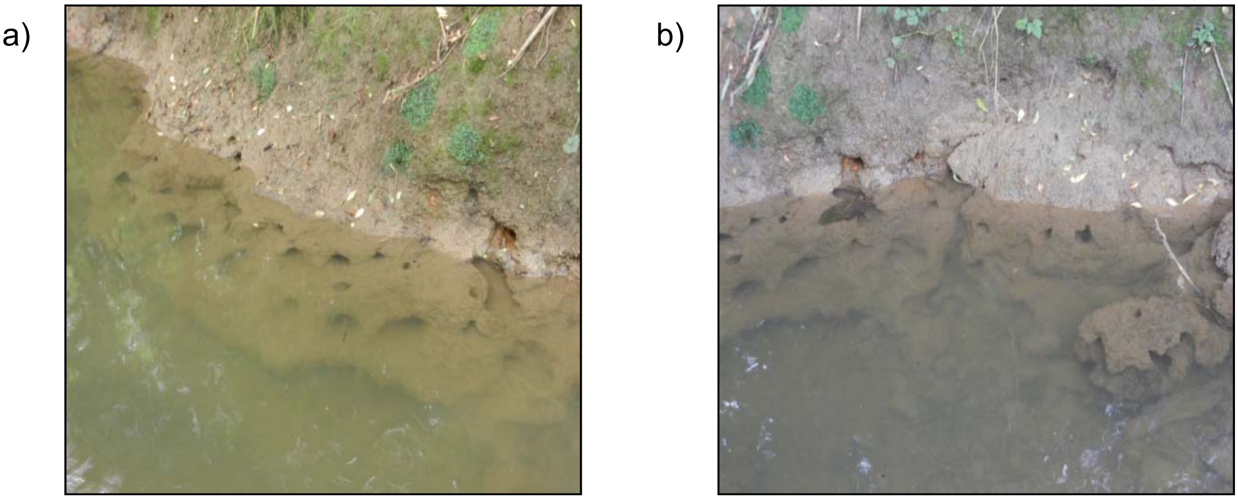

Figure 4.4 a) Evidence of extensive burrowing activity in the banks and clay river bed and; b) enhanced bank collapse as a result of signal crayfish burrowing activities. Photos taken at Brooke mid-reach in 2014.

4.3.2 Crayfish activity

Throughout the sampling campaign, crayfish trapping data was used as a surrogate for crayfish activity. Periodically (n=14), baited “trappy” traps (50 x 20cm with an opening of 5 cm and mesh size 3 cm) were deployed at Brooke in three pool locations throughout the reach (upstream, middle and downstream). On each occasion traps were set in a location during the afternoon and retrieved the following morning, with a total of two traps per site. The number of sites trapped on each occasion varied as a function of trap availability associated with a wider investigation on crayfish induced sediment fluxes (see Table 4.2 for a summary of number of sites trapped on each occasion). The minimum distance between each trap was 5 m and traps were located in the same place on each occasion. For each trapped individual, carapace length (mm; measured from the tip of rostrum to end of carapace), sex and evidence of damage was recorded. Catch Per Unit Estimates (CPUE) were calculated from the total number of individuals caught at each location for each sampling set and employed as an abundance index. Assessing the true abundance of crayfish is problematic because of the sampling difficulties previously discussed (Section 4.3.1) and consequently studies often report CPUE to enable comparison between datasets. CPUE standardises the data based on the effort (i.e. the number of individuals caught per number of traps and total time duration) and has been shown to be significantly correlated with other measures (Zimmerman and Palo, 2011). It should also be noted that trapping has a strong bias towards the largest individuals (Westman et al., 1999; Moorhouse et al., 2011a), often leaving the juvenile populations uncharacterised (Holdich et al, 1999), such that trapping is unable to accurately represent the true densities of crayfish present in the reach. To assess for any differences in crayfish parameters over time and by site, a one-way ANOVA was employed. Trapping was conducted on four occasions at Ridlington to confirm the absence of crayfish during the sampling period.

4.3.3 Turbidity records

Turbidity (nephelometric turbidity unit (NTU)) stage and water temperature were measured at both the upstream (U/S) and downstream (D/S) end of the reach at Brooke (5 minute resolution) using a Measurement Specialities, Eureka 2 Manta sonde fitted with a self-wiping turbidity sensor (International Organisation for Standardisation (ISO) 7027; 0-3000 NTU, quoted error ± 1%), vented pressure transducer (0 -10m, quoted error ± 0.003%) and thermistor (-5^{o}c – 50^{o}c, quoted error ± 0.1%). Turbidity, stage and temperature measurements were made at one location at Ridlington at the upstream boundary of the reach using a Seametrics, Instrumentation Northwest, Inc (INW) self-wiping Turbo sensor (0-3000 NTU, quoted error ± 2%). Water pressure and temperature were measured using a vanEssen Instruments Mini-Diver DI501 pressure transducer (0-10m, quoted error ± 0.5%; -20^{o}c – 80^{o}c, quoted error ± 0.1%) with stage calculated through barometric atmospheric pressure compensation using a vanEssen Instruments Mini-Baro DI500 pressure sensor (quoted error ± 0.5%). Turbidity sondes were mounted horizontally 0.1m above the river bed with the sensors approximately 0.3m from the left bank.

Recording problems during the study were intermittent. Where records were affected by timing problems (i.e. a record was missed resulting in a 10-minute resolution at times), records were interpolated by using a local average (of the previous and subsequent record). Where data series consisted of large sections of missing data, this was unable to be interpolated and remained as gaps in the time series. Ridlington datasets ran from 17th June 2015 – 31st October 2015 (136 days) with 12.0 days being removed as a result of biofouling problems. Upstream (U/S) measurements at Brooke ran from 8th June 2015 – 31st October 2015 (145 days) with 18.1 days missing due to recording problems. Brooke downstream (D/S) records ran from 8th June 2015 – 12 October 2015 (126 days) and include 7.32 days of missing data (Table 4.2 indicates the time periods affected for all three sondes).

The performance of the turbidity sensors were tested to ensure measurements were not adversely affected by local environmental conditions such as daily fluctuations in incident radiation and temperature (Rice et al., 2016). At each site on separate occasions, a second identical sensor was installed immediately adjacent to the main sensor but located inside a rectangular Perspex container (internal dimensions 0.13 m x 0.75 m x 0.4 m) fixed to the river bed (Figure 4.5). The box was water tight around the base but was without an upper surface and therefore the sonde experienced the same daily fluctuations in temperature and light but was filled with clean tap water. In the absence of any temperature or incident light fluctuations it was anticipated that the sonde would read a constant low turbidity reading compared to that within the stream. Turbidity measurements were not affected for either model of turbidity sensor; the turbidity time series in the box did not fluctuate whilst variations were present in the stream series (Figure 4.6). Water temperature measurements inside and outside the box confirmed that the temperature and light fluctuations were similar during each test.

Figure 4.5 Equipment integrity testing. One sensor was located in stream water and as such experienced natural variations in turbidity. A second was placed adjacent in a perspex box filled with clean tap water. Both experienced the same incident light and temperature fluctuations.

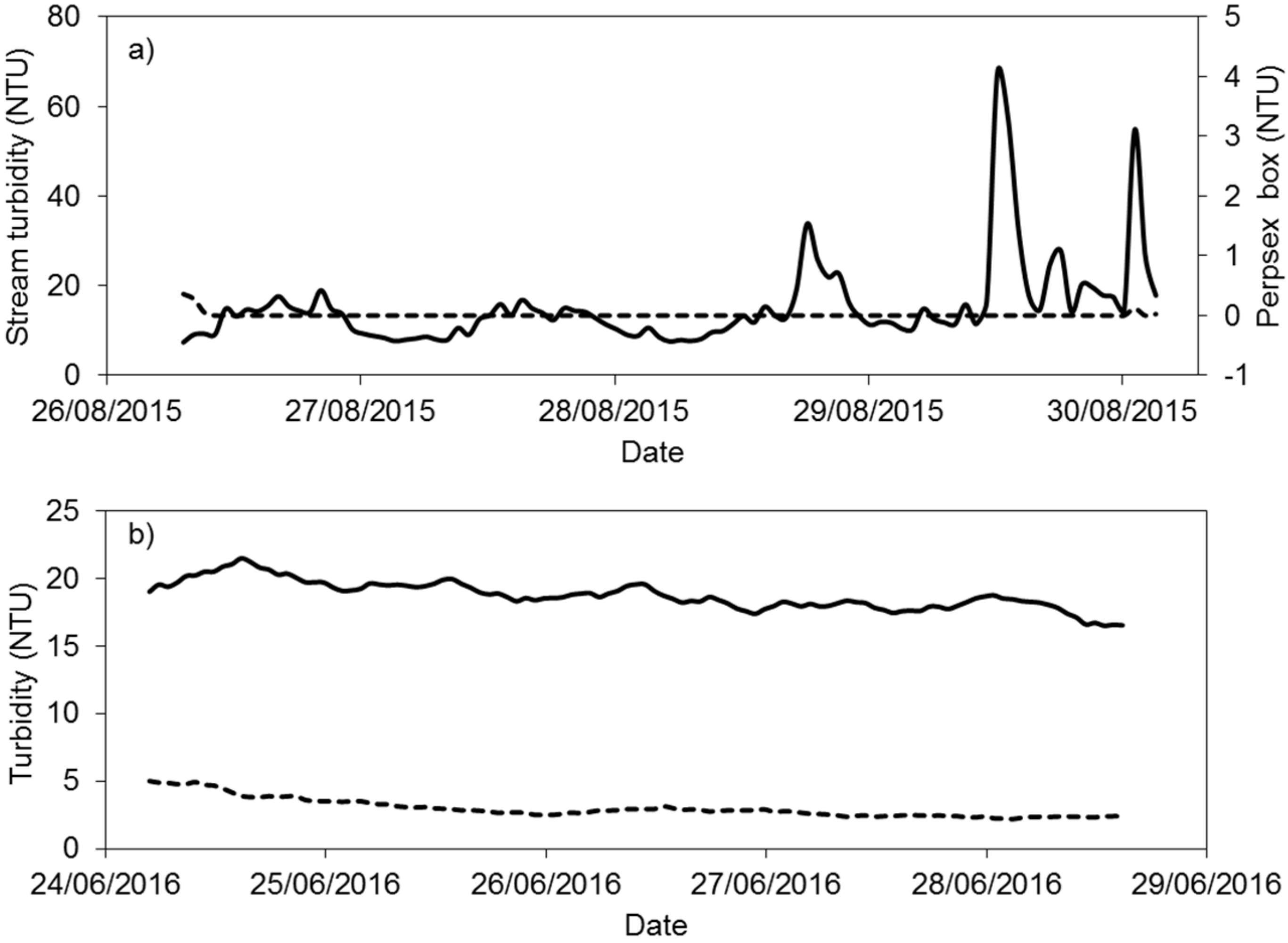

Figure 4.6 The effect of light and water temperature on sensor performance for: a) Eureka Manta 2 sensor and; b) INW turbo sensor. The solid line represents the sensor in the stream and the dashed line is for the instrument in a perspex box adjacent to it. Hourly averaged turbidity is plotted. Tick marks are at midnight. The large spikes at the end of the record in a) represent a number of storm events.

The time series of turbidity measurements were analysed to determine the presence of a diurnal bioturbation signal as a result of crayfish presence and activity. Dominant periodicities in the turbidity measurements were examined by calculating periodgrams of the time series using the software PAST version 3.12. Periodgrams enable the investigation of periodic components (or frequencies) of a time series to determine the presence of statistically significant oscillations (Hernandez, 1999). Prior to analysis, data were despiked by replacing individual data records that were greater than 1 SD from the monthly average with the local average (of the previous and subsequent 5-minute record). Periodgrams were then calculated to provide a graphical representation of the measure of relative importance of all frequency values that may describe the oscillation pattern within the data; thereby enabling the dominant frequencies in the series to be identified (Stoica and Moses, 2005). Periodgrams were calculated using the Discrete Fourier Transform (DFT).

4.3.4 Suspended sediment concentrations

At each site, water samples were collected to enable the determination of suspended sediment concentration (SSC). Samples were taken using an ISCO 3700 automated water sampler fitted with a stage-activated trigger that drew water up from an inlet hose located immediately adjacent to the turbidity sensor (Brooke D/S and Ridlington). A total of 240 500 ml samples were collected at Brooke during six storms and by periodic sampling over 12 days (samples were collected at midday and midnight) on four occasions. At Ridlington 168 samples were collected during three storms and during two occasions of periodic 12-day sampling. 75 samples had to be discarded from Ridlington and 34 from Brooke because elevated turbidity values in the series which persisted for longer than a 15 minute period indicated that material may have built up on the sensor, or that recordings were affected by technical issues. This resulted in a total of 93 and 206 samples respectively from Ridlington and Brooke. Collection of periodic samples every 12-hours enabled visual corroboration of diurnal variability in SSC as inferred from turbidity measurements. Storm samples over a range of flows provided a large range of SSC values to enable a more accurate calibration model to be constructed.

The single point measurements of turbidity and sediment concentration were assumed to be representative of the average cross-section values based on the small size of the streams (Rice et al., 2016). Samples were filtered using Whatman 0.7μm glass microfiber filters and routinely analysed for percent organic matter by weight (% TOC) through oven drying at 105^{o}c overnight and carbonate content by weight (% TC) through Loss-On-Ignition (LOI) at 550^{o}c (2 h; % C-organic; Dean, 1974). Using continuous measurements of turbidity as a surrogate of SSC should be undertaken with caution since turbidity measurements are sensitive to the physical characteristics of the material including the presence of organic detritus (Lewis, 2003; Bilotta and Brazier, 2008). The average organic component of samples at Brooke was 21.5% (SD = 5.36%) and 26.31% at Ridlington (SD = 7.77%) and as a result SSC was calculated using only the mineral mass.

A site-specific calibration was constructed using a LOESS model (Hicks et al., 2000; Gray et al., 2015; Rice et al., 2016) that best described the nonlinear relationship between turbidity and SSC. Preliminary testing indicated that an alpha smoothing value of 0.4 provided the best fit at both sites. For both the U/S and D/S sites at Brooke LOESS models utilized one data set of SSC values extracted from water samples, but models were fitted to corresponding local turbidity measurements. These models were used to extract SSC values for the entire time series at the three locations (Figure 4.7). Despite fluxes not being calculated for Ridlington (described in the subsequent section, 4.35, for Brooke), SSC calibration was conducted to enable validation of the turbidity measurements and overcome site-specific differences in transported material (Grayson et al., 1996). Conversion of the data also provides a continuous record of SSC which enables the potential ecological consequences of sediment levels to be evaluated (Bilotta and Brazier, 2008) and which can help inform management strategies given the paucity of high resolution SSC records to date (Duvert et al., 2011).

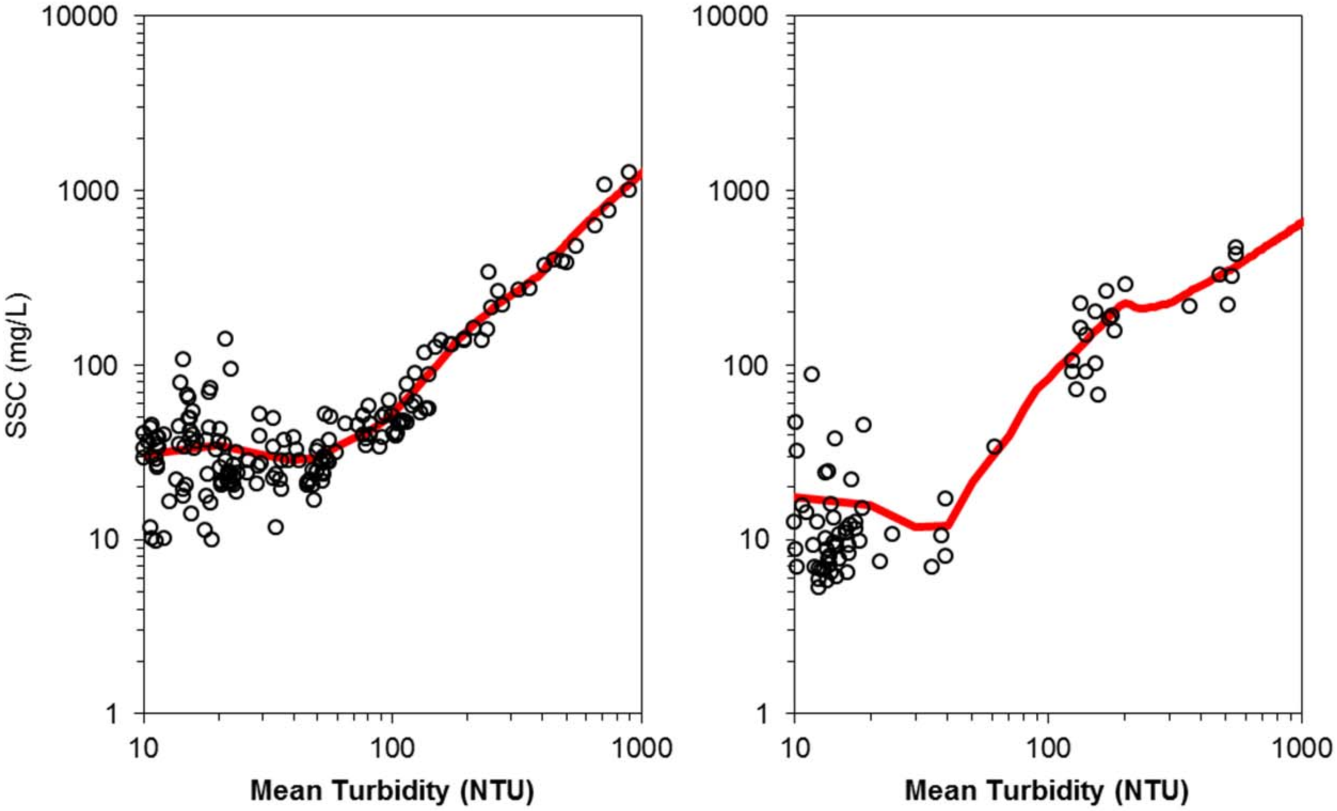

Figure 4.7 LOESS calibration model (smoothing parameter α = 0.4) for: a) Brooke (n = 206) and b) Ridlington (n = 93) based on concurrent measurements of turbidity and suspended sediment concentration.

4.3.5 Sediment flux estimation at Brooke

Sediment fluxes at Brooke were quantified in order to assess the implications of a crayfish infested reach on suspended sediment budgets. Stage measurements associated with a pressure transducer (0.001 - 3.05 m, quoted error ± 0.003 m; Teledyne ISCO 2150) were recorded at a 15-minute resolution. The sensor was mounted horizontally on a metal plate resting just above the river bed in the centre of the upstream cross section at Brooke. Physical measurements of discharge were taken on ten occasions across a range of flows using the velocity - area method (Herschy, 1993). Measurements were made at a cross section 1 m upstream of the turbidity sonde (cross sectional area) with 30 second averaged velocity values ($m\ s^{-1}$) recorded using a Valeport electromagnetic current meter at 0.4 of the water depth.

The correlation between ISCO measured water depth values (D) and measured discharge calculations was significant ($r = 0.98$, $P<0.001$) and a first order polynomial regression model ($R^2 = 0.99$) was fitted to determine discharge (Figure 4.8): $Q = 1.69D^2 – 0.18D – 0.09$. ISCO depth measurements were spilt into 5 minute resolution (i.e. one 15-minute depth measurement was employed for the three 5-minute corresponding time values). The ISCO velocity module was not deployed until later on in the sampling campaign, July 18th 2015, and as a result U/S Manta depth values were converted to ISCO depth values for use in the polynomial model for this preceding time period. Correlation between the ISCO depth measurements and U/S Manta depth measurements was significant ($r = 0.99$, $p <0.001$) and a linear regression model ($R^2 = 0.98$) was fitted: $D = 0.96x+ 0.13$ (Figure 4.9). The polynomial model was subsequently used to estimate discharge for the corresponding time series. Discharge was assumed to be similar at the U/S and D/S reach locations due to the spatial proximity and small nature of the streams.

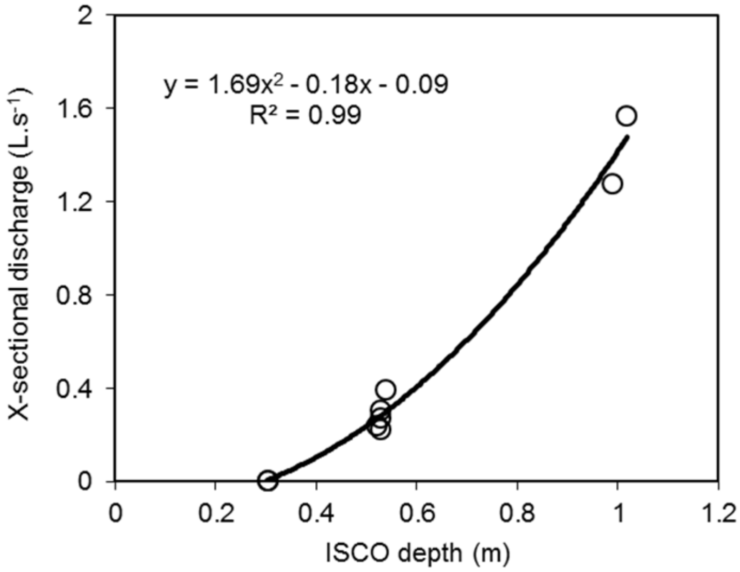

Figure 4.8 First order polynomial regression model based on physical measurements of cross sectional discharge and ISCO water depth values at Brooke.

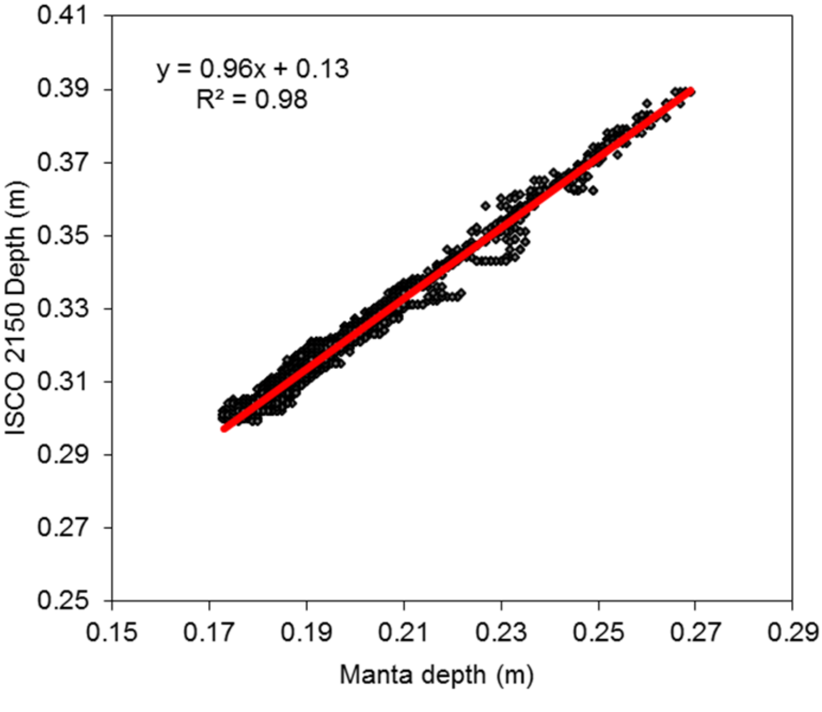

Figure 4.9 Linear regression model based on measured water depth by Manta and ISCO sensors at Brooke U/S (n = 13293).

Discharge measured by an Environment Agency gauge located at Manton approximately 3.2km downstream of the monitoring site provides a means to check the quality of the data derived from Brooke. The measurements are closely matched with a correlation of 0.95 at a lag time of 1.5 hours. Moreover at this lag rate, the discharge is on average 1.4 times smaller which is consistent with a 1.3 fold increase in discharge area at Manton. Discharge values are therefore reliable and were used with corresponding estimates of SSC to calculate sediment fluxes SF (mg s^{-1}) for each 5 minute interval at Brooke (both U/S and D/S). For a desired time period the suspended sediment load SL (kg) was calculated as:

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

[1]

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

4.3.6 Isolation of abiotic and biotic components of sediment load at Brooke

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

$$SL_{bf} = SL_{bfB} + SL_{bfA}$$

[2]

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

There is one significant uncertainty in this method in that the abiotic value of turbidity is not known. A minimum estimate was employed which constituted the minimum measured value of turbidity each day (Figure 4.10). However, minimum turbidity values are likely to be elevated by the residual effects of the previous night's bioturbation and as result it is possible that in the absence of such activity, turbidity levels could reach lower values resulting in estimates being much smaller than in reality. No efforts were made to decompose flood periods as it is not anticipated that bioturbation would have a significant effect on entrainment during high flow events (Moore, 2006; Albertson and Allen, 2015) and is therefore assumed to be negligible.

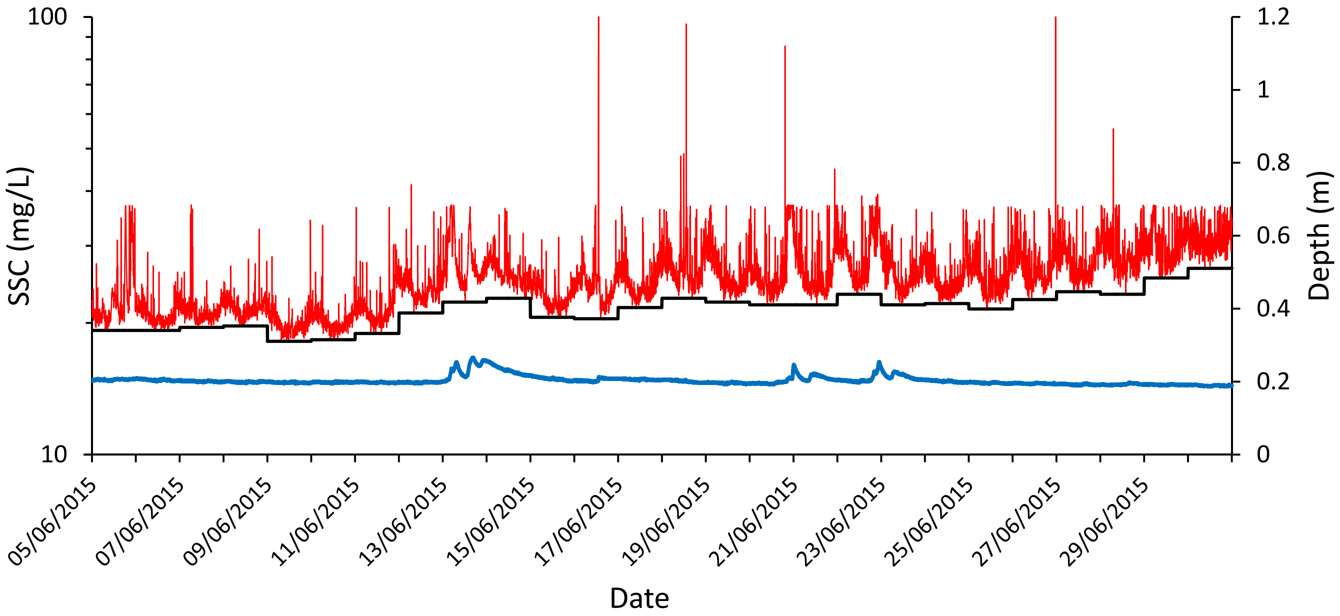

Figure 4.10. Example plot of decomposing the turbidity data into biotic and abiotic components. The red line is five minute turbidity data, the blue line is five minute stage data and the black line indicates the minimum turbidity value used as a surrogate for the abiotic fine sediment load. The area above the black line and below the red is assumed to represent enhanced fine sediment fluxes associated with biota.

4.3.7 Sediment balance at Brooke

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

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

where I is the sediment input, O is the sediment output and ΔS is the change in sediment storage.

4.3.8 Sediment ingress rates

4.3.8.1 Experimental setup

At both Brooke and Ridlington, sediment traps were installed that measured fine sediment ingress rates with the aim of evaluating whether crayfish presence and corresponding impacts on turbidity have a significant effect for fine sediment storage. Each trap comprised a PVC cylinder (diameter 65 mm, height 200 mm) perforated with twelve horizontal holes (diameter 6 mm) to permit both horizontal and vertical exchange of flow and fine sediments (Mathers and Wood, 2016). All cylinders were filled with a prewashed gravel framework collected from each of the respective sample sites (truncated at 8 mm) that was enclosed in a net bag (7 mm aperture) within each cylinder. Application of a local gravel framework negates the potential influence that differing framework matrices have on ingress rates (Petticrew et al., 2007).

Cylinders were inserted into the river bed by placing the PVC cylinders onto a steel pipe (35 mm diameter) that was then driven into the bed sediments by hand using a sledge hammer and subsequently moved from side to side until a sufficient sized hole was formed (Figure 4.11). Cylinders were inserted flush with the sediment surface to a depth of 200 mm (Figure 4.12). The surrounding stream bed remained unchanged and consisted of non-uniform cobbles and gravel. Cylinders were left *in-situ* for the entire sampling campaign, but every 14 days the gravel netting bag was removed and replaced, providing a constant record of sediment accumulation at a 14 day resolution. At the end of each 14-day sampling period, the net bag (containing the gravel clasts) was carefully lifted out and retained with a 250 µm net held directly downstream to catch any material mobilised during extraction. Empty cylinders were then replaced with a clean gravel bag. Sediment traps were installed 21st May – 24th September providing a record of 126 days (9 sample sets).

Figure 4.11 Sediment trap installation process**.**

Figure 4.12 Sediment traps *in-situ.*

Three riffle sites were examined at Brooke and two at Ridlington (initially one until 2nd July 2015) at Ridlington. At each riffle four cylinders were installed providing a total of 12 replicates at Brooke and 8 at Ridlington (4 initially for 3 sample sets). Samples were evenly spaced across the riffle unit (head through to tail) as fine sediment accumulation can vary as a function of longitudinal vertical hydrological gradients (Mathers and Wood, 2016). In total 105 and 57 ingress samples were examined from Brooke and Ridlington respectively (3 ingress cylinders were lost at both sites during the campaign; Table 4.2 provides a breakdown of sample and riffle replicates over time).

4.3.8.2 Laboratory and statistical analysis

In the laboratory, the contents of the cylinder samples were passed through 4 and 2 mm sieves to remove the artificial substrate. The remaining sediment was passed through a 250 µm sieve to retain invertebrates (subsequently presented in Chapter 5) and larger clasts, with residual fine sediment (< 250 µm) collected and retained in a settling container. Once samples had been processed for invertebrates all grains (< 2 mm) were combined with the residual fine sediment in the container and left to settle. Fine sediment samples (< 2 mm) were oven dried at 60 ^{o}C until a constant weight was recorded (Pacioglu et al., 2012). Samples were gently disaggregated, passed through a sieve nest (1000 μm and 125 μm) and each fraction weighed to determine the grain size distribution (1000-2000 μm, 125-1000 μm; <125μm; Gordon et al., 1994). Grain sizes were examined because the rate of fine sediment ingress is inherently associated with the ratio of pore filling / infiltrating particles to the framework matrix (Fings et al., 2008).

Prior to analysis sediment weights for each grain size were converted to deposition rates (kg m^{-2} d^{-1}) for each sample set. A linear mixed effects (LME) model was employed to examine grain size differences with regards to site (Brooke or Ridlington) and over time. Models were fitted using the 'nlme' package in R Version 3.1.2 (R development Core Team, 2014). Two model types were employed for each grain size fraction; one in which temporal differences were considered with site and time specified as a fixed factors and riffle as a random factor (reflecting that cylinders at individual riffles are less independent); and a second model structure considered rates independent of temporal differences with riffle nested in time as a random factor. Pairwise comparisons of rates for each individual time period were also conducted. All models were fitted using the restricted maximum likelihood (REML) estimation function.

4.3.9 Relationship between suspended sediment, hydrology and sediment ingress rates

Hydrological variability over the sampling period was analysed using data collected from local Environment Agency gauging stations on the River Chater (Fosters Bridge) and River Gwash (Manton) at 15 minute resolution. Discharge data (m^3 s^{-1}) were converted to hourly averages and scaled based on catchment drainage area to facilitate the identification of marked differences in the series including known hydrological events (floods or low flows). To measure the association between flow and turbidity, Spearman's rank correlation (data was not normally disturbed) was conducted on hourly averaged time series.

To assess whether aspects of the turbidity and discharge time series varied by site and time, 23 turbidity and 14 flow indices (Table 4.3) were calculated for each 14-day sampling period at Ridlington and Brooke D/S (selected as the most consistent record). Indices were based around the five facets of the two regimes which consist of the following components; magnitude – amount moving past at a given time and includes minimum and maximum; frequency – how often the time series goes above a given magnitude; duration – the period of time over a specific threshold and; rate of change – how quickly the time series changes from one magnitude to another (Richter et al., 1996; Poff et al., 1997). Timing of events was not considered due to the short temporal scale of the study. Much of the work to date focussed on characterising hydrological series for the purposes of hydroecological relationships have done so over long time scales (multiple years) and as such the most relevant indices from previous studies were adapted for this study (Richter et al., 1997; Olden and Poff, 2003; Monk et al., 2007).

In addition, a number of the indices were calculated which aimed to characterise the potential effect of biotic diurnal bioturbation on the turbidity series (average night turbidity – AVNt, average day turbidity – AVDt, difference in day – night turbidity – DDNt and periodicity – PERt). Night was employed as a fixed time window (18:00-6:00; Rice et al., 2014). Hydrological data were scaled to Z-scores to enable comparison across sites in subsequent analyses (one-way ANOVA indicated that discharge values differed as a function of site). The relationship between standardised discharge, turbidity and mass of fines was explored using spearman's rank correlation for all 37 indices and 4 ingress size categories.

Both hydrological and turbidity indices were analysed using principal component analysis (PCA) to identify redundant interrelated indices whilst retaining the major sources of statistical variation (Jolliffe, 1986). A series of PCAs were undertaken on turbidity and hydrological data in isolation and as a combination using the '*prcomp'* function from the '*stats*' package in 'R'. PCAs were conducted to identify the dominant principal indices following the PCA redundancy reduction approach outlined by Olden and Poff (2003). Previous research employing this approach has typically utilized a maximum of six indices to sufficiently characterise the regimes (Monk et al., 2006; Belmar et al., 2013; Worrall et al., 2014) and consequently the six indices with the highest loadings on the first two principal component (PC) axes were identified for each set of variables (turbidity, hydrological and combined). Following Olden and Poff (2003), the number of indices selected from each axis was proportional to the variance explained by each PC relative to the others. For example, based on the turbidity data the first PC explained 48.4% of the total 68.5% of the variance explained by the two significant components, resulting in four indices being selected from PC1 and two from PC2. Highly correlated indices (r values greater than 0.95 as determined through employment of a correlation matrix) were considered redundant and removed to attain a selection of six indices which effectively characterised statistical variability whilst minimising collinearity (Monk et al. 2006).

Table 4.3 Summary of turbidity and flow indices calculated in this study.

Turbidity indices	Description	Flow indices	Description
MAXt	Maximum turbidity	MAXd	Maximum discharge
MINt	Minimum turbidity	MINd	Minimum discharge
RANt	Turbidity range	RANd	Discharge range
STDt	Standard deviation of turbidity	STDd	Standard deviation of discharge
AVt	14 day average turbidity value	AVd	14 day average discharge
MEDt	Median turbidity value	MEDd	Median discharge
D10t	Duration over 10 NTU	D1d	Duration over 0.1 (z standardised score)
D20t	Duration over 20 NTU	D2d	Duration over 0.2 (z standardised score)
D50t	Duration over 50 NTU	DUn1d	Duration under - 0.1 (z standardised score)
D100t	Duration over 100 NTU	DUn2d	Duration over - 0.2 (z standardised score)
DU10t	Duration under 10 NTU	D14AVd	Duration over 14 day average discharge
D14AVt	Duration over 14 day average turbidity value	DTAVd	Duration over total average discharge
DTAVt	Duration over total average turbidity value	NPTAVd	Number of peaks over total average discharge
PERt	Periodicity	NRd	Number of rises in discharge series
AVNt	Average night turbidity value		
AVDt	Average day turbidity value		
DDNt	Average difference in day and night turbidity		
NP20t	Number of peaks over 20 NTU		
NP50t	Number of peaks over 50 NTU		
NP100t	Number of peaks over 100 NTU		
NRt	Number of rises in turbidity series		

The PC components resulting from the reduced set of variables in each dataset were used as independent variables in the development of multiple linear regression models to examine the ability of flow and turbidity variables to account for variation in the mass of grains deposited for each sampling set for each grain size; hereafter referred to as *m*. PC components with eigenvalues >1 were considered for inclusion in each model, and stepwise selection using the '*stepAIC*' function in the '*MASS*' package was used to select the best combination of variables. As a result of the removal of highly correlated and redundant variables through PCA selection and the subsequent compartmentalisation of the data to reduce its dimensionality, overfitting of models is minimal. This approach yielded a total of three models (discharge, turbidity and discharge + turbidity) for each of the grain sizes to enable an evaluation of the relative contribution of explanatory power that each process exerted over *m*. To assess whether the turbidity regimes differed by site or time as a function of any facets of the series (magnitude, duration etc.), a Generalised Linear Model (GLM) was fitted to the PC component scores. Models were developed using the '*glm*' function in the '*stats*' package with a Gaussian error distribution and identity link (as determined by the Akaike's information criteria - AIC).

4.4 Results

4.4.1 Signal crayfish demographics at Brooke

Catch per unit effort (CPUE) numbers exhibited variability during the sampling period, with spatial and temporal differences in individuals trapped (average 3.9 adults, range 9.66 - 1.5 adults per trap night; Figure 4.13a). There was little variation in the size of adults trapped spatially or over time (average 34.82 mm, range 28.62 mm – 40.6 mm; Figure 4.13b). Populations were dominated by females (average 69.43%) with 21.43% exhibiting some form of damage. None of the parameters were statistically different when time or site was considered (one-way ANOVA, $P > 0.05$).

