Ecosystem engineering impacts of invasive species on river banks: signal crayfish and Himalayan balsam

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Abstract

This thesis investigates the impact of two invasive ecosystem engineers on the river banks. Invasive species generate significant global environmental and economic costs and represent a particularly potent threat to freshwater ecosystems. Ecosystem engineers are organisms that modify their physical habitat. Therefore this thesis will explore the interaction of these two types of species and their impacts on the example of the impact of signal crayfish and Himalayan balsam on river banks. The work included analyses and development of conceptual models for the understanding of invasive ecosystem engineers, followed by four research chapters aimed at answering specific questions.

A study of signal crayfish impact is primarily focused on the impact of burrows that crayfish dig as shelter and their influence on riverbank erosion. The interaction between habitat characteristics, the occurrence of burrows and erosion is analysed on three different levels of spatial scale: bank section in reach, reach in the catchment and bank section in the catchment.

Bank section in reach survey (Chapter 4) focused on a reach heavily impacted by crayfish burrowing on the River Windrush, UK, in order to study the maximum effect of burrowing. Also, smaller spatial extent enabled detailed study of three sets of variables as well as an assessment of the impact that signal crayfish population density has on burrowing. Reach in catchment spatial scale expanded the survey to cover 103 river reaches in the Thames catchment and was based on a combination of habitat information from publicly available online data sets, primarily the River Habitat Survey database and rapid field surveys that recorded burrows and erosion. Bank section in catchment-scale was based on the same 103 sites, but the main focus of field observations were ten metres long bank sections for which habitat, burrows and erosion information were collected. Overall, burrowed banks were more likely to be characterised by cohesive bank material, steeper bank profiles with large areas of bare bank face, often on outer bend locations and were associated with bank profiles with signs of erosion. There were indications that signal crayfish burrowing is contributing to the river bank erosion, but no conclusive results have been made.

Study of the impact of the Himalayan balsam was undertaken on eight sites at the River Brenta in Italy and it was focused on three main aspects. Firstly it was established that extent of Himalayan balsam domination over native vegetation varies widely depending on the habitat conditions and native plants encountered. Secondly, it was established that there are no conclusive differences in the extent of erosion and deposition on transects covered by native vegetation and Himalayan balsam. Thirdly, measurement of traits of individual plants showed significant differences in traits of individual plants that are known to have consequences for river bank erosion and deposition.

The obtained results indicate that there are few avenues through which invasive ecosystem engineers can influence river bank processes. While many uncertainties remain, due to the intrinsic complexity of river ecosystems, a multitude of anthropogenic stressors that they are increasingly subjected to and a wide array of ecosystem services that rivers provide to people, it is important to consider the role of invasive ecosystem engineers in river management practices.

Table of Contents

List of Figures

List of Tables

CHAPTER 1: Introduction

Rivers are complex ecosystems, facing a multitude of management challenges (Newson, 2002; Macleod et al. 2007), understanding of which requires an interdisciplinary approach across fluvial geomorphology, stream ecology and hydraulic engineering (Rice et al. 2010). The complexity of river systems is evident in many aspects - from the concept of habitat (Clifford et al. 2006), the interaction between different hierarchical levels of organisation (Parsons and Thoms, 2007) to the contrasting perspectives revealed by qualitative and quantitative models (Carbonneau et al. 2012). In addition, all those interactions interplay over different spatial and temporal scales (Schumm and Lichty 1965; Frissell et al. 1986; Thorp et al. 2006).

Therefore, rivers are complex ecosystems and from that complexity stems their importance for society at large (Costanza et al. 1997; Helfenstein and Kienast, 2014). The importance of river systems is based on the direct value provided by ecosystem services (Gilvear et al. 2013; Palmer, 2013) and from the intrinsic value of ecosystems (Cafaro and Sandler, 2007). However, this complex and valuable system is under multiple threats, ranging from water quality issues (Krueger et al. 2007), biodiversity loss (Ward, 1998), river bank engineering (Surian and Rinaldi, 2003) and climate change (Johnson et al. 2009; Harries and Penning-Rowsell, 2011). However, the special case that will be the focus of this thesis are invasive species (Pejchar and Mooney, 2009).

Out of above-presented threats, invasive species will be the special focus of this thesis. Invasive, species are recognised as a second most important factor causing biodiversity loss (Sala et al. 2000) and also cause of significant economic loss (Pimentel et al. 2001). Their negative impact on ecosystems occurs through multiple mechanisms (Ehrenfeld, 2010), out of which direct competition and predation in relation with native species are the most significant (Vitousek, 1990; Lodge, 1993; Thomsen et al. 2011). However, the special case of invasive species and further focus of this study are invasive ecosystem engineers.

The term "ecosystem engineer" was coined to include all organisms that influence their habitats (Jones et al. 1994). For a long time, it was assumed that the biological component of rivers is relatively passive and acting in response to hydrogeomorphological processes (Corenblit et al. 2007). That perspective changed with an increasing recognition of the role of vegetation (Gurnell, 2014) as well as animals (Butler and Sawyer, 2012). Therefore, one of the key issues and the main topic of this thesis is the interaction between the physical and biological components of rivers ecosystems.

The two key terms introduced above, ecosystem engineers and invasive species were individually subjected to intensive studies, but with the exception of few key studies (Cuddington and Hastings, 2004; Gonzalez et al. 2008) their interaction mainly remained understudied. This thesis will explore the traits of invasive ecosystem engineers on the river banks. In order to focus the study, two case studies are analysed, an invasive animal and plant that are known for their ecosystem engineering traits: signal crayfish (*Pacifastacus leniusculus*) and Himalayan balsam (*Impatiens glandulifera*). Signal crayfish is the most widespread invasive species of crayfish in the United Kingdom and its ecosystem engineering nature is reflected in digging burrows in the river banks (Holdich et al. 2002). Himalayan balsam is an invasive plant that is widely spread in both, continental Europe and British Isles (Beerling and Perrins, 1993). Its ecosystem engineering aspect is manifested in observations that due to its morphology, it does not provide protection to the soil from erosion like native vegetation (Dawson and Holland, 1999). Therefore, the focus of this study is to assess ecosystem engineering aspects of these two invasive species on river banks.

One of the main challenges in this thesis was to address the differences in impacts done by two case study species, while simultaneously providing an overarching framework for addressing their impact as invasive ecosystem engineers. This difference was based primarily with the current state of knowledge of ecosystem engineering by plants and animals as well as the difference in invasive status of two species. Therefore in order to organise the thesis, firstly a shared part is presented in the literature review and research design and followed by four main results chapters. Finally, the overview of findings and implications are discussed in the conclusion chapter. The more detailed overview of chapters is given below.

Literature review (Chapter 2) gives a basic overview of the important concepts on which this thesis is based. It starts by introducing the concept of morphological activity, a term used for the joint effect of erosion and deposition and further expands on the main types of processes. Further, basic principles of studying ecosystem engineers and invasive species are given and they served as a basis for developing a main framework of the thesis. A conceptual framework for the study of invasive ecosystem engineers was developed and specifics of two species interpreted in it. This enabled a good identification of key questions that required answering for both studied species.

While literature review identified key questions required answering, research design (Chapter 3) elaborated on practical aspects of these questions. This primarily dealt with choice of research sites and aspects of the methodology used in all chapters. For signal crayfish that primarily meant the discussion of spatial scale and implications it has on survey methodology. For Himalayan balsam, research design covered shared aspects of the methodology. Therefore, chapter three established a bridge between research questions as they were identified at the end of literature review and practical aspects that were required for answering them. In research design chapter, research questions as identified at the end of literature review were modified to include practical aspects and linked with main research chapters aimed at answering them.

The signal crayfish analysis is covered by three chapters (Chapter 4, 5 and 6). While all three chapters answer the same question about the interaction between habitat characteristics, the presence of burrows and erosion they address those questions on a different spatial scale. In line with that, different factors are assessed. The broad topic of the chapters five and six is published as Faller et al. (2016).

Therefore, Chapter 4, explored the signal crayfish by analysing it on the level of one reach. This enabled the study of crayfish population density and detailed observations of burrows presence and erosion. Additionally, it enabled a link between above and below water line burrowing which was the basis for observation in the following two crayfish chapters. Chapter 5, covered 103 sites at seven tributaries of the Thames catchment. In doing so, it combined the existing publicly available data and field surveys. As such it gave insight into the extent of signal crayfish burrowing as well as habitat traits leading to burrowing on that scale. Information about a number of burrows that can be expected also enabled assessments of the volume of sediment excavated. Chapter 6 explored the same reaches as Chapter 5, but analyses them on the level of bank sections. This increase in analysis resolution enabled better assessment of links between habitat, burrows and erosion.

Chapter 7 explores multiple impacts that Himalayan balsam has on native vegetation and processes on the riverbanks. It starts by assessing habitat preferences and abundance of Himalayan balsam in comparison with native vegetation. This is followed by analysis of the difference in morphological activity on transects with native vegetation and Himalayan balsam. Thirdly, the difference in characteristics of individual plants between two vegetation types was assessed.

Finally, Chapter 8 summarises results presented in chapters 4, 5, 6 and 7. On the basis of those results, recommendations for improvements to methodology in future work is given. Additionally, implications of outcomes for the habitat conservation and river system management are presented. Finally, recommendations for future research are given.

CHAPTER 2: Literature review

2.1 Introduction

This chapter reviews the current literature relevant to the study of ecosystem engineering impacts of signal crayfish and Himalayan balsam on river banks. Overall, this section deals with interaction of three principal themes: physical processes of erosion and deposition on the river banks; interactions between those physical processes and a biological component which are encompassed by the term ecosystem engineers and finally, a special case of invasive species which deals with explores a specific type of interactions that occur between invasive and native species. While these three components influence each other, for the sake of simplicity, the relevant knowledge will be presented in linear order, before integrating them into a conceptual model that will be applied to two case study species. Firstly, an overview of the physical factors influencing river banks is given in order to provide a general context for this thesis. Secondly, the role of ecosystem engineers in general and animals and plants in specific is examined. Thirdly, invasive species as a special group with specific impacts on biological communities will be discussed. Fourthly, a basic background on the ecology of two species will be given. Finally, a conceptual model for the study of the invasive ecosystem engineers will be developed and within it, knowledge gaps and research questions will be formulated for signal crayfish and Himalayan balsam.

2.2 Morphological activity on the river bank morphology and analysis of factors that influence it

Morphological activity, a joint term that incorporates interaction of erosion and deposition (Hjulström, 1935; Henshaw et al. 2012), is one of the key natural geomorphic processes which shapes river banks. The main factors that decide whether a specific particle in the water column will be eroded or deposited are the size of particle and water velocity. That relationship was first recognized by Hjulström (1935) and later adapted in the form of Hjulström curves which demarcate conditions under which sediment particles are being eroded, transported or deposited. An additional factor in erosion are the cohesive forces between very small particles which provide a binding force and are therefore harder to erode than particles of middle size. Due to this effect, most studies of erosion distinguish between cohesive and non-cohesive sediment (Thorne, 1982). What is important to establish, is that erosion and deposition are coupled processes since all sediment on river banks was once deposited, and the majority of eroded sediment in rivers will be deposited in the same river channel. Therefore throughout this thesis, a term morphological activity will be used as a term that encompasses erosion and deposition.