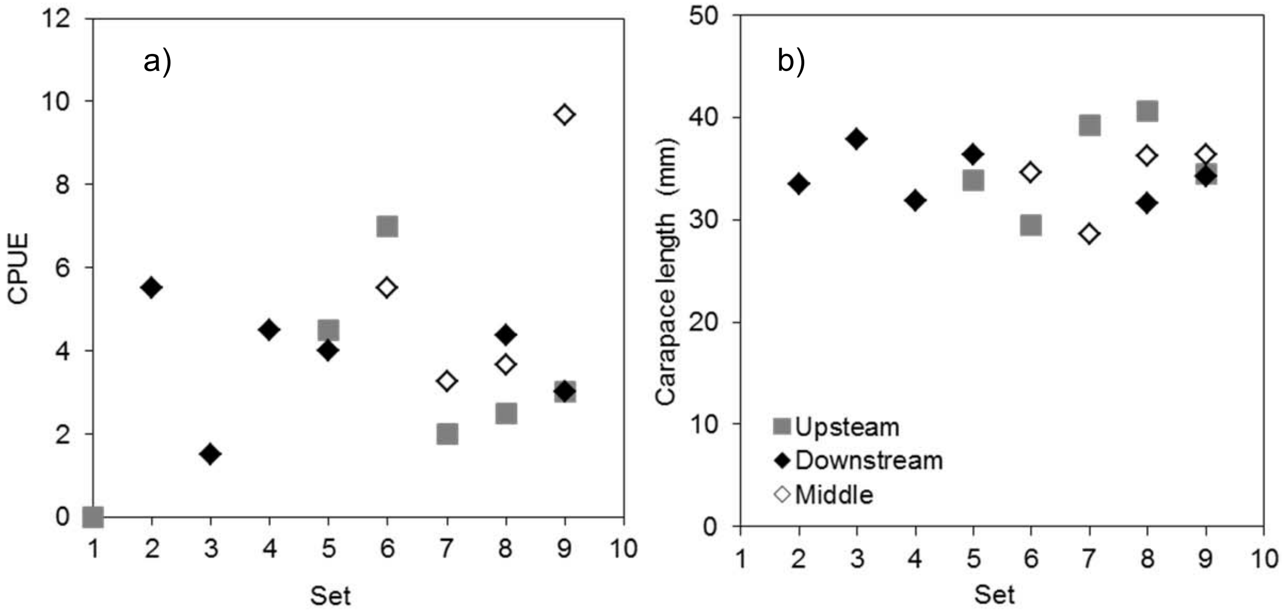

Figure 4.13 Signal crayfish a) catch per unit effort (CPUE) and; b) average carapace length (mm) for each sample set at Brooke (21st June – 24th September 2015).

4.4.2 Crayfish presence and turbidity time series

Examination of the turbidity series at Brooke indicated that the patterns recorded at the U/S and D/S sites were similar (Figure 4.14) and therefore only Brooke D/S as the most consistent record is presented in the main text to avoid duplication (see Appendix 3 for Brooke U/S record). The turbidity time series at Brooke D/S is variable in nature, however there is clear evidence of diurnal fluctuations (Figure 4.15). The strength of the pattern is weak during Set 2 and Set 3 (8th June – 2nd July), however there is a notable increase in fluctuations during Set 4 which remain strong until the latter half of Set 9. Periodgrams for the turbidity time series at Brooke

D/S corroborate these visual observations exhibiting peaks in power predominately at the period of 1 day in all (Sets 3 – 8) but one instance (Set 9; Figure 4.16). For set 9, data was analysed in two parts due to missing data, with the first half of the set (10th -14th Sept) indicating a peak in power at 1 day but the latter half (17th – 24th Sept) at 0.5 days.

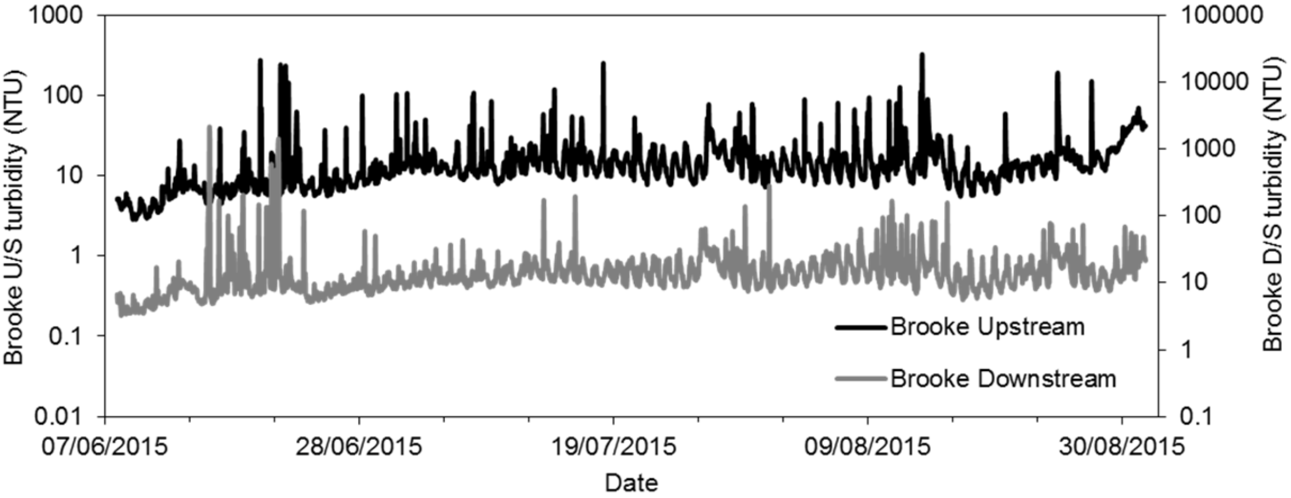

Figure 4.14 Turbidity record (hourly average) at the two monitoring sites at Brooke; upstream (black line) and downstream (grey line) of the sampled reach between 8th June and 31st August 2015. Note the difference in scale representation to enable comparison of both series. Both turbidity series represent similar turbidity values. Tick marks are at midnight.

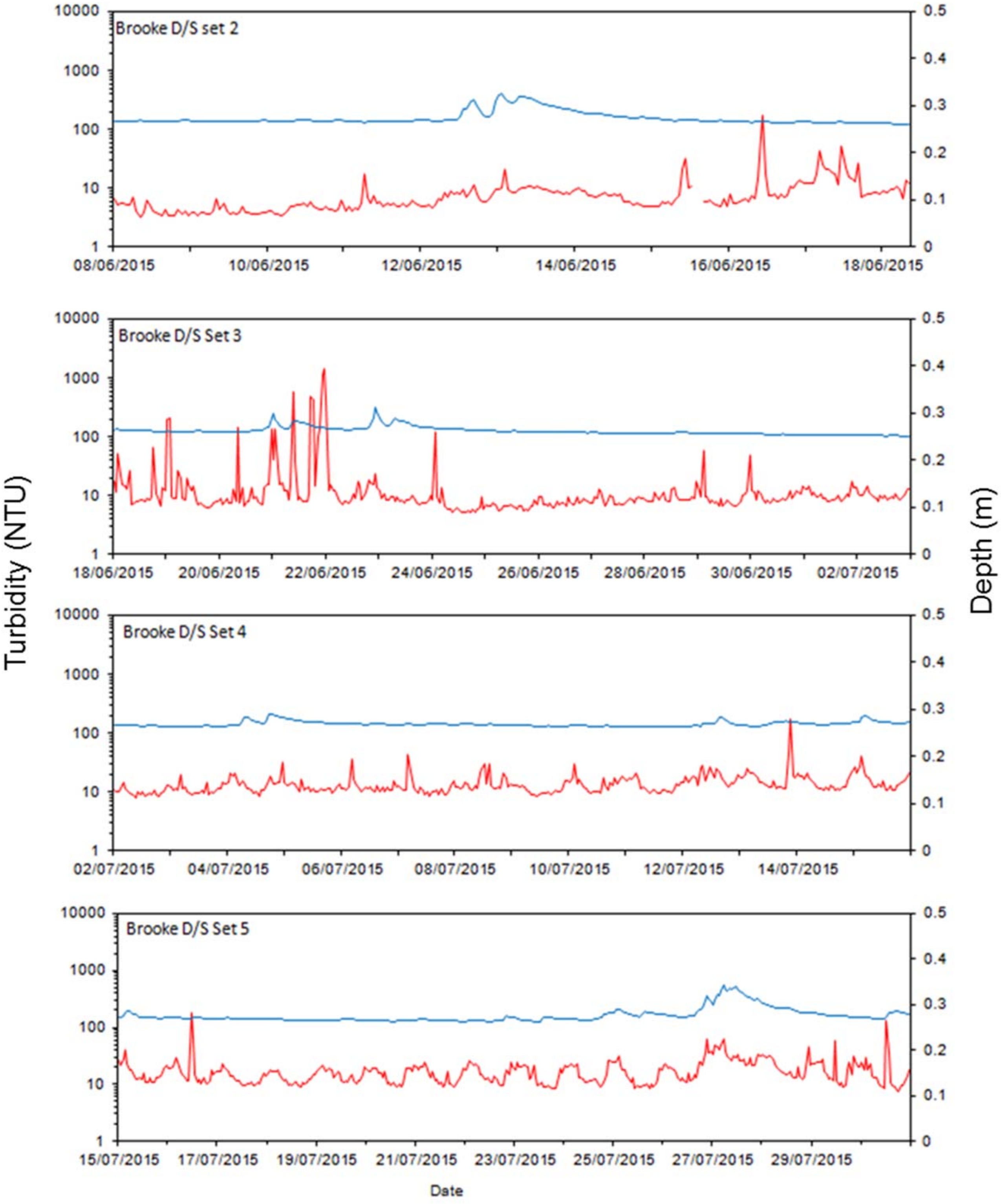

Figure 4.15 Turbidity and water depth (hourly average) at Brooke D/S for the corresponding two week sampling periods (4th July – 24th September 2015). Note no turbidity or water data was collected during the first set (21st June – 4th July 2015) due to equipment problems and set 2 is missing data at the start of the record (4th June – 8th June 2015). Gaps in record reflect missing data. Tick marks are at midnight.

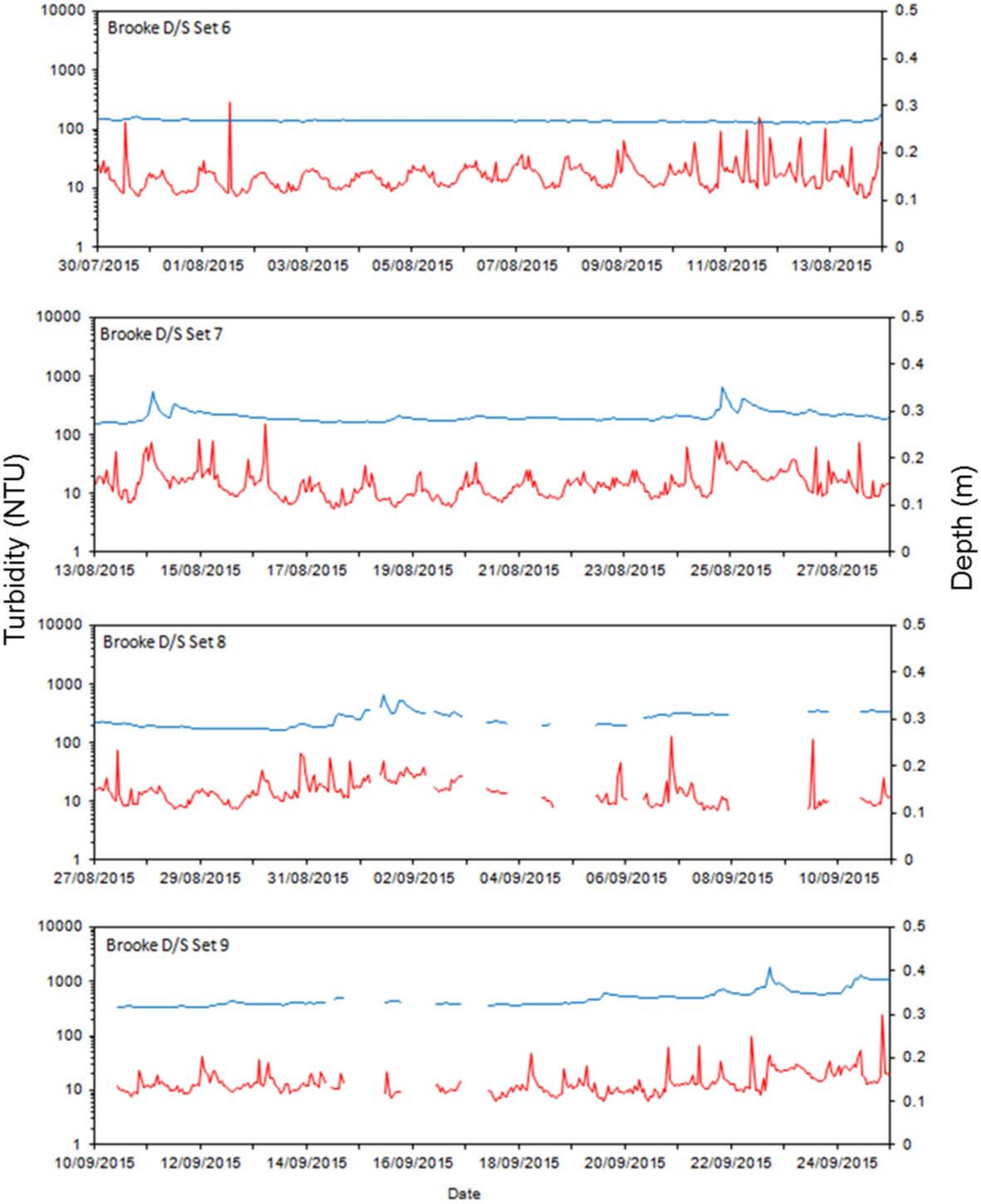

Figure 4.15 continued. Turbidity and water depth (hourly average) at Brooke D/S for the corresponding two week sampling periods (4th July – 24th September 2015). Note no turbidity or water data was collected during the first set (21st June – 4th July 2015) due to equipment problems and set 2 is missing data at the start of the record (4th June – 8th June 2015). Gaps in record reflect missing data. Tick marks are at midnight.

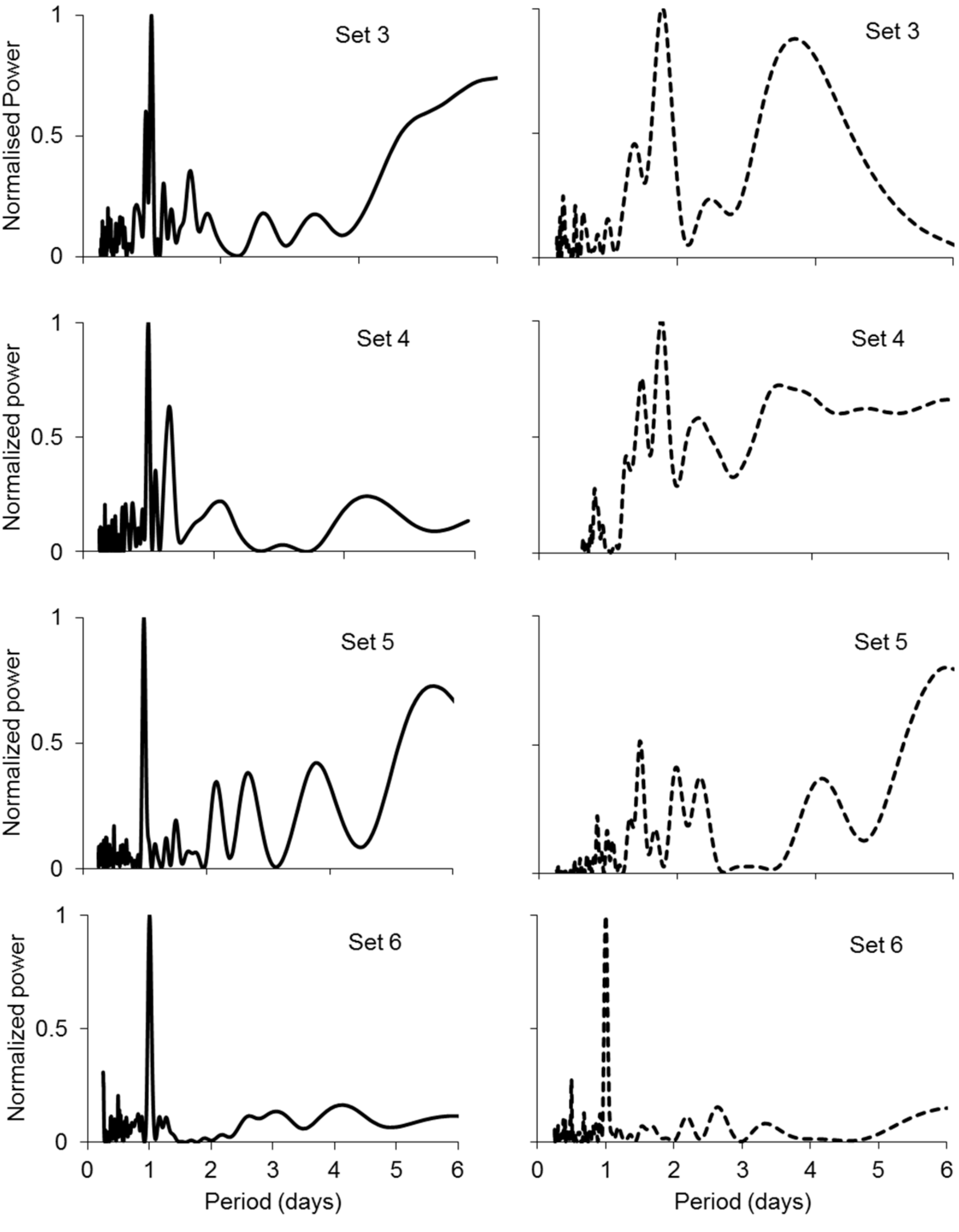

Figure 4.16 Periodgrams of turbidity time series from June – Sept 2015. Data that were more than one standard deviation from the monthly mean were replaced with a local average. Power is normalized by the maximum value for the respective time series. Black solid lines represent Brooke D/S and black dashed Ridlington. The main peaks are significant in all instances ($P<0.05$).

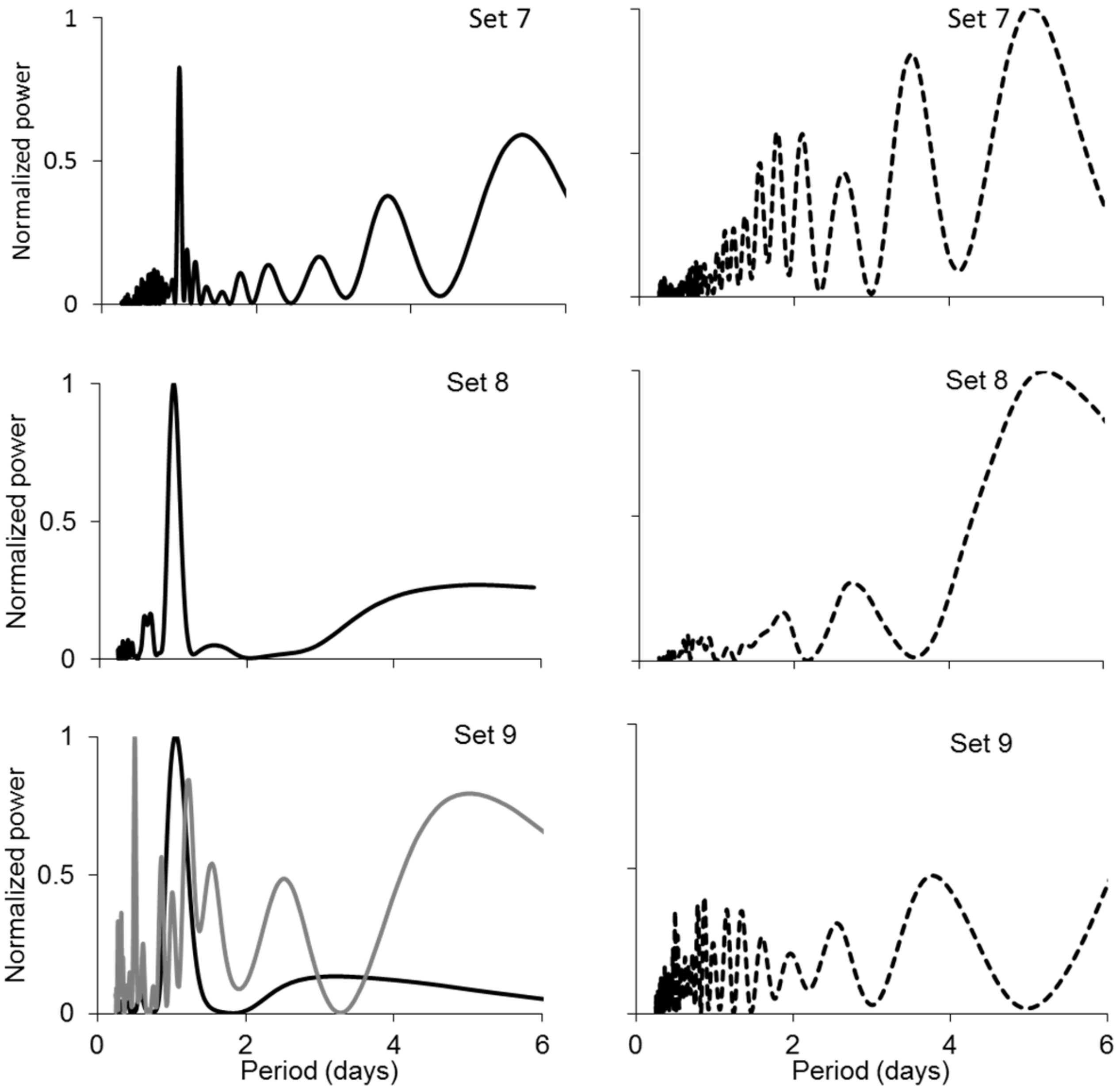

Figure 4.16 continued. Periodgrams of turbidity time series from June – Sept 2015. Data that were more than one standard deviation from the monthly mean were replaced with a local average. Power is normalized by the maximum value for the respective time series. Black and grey solid lines represent Brooke D/S and black dashed Ridlington. The main peaks are significant in all instances (P<0.05).

A similar pattern is evident at Brooke U/S (Appendix 3) with weak diurnal fluctuations in turbidity evident during Set 2 – Set 3 (secondary peak at 1 day). The strength of these fluctuations notably increases halfway through Set 4 (power peak at 1 day for sets 4-7). There is no obvious hydraulic explanation for the observed diel patterns with water depth remaining consistent during baseflow periods (Figure 4.15). As stage is a useful index of change in hydraulic parameters relevant to sediment entrainment (shear stress and shear velocity), the independence of the diel turbidity fluctuations suggest that hydrological conditions were not responsible for this pattern. Crayfish population data (CPUE) exhibited a strong negative correlation with average D/S turbidity for each of the 14-day sample sets ($r = -0.725$, $P > 0.05$).

A persistent feature in the raw data (five minute resolution) at Brooke is the presence of large but short-lived spikes in turbidity from the mean, often reflecting one 5 minute data point (Figure 4.17). This characteristic has also been documented by Rice et al., (2014) and analysis of this feature was conducted following the procedure outlined by the authors. Spikes were defined as individual turbidity values that exceeded the local hourly mean by more than one global standard deviation (68.31 NTU at Brooke D/S). For five sampling sets, the number of turbidity spikes was greater at night then during the day (day range – 1 - 12, night 6 - 38), for set 8 the number was equal (8 in both instances) and for set 3 there was a larger number during the day (13 in the day, 7 at night). On average, there were 13 spikes per 14-day period at night and 8.38 during the day (excluding flood periods) indicating that spikes are 1.63 times more common at night. A corresponding plot for Ridlington is not able to be presented or interpreted due to a large degree of equipment instability which resulted in a high number of erroneous spikes being evident in the dataset (including negative spiking). The inherent problems associated with turbidity measurements are reflected on in the discussion.

Turbidity at Ridlington demonstrates considerable variability with the series being characterised by intermittent spikes (Figure 4.18). Periodgrams for the time series indicate an absence of a regular dominant frequency with all sampling sets providing differing peak frequencies (average 6.02 days, range 1 - 11.63 days; Figure 4.16). Only one sampling set indicated a periodic peak at 1 day (set 6) which is evident in the turbidity series (Figure 4.18). This diurnal pattern is very spiky in comparison with the gradual rising and falling limbs evident at Brooke and in other crayfish zoogeomorphic studies (Harvey et al., 2014; Rice et al., 2014; 2016). This pattern also coincides with slight diurnal fluctuations in stage (0.1 - 0.2 m) between mid-afternoon and midnight evident in Figure 4.18. These fluctuations in stage are likely to reflect summertime variations in evapo-transpiration during periods of soil moisture deficit (Bond et al., 2002; Gribovski et al., 2010) and coincide with baseflow periods in which there are no flood flows. As these fluctuations are out of synchronization with the turbidity spikes (peaks in stage are associated with turbidity minima) it is unlikely that these small fluctuations are driving changes in turbidity but may indicate the presence of another zoogeomorphic agent (see section 4.5.1 for discussion). During flood events, turbidity responded as expected with corresponding peaks at both Brooke and Ridlington suggesting the presence of widespread sediment availability at both sites. Average SSC over the sampling period were 32.19 mg L^{-1} at Ridlington and 38.04 mg L^{-1} at Brooke.

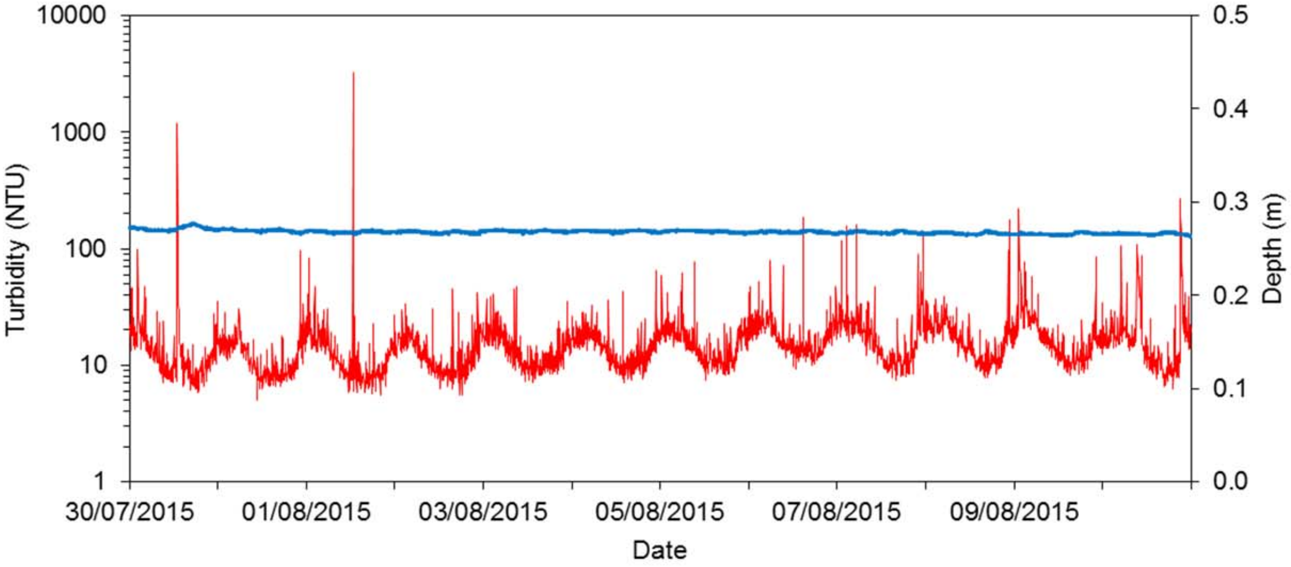

Figure 4.17 Example of turbidity and depth series for a 10-day period in August 2015 at Brooke D/S demonstrating the spiky nature of the turbidity record particularly, at night despite no changes in stage. Tick marks are at midnight. The red line is five minute turbidity data and the blue is five minute stage data.

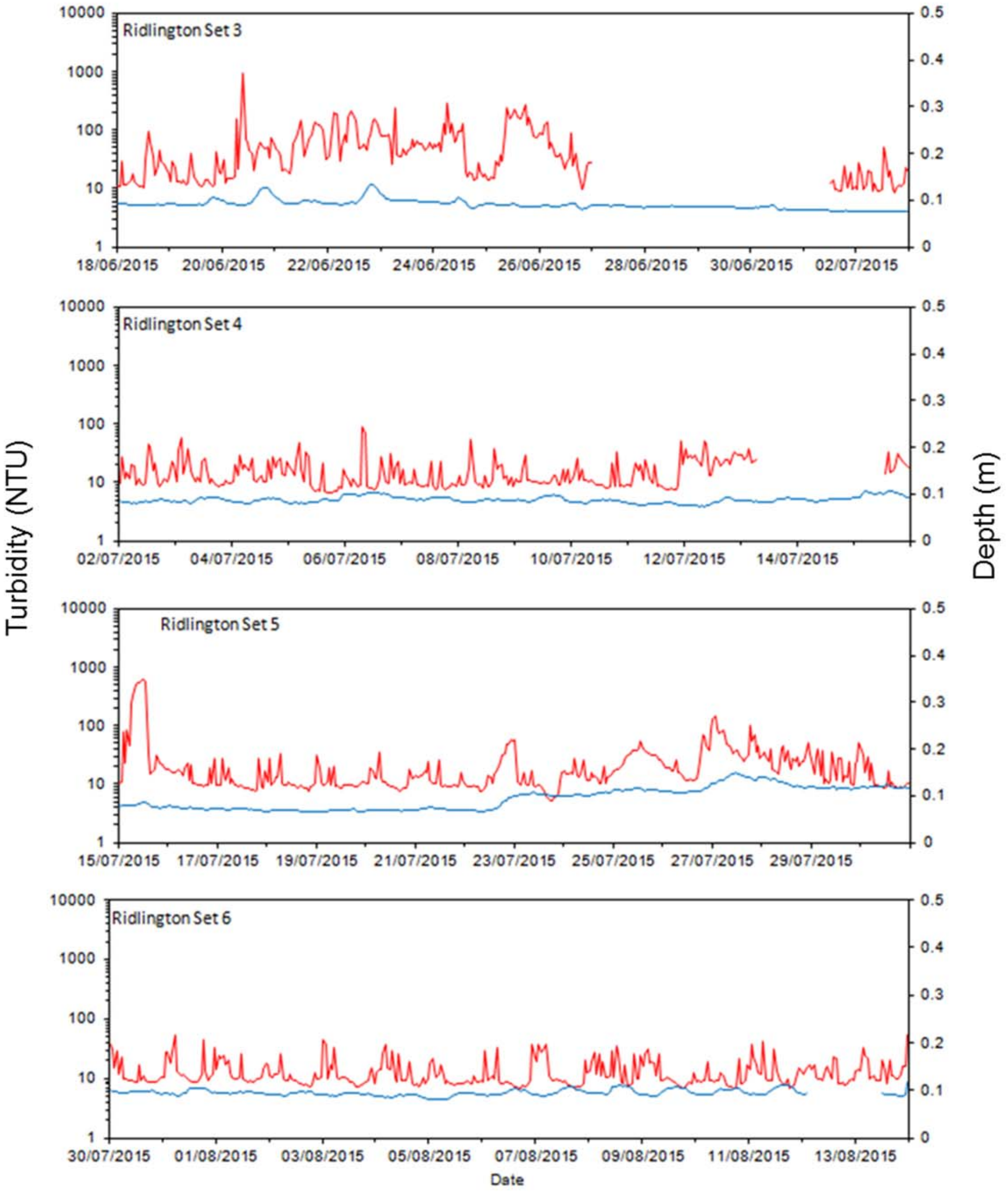

Figure 4.18 Turbidity and water depth (hourly average) at Ridlington for the corresponding two week sampling periods (18th July – 24th September 2015). Note no turbidity or water data was collected during the first two sets (21st June – 18th July 2015) due to equipment problems and gaps in record reflect missing data. Tick marks are at midnight.

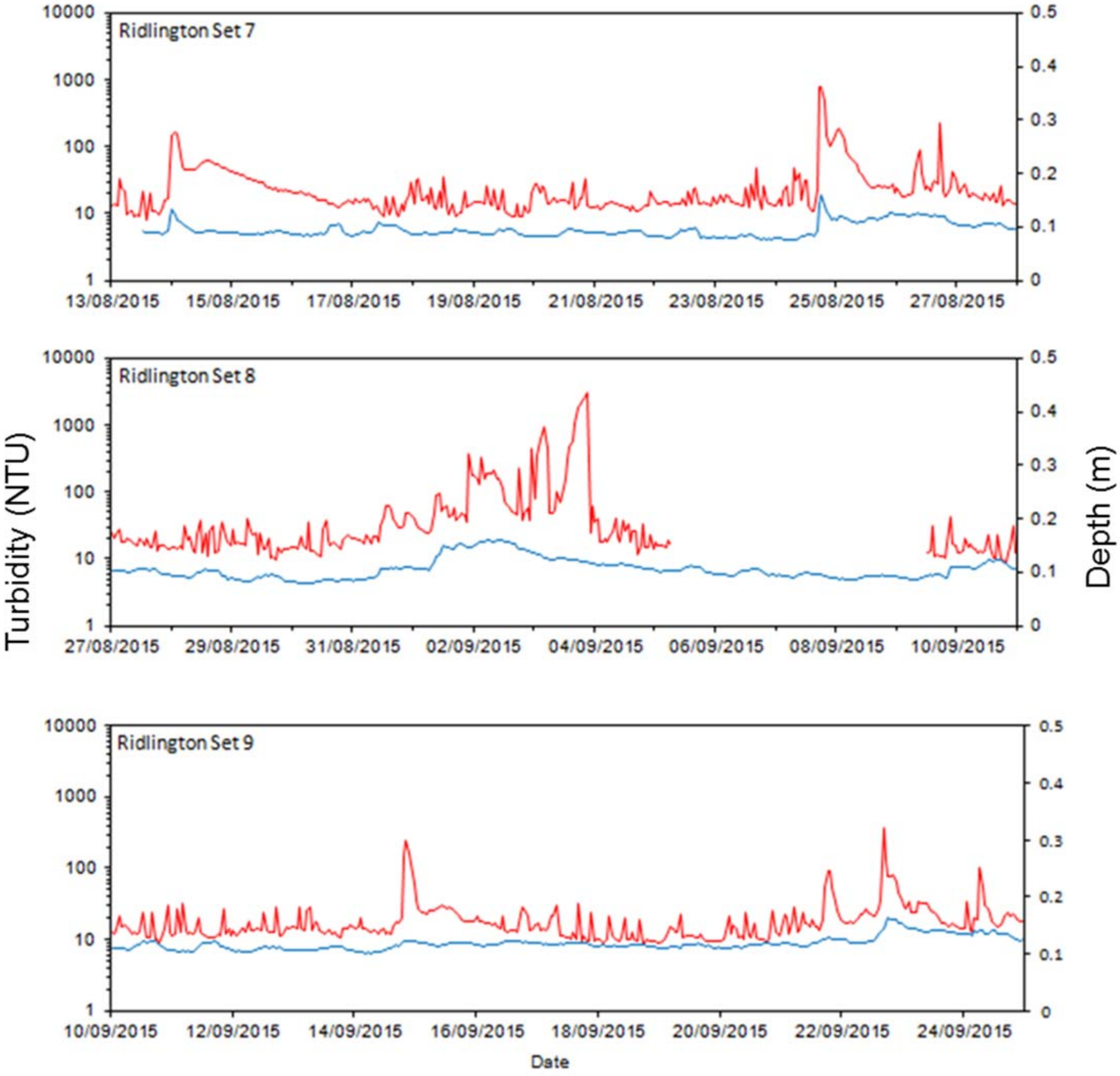

Figure 4.18 continued. Turbidity and water depth (hourly average) at Ridlington for the corresponding two week sampling periods (18th July – 24th September 2015). Note no turbidity or water data was collected during the first two sets (21st June – 18th July 2015) due to equipment problems and gaps in record reflect missing data. Tick marks are at midnight.

4.4.3 Biotic and abiotic contributions to suspended sediment load at Brooke

Biotic and abiotic contributions to baseflow suspended sediment load (SL_{bf}) and total suspended sediment load (SL) are presented in Table 4.4a. Conservative estimates (using minimum daily turbidity values) of biotic contributions to sediment fluxes indicate that crayfish added on average 20.0% (standard error = 1.2%) to baseflow loads during the sampling period. Estimates range from 93.0 kg (based on 11 days equivalent to 8.45 kg d^{-1}) through to 317.4 (14 days or 22.6 kg d^{-1}) with a mean of 230.9 kg per 14-day set (equivalent to 12.0% - 25.5%). Biotic contributions during baseflow conditions vary as a function of time and space. On average, bioturbation additions were greater at the D/S site (average 21.6 %, range 16.4% - 25.5%) when compared to the U/S site (average 18.2%, range 12% - 23.7%).

The distribution of crayfish is highly variable (Figure 4.13), in space but also time (crayfish tend to not remain in the same location for more than a few days) and it is likely that these differences reflect such population dynamics. Crayfish activity is heavily associated with temperature (Johnson et al., 2014) and the gradual increase in biotic contributions as the summer progresses (particularly in the case of the U/S site) reflects this. Sets 2 and 3 had moderate crayfish additions to the sediment load which increased considerably during set 4 when water temperature began to increase (Figure 4.19). CPUE estimates during the sampling period (Brooke set 2 - 9) exhibited moderate negative correlation with temperature range ($r = - 0.5$, $P > 0.05$).

85.3% of total suspended sediment was transported as a result of abiotic processes when high flow periods were included in calculations. That is, when flood spates are included, bioturbation contributions reduce to an average of 14.7% (note that 2 sample sets did not include any flood periods, set 4 and 6) and ranged from 5.6% - 24.7% (Table 4.4b). The monthly figures are highly variable, mainly as a function of the number of flood days and the magnitude of such flows (Figure 4.19).

Table 4.4 Estimates of biotic and abiotic contributions ± 1 standard deviation to a) base flow and; b) total suspended sediment load at Brooke. Estimates denoted in bold italics are sample sets which do not contain any flood days.

a)

	Upstream				**Downstream**			
Sample set	**Abiotic load, SL_{bfA} (kg)**	**Biotic Load, SL_{bfB} (kg)**	**Biotic contribution (%)**	**Days missing***	**Abiotic load, SL_{bfA} (kg)**	**Biotic Load, SL_{bfB} (kg)**	**Biotic contribution (%)**	**Days missing***
2	682.0 ± 44.0	93.0 ± 58.9	12.0	3.0	768.6 ± 145.9	161.8 ± 66.0	17.4	3.0
3	779.04 ± 184.5	151.3 ± 14.5	16.3	3.8	890.62 ± 18.0	175.1 ± 44.3	16.4	3.7
4	1268.3 ± 47.6	294.9 ± 47.4	18.9	0.0	1229.5 ± 46.4	311.4 ± 119.6	20.2	0.0
5	960.1 ± 40.7	298.7 ± 113.3	23.7	2.4	1288 ± 40.7	307.5 ± 54.7	23.9	3.4
6	969.1 ± 21.8	294.3 ± 37.1	23.3	0.0	968.6 ± 18.1	317.4 ± 65.0	24.7	0.0
7	1035.2 ± 49.2	180.56 ± 32.3	14.9	3.9	672.0 ± 71.5	230.2 ± 40.9	25.5	5.5
8								
9					377.1 ± 34.9	114.8 ± 31.7	23.3	5.33

N.B. * comprises of missing data and flood days, set 2 record is missing data at the start and commences on 8th June 2015.

b)

	Upstream		**Downstream**	
Sample set	**Abiotic load, SL_{bfA} (kg)**	**Biotic contribution (%)**	**Abiotic load, SL_{bfA} (kg)**	**Biotic contribution (%)**
2	1032.9 ± 163.6	9.0	2159.4 ± 129.5	8.04
3	1556.9 ± 127.8	9.7	3110.5 ± 105.9	5.6
4	***1268.3*** **± 47.6**	***18.9***	**1229.5 ± 46.4**	***20.2***
5	1646.3 ± 479.4	17.9	1561.5 ± 321.8	20.1
6	**969.1 ± 21.8**	***23.3***	**968.6 ± 18.1**	***24.7***
7	1543.1 ± 131.8	9.5	1852.5 ± 140.4	12.4
8				
9			747.5 ± 84	11.2

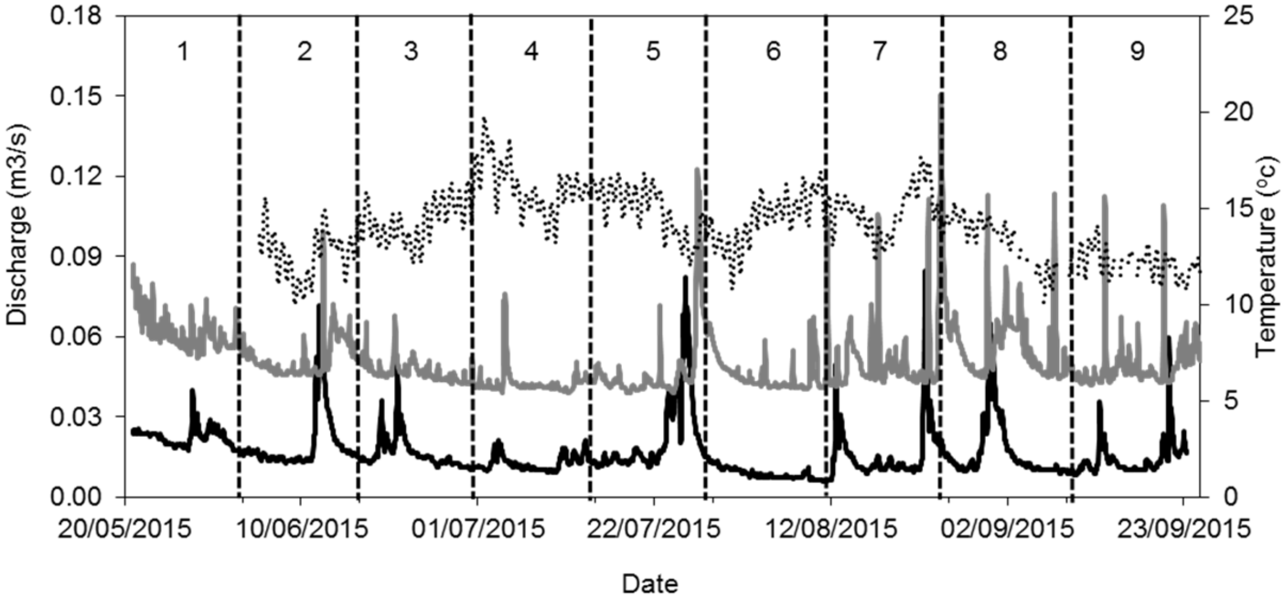

Figure 4.19 River discharge (hourly average $m^3 s^{-1}$) for the River Gwash (black) and River Chater (grey) Rutland, UK during the sampling campaign. Dotted black represents water temperature recorded at Brooke (hourly averaged). Ridlington temperature is a parallel series and is therefore not presented. Dashed lines indicate the two week sampling periods (21st June - 24th September 2015).

4.4.4 Sediment flux estimation at Brooke

Sediment fluxes during the sampling period varied considerably with an overall net loss of fine material (2484.72 kg). For five out of the seven sampling sets (Set 4 - Set 7) the sediment budget remained in equilibrium with a negligible net gain of 25kg $14d^{-1}$ (Figure 4.20). Sediment fluxes during this period remained consistent (average 132.61 kg d^{-1}, range 105.41 – 146.18 kg d^{-1}). Fluxes during set 2 and 3 resulted in an overall net loss of material from the reach (-95.65 and -110.97 kg d^{-1}) associated with three storm flows entraining greater amounts of fine sediment at the downstream end of the reach (Figure 4.15; Appendix 3). In addition, a large number of turbidity spikes between 16th June and 20th June 2015 at the downstream end of the reach contributed large quantities of fines to the suspended sediment load (Figure 4.15). This process may be as a result of crayfish activity given the lack of hydrological explanation present at that time.

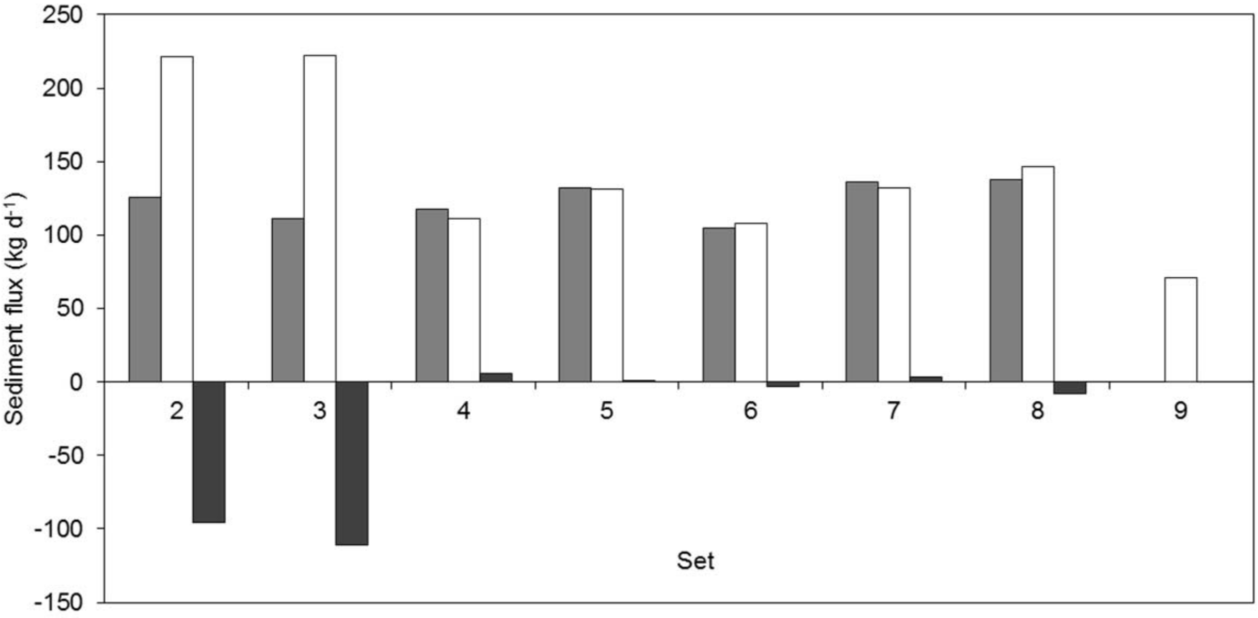

Figure 4.20 Daily sediment fluxes (kg d^{-1}) for each two week period of the sampling campaign at Brooke (8th June – 24th September 2015). Light grey bars = upstream reach; white bars = downstream reach and; dark grey bars = change in storage (not measured directly but calculated from sediment input and output values). Note no data was collected during the first set (21st June – 7th July 2015) due to equipment problems, set 8 includes 2.68 missing days and only data from the D/S site was available for Set 9.

4.4.5 Fine sediment ingress

There were no differences in ingress rates between Brooke and Ridlington when overall differences or pairwise comparisons were considered for any of the size fractions ($P > 0.05$, LME). There was a significant time interaction with ingress rates varying significantly at both sites for all grain sizes (Figure 4.21). Grains in the size fraction 1000-2000 µm demonstrated a significant decline in ingress rates over the sampling period, with rates peaking during set 2 at both sites followed by a reduction to negligible rates by set 6 (time interaction; $F_{1,155} = 19.15$, $P < 0.001$, LME). Rates were greatest at Ridlington during the first three sets, Brooke for sets 4 and 5, and Ridlington during sets 8 and 9. Overall ingress of this size fraction was the lowest of the three measured grain sizes, most likely being supply limited (Figure 4.2). Rates of ingress of the three sampled grain sizes were greatest in the size fraction 125-1000 µm, with peak rates being recorded during set 2 and a secondary peak at Ridlington evident during set 8 (time interaction $F_{1,155} = 9.629$, $P = 0.002$, LME). Ingress was greatest at Ridlington during set 2, Brooke during set 4 and 6 and

Ridlington during set 8 and 9. Grains <125μm peaked during set 2 and in the instance of Ridlington during set 8 (time interaction $F_{1,155} = 10.64$, P = 0.001, LME). When all size fractions were considered as a whole (dry weight), a slow decline in infiltration was evident over the course of the sampling period, with maximum infiltration taking place during set 2 (time interaction $F_{1,155} = 17.42$, P < 0.001).

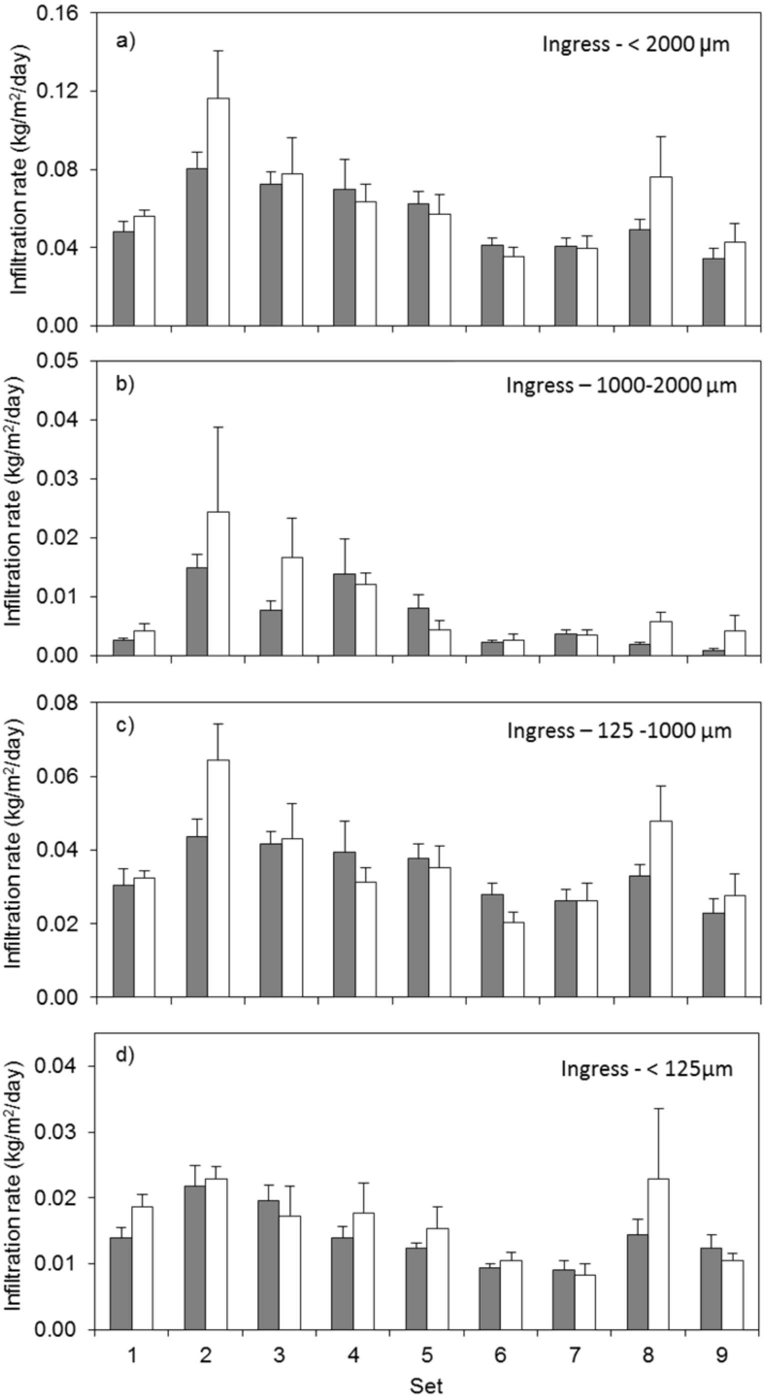

Figure 4.21 Mean (± 1 SE) infiltration rates (kg m^{-2} day^{-1}) for each period of the sampling campaign (21st June – 24th Sept 2015) for: a) <2000 μm (total dry weight); b) 1000-2000 μm; c) 125 – 1000 μm and; d) < 125μm. Solid grey bars = Brooke and white bars = Ridlington.

4.4.6 Characterisation of turbidity and hydrological series

When principal component analysis (PCA) was employed to determine which turbidity and hydrological indices were the most influential in characterising the dominant sources of variability, the percentage of variance explained by the differing sets of models ranged from 87.07% for the combined variables through to 98.18% for the reduced hydrological dataset (Table 4.5). Turbidity indices demonstrated greater variability than the hydrological datasets with less variance explained on the first axis in both instances (full and reduced dataset). Using the PCA selection procedure, three indices were identified which represented magnitude of turbidity (MEDt, AVNt and DDNt), two that represented duration of turbidity events (D10t and D100t) and one which characterised the frequency of change (NRt; Figure 4.22). Within the subset of six hydrological variables identified, the majority represented magnitude of discharge (MINd, AVd and STDd), two characterised duration of events (DUN1d, D14AVd) and one the frequency of events (NRd; Figure 4.23). When all variables were considered together, turbidity accounted for a larger proportion of variance with four dominant indices identified and two hydrological indices. Magnitude of the series was the primary source of variability (MEDd, STDd, MEDt, MAXt and AVt) with the remaining two indices representing the duration of low magnitude events (DUN1d, Du10t; Figure 4.24).

Table 4.5 Summary of the percentage variability explained on axes 1-4 for each of the six sets of variables.

	Principal component (% variance explained)				**Total (%)**
	1	**2**	**3**	**4**	
All turbidity	48.39	20.06	11.47	7.15	87.07
Reduced turbidity	52.48	25.59	11.84	8.74	98.65
All hydrological	66.68	15.5	11.45	4.04	97.67
Reduced hydrological	55.41	19.87	16.30	6.60	98.18
Turbidity and hydrological combined	39.08	21.23	13.06	8.51	81.88
Reduced turbidity and hydrological	48.19	27.37	16.93	4.9	97.39

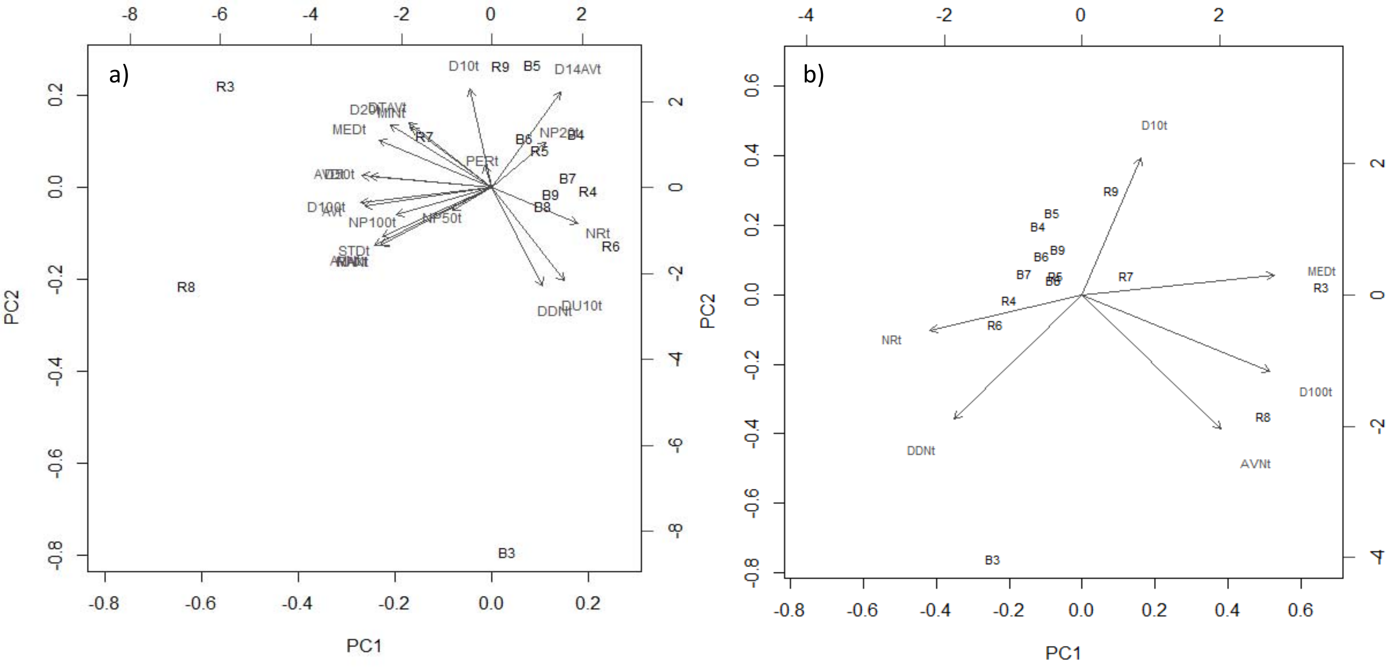

Figure 4.22 Principal component analysis plots of turbidity indices and sample set (Brooke - B3 – B9, Ridlington R3 –R9) for a) 23 turbidity indices and; b) 6 PCA selection indices (see Table 4.3 for abbreviations).

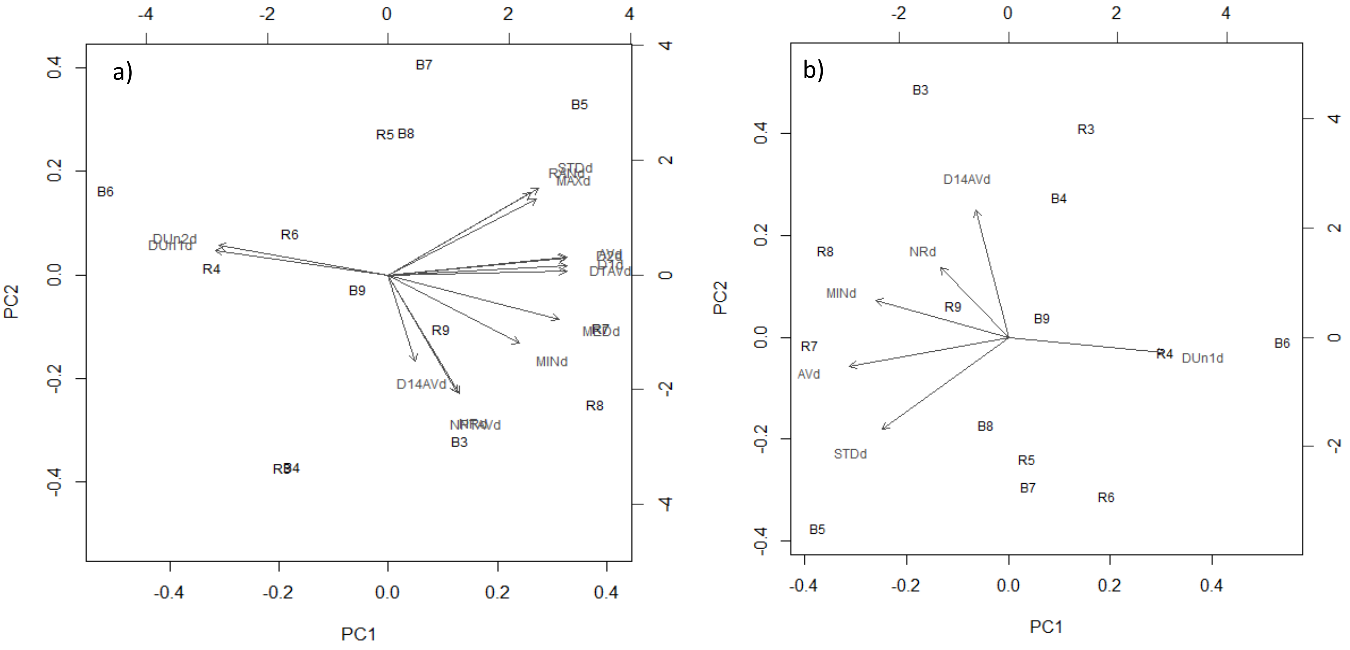

Figure 4.23 Principal component analysis plots of hydrological indices and sample set (Brooke -B3 – B9, Ridlington -R3 –R9) for a) 14 hydrological indices and; b) 6 PCA selection indices (see Table 4.3 for abbreviations).

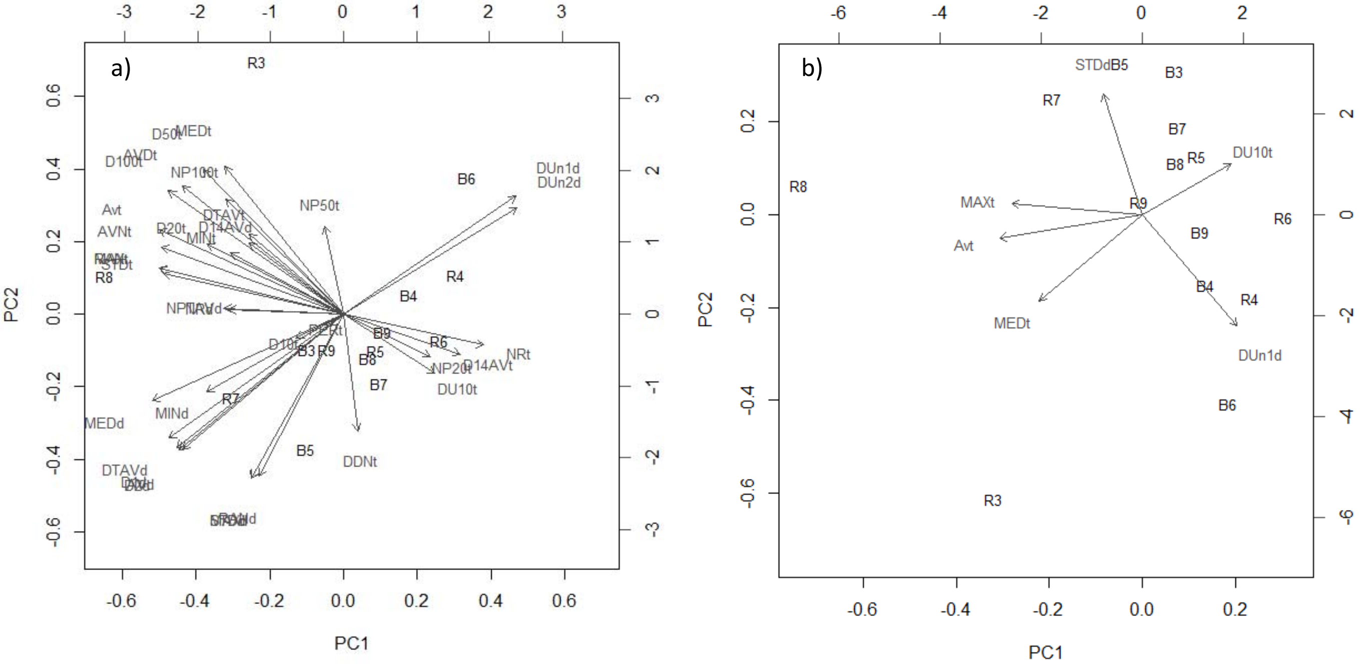

Figure 4.24 Combined principal component analysis plots of turbidity indices, hydrological indices and sample set (Brooke - B3 – B9, Ridlington - R3 –R9) for a) 21 turbidity indices and; b)) 6 PCA selection indices (see Table 4.3 for abbreviations).

Examination of the sample sites on the ordination plots indicates that the turbidity series were similar overall in character temporally regardless of crayfish presence (Figure 4.22). Despite this, Ridlington exhibits greater variation in turbidity over time, with the majority of Brooke sites forming a cluster at the centre of the plot. Three turbidity series represent extreme outliers, with R3 being strongly associated with higher than average MEDt, R8 by AVNt and D100t and B3 by DDNt. The dominant vectors of variation are associated with duration over 10 NTU and difference in day / night turbidity. Discharge exhibited greater variability with a wide spread of sites and time periods evident, with the majority of sites being heavily loaded on PC1 associated with the characterisation of low flow conditions (Figure 4.23). Time periods in which baseflow conditions were dominant (e.g. B4, R3, R6, B6) plot to the right of the ordination and those with high flow events to the left (e.g. R8, R7, B5). When hydrological and turbidity variation at sites was considered in combination, sites demonstrated consistent variation over time being influenced by both discharge and turbidity variability (Figure 4.24). The dominant vectors of variation are associated with the characterisation of low flow periods (Dun1d and STDd) with two outliers being strongly influenced by turbidity (MEDt -R3 and MAXt - R8). When all facets of the turbidity regime were considered in site / time comparisons, no significant differences were evident ($P > 0.05$, GLM).

4.4.7 Relationship between discharge, turbidity and ingress

Correlation between turbidity and discharge indices indicated moderate relationships ($|\rho| > 0.5$) between turbidity and discharge in a number of instances (Table 4.6). Hydrology was predominantly associated with the magnitude of turbidity (MAXt, MINt RANt, STDt) with 12 out of 23 variables being characterised as such (nine of which were significant). Of the remaining cross correlations, five were associated with average turbidity parameters (AVt, AVNt, D14AVt) as characterised by average discharge (D14AVd, MEDd, DTAVd); three of which were significant. The strongest correlation was between 14-day averaged discharge (D14AVd) and number of peaks over 100 NTU (NP100t). When the hourly averaged raw discharge and turbidity series were correlated, both sites yielded weak relationships (Brooke $\rho = 0.040$; $P < 0.05$; Ridlington $r = 0.211$; $P < 0.001$).

Correlations between standardised hydrological, raw turbidity values and *m* fines (see section 4.3.9 for derivation) demonstrated a poor relationship between individual discharge and turbidity indices (Table 4.7). Only three turbidity indices and one discharge index had a moderate correlation ($|\rho| > 0.5$) with the different size fractions of *m.* The strongest correlation was between duration of discharge over 14 day average (D14AVd) and fines 125-1000 µm ($\rho = 0.617$; $p \leq 0.05$). Grains in the size fraction of 1000-2000 µm demonstrated the strongest correlation with turbidity with three indices having a moderate correlation, whilst dry weight was correlated with D14AVd (Table 4.7). Correlations between raw hydrological indices and ingress yielded no relationships.

Table 4.6 Spearman's rank correlations for all discharge (standardised) and turbidity indices (only those with a moderate correlation stronger than |ρ | > 0.5 are presented).

Discharge index	Turbidity index	r value
MINd	MAXt	0.546 *
MINd	RANt	0.546 *
MEDd	MAXt	0.596 *
MEDd	RANt	0.596 *
MEDd	AVt	0.595 *
MEDd	D100t	0.519
MEDd	STDt	0.522
NPTAVd	MINt	0.504
NPTAVd	NRt	-0.613
D14AVd	MAXt	0.709 ***
D14AVd	RANt	0.709 ***
D14AVd	AVt	0.630 *
D14AVd	D50t	0.570 **
D14AVd	D100t	0.720 *
D14AVd	AVNt	0.522
D14AVd	NP50t	0.541 *
D14AVd	NP100t	0.782 ***
D14AVd	STDt	0.674 *
D14AVd	D14AVt	-0.617 *
DUn1d	MAXt	-0.525
DUN2d	MAXt	-0.560 *
DUN2d	RANt	-0.560 *
DTAVd	AVt	0.530

* p ≤ 0.05, ** P ≤ 0.01, ** p ≤ 0.005

Table 4.7 Spearman's rank correlations for discharge (standardised) and turbidity indices and ingress grain size characteristics (g; only those with a moderate correlation stronger than | ρ | > 0.5 are presented).

Grain size	Index	r value
Dry weight	D14AVd	0.566 *
1000 - 2000 µm	NP100t	0.592 *
1000 - 2000 µm	AVNt	0.56 *
1000 - 2000 µm	D100t	0.531
1000 - 2000 µm	D14AVd	0.617 *

* p ≤ 0.05, ** P ≤ 0.01, ** p ≤ 0.005

Multiple linear regression models developed for *m* using the PC scores explained between 8.78% and 53.92% of the variance in the ingress rates (Table 4.8). For grains 1000- 2000 µm, discharge was the most influential predictor with the model accounting for an additional 15.96% compared to turbidity and 9.56% when both turbidity and hydrology were considered together. PC2, which characterised the duration and magnitude of high flow events, were the most significant predictor variables (p = 0.004; Table 4.9). Grains 125-1000 µm were strongly influenced by turbidity with the model accounting for 45% of variation, an additional 10% compared to discharge. Both PC compartments were significant predictors, with magnitude of high turbidity values being the dominant explanatory factors followed by the average turbidity conditions of the time period. The combination of discharge and turbidity parameters only accounted for an additional 0.9% of variation, with the final model developed using PC components which only characterised turbidity (PC1 and PC3). Similarly, grains <125 µm were predominantly explained by turbidity with the model explaining 53.52% of variation, 32.42% more than the discharge model alone. PC2 was the most significant predictor (p = 0.005) which characterised average turbidity conditions. When total mass (<2000 µm) was considered, turbidity was the most influential factor (37.15%) with magnitude and frequency of high turbidity being the dominant predictors (p = 0.047). Similarly, the combined model provided the best fit with only PC components which characterise turbidity (average, maximum and duration of low turbidity) being significant influential factors. A summary of all linear regression models and the interpretations of the PC loadings for each of the compartments are provided in Tables 4.8 and 4. 9.

Table 4.8 Summary of multiple linear regression models fitted to ingress rates using PC scores from turbidity, discharge and turbidity + discharge datasets (reduced). * $p \leq 0.05$, ** $P \leq 0.01$, ** $p \leq 0.005$.

Datasets	Predictor	Adjusted R^2	F	Model p value	Variable p value	
Total mass						
Turbidity	PC1 + PC2	37.15	4.48	0.03 *	PC1 0.047	PC2 0.053
Discharge	PC2	30.03	6.58	0.03 *		
Turbidity + Discharge	PC1 + PC3	32.39	4.11	0.05 *	PC1 0.0394	PC3 0.125
1000- 2000 µm						
Turbidity	PC1	8.78	2.25	0.16		
Discharge	PC2	24.74	5.27	0.04 *		
Turbidity + Discharge	PC2	15.18	3.33	0.15		
125 – 1000 µm						
Turbidity	PC1 + PC2	45.00	6.31	0.02 *	PC1 0.020	PC2 0.043
Discharge	PC1 + PC2	35.00	4.58	0.03 *	PC1 0.106	PC2 0.032
Turbidity + Discharge	PC1 + PC3	45.90	6.52	0.01 *	PC1 0.107	PC3 0.150
<125µm						
Turbidity	PC1 + PC2	53.52	8.49	0.01 *	PC1 0.056	PC2 0.005
Discharge	PC2	20.90	4.43	0.06		
Turbidity + Discharge	PC1 + PC3	53.92	8.61	0.01 *	PC1 0.020	PC3 0.010

Table 4.9 Principal component loadings for the variables within the principle components analysis.

Dataset	PC1		PC2		PC3	
	Variable loadings	**Interpretation**	**Variable loadings**	**Interpretation**	**Variable loadings**	**Interpretation**
Turbidity	MEDt (0.52), D100t (0.51), NRt (-0.41)	Magnitude and frequency of turbidity (high)	D10t (0.56), AVNt (-0.5), DDNt (-0.51)	Average turbidity		
Discharge	MEDd (-0.47), DUn1d (0.47), Avd (-0.47)	Duration of low flow and average discharge	D14AVd (0.71), STDd (-0.55), NRd (0.33)	Duration and magnitude of flow (high)		
Turbidity + discharge	Avt (-0.55), MAXt (-0.51)	Average and extreme turbidity	STDd (0.62), DUn1d (-0.57), MEDt (-0.44)	Flow conditions and turbidity distribution	DU10t (-0.66)	Duration over low turbidity threshold

4.5 Discussion

4.5.1 Crayfish presence and local turbidity records

The results presented in this chapter provide the first direct comparison of a turbidity series at a pair of sites where signal crayfish are present in high numbers at one site and are absent at the other. A number of other studies have documented the presence of diurnal fluxes in fine sediment which are not associated with hydraulics. Signal crayfish activity is predominantly nocturnal (Bubb et al., 2002; Johnson et al., 2014) and it is therefore reasonable to assume that an effect on fine sediment dynamics would be more likely during these hours. Crayfish are significant bioturbators and can alter bed sediment resuspension through foraging, pitt construction, walking, tail flipping and fighting activities (Creed and Reed, 2004; Rice et al., 2014; Albertson and Daniels, 2016a). In addition, burrowing activities by signal crayfish can result in pulses of fine sediment of sufficient magnitude to increase ambient turbidity levels (Harvey et al., 2014). The pattern recorded during a 16-week period over the course of a summer provides further evidence to corroborate the observations made by Harvey et al. (2014), Rice et al. (2014; 2016) and Cooper et al., (2016). The turbidity signal has a clear and distinctive nature, demonstrating a gradual increase in ambient sediment concentrations of between 10-20 NTU, presumably associated with the additive effects of fine sediment mobilisation as the number of crayfish and the level of activity enhance over the course of the night. Turbidity levels subsequently remain elevated for a few hours before gradually declining over the course of early morning as crayfish activity declines.

Periodgram analysis supports these arguments. At the D/S site the dominant frequency of turbidity is one day for sets 3-8 and for the U/S site sets 4-7. The absence of clear diurnal trends in turbidity during the first few sample sets, early in the summer, is likely to be associated with water temperatures being low and consequently corresponding crayfish activity being minimal (Cooper et al., 2016). There was a notable increase in water temperatures during set 4 (July) and this is associated with a diurnal pattern in turbidity becoming more discernible (both visually and through the periodgram analysis). Similarly, the final set at the D/S end (late September) had two dominant frequencies, with the start of the record again having a dominant periodicity of one day, whilst the latter half of the record became more noisy with a peak frequency of 0.5 days being identified. One reason could be associated with the reproductive behaviours of crayfish which may alter during the periods of activity. Spawning behaviour of *P. leniusculus* typically occurs during October in the majority of populations (Lewis, 2002) and it is likely that activity levels alter in the lead up to mating season. Visual observations indicated that crayfish were more active in the day during this time period, and Rice et al., (2016) noted a similar pattern with increased activity levels (as determined by passive integrated transponder (PIT) data) and a corresponding weakening in diurnal turbidity fluctuations. Consequently when investigating the role of biota as zoogeomorphic agents, consideration should be given to behavioural and life cycle attributes which may influence the extent of their geomorphic potential; that is their potential to modify the amount of material transported and the modification of geomorphic features (Wolman and Miller, 1960).

In the case of Ridlington, the turbidity series was not as anticipated, in that in the absence of crayfish acting as geomorphic agents, it was assumed that turbidity levels would represent a more consistent low level than is demonstrated. Instead some diurnal variation was observed in one of the seven sets of data analysed. However, the nature of this diurnal pattern is quite distinctive from that at Brooke with the turbidity data lacking the characteristic slow increase in turbidity evident at Brooke in the presence of crayfish. The turbidity series at Ridlington is spiky in nature with a large number of noisy peaks throughout the day. These peaks represent short time frames where turbidity spikes for an hour and then returns back to base levels. It is difficult to attribute the cause of these turbidity fluxes, but as the periodgram confirms, these spikes do not appear to be associated with any form of consistent periodicity with dominant frequencies demonstrating no pattern but rather appear as ‘noise’.

Long term monitoring of suspended sediment concentrations or turbidity are rare with much of the historical monitoring taking place at low resolutions (Duvert et al., 2011) or being heavily focussed towards hydrological events (i.e. to investigate sediment hysteresis) reflecting the conventional view that energy conditions control the transport of fine sediment (e.g. Lewis, 1996; Walling and Collins, 2016). In the absence of continuous or near-continuous SSC data, hydrologists have typically used rating (sediment transport) curves to predict daily SSCs for flux calculations on the presumption that the link between discharge and SSC is strong (Horowitz et al., 2001; Horowitz, 2003). The development of effective turbidity meters which commonly employ optical backscatter (OBS) sensors now offer a means of collecting a continuous surrogate record of SSC (Gippel, 1995; Voichick and Topping, 2014). Despite this, the continued focus of sediment programmes around high discharge monitoring events dictates that baseflow data is limited. As such it is difficult to compare the observed patterns in this study at Ridlington with baseline data from other locations.

It is certainly possible that the assumption that turbidity remains fairly consistent during baseflows is unfounded and that variations in levels of SSC unrelated to flow are natural (Lewis, 2003; Duvert et al., 2011) and may contribute significantly to sediment fluxes, particularly in river reaches which are not transport limited. Grove et al. (2015) suggest that these temporal variations in SS should be expected given the temporally variable contributions of fine sediment from channel and non-channel sources. The classic and principal sources of fine sediment from channel sources are river banks, channel and point bars, bed material, natural backwaters, fine particles associated with vegetation and other biotic particles including phytoplankton ad zooplankton (Wood and Armitage, 1997; Cotton et al., 2006). Invertebrate faecal material is also a significant source of fine material (Ward et al., 1994).

The possibility that animals may also act to entrain and suspend material again highlights the distinct paucity of studies which consider this process and the possibility that a whole array of organisms may be influencing fine sediment dynamics which to date have not been detected (Rice et al., 2016). These potential geomorphic agents are not limited to aquatic flora and fauna (such as vertebrates, invertebrates and fish) but could also include large semi-aquatic organisms such as birds, otters, mink and water voles, which are capable of having a large impact on fine sediment dynamics when foraging or burrowing. Information from local landowners indicated a large number of sightings of mink in the area (*per comms.*) and a number of crayfish traps were destroyed by an unknown aquatic animal at another local site. It is therefore plausible that the large increases in sediment could be attributed to mink (or another large mammal such as badger) navigating and foraging in the stream, particularly as the increase in peaks often occurs around midnight corresponding with this taxon also being predominantly nocturnal (Gerell, 1969). This explanation is conceivable given that approximately 100-200 m upstream a number of unidentified hollows were observed (Figure 4.25) which could be mink excavations and again could contribute to sediment fluxes. Otter and mink are numerous in the two catchments (Reeds, *per comms.*) and it therefore seems reasonable that another large zoogeomorphic agent may be at work which is capable of influencing fine sediment dynamics. During electrofishing no fish species were determined which are capable of disturbing large quantities of fine sediment.

Figure 4.25 Evidence of bank excavations at Ridlington 200 m upstream of the sample site. Potential mink evidence? Photos taken in 2014.