Morphological activity is one of the key factors affecting dynamic geomorphological features on river banks. River banks are dynamic geomorphological features that represent the interface between aquatic and terrestrial environments (Florsheim et al. 2008). Their shape and position evolve in response to a diverse range of physical processes and this morphological activity can have important ecological and socio-economic consequences. For example, the lateral migration of meandering rivers across their floodplains through bank erosion has been identified as a major cause of disturbance in forest ecosystems with significant implications for local biodiversity (Salo et al. 1986). Likewise, bank erosion poses a threat to flood defences and floodplain infrastructure through its capacity to undermine structures and change the spatial distribution of overbank flows (Plate, 2002). Additionally, river bank erosion can have effects that extend beyond the immediate location of its occurrence (Collins and Anthony, 2008). While sedimentation is a part of natural river functioning increase in fine sediment can have multiple negative impacts on river ecosystem (Bull 1997; Wood and Armitage, 1997). These consequences include reduced light penetration through the water column which interferes with photosynthesis (Köhler et al. 2010), increased mobilisation of pollutants (Krueger et al. 2007) and interference with gills of aquatic animals (Rosewarne et al. 2014).

Previous examples demonstrate the myriad pathways by which change in erosion and deposition can cause an impact on river ecosystems. Therefore morphological activity is a crucial component of the river system. Before proceeding further to examine the contribution of living organisms to those processes, a short overview of four main physical components of morphological activity will be given. The processes which govern the erosion of river banks can be divided into three main types: subaerial, fluvial and mass failure (Thorne, 1982) and in addition to those, the deposition will be also explained. Those four components of morphological activity will be discussed in the following sections.

2.2.1 Subaerial processes

Bank weakening and weathering are considered to be preparatory processes, ones that make the soil more susceptible to erosion by other means. Subaerial processes are a heterogenic group of activities whose main trait is that they are not primarily influenced by characteristics of river flow (Thorne, 1982), but a wide range of other factors. They act either within the bank, effectively reducing its strength or on the surface of the banks, therefore increasing soil erodibility (Lawler et al. 1997; Grabowski et al. 2011). An additional type of subaerial processes is precipitation, which directly causes erosion and depends primarily on the nature and frequency of rain (Hooke, 1979). These three main types of impacts will be addressed below.

The strength of the river bank is primarily impacted by pore water pressure (Simon et al. 2000). Positive pore water pressure, a condition that occurs during saturated conditions, leads to a reduction of the bank strength. Therefore any circumstance that leads to wet conditions like poor drainage, heavy precipitation, snowmelt or sudden drawdown of the river stage, leads to a reduction of the bank strength and higher likelihood of mass bank failure (Thorne, 1982; Lawler et al. 1997).

In addition to this, Grabowski et al. (2011) gave a lengthy overview of physical, geochemical and biological factors that influence soil erodibility. However, Thorne (1982) identified desiccation and freeze-thaw cycles (Thorne, 1982) as major factors that can lead to an increase in soil erodibility. Desiccation on its own can either increase (Couper, 2003) or decrease erodibility (Hooke, 1979). On the other hand, freeze-thaw cycles lead to increases in erodibility, due to the formation of cracks that happen due to of differences in volume of water between liquid and solid state (Lehrsch, 1998). The impact of these cycles depends on the type of particles interlocking and their size (Lawler et al. 1997) and especially on soil parameters like clay content (Couper, 2003).

The most significant form of precipitation, rain, causes dislodgement of individual particles by kinetic energy upon impact. Therefore it is primarily intensity of rain drops as well as the slope of the surface that are defining the impact (Battany and Grismer, 2000). In the case of intense rain, when infiltration rates cannot infuse all the water, rilling and gulling occurs and with them extra erosion effects (Castillo and Gomez, 2016).

2.2.2 Fluvial entrainment

Fluvial entrainment is defined as a detachment of sediment particles or aggregates from the bank surface by water (Thorne, 1982; Lawler et al. 1997). Therefore entrainment of an individual particle happens when disturbing forces, generated by shear stress by flow, overpower restoring forces of gravity and inertia (Thorne, 1982). These two processes interact differently in cases of cohesive and non-cohesive material and therefore the factors influencing them will be analysed separately.

In the case of non-cohesive material, main disturbing force is shear stress. Shear stress is impacted by the velocity of water and extent of the surface of the grain on which the force of water acts. Since calculating the velocity of water near individual particles is often not directly possible, proxy variables like mean water velocity (Lawler et al. 1997) or slope (Parker et al. 2011) are used as an approximation. Main restoring force is gravity, which depends on the weight of the grain and presence of reinforcement like interlocking of the grains. Therefore it can be concluded that in the case of non-cohesive material, that erosion depends on the relationship between water velocity and the characteristics of individual grains.

In the case of cohesive materials, in addition to the forces described above, cohesive forces, based on the chemical interactions between particles, contribute greatly to the strength of the soil (Thorne, 1982). While the same forces exist in non-cohesive soils too, only in cohesive soils, which have smaller particles and therefore bigger active surface per unit of volume and mass do these forces achieve significance. The existence of those binding forces is twofold. Firstly on every scale, particles are connected and therefore resist disturbing force much more strongly than can be attributed to gravity only. Secondly, cohesive soils form aggregates of smaller particles which since they are bigger in size and also less dense than respective non-cohesive sediment, start to act like non-cohesive sediment. Therefore, fluvial entrainment is mainly influenced by the size of particles and nature of chemical interactions (Grabowski et al. 2011; Parker et al. 2011).

2.2.3 Mass failure

Mass bank failure refers to situations when blocks of bank material, much bigger than individual particles that make it, slide or fall toward the toe of the bank (Thorne, 1982; Lawler et al. 1997). This happens when driving (gravitational) forces acting on the bank overcome the resisting forces of the bank material (Simon et al. 2000). The driving forces leading to a failure are a function of the weight of the block of soil and the bank angle, while resisting forces or the shear strength of soil are mainly influenced by the cohesion of the soil and the pore water pressure. In the case of non-cohesive (sand, gravel) banks, due to the low cohesion of the material, mass failure happens only on a small scale and occur as shallow slips. However, banks dominated by cohesive material (clay, silt), due to the bonding of individual particles resist the gravitational forces until they finally collapse in relatively big chunks of material. Because of that, mass failure as a process is much more important for the banks made of cohesive material. The environmental conditions that influence main factors determining bank stability will be examined.

Mass bank failure in the cohesive sediment river banks depends on a variety of factors, primarily bank geometry and properties of bank material like the type of sediment particles (Pollen-Bankhead et al. 2009; Davies and Harden, 2012). Except for the sediment material which can be considered uniform within certain reach of the river, the main factors are bank angle and overall bank geometry. Bank geometry as a factor is relevant to the notion of a factor of safety, namely relationship between the actual angle of the river bank and angle that leads to bank failure. The models for such an idealised river banks are developed and can predict the likelihood of bank failure for specific conditions (Simon et al. 2000).

2.2.4 Sediment deposition

Sediment deposition occurs when lift forces acting on the individual particle are weaker than gravitational forces and this interaction depends mainly on the size of the particle and water velocity (Thorne, 1982). Since particles are dissolved in water, cohesive interactions between them are not impacting sedimentation processes. Therefore once sediment is eroded, it remains transported by the water flow until water velocity drops to a critical level and as a result, the particle is deposited (Othman et al. 2003). This effect has important implications for fluvial forms in the longitudinal direction and at cross-sectional of the river channel. Longitudinally, it results in a downstream gradient of decreasing sediment size or downstream fining (Menting et al. 2015) which has multiple impacts on physical and biological processes in rivers. In the symmetrical cross-sectional area of the river, the highest velocity is in the middle of the river and is reduced toward the edges, while in meanders the inner bend of channel demonstrates low water velocity while the outer a faster one (Thorne et al. 1985; Harvey and Clifford, 2009). Therefore the prevailing trend is that in the middle of the symmetrical channel and the outer bend of the meander bigger sediment particles prevail, while toward the edges and in the inner bend of meander are dominated by smaller sediment.

2.2.5 Spatial scale in geomorphology

The spatial scale is often conceptualised through the spatially nested hierarchical model in which an element of the higher order consists of multiple elements of lower order (Frissell et al. 1986; Charlton, 2008). One typical example is given by Brierley and Fryiers (2005), in which seven spatial levels are defined, from an ecoregion and catchment at the broadest spatial level, a reach at the middle level and a microhabitat at the most narrow level. While exact definitions of such levels vary between authors (Charlton, 2008; Brierley and Fryiers, 2005), all recognise the hierarchical order of different spatial scales. In order to study spatial scale, two contrasting approaches are used in geomorphology: one is an extensive method which uses a large number of samples and other is an intensive method that is focused on a small number of case studies (Richards, 1996). While both approaches have their merits, a study of the same process on a different spatial scale involves a change of methodology and often requires inputs from different disciplines (Rice et al. 2010).

2.2.6 Factors to consider in study of morphological activity

All three presented morphological activity processes occur in rivers all the time, however, their relative importance varies according to a number of factors. Abernethy and Rutherfurd (1998) found that subaerial processes, fluvial entrainment and mass failure erosion dominate upstream, midstream and downstream sections of the river respectively. However, Henshaw et al. (2012) found that fluvial processes dominate the upstream section of the small catchment and therefore it can be argued that due to multiple factors influencing each erosion process, predictions of the influence of specific processes are dominated by uncertainty.

Previous work outlined physical factors that influence erosion processes. However, since the early days in the study of erosion (Hickin, 1984), the role of vegetation in the protection of soil from erosion was recognised (Thorne, 1982). Therefore the idea that living organisms can significantly impact physical processes has led to the introduction of the concept of biogeomorphology (Viles 1988).

2.3 Ecosystem engineers in river processes, animals and plants

The notion that living organisms influence physical environment appeared early, most notably in the work of Darwin (1881) who explored the impact of earth worms on the soil. However, the first systematic overview of interactions between living organisms and physical world was given a century later by Viles (1988) who introduced the term biogeomorphology. Despite this, the influence of living organisms on physical processes remained understudied phenomenon (Wright, 2006).

The lack of systematic study of interactions between living organisms and physical environment has its root in the dual nature of these interactions. Butler and Sawyer (2012) recognised that each of those interactions can be studied from two perspectives and consequently is covered by two disciplines, ecology and geomorphology. That dualism was also represented in terminology used for the otherwise same topic. Geomorphologists used the terms biogeomorphology to describe changes in the physical environment caused by the influence of living organisms (Viles, 1988), while ecologists used the term ecosystem engineers to describe activities of living organisms that had an impact on the physical environment (Jones et al. 1994). For the purpose of this study the term “ecosystem engineer” will be used throughout the text and the meaning is that of an organism that modifies its physical environment.