Natural variability in sediment inputs may also be evident in external channel sources of material such as mass bank failures, exposed soils subject to erosion, atmospheric deposition due to aelioan processes and litter fall (Wood and Armitage, 1997). Although a number of these processes are associated with high intensity events such as rainfall and runoff, it is likely that periodic aeolian transportation will occur at streams directly adjacent to bare agricultural land (as in this study) in addition to frequent and episodic inputs of material from litter fall. This may be natural dieback (Greenwood and Kuhn, 2014) or may be associated with physical disturbance by terrestrial biota. As the study site was located directly downstream of a heavily vegetated area which was overhung by a large quantity of dead wood, inputs of leaf litter may have been possible.

It is unlikely however, that these processes would alone account for the large variation in turbidity observed, leaving the most plausible explanation as unaccounted for biotic interactions with fine sediments. Short term records collected by the author at a number of other sites across Rutland, Leicestershire and Northamptonshire, in which crayfish are absent, also possess random turbidity fluxes unassociated with flow but without the signature pattern of crayfish induced elevated levels. As such there is a need for improved continuous monitoring of SSC which extends our knowledge of sediment fluxes beyond that of hydrological flows and into natural temporal variations (at sufficient resolutions) that are unassociated with hydraulic controls (Lewis, 2003).

The application of nephelometric turbidimeters (which measure the degree of scattering that a beam of radiation undergoes; Minella et al., 2008), should not however be undertaken without serious considerations for its limitations (Billotta and Brazier, 2008), and how these affect the reliability of the data collected. Turbidity readings are strongly influenced by the particle size, shape, colour and physical composition of the grains (Clifford et al., 1995; Gippel, 1995; Sutherland et al., 2000). The quality of turbidity data is therefore less consistent than physical SSC samples, often being affected by biofouling, detritus and waterbourne debris. Automatic wipers can limit and prevent fouling from small particles but large debris must be manually removed (Lewis, 2003). Similar issues were encountered in this study with a number of periods in which large quantities of organic debris had built up on the sonde or where biofouling was evident. Operational *in-situ* maintenance is therefore vital in order to gain accurate and representative turbidity records in conjunction with manual screening of data to remove affected records.

To overcome the issues associated with particle size and shape, site-specific calibrations can be conducted with manually collected suspended sediment concentration data. Calibrations typically require 20-30 samples collected over a range of hydrological conditions to be effective (Christensen, 2001) and hence continuous SSC data sets still remain rare (Horowitz, 2003). SSC calibrations were conducted at both the sample sites in this study to overcome such issues and corroborate the observed diurnal trend at Brooke and spikes at Ridlington (Figure 4.26). It is evident that SSC levels are much higher at Brooke than Ridlington and exhibit temporal variability at both sites. It is also apparent that the rate of change in concentration is also much greater at Brooke.

A final issue which was encountered over the course of this study is related to instrument errors associated with the equipment. These errors can be systematic or random either reflecting instrument drift in the case of the former or instability in the signal associated with variations in the voltage or temperature changes in regards to the latter (Minella et al., 2008). There were a number of random errors present in the turbidity record at Ridlington associated with such instrumentation problems, however through application of hourly averaged records these errors were addressed. Caution should however be exercised when interpreting turbidity records. The data presented in this study has been subjected to rigorous quality control checks, with all erroneous or ambiguous data being removed from subsequent analysis and it is therefore anticipated that the patterns presented are real.

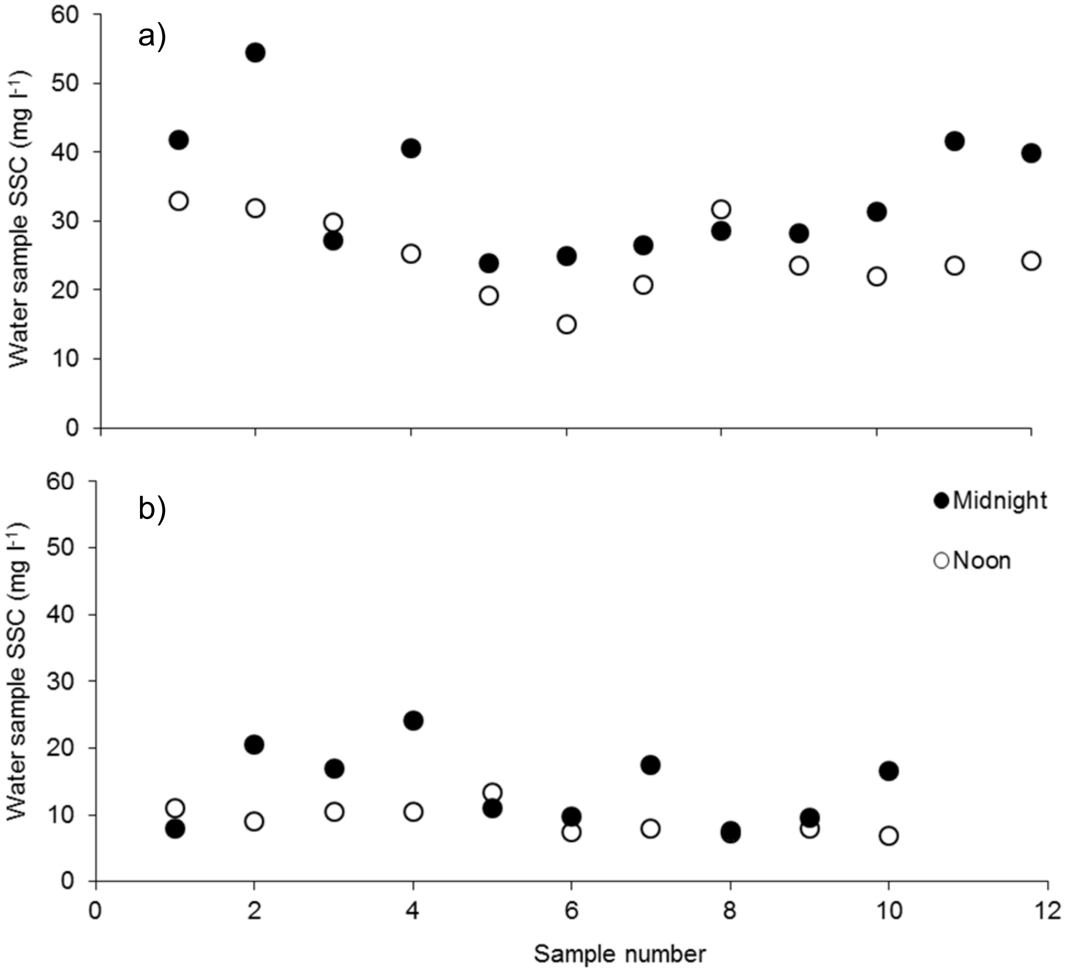

Figure 4.26 Suspended sediment concentrations for water samples collected noon (open circles) and midnight (closed circles) for a) Brooke D/S commencing 19th June at noon; and b) Ridlington commencing 21st June at noon.

4.5.2 Crayfish contribution to suspended sediment loads

Based on the results of this chapter, on average crayfish added 271 kg to 14 day baseflow sediment loads with a maximum of 230 kg within the study reach. This estimate is equivalent to 20 % (maximum of 26%) of the sediment load and highlights the potential importance of biotic interactions with fine sediment dynamics during baseflow conditions. If flood periods during the study (which are low in number associated with the summer time period employed) are incorporated in the calculations this contribution reduces to 14.7%, which still represents a significant contribution to sediment fluxes in a small lowland stream. It should be noted that discharge plays a significant role in mediating the magnitude of biotic contributions (Moore, 2006; Albertson and Allen, 2015). Rice et al. (2016) documented similar additions as a consequence of crayfish presence with an average annual contribution of 31.8% during baseflow flows reduced to 1.46 % with flood periods included. The results of this study further corroborate the growing evidence that biota are significant bioturbators and that their influence on sediment dynamics needs to be considered more seriously during the development of sediment transport models which are severely constrained without incorporation of such interactions (National Research Council, 2010; Corenblit et al., 2011).

Invasive crayfish are not the only taxa capable of such consequences on fine sediment dynamics, dam building by beavers has the potential to completely alter the retention and deposition of fine sediment (Levine and Meyer, 2014; Giriat et al., 2016), with some estimates suggesting that initial aggradation of rivers can be as high as 0.47 m yr^{-1} (Pollock et al., 2007). A number of species of fish have been found to mobilise fine sediments during foraging activities including Barbel (*Barbus barbus),* gudgeon (*Gobio gobio*), bream *(Abramis brama),* tench (*Tinca tinca)* and common carp *(Cyprinus carpio;* Statzner et al., 2003a; Persson and Svensson, 2006; Matsuzaki et al., 2009; Weber and Brown, 2009) and the most well studied zoogeomorphic agent, salmonids, can rework sediments through spawning activities (DeVries, 2012; Hassan et al., 2015). Macroinvertebrates (Plecoptera, Ephemeroptera, freshwater shrimp, tubificids and Chironomidae) have also been documented to alter fine sediment dynamics despite their relatively small size (Soluk and Craig, 1990; Zanetell and Peckarsky, 1996; March et al., 2002; Nogaro et al., 2009). Given the large number of biota which inhabit aquatic ecosystems, the impact of such interactions on fine sediment dynamics has the potential to be considerable (Rice et al., 2012b; Statzner, 2012).

Within this study, the contribution of biotic induced sediment loads demonstrated significant variability both temporally and spatially. Biotic fluxes were on average greater at the D/S reach (22%) compared to the U/S reach (18%). Furthermore, temporal differences in rates were most prominent at the U/S reach with a considerable increase during set 4 (July) from an average of 16% to 24 % for the next four weeks. The implications of biota on the physical environment are heavily dependent on three biological characteristics; body size, abundance and behaviour (Moore, 2006). Within this study, the body size of individuals did not vary over time or space and consequently is unlikely to have affected the flux rates measured. Behavioural effects on bioturbation associated with reproductive behaviours were possibly evident in the weakening of the diurnal turbidity pattern as discussed in the previous section. The CPUE however did demonstrate some variability over time with estimates being highly correlated with temperature (Johnson et al., 2014).

The variability in the contribution of crayfish to sediment fluxes, particularly in the instance of the U/S reach, is most likely associated with spatial differences in crayfish populations throughout the reach (and U/S of the reach which were not accounted for directly). Crayfish typically remain in the same location for days to weeks but then sporadically move to a new location (Bubb et al., 2002). As such these alterations to localised abundances will have repercussions on the extent of biotic interactions with the environment (Albertson and Allen, 2015). Consequently, when considering the role of biota as geomorphic agents' attention should be paid to localised population dynamics of the taxa over time as opposed to purely presence / absence.

Within the study reach, the spatial distribution of crayfish over time affected channel storage and ingress rates. Sediment fluxes demonstrated a net loss of material (2510 kg) during the first four weeks (June) with three high flow events entraining a large amount of material at the D/S end of the reach. However, in the most part sediment budgets remained largely in equilibrium during the sampling period with a negligible net gain of 25 kg (average flux of 1593.45 kg). It is likely that this estimate reflects the highly dense population structure of crayfish throughout the river Gwash.

Selection of the river reach was focussed around a riffle-pool structure which supported a highly abundant population of crayfish. However, within this river the distribution of crayfish remains high throughout with a number of sites on the river supporting high abundances of crayfish; CPUE estimates based on 3 nights trapping during 2014 - 6.8 adults at a site 1.7 km U/S (Braunstone - SK8345506432) and 6.2 individuals at a site 2 km D/S (Gunthorpe - SK8660305165). As a result, the amount of fine sediment entering and leaving the reach is likely to be similar and in this river crayfish do not act as a net source of fine sediment to reaches downstream. However, in a river which is undergoing crayfish colonisation and is in the early stages of invasion or in one which supports isolated pockets of abundant populations, the implications of crayfish on downstream fluxes may be notable. Sites in which crayfish are present may act as a source of material whilst those D/S may act as a store.

4.5.3 Fine sediment ingress over time as a function of crayfish presence

Fine sediment ingress rates demonstrated no overall differences when crayfish presence was considered for any of the two week time periods. Similar amounts of fine sediment accumulation were present at both Brooke and Ridlington which may reflect that despite the distinctive diurnal fluxes in fine sediment associated with crayfish bioturbation, the overall facets (i.e. duration, magnitude, frequency of turbidity over thresholds) of the two turbidity regimes did not differ in these study sites (as determined by the PC analysis). A number of other studies have documented a reduction in sediment accrual associated with the presence of crayfish (Parkyn et al., 1997; Creed and Reed, 2004; Usio and Townsend, 2004; Helms and Creed, 2005; Albertson and Daniels, 2016a), but these studies have significant limitations in that they are conducted under controlled conditions utilising *in-situ* enclosures or through flume studies (*in-situ* experimental channels or *ex-situ*). In such experiments it is unsurprising that sediment deposition rates were greater in enclosures free from crayfish compared to those with crayfish. Crayfish activity within these studies was as a consequence of repeated foraging within a small spatial area and therefore these studies directly measure the potential of crayfish to act as geomorphic agents in the remobilisation of fine sediment. In reality crayfish activity is not confined to a small spatial area but distributed across multiple foraging patches which are likely to differ each night.

This study therefore aimed to scale up the impacts of crayfish on fine sediment deposition by measuring accrual rates over a two week period between a control and invaded reach. Moreover, this study differed in environmental context, with the previous studies being located in rivers or flumes which are characterised by predominantly gravelly substrates. Consequently, inputs of fine sediment through suspended sediment fluxes (biotic and abiotic) are likely to be limited, compared to the quantity of fine sediment available in the rivers in this study. As a result, the findings of this study take into account the cumulative effect of crayfish on fine sediment deposition as a function of inputs (burrowing and fluxes) in addition to outputs (remobilisation).

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

4.5.4 Biotic contribution to fine sediment dynamics

To summarise, the consequences of biota on fine sediment dynamics is heavily dependent on a number of factors. Firstly, the abundance of biota in time and space (also dependent on the stage of invasion if non-native) which controls the net change in sediment dynamics. Secondly, life cycle attributes that often alter an organism’s behaviour and therefore their interaction with the physical environment, and thirdly environmental controls such as discharge and temperature which exert an influence over activity levels and the overall contribution of the biota to sediment fluxes.

Despite the growing body of literature focussed on the role of organisms as geomorphic agents, studies which examine the implications of their behaviour on the physical environment associated with the above attributes are limited (Moore, 2006; Johnson et al., 2011; Albertson and Allen, 2015). Further work is therefore imperative to enhance our understanding of the potential biogeomorphic contributions that biota may have on the physical environment as a function of time and space.

4.5.5 The relationship between discharge, turbidity and fine sediment ingress

This study represents the first attempt to characterise the relationship between the physical controls of discharge (transport capacity), turbidity (sediment availability) and mass of fine sediment ingress (*m*) focussed on the intermediate time scale. Application of simultaneous monitoring of all three processes enables an enhanced understanding of the catchment scale processes which drive fine sediment deposition at the catchment scale. Major limitations in our understanding of the relationship between ingress and broad-scale physical controls have been an absence of high resolution sediment time series data which historically lags behind discharge monitoring (Gray and Gartner, 2009). This study utilised the surrogate measurement of turbidity (cross checked with SSC calibration data; Bilotta and Brazier, 2008) and gauged discharge data over an 18-week period at two sites to gain a better understanding of how localised and temporal variations in discharge and turbidity influence the mass of fine sediment ingress. The methodological approach employed demonstrates the value of undertaking principal component analysis to characterise the overall facets of discharge and turbidity which influence fine sediment ingress and which can therefore inform large scale catchment sediment management.

Despite the specific controls on ingress being associated with localised differences in hydraulics and bed sediment composition, amongst other factors (Carling, 1984; Lapointe et al., 2004), these variables are difficult to incorporate into sediment management practices particularly as they are highly variable in space and time. Therefore understanding the controls on sediment loading (within the channel) relies on a generic knowledge of site specific relationships between ingress, stream capacity and sediment availability. Correlation analysis indicated that the hourly-average turbidity series was not highly associated with discharge regimes at either site. Historical monitoring of SSC is typically limited to low resolution data with the focus predominantly on high discharge events (Walling and Fang, 2003). However, the lack of apparent correlation between suspended sediment availability and discharge indicates that other processes may control sediment rates, potentially biotic processes. Whatever the cause, the conventional view that discharge alone controls sediment fluxes may overlook important contributors to temporal variations in suspended sediment transport.

When individual facets of the regimes were considered, the evidence further corroborates the lack of association. Hydrology is predominantly correlated solely with the magnitude of turbidity, which is not unexpected. Visual observations of ingress (Figure 4.21), periods of high flow (Figure 4.19) and the loading of sample sites on the PCA plot (Figure 4.23) indicate no relationships between discharge variables and fine sediment deposition. Periods of high discharge do account for the highest *m* in the case of set 2 at Brooke (B2) and set 8 at Ridlington (R8), however sets 5 and 7 at Brooke (B5 and B7), which are heavily weighted to high flows, demonstrate relatively low *m*. Construction of correlation matrices between the individual facets of turbidity, discharge and *m* (Table 4.7) indicated that the individual facets of discharge and turbidity had a poor relationship with *m.* Construction of linear regression using multiple components of discharge and turbidity yielded improved predictive models, suggesting that it is not one element of discharge or turbidity which controls *m* but a combination of multiple facets.

Grains 125 -1000 µm exhibited strong correlation with average turbidity conditions and magnitude of turbidity. Regression analysis indicated that both average and magnitude characteristics of turbidity were significant predictors of ingress rates explaining 45% of the variance, with the latter being the strongest factor. Incorporation of discharge indices into the model made little difference to the amount of variance explained (0.9% addition). Grains in this size fraction are more likely to be influenced by extreme sediment events as it is unlikely that they will be transported as fluxes over large distances during low flow events. Consequently, the mobilisation of these grains is likely to be associated with high intensity events (with corresponding high critical bed shear) which produce enough energy to initiate entrainment (Gordon et al., 1992). Of all the linear models developed using the discharge regime, grains in this size fraction are associated with the greatest amount of variation being explained. Magnitude of discharge is the most significant predictor within the model and this therefore provides a controlling link over the magnitude of turbidity. Average turbidity conditions are however not associated with discharge and therefore vary independently of discharge in time.

The strongest association was between *m* <125 μm and turbidity with the regression model accounting for 54 % of the variation (with an additional 0.4% explained with discharge incorporated). The component which characterised the duration of turbidity values below 10 NTU was the most significant explanatory variable. Grains in this size fraction, once in suspension, can be transported long distances given the low hydraulic energy conditions (shear stress) needed to entrain them (Lambert and Walling, 1988). Consequently, as the time in which turbidity levels fall below the threshold of 10 NTU, ingress rates of this size range may increase as grains are more liable to vertical ingress rather than being in suspension in the water column. Discharge has the least association with this size fraction (21 % variance explained) with many rivers often acting as an effective conveyance system for silt sized particles irrespective of hydraulic energy.

The only grain size to be associated predominantly with discharge is the size fraction of 1000-2000 μm. The discharge facets of duration and magnitude of high flows, accounted for 25 % of the variability in ingress rates compared to 9 % and 15 % within the turbidity and combined model respectively. Grains in this size fraction are heavily reliant on sufficient hydraulic force for entrainment which is typically a function of hydrological flow (Schálchli, 1995). Consequently, it is unsurprising that turbidity has little association with ingress of this size fraction as the grains are unlikely to remain in suspension for long periods of time during baseflows as per the critical Shields Parameter concept (Rathburn and Wohl, 2003).

This study demonstrates that an adapted PCA- based method (*sensu* Olden and Poff, 2003) can effectively be used to identify the dominant facets of turbidity and discharge regimes (and which can be expanded to incorporate other broad scale controls) that influence the mass of fine sediment ingress. The results of the study suggest average and magnitude facets within turbidity regimes are important for the ingress of grains 125 – 1000 μm, whilst the duration of turbidity below 10 NTU is associated with grains in the size fraction <125 μm. Discharge was positively related to only one grain size, that of 1000-2000 μm which was associated with the magnitude and duration of high flow events. It should be noted that it is important to exercise caution when employing data redundancy approaches as they may reject variables of importance due to the assumption that statistically dominant sources of variability are the principal drivers of the association they are being used to describe (Monk et al., 2007). Despite this, application of the methodological approach undertaken within this study enables incorporation of a multitude of parameters that characterise various facets of hydrological and sedimentological regimes whilst minimizing the problems associated with collinearity and overfitting of models. As such the analysis tool enables an enhanced knowledge base of the processes which are relevant to sediment loading but at a scale which is appropriate for management strategies.

Results from this chapter indicate that discharge is weakly associated with ingress rates during baseflow conditions and that localised turbidity variations explain a greater amount of variance. The study highlights the need for additional research which simultaneously monitors sediment concentrations, discharge and ingress rates during low flow conditions. It is widely acknowledged that discharge during extreme flow periods exerts a strong control over ingress rates (Frostick et al., 1984), but much less is known about deposition rates during baseflows conditions. Further understanding could be ascertained by monitoring the gradients of vertical and lateral hydrological exchange as a function of discharge, as these exchanges exert a significant influence over ingress rates during baseflow conditions (Pettricrew et al., 2007). Incorporating the role of biotic processes on fine sediment fluxes may also enhance the fundamental knowledge base and may provide some explanation as to why turbidity drives sediment dynamics independent of hydraulic forcing.

4.6 Summary

The results of this chapter demonstrate the significance of crayfish as zoogeomorphic agents. Observations of fine sediment fluxes over 145 days indicated that signal crayfish contributed on average 20% extra to baseflow loads than would otherwise be observed under abiotic forcing alone. During spate periods the contribution of crayfish declined considerably highlighting the importance of considering environmental controls when examining biotic-abiotic interactions. In contrast, no direct evidence of crayfish influencing fine sediment ingress rates was determined relative to the control site. This finding is probably associated with the invaded site being densely populated by crayfish resulting in fine sediment losses and inputs associated with zoogeomorphic activity being in equilibrium. The chapter also presented one of the first accounts of organisms influencing sediment budgets; with implications evident early in the crayfish season, which dissipated as the season proceeded, most likely associated with the temporal distribution of crayfish throughout the river reach. The results from these studies suggest that the implications of crayfish for fine sediment dynamics are highly dependent on three main factors. Firstly, the abundance of the organism spatially and temporally; secondly, life cycle attributes which alter their behaviour over time and finally; environmental controls which exert an influence over activity levels and overall biotic contributions.

Concurrent examination of turbidity at a control site demonstrated random and intermittent spikes in suspended sediment concentrations not associated with hydraulic forcing. This raises the strong possibility that a number of organisms may be influencing fine sediment dynamics which to date have not been detected. This was further sustained when the controlling processes of fine sediment ingress were examined. Discharge was not determined to be strongly correlated with turbidity or the mass of fine sediment ingress, whilst turbidity levels explained a greater proportion of variability in the mass of fine sediment ingress. Understanding localised turbidity fluctuations which occur independent of hydraulic forcing therefore represents a key challenge to enable enhanced comprehension of the controls on fine sediment ingress. Biotic interactions with fine sediment signify an important process within this research area.

Chapter 5 – Temporal variability of invasive crayfish effects on macroinvertebrate communities at the reach scale

5.1 Introduction

Across the globe invasive species are spreading rapidly and represent one of the most significant threats to biodiversity, economic development and human health (Simberloff et al., 2013; Early et al., 2016). Despite biological invasions being a natural facet of ecological change, the rate of contemporary invasions far exceeds that of historic events and it is likely that this trend will increase in the future associated with climatic modifications (Gillson et al., 2008; Walther et al., 2009; Brown et al., 2016). The establishment of a non-native taxon can have significant implications for the entire ecosystem and biomonitoring tools (see Chapter 3), from the replacement of an individual species through to the decoupling of food webs with resultant cascade effects throughout the ecosystem (Strayer, 2010; Walsh et al., 2016).

Despite an increasing number of studies on the ecological implications of invasive crayfish, much of the research has been conducted in lentic ecosystems (e.g. Nyström et al., 2001; Ercoli et al., 2015a,b, Ruokonen et al., 2016) and is typically focussed on understanding the overall effect for the ecosystem with only a limited number of studies undertaking repeated sampling at the same sites. Much less is known about how stream communities are affected by such invasions and even less so regarding the temporal effects of invaders. To date, few studies have considered the long term effect of signal crayfish on macroinvertebrate communities (see Wilson et al., 2004; McCarthy et al., 2006; Ruokonen et al., 2016; Chapter 3) and none have considered the intra-annual temporal dynamics at smaller time scales once an invasive population is established (i.e. associated with key life history characteristics). Understanding the full extent of invader effects will continue to be constrained until studies are conducted that span the appropriate spatial and temporal scales (McCarthy et al., 2006).

Community composition of lotic macroinvertebrate populations vary over space and time associated with physical properties such as flow, water quality and the availability of resources, but also demonstrate short term (seasonal) temporal shifts related to individual taxon life-cycles / histories (Hynes, 1972). Many taxa exhibit seasonal life cycles that are timed to take advantage of optimal environmental conditions including temperature (Huryn and Wallace, 2000), flow (Bunn and Arthington, 2002) and food availability (Anderson and Cummins, 1979) or to avoid competition via temporal niche separation (Grant and Mackay, 1969). Crayfish also exhibit variations in levels of activity, which generally increase with rising water temperatures (Johnson et al., 2014). These seasonal changes in macroinvertebrate abundance and crayfish activity levels may affect the magnitude of crayfish effects within the invaded ecosystem, particularly if preferential prey items are depleted over the course of the seasonal timeframe when crayfish are active.

The physical habitat template of the ecosystem in which biological invasions take place will most likely control the effect the invader has on the receiving ecosystem. A number of studies have documented highly variable effects of non-native taxa as a function of the physical characteristics of the ecosystem (Vilà et al., 2011; Klose and Cooper, 2012). Heterogeneous habitats, which contain boulders and cobbles, macrophytes and interstitial space, provide shelter, potentially reducing the effects of predators. In contrast, areas with low habitat complexity may increase predation vulnerability (Crooks, 2002). Fine sediment loading can lead to the homogenisation of lotic ecosystems and loss of habitat (Wood and Armitage, 1997) but can also lead to diminished macroinvertebrate diversity through direct burial or enhanced drift (Wood et al., 2005; Larson and Ormerod, 2010; Jones et al., 2012). These alterations in resident macroinvertebrate assemblages (in particular species richness) associated with the physical template may modify the interactions and effects of invasive crayfish with the wider macroinvertebrate population (Fitzgerald et al., 2016).

The quantity of fine sediment stored within riverbeds is widely considered to be a global threat to freshwater biodiversity (Owens et al., 2005; Heppell et al., 2009). Elevated levels of fine sediment delivery are typically associated with anthropogenically driven alterations to fine sediment loading (Walling and Collins, 2016), however crayfish themselves represent significant ecosystem engineers capable of modifying the fine sediment dynamics of a river (Harvey et al., 2011) Increasingly aquatic ecosystems are being subjected to multiple stressors (Jackson et al., 2016b). It is therefore important to consider the additive effects of invasive species and habitat modifications (e.g. via fine sediment loading) upon the macroinvertebrate community to fully understand the implications and enable effective management (Strayer, 2010). Few studies have investigated the interactive effects of invasive crayfish and fine sediment and of these the majority consider the erosion of fines characteristic of gravel river beds in North America rather than lowland agricultural settings (e.g. Helms and Creed, 2005; Albertson and Daniels, 2016a).

5.2 Research Aims

In this chapter the additive effect of invasive signal crayfish and fine sediment loading on macroinvertebrate communities was examined within a high resolution sampling timeframe. Two lowland rivers in England (UK) were employed, one which supported a well-established non-native crayfish population (invaded) and one in which crayfish have not been recorded (control). In contrast to other studies which have examined the net effect of large established populations of crayfish on stream communities via spot sampling throughout the year, this study aimed to examine the temporal evolution of crayfish effects (if any) throughout the main crayfish activity period. That is, does the effect on the community intensify as the main activity season proceeds with continuing adjustments in the macroinvertebrate community, or are the impacts on the macroinvertebrate community consistent regardless of levels of crayfish activity? The study also considers the potential additive effective of fine sediment loading in combination with invasive crayfish predation under field conditions. Finally, monitoring crayfish populations is difficult due to the size-bias of commonly employed trapping methods. Here the potential value of colonisation cylinders to quantify the temporal dynamics of crayfish juveniles (young of the year) was examined.

Specifically the following research questions are addressed:

1) Are the implications of established *P. leniusculus* populations persistent for macroinvertebrate communities, or do they vary intra-annually associated with life histories (invader and resident macroinvertebrates)?

2) What are the main taxa affected by the presence of *P. leniusculus* in lotic ecosystems and are the trends similar to those identified in long term evaluations of macroinvertebrate impacts (Chapter 3)?
3) Do the effects of fine sediment loading and crayfish presence have independent or additive effects on the wider macroinvertebrate community?

5.3 Methods

5.3.1 Field sites

The study took place on two small lowland rivers in Rutland (UK) both of which were the focus of research presented in Chapter 4; the River Gwash (SK8497705995) and the River Chater (SK8494303710). Historic routine sampling by the Environment Agency and contemporary sampling during the study period by the author has not recorded any signal crayfish in the River Chater (control river), whilst density estimates in the Gwash (invaded river) during 2014 – 2015 indicated a mean catch per unit effort of 4.7 individuals per trap per night (n = 20). Both of these rivers were also part of the ecological long-term analysis conducted in Chapter 3 with the River Gwash demonstrating a significant divergence in assemblage composition following crayfish invasion in 1996 compared to the River Chater (and other control rivers). Community composition was originally similar and the divergence in communities associated with crayfish presence persisted over time. The rivers therefore represent two different community types as a function of crayfish which can be investigated in more detail within this study. For more detailed site characteristics and information see section 4.3.1.

5.3.2 Colonisation cylinders

This study utilised the same cylinders employed in Chapter 4. At both sites, colonisation cylinders were employed to provide a constant record of the macroinvertebrate community with the aim of evaluating whether the effect of signal crayfish presence remained consistent over time. Each colonisation cylinder comprised a PVC cylinder (diameter 65 mm, height 200 mm) perforated with twelve horizontal holes (diameter 6 mm) to permit both horizontal and vertical exchange of flow, macroinvertebrates and fines (Mathers and Wood, 2016). All cylinders were filled with a prewashed gravel framework collected from each of the respective sample sites (truncated at 8 mm) that was enclosed in a net bag (7 mm aperture) within each cylinder.

A second cylinder treatment was also employed, in which 250g of fine sand (63 – 2000 µm) was added to the gravel framework, and which preliminary tests indicated filled 100% of interstitial volume. Signal crayfish have the potential to directly alter the input and output of fine sediment, which may have consequences for the storage of fine sediment. Burrowing activities may enhance the delivery of fine sediment (Faller et al., 2016), whilst the diurnal bioturbation of fine sediment associated with crayfish activity increases sediment fluxes out of the reach (Chapter 3; Rice et al., 2016). It is likely that the dominance of these processes will vary depending on the spatial distribution of crayfish within a river reach and therefore the effect of crayfish on fine sediment loading may not be consistent. Consequently, the application of two sediment treatments in this study (i.e.no fine sediment and interstitial pore space filled with fines) enabled the potential effect of differing fine sediment loading and severity of crayfish impacts for the receiving ecosystem to be examined.

For the cylinders with fines (hereafter referred to as clogged), a circular disk (64 mm diameter) was attached to the mesh bag which effectively sealed the base of the cylinder and prevented the loss of fine material vertically into the riverbed. The cylinder installation process is described in the previous chapter (Section 4.3.8.1). Cylinders were left *in-situ* for the entire sampling campaign, but every 14 days the gravel netting bag was removed and replaced, providing a constant record of the macroinvertebrate communities at this resolution. At the end of each 14-day sampling period, the net bag was carefully removed and placed directly into a sample bag. Empty cylinders were then replaced with the corresponding gravel bag treatment (clean or clogged). All invertebrate samples were preserved in the field in 10% formaldehyde and returned to the laboratory for processing and identification.

Colonisation cylinders were installed 21st May – 24th September 2015 (as in Chapter 4) providing a record of 126 days (nine 14-day sample sets). At each riffle (three at the invaded reach and two at the control; one until 2nd July 2015), four cylinders of each type (clean or clogged) were installed providing a total of 12 replicates in the invaded reach and 8 (4 initially for 3 sample sets) at the control. In total, 105 and 57 clean substrate samples and 108 and 55 clogged substrate samples were examined from the invaded and control sites respectively (3 clean cylinders were lost at both sites and 5 clogged cylinders at the control site during the sampling campaign; Table 5.1 provides a breakdown of sample dates and riffle replicates over time).

In addition to the 2 week samples, two additional sampling timeframes (ca one month: 28 days and ca two months: 56 days) were examined to ascertain whether sampling duration had an effect on the ability to detect the presence of crayfish effects on macroinvertebrate communities. These samples were more susceptible to the cumulative effects of multiple spate conditions and the additive effect of crayfish over the season. In total, 39 samples were retrieved over these time frames respectively (Table 5.1; 1 clean cylinder was lost at the control site during the one month period and one clogged sample from the invaded site in the 2 month sample set).

Table 5.1 Summary of datasets collected for this study at the invaded (Brooke) and control sites (Ridlington) during 2015.

		Invaded site		Control site
Sample Set	**Dates covered**	**Sediment traps**	**Crayfish data**	**Sediment traps**
1	21st May - 4th June	n = 23	n = 1	n = 7
2	4th June - 18th June	n = 24	n = 1	n = 7
3	18th June - 2nd July	n = 24	n = 1	n = 8
4	2nd July - 15th July	n = 24	n = 1	n = 16
5	15th July - 30th July	n = 23	n = 2	n = 15
6	30th July - 13th August	n = 24	n = 1	n = 14
7	13th August - 27th August	n = 24	n = 2	n = 15
8	27th August - 10th September	n = 23	n = 3	n = 15
9	10th September - 24th September	n = 24	n = 3	n = 16
1 month	2nd July – 30th July	n = 24	n = 3	n = 15
2 month	2nd July – 27th August	n = 23	n = 6	n = 16

5.3.3 Crayfish activity

Trapping was conducted on an intermittent basis throughout the sampling campaign as a surrogate for adult crayfish activity. Periodically (n=14), baited “trappy” traps (50 x 20cm with an opening of 5 cm and mesh size 3 cm) were deployed at the invaded site at three locations throughout the reach (upstream, middle and downstream). This sampling strategy enabled a spatially representative record of crayfish activity as crayfish are known to move sporadically to new locations and therefore not reside at a single location (Bubb et al., 2002). On each occasion traps were set at a location during the afternoon and retrieved the following morning, with a total of two traps per site. Catch Per Unit Estimates (CPUE) were calculated from the total number of adult individuals caught for each sampling set and presented as an abundance index. Trapping often leaves juvenile crayfish population's uncharacterised (Holdich et al., 1999), however juvenile crayfish were regularly recorded in the colonisation cylinders. This provided a means of consistently assessing the abundance of juvenile crayfish present in the river. The number of juvenile crayfish recorded in the cylinder samples for each sample set was standardised to the number of individuals per m^2 by dividing the total number of crayfish for each sample set by the total sample surface of the cylinders (ind / m^2).

5.3.4 Laboratory procedures and statistical analysis

Within the laboratory, samples were processed for invertebrates using a 250 µm sieve. All macroinvertebrates were identified to the lowest taxonomic level possible usually species or genus with the exception of Oligiochetea (order), Diptera families (including Ephydridae, Ptychopteridae, Chironomidae, Psychodidae, Simuliidae, Ceraptogonidae and Stratiomyidae), Sphaeriidae and Zonitidae (family) and Ostracada, Hydracarina and Collembola which were recorded as such.

To identify temporal changes in macroinvertebrate communities associated with crayfish activity and macroinvertebrate lifecycles (by sample sets), non-metric multidimensional scaling (NMDS) centroid plots were employed over time for the invaded and control sites (sample sets 1-9). Distances among centroid matrices were constructed by calculating the averages (e.g. the centroid - the centre-point of all replicates for each sample set in multi-dimensional space) using Bray-Curtis similarity coefficients (Anderson et al., 2008). Compositional differences in communities between the control and invaded sites were examined using non-metric multidimensional scaling (NMDS) plots using Bray-Curtis similarity coefficients for the overall data set and for each individual sample set. This approach enabled examination of whether community effects were consistent or whether they varied as a function of time (e.g. crayfish activity or environmental conditions such as changes in discharge or water temperature; 14-day periods).

A One way ANOSIM (Analysis of Similarities) was used to examine differences in the communities amongst the control and invaded rivers for the overall data set and for each sample set (1-9). For each dataset, a random Monte Carlo permutations test was performed (999 random permutations). Both P and R ANOSIM values were examined, with R values >0.75 indicating strong separation amongst groups, R = 0.75–0.25 indicating separate groups with overlapping values and R <0.25 as barely distinguishable groups (Clarke and Gorley, 2006). To examine if invaded or control communities were more or less heterogeneous than the other, homogeneity of multivariate dispersions (beta diversity) between aquatic macroinvertebrate assemblages based on Bray-Curtis distance matrices from the centroid were calculated using the PERMDISP function and compared using One-Way ANOVA (Anderson, 2006a,b; Anderson et al., 2008). Multivariate dispersion measures the spread of samples around the central tendency measurement (in this case the centroid) based on sample groups (for this study invaded and control). A non-significant ANOVA indicated that the sample groups were similar in heterogeneity. Taxa contributing to the divergence of communities were identified through the application of the similarity percentage (SIMPER). Taxa that SIMPER identified to be driving dissimilarity between invaded and control rivers or that have been cited in previous literature associated with crayfish invasions were selected for further statistical analysis. All ordination analyses were performed in PRIMER Version 7.0.11 (PRIMER-E Ltd, Plymouth, UK).

Community abundance and taxa richness metrics were derived from the raw data, in addition to richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) groups. Abundances of taxa characterised as sensitive to sediment (as defined under the sensitivity weights provided in the Empirically-weighted Proportion of Sediment-sensitive Invertebrates index (E-PSI; Turley et al., 2016)) were also calculated for each sample. To examine differences in macroinvertebrate metrics and individual taxon abundances associated with crayfish presence, generalised linear mixed effects models were developed (GLMMs). Models were fitted using the '*lme4*' package in R version 3.2.2 using the '*glmer*' function (R development Core Team, 2014). Site and time were specified as fixed interacting factors (Site x Time) and sediment treatment was nested within riffle as a random factor (columns within sediment treatments in individual riffles are less independent). Models were fitted using a Poisson error distribution and log link structure. For a full list of model outputs including interactions between sediment treatment and time see Mathers et al. (2017).