Today the concept of ecosystem engineers is well recognised and their specific effects are even considered for use in ecosystem restoration (Bryers et al. 2006). By now, different aspects and principles related to ecosystem engineers are studied, including: work on classification of included processes (Naylor et al. 2002), mutual dependency of processes (Stallins, 2006), key current challenges (Wright and Jones, 2006), feedback mechanisms (Corenblit et al. 2011), hierarchy of processes (Parsons and Thoms, 2007) and impact of population density (Jones, 2012). In all mentioned processes, the impact of engineers is the result of the interaction of two key traits: characteristics of an individual organism and their density. Despite this increased knowledge, there remains a major divide in the field, not between disciplines, but between organisms groups, namely animals and plants.

In the case of studies of morphological activity on the river banks, there is a noticeable difference in understanding of the roles played by different groups of organisms. While the role of microorganisms is recognised as important (Viles, 2012), in river systems there is a visible difference in the study of impacts caused by animals and plants. The role of plants is well recognised and is part of every significant book on erosion processes (Thorne, 1982), while the role of animals is mainly restricted to the limited inclusion of impacts done by individual high profile species like salmon (DeVries, 2012). Current understanding of ecosystem engineering concepts relevant for the study of two case study species will be given in the further text.

2.3.1 Animals as ecosystem engineers in river systems

The role of animals is recognised in studies of river bank erosion, primarily through their influence on sediment erodibility (Le Hir, 2007; Grabowski et al. 2011). Statzner (2012) provides an excellent review of the ecosystem engineering role and intensity of caused effects for dozens of individual species. Depending on their interaction with sediment, animals are classified as either bioturbators or bioconsolidators and on the basis of that contribute to either increase in or a reduction of erosion. While bioconsolidation can achieve significant impacts on sediment transport (Botto and Iribarne, 2000), it can be argued that in the case of animals, bioturbation is a much more dominant process. In that light, animal activity in contribution to erosion through bioturbation can be attributed to two main processes: movement and creation of specific structures.

The basic process of movement causes disturbance of surface particles and therefore contributes to erosion. Almost all animals are involved in this process with detailed studies covering impacts of stoneflies (Zanetell and Peckarsky, 1996), shrimps (Pringle et al. 1993), crayfish (Statzner and Peltret, 2006; Johnson et al. 2010), invertebrates in general (Fernandes et al. 2009), salmon (DeVries, 2012), comparison of crayfish and fish (Statzner and Sagnes, 2008) and signal crayfish (Harvey et al. 2014). The overall conclusion from these studies is that impact of animals is in direct proportion to their weight and movement activity. The second main process is linked to the creation of specific structures which cause a change in physical environment. For instance, beaver dams have a significant impact on the flow of rivers and act as sediment traps (Butler and Malanson, 2005), while caddisflies bring together sand particles into aggregates and therefore increase the effective size of sediment (Statzner and Dolédec, 2011). In this study, the focus is on crayfish burrows and therefore a brief overview of the general state of knowledge regarding animal burrows and their impact on erosion will be given.

Impact of burrows on physical processes in rivers is mainly focused on two aspects: influence on the flow of water and an indirect impact this produces (Ridd, 1996; Ziebis et al. 1996; Xin et al. 2009) and studies that directly measure erosion (Onda and Itakura, 1997; Needham et al. 2013).

However, none of these studies gave a clear assessment of the contribution of burrowing to the standard erosion processes at the respective study sites. Also, a Chinese mitten crab has attracted a lot of attention exactly because of its burrowing activity (Rudnick et al. 2003; Rudnick et al. 2005), however even in that case, there is a lack of quantitative studies covering the influence of burrows and erosion.

In addition to the lack of specific studies on burrowing, it is important to note that standard bank stability models like BSTEM (Midgley et al. 2012) do not provide an option for input of burrow parameters like dimensions and density. Therefore in the design of a study of signal crayfish burrowing, there was no established framework to analyse interactions between burrows and morphological activity.

Signal crayfish burrowing has been studied on several occasions. One of the first studies, Guan (1994) identified the occurrence of burrows in the UK. It further provided basic information about dimensions, the density of burrows and association between burrows and cohesive sediment. Roberts (2012) expanded that study by undertaking a survey in the Thames catchment and provided information about burrow occurrence, habitat types favouring burrowing and potential implications for the erosion processes. Finally, Harvey et al. (2014) outlined a range of implications that signal crayfish burrowing can have on river bank erosion and sediment management in rivers. However, the extent of burrowing over a range of spatial scales and environmental factors leading to their occurrence remained unknown.

2.3.2 Plants as ecosystem engineers in river systems

The role of vegetation in shaping river processes is well established and it is known that plants influence processes as diverse as bank stability, sediment dynamics and flow velocity and that these processes in combination impact the overall erosion and deposition (Osterkamp and Hupp, 2010; Gurnell, 2014). In order to study the impact of vegetation on overall processes, influence on each erosion process will be reviewed.

Influence of vegetation on subaerial processes depends on the type of process in question. The soil strength, mainly influenced by pore water pressure (Simon and Collins, 2002) is impacted by vegetation due to its water suction activity. Vegetation continuously takes water from the environment, effectively reducing the pore water pressure and causing an increase in the soil strength (Zhu and Zhang, 2015). However the existence of shoots (above-ground part of the plant) has an important effect on the impact of rain. On one side it intercepts rain drops and therefore reduces their kinetic energy at the point of impact, which leads to protection of soil (Battany and Grismer, 2000; Burylo et al. 2011). However on the other side, especially in the case of the tree canopy, branches collect rain and lead to the creation of concentrated flow which can further cause direct erosion or increase pore water pressure and therefore weaken the soil (Pollen, 2007; Pollen-Bankhead and Simon, 2010; Briggs et al. 2016). Additionally, in dry conditions, vegetation has an impact on soil desiccation since it contributes to drying of soil via transpiration but also creates a protective cover that holds moisture following rain events. Another important impact of vegetation is the effect of temperature insulation and subsequent reduction in temperature extremes which leads to less weakening as a consequence of freeze-thaw cycles (Barnes et al. 2016).

Influence of vegetation on fluvial entrainment is mainly divided into two aspects namely impact on surface roughness by shoots and soil reinforcement by roots. Plant shoots increase surface roughness and this concentrates the flow toward the middle of river cross section. The result is the direction of flow to the centre of the channel and away from the river banks and reduction of water velocity near banks and soil – water interface (Thorne and Furbish, 1995; Stephan and Gutknecht, 2002; Cantalice et al. 2015). An additional effect of this process is the creation of drag force on the surface of plants. If that drag force exceeds anchoring strength of the roots it leads to uprooting and loss of protective vegetation cover (Bociag et al. 2009; Liffen et al. 2011; Schoelynck et al. 2013). The second main influence of vegetation on fluvial entrainment is the impact of fine roots on improving soil cohesion and therefore reduction of erodibility (De Baets and Poesen, 2010; Burylo et al. 2012). The main factor in this process is structure of roots and that is the main difference between monocotyledonous plants (mainly grasses and sedges) with their uniform network of fine roots and dicotyledonous (majority of herbaceous, ground level vegetation) plants which have a dominant root with separate branches (De Baets et al. 2006; Fattet et al. 2011).

Influence of vegetation on mass failure erosion is primarily considered through reinforcing acts of roots (Greenway 1987). While soil is weak in resistance to a tension force, roots are strong and therefore reinforce the soil (Thorne, 1990; Pollen, 2007). The main factor in that is the root tensile strength which is primarily influenced by plant species and root diameter (Zhang et al. 2014). The presence of roots reinforces the soil and resists mass failure until roots are either pulled out or broken. Model of roots breakage by Wu et al. (1979) assumed that all roots break at the same moment and that was later improved by application of more realistic model based on the gradual breakage of roots (Gray and Barker, 2004; Tosi 2007; Pollen-Bankhead et al. 2009). Therefore it can be concluded that the impact of vegetation on erosion and deposition processes is extremely complex as it is influenced by multiple aspects of both the physical environment and vegetation. Therefore invasion of Himalayan balsam can influence morphological activity through multiple avenues.

Morphology, lifecycle and growth of Himalayan balsam differ in a few key characteristics from the dominant native vegetation in Europe and (Beerling and Perrins, 1993; Ennos et al. 1993; Dawson and Holland 1999; Hejda and Pyšek, 2006). These differences primarily focus on Himalayan balsam relatively shallow and weak roots, tall and dominant shoot (above-ground part of the plant), high shoot to root ratio and weak resistance to uprooting. In addition to points raised above, a peculiar feature of the Himalayan balsam, described by Dawson and Holland (1999), is a winter die back. It refers to death and disappearance of the Himalayan balsam which dies in the autumn, leaving the soil exposed to winter runoff and rain (Dawson and Holland, 1999) and the consequential lack of protective vegetation cover leaves the soil more prone to erosion. Therefore it is hypothesised that due to differences in morphology and life cycle, in comparison to native vegetation, Himalayan balsam has a different role in the protection of soil from erosion (Dawson and Holland 1999), however, these have to date never been tested.

2.3.3 Factors to consider in study of ecosystem engineers

Interactions between ecosystem engineers and physical environment can be extremely complex. One of the best examples is the impact of large predators on riverine communities described by Beschta and Ripple (2012). The reintroduction of wolves into Yellowstone National Park has resulted in a change in the behaviour of elk, which have altered their habitat preference from open grassland to forest. This has led to a recovery of previously overgrazed riparian vegetation. Regrowth of vegetation had multiple impacts on bank stability, shading and biotic communities in local streams and rivers.

Despite these complexities, there are some general trends in the study of animal and plant ecosystem engineers. It can be argued that impacts of animals are much more specific and therefore certain effects are only present if the respective engineer is present. For instance, beaver dams are a very specific structure and replacement of beavers by an animal that occupies a similar ecological niche (for example coypu) will not have similar effects on physical processes. Contrary to that, despite all the stated differences, most vegetation types within a few basic morphotypes (trees, shrubs, grasses, herbs) have a relatively similar impact. Therefore it could be argued that the study of ecosystem engineering impact of animals is a study between the situation in which animal is present and absent, while the study of the impact of plants is more a study of comparison between different plant species. However, before proceeding further, the concept of invasive species and implications to the topic have to be discussed.

2.4 Invasive species

Invasive species are known to have a detrimental impact on biological and physical aspects of the ecosystem (Vitousek et al. 1996). While alien species refer to all living organisms that are not native in a specific area, invasive species are characterised by their significant, negative impact on other species either through competition, predation or other specific actions (Thomsen et al. 2011). Therefore each invasive species is defined by its place of origin, the new area which it has invaded and the impact it has on native communities (Bennett et al. 2012). However, for the overall conceptualisation of the research performed on two case study species, it is important to discuss two concepts: ecological niche and phase of the invasion.

2.4.1 Concept of ecological niche

The ecological niche can best be described as a role of a species in an ecosystem (Begon et al. 2005). Due to inherent heterogeneity of habitats, each species adjusts to a specific set of ecological (biotic and abiotic) parameters to which it is better adjusted than other species (Jackson et al. 2014). An example of ecological niche can be defined in trophic terms or a set of environmental conditions to which plants are best suited to grow (Willis and Hulme, 2002; Barbaresi et al. 2007). The important implication is that if niches of two species overlap, species compete for the same resources and usually one species is more dominant within specific conditions. This concept has different implications for research of two case studies species as it will be illustrated below.