5.4 Results

5.4.1 Community composition associated with crayfish presence

A total of 69 taxa were recorded from the 169 colonisation cylinders; of these 57 were recorded in the invaded river (mean 6.62 range 1-14) and 54 in the control river (mean 7.06, range 2 – 16). In all, 17,734 individuals were recorded from the nine sampling sets (invaded river mean 55.02 per cylinder / sampling set, range 14-168; control river mean 54.68, range 9-136). Communities at the invaded site were dominated by *Gammarus pulex* (56.69% of total abundance), Chironomidae larvae (14.10%) and *Potamopyrgus antipodarum* (9.92%). The most abundant taxa at the control site were *Gammarus pulex* (69.70% of total abundance), Oligochaeta (5.63%) and Chironomidae (4.66%). A total of 11 taxa were unique to the invaded site (4 Trichoptera, 4 Diptera, 1 Tricladida, 1 Gastropoda and 1 Ostrocoda) and 10 to the control (5 Coleoptera, 2 Trichoptera, 1 Hirudinea, 1 Gastropoda and 1 Diptera).

Non-metric Multi-Dimensional Scaling (NMDS) ordination diagrams for the entire dataset and the nine individual sampling sets indicated distinct clusters of macroinvertebrate communities in the invaded and control rivers on all occasions (Figure 5.1). The degree of separation between the groups remained consistent over time with all sample sets indicating highly significant differences for all pairwise comparisons (ANOSIM; eight of nine sets and global dataset p = <0.001 and set 2 P = 0.002; Table 5.2).

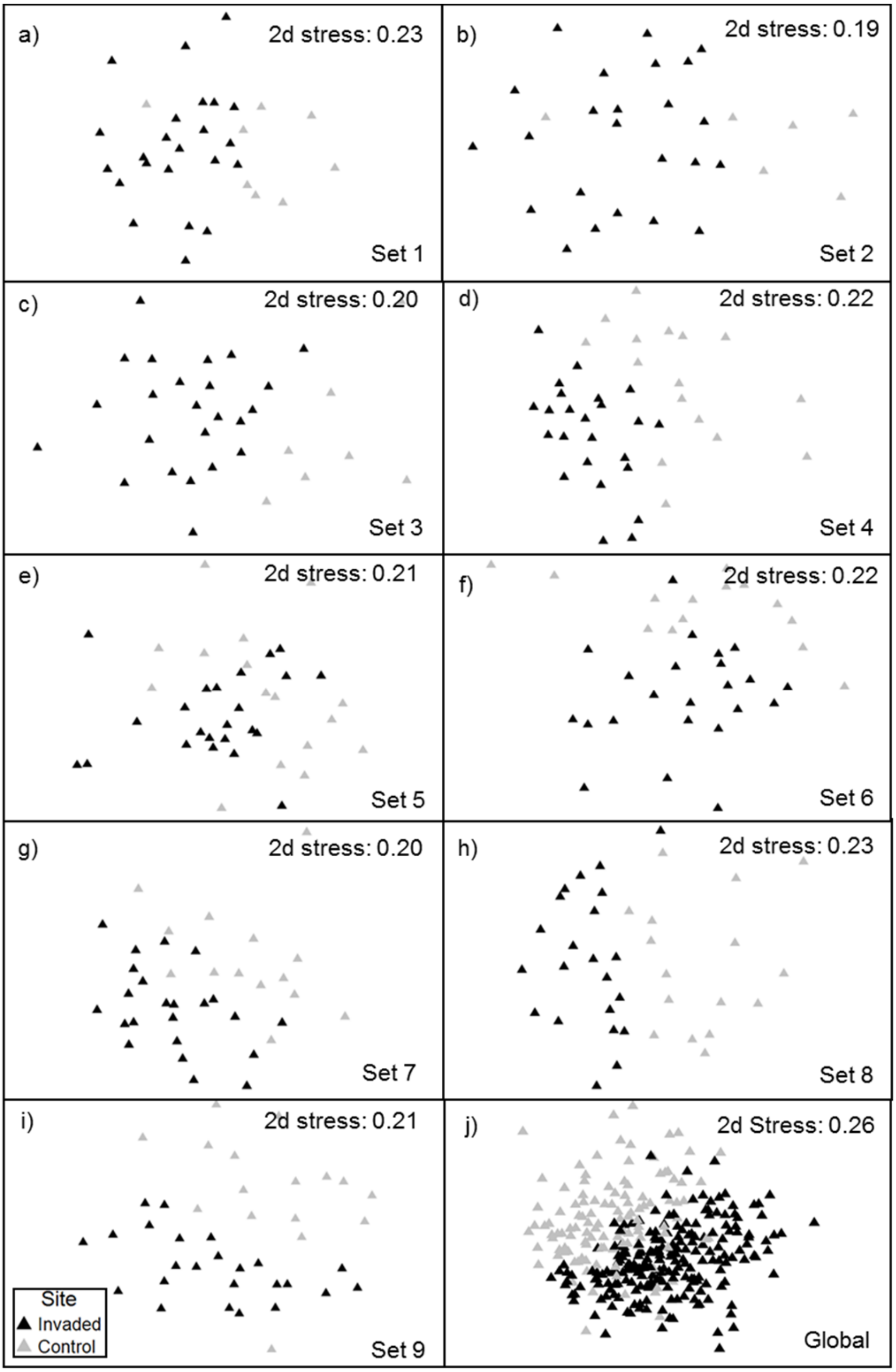

Figure 5.1 Non-metric multidimensional scaling (NMDS) of macroinvertebrate community data using the Bray-Curtis similarities coefficients for cylinder sets 1 -9 (panes a-i) and global data set (pane j). Black triangles = invaded river (Brooke) and grey triangles = control river (Ridlington).

Table 5.2. Summary of ANOSIM values over time by crayfish presence and the combinations of sediment treatment and crayfish presence.

Set	**Site differences**		**Clean vs clean**		**Clog vs clog**		**Control x sediment**		**Invaded x sediment**	
	r value	**p value**	**r value**	**p value**	**r value**	**p value**	**r value**	**p value**	**r value**	**p value**
1	0.325	0.001	0.409	0.018	0.249	0.078	0.094	0.375	0.076	0.078
2	0.407	0.002	0.545	0.006	0.116	0.363	0.179	0.333	0.245	0.005
3	0.552	0.001	0.812	0.002	0.402	0.012	0.296	0.143	0.025	0.276
4	0.417	0.001	0.424	0.001	0.524	0.001	0.163	0.056	0.188	0.006
5	0.252	0.001	0.413	0.001	0.208	0.015	0.239	0.006	0.125	0.033
6	0.306	0.001	0.348	0.001	0.34	0.004	0.155	0.050	0.134	0.032
7	0.367	0.001	0.368	0.002	0.277	0.016	0.027	0.008	0.104	0.064
8	0.375	0.001	0.399	0.001	0.394	0.030	0.270	0.010	0.020	0.338
9	0.411	0.001	0.281	0.006	0.487	0.001	-0.046	0.690	-0.027	0.671
Overall	0.342	0.001	0.306	0.001	0.306	0.001	0.108	0.001	0.084	0.001
1 month	0.537	0.001	0.494	0.001	0.55	0.001	0.090	0.116	0.059	0.128
2 month	0.567	0.001	0.538	0.001	0.588	0.001	-0.048	0.832	-0.029	0.601

When sediment treatment was considered, it was clear that crayfish invasion had altered the wider macroinvertebrate community composition compared to the control site (see Chapter 3). However, it was also evident that the sediment treatment had a significant effect on community composition which was independent to that of crayfish. Four distinct clusters were evident in the ordination plots as a function of crayfish and substrate treatment (Figure 5.2; only one sampling period, set 4, is shown for conciseness. For all sampling periods see Appendix 4). Clean substrate communities demonstrated the greatest separation between invaded and control communities with all pairwise comparisons being significant (including 7 sets $p < 0.005$) compared to 7 of the clogged sets (where only 4 sets $p < 0.005$; Table 5.2). When the effects of sediment treatment were considered at the respective sites, communities demonstrated less marked effects on community composition than that associated with crayfish presence (Table 5.2). Only four sampling periods were significantly different (respectively at both sites) with R values being on average a magnitude of 2.5 (control) and 3.9 (invaded) less than those associated with crayfish presence.

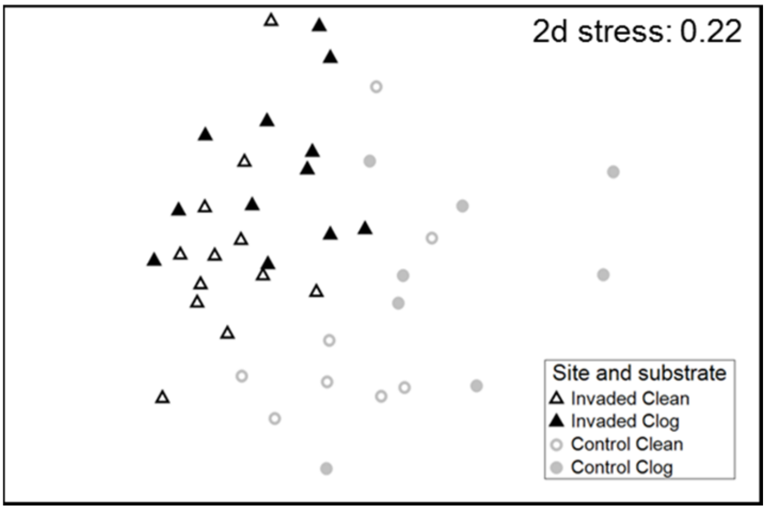

Figure 5.2 Non-metric multidimensional scaling (NMDS) of macroinvertebrate community data using the Bray-Curtis similarities coefficients for cylinder sampling set 4 (2nd – 15th July 2015) as a function of combined crayfish presence / absence and sediment treatment (clean or clogged). Black open triangles = invaded clean substrates; black solid triangles = control clog substrates; grey open circles = control clean substrates and; grey solid triangles = control clog substrates.

Both the invaded and control site demonstrated comparable temporal patterns in assemblage composition over time, and followed similar trajectories with a gradual shift from the left to right in the ordination space (Figure 5.3). However, the change in composition over time remained consistent at the control site, whilst sets 4-8 at the invaded site cluster together in the right of the ordination plot followed by another shift in composition for Set 9. Multivariate dispersion indicated a shift in the heterogeneity of the communities over time. Invaded communities demonstrated greater or similar beta diversity as the control site for the first three sample sets (average distance for invaded 29.30 and 29.04 for control communities), after which control communities displayed greater heterogeneity (sets 4-9; control site average distance 31.58) with invaded sites demonstrating lower beta diversity (average distance 28.17). Only set 4 of the pairwise distances was determined to be significantly different (T = 3.13, P = 0.008; Table 5.3). When the global dataset was considered, the control site was significantly more heterogeneous (T = 3.77, P = 0.001) than the invaded site (average distances 34.44 control and 31.21 invaded). The top ten taxa driving dissimilarity overall between control and invaded sites were Chironomidae (5.65% dissimilarity), Oligochaeta (5.11%), *P. antipodarum* (5.03%), *G. pulex* (4.26 %), *Erpobdella octoculata* (3.81%), *Dicranota* sp. (2.81%), *Habrophlebia fusca* (2.79%), *Baetis* sp. (2.29%), *Elmis aenea* (adult; 2.01%) and Sphaeriidae (1.90%).

Table 5.3 Summary of PERMDISP analysis by crayfish presence.

	Average distance		
Set	**Invaded**	**Control**	**p value**
1	28.18	27.53	0.852
2	30.23	29.69	0.856
3	29.61	29.90	0.956
4	26.04	32.02	**0.008**
5	27.62	31.62	0.224
6	28.08	29.74	0.561
7	28.31	31.66	0.223
8	27.36	30.78	0.129
9	31.60	33.67	0.438
Global	31.213	34.443	**0.001**

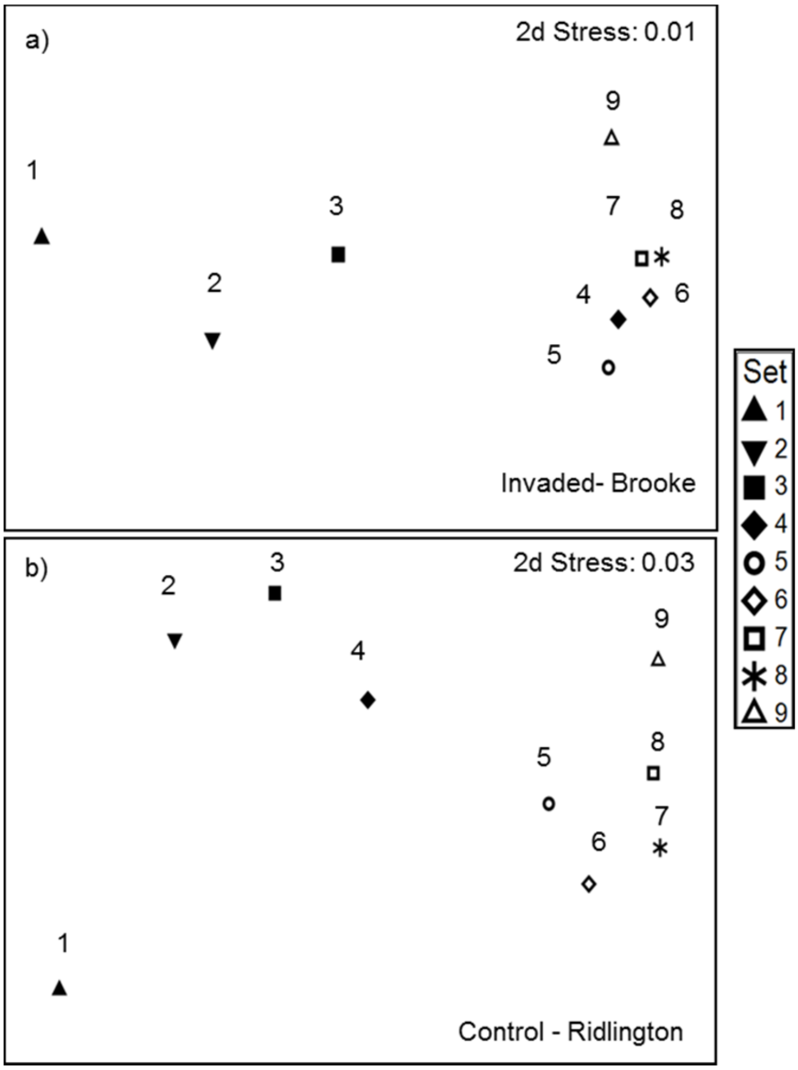

Figure 5.3 Non-metric multidimensional scaling (NMDS) temporal centroid ordinations of community data for cylinder sets 1- 9 at: a) the invaded and; b) the control site.

5.4.2 Community metrics and individual taxon abundances associated with crayfish presence

Total community abundance did not vary significantly by site or time ($p > 0.05$). Taxa richness varied significantly over time ($Z_{10,320} = -3.64$, $p < 0.001$) and demonstrated significant site: time interactions ($Z_{10,320} = 2.17$, $p = 0.03$) with lower numbers of taxa on most sampling occasions at the invaded site (Figure 5.4). EPT abundance and richness, and abundance of sediment sensitive taxa varied over time (all $p < 0.001$) but not by site ($p > 0.05$).

When individual taxon abundances were considered, the Hirudinea species, *E. octoculata,* consistently demonstrated significantly lower densities at the invaded site ($Z_{10,320} = 2.03$, $p = 0.043$; Figure 5.5a) with only ten individuals recorded across the whole series. Mollusca responses varied, with *P. antipodarum* displaying greater abundances at the invaded site on a number of occasions (Site: time interaction $Z_{10,320} = - 2.35$, $p = 0.019$; Figure 5.5b) whilst Sphaeridae was recorded in greater numbers at the control site ($Z_{10,320} = 3.427$, $p < 0.001$), varied over time ($Z_{10,320} = 3.56$, $p < 0.001$) and demonstrated a site: time interaction ($t_{10,310} = -2.254$, $p = 0.025$). *Dicranota* sp. demonstrated significant differences in abundances associated with site ($Z_{10,320} = - 3.38$, $p <0.001$; Figure 5.5c) and over time ($Z_{10,320} = - 13.61$, $p <0.001$). The coleopteran Elmidae (comprising multiple species; *Limnius volckmari*, *Elmis aenea* and *Oulimnius* sp.) were recorded in significantly greater abundances at the control site in both larval ($Z_{10,320} = 2.49$, $p = 0.013$) and adult life stages ($Z_{10,320} = 3.178$, $p = 0.001$) which was consistent across the sampling period (Figure 5.5d). Crayfish presence did not affect all taxa within the order of Ephemeroptera. The crawler *H. fusca* demonstrated significantly lower abundances on a number of sampling occasions at the invaded site (Site: time interaction $Z_{10,310} = 3.6$, $p < 0.001$; Figure 5.5e), whilst the swimmer *Baetis* sp. demonstrated no significant differentiation between the invaded and control site but did vary in abundance over time ($Z_{10,320} = -9.67$, $p < 0.001$; Figure 5.5f).

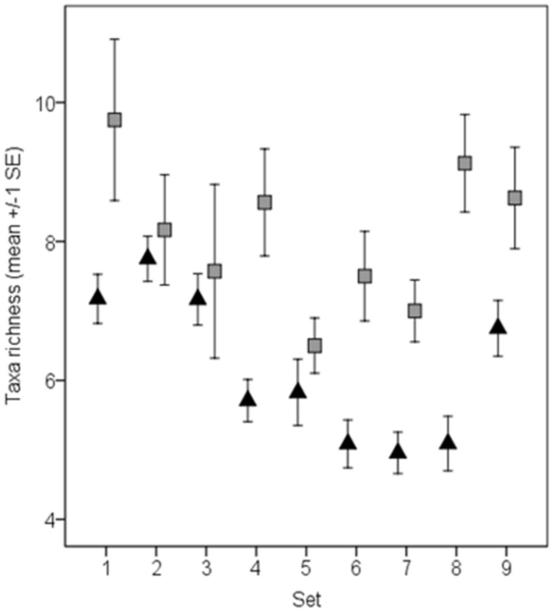

Figure 5.4 Mean (+/- 1 SE) taxa richness over the nine sample sets. Black triangle = invaded communities and grey square = control communities.

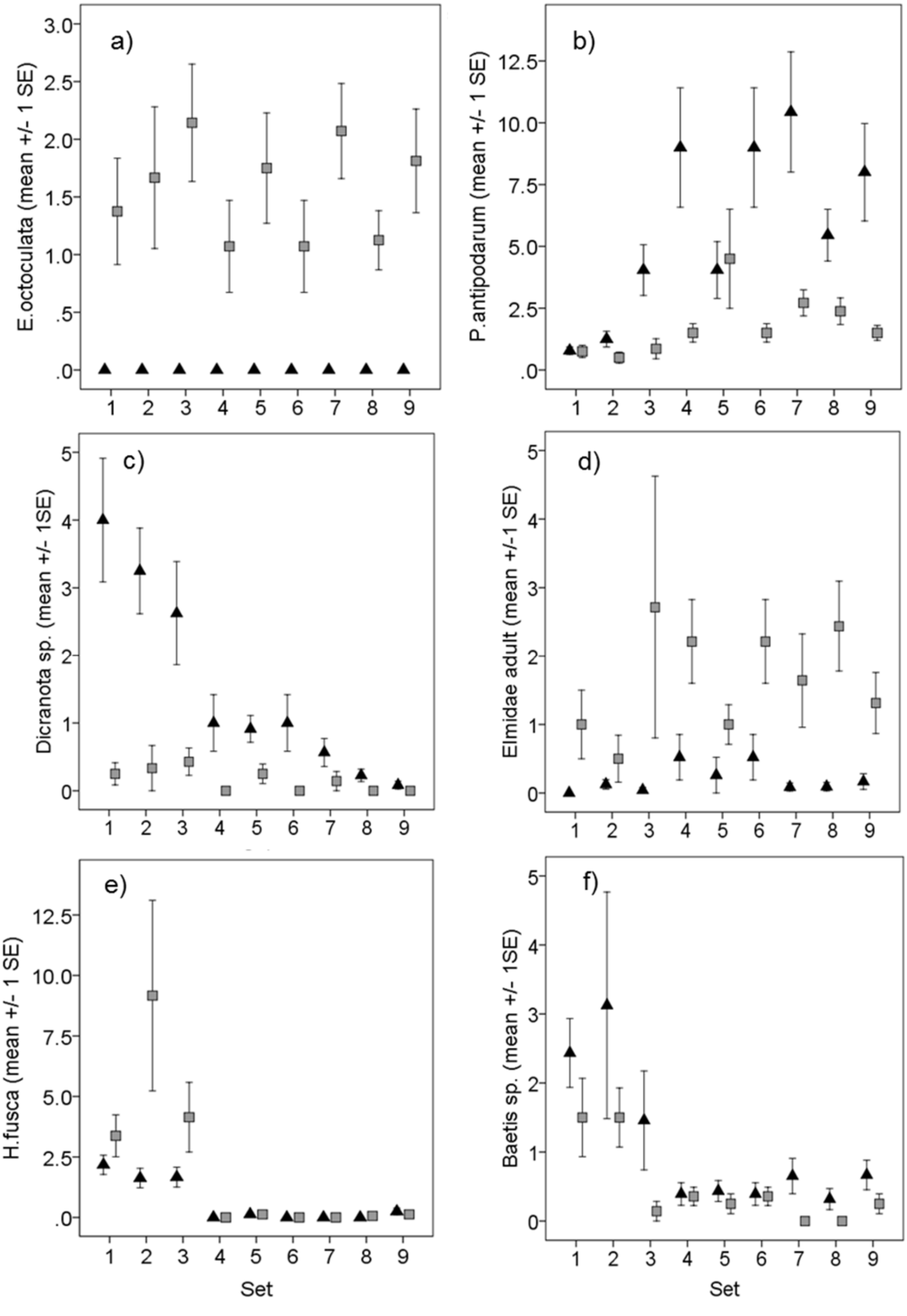

Figure 5.5 Mean abundances per site (+/- 1 SE) of: a) *Erpobdella octoculata*; b) *Potamopyrgus antipodarum*; c) *Dicranota* sp; d) Elmidae adult; e) *Habrophlebia fusca* and; f) *Baetis* sp. over the nine sample sets. Black triangle = invaded communties and grey square = control communities.

5.4.3 Signal crayfish activity

A total of 25 juvenile signal crayfish were recorded in the cylinders over the course of the sampling campaign. Individuals first appeared in the sampling record in set 2 (early June), with this time frame supporting the greatest abundance of 12 individuals (150.5 ind / m^2). Individuals remained in the record until set 7 (late August), with a second peak being evident during set 5 (82 ind / m^2; Figure 5.6). There was no preference displayed for clean or clogged cylinder substrate (22 .3 and 24 ind / m^2 respectively).

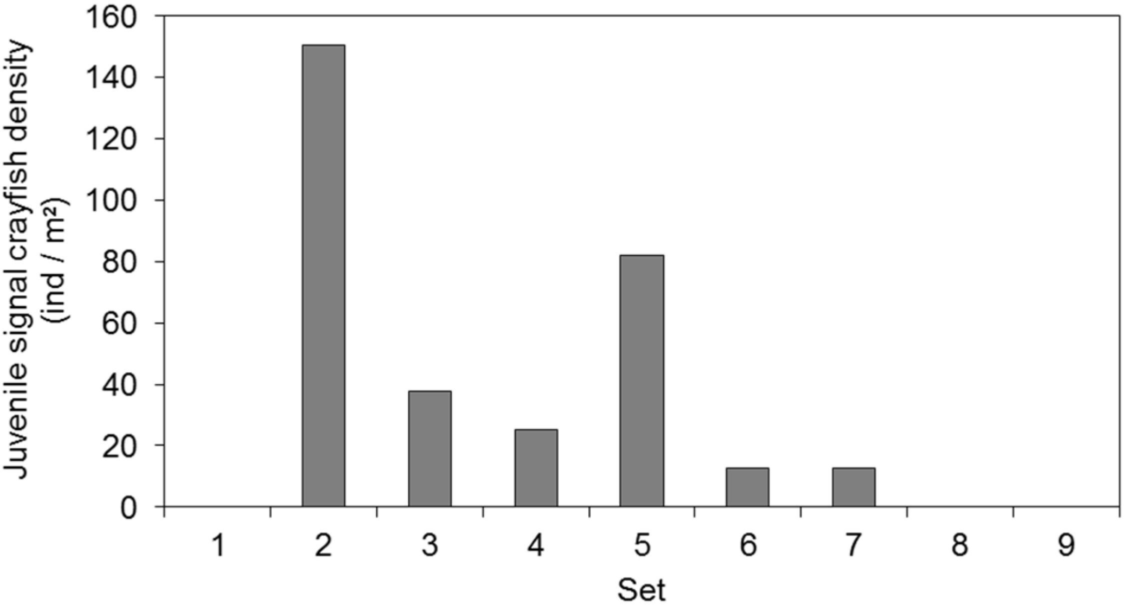

Figure 5.6 Density of juvenile signal crayfish recorded during individual sampling sets (21st May – 24th September) via the colonisation cylinders at the invaded site (Brooke).

Trapping of the adult component of the population indicated temporal differences in the number of individuals trapped (average 3.9 adults, range 0 – 5.55 CPUE; Figure 5.7). No crayfish were trapped during set 1 and were recorded in low abundances during set 3. Set 2 recorded large CPUE numbers similar to those recorded during sets 4-9 and also corresponded to the first occurrence of juvenile crayfish in the records. Crayfish activity levels can also be inferred from the level of diurnal suspended sediment patterns (Rice et al., 2016; Cooper et al., 2016), with fluctuations in turbidity becoming evident during set 4 which begin to break down during set 9 (Figure 4.14; Section 4.42).

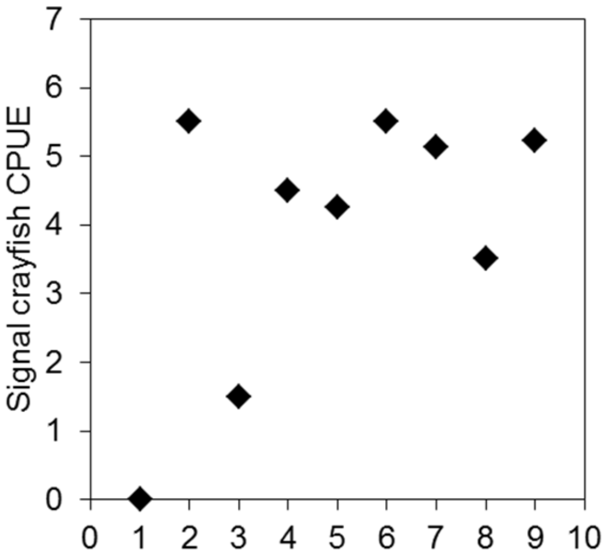

Figure 5.7 Adult signal crayfish catch per unit effort (CPUE) for each sample set at the invaded site (Brooke).

5.4.4 Crayfish community effect associated with sampling time frame

When longer time frames were considered, the effect of crayfish remained consistent with both one month (28 days) and two month (56 days) ordination plots indicating distinct clusters associated with crayfish presence (Figure 5.8). The degree of separation was significant in both instances ($p < 0.001$) with two of the largest R values obtained when all sampling times are considered ($R = 0.537$ and $R = 0.538$ for one month and two month data respectively) suggesting a greater divergence in communities as the crayfish season proceeds. When sediment treatment was considered, clogged substrate communities demonstrated the greatest separation associated with crayfish presence with the degree of divergence (as determined by the R value) increasing with cylinder residence time (Table 5.2). Multivariate dispersion indicted that the control river supported greater heterogeneity in communities for one month (average distance 26.05 invaded, 36.35 control group) and two month samples (27.81 and 32.15) which was significant in the instance of the one month dataset ($t = 4.00$, $p = 0.001$) but not for the two month data ($p > 0.05$).

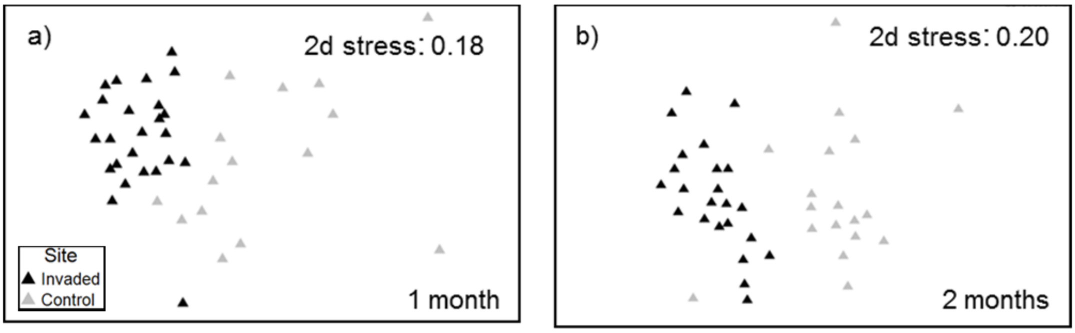

Figure 5.8 Non-metric multidimensional scaling (NMDS) of macroinvertebrate community data at Brooke and Ridlington by crayfish presence using Bray-Curtis similarities coefficients for cylinder sets over a) one month (28 days) and b) 2 months (56 days). Black triangles = invaded communities (Brooke) and grey triangles = control communities (Ridlington).

5.5 Discussion

5.5.1 Crayfish effects for macroinvertebrate communities

A number of studies have demonstrated the effects of invasive crayfish for lentic ecosystems (e.g. Usio et al., 2006; Ercoli et al., 2014), however knowledge regarding the implications for lotic communities remains limited and repeated sampling surveys that provide information about seasonal patterns of impact are rare. The results presented in this chapter demonstrate that invasive signal crayfish have significant and consistent effects on the wider lotic macroinvertebrate communities once populations are established. Ordination analysis indicated distinct communities at invaded and control sites throughout the sampling period (21st May – 27th August) and for each of the nine individual 14-day sampling sets. All pairwise comparisons were determined to be highly significant (all $P < 0.002$) demonstrating the strong and persistent modifications to macroinvertebrate assemblages once ecosystems are invaded (Wilson et al., 2004; McCarthy et al., 2006). Crayfish also had an overall significant effect on beta diversity, with control communities demonstrating a greater degree of community heterogeneity compared to those at the invaded site.

One advantage of the use of repeated colonisation samplers is that it provided a consistent record of macroinvertebrate populations without depleting resident populations and therefore affecting longitudinal data collection, a problem associated with other methods (i.e. Kick and Surber sampling). When the temporal community effects and activity of crayfish were considered, both invaded and control communities demonstrated similar temporal trajectories of change reflecting natural variability in macroinvertebrate assemblages as a function of taxon life histories (Johnson et al., 2012). However, invertebrate communities at the crayfish site demonstrate some deviations most likely reflecting fluctuations in crayfish activity levels over the sampling period.

During the first three sets of samples (late May – early July) both rivers demonstrated similar temporal changes and there was therefore some evidence to suggest that community effects of crayfish were less marked following periods of lower water temperatures (i.e. over winter and early spring). Both invaded and control sites also displayed similar community heterogeneity during the early surveys (set 1 -3) when adult crayfish activity was low (as determined by CPUE; excluding set 2 which coincides with egg release but does not correlate with activity as determined by SSC increases; Section 4.42; Figure 4.14). However, set 4 represents a discrete period during which the community trajectory differed markedly. At the crayfish site, communities' cluster together during sets 4-8 (early July – Mid September), whilst at the control site, assemblages continue to demonstrate more marked changes over time. This period coincides directly with an increase in adult crayfish activity associated with elevated water temperatures (Figure 4.18; Bubb et al., 2006). CPUE abundances increase considerably during Set 4 and remain consistently high throughout the remainder of the sampling campaign. Consequently, it is likely that despite crayfish having significant and omnipresent effects for the wider macroinvertebrate communities, there are notable and small scale differences in their effects over time. Notably, the only sample set to demonstrate significant differences in beta diversity between invaded and control rivers was set 4, the time period when crayfish activity intensifies.

Set 9 (Mid – late September) demonstrates another shift in temporal community composition, potentially reflecting another alteration in crayfish behaviour, with this time period coinciding with the mating season (Lewis, 2002). The high temporal resolution dataset utilised in this study enables the key stages in crayfish activity and their lifecycle to be identified. This study was conducted in a river which supported a well-established and abundant crayfish population (20 + years) and thus the overwhelming effect of crayfish presence is such that community composition has been completely altered (corroborating the results of Chapter 3). These life history behaviours of crayfish populations (increased activity in late spring and during mating) may have more marked effects for invertebrate populations in rivers where the invasion is more recent or abundances are low as a result of preferential prey (hirudinea and gastropods) still being present. The residual effect of crayfish for macroinvertebrates most likely intensifies over the main period when individuals are active, with results from the two longer sampling durations (1 and 2 months) indicating a greater degree of separation associated with crayfish presence than the majority of the other shorter sampling periods. Similarly, beta diversity was determined to be greater in the control communities in both instances.

When sediment treatment was taken into account during the 14 day-periods, clean substrates demonstrated the greatest degree of separation at sites where crayfish were present. Clean substrates are widely acknowledged to support a greater diversity of macroinvertebrates (Richards and Bacon, 1994; Wood and Armitage, 1999). Consequently, the reduced numbers of taxa at the invaded site are more likely to be evident in highly diverse habitats than those which are species poor and characteristic of silted environments. However, in contrast, when longer colonisation time frames were employed, silted substrates demonstrated more marked divergence in communities (stronger ANOSIM R values). This shift may reflect the sustained effect of crayfish on the taxa, with those taxa in the clogged substrates potentially being more susceptible to predation through a loss of refugia.

Within boreal lakes, Ruokonen et al., (2014) documented habitat specific effects of signal crayfish for resident macroinvertebrate taxa. It is likely that the effects of crayfish invasion will vary dependent on local habitat conditions which act as a physical template for resident taxa. Consequently, the effects of invasive species should be evaluated across a range of relevant habitats and spatial scales in order to enable the full extent of invaders to be ascertained. Nevertheless, the results from this study indicate that when substrate conditions are considered, the effect of invasive crayfish is stronger and more consistent than the differences in communities associated with the volume of fine sediment present. Macroinvertebrate communities demonstrate a consistent and highly significant difference in composition as a function of the established invasive crayfish populations regardless of the substrate conditions. To analyse the independent or additive effects of substrate conditions on the wider macroinvertebrate community, resident communities most likely need to be minimally impacted by invasion effects (i.e. early on in the invasion process and thereby unaffected) or investigated through controlled ex-situ experiments. Chapter 6 will investigate the interaction of fine sediment dynamics, invasive crayfish and macroinvertebrates via detailed mesocosm experiments in order to try and untangle the interactive and additive effects of the three factors.

5.5.2 Taxa – crayfish interactions

Crayfish presence did not significantly affect total macroinvertebrate abundance within this study. The effect of crayfish presence on invertebrate densities is highly variable with some studies indicating a reduction (Nyström et al., 1999; Crawford et al., 2006) whilst others reported no differences (Lagrue et al., 2014; Ercoli et al., 2015a). The inconsistent results most likely suggest that any effect on community abundances is weak and probably a function of original community composition and thereby highly dependent on species specific responses. Within this study, taxa richness was significantly lower at the invaded site compared to the control site. This effect remained consistent throughout the sampling period, but was not as marked during sets 2 and 3, a factor reflected in the site: time interaction. Reduced taxa richness has also been documented in a number of other studies following signal crayfish invasion (Crawford et al., 2006; Ruokonen et al., 2014; Ercoli et al., 2015a,b).

When individual species were considered, the most widely cited taxa affected by crayfish invasion were the class of Hirudinea (leeches), which typically demonstrate significant reductions in abundance (Stenroth and Nyström, 2003; Crawford et al., 2006; Chapter 3). Results from this study provide further evidence to support this finding, with only 11 individuals in this class being recorded at the invaded site compared to a total of 205 individuals at the control site. Moreover, one Hirudinea species, *Helobdella stagnalis* was unique to the control site. *E. octoculata*, the most abundant taxon in this class, demonstrated consistently low abundances throughout the sampling period with no temporal variation in numbers evident. The unprotected soft bodies and relative slow mobility of these taxa make them ideal prey items for crayfish (Stenroth and Nyström, 2003).

Another group of taxa which are typically associated with reductions in density, biomass and richness are molluscs (Weber and Lodge, 1990; Lodge et al., 1994; Dorn, 2013). Similar to Hirudinea, their reduced rate of mobility makes them susceptible to predation. However, the effects vary depending on the species considered, which most likely reflects varying life history characteristics and the ability to adapt behaviours that reduces the threat of predation. A number of species have been documented as demonstrating reduced reproductive rates whilst enhancing their growth rates (Hoverman et al., 2005), whilst others display avoidance behaviour by migrating to the waterline for several hours (Alexander and Covich, 1991a,b; Turner et al., 1999).

The latter strategy of avoidance has been recorded in *P. antipodarum* under experimental conditions (Haddaway et al., 2014) and may explain the ability of this species to maintain populations that are even greater than those at the control site within this study. This non-native taxon is tolerant of fine sediment and typically burrows into silted river beds (Holomuzki and Biggs, 2000; Suren, 2005), a factor which may also facilitate predation evasion. In contrast, the bivalve Sphaeriidae was recorded in greater numbers at the control site, although there was a significant site: time interaction with the effect not being consistent over time.

Nyström et al., (1999) suggested that benthic sediment dwelling taxa may dominate crayfish communities. Within this study, in addition to *P. antipodarum,* both Chironomidae and *Dicranota* sp., which have a high affinity for fine sediment, were recorded in greater abundances at the invaded site (Fitter and Manuel, 1986). *Dicranota* sp. had high abundances during sets 1-3 (when crayfish activity was minimal) but then displayed a marked reduction in numbers during the remaining sampling events. This taxon has a soft unprotected body similar to Hirudinea and may therefore still be susceptible to predation indicating the importance of considering temporal dynamics (associated with life cycle stages of the invader) in biological invasion studies.

Within this study, the abundance of the coleopteran family Elmidae (consisting of *E. aenea*, *L. volckmari* and *Oulimnius* sp.) was reduced at the crayfish site for both larval and adult life stages. Despite being highly mobile, the semivoltine life cycle (taking more than one year to complete its life cycle) of this taxa makes them more susceptible to disturbances (Elliot, 2008) and may therefore make them more vulnerable to predation than comparable mobile taxa. Gut analysis led Guan and Wiles (1998) to conclude that Coleoptera made up a large component of lotic signal crayfish diets and a number of field studies in lentic environments have suggested that the presence of Elmidae may indicate an absence of crayfish (Bjurstrom et al., 2010; Ruokonen et al., 2014; 2016).