Signal crayfish fills a trophic niche of a large invertebrate omnivore (Almeida et al. 2012). That niche used to be occupied by the native white clawed crayfish (*Austropotamobius torrentium*), however since signal crayfish is bigger, more resistant to diseases and more aggressive, it has completely outcompeted native white clawed crayfish in the majority of water systems in the UK (Holdich et al. 1999). Therefore, due to the disappearance of white clawed crayfish from river systems in the UK, the signal crayfish has achieved almost complete dominance in its niche and competition with a native species is not a relevant factor.

Himalayan balsam together with many other plant species (Hejda and Pysek 2006), fills an ecological niche of riparian vegetation. Each of those plant species is more competitive in a narrow range of environmental conditions (shade, soil moisture, flooding regime) but due to the intrinsic heterogeneity of the river banks, vegetation cover is a mix of different plant species (Schmitz and Dericks 2010). Only in extreme conditions, in the case of uniform environment that favours one plant species will a significant dominance occur. Therefore, Himalayan balsam, while dominant species on some microhabitats, usually does not completely replace native vegetation and achieves only partial dominance.

2.4.2 Phase of invasion concept

The phase of invasion is a concept linked to time considerations related to invasive species

(Václavik and Meentemeyer, 2012). When invasive species first arrives to a new geographic area, it spreads from that initial point to the surrounding areas. Exact time and place are either well known or approximated. From that point of initial invasion, invasive organism spreads to surrounding areas where it can successfully compete and reproduce. This expansion continues as long as invasive species is in contact with good quality habitat. Therefore two types of areal are defined for each invasive species. Realised areal is the area in which invasive species is present, while potential areal is an area that has required ecological conditions for the success of invader, but invader has not yet reached it (Bennett et al. 2012). In this aspect two studied species are different.

Signal crayfish was introduced to the UK for the purpose of aquaculture around 1976 and has since spread rapidly. Therefore its current areal is similar to its potential areal (Souty-Grosset et al. 2006). Due to sufficient time since invasion, knowledge about average migration rates (Bubb et al. 2004), overall connectivity of freshwaters in UK due to the canal system and information on the signal crayfish actual distribution (National Biodiversity Gateway, 2016) it can be argued that signal crayfish has spread to the majority of suitable habitats in the UK (Holdich, 1999).

Himalayan balsam was introduced around 19th century to Europe, mainly for the purpose of horticulture. Despite longer time since the invasion and probably because of a stronger competition from the native vegetation, Himalayan balsam spread is slower (Pyšek and Prach, 1995). While Himalayan balsam is also spread through Europe, it has not occupied all the microhabitats on which it is more competitive and therefore it is probably still in the phase of expansion (Malíkova and Prach 2010).

2.4.3 Factors to consider in study of invasive species

As presented above, two invasive species are quite different in their traits as invaders. Signal crayfish has completely outcompeted and replaced native species and therefore the study will focus only on signal crayfish. Since it has achieved its potential areal, any impacts are likely not going to increase in future. On the other hand, Himalayan balsam coexists with other plant species and therefore the study will focus primarily on a comparison between native vegetation and Himalayan balsam. However, due to expanding areal, any impacts are likely to be more pronounced in future. Those differences have to be considered when designing the survey and interpreting the results. Before proceeding to the specific challenges of studying invasive ecosystem engineers, ecology and biology of two species will be shortly presented.

2.5 Physical habitat preferences and ecology of signal crayfish

Physical habitat, as defined by Maddock (1999), is a spatially and temporally dynamic environment that represents the living space of animals in river systems, defined by the interaction between structural features and hydrological regime. In case of signal crayfish, physical habitat preferences depend on the spatial scale. In river catchments, signal crayfish are present from upstream sections (starting from few kilometres from the source), followed by continuous presence throughout the whole length of the river and are usually absent from the downstream sections (Souty-Grosset et al. 2006; NBN, 2016). This type of presence can be explained by the good adaptability of signal crayfish to lowland rivers in the UK (Almeida et al. 2013) and its good dispersal abilities (Bubb et al. 2004). Increased pollution is probably responsible for the absence of signal crayfish in most downstream sections of lowland rivers (Holdich, 2002). On the individual reach, signal crayfish demonstrate similar patterns of mesohabitat selection as most other crayfish species. This refers to generally continuous presence throughout the length of the reach, but with a high preference toward lentic areas dominated by deeper water and slower water flow (Hudina et al. 2009). At the microhabitat level, physical habitat preference of crayfish is dominated by the search for shelter (Alonso and Martinez, 2006). The shelter takes the form of large wood, roots of riparian trees, stones and burrows dug by crayfish themselves (Johnson et al. 2010) (Figure 2.1).

Figure 2.1 Signal crayfish in front of burrow, bank of the River Windrush, UK (9th October 2013).

Ecology of signal crayfish is primarily characterised by its tolerance to a wider range of environmental conditions in comparison to native crayfish species in Europe (Holdich, 2002). This is the case in terms of tolerance to water temperature, pH and various aspects of chemical pollution. In terms of oxygen demand, signal crayfish has relatively high demand and can suffer heavy mortality during summer months and be absent from lower sections of large rivers (Souty-Grosset et al. 2006). Signal crayfish is a chronic carrier of crayfish plague but is mainly resistant to its mortal effects due to long coexistence between crayfish and the parasite that is typical for all alien crayfish species in Europe (Longshaw, 2011).

The position of signal crayfish in trophic web of the river ecosystem is primarily characterised by a “direct link” that a signal crayfish provides between organic matter it eats and high-level predators that pray upon it (Guan and Wiles, 1998; Jackson et al. 2014). Signal crayfish is an opportunistic feeder that feeds on most types of organic material available (Holdich, 2002). Still, it is found that crayfish diet shifts with age (Peay et al. 2009; Ahvenharju and Ruohonen, 2006). Young specimens predominantly feed on aquatic insects, but as they age there is a strong increase in plant material. Therefore adults consumed mainly dead leaves of riparian trees, macrophytes and periphyton, which is similar to other aquatic invertebrates like insect larvae. What is specific with crayfish, is that due to their size they are consumed by top predators in the river, like predatory fish (pike, perch, trout, catfish), otters and birds (heron) (Souty-Grosset et al. 2006). However, predation on crayfish is also dependant on the size of crayfish in relation to a predator.

Another important aspect of signal crayfish ecology, especially when taking into account focus of this thesis on invasive species is its interaction with native, white clawed crayfish (*Austropotamobius pallipes*). Signal crayfish occupies roughly the same ecological niche as native species but it is much more competitive and it has caused the almost complete disappearance of the native species (Holdich, 1999). That competitiveness is primarily based on larger size and broader tolerance of adverse environmental conditions. Additionally, signal crayfish is also a carrier of crayfish plague, a viral disease to which it is resistant, but which is fatal for the native species (Longshaw, 2011). Combination of these factors mean that presence of signal crayfish means the disappearance of the native one. Only water bodies that were physically separated from the main river networks remained a safe habitat for the native species and special effort is placed to preserve them that way through the Ark sites project (Whitehouse et al. 2009).

2.6 Physical habitat preferences and ecology of Himalayan balsam

Physical habitat preferences of Himalayan balsam are primarily influenced by its origin as a riparian species in its native habitat (Beerling and Perrins, 1993) (Figure 2.2). While it was introduced to UK and Europe as a horticultural species, after it escaped to the wild, it spread mainly along the river banks (Pyšek and Prach, 1995; Chittka and Schürkens, 2001). Therefore, while Himalayan balsam can be encountered in other habitats, in context of this thesis it is primarily considered a riparian species (Figure 2.2). Himalayan balsam requires high soil moisture while tolerating a wide range of slopes (from flat ground to 40° angle) and grows under moderate shade (Beerling and Perrins, 1993). As with other plant species, it is in constant competition with the rest of vegetation and its dominance depends on the local conditions. Therefore habitat requirements and physical habitat preferences of Himalayan balsam depend on the level of spatial scale that is assessed. On the level of river catchments, the Himalayan balsam distribution follows the course of large rivers representing an important element of the riparian vegetation (Dawson and Holland, 1999; Hejda and Pyšek, 2006). On the level of individual reach, Himalayan balsam dominates on the sites with less shade and sufficient moisture (Beerling and Perrins, 1993). Finally on the microhabitat level, exact conditions that lead to the competitiveness of Himalayan balsam are not yet established, however, it is known that flooding and water-table regime are not a major influence on growth (Tickner et al. 2000).

Ecological requirements of Himalayan balsam are primarily defined by its designation as a riparian vegetation. Therefore it grows well in moist and nutrient-rich soils, conditions where it successfully outcompetes native vegetation. Additionally, temperature sensitivity is known to be a limiting factor in the distribution of Himalayan balsam globally, however, in the UK context where frost is rare outside winter period, this is not a defining factor in the distribution (Willis and Hulme, 2002). However, in Italy, especially in the subalpine area, low temperatures could be one of the factors influencing its distribution (Skálová et al. 2011).

The interaction of Himalayan balsam with native riparian fauna is a complex one, due to the diversity of species that compose native vegetation and different habitats in which those plants coexist. Himalayan balsam, in general, outcompetes native vegetation in the riparian area, primarily native nitrophilous perennials like sting nettle (Urtica dioica) (Tickner et al. 2001). This is one of the rare examples that an annual plant is able to outcompete a perennial one.

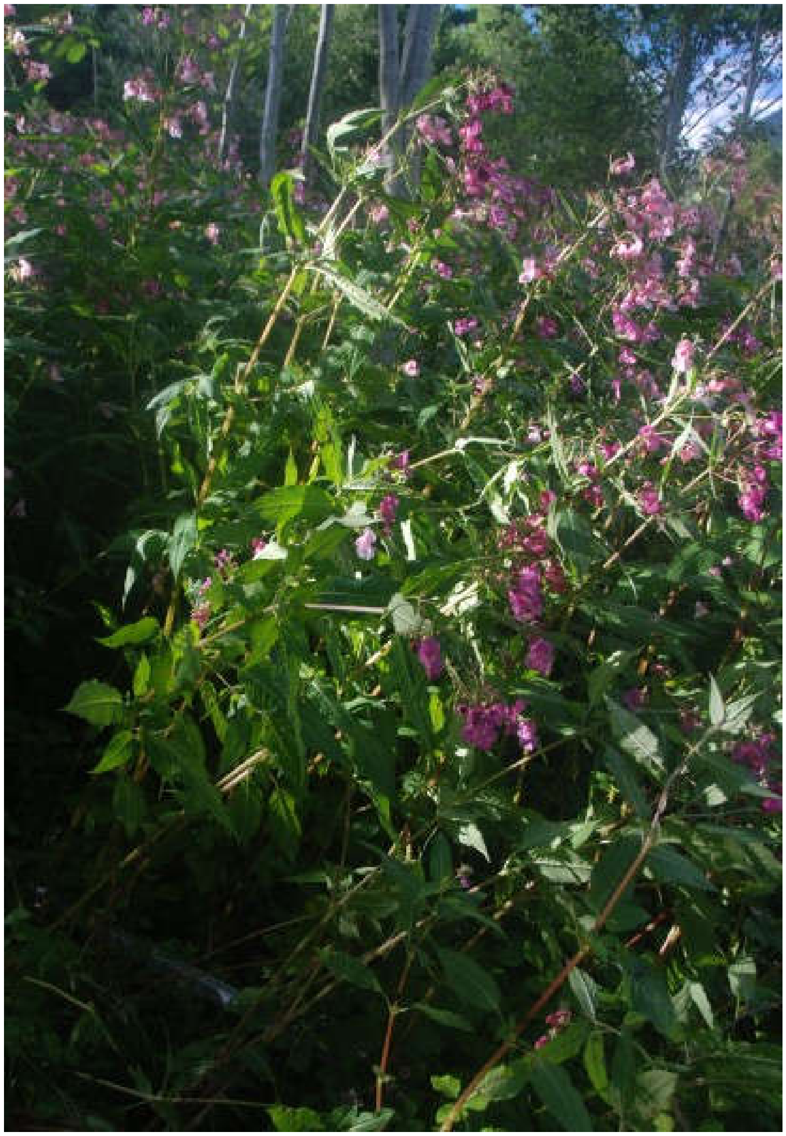


Figure 2.2 Himalayan balsam, bank of the River Brenta, Italy (17th August 2014).