Taxa in the order of Ephmeroptera have also attracted considerable attention when examining crayfish effects on macroinvertebrate communities with highly variable responses being documented (Chapter 3). Reductions in abundances (McCarthy et al., 2006) through to no change or enhanced abundances have been reported (Keller and Ruman, 1998; Usio and Townsend, 2004). Within this study contrasting effects were recorded for the swimming mayfly larvae *Baetis* sp. and the crawling taxon *H. fusca.* These differences most likely reflect the mode of locomotion with swimmers (*Baetis* sp.) demonstrating enhanced mobility associated with characteristics that make them adapted to faster flow velocities, whilst crawlers (*H. fusca*) display slower locomotion (Peckarsky, 1996). *H. fusca* typically inhabit slacker waters, predominantly pools and margin areas (Elliott et al., 1988), which may make them particularly vulnerable to predation by larger crayfish which also favour pools (Clark et al., 2013).

5.5.3 Application of colonisation cylinders in the monitoring of juvenile crayfish populations

This study utilised a novel application of commonly employed colonisation cylinders to obtain a quantitative record of benthic invertebrate densities over the course of 126 days. Deployment of the cylinders occurred before the main period of crayfish activity (late May) when water temperatures were still low (average 12.78^{o}c) and therefore provided an opportunity to assess the ability of the method to quantitatively monitor juvenile crayfish abundances. Results from the study, suggest that colonisation cylinders may have effectively determined abundances throughout the sampling period, with peak densities occurring during set 3 (late June); however further testing is required to assess the validity of such an approach. Egg hatching of signal crayfish populations occurs between late March and the end of July dependent on water temperatures, and it is therefore likely that this peak in numbers reflects the time when eggs were released in this population of signal crayfish. The densities recorded during this time frame were 150.5 ind / m^2 reflecting the high fecundity of this species which make them such a successful invader (Kouba et al., 2015).

Densities remained high (37 – 25 ind / m^2) during the following four weeks, with another spike in abundances in set 5 (mid July; 82 ind / m^2) which may represent a secondary period of egg release. Abundances declined over the next four weeks, with no juveniles recorded in the cylinders during the final two sample sets (September). This decline and absence toward the end of the record may reflect the cannibalistic nature of signal crayfish with adult populations often eating their young (Guan and Wiles, 1998) but could also reflect the rapid growth rates of signal crayfish and therefore larger body sizes at this stage inhibiting access to the subsurface substrates. The high number of juvenile crayfish recorded in this study indicates that interstitial habitats are likely to provide a safe refuge for juvenile crayfish and an absence of such habitat (i.e. an inaccessible hyporheic zone for example within urbanised rivers or upland streams) may limit the reproductive successes of crayfish populations through reduced survivorship.

5.6 Summary

Non-native crayfish are widely acknowledged to have significant and deleterious effects for the wider ecosystem once established (Twardochleb et al., 2013; Chapter 3), however little is known about the intra-annual variability of such effects. Results from this chapter suggest that alterations to the wider macroinvertebrate community are dynamic reflecting short term temporal patterns. These are likely to be a function of the life history characteristics (of the invader and resident taxa) such as reproduction or invertebrate flight periods. Although in this study, the alterations over time were relatively weak (but still evident), most likely associated with the well-established and abundant crayfish population which had substantially altered resident communities before sampling took place (overall reduced beta diversity), the variation in newly invaded or sparsely populated communities may be notable. The effect of crayfish within this river was so strong that changes in the community were evident regardless of substrate conditions and the effect of fine sedimentation and crayfish therefore resulted in independent and distinct macroinvertebrate communities.

Results from the chapter also highlight the effectiveness of colonisation cylinders in the collection of spatially replicated, high resolution macroinvertebrate data without depletion of resident macroinvertebrate communities. Colonisation cylinders are gaining increasing recognition in the field of aquatic ecology but have been used exclusively for one off sampling efforts to date (e.g. Pacioglu et al., 2012; Descloux et al., 2013; 2014; Mathers and Wood, 2016). Data presented within this chapter demonstrates the applicability of this method, and highlights the potential for its novel applicability in characterising juvenile crayfish populations which are notoriously difficult to sample (Moorhouse et al., 2011a). Further research is needed to ascertain its accuracy in detecting true abundances of juvenile crayfish present, but given the large abundances of juveniles recorded in this river (peak of 150 m^{-2}) it is not surprising that invasive crayfish represent such a significant threat to ecosystems globally.

Chapter 6 – The interaction of zoogeomorphology, fine sediment and predator-prey interactions - avoidance behaviour of a freshwater shrimp to signal crayfish

6.1 Introduction

Many of the problems associated with invasion of non-native taxa within an ecosystem (i.e. terrestrial, freshwater or marine) arise from the consumption of other indigenous taxa (Albins and Hixon, 2013). Invasion of non-native species may drive reductions in prey densities, but may also lead to modifications and / or adaptations to life history, behavioural and morphological characteristics (Lambrinos, 2004; Nunes et al., 2014). Predation is an important driver of evolutionary change (Vermeij, 1982); with prey / predator interactions receiving a large amount of attention historically (e.g. Heck and Crowder, 1991; Chivers and Smith, 1998). It is widely documented that many species possess a repertoire of strategies and defence mechanisms towards competition, parasites and predation by native species as a result of adaptations initiated by millennia of ecological interactions (Strauss et al., 2006).

Typically, prey respond to the presence of predators by reducing activity levels and by increasing their use of ‘safe’ microhabitats (Lima and Dill, 1990; Sih and McCarthy, 2002). However, the predatory effect of non-native species may be exacerbated as a result of novel predation strategies that are different to that of native species or because the prey cannot recognise non-native species or be able to respond to them with appropriate avoidance or survival strategies (Sih and McCarthy, 2002). One mode of rapid learning is through the pairing of visual or chemical cues and it has been widely documented that the release of a chemical signal from injured conspecifics (‘alarm cues’) elicits a dramatic response when in the presence of a novel predator (Dickey and McCarthy, 2007; Ferrarai et al., 2007).

Crayfish represent one of the most successfully translocated species globally (Kouba, Petrusek, and Kozák, 2014), and where populations become established, can have substantial and far reaching consequences for aquatic ecosystems (Jackson et al., 2014). Signal crayfish (*Pacifastacus leniusculus*; Dana) are widespread and abundant across much of Europe and have been documented as having negative effects on the diversity and biomass of macroinvertebrate assemblages where they have been introduced (Crawford et al., 2006; Nilsson et al., 2012; Chapters 3 and 6). Much of the work conducted on the interaction of crayfish and macroinvertebrates to date, has focused on freshwater snails. Migration to the waterline or utilisation of near-surface habitats (Alexander and Covich, 1991a, b; Turner et al., 1999; Hoverman et al., 2005), vertical movements into the river bed (Haddaway et al., 2014), morphological changes in shell design (Hoverman et al., 2005), and enhanced growth rates and altered reproduction cycles (Crowl and Covich, 1990; Hoverman et al., 2005) have been documented as predator-induced reactions in a number of laboratory experiments using aquatic snails. Gastropods are one of the most widely cited prey taxa of crayfish due to their limited locomotion, with many *in-situ* studies documenting a reduction in richness, abundance and / or biomass associated with crayfish presence (Stenroth and Nyström, 2003; Rosewarne et al., 2013; Ruokonen et al., 2014).

Despite a large number of studies on crayfish-prey interactions, studies which examine the response of taxa which are typically not documented to be affected by crayfish predation are limited (but see Haddaway et al., 2014). A number of avoidance strategies which taxa may adopt in response to invasive crayfish have been suggested such as enhanced locomotion, increased drift propensity, and vertical migration into the river bed and subsurface substrates (Alexander and Covich, 1991a,b; Nyström; 1999; Haddaway et al., 2014). However, utilization of the river bed as a refuge is dependent on the availability of pore space and consequently is linked to the dynamic nature of the physical environment. Sedimentation and clogging of riverine substrates is increasingly being recognised as one of the greatest threats to the ecological integrity of riverine ecosystems globally (Boulton et al., 2010; Jones et al., 2015). Many rivers currently exceed natural background levels for fine sediment (suspended and deposited) and the delivery of fine sediment is anticipated to increase in future as a result of climatically driven changes to rainfall and runoff regimes (Bilotta and Brazier, 2008; Collins et al., 2011).

In addition to the classic view of fine sediment dynamics (that based on the physical characteristics of the river and hydromorphological processes), organisms that inhabit the riverbed can also alter the accumulation and distribution of fines. Signal crayfish have been recorded to alter fine sediment dynamics by increasing the flux of suspended sediment (Harvey et al., 2014; Rice et al., 2014; 2016; Chapter 4). They may also enhance the input and loading of fine sediment associated with burrowing activities which may lead to enhanced fine sediment infiltration rates (Guan, 1994; Harvey et al., 2016). Fine sediment deposition has the potential to infill interstitial spaces, alter substrate composition and thereby reduce resources and available habitat (benthic and sub-surface) for macroinvertebrates (Rabeni et al., 2005; Sarriquet et al., 2007; Simpson and Meixner, 201). Clogging can lead to the disconnection of benthic and hyporheic habitats (Descloux et al., 2013; Mathers et al. 2014). Consequently, if prey taxa possess predator adaptations which rely on vertical movement into the river bed, the presence of high concentrations of fine sediment may limit their ability to avoid competition or predation effects. As a result, by engineering increased sediment content of the river bed, crayfish may inadvertently improve their foraging success, an example of extended phenotype engineering (whereby the organism creates structures or effects that directly influence their fitness and survival; Jones et al., 1994; Wright and Jones, 2006).

However, a number of macroinvertebrate species (including Chironomids, tubificids Plecoptera, Ephemeroptera and Amphipoda) have been reported to act as bioengineers through the winnowing of fine sediment from interstitial spaces, reducing clogging of bed sediments and thereby maintaining / re-establishing vertical connectivity and migration pathways (Visoni and Moulton, 2003; Mermillod-Blondin et al. 2003; 2004; Nogaro et al., 2006; 2009). This activity may enable the vertical movement of taxa as a response to crayfish, even in the presence of fine sedimentation. The amphipod *Gammarus pulex* is common, widespread and locally abundant within rivers in the UK (Gledhill et al., 1993) and in many riverine communities often dominates macroinvertebrate communities in terms of biomass and / or numbers (MacNeil et al., 1997). *G. pulex* can tolerate low oxygen concentrations and is known to colonise both benthic and hyporheic habitats. Studies have documented vertical movement of *G. pulex* into subsurface sediments to actively avoid inter-specific predation (McGrath et al., 2007) and during adverse surface conditions associated with drought events (Wood et al., 2010). *G. pulex* are opportunistic and are highly successful in colonising and invading habitats due to their feeding plasticity and omnivorous nature (MacNeil et al., 1997). *G. pulex* play a key role in ecosystem functioning, including detrital processing rates (Navel et al., 2010) and represent important prey items for many carnivorous invertebrates, fish and crayfish (Armitage and Young, 1990; Sutcliffe, 1991). A highly mobile taxa, capable of burrowing through fine sediment and winnowing fine sediment to find resources and habitat (Pringle and Blake, 1994; March et al., 2002), the response of this taxon to signal crayfish presence and its interaction with fine sedimentation may reflect responses for a range of mobile taxa and thus acts as a model organism.

Understanding the interaction of organisms with the physical environment in association with the behaviour of predator / prey interactions is important. Investigating the two processes in parallel, addresses key contemporary questions regarding whether organisms engineer habitats, with important outcomes for ecosystem functioning and feedbacks and geomorphic processes (Crain and Bertness, 2006). Despite a handful of studies which investigate the role of biota as geomorphic agents, and similarly studies investigating predator prey interactions as separate entities, the issue of how biota interact with both the physical environment and other organisms simultaneously, and how these factors mediate and interlink with each to effect the outcome of such interactions has yet to be explored. Moreover, investigations which consider the additional effect of external stressors and / or disturbances within the environment are lacking. Understanding the effect of stressors on the natural dynamic of predator-prey relations is important in order to inform and underpin management strategies, particularly aimed at controlling invasive species. This study examines the relationship of predator-prey interactions in combination with the physical environment. For the first time the indirect effect of predators and / or prey organisms modifying the physical environment and how this affects predator-prey interactions is considered, with the aim of stimulating further interdisciplinary research which considers the role that both factors play in ecosystem functioning (biotic and abiotic outcomes).

6.2 Research Aims

In this chapter the vertical distribution of *Gammarus pulex* (L.) (Amphipoda: Crustacea) within experimental running water mesocosms was examined in response to different fine sediment treatments (<4 mm) in the presence and absence of signal crayfish (*Pacisfastcus leniusculus;* Dana). This experiment sought to examine if *G. pulex* displayed avoidance strategies in the presence of signal crayfish and if this behaviour was altered due to fine sediment deposition. The experiment also sought to examine if either *G pulex* or *P. leniusculus* modified fine sediment infiltration rates and whether this therefore affected the predator / prey interactions.

Specifically, the following research questions were examined:

1. Does the vertical distribution of *G. pulex* vary as a function of sediment grain size and loading?
2. Does *G. pulex* display predator avoidance behaviour in the presence of *P. leniusculus* via vertical movement into subsurface sediments?
3. Does coarse sand sedimentation limit the process of vertical avoidance behaviour of *G. pulex* by preventing movement into subsurface habitats; and does burrowing by *G. pulex* enable vertical avoidance under fine sand treatments?
4. Do high sediment loadings result in enhanced predation risk and a reduction in survivorship of *G. pulex?*
5. Does the presence of *G. pulex* and *P. leniusculus* (alone and combined) modify fine sediment infiltration rates?

6.3 Methods

6.3.1 Experimental setup

Experiments were undertaken in three identical sediment columns located in large water containers (following Mathers et al., 2014) that comprised two interlocking sections which represented surface and sub-subsurface substrates (Figure 6.1). Each section was 32 cm in diameter and contained a 50 mm thickness of coarse fluvial sediment (gravel particles 20-64 mm in diameter). This size distribution reflected natural coarse river framework gravels and included grain sizes that signal crayfish have been shown to displace (up to 38 mm in diameter; Johnson et al., 2010a). The two sections were stacked vertically to provide a total depth of 100 mm. To allow water, fine sediment and organisms to pass between the sections, 6 mm holes were drilled into the base of the top section (0 - 50 mm depth) at a density of 0.06 cm^{-1}. The bottom section (50 -100 mm) was perforated with smaller holes (2 mm diameter at a density of 0.09 cm^{-1}) to limit the movement of *G. pulex* and fine sediment from the column, whilst permitting the vertical flow of water. In addition, a 0.25 mm aperture net was secured around the base of the bottom section and a 5 mm rubber seal created around the base of the top section to prevent migration of individuals outside the column. 5 mm sieves were placed over the top of the sediment column to prevent the movement of crayfish out of the column. Permeable sieves rather than solid lids were employed to enable the infiltration of natural light into the columns and therefore not influence crayfish activity or *G. pulex* movement behaviour. *G. pulex* are phototatic and display negative migration behaviour in response to light (movement away from the light source; MacNeil et al., 1999) whilst signal crayfish activity is strongly diurnal with most activity occurring at night (Guan and Wiles, 1998; Nyström, 2005).

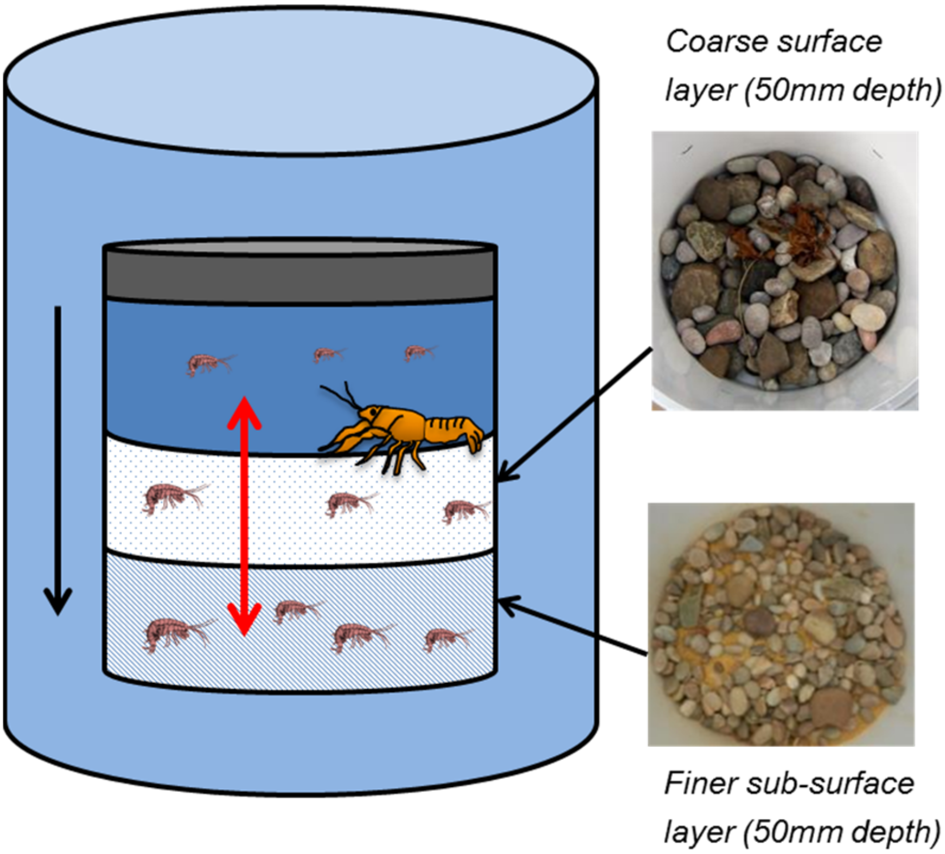

Figure 6.1 Conceptual diagram of the experimental setup consisting of a coarse surface layer and finer sub-surface layer. The red arrow represents the migration pathways available to *Gammarus pulex*, and the black arrow represents the flow of downwelling water and direction of sediment transport. Photographs represent the grain size matrix prior to sediment addition.

Previous experiments within this facility established an affinity of *G. pulex* within clean surface substrates under downwelling water (as a result of their rheophilic nature). Upwelling water resulted in a reversal in patterns, with the majority of individuals migrating to the base of the column (Mathers et al., 2014). Consequently, to facilitate the establishment of crayfish avoidance behaviour in the form of vertical movements into the riverbed, downwelling flow conditions were selected to act as the ‘model control’ distribution. The sediment columns were placed inside separate large cylindrical black plastic water containers (97 x 57 cm, volume = 210 L; Figure 6.2). Three external pumps delivered flowing water to the columns which was allowed to pass through the column under gravity. A sprinkler rosette was attached to the end of the pump outlet to disperse the water (2.7- 2.8 L min^{-1}). Visual observations indicated that this flow of water was sufficient to maintain low interstitial flow through the sediments but not large enough to initiate sediment transport.

Consequently, any movement of fines during the experimental period was primarily a function of gravity and bioturbation associated with the movement of *G. pulex* and / or signal crayfish.

Figure 6.2 The experimental mesocosm facility in which the experiments were conducted.

The experimental containers were aerated throughout the experiments using an aquarium aeration pump and temperatures were held constant (15^{o}C ± 0.4^{o}C) via an external water cooler (Aqua medic, Titan 150). Water temperature is a strong regulating factor in crayfish activity (Gheradi et al., 1998; Bubb et al., 2004). The temperature selected for the experiments corresponds with peaks in crayfish activity under field conditions in the summer months within the UK (Johnson et al., 2014) and is similar to that recorded during other laboratory studies (Basil and Sanderman, 2000; Johnson et al., 2010a). Experiments took place during late spring and summer (May - July 2014) to coincide with the natural crayfish lifecycle and periods of increased foraging activity.

Fine sediments used in the experiment consisted of pre-washed fine riverine sands (0.125 µm – 1 mm) and very coarse sands (1 – 4 mm; Figure 6.3). Fine sediment, silt and clay fractions (< 0.125 µm) were removed by wet sieving to ensure that turbidity did not vary between the experimental trials. Prior to each experimental run, fine sediment was applied evenly to the surface of wet gravel in the top section using a 1 or 4 mm sieve. Preliminary tests indicated that the application of 5kg m^{-2} filled all interstices (100% of interstitial volume) under the fine sediment treatment and covered the surface of all gravel particles. In addition to this heavy sediment loading, an application of 3 kg m^{-2} was selected to represent a moderate sediment loading. The two size fractions were chosen to include one with a low propensity to clog interstitial spaces (0.125 µm – 1 mm) and one with a high propensity to bridge between framework clasts and thus prevent further subsequent infiltration (1 – 4 mm). The appropriate range of grain sizes to be examined in the study were determined using calculations based on studies by Gibson et al., (2009b) and Frings et al., (2008) which provide ratios to discriminate between pore filling loads and bed structure loads. For each experimental trial a mixture of both size fractions (equivalent to 2 kg m^{-2} of each size fraction) was mixed thoroughly with the gravel matrix in the bottom section. This mixture acted as sediment trap but did not infill interstitial spaces sufficiently to preclude *G. pulex* from migrating into the subsurface layer.

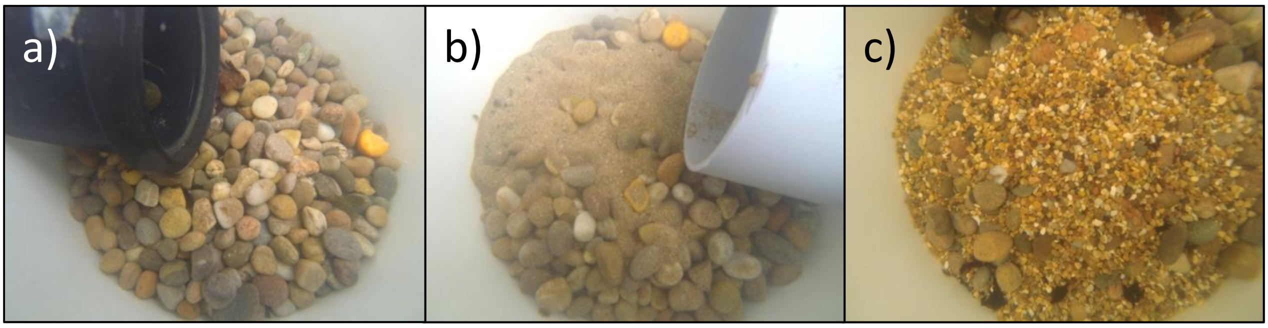

Figure 6.3 Sediment treatments used in the experimental trials. a) Clean gravel framework; b) fine sediment in the grain size fraction 0.125µm - 1mm and; c) coarse sedimentation in the grain size fraction 1- 4mm. Photos of the respective sediment applications represent a 5 kg m^{-2} treatment in both instances.

Five sediment treatments were examined: (1) an open gravel framework (no fine sediment treatment); (2) 3 kg m^{-2} fine sand sedimentation in the surface section; (3) 5 kg m^{-2} fine sand sedimentation in the surface section; (4) 3 kg m^{-2} coarse sand sedimentation in the surface section and; (5) 5 kg m^{-2} coarse sand sedimentation in the surface section. These treatments represented a continuum of fine sediment loading (Figure 6.4). Each treatment was undertaken for four different scenarios: (a) sediment treatments with no organisms present; (b) 75 *G. pulex* and sediment treatments; (c) one crayfish and sediment treatments and; (d) one crayfish, 75 *G. pulex* and sediment treatments. The sediment treatments (n=5), crayfish presence (n=2) and *G. pulex* presence (n=2) were combined in a full factorial design giving 20 treatment combinations. Each combination was replicated five times to give a total of 100 experimental runs. Treatments were randomly allocated to an experimental trial.

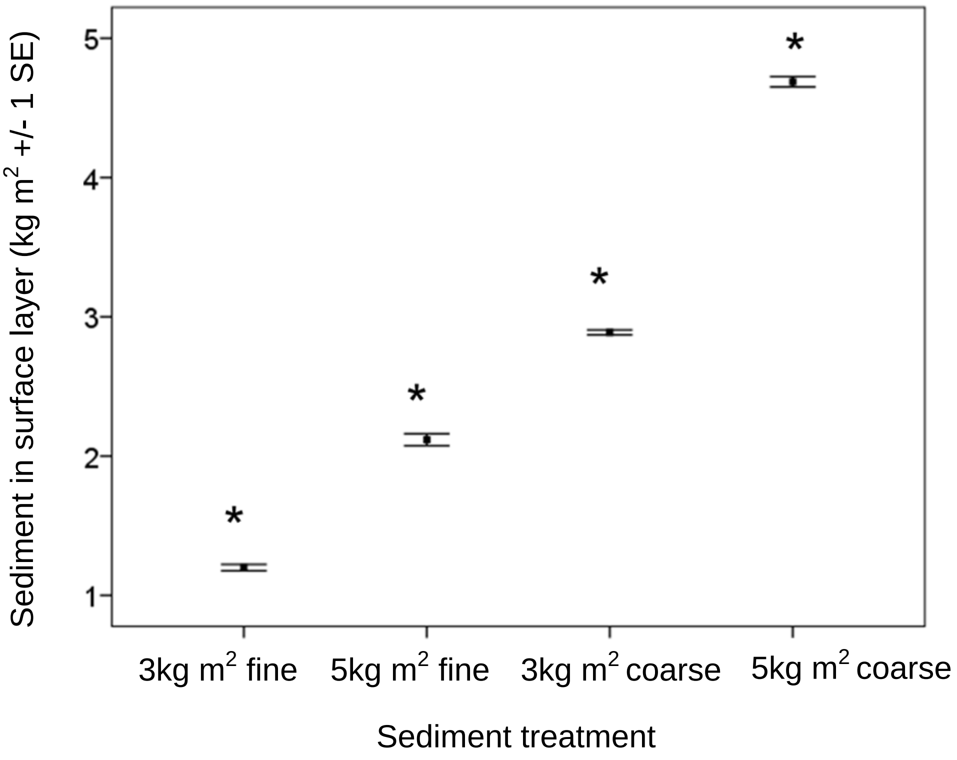

Figure 6.4 Mean amount of fine sediment (kg m^{-2} ± 1 SE) remaining in the surface layer (0-50mm) at the end of the experiment (24-hours). Sediment treatments where the amount of sediment is significantly different are indicated with * (Tukey, $p < 0.05$).

6.3.2 Animals used in experiments

All crayfish were collected from a local stream (Wood Brook, Loughborough, UK, 52° 75’ 69’’ N., -1° 22’ 74’’ W.) using baited traps (Environment Agency Trapper Number EE073-L-487) and transported to the laboratory under licence from the Department for Environment, Food and Rural Affairs (DEFRA Licence Number 62). To limit the variability of impact that might be associated with differing size and age, only individuals with a carapace length of 40 ± 5 mm were selected. Signal crayfish typically attain a maximum carapace length of 50-70 mm, although individuals up to 95mm have been recorded in the UK (Lewis, 2002), and thus the crayfish selected for the experiments represent medium sized individuals. Selected individuals were also without obvious injury (such as damaged carapace or loss of chelae, legs or antennae), or regenerating chelae (those which are in the process of growing back) as this affects their foraging behaviour (Basil and Sandeman, 2000; Koch et al., 2006). The sex of crayfish was recorded, however males and females have been documented as exhibiting no significant differences in behaviour (Guan, 1994), so this influence was not considered in experiments. Only intermolt individuals were used in the experiments (Kuhlmann et al., 2008) as activity and feeding behaviour is known to be modified during some stages of ecdysis (moulting; Reynolds, 2002).

Each crayfish was housed individually between experiments, within a plastic aquarium (0.6 x 0.4 x 0.4 m) that had black, opaque sides because crayfish survival is known to be enhanced in dark environments (Lewis, 2002). Each aquarium had a secure lid with a central opening of 480 × 240 mm that was covered in wire mesh to prevent escape. Water temperature was allowed to fluctuate with ambient conditions, and a filter pump circulated water through the tank, removing waste and aerating the water. Lettuce was provided *ad libitum* and supplemented with crayfish pellets (Tetra: TetraCrusa Menu) every other day when not involved in experiments. Preliminary tests indicated that when crayfish were starved prior to experiments, insufficient numbers of *G. pulex* survived the experimental trials due to predation to enable analysis. All *G. pulex* specimens were collected from a local stream (Burleigh Brook, Loughborough, UK, 52°76’09’’N., -1°24’58’’W) where they occur at high abundances (>100 individuals per m^{-2}) using a standard pond net (mesh size, 1 mm) prior to each experimental run. Individuals used in the experiments consisted of mixed size classes; 5-10 mm.

6.3.3 Experimental procedure

For experimental permutations in which no organisms were present (‘control’ sediment application experiments), fine sediment was applied to the surface of the top section as described above and left to infiltrate under gravity for 24 hours. Experimental runs with crayfish present were initiated in the same manner but with the addition of one signal crayfish in the surface section after the application of the fine sediment treatment. For experimental trials which included *G. pulex*, seventy-five individuals (Figure 6.5) of mixed size (> 1mm) were released onto the top section and left for 24-hours to redistribute themselves. Preliminary experiments indicated that this was a sufficient number for appropriate survival rates at the termination of the experiments to enable the detection of avoidance behaviour(s) if present. In experimental runs where crayfish were present at the same time as *G. pulex*, all *G. pulex* individuals were placed in the experimental facility and left to acclimatise to the environment for an hour prior to the addition of crayfish. A single pre-conditioned (soaked in water) horse chestnut (*Aesculus hippocastanum*) leaf was placed in both sections as a food source for the *G. pulex* to reduce intra-specific predation (Joyce et al., 2007) which has been observed in low food environments (Little et al., 2006). A slice of carrot (c.10g) and crayfish pellets (following Bubb et al. 2002; Kuhlmann et al., 2008) were provided as alternative food sources for the crayfish, to avoid excessive predation due to the absence of an alternate sedentary food source which they are documented to prefer (e.g. Hirudinea and Gastropods; Dorn, 2013; Ruokonen et al. 2014; Chapters 3 and 5). Shelter, in the form of an open ended drainpipe (110 x 100 mm; Figure 6.6) was provided for the crayfish, to reduce pit digging behaviour (Johnson et al., 2010a) due to the absence of an obvious refuge.

Figure 6.5 *Gammarus pulex* (Amphipoda: Crustacea).

Figure 6.6 Refuge provided for the crayfish in each experimental trial.

At the end of each experimental run (24 hours), *G. pulex* individuals were collected and counted from each section by washing the contents of each section through 4-mm sieves. All fine sediment was removed from the column and subsequently oven dried at 60^{o}C until a constant weight was recorded to determine mass per section. For the sub-surface section, initial fine sediment quantities within the matrix were deducted from the total fine sediment mass to enable the fraction which had infiltrated to be calculated. New *G. pulex* specimens were used for each experimental run. One crayfish was used per experimental trial, and each individual crayfish was used once for each treatment.

6.3.4 Statistical analysis

Differences in the abundance of *G. pulex* in the sub-surface as a function of sediment treatment, crayfish presence and the interaction of the two factors were tested via a linear model using the function '*lm*' in the '*stats*' package in R version 3.12 (R development Core Team, 2014). Differences between all experimental treatments were tested using a Tukey *post hoc* test using the '*glht*' function in the '*multcomp*' package. To assess differences in the vertical distribution of *G. pulex* (associated with avoidance behaviour) within each sediment treatment and each organism combination (crayfish presence or absence) a linear mixed effects model was employed with treatment specified as a fixed factor and bucket nested within the experimental replicate (column) as a random factor (reflecting that buckets within individual columns are not independent from each other). Post hoc tests were conducted using the '*glht*' function to determine the effect of the different sediment loadings on *G. pulex* movement patterns with and without crayfish. Survivorship of *G. pulex* (number of individuals retrieved at the termination of the experimental run) in the presence of crayfish and as a function of the sediment treatment was examined within a general linear model (GLM) using the '*glm*' function in the '*stats*' package. A Poisson error distribution and log link structure was fitted to account for non-normal residuals. Treatment was specified as a fixed factor and bucket was nested within the experimental replicate (column) as a random factor. Sediment masses added to the sub-surface layer during the experimental trial were converted to infiltration rates (kg / m^{-2} / day) to enable the amount of sediment mobilised by the organisms to be ascertained. Differences in infiltration rates between organism combinations for each sediment treatment were examined via a linear model and tested using a Tukey *post hoc* test.

6.4 Results

Recapture rates of amphipods for all experiments averaged 80% but showed high variability as a function of crayfish presence / absence. Those experiments conducted in the absence of crayfish had an average recapture rate of 89% (range = 80 - 100%). When crayfish were present, the average retrieval rate was 52% (range = 34 - 76%). The distribution of *G. pulex* between layers was dependent on the presence of crayfish (p <0.001), fine sediment treatment (p < 0.001) but did not vary as a function of the interaction of these two factors (p = 0.247; Table 6.1; LMM).

Table 6.1 Univariate linear model (LM) analysis for the abundance of *Gammarus pulex* within the subsurface associated with the presence of invasive crayfish, sediment treatments (n=5) and the interaction between these factors.

Factor	*F value*	*P value*
Crayfish presence	22.14	<0.001
Sediment Treatment	13.42	<0.001
Sediment Treatment x Crayfish Presence	1.42	0.247

6.4.1 Vertical distribution of G. pulex as a function of sediment load

When comparisons between sediment treatments, with either crayfish present or absent were considered, there were distinct differences in the vertical distribution of *G. pulex* within the column (Tables 6.2 and 6.3). In the absence of crayfish, on average 18 individuals were recorded in the sub-surface under control conditions (open gravel framework) and the two fine sand treatments (3 kg and 5 kg m^{-2}). The addition of the heaviest loading of coarse sand (5 kg m^{-2}) resulted in *G. pulex* being unable to migrate vertically with an average of 8 individuals being recorded in surface layer with significant differences, 3 kg m^{-2} fine sand (p = 0.022) and 5 kg m^{-2} fine sand (p = 0.005). In the presence of crayfish, the disconnection of surface and subsurface layers caused by coarse sand sedimentation was even more marked with both loadings (3 kg m^{-2} and 5 kg m^{-2}) resulting in reduced numbers of individuals being recorded in the sub-surface layer compared to clean gravel (p = 0.03 and p = <0.001 respectively), 3 kg m^{-2} fine sand (p = 0.006 and p < 0.001 respectively) and 5 kg m^{-2} fine sand (both instances p = <0.001). In the presence of crayfish, on average 26 individuals were recorded in the subsurface layer control conditions (open gravel framework) and the two fine sand treatments compared to 12 and 6 individuals under the two coarse sedimentation treatments. The addition of fine sediment, in this instance coarse sand, which has a high propensity to bridge interstitial spaces, disconnected surface and subsurface habitats and impeded the vertical movement of invertebrates.

Table 6.2 Tukey post-hoc comparisons of *Gammarus pulex* abundances in the sub-surface layer in the absence of crayfish. p-values are presented for pairwise comparisons between sediment treatment. Significant ($p < 0.05$) results are emboldened.

Sediment treatment	3 kg m^{-2} fine	5 kg m^{-2} fine	3 kg m^{-2} coarse	5 kg m^{-2} coarse
Open framework	1	0.989	0.069	0.073
3 kg m^{-2} fine		1	0.38	**0.022**
5 kg m^{-2} fine			0.14	**0.005**
3 kg m^{-2} coarse				0.942

Table 6.3 Tukey post-hoc comparisons of *Gammarus pulex* abundances in the sub-surface layer in the presence of crayfish. p-values are presented for pairwise comparisons between sediment treatment. Significant ($p < 0.05$) results are emboldened.

Sediment treatment	3 kg m^{-2} fine	5 kg m^{-2} fine	3 kg m^{-2} coarse	5 kg m^{-2} coarse
Open framework	1	0.942	**0.03**	**<0.001**
3 kg m^{-2} fine		1	**0.006**	**<0.001**
5 kg m^{-2} fine			**<0.001**	**<0.001**
3 kg m^{-2} coarse				0.651

6.4.2 Vertical migration of G. pulex in response to crayfish presence

Clean gravel: In the absence of crayfish, the majority of individuals remained in the surface layer but the addition of signal crayfish resulted in an equal distribution of *G. pulex* in the surface and subsurface (Figure 6.7). There were no differences in the number of *G. pulex* recorded in the surface or sub-surface layers in treatments when crayfish were present ($p > 0.05$), but statistical differences were apparent when crayfish were absent, with a greater number o*f G. pulex* recorded in the surface layer ($t_{1,8} = -7.339$, p = <0.001; Table 6.4). This indicates the use of vertical avoidance behaviour in the presence of a predator when open interstitial space is available beneath the surface.

3 kg m^{-2} fine sand sedimentation: As with clean gravels, the presence of crayfish resulted in a greater number of *G. pulex* migrating to the subsurface (Figure 6.7). In the absence of crayfish, 25% of individuals were located in the sub-surface layer at the end of the experiment, but with the addition of crayfish this rose significantly to 50%. During experiments where crayfish were absent, there were significant differences in the vertical distribution of individuals ($t_{1,8}$ = -7.443, p = <0.001), but no differences were evident in the presence of crayfish (p > 0.05 ; Table 6.4).

5 kg m^{-2} fine sand sedimentation: As in clean gravels and with 3 kg m^{-2} fine sand sedimentation, there were no significant differences in surface and sub-surface abundances of *G. pulex* when crayfish were present (p > 0.05), but when crayfish were absent the surface layer contained a greater number of individuals ($t_{1,8}$ = -6.304, p = <0.001; Table 6.4; Figure 6.7).

3 kg m^{-2} coarse sand sedimentation: The addition of coarse sand sedimentation resulted in a change in the distribution of *G. pulex* in the presence of crayfish. No differences in the number of amphipods in the surface layer were detected irrespective of whether crayfish were present or absent (Figure 6.7). In both cases, the majority of amphipods were located in the surface layer: The number of *G. pulex* in surface and sub-surface layers was significantly different in both experiments with ($t_{1,8}$ = -3.933, p = 0.010) and without crayfish ($t_{1,8}$ = -12.044, p = <0.001; Table 6.4). The addition of sand with a high propensity to bridge interstitial space limited the ability of *G. pulex* to migrate vertically in order to avoid predatory crayfish.

5 kg m^{-2} coarse sand sedimentation: The heavy loading of coarse sand was associated with retention of the largest count of *G. pulex* in the surface layer, irrespective of crayfish presence (Figure 6.7; Table 6.4). The surface layer contained significantly greater numbers of individuals than the subsurface layer in the presence ($t_{1,8}$ = -4.973, p = <0.001) and absence of crayfish ($t_{1,8}$ = 13.455, p = <0.001 ; Table 6.4).

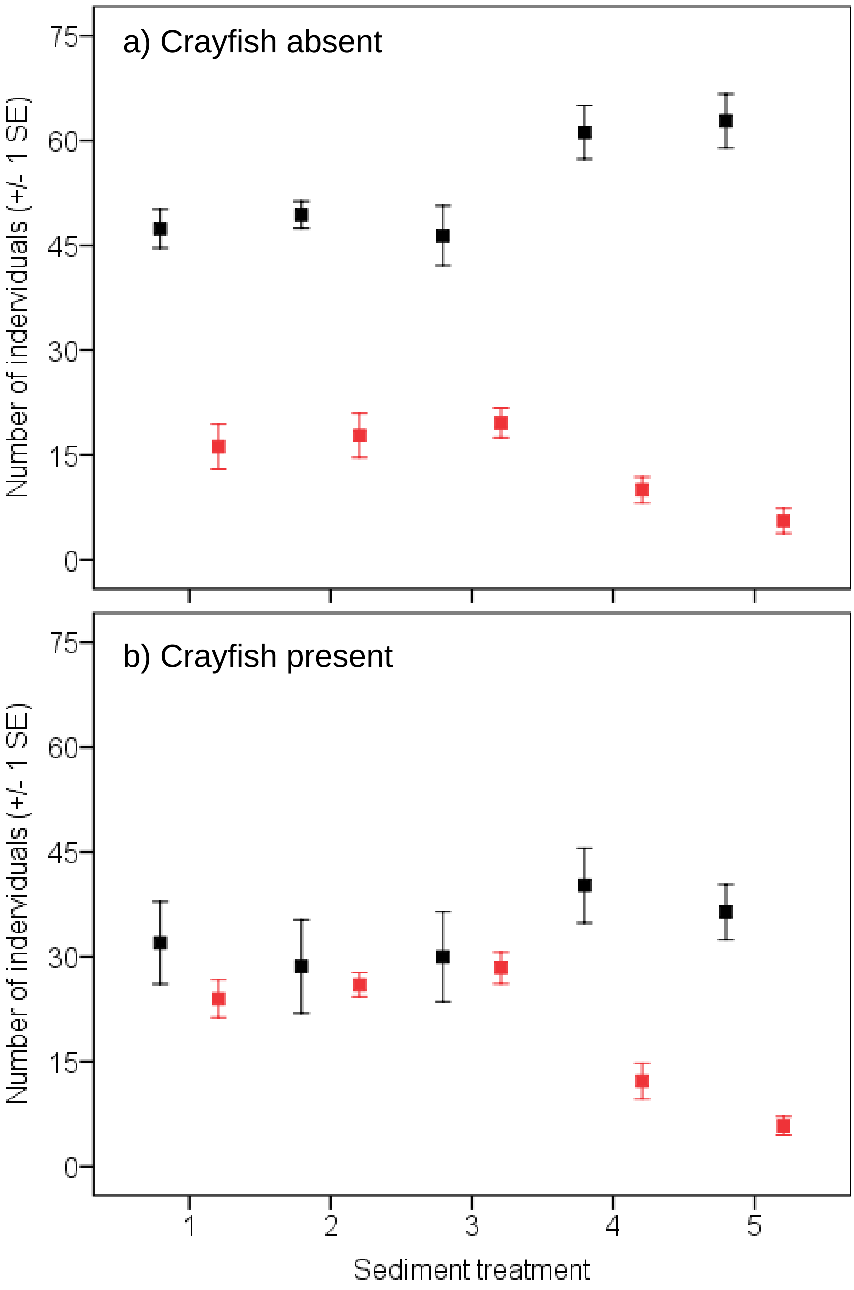

Figure 6.7 Mean number of *Gammarus pulex* (± 1 SE) recorded at the end of the 24-hour experiment within surface (black) and subsurface (red) for each sediment treatment in a) the absence and b) presence of crayfish. Sediment treatments; 1 = open gravel framework; 2 = 3 kg m^{-2} fine sedimentation; 3 = 5 kg m^{-2} fine sedimentation; 4 = 3 kg m^{-2} coarse sedimentation; 5 = 5 kg m^{-2} coarse sedimentation. Sections where the number of individuals are significantly different are indicated with the same letter (Tukey post-hoc test, $p < 0.05$).

Table 6.4 Tukey post-hoc comparisons for the abundance of *Gammarus pulex* between sections. p-values are presented for pairwise comparisons in the presence / absence of crayfish for each sediment treatment. Significant ($p < 0.05$) results are emboldened.

Sediment treatment	t-value	p-value
Crayfish absent		
Open framework	-6.770	**<0.001**
3 kg m^{-2} fine	-6.856	**<0.001**
5 kg m^{-2} fine	-5.815	**<0.001**
3 kg m^{-2} coarse	-11.109	**<0.001**
5 kg m^{-2} coarse	-12.411	**<0.001**
Crayfish present		
Open framework	-1.199	0.972
3 kg m^{-2} fine	-0.390	1.000
5 kg m^{-2} fine	-0.240	1.000
3 kg m^{-2} coarse	-4.197	**0.001**
5 kg m^{-2} coarse	-4.587	**<0.001**

6.4.3 Survivorship to crayfish presence as a function of sediment load

There were marked differences in the abundance of *G. pulex* between the layers of the column when subjected to varying levels of sedimentation in the presence of crayfish (Figure 6.8). With clean gravels, 3 kg m^{-2} fine sand sedimentation and 5 kg m^{-2} fine sand sedimentation, the number of individuals in both the surface and sub-surface layers were similar (average = 28, range = 24 - 32). In contrast, coarse sand sedimentation (3 kg m^{-2} and 5 kg m^{-2} treatments) resulted in greater numbers of *G. pulex* being recorded in the surface layer at the end of experiment (average= 38) and a reduction in the numbers recorded in the sub-surface (average = 7). Survivorship of *G. pulex* when all treatments were considered was significantly different ($F_{4,20} = -3.612$, $p < 0.001$). Post-hoc pairwise tests indicated that 5 kg m^{-2} of coarse sedimentation resulted in a significantly lower survivorship (56.27%) of individuals compared to clean gravel treatments (79.73%; $p < 0.001$), 3 kg m^{-2} of fine sedimentation (69.67%; $p = 0.040$) and 5 kg m^{-2} of fine sedimentation (77%; $p = 0.003$; Tukey; Figure 6.9). No other significant differences in *G. pulex* survivorship among treatments were observed (Table 6.5). Results indicate that the addition of fine sediment at high loadings and appropriate grain sizes enhances the risk of *G. pulex* predation by signal crayfish.

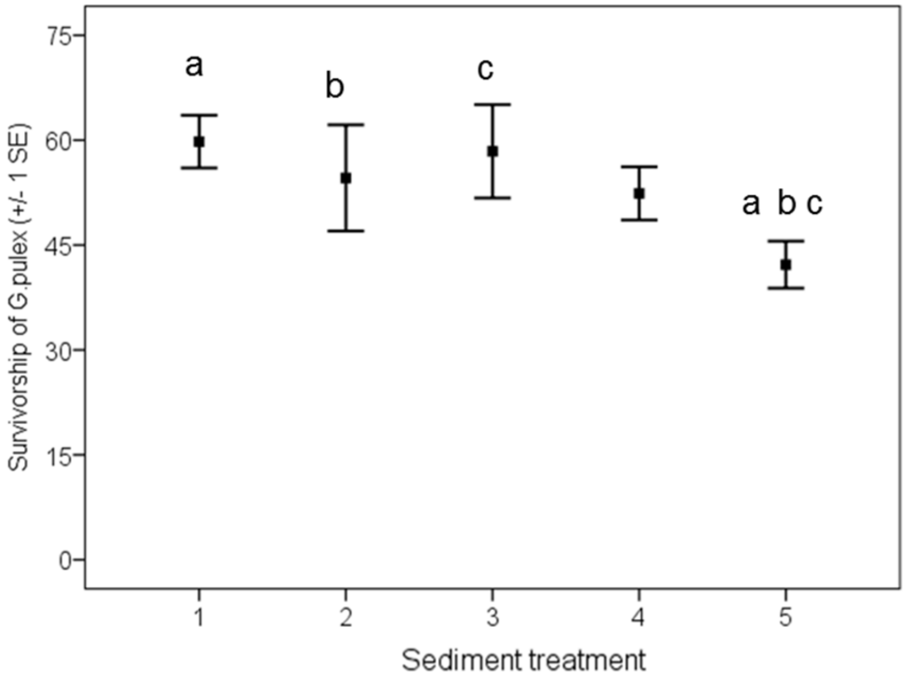

Figure 6.8 Survivorship of *Gammarus pulex (n = 75)* in the presence of crayfish for each of the sediment treatments. Sediment treatments; 1 = open gravel framework; 2 = 3 kg m^{-2} fine sedimentation; 3 = 5 kg m^{-2} fine sedimentation; 4 = 3 kg m^{-2} coarse sedimentation; 5 = 5 kg m^{-2} coarse sedimentation. Treatments where survivorship numbers were significantly different are indicated by the same letter (Tukey post-hoc test p <0.05).

Table 6.5 Tukey post-hoc comparisons for survivorship of *Gammarus pulex* individuals in the presence of crayfish between sediment treatments. P-values are presented for pairwise comparisons between sediment treatments. Significant ($p < 0.05$) results are emboldened.

Sediment treatment	3 kg m^{-2} fine	5 kg m^{-2} fine	3 kg m^{-2} coarse	5 kg m^{-2} coarse
Open framework	0.813	0.999	0.522	**<0.001**
3 kg m^{-2} fine		0.931	0.989	**0.040**
5 kg m^{-2} fine			0.707	**0.003**
3 kg m^{-2} coarse				0.132

6.4.4 Sediment infiltration rates

3 kg m^{-2} fine sand sedimentation: Infiltration rates of fine sand into the subsurface layer were greatest in experiments with crayfish present (average 1.93 kg m^{-2}, 63.3% of the sediment initially applied on the surface of the upper layer). These rates were significantly greater ($P = 0.006$ Tukey) than under control conditions with no organisms present (1.61 kg m^{-2}, 53.6%). Infiltration rates for experiments with both 75 *G. pulex* and crayfish were intermediate (1.78 kg m^{-2}, 59%) to that of a single crayfish and 75 *G. pulex* (1.73 kg m^{-2}, 58%; Figure 6.9a; Table 6.6). The addition of biota significantly enhanced the vertical ingress of fines into the sub-surface, with crayfish as the single agent representing the most influential factor.

5 kg m^{-2} fine sand sedimentation: As with the 3 kg m^{-2} fine sand sedimentation experiments with crayfish had the greatest infiltration rates (average 3.05 kg m^{-2}, 61% of initial sediment), which were higher than control experiments (2.68 kg m^{-2}, 54%) and those with 75 *G. pulex* (2.71 kg m^{-2}, 54.2%). Treatments with crayfish and 75 *G. pulex* had intermediate infiltration rates (2.86 kg m^{-2}, 57.2%; Figure 6.9b).None of the pairwise comparisons were determined to be statistically different (Table 6.6).

3 kg m^{-2} coarse sand sedimentation: In contrast to fine sand additions, the application of coarse sand at moderate loadings resulted in no significant differences between infiltration rates with and without organisms (Table 6.6). All organism treatments displayed similar low sediment infiltration rates (range 0.095 – 0.111 kg m^{-2}, 3.1 – 3.7% of initial sediment application Figure 6.9c). In the presence of fine sediment which has a high propensity to clog, biota did not influence the ingress of fines into the substrate.

5 kg m^{-2} coarse sand sedimentation: The heavy loading of coarse sand produced results similar to those of fine sediment with biota impacts of ingress rates being evident. Infiltration of fines into the subsurface was greatest when both crayfish and 75 *G. pulex* were present and the rate was statistically greater than under control conditions ($P < 0.001$ Tukey), 75 *G. pulex* ($P < 0.001$ Tukey) and an individual crayfish ($P = 0.009$ Tukey). However, infiltration rates for all organism treatments were low when compared to the fine sand treatments (range 0.082 – 0.286 kg m^{-2}, which represent only 1.6 – 5.7% of initial sediment application; Figure 6.9d).

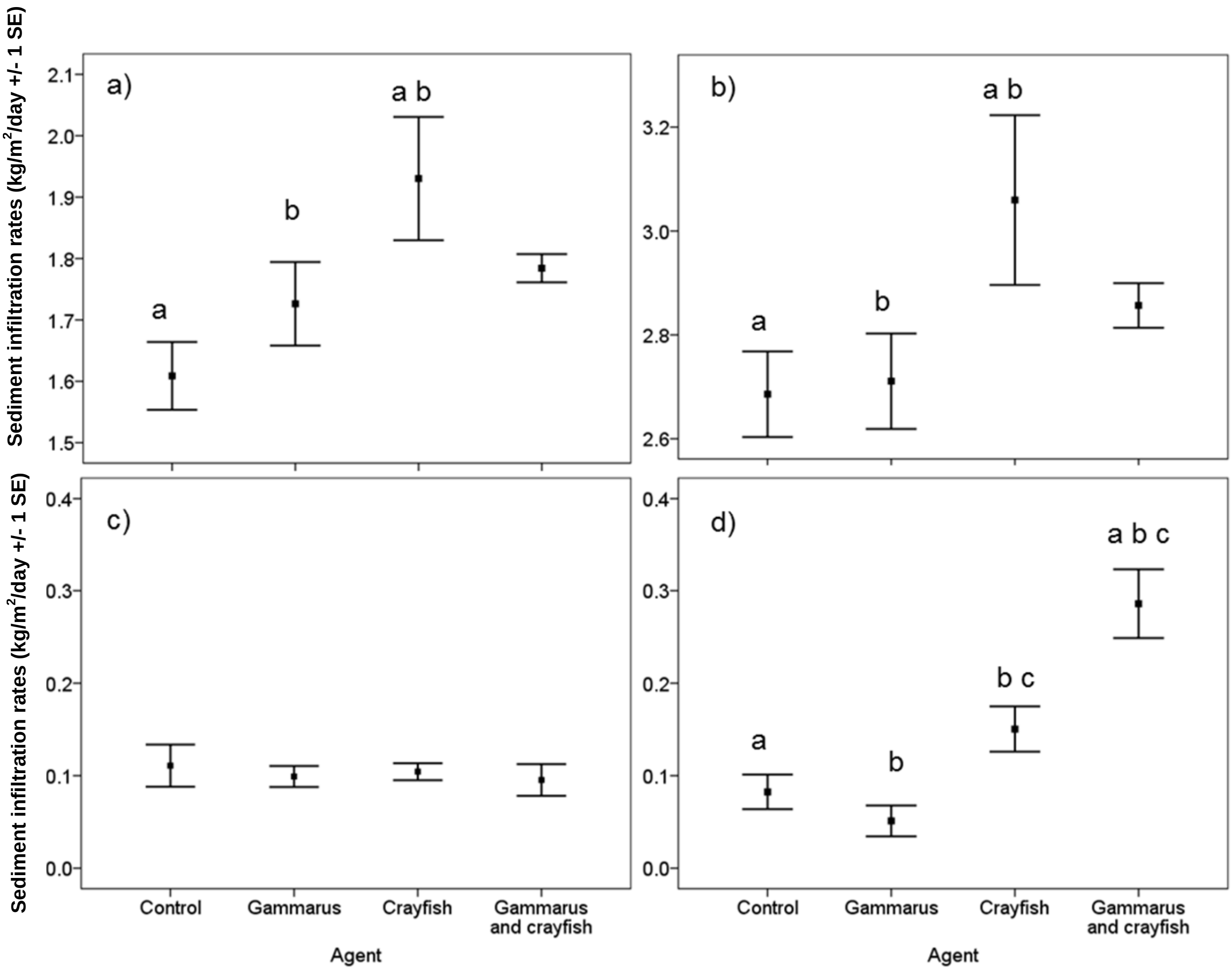

Figure 6.9 Mean infiltration rates (kg/m^2/day ± 1 SE) of each organism combination for: a) 3 kg m^{-2} fine sedimentation; b) 5 kg m^{-2} fine sedimentation; c) 3 kg m^{-2} coarse sedimentation and; d) 5 kg m^{-2} coarse sedimentation. Experiments where infiltration rates are significantly different by organism are denoted by the same letter ($p < 0.05$ Tukey post-hoc test). Note y-axis scales are different dependent on the sediment treatment.

Table 6.6 Tukey post-hoc comparisons sediment infiltration rates over the experimental period (24-hours) for each sediment treatment. p-values are presented for pairwise comparisons between organisms. Significant ($p < 0.05$) results are emboldened.

3 kg m^{-2} fine sedimentation

Organism	*G. pulex*	Crayfish	*G. pulex* and crayfish
Control	0.609	**0.026**	0.343
G. pulex		0.172	0.926
Crayfish			0.497

5 kg m^{-2} fine sedimentation

Organism	*G. pulex*	Crayfish	*G. pulex* and crayfish
Control	0.998	0.098	0.673
G. pulex		0.110	0.774
Crayfish			0.546

3 kg m^{-2} coarse sedimentation

Organism	*G. pulex*	Crayfish	*G. pulex* and crayfish
Control	0.955	0.992	0.902
G. pulex		0.996	0.998
Crayfish			0.978

5 kg m^{-2} coarse sedimentation

Organism	*G. pulex*	Crayfish	*G. pulex* and crayfish
Control	0.821	0.275	**<0.001**
G. pulex		0.062	**<0.001**
Crayfish			**0.009**

6.5 Discussion

6.5.1 Faunal predator avoidance and the interaction with the physical environment

The experiments outlined in this chapter sought to examine the avoidance behaviour of the freshwater shrimp, *Gammarus pulex,* in the presence of signal crayfish, but also how interaction(s) with the physical environment (in this instance, the stressor of fine sediment) affects both predator-prey relations and fine sediment ingress into gravel beds. Numerous studies have examined the ingress of fine sediment into gravel beds, but none have examined how this process might be mediated by single organisms or organism interactions. Similarly, a number of studies have examined the response of a range of snail species to crayfish presence in laboratory settings (Crowl and Covich, 1990, Correia et al., 2005) but studies of mobile taxa are lacking and those which examine the response in combination with external stressors are absent (Figure 6.10). Results from this study, indicate that in the presence of crayfish and where interstitial space permits, a large number of *G. pulex* migrate vertically into the sub-surface to avoid predation. Connectivity between subsurface and surface layers which enabled vertical movement behaviour was strongly associated with the grain size and fine sediment loading.

Fine sand applications (grain size 0.125 µm – 1 mm) under both loadings (3 & 5 kg m^{-2}) resulted in high infiltration rates under control conditions (gravity and downwelling flow) and for all organism combinations. This reflects the fairly large interstitial spaces between the framework gravels, which enabled the relatively unimpeded movement of fines and therefore maintained connectivity between the surface and sub-surface layers (Xu et al., 2014; Mathers et al., 2014). Consequently, with clean gravels and both loadings of fine sand, a large proportion of *G. pulex* (around 50%) were able to migrate vertically into the sub-surface when crayfish were present. In the equivalent sediment treatments (clean and fine sand applications) but with crayfish absent, the majority of *G. pulex* remained in the surface layer where the highest flow velocities were, reflecting their rheophilic nature (Gledhill et al., 1993). Results from the study indicate that the presence of crayfish significantly alters the vertical distribution of *G. pulex,* providing evidence of avoidance behaviour and thus evidence to answer the second research question.

The addition of coarser sand sediments (1 - 4 mm) to the gravel framework resulted in bridging of interstitial spaces within the surface layer and the development of clogs that disconnected the surface and sub-surface layers. Infiltration rates were significantly lower than for fine sand treatments, with the majority of the applied sediment remaining in the surface layer for both organism combinations (Figure 6.4). This resulted in no significant differences in the vertical distribution of *G. pulex* with and without crayfish (research question 1). The formation of clogs in the substratum limited the ability of *G. pulex* to penetrate the surface layer of the substrate and migrate into sub-surface sediments (research question 3). This interaction of predator avoidance behaviour with the physical environment significantly influenced predator-prey relationships, in this instance survivorship of *G. pulex* (Figure 6.10b and c).

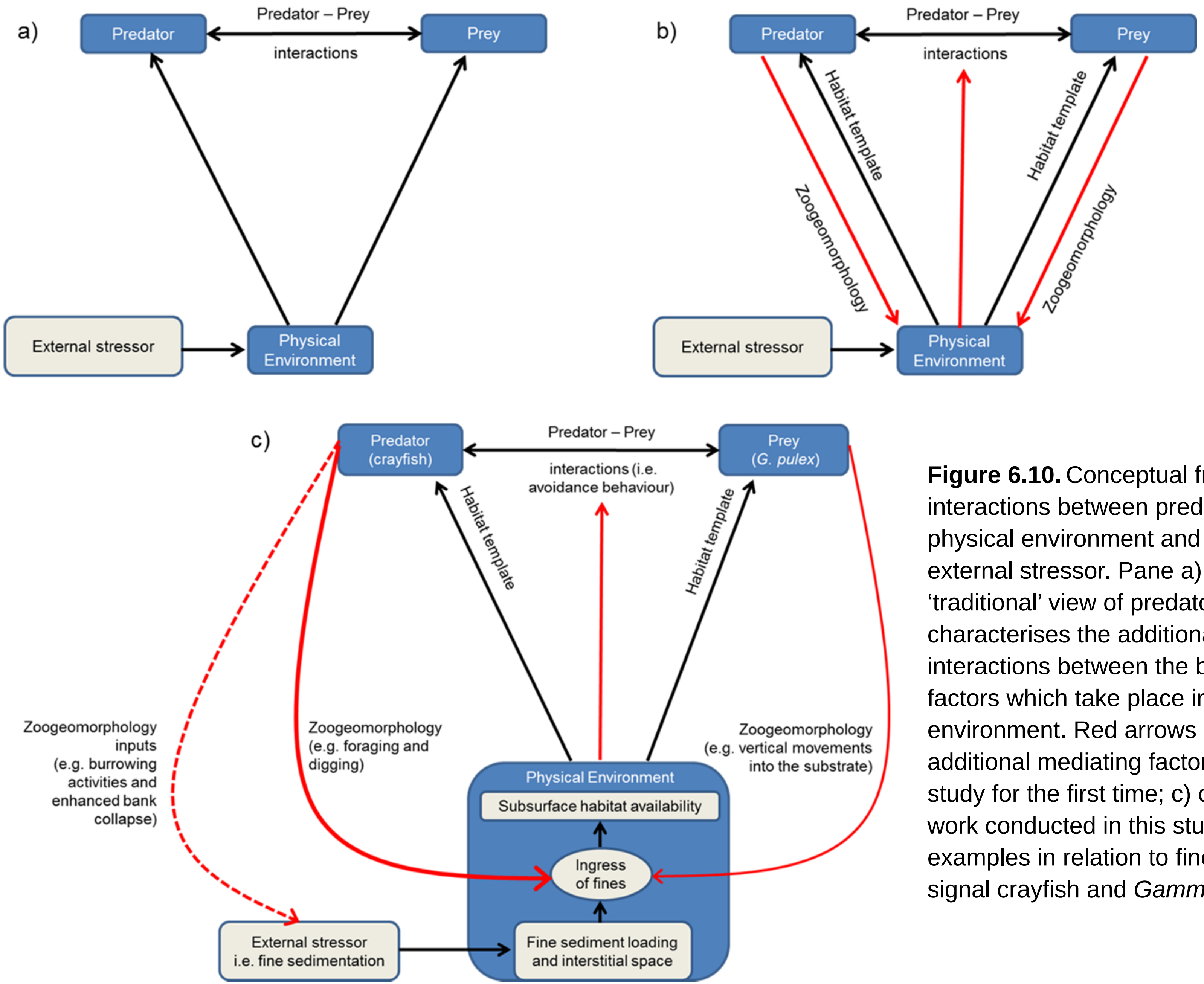

Figure 6.10. Conceptual framework of the interactions between predator-prey relations, the physical environment and the addition of an external stressor. Pane a) represents the 'traditional' view of predator-prey interactions; b) characterises the additional processes and interactions between the biotic and abiotic factors which take place in the natural environment. Red arrows represent the additional mediating factors considered in this study for the first time; c) conceptualises the work conducted in this study providing specific examples in relation to fine sediment dynamics, signal crayfish and *Gammaurs pulex.*

In experiments, where *G. pulex* were able to successfully migrate and display avoidance behaviour, survivorship rates were on average 78% with no significant differences evident for any of the fine sand or clean gravel control treatments. The addition of coarser sand clogged the substrate interstices and prevented vertical avoidance behaviour, resulting in larger numbers of individuals being present in the surface layer where they were less able to evade crayfish. 3 kg m^{-2} coarse sand resulted in slightly lower survivorship rates of *G. pulex* (70%). However, the addition of 5 kg m^{-2} coarse sand significantly reduced *G. pulex* survival to 56%, a reduction of 28% compared to the open gravel framework (control) where the substrate was not clogged and thereby permitted vertical movement. Consequently, the addition of fine sediment under appropriate loadings and grain sizes has the potential to render a prey's avoidance behaviour ineffective and therefore make them more susceptible to predation (research question 4).

Results from the study emphasise the importance of enhancing our knowledge in relation to the interaction of predator-prey relationships and their physical environment, in order to acknowledge and mitigate the potential effect of environmental stressors (Figure 6.10b). Alterations to the physical environment which inhibit avoidance behaviour may alter predator-prey dynamics which may, in turn, have indirect consequences for the wider ecosystem such as altered detrital processing rates, changes to the dominant algae cover and restructuring of macroinvertebrate communities (Matsuzaki et al., 2009). In the case of signal crayfish, it is likely that crayfish themselves may alter the delivery of fine sediment within lotic ecosystems, via burrowing activities and associated bank collapse (Faller et al., 2016; Rice et al., 2016). Consequently, crayfish most likely inadvertently improve their foraging success if they deliver coarse sand, an example of phenotype engineering.

Taxa are widely documented to utilise different avoidance strategies in the presence of discrete predators. Haddaway et al. (2015) demonstrated that *G. pulex* and *Potamopyrgus antipodarum* behave differently in the presence of native benthic fish, invasive crayfish and native crayfish. A number of other snail species have been documented to migrate to the waterline in the presence of crayfish but often seek benthic refuge from fish or water bug (Hemiptera) predators (Turner et al., 1999; Hoverman et al., 2005). In contrast to the nocturnal activities of crayfish, benthic fish, which typically rely on visual sightings of prey, instigate daylight refuge in *G. pulex* and increased night time activity and / or drift propensity (Allan, 1984; Holomuzki and Hoyle, 1990; Andersson et al., 1986; Haddaway et al., 2014). Vertical movement of *G. pulex* into interstitial spaces has been documented as a refuge mechanism to avoid inter-species predation (McGrath et al., 2007). Consequently, it is not unexpected that vertical movement may be one of the strategies employed by Gammaridae to avoid predation by crayfish, especially as signal crayfish activity is strongly linked to the transition between daytime and night (Nyström, 2005). It is likely that Gammaridae and other macroinvertebrate species possess a repertoire of avoidance mechanisms which enhance their probability of predator evasion, and therefore employ differing strategies dependent on the habitat characteristics and dynamics of the ecosystem. This work demonstrates that given suitable substrate conditions, specifically matrix and framework grain sizes that promote surface-subsurface connectivity, vertical avoidance behaviour into subsurface substrates by macroinvertebrates may be one such strategy.

6.5.2 Impact of organisms on fine sediment infiltration rates –the role of predator and prey relationships

This study also examined the two-way interactions of biota and the physical environment and in particular if organisms exert a significant zoogeomorphological influence on the physical processes of sediment ingress into a gravel substrate (Figure 6.10b). Results from the study provide evidence to answer the fifth research question; that the presence of *G. pulex* and signal crayfish enhanced infiltration rates. However, the influence of the two organisms on fine sediment infiltration rates was not consistent and varied as a function of sediment loading and grain size, and the interactions between the organisms themselves.

For the fine sand treatments (grain size 0.125 µm – 1 mm), the greatest geomorphic impact was associated with individual crayfish, with significantly greater infiltration rates than under control conditions (no organisms present) or for 75 *G. pulex*. The presence of crayfish resulted in approximately 10% more fine sand infiltrating into the substrate compared with control conditions under both loadings (3 and 5 kg m^{-2}). When sediment masses were considered, the heavier sediment loading resulted in greater weights of fine sediment infiltrating the substrates (average of 1.93 and 3.05

kg m^{-2} for crayfish treatments compared to 1.61 and 2.69 kg m^{-2} with no organisms present), despite the rates of infiltration being similar. In this instance, sediment loading controlled the total mass of ingress rather than influencing the contribution that crayfish had over ingress rates (i.e. more sediment did not result in greater ingress rates but remained consistent at 10% enhancement). Crayfish have been documented to reduce surface deposition of fine sediment (Usio and Townsend, 2004; Helms and Creed, 2005), with a number of field and laboratory studies documenting increases in suspended sediment concentrations associated with crayfish movement (Harvey et al., 2014; Rice et al., 2014; 2016). However, no studies have considered the vertical ingress of fines into a gravel framework or how this may influence the wider ecosystem. The significant influence of an individual crayfish in these experiments, suggests that under field conditions, where pore space permits, sediment infiltration may occur at greater rates where crayfish densities are high. As invasive signal crayfish are widespread and can reach high densities (up to 15 m^{-2} in riffle habitats in a small UK lowland river; Guan and Wiles, 1996), the presence of this organism may significantly alter fine sediment movements between the surface and subsurface layers.

G. pulex displayed some evidence of enhancing sediment ingress in the case of the lowest and finest sand loading (3 kg m^{-2}). Given their relatively small individual size, this modest impact was not unexpected, with significant effects on fine sediment dynamics most likely not being evident until densities of this organism reach considerable numbers (Moore, 2006). The results do imply however that over a wider scale, the cumulative effect of benthic and hyporheic macroinvertebrates (the community as a whole) might exert a significant influence on interstitial fine sediment concentrations and the availability of suitable habitat. The results also indicate that organisms interact with their environment in such a way as to maintain and regulate suitable meso-habitats for the biota themselves (Zantell and Peckarsky, 1996; Nogaro et al., 2009). The presence of bioengineers may result in the creation of a mosaic of benthic habitats, through the suspension and bioturbation of fine sediment at differing scales (Figure 6.10c). The relationship between fine sediment and macroinvertebrates is therefore not straightforward but a two-way process (Zanetell and Peckarsky, 1996; Rice et al., 2012b, Statzner, 2012), with important repercussions for the wider ecosystem functioning.

Under settings where both the predator and prey were present (crayfish and 75 *G. pulex*), sediment infiltration rates were found to be the second greatest with ingress rates being 5% higher than control conditions (no organism present) and in the presence of just 75 *G. pulex*. It is likely that infiltration rates were reduced during these experiments as a result of two prey-predator interactions. Firstly for experiments without crayfish, the majority of *G. pulex* were located in the surface layer and therefore had a greater opportunity to influence the ingress of fines over the course of the 24 -hours. In contrast, in the presence of crayfish, on average 25% more individuals migrated into subsurface habitats and consequently once they had migrated they were unable to influence the ingress of finer sediments.

Secondly, it was evident that in experiments where crayfish were the only organism present, a large proportion of energy was exerted in foraging for food. In a number of experiments, crayfish exhibited bulldozing behaviour by piling sediment to one quadrant of the mesocosm (Figure 6.11; Helms and Creed, 2005; Johnson et al., 2010a). This foraging behaviour would have significantly affected the movement of fine grained sediments. The addition of prey items in the form of *G. pulex* resulted in a reduction of foraging behaviour, with food availability being significantly greater (50% of *G. pulex* remained in the surface layer despite many individuals displaying avoidance behaviour). It is presumed that foraging activity would have declined over the 24-hours as the crayfish consumed prey items (Haddaway et al., 2012) and time between foraging activity would have increased. Prey availability may therefore be a key driver on the influence that biota exert over physical processes. Reductions in prey availability may enhance foraging behaviour and inter-species competition (especially for signal crayfish which are widely documented as being aggressive to conspecifics; Pintor et al., 2008) and may therefore enhance fine sediment mobilisation (suspension and ingress). These results support findings of other studies on predaceous stoneflies, which surmise that increased hunger levels accentuate the rate of predator movement and thus the agitation of fine sediments (Zantell and Peckarsky, 1996; Statzner et al., 1996). Consequently, as invading species become more established and if resources become depleted, the implications of biota on the environment may become more prominent and may increase the rate of range expansion associated with increased mobility.

Figure 6.11 Substratum piling as a result of foraging behaviour by crayfish after 24-hours.

In stark contrast to the fine sand additions, the greater propensity of coarse sand to form a bridge between clasts and thus prevent further subsequent infiltration, resulted in little or no implications of biota on infiltration rates. Under 3 kg m^{-2} loadings, no significant differences in infiltration rates were recorded for any of the organism combinations, with between 3 - 4% (0.1 kg m^{-2}) of the initial sediment application penetrating into the subsurface. 5 kg m^{-2} resulted in some differences in infiltration rates as a result of biota presence although these were small relative to the fine sand treatments. As with fine sand applications, crayfish as a single agent were associated with significantly greater infiltration rates (an extra 0.1 g m^{-2} on average) than control conditions and 75 *G. pulex*. However, in contrast to fine sand applications, the combination of both *G. pulex* and crayfish resulted in the greatest infiltration rates. Under these conditions, *G. pulex* were unable to migrate to the sub-surface substrates, and therefore around 95% of individuals would have been present in the surface layer. It is assumed that some individuals would be attempting to burrow through the coarse sand to avoid the predatory crayfish. For experiments without crayfish, smaller numbers of *G. pulex* exercised vertical avoidance behaviour and therefore less energy would have be exerted to burrow through coarse sand particles blocking vertical pathways.

6.6 Summary

Within this study, *G. pulex* demonstrated vertical avoidance behaviour in the presence of crayfish where the interstitial pore space permitted. However, the addition of fine sediment under appropriate loadings and grain sizes, disconnected surface and sub-surface habitats and *G. pulex* were unable to reach substratum refugia making them more susceptible to predation. These results highlight the link between fine sedimentation loading and the availability of suitable refugia. The study also highlights the zoogeomorphological potential of biota such that they may exert a significant influence on physical processes if they are large (e.g. signal crayfish) or when populations (e.g. *G. pulex*) or communities reach very high densities. Crayfish significantly enhanced fine sediment infiltration rates, but under natural conditions with both prey and predator present, infiltration rates were not as high. Prey availability therefore plays a key role in the interaction of biota and the physical environment.

The results of this study demonstrate that predator-prey interactions are complex and are strongly mediated by the interactions of the organisms and their physical environment (Figure 6.10). Where possible these predator-prey interactions should not be studied in isolation from the influence of the physical environment, and similarly the role of zoogeomophic agents should be considered in the context of resource availability. There is a need for further studies which explore beyond the classic approach of one way interactions such as the direct influence of predators on communities (Figure 6.10a), or the implications of biota as biogeomorphic agents, but which investigate the mechanisms behind such interactions through the application of truly interdisciplinary research (Stazner and Sagnes, 2007; Figure 6.10b and c).

Chapter 7 - Summary, key themes, future research and concluding remarks

7.1 Introduction

At a time when invasive species are expanding their ranges and threatening native biodiversity (Early et al., 2016), the principal aim of this thesis was to examine and quantify the abiotic and biotic implications of invasive signal crayfish in lowland UK rivers. The thesis focussed in particular on two main elements; macroinvertebrate community changes and fine sediment dynamics. The research also considered the dynamic and interlinked connections between biota and abiotic processes and how these interactions mediate the outcomes of associated zoogeomorphic activity. Specifically this research has sought to address the following objectives;

1. Quantify the temporal and spatial extent of signal crayfish effects for instream macroinvertebrate communities (Chapters 3 and 5).
2. Examine the potential effect of invasive signal crayfish on commonly employed biomonitoring tools (Chapter 3).
3. Quantify the role of signal crayfish on fine sediment dynamics within lotic ecosystems (Chapters 4 and 6).
4. Experimentally examine the predator-prey interactions of signal crayfish and macroinvertebrates in association with fine sediment loading (Chapter 6).

Data presented within Chapters 3-6 examined the interaction of invasive signal crayfish with fine sediment dynamics and macroinvertebrate communities at multiple spatial scales (national, reach and meso-scale) within lowlands rivers in the UK. The research undertaken has addressed all four objectives. The outcomes and implications of the results presented in this thesis will be examined in further detail in the following sections and key findings highlighted. This chapter also considers the key themes arising from the research and considers how the research may be integrated into contemporary river management and conservation. The thesis concludes with consideration of how research in the field may be developed in the future.

7.2 Fulfilment of thesis objectives

Given the ongoing concern regarding the long term effects of invasive taxa, Chapter 3 aimed to quantify the temporal and spatial extent of invasive signal crayfish effects on macroinvertebrate communities. The research examined long term Environment Agency of England data from three English regions to assess whether the effects of crayfish invasion were persistent over time and space and addressed the first objective of the thesis.

1. *Quantify the temporal and spatial extent of signal crayfish effects for instream macroinvertebrate communities.*

Despite invasions of aquatic ecosystems becoming more frequent (Brown et al., 2016), there is a paucity of studies which examine the long term effects of biological invasions, particularly within lotic ecosystems (McCarthy et al., 2006). Using non-metric multidimensional scaling (NMDS) of macroinvertebrate community data the results demonstrate that the effects of crayfish invasion are persistent over time and space. Crayfish invasion resulted in marked changes to the macroinvertebrate community when control and invaded rivers were considered. The effects of crayfish invasions on the wider community were evident over ten years later, despite shifting hydrological conditions, and there was no evidence of recovery within the communities. The modifications to macroinvertebrate communities were consistent across multiple English regions in spite of being characterised by differing lithologies, flow regimes and habitat characteristics.

The individual taxa negatively affected by crayfish invasion (associated with reduced numbers) were consistent with that reported in the wider literature, with Hirudinea (leeches) being the most significantly affected (Stenroth and Nyström, 2003; Ruokonen et al., 2014) in addition to some species of Moullusca (e.g. *Radix* spp., Sphaeriidae; Lodge et al., 1994; Dorn, 2013; Table 2.1). The study highlighted the need for greater taxonomic resolution (species or genus where possible) when considering the effect of stressors. It is likely that life history characteristics (i.e. habitat and feeding preferences) most likely control the implications of invasions for specific taxa and these vary considerably at coarse taxonomic resolutions (such as family or order level). Not all Mollusca taxon were affected by invasion (e.g. *Potamopyrgus antipodarum*) and similarly the order of Ephemeroptera demonstrated variable responses (e.g *Caenis* spp and *Baetis* spp; Usio and Townsend, 2004; McCarthy et al., 2006).

Chapter 5 provided further evidence for the first objective but at different temporal and spatial scales. The chapter considered the temporal dynamics of crayfish effects over short time frames (associated with taxon life history cycles) and in conjunction with fine sediment loading at the reach scale. The chapter considered the additive effect of substrate conditions (fine sediment content) and crayfish presence on macroinvertebrate communities.

There is an absence of studies which consider the temporal dynamics of biological invasions for ecosystems, with relatively few studies undertaking repeated sampling (with regard to both short and long time periods). This chapter aimed to examine the influence of temporal variability of crayfish implications on macroinvertebrates associated with life history characteristics of both crayfish and invertebrates. The results of the chapter indicated that communities which support invasive crayfish populations were consistently distinct compared to those where crayfish were absent. In addition communities that were invaded consistently display reduced beta diversity compared to control (non-invaded) sites.