2.7 Conceptual background for the study of invasive ecosystem engineers

Since introduction of the concept of ecosystem engineers, several definitions and corresponding frameworks for understanding ecosystem engineers were proposed, focusing on the role of invasive species (Cuddington et al. 2009), identifying individual interactions between environment and ecosystem engineer (Jones et al. 2010), feedback mechanisms between geomorphology and biota (Corenblit et al. 2011) and the role of plants in rivers (Gurnell, 2014). Out of those models, the framework proposed by Jones (2010) includes the most comprehensive outline of potential interactions between organisms and the environment (Figure 2.3).

The most significant feature of Jones' model is that it identified four main elements that define the interaction between organism and the environment: ecosystem engineer, structural change, abiotic change and biotic change. In addition to that, it also listed connections between those four elements. The ability of the Jones model to accommodate all potential interactions between an ecosystem engineer and the environment was the primary reason to choose it as a basis for a framework to study the impact of signal crayfish and Himalayan balsam on physical processes. However, two modifications of the Jones model had to be introduced in order for it to be fully applicable to the study of these two species. These are broadening the definition of an ecosystem engineer and recognising additional interactions that occur between a native organism and an invasive species.

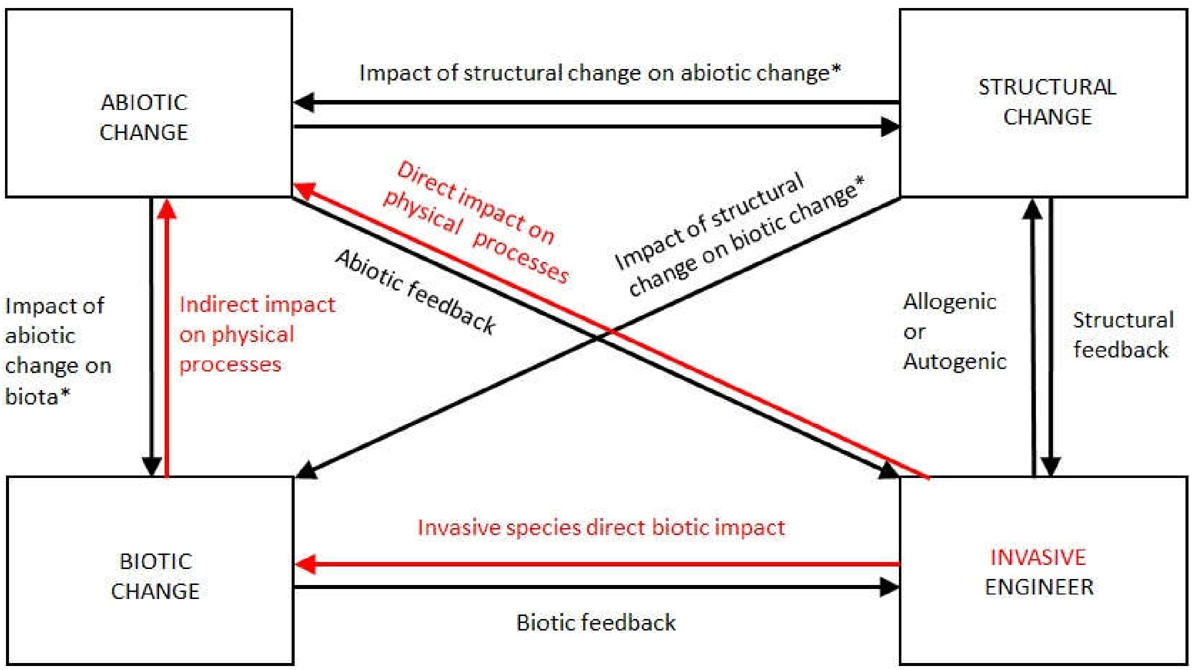


Figure 2.3 The conceptual model of the physical ecosystem engineering by organisms and possible interactions between main components (redrawn from Jones 2010 in black colour). Red text and arrows indicate three extra interactions that occur when a broader definition of an ecosystem engineer (*direct impact on the physical process) is used and when the ecosystem engineer is an invasive species (**direct biotic impact, indirect impact on the physical process). Interactions marked by * are not explicitly named in the Jones model but are discussed in the text of the original paper.

The definition of an ecosystem engineer by Jones (2010) is that of an “organism that creates physical structures in the environment through either autogenic or allogenic means”. Such structures are further distinguished between an autogenic structure which is a direct manifestation of the living organism (trees, coral reefs) and an allogenic structure which is formed by the engineer from the surrounding material (burrows, dams). Many sessile organisms (plants, corals) are usually autogenic engineers, while mobile ones (beaver, caddisflies) are allogenic, although combinations of the two groups are known. Therefore, these two categories only include organisms that modify the environment via the direct creation of physical structures. However, many definitions of ecosystem engineer also recognise the modification of physical processes in the environment as valid criteria for categorising an organism as ecosystem engineer (Cuddington et al. 2009; Gurnell, 2014). For instance, river bank vegetation influences processes of erosion and deposition through its root structure without creating a specific structure (Gurnell, 2014) and benthic animals act as both bioturbators and biostabilisators of the bottom sediment (Statzner, 2012). That type of interaction can best be described as a direct impact of the engineer on the physical processes (without creating a specific structure) and therefore it was added to Jones' (2010) model (Figure 2.3).

The original model by Jones (2010) describes interactions between organisms and their environment but does not account for additional interactions which occur when the ecosystem engineer is an invasive species. Invasive species exhibit a direct negative impact on native populations mainly through competition or predation (Cuddington and Hastings, 2004). In addition, changes in biological communities caused by that direct impact further influence the environment and that impact can best be described as an indirect impact of the ecosystem engineer. Therefore, it was necessary to add these two additional interactions to the conceptual framework of the invasive ecosystem engineer impacts (Figure 2.3).

In this section, a holistic framework for the study of invasive ecosystem engineers was defined by a modification of the original Jones model through three additions: broadening the definition of ecosystem engineer, accounting for the direct biological impact of invasive species and indirect impact of that change on the physical processes (Figure 2.3). In the following text, details of how signal crayfish and Himalayan balsam fit into this framework will be presented.

2.8 Conceptual model for study of ecosystem engineering impact of the signal crayfish

The role of signal crayfish as an ecosystem engineer is the most easily interpreted in a counter-clockwise direction in the modified Jones' (2010) model (Figure 2.4). The four main elements in the model are: signal crayfish (I) whose creation of structural change or burrows (II) leads to an abiotic change in the form of more erosion (III) and that leads to biotic change (IV). Between these four elements, five couples of interactions occur (consisting of actions and reactions which have positive or negative impacts). Each consists of action and reaction which has a positive or negative impact (positive or negative feedback loop). Some are well established, while other are hypothesised.

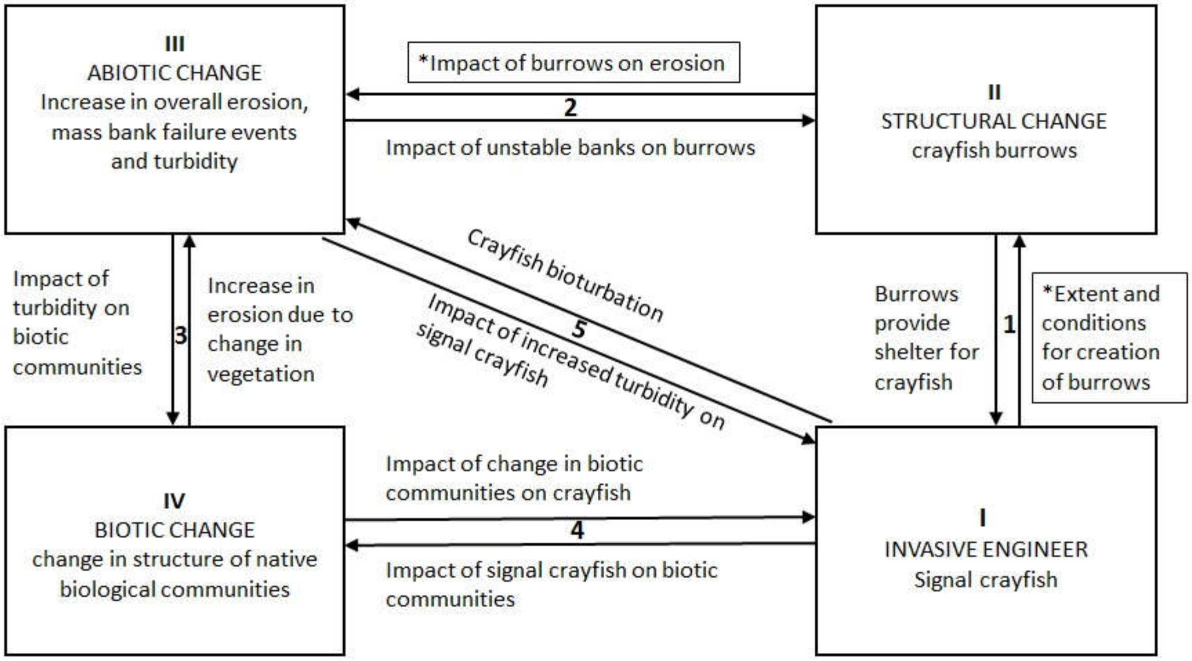


Figure 2.4 Application of the modified Jones (2010) model to the impact of signal crayfish as an invasive ecosystem engineer. Potential research questions are indicated with the *

The first pair of interactions is between invasive engineer (signal crayfish) and structural change (burrows) it creates. The creation of signal crayfish burrows is well recorded (Guan 1994, Harvey et al. 2014) while attempts to explain the extent of burrowing and conditions that lead to burrowing (Roberts, 2012) are not conclusive. The resulting impact of those burrows is positive for the crayfish since burrows provide a shelter and increase crayfish safety and survivability (Hudina et al. 2010).