Despite the consistent effects on macroinvertebrate communities, residual effects for macroinvertebrates appear to differ over the main period when crayfish are active. NMDS plots of site / temporal centroids indicated a distinct change in temporal trajectories associated with this period. These differences probably reflect the life history behaviours of crayfish (intensification of activity with increasing water temperatures and spawning behaviour) but also the life-cycles of macroinvetebrates. Although relatively minor within this study, these alterations in effects may be more noteworthy in recently established populations of invasive crayfish. Sediment loading had no significant effect on the magnitude of crayfish effects for macroinvertebrate communities with differences remaining consistent regardless of substrate composition. Similar taxa were observed to be affected as those documented in Chapter 3 and other studies (Crawford et al., 2006; Ruokonen et al., 2014) including riffle beetles (Elmidae) and taxa within the class of Hirudinea. Variable effects within Ephemeroptera and Mollusca were also evident.

Chapter 3 considered how the resultant changes to the macroinvertebrate community composition may affect the effectiveness of freshwater biomonitoring metrics currently used to assess the ecological status of waterbodies for EU water framework directive purposes. This fulfilled the second objective;

2. *Examine the potential effect of invasive signal crayfish on commonly employed biomonitoring tools.*

Crayfish invasions were instrumental in modifying community composition and a number of other studies have documented that assemblages typically shift to those characterised by mobile taxa at the expense of slower moving, more sedentary taxa (Parkyn et al., 1997; Keller and Ruman, 1998). This research demonstrated that these modifications to community composition may influence the results of biomonitoring tools which incorporate abundance weightings in their derivation. Indices which characterise the flow regime (Lotic Invertebrate index for Flow Evaluation, LIFE) and storage of fine sediment (Proportion of Sediment-sensitive Invertebrates, PSI) both demonstrated significant inflations following signal crayfish invasion when compared to control rivers over the same timeframe. In effect, this could lead to the incorrect overestimation of the amount of fines and water present in a river. In contrast, scores which only incorporate presence / absence of taxa were not significantly affected (Biological Monitoring Working Party score, BMWP; Average Score Per Taxon, ASPT, NTAXA and; EPT richness), most likely as local extinctions of prey taxa were rare whilst reductions in taxon abundances were common. Crayfish activity is strongly associated with water temperatures (Johnson et al., 2014) and within this study temperature was also found to have a significant influence on the results derived for individual metrics. LIFE and PSI scores were most strongly affected during the autumn sampling period when crayfish activity was at its peak.

Chapter 4 examined the implications of signal crayfish for fine sediment dynamics at the reach scale within two lowland rivers in the UK; the River Gwash (invaded) and the River Chater (control). Specifically it addressed the third objective;

3. *Quantify the role of signal crayfish on fine sediment dynamics within lotic ecosystems.*

A number of studies have examined the implications of crayfish for fine sediment remobilisation, with crayfish presence often being characterised by diurnal peaks in suspended sediment concentrations (Harvey et al., 2014; Rice et al., 2014; 2016; Cooper et al., 2016). However, little attention has been given to as to how these modifications affect the overall storage of fine sediment (in particular associated with the documented burrowing behaviour of crayfish within the UK; Faller et al., 2016) and what the cumulative impact is for localised reach scale sediment budgets. Results from this chapter demonstrate that signal crayfish are significant zoogeomorphic agents and enhanced the transport of fine sediment by 20.0 % under conservative estimates (range of 8.45 kg d^{-1} and 22.6 kg d^{-1}); a figure which is comparable to other lowland UK streams (Rice et al., 2014; 2016). Temporal variations in suspended sediment concentrations were also observed in the control site. However these were different in character and exhibited no clear temporal pattern or consistency. These variations in sediment concentrations at the control site in the absence of other plausible explanations (i.e. change in flow) suggest that a whole array of biota and processes could be influencing fine sediment dynamics which have not yet been studied in this thesis or acknowledged more widely.

No significant differences in the mass of fine sediment ingress were observed between the control and invaded reaches, most likely as a function of the spatial distribution of crayfish. The River Gwash is a heavily invaded river, with populations being present throughout the river and consequently sediment inputs are likely to equal outputs; a feature evident in the reach sediment budget. For the majority of the sampling period, sediment storage remained in equilibrium, but for a number of sampling sets (14-day periods), net losses in fine sediment were observed (956.53kg $14d^{-1}$and 1553.57kg $14d^{-1}$). These differences in fine sediment fluxes suggest that the implications of crayfish for fine sediment dynamics are heavily dependent on a number of key factors; (i) spatial and temporal variability in abundances, (ii) life cycle attributes and (iii) environmental controls (i.e. discharge and temperature). These themes will be discussed further below (Section 7.3.2).

Chapter 4 also examined the relationship between discharge, turbidity and fine sediment ingress through the application of a novel ‘data reduction’ method within the field of geomorphology. Examination of the dominant facets of flow and turbidity regimes (duration, frequency, magnitude and rate of change in flow events; Richter et al., 1996) using a principal components redundancy approach (*sensu* Olden and Poff, 2003) enabled identification of the primary drivers of fine sediment ingress within the two studied rivers. Discharge and turbidity were poorly correlated with each other and discharge also demonstrated little association with the mass of fine sediment ingress. In contrast, localised turbidity variations appear to explain a greater amount of variation, indicating the strong potential that localised biotic processes drive turbidity independent of hydraulic forcing.

Chapter 6 investigated potential predator avoidance strategies of the freshwater amphipod, *Gammarus pulex*, and considered the direct interaction of fine sediment loading and crayfish presence on survivorship rates. In parallel to this, the study also examined the zoogeomorphic potential (the effect a species can have on the physical environment) of signal crayfish for fine sediment ingress and reflected on the ecological feedbacks of predator-prey interactions upon the observed zoogeomorphic activity of biota. Specifically it addressed the fourth objective;

4. *Experimentally examine the predator-prey interactions of signal crayfish and macroinvertebrates in association with fine sediment loading.*

Ex-situ experiments demonstrated that signal crayfish enhanced fine sediment infiltration rates by up to 10% when compared to control conditions and when the substrate was exposed to smaller freshwater amphipods. The combination of both organisms (i.e. predator- prey interactions permitted) resulted in the second greatest rate of ingress. Incorporation of biotic interactions within the geomorphic framework is vital in order to gain a more comprehensive and accurate representation of the full zoogeomorphic potential that organisms may have for the physical environment. The results of this chapter suggest that reductions in prey availability may enhance foraging behaviours (Soluk and Craig, 1990; Visoni and Moulton, 2003) and therefore as invading species become more established and if resources become depleted, the implications of such biota on the environment may become more prominent. The chapter also considered the potential avoidance mechanisms that prey may utilise to evade crayfish predation and the interactions that fine sediment engineering by crayfish may have on such behaviours. Within these experiments, *G. pulex* displayed vertical avoidance behaviour by migrating into subsurface substrates to avoid crayfish predation. Fine sediment loading (of appropriate grain sizes and loading) was found to restrict the ability of individuals to utilize subsurface habitats and left individuals more susceptible to predation (control experiments survivorship 60% and worst case scenario 42%). Therefore, if crayfish increase fine sediment loading via burrowing and other sediment recruitment activities (Faller et al., 2016) they may modify the physical environment in a way that enhances their ecological successes (i.e. predation).

7.3 Research themes

This thesis sought to examine the biotic and abiotic implications of signal crayfish invasions. Throughout the study, aspects of geomorphology, ecology and hydrology have been examined in isolation, and in combination, to provide a holistic overview of the effects on lowland lotic ecosystems. The factors influencing the severity of environmental effects experienced by the ecosystem following invasion have been examined in detail through a number of studies over a range of temporal and spatial scales. This approach was adopted to enable the implications of such invasions to be assessed over environmentally relevant spatial and temporal scales. This section concludes by considering the wider implications of crayfish invasions for fine sediment dynamics and biotic communities.

7.3.1 Multidisciplinary work – crossing the boundaries of geomorphology, ecology and hydrology

This thesis was primarily founded on two key concepts; ecosystem engineering (Jones et al., 1994) and zoogeomorphology (Butler, 1995). By undertaking detailed work in both the geomorphological and ecological disciplines throughout this thesis it is clear that these concepts share many commonalities and are centred upon similar fundamental frameworks. Research conducted in both disciplines should not lose sight of the fact that biotic and abiotic processes do not work in isolation but are intimately connected and should be examined as such. Until such multidisciplinary work is conducted, both fields will continue to be constrained in their academic breakthroughs and ultimately the accuracy of their findings (e.g. Figure 6.11).

The focus of this thesis was to consider the biotic and abiotic implications of invasive crayfish. Invasive crayfish had clear effects on macroinvertebrate communities with direct modifications (most likely via predation) being evident at the national and / or long time scale (Chapter 3), through to the temporally dynamic reach scale (Chapter 5). Crayfish also had significant implications on fine sediment dynamics through the remobilisation of fines in the field (Chapter 4) through to the enhancement of fine sediment infiltration rates within mesoscale experiments (Chapter 6). These results also support the wider literature pertaining to the zoogeomorphic effects of invasive crayfish (Harvey et al., 2014; Rice et al., 2014; 2016; Cooper et al., 2016; Albertson and Daniels, 2016a).

However, when ecological factors were introduced into the zoogeomorphic equation and similarly when the physical habitat is considered within the ecological implications, the outcomes of the separate components yielded different results. Many ecological studies which examine the implications of invasive taxa typically do so within controlled experimental studies with limited habitat complexity or physical environmental controls and thereby do not always accurately represent the complexity of such invasions (e.g. Haddaway et al., 2014; Dodd et al., 2014; Taylor and Dunn, 2017). It was evident within the experiments conducted within this thesis (Chapter 6) that habitat availability (in this instance interstitial pore space as a function of fine sediment loading) is an important control on the magnitude of the invader effects experienced and future studies should therefore consider controlling for such influential effects.

Similarly, when considering the geomorphic outcomes of invasive taxa, the addition of prey items within the experiments, and therefore the introduction of natural biotic interactions, reduced the observed impact that signal crayfish had for fine sediment infiltration rates (Figure 6.11). Typically, the geomorphic potential of taxa is examined purely as a function of individual taxa through flume or mesocosm experiments with little consideration for the dynamic interactions with other organisms (e.g. Statzner et al., 2003b; Johnson et al., 2011; Pledger et al., 2014). These studies may therefore overestimate the potential impact that taxa have on the environment. Experimental manipulations in the field also commonly employ in-situ enclosures (e.g. Creed and Reed, 2004; Albertson and Daniels, 2016a) which do not fully represent the complexity of geomorphological processes operating and therefore provide a gross estimation of the ‘potential’ geomorphic work a biota is capable of. These crude experiments and field studies yield estimations which are vitally important and enhance our essential mechanistic understanding of the processes operating but studies should reflect on the realism and therefore wider applicability of their results when relevant spatial and temporal scales are considered.

7.3.2 Spatial and temporal scales

This thesis has taken a multiple scale approach to investigating the implications of crayfish for biotic and abiotic processes in both space and time. It is important to consider the results of such processes at relevant spatial and temporal scales. Many studies which have investigated the environmental implications of invasions typically do so at the micro-scale (through controlled laboratory experiments) over very short time frames; the results of which provide useful and mechanistic information regarding the processes taking place. Studies have also predominantly been conducted at the intermediate scale; over a number of years, commonly between one to three years or effectively the duration of a research project, and typically at one or two focus sites. These studies provide snapshots of the overall effect that invasive taxa may have for the physical environment but do not provide any temporal or wider spatial context for the results; i.e. is this within the range of natural variability and are these results consistent across space and time?

As a result of the temporal and spatial scales employed throughout the research presented in this thesis, a number of recurring themes have emerged which highlight the importance of the following factors when considering the role of invading species;

- ***(i)*** ***Spatial and temporal population dynamics;***
- ***(ii)*** ***Life cycle attributes and histories (for both invaders and the receiving ecosystem);***
- ***(iii)*** ***Environmental controls and;***
- ***(iv)*** ***Biotic interactions / original resident community composition***

Whether considering the geomorphological or ecological consequences of invading taxa, the environmental assessments of such processes share all of the above key components to varying degrees. These will be examined in detail in the following subsections.

7.3.2.1 Zoogemorphic activity

Many organisms are considered to be agents of geomorphic change, capable of modifying landscape evolution processes (Flecker et al., 2010; Jones, 2012). However, the effects of zoogeomorphic activity will not be spatially and temporally consistent; the effects may be minimal in some ecosystems whilst in other systems they may dominate. Moore (2006) and Johnson et al., (2011) suggested a general framework of four interacting factors that may influence the geomorphological impact of animals; behaviour, body size, density and abiotic context. In the section below, these factors are reflected on and a number of additional factors proposed which should be considered when evaluating the role of zoogeomorphic agents (outlined in Figure 7.1).

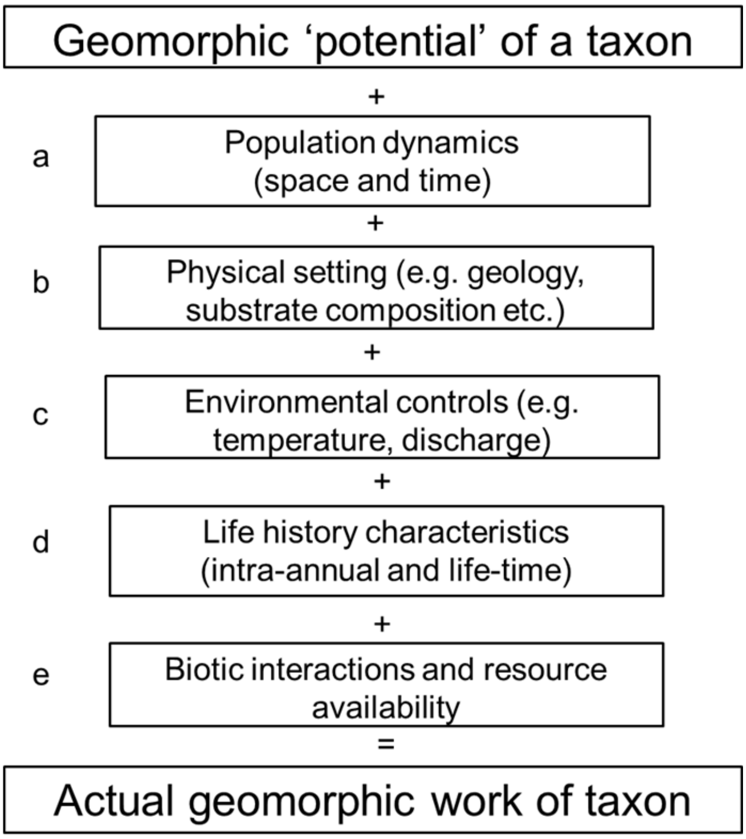

Figure 7.1 Conceptual framework of the interacting factors which influence the potential geomorphic impact of a taxon.

Population dynamics (space and time; Figure 7.1a): The impact of a species for an ecosystem is a function of its population density, with larger populations most likely having greater impacts (Moore, 2006). Experiments examining the zoogeomorphic potential of animals which utilize high density treatments are associated with a 66% greater effect size than low density treatments (meta-analysis conducted by Albertson and Allan, 2015). However, the patterns observed are not always clear, when all documented organism effects are considered (ranging from macroinvertebrates through to fish) no significant effect of density on sediment transport was evident (Albertson and Allan, 2015). This is most likely a function of body size, with larger animals having a greater effect on the environment than smaller organisms. Despite this, when considering natural population size, the effect of smaller animals, such as macroinvertebrates and crayfish (Soluk and Craig, 1990;

Visoni and Moulton, 2003), is often similar or greater than that of larger organisms, for instance fish or macrophytes, due to their much greater abundances (Fritz and Feminella, 2003; Hassan et al., 2015). Natural population dynamics control such effects with the cumulative effect of large numbers of macroinvertebrates counteracting the less dense but larger species such as fish.

All natural populations fluctuate in time and space (Tilman and Kareiva, 1997; Lande et al., 2003) and this will have significant implications for the overall effect that organisms have within the ecosystem (Statzner et al., 2003b). This is especially true when considering the role that animals have for sediment transport models and ultimately the overall implications they may have for sediment budgets. Highly dense but localised populations of organisms will have significant geomorphic effects which may cascade downstream. In contrast, if densities of organism are consistent throughout a study reach, the effects on the environment may not be as substantial and may result in no overall biotic effect being evident, despite the potential modifications to abiotic processes. Similarly, density fluctuations in time will alter the relative importance of an organism's geomorphic work, which may cause considerable imbalances in mass transport equations if the shift in populations is considerable. Population densities are an important factor in the potential importance of geomorphic activity and have been the focus of a large proportion of studies (Stazner and Pelret, 2006), however future studies should reflect on the highly dynamic nature of t over both space and time (Figure 7.1a).

Physical setting (Figure 7.1b): The effect of organisms on the physical environment will vary significantly as a function on the physical context of the study. Substrate characteristics exert a significant control over the potential amount of geomorphic work an organism can perform. Bioturbation activities will have greater effects within streams dominated by fine sediment, but may be reduced in gravel bed rivers. The behaviour of animals may also vary as a function of the physical characteristics of the ecosystem. For example the burrowing behaviour of crayfish is most likely associated with the composition of bank material (Faller et al., 2016) which is often a function of local geology properties.

Environmental controls (Figure 7.1c): Hydraulic energy plays a direct role in controlling the magnitude of biotic effects with increasing discharge typically having a negative relationship with biotic effects. Within larger streams (and in small streams associated with flood periods), physical processes dominate and not biological forces (Albertson and Allan, 2015; Rice et al., 2016). However, environmental controls also exert an indirect influence on the geomorphic effect of organisms associated with activity levels. Many taxa exhibit seasonal life cycles which are often timed to coincide with optimal environmental conditions (Verberk et al., 2008). As a result, environmental conditions may dictate the activity levels of a species in time and in space. Higher water temperatures are often associated with enhanced activity levels of cold-blooded biota (Bubb et al., 2006; Canal et al., 2016) and this may control the effect an organism has: (i) annually associated with seasonality; (ii) geographically associated with the world’s biomes and; (iii) in time associated with climatic modifications to global temperatures.

Life history characteristics (Figure 7.1d): Taxa most likely exhibit variability in their zoogeomorphic behaviour during the course of an individual’s life cycle. Many species demonstrate ontogenetic changes in feeding habits (Parkyn et al. 2001; Litz et al., 2017) and these modifications in the way taxa forage for food may alter the outcome of biotic effects. Shifts in the behaviour of taxa associated with life history events such as reproduction periods may also affect the geomorphic potential of organisms.

Biotic interactions and resource availability (Figure 7.1e): The act of bioturbation is one of the most widely cited activities associated with zoogeomorphic agents. Foraging, refuge creation and movement are three of the primary types of bioturbation activities that commonly occur in the natural environment (Moore, 2006). All of these activities are intimately connected through inter- and intra-specific interactions which may also directly or indirectly control resource availability. Biotic interactions play an influential role in the propensity of taxa to seek refuge and aggressive fighting behaviours have been cited as being associated with the most significant effects for biotic - environment energy transfers (Statzner et al., 2003b; Rice et al., 2014).

The availability of food and predator-prey interactions also directly affects the intensity and duration of foraging behaviour (Zanetell and Peckarsky, 1996; Statzner et al., 1996), with limited food resources most likely leading to increased geomorphic potential as a function of the enhanced foraging behaviours. Similarly, the composition of food resources will most likely have an effect on the foraging behaviour and subsequent geomorphic effects. For example, consumption of macrophytes will have minimal direct implications for sediment processes but will indirectly affect the storage of fines through flow modifications (Wharton et al., 2006). In contrast, predation of certain macroinvertebrates may cause some physical disturbance (Parkyn et al., 1997), whilst predation of other species of macroinvertebrates may not require as much energy. As preferential resources are depleted through time, the implications of biota on the physical environment may also alter.

Consideration of the temporal and spatial dynamics of environmental and ecological controls will enhance our fundamental understanding of the cumulative importance and role that zoogeomorphic organisms play within our ecosystems. Figure 7.1 provides a conceptual framework in which the potential geomorphic activity of a taxon can be evaluated within. Taxa can have large effects for many of the fundamental processes taking place in ecosystems and as such understanding the spatial and temporal context of such activities is vital.

7.3.2.2 Ecological implications

The ecological implications of invasive taxa for biota are highly variable with the effects being dependent on a number of interacting factors which have been drawn out throughout the thesis and are presented in Figure 7.2. These are briefly outlined below.

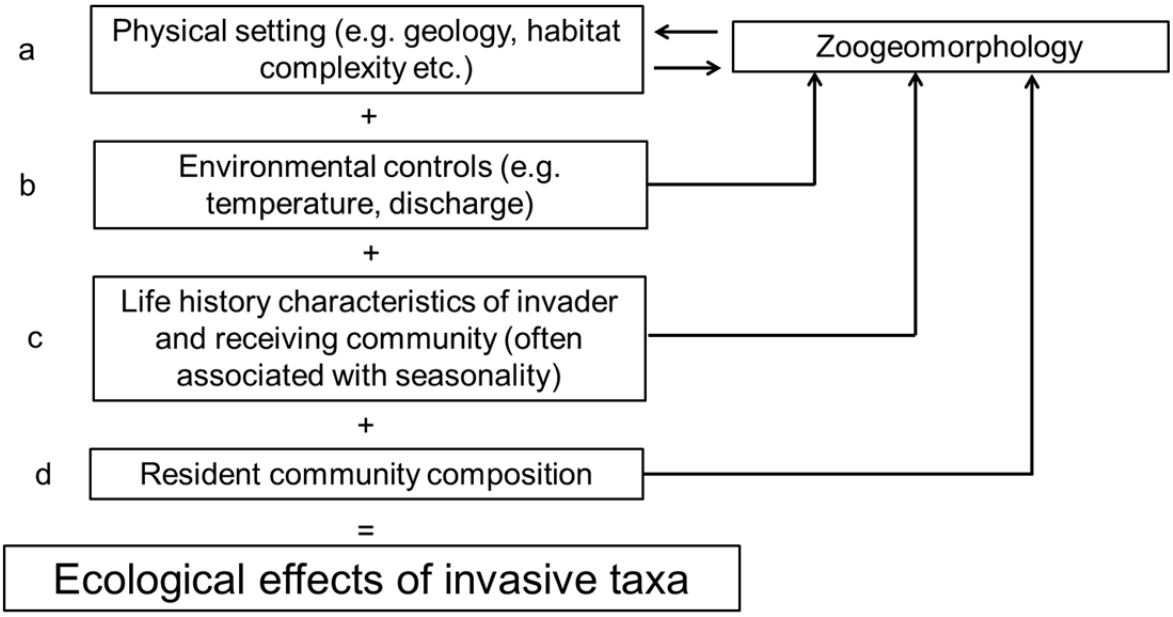

Figure 7.2 Conceptual framework of some of the interacting factors which influence the potential ecological effect of invasive taxa considered in this thesis.

Physical setting (+ zoogeomorphology; Figure 7.2a): The physical habitat conditions in which a biological invasion takes place will most likely control the effect the invader has for the receiving ecosystem. Heterogeneous habitats, which contain boulders and cobbles, macrophytes and interstitial habitat provide shelter, reducing the effects of predators. In contrast, areas with low habitat complexity may increase predation vulnerability and artificial habitat homogenisation may even enhance the establishment of non-native taxa (Crooks, 2002; Macneil and Platvoet, 2013). The effects of invasive taxa may also be further enhanced by engineered habitat changes (Gallardo et al., 2016). By altering channel morphology and bed material characteristics, such modifications can affect the availability of habitats for other organisms, with implications for ecosystem health and wider community composition. Despite the strong control the physical environment has over invasive taxa impacts, the two-way interaction of invasive species and geomorphic processes has frequently been overlooked to date (Fei et al., 2014).

The effects of invasive taxa are also likely to be function of the invaded waterbody (lentic or lotic). Making predictions of how ecosystems will be affected are difficult as many taxa are able to survive in a variety of environments and are able to readily adapt to changes in the environment and resources associated with their high feeding plasticity (Thompson et al., 2007). Studies suggest that the implications of non-native taxa vary as a function of the physical characteristics of the ecosystem (Vilà et al., 2011; Klose and Cooper, 2012).

Environmental controls (Figure 7.2b): Activity levels of many predacious taxa demonstrate a strong relationship with temperature (Öhlund et al., 2015). Temperature can also control the structure of predator populations through the regulation of prey abundance and size availability (Adams et al., 1982). Inter and intra-annual variations in temperatures will therefore be a strong determining factor in the severity of implications felt for the receiving ecosystem. Future climatic modifications may also act to alter the competitive and predatory effect on native species by reducing seasonally unfavourable conditions (Rahel and Olden, 2008). Environmental controls such as discharge may act to alter community effects through demographic alterations to invader populations. Using crayfish as an example, densities have been documented to decline following intense wet spates (indervideuals are entrained downstream; Light, 2003); whilst a number of species have been reported to survive during stream bed drying events (Datry, 2012). As these communities will be heavily stressed (Larned et al., 2010) they may be less resilient to invasion effects but also the adverse environmental conditions themselves.

Life history characteristics (Figure 7.2c): All organisms demonstrate life cycle characteristics which may affect forging behaviour and activity levels (including aggression levels) temporally. Ontogenetic shifts in the preferential food choice of taxa may affect the components of the ecosystem which are most severely affected dependent on the demographic makeup of invasive populations, with the implications of such invasions developing over time as the invasion process proceeds (Števove and Kováč, 2016). Similarly taxon vulnerability will be at its highest if peak activity levels of the invader coincide with life cycle stages which make prey effective and distinct targets such as during pupation. Pupae are particularly vulnerable as they represent trophically efficient resources for little energetic cost. A number of taxon are also able to readily adapt their life history behaviours in the presence of predators. Some caddisfly species select harder materials for case building whilst snails alter their reproductive and growth rates in the presence of certain predators (Crowl and Covich, 1990; Cerezer et al., 2016).

Resident community composition (Figure 7.2d): Consumptive effects of invasive taxa are strongly aligned to preferential feeding behaviours associated with the most trophically efficient food sources (Worischka et al., 2015). Original resident community composition therefore exerts a strong control over the extent and severity of effects experienced for all trophic levels of invaded ecosystems and may even moderate the overall impact (Hoy et al., 2015; Hewitt et al., 2016). Resident community composition is strongly influenced by a number of the above factors. Habitat modifications, through urbanisation or agricultural intensification, often results in diminished community diversity and may result in impoverished communities which are highly vulnerable to invasions (Fitzgerald et al., 2016). Similarly, environmental controls such as flow are regulatory physical templates for resident macroinvertebrate communities (Lobera et al., 2017). Communities that are dominated by highly mobile organisms, characteristic of strong flows, may have a greater ability to evade and resist predation based invasion effects. In contrast sedentary communities which are more common in slower flowing waters may be more susceptible to predation.

The factors outlined above provide an overview of some of the key factors (also highlighted in Figure 7.2) which may influence the effect of an invader upon the receiving ecosystem. However, given the dynamic and complex interactions within ecosystems the list is not exhaustive and other abiotic (e.g. physicochemical conditions of the waterbody) and biotic (e.g. multiple invasive species) factors may need to be considered at different spatial and temporal scales.

7.3.3 Crayfish invasions – dynamic and multi-faceted

Crayfish are both ‘ecosystem engineers’, and ‘zoogeomorphic agents’; whereby they regulate the supply of resources to other organisms through altering the physical landscape (Jones et al., 1994; Cavin and Butler, 2015). The effects therefore of signal crayfish invasions for ecosystems are not straightforward but represent complex and dynamic feedback loops. Focussing in particular on the implications of crayfish invasions for macroinvertebrate community composition there are a multitude of pathways through which assemblages could be affected (Figure 7.3). As this thesis focussed on the two main processes of predation (Figure 7.3a) and fine sediment dynamic alterations by invasive crayfish (Figure 7.3b; which indirectly affects nutrient cycling Figure 7.3c), these processes will form the fundamental basis of the holistic overview with a particular focus on how abiotic and biotic process are intimately connected.

Direct predation is the primary affect upon macroinvertebrates communities (Hanson et al., 1990; Charlebois and Lamberti, 1996; Figure 7.3a and d; Chapter 6), however there are a number of indirect effects which may also alter the composition of macroinvertebrate assemblages. Fine sediment dynamics is one of principal factors regulating macroinvertebrate community composition (Jones et al., 2012). Crayfish are widely acknowledged to alter the distribution and storage of fine sediment (Harvey et al., 2011) and it is likely that these modifications have subsequent effects for the structure of macroinvertebrate communities. Bioturbation of benthic sediments has been cited as one possible process responsible for the restructuring of benthic communities (Parkyn et al., 1997; Statzner et al., 2000) with this process also leading to enhanced nocturnal turbidity levels (Harvey et al., 2014; Rice et al., 2014; 2016). This increase in fine sediment suspension may leave invertebrate populations susceptible to physical disturbance by saltating grains leading to catastrophic drift (Culp et al., 1986; Larsen and Ormerod, 2010; Figure 7.3b).

In addition to the potential saltation of individual taxa, invertebrates entering into diurnal drift as a function of elevated suspended sediment concentrations of fine sediment loading (voluntarily or as a result of physical disturbance; Doeg and Milledge, 1991; Gomi et al., 2010) may be more susceptible to predation. Enhanced sedimentation rates (Richards and Bacon, 1994; Zweig and Rabeni, 2001; Descloux et al., 2013) and alterations to organic matter processing (Usio, 2000; Creed and Reed, 2004) may also influence invertebrate communities in a variety of ways. Furthermore, elevated sediment inputs as a consequence of burrowing behaviour (Guan, 1994) may clog substrates which could provide refugia habitat for macroinvertebrates from intra and inter specific predation (McGrath et al., 2007; Chapter 6) thereby enhancing a taxon's predation risk (Figure 7.3b) or may adversely affect ecologically homologous species such as *A. pallipes* which are highly susceptible to gill damage by suspended sediment (Rosewarne et al., 2014).

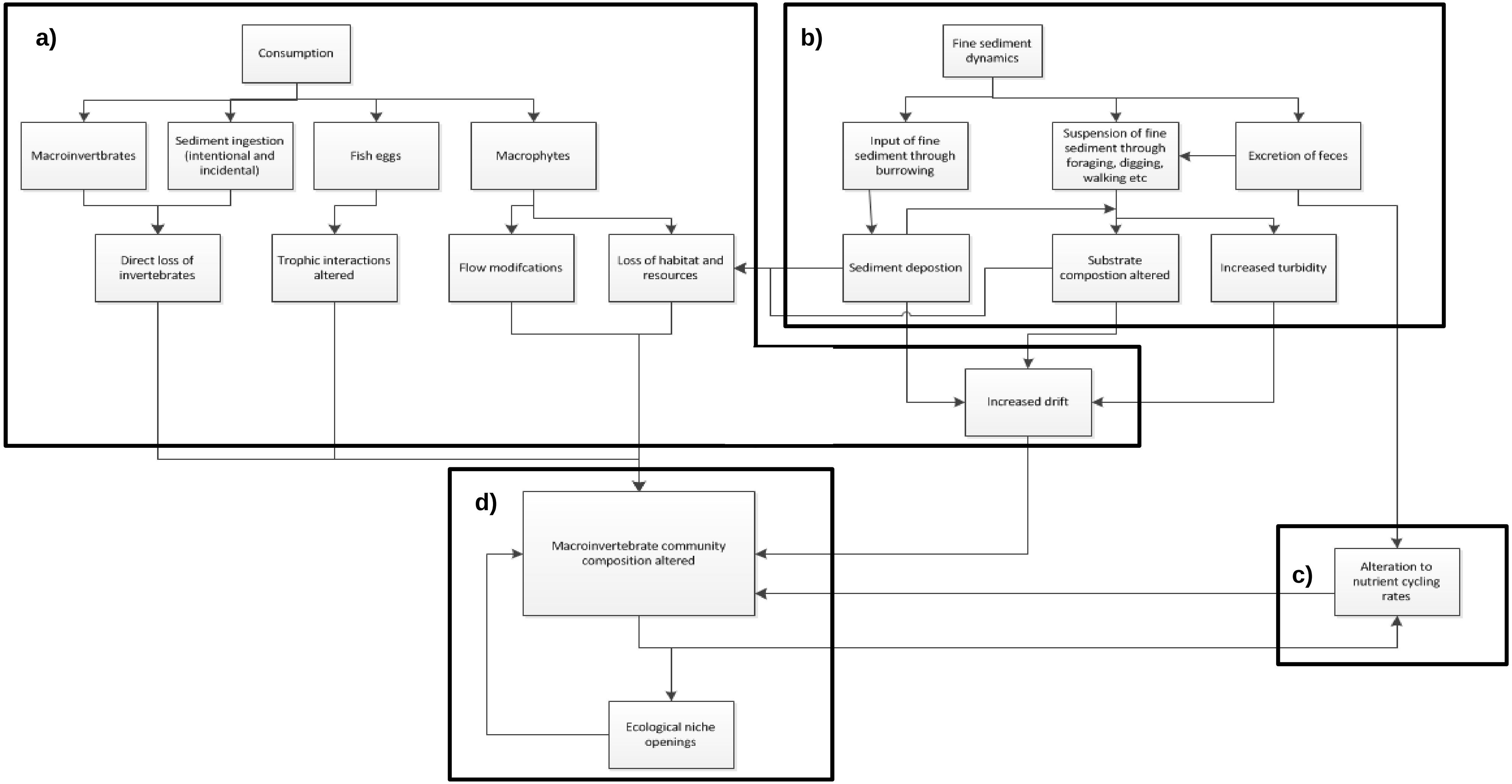

Figure 7.3 Conceptual diagram highlighting the complexity of crayfish invasions with a focus on fine sediment dynamics and macroinvertebrate communities. Box a) refers to biological processes; b) to fine sediment dynamics; c) biogeochemical processes and; d) the resultant macroinvertebrate community changes. Boxes represent the distinct biotic and abiotic processes but a number of interlinked processes are present.

The act of bioturbation by crayfish can also alter the transport of nutrients (Figure 7.3b and c). By increasing oxygen penetration to benthic sediments, mineralisation rates are enhanced which increases the release of phosphorus to the water column (Hansen et al., 1998; Bronmark and Hansson, 2005). One study which focussed on crayfish as bioturbators (with an absence of food to minimize egestion inputs), documented that crayfish activities altered aerobic conditions and consequently phosphorus solubility. In the presence of crayfish (and aeration of aquaria water) the percentage of Total Phosphorus (TP) released from the sediments to the water column was 7.5% compared to just 0.9% in control treatments (Ottolenghi et al., 2002). Within freshwater systems, phosphorus is often the limiting nutrient for plant growth (Carr and Chambers, 1998). Increasing phosphorus availability can therefore increase the primary productivity of rivers leading to the excessive growth of plants, mainly in the form of algae and rooted macrophytes (Mainstone and Parr, 2002). Animal egestion can also be an important source of nutrients within aquatic ecosystems, with crayfish faeces documented to contribute significantly to the growth of plants (Flint and Goldman, 1975). Crayfish may also alter detrital processing rates directly through consumption of leaf litter and indirectly through predation of macroinvertebrates (Carvalho et al., 2016; Figure 7.3c).

Indirect effects (and synergistic interactions) may also be evident through the consumption of macrophytes (Figure 7.3a) which may alter community composition of invertebrates via reductions in habitat and resources (Feminella and Resh 1998; Nyström et al., 2001; Usio et al., 2006). The removal of macrophyte cover is however associated with multiple feedback loops. Macrophytes are key elements of roughness in lowland rivers and often influence flow behaviour (Marjoribanks et al., 2017). Alterations to macrophyte species and thus near bed hydraulics through selective consumption (Nyström and Strand, 1996) may affect invertebrate populations via flow trait preferences (Dolédec et al., 2015), but may also create a mosaic of depositional and erosional areas. These small scale variations in flow dynamics will determine the distribution of sediment (Rovira et al., 2016) and therefore the diversity of mesohabitats which are essential in regulating macroinvertebrate diversity (Armitage and Cannon, 2000).

The discussion above does not provide an exhaustive summary of the direct and indirect mechanisms in which crayfish could alter macroinvertebrate communities but highlights the complex and dynamic nature of biological invasion impacts. Disentangling and identifying the potential impacts (direct and indirect) of non-native crayfish on lotic ecosystems remains a key challenge in order to fully comprehend the implications and severity of impacts facing ecosystem health and functioning. Crayfish represent keystone species of aquatic ecosystems, interacting with all trophic levels of the food web (Creed, 1994; Momot, 1995). There is therefore a need for further multi-scale research (temporal and spatial) in order to fully understand the dynamic nature of crayfish invasions in aquatic ecosystems which are not able to be captured in mesocosm studies (Wilson et al., 2004; McCarthy et al., 2006).

7.4 Future research directions and considerations

This thesis provides one of the first studies to address the dynamic and complex interactions that invasive taxa have for the receiving ecosystem within a multidisciplinary framework. This thesis has contributed to the growing literature of both the ecological and physical implications that invasive taxa have once established within aquatic ecosystems. The work contributes to our understanding of how these processes operate on differing spatial and temporal scales and has highlighted the key role that both biotic and abiotic processes play in driving the effects. The following section provides a number of key considerations for future research.

- This study has highlighted the need for zoogeomorphic and biological invasion research to be conducted on relevant environmental scales. Further work should investigate these processes over longer time scales (multiple years) and at multiple spatial scales and sites in order to fully establish the extent of impacts which are typically observed in mechanistic studies.
- Greater integration of ecological and geomorphological theories is needed particularly in association with invasive species (Fei et al., 2014). Despite a number of calls for multidisciplinary work, the number of studies which conduct work considering theories and concepts from both disciplines remains rare. This thesis has demonstrated that biotic and abiotic processes are intimately linked and should be examined as such.

- A greater awareness of the taxonomic resolution that studies are conducted at is required. The reported effect of biological invasions is likely to be significantly influenced by highly dynamic and variable life history traits and characteristics (Hewitt et al., 2016). These can differ extensively at the family level which is often the reported taxonomic resolution that biological effects are evaluated to.
- This study is one of the first considering the effect of invasive taxa for biomonitoring tools (but see Macneil et al., 2013a). Further work is therefore required on a range of invasive taxa and future studies should examine the effects of biological invasions for biomonitoring techniques in association with the potential ecosystem engineering changes that may be taking place (i.e. enhanced fine sediment availability).

7.5 Concluding remarks

Invasive species represent a significant global threat to ecosystem functioning. This thesis has investigated the implications of a non-native crayfish species, *Pacifastacus leniusculus,* for biotic and abiotic processes in lowland rivers within England. A holistic approach was employed utilizing techniques from ecology, geomorphology and hydrology at the micro, meso and macro-scale. The study has demonstrated the significant threat that signal crayfish pose for lotic ecosystems, with considerable implications for the organisms inhabiting them and the physical processes which operate and maintain healthy ecosystem functioning. In addition, the results have highlighted the need for greater understanding of the interconnected nature of these dynamic processes in order to further enhance our understanding within the fields of zoogeomorphology and invasion biology.

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