The second pair of interactions is between structural change (burrows) and abiotic change (increase in erosion) it causes. Burrows are hypothesised to contribute to an increase in erosion through reduction of the bank stability and increased likelihood of mass bank failure events (Souty-Grosset et al. 2006, Harvey et al. 2011). While this is not specifically proven for crayfish burrows, it can be assumed from the theory of bank stability (Pollen-Bankhead and Simon, 2010). Increased erosion is further expected to lead to an increase in sediment supply and increase in turbidity. However, the exact conditions that cause burrows to lead to erosion and extent of that action are not known. The mass bank failure is likely to exhibit a negative feedback on crayfish burrows since it would bury the entrance of the burrows.

The third pair of interactions is between abiotic change (increase in turbidity) and biotic change (structure of animal and plant communities) it would cause. Increase in turbidity is well known to influence macrophytes, invertebrates and fish, and would therefore cause a significant change in the structure of the biological community in the direction of increasingly turbidity tolerant organisms (Lunt and Smee, 2014). Furthermore, it can be hypothesised that increasingly unstable banks would cause a change in bank vegetation. The feedback caused by the loss of macrophytes could lead to a further increase in erosion due to an increase in the velocity of water.

The fourth pair of interactions is between biotic change (different composition of biological communities) and invasive engineer (signal crayfish). These changes in the biological community have multiple impacts on signal crayfish, ranging from loss of alternative shelter due to loss of macrophytes, reduction of predation due to lesser visibility and expected reduction in the salmonid species which are a known predator of crayfish to change in diet due to alteration of the trophic chain. Lastly, the biotic feedback of signal crayfish on biota is relatively well known and includes a change in the composition of macrophytes, macrozoobenthos and fish (Crawford et al. 2006).

The fifth pair of interactions is between invasive engineer (signal crayfish) and abiotic change (increase in erosion and turbidity). The direct impact of the signal crayfish on the turbidity was demonstrated by Johnson et al. (2010). The abiotic feedback on signal crayfish through the increase in turbidity could be positive, due to reduced risk of predation, and negative due to interference with gills and breathing (Holdich, 2002).

2.9 Conceptual model for study of ecosystem engineering impacts of Himalayan balsam

The role of Himalayan balsam as an ecosystem engineer is most easily interpreted in a clockwise direction in the modified Jones' (2010) model (Figure 2.5). The four main elements in the model are: Himalayan balsam (I) causes biotic change (II) which leads to an abiotic change in the form of more erosion (III) and that leads to structural change (IV). Between those four elements, five couples of interactions occur (consisted of action and reaction which has a positive or negative impact). Each consists of action and reaction which has a positive or negative impact (positive or negative feedback loop). Some are well established, while other are hypothesised. The most important feature of Himalayan balsam is that it does not directly cause structural changes in the riverbank (through burrowing or any other effect).

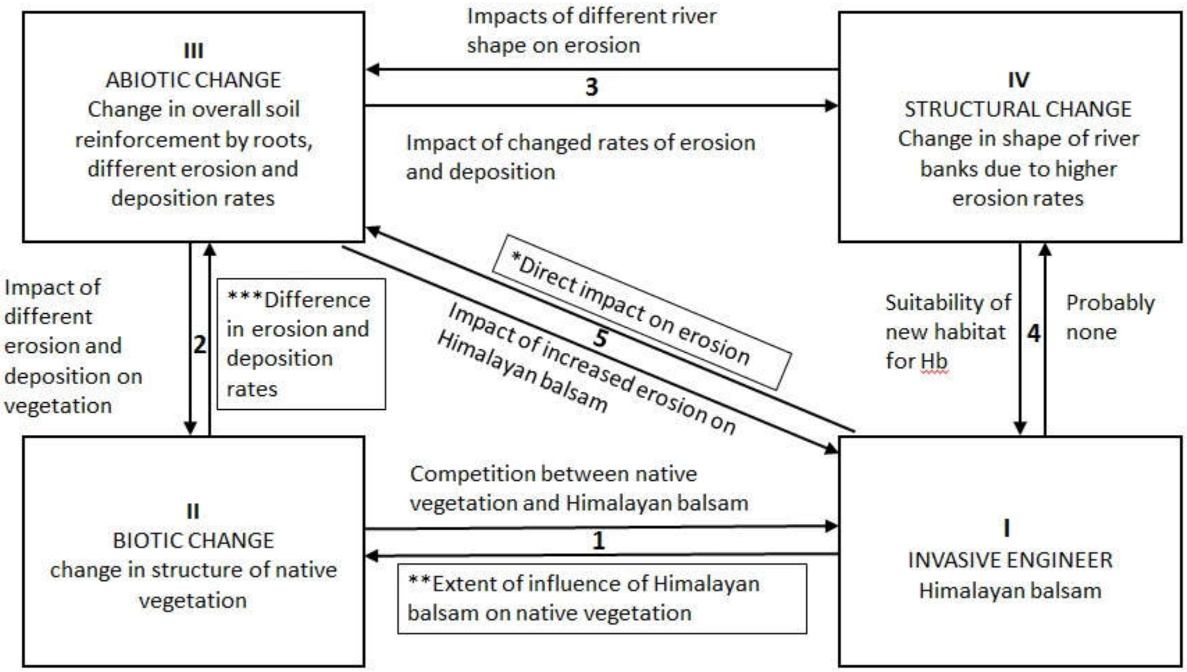


Figure 2.5 Application of the modified Jones' (2010) model to the impact of Himalayan balsam as an invasive ecosystem engineer. Potential research questions are indicated with the *

The first pair of interactions is between invasive engineer (Himalayan balsam) and biotic change (change in native vegetation) it causes. Himalayan balsam also has a direct biotic impact on vegetation because of competition with native species and resulting vegetation is a mix of native species and Himalayan balsam. Hejda and Pysek (2006) correctly argued that impact of Himalayan balsam on riparian vegetation does not lead to significant changes. However, that study was focused on the macroscopic level of analyses while small scales effects of Himalayan balsam were not addressed. Therefore, the extent of Himalayan balsam dominance over native vegetation will be explored through research question number 2. The second pair of interactions is between biotic change (mix of native and invasive vegetation) and abiotic change (increase in erosion) it causes. The change in vegetation structure is expected to cause a change in erosion and deposition processes, and these will be explored through research question number 3. The third pair of interactions is between abiotic change (increase in erosion) and structural change (shape of the river) it would cause. Firstly, it can be hypothesised that change in soil reinforcement and differential erosion and deposition rates could over time cause a structural change in the shape of river banks. The fourth pair of interactions is between structural change (different river) and invasive engineer (Himalayan balsam). Feedback caused by different riverbanks might occur as well, based on the impact of the increased erosion on both Himalayan balsam and native vegetation. The fifth pair of interactions is between invasive engineer (Himalayan balsam) and abiotic change (increase in erosion). However, due to differences in morphology of the individual plant, Himalayan balsam is hypothesised (Dawson and Holland, 1999) to increase the rates of erosion compared to the native vegetation and the research question number 1 will explore these impacts in more detail.

2.10 Research questions

The overall aim of this thesis is to improve current understanding of the role that invasive ecosystem engineers have on the river ecosystem. Analysis of specific impact caused by each of two case study species (illustrated in Sections 2.8 and 2.9) identified six main research questions.

1. What is the extent of signal crayfish burrowing over a wide range of spatial scales?
2. Which environmental conditions are the most conducive to the occurrence of burrowing?
3. What is the impact of burrowing on river bank erosion?
4. How does the presence of invasive Himalayan balsam influence the structure of native vegetation communities?
5. How does the presence of Himalayan balsam influence erosion and deposition processes on river banks?
6. What is the difference in plant morphology between Himalayan balsam and native vegetation and how is that relevant to the erosion processes?

These six questions identified the research gaps that stem from the literature review. In the following chapter, a practical approach to answering those questions will be presented and linked to individual research chapters.

CHAPTER 3: Research Design

3.1 Introduction

This chapter outlines the overall research design employed to answer the research questions identified at the end of the literature review. The results from the PhD research are presented in three results chapters dealing with invasive crayfish (Chapters 4, 5 and 6) and Himalayan balsam (Chapter 7). This chapter outlines the study sites, overall research design and elements of the methods that are common for all chapters. Methodological details specific to each results chapter are then dealt with within a specific chapter.

Signal crayfish and Himalayan balsam are widespread throughout the UK and Europe (Holdich, 2002; Dawson and Holland, 1999). In choosing study areas for those two species, an important role was played by the international context of the project that this thesis was a part of. The SMART Erasmus Mundus Joint Doctorate Programme was a result of a cooperation of three universities (SMART, 2016). Due to this circumstance, a signal crayfish research is done in the UK, while Himalayan balsam one in Italy. The process of selection of study area and overall research design are closely intertwined and therefore both will be firstly outlined for the signal crayfish and then for the Himalayan balsam.

3.2 Signal crayfish site selection rationale

Processes in rivers are known to be defined by different drivers at different spatial scales (Brierley and Fryiers, 2005; Charlton 2008), as demonstrated for the distribution of a large wood in the River Murray (Parsons and Thoms, 2007), invasive plants (Collingham et al. 2002) and impact of anthropogenic stressors on river biota (Kail and Wolter, 2003). Addressing research questions across multiple spatial scales was considered particularly important for the research on invasive crayfish burrowing because of combination of wide geographical distribution of signal crayfish (DAISIE, 2016) and the potential for intensive local impacts (Guan, 1994). Therefore answering stated research questions requires a study design that includes a survey on different spatial scales.

Secondary data sets are useful in providing coverage of the large numbers of sites used in ‘large N’ research, as defined by Richards (1996) that were employed in this study. The Environment Agency’s River Habitat Survey (RHS) (Environment Agency, 2003) was used to provide site data on biophysical river properties. Surveying was undertaken on a 500 m long river reach on two levels: spot checks which are done on ten equally spaced (each 50 m) transects and a sweep up, which provides information for the whole reach. More than hundred variables relevant to the physical characteristics, vegetation and general features are collected on each site and as of the year 2016, more than 24,000 sites across the UK have been surveyed (RHS 2016). The National Biodiversity Network (NBN, 2016) collects data on species presence and absence from a range of secondary data sets. While the majority of data entries are positive findings with a limited number of negative records, it provides a good information on the signal crayfish distribution in the UK. Due to the high number of data points in both databases and the extensive details recorded, it can be argued that combination of the RHS and the NBN data represents a good framework on which to base the research design.

This study was based on three spatial levels. The first two levels are based on the RHS reach and transect concepts. However, two modifications of this methodology will be applied when using it for the study of crayfish burrowing. The first one is related to the length of the individual reach, which might, depending on availability of access to the site, be shorter than 500 m. The second one is related to a terminology of naming ten metre long stretches of the river in which the term transect will be used when both river banks are surveyed while the term bank section will be used when only one river bank is surveyed. Therefore this survey was designed by using the same spatial levels (reach and transect / bank section) as the RHS in order to enable easier coupling of two datasets. For the higher level of spatial organization, as a third spatial level, the river catchment seemed the most appropriate since it is a scale that is most consistently identified in discussions related to scale in river science (Charlton, 2008, Brierley and Fryirs 2005) and it is also used in studies regarding crayfish ecology (Almeida et al. 2013). Therefore, three spatial levels that will be used in this study are catchment, reach and transect / bank section.

When designing studies spanning multiple spatial scales, it is important to note that there is no single natural spatial level at which a study should be performed, but the relationship to the research questions should be meaningful and clear (Levin, 1992). Turner et al. (1989) specified two main components which define the spatial scale: a grain (or pixel) and an extent. The pixel is the minimum size of a unit for which data are collected while the extent is an overall area included in the investigation. Therefore these two traits, a pixel and an extent, define each spatial scale.

In that regard, all three spatial levels are justified from the perspective of this study. A catchment is the broadest isolated river system and therefore represents a natural border for a population of signal crayfish (Holdich, 2002). A reach represents river stretch that is sufficiently big to support and influence populations of signal crayfish and is also in the range of the annual migration of the individual animal (Bubb, 2004). The transect is the smallest unit which corresponds to the daily migration of individual signal crayfish and therefore influences decisions of an individual animal (Bubb, 2004).

Once the spatial levels of study are defined, it is important to assess how their combination determines a specific spatial scale. Turner et al. (1989) specified two main components which define spatial scale: a grain (or pixel) and an extent. The pixel is the minimum size of a unit for which data are collected while the extent is an overall area included in the investigation. Therefore these two traits, a pixel and an extent, define each spatial scale. The design of the signal crayfish research will address research questions on three arbitrarily defined scales: bank section within reach, reach within the catchment and bank section within the catchment (Figure 3.1). The first spatial scale, bank section in reach, enables detailed survey of a small uniform area and will be further explored in Chapter 4. The second scale, reach in the catchment, aims to identify which reaches of river support signal crayfish populations and in which conditions they start burrowing, therefore giving a more generalised answer to the research questions and that is covered in Chapter 5. The third spatial scale, bank section in the catchment, is focused more on localised effects which are more likely to influence the creation of individual burrows and is analysed in Chapter 6. The relationship between these three spatial scales are shown in Figure 3.1 and the process of site selection for each one will be presented below.

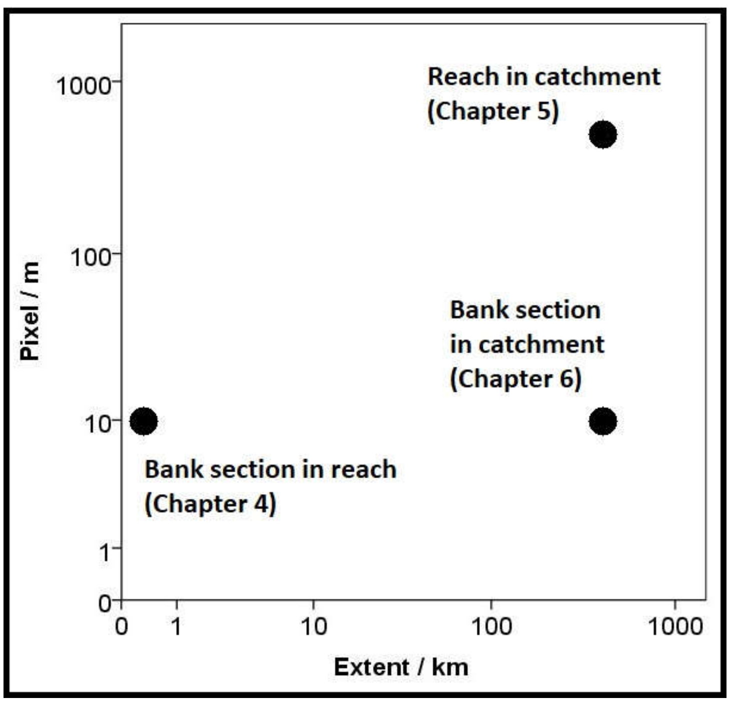


Figure 3.1 Relationship between pixel and extent for three spatial scales used in this research.

The signal crayfish is spread throughout the UK with an especially consistent presence in the south-east of England (Figure 3.2). However, for practical reasons, it was necessary to limit the survey to a more manageable area. The first principle to guide that process was the awareness that impacts of the invasive species are the most pronounced in ecosystems that are already under anthropological stress (Catford et al. 2012) and therefore the Thames river catchment was chosen as a principal area for the signal crayfish study.

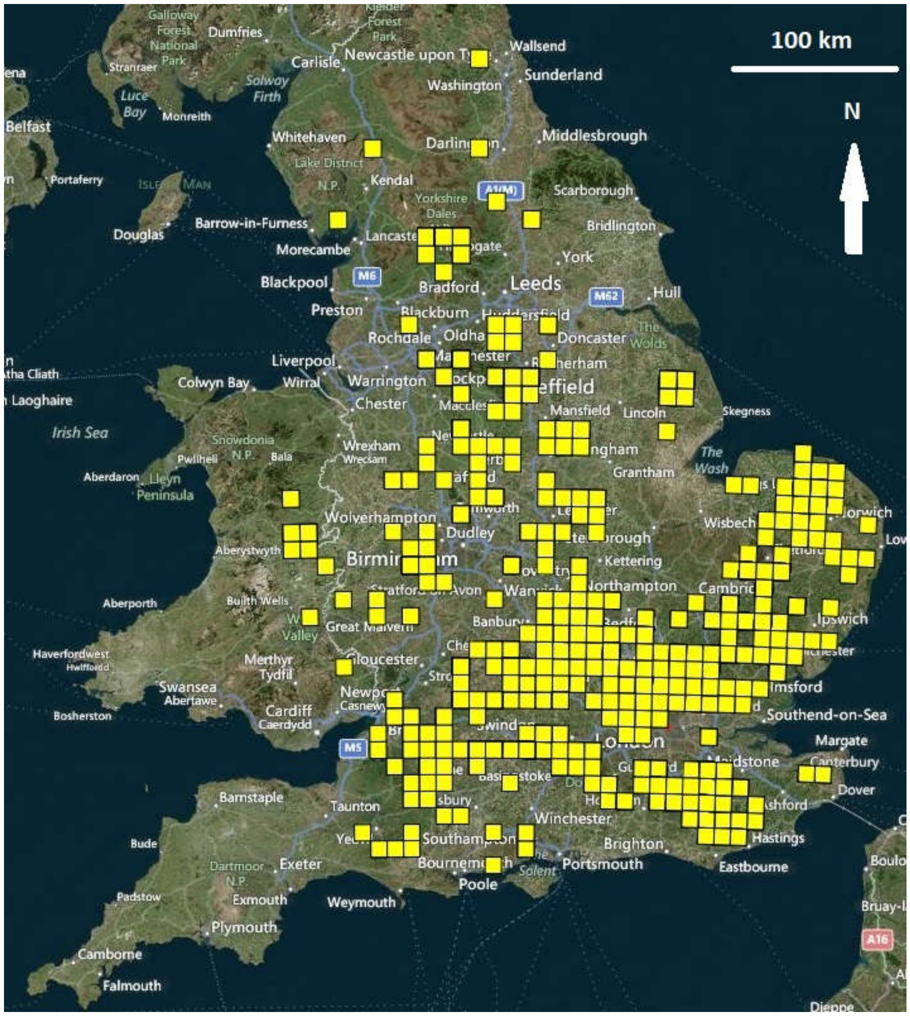


Figure 3.2 The distribution of signal crayfish in England and Wales (NBN, 2016).

The wider Thames catchment is large in area (16,000 km^2), includes 38 main tributaries and contains the most densely populated urban areas in the UK as well as Areas of Outstanding Natural Beauty. With 690 mm of rainfall, the area of the Thames catchment is drier than a national average (897 mm) and in combination with a high population density (13 million people) (BGS, 2015) this puts even more pressure on water resources. The primary river management challenges are flooding, water abstraction and diffuse and point sources of pollution (BGS, 2015). The seven rivers selected for study are predominantly lowland, low energy rivers (altitude < 83 m a.s.l.; slope < 0.001) underlain by chalk, sandstone, limestone and clay (BGS, 2015). They achieve good geographic coverage of the wider Thames catchment and are representative of the high proportion of lowland, low energy rivers in the UK (Harvey et al. 2008). Invasive crayfish are widespread in the Thames and include narrow-clawed (*Astacus leptodactylus*), virile (*Orconectes virilis*) and red-swamp (*Procambarus clarkia*) but signal crayfish (*Pacifastacus leniusculus*) are by far the most successful invader to date (Souty-Grosset et al. 2006). The native white-clawed crayfish (*Austropotamobius pallipes*), initially widespread within the Thames, gradually disappeared from the mid-1970s onwards when signal crayfish was introduced, and with a particularly steep decline between 2001-2010 (Almeida et al. 2013).

Seven tributaries in the Thames catchment longer than 40 km were arbitrarily chosen as a focus of this study (Figure 3.3). All seven rivers are predominantly low land, low energy rivers. Rivers Kennet, Colne and Lee are partially on a chalk bedrock, while the rest: Windrush, Loddon, Wey and Mole, are mainly on sandstone, limestone and clay bedrock (BGS, 2015). The choice of tributaries aimed to achieve a good balance between left and right tributaries of the Thames and also between tributaries in the western and eastern part of the catchment. Therefore the chosen tributaries are representative of the overall conditions in the Thames catchment.

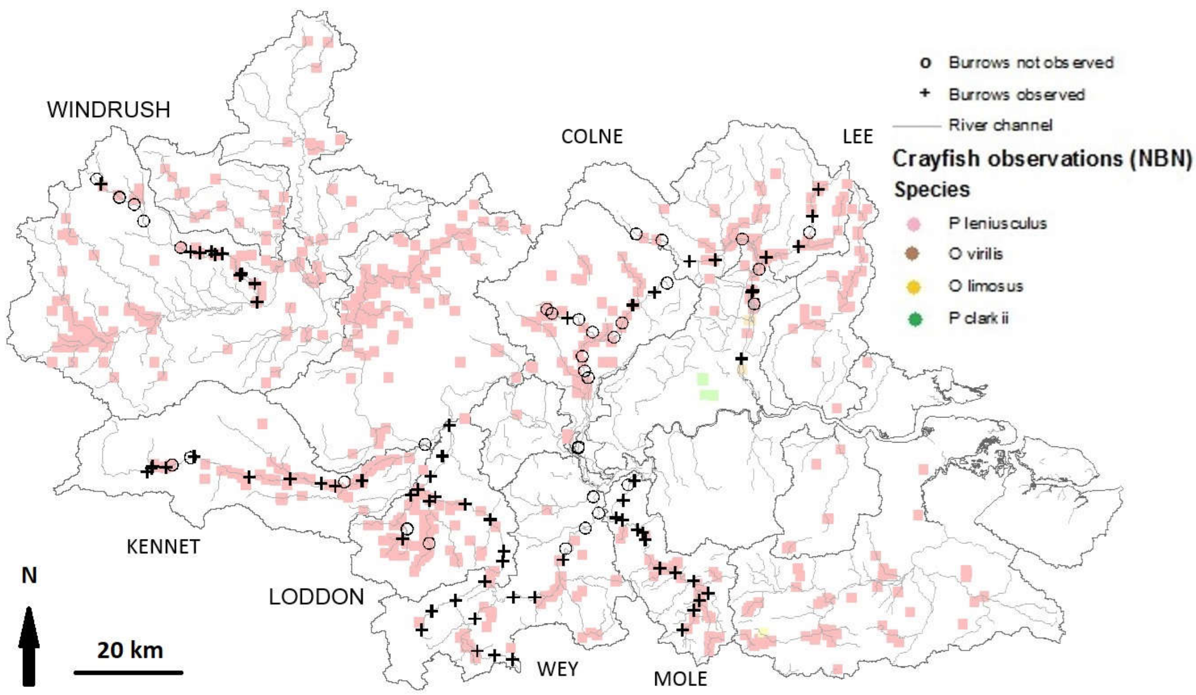


Figure 3.3 Map of the Thames catchment indicating features of interest for the research design: distribution of signal crayfish (*Pacifastacus leniusculus*) and three other invasive crayfish species as well as the location of sites chosen for the reach in catchment and transect in catchment study (NBN, 2016).

Each chosen tributary has a well-recorded presence of the signal crayfish along its length (NBN, 2016) (Figure 3.3). While other invasive species are also present in the Thames catchment, signal crayfish is by far the most widely spread. Despite a high overall number of records, on each studied tributary, there are stretches of the river without records of signal crayfish absence or presence. However, it is considered that signal crayfish had a chance to spread to all sites on each river, due to following reasons. Firstly, because of a long time since initial invasion occurred around the 1960s (Holdich et al. 1978), signal crayfish had sufficient time to spread to all suitable habitats. Secondly, a speed of the signal crayfish spread, which can range from 1 km (Peay et al. 2009) to 24 km per year (Hudina et al. 2009), ensures that within the time available, crayfish could have migrated along the studied rivers, especially since their migration is only weakly biased in downstream direction (Bubb et al. 2004). Thirdly, upstream parts of rivers are more likely to stay separated from established populations due to natural isolation (Peay, 2001). However, channel locks and dams that could prevent migration are rarely positioned in headwaters, while at the same time, due to mainly lowland character of these rivers, instances of natural barriers are rare. Fourthly, the spread of invasive crayfish can additionally be increased by anthropogenic activities like fishing and other river-related human activities (Bohman et al. 2011). Fifthly, there are very few records of signal crayfish absence in NBN Gateway database (NBN, 2016). Finally, there is a general understanding that records of invasive species presence always lag behind the situation in the field, due to the time required for species detection (Hulme et al. 2012, Pyšek et al. 2008). Under these assumptions, the population density of the signal crayfish on individual sites is a consequence of suitability of local conditions and not the isolation of the site. Therefore, for the purpose of this study, it can be assumed that each chosen site was exposed to the signal crayfish presence.

The first spatial scale (bank section in reach), is designed as an intensive study and therefore a reach with the well-known presence of crayfish and burrows was chosen. Since this survey was undertaken in the September 2015, data from the catchment-wide survey were available. Those data demonstrated that the River Windrush is the river with the highest presence of burrows. On the River Windrush, in addition to the presence of crayfish burrows, an extra consideration had to be made in regard to water voles. Water voles are protected species that can be caught in crayfish traps and drown. Because of that, use of traps in proximity to water vole habitat is prohibited (EA, 2010). In order to address this problem, a local environmental non-government organisation was contacted and in coordination with them, potential sites were discussed. The main criteria for the choice of the site was that it had to be outside of the known distribution of the water voles. Since there is an intensive survey going on, two potential areas were identified, both in the downstream section of the River Windrush. Out of those two, a site with a well-known high presence of crayfish burrows was identified near the town of Hardwick (Oxfordshire) and chosen as a location for this study.

The choice of sites for the remaining two spatial scales (reach within the catchment and bank section within catchment) was done on the basis of existing RHS sites in order to enable coupling of existing data and field survey (Figure 3.3). The field survey for research on both scales was done during the autumn 2013 and spring 2014, by revisiting river reaches covered by the RHS database. In order to achieve a good representation of different parts of the river, and still maintain an element of randomness in the site selection, a stratified random sampling was applied (Krebs, 1999). On each tributary, three to four longitudinal parts were identified and within them, RHS sites were chosen randomly. In the end, a total of 103 sites on seven tributaries of the Thames were surveyed (Figure 3.3).

It can be argued that since sites were chosen from the RHS database, the sampling procedure is not completely random. However, the fact that originally RHS sites are chosen on the basis of randomness makes the original decision justified (RHS, 2015). Another factor that influenced the site selection was the right of access to river banks. Only 2% of river banks in England and Wales have a public right of access and that was the object of public campaigns to allow access to rivers like the River Access Campaign (RAC, 2015). Sites surveyed during this research either had public access or there was no strict ban (in terms of fences and signs) that prohibited access. Therefore, it can be said that this study has a slight bias toward locations with public access at the expense of sites on private land. However, a number of potential sites that could not be assessed was relatively small and it is not expected to alter the results of the study in a significant way. Overall, the main advantage of this research approach is that it provides an information on fine and coarse spatial scale (bank section and reach) following the same principles like the RHS, country's most extensive river habitat database.

3.3 Signal crayfish study research design

While the previous section identified the main spatial aspects of this study, in this section an approach used for answering individual research questions will be discussed. The research design is guided by two principles. Firstly, it can be argued that there is a hierarchy of three stated research questions. On every given spatial scale, first, it is required to establish the extent and distribution of burrows. Only then, the second research question, dealing with the interaction between habitat characteristics and burrows presence can be answered. Finally, the third research question can be answered if extra information on erosion is collected. All three research questions are answered on each scale using the most appropriate approach, which is outlined in Table 3.1. Therefore in the following text, general features of research design used for each one of three spatial scales will be presented, while further details of the methodology applied will be described in the respective chapters.

Table 3.1. Crayfish research design: an overview of data sources for four categories of data (burrows, habitat, erosion and crayfish) for each of the three spatial scales studied.

Spatial scale	Burrows	Habitat	Erosion	Crayfish population
Bank section in reach	Visual observations (close up)	Field survey	Visual signs of erosion	Trapping data
Reach in catchment	Visual observations (from bank)	Secondary data	Volume of sediment	NBN only
Bank section in catchment		Field survey	Visual signs of erosion	presence confirmed by burrows observation

The research on the bank section in reach scale is focused on one 410 m long reach on the river Windrush near the town of Hardwick. The reach was surveyed across 41 transects (covering both left and right banks) for habitat, burrows and erosion information as well as an assessment of crayfish density. Each transect provided information for two bank sections, resulting in a total of 82 main data inputs. Habitat information was collected on a similar principle as in the bank section in catchment scale. Burrows were recorded by detailed observation from the river channel. Direct signs of erosion were recorded on each transect. In addition to these three categories of data, limited length of this reach (410 m) enabled collection of data on crayfish density through trapping. Traps were positioned at each 10 m of river length and standard methodology for assessment of crayfish population density was applied (Hudina et al. 2009; Moorhouse et al. 2014). Combination of these methods enabled a more detailed assessment of factors influencing burrowing and erosion.

The remaining two spatial scales, reach in the catchment and bank section in the catchment, aimed to cover a wide spatial extent of the Thames and its tributaries. Therefore, they were designed under similar principles as the RHS field survey and rely on visual observations of features without specific field measurements. In order to improve the relevance of the records, especially in regards to crayfish burrows and erosion, the survey was undertaken during conditions of low flow in the autumn (September and October 2013) and spring (March and April 2014) when vegetation was sparse. In order to ensure a good view of the bank face, banks were observed by walking either through a river channel or on the opposite bank. Therefore, field data for reach in the catchment and bank section in catchment scales were collected on the same occasion for each of 103 sites in the River Thames catchment. Details of the research design will be presented below.

On the reach in catchment scale, research approach combined a secondary data from the publicly available databases with the field observations of burrows presence. The primary source of publicly available data was the RHS for the river habitat characteristics, supplemented with the information from the British Geological Survey (BGS, 2015) for geological information and Digimap (Digimap, 2015) for calculation of map derived variables. RHS records information of river banks and channel characteristics at ten equally spaced transects as well as a “sweep up” observation of the whole reach. Therefore for each surveyed site, over hundred variables recorded in nominal, ordinal or ratio format are collected (Environment Agency, 2003). In order to effectively use this diverse information, a range of reach level indices were designed and successfully used for the analysis of traits of geomorphic units (Emery et al. 2003), classification of urban rivers (Davenport et al. 2004) and relationship between physical habitat and lithology (Harvey et al. 2008). In a similar manner, specific indices will be designed to capture information considered relevant for the crayfish burrowing. The field survey consisted of revisiting RHS sites and recording several aspects of burrows presence (number of burrows, length of the bank impacted and density of burrows). Erosion information was not directly recorded, however the volume of the burrowed material was calculated for each site on the basis of the average size of burrows available from the literature.

On the bank section in catchment scale, information was collected on the same principle as the RHS spot check survey, by observing between 4 and 10 bank sections along the 500 m reach. In total, 1,095 ten metre sections were surveyed. On each reach, bank sections were selected to cover a representative sample of bank sections with and without burrows (Figure 3.4). Habitat characteristics were collected for bank and channel features on the basis of a modified RHS survey. Information on crayfish burrows was collected for the length of bank impacted, number and density of burrows. Erosion was analysed by directly observing physical manifestation of erosion on the basis of simplified Stream Reconnaissance procedure (Thorne, 1998).

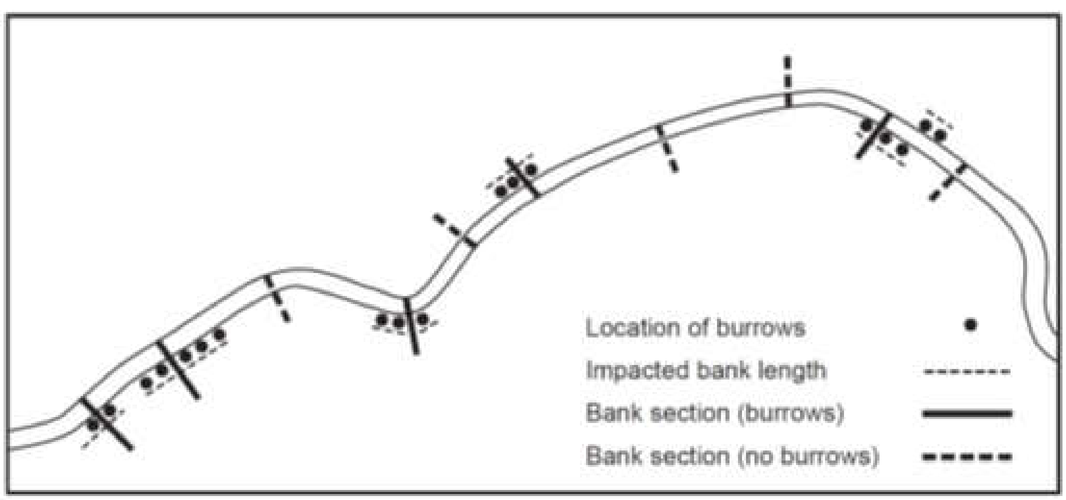


Figure 3.4 Scheme for collecting data on bank section and reach scale

3.4 Himalayan balsam site selection rationale

Himalayan balsam is widely spread in Europe, in Italy covers the north of the country, while its distribution in the Trentino region mainly follows major rivers (Figure 3.5).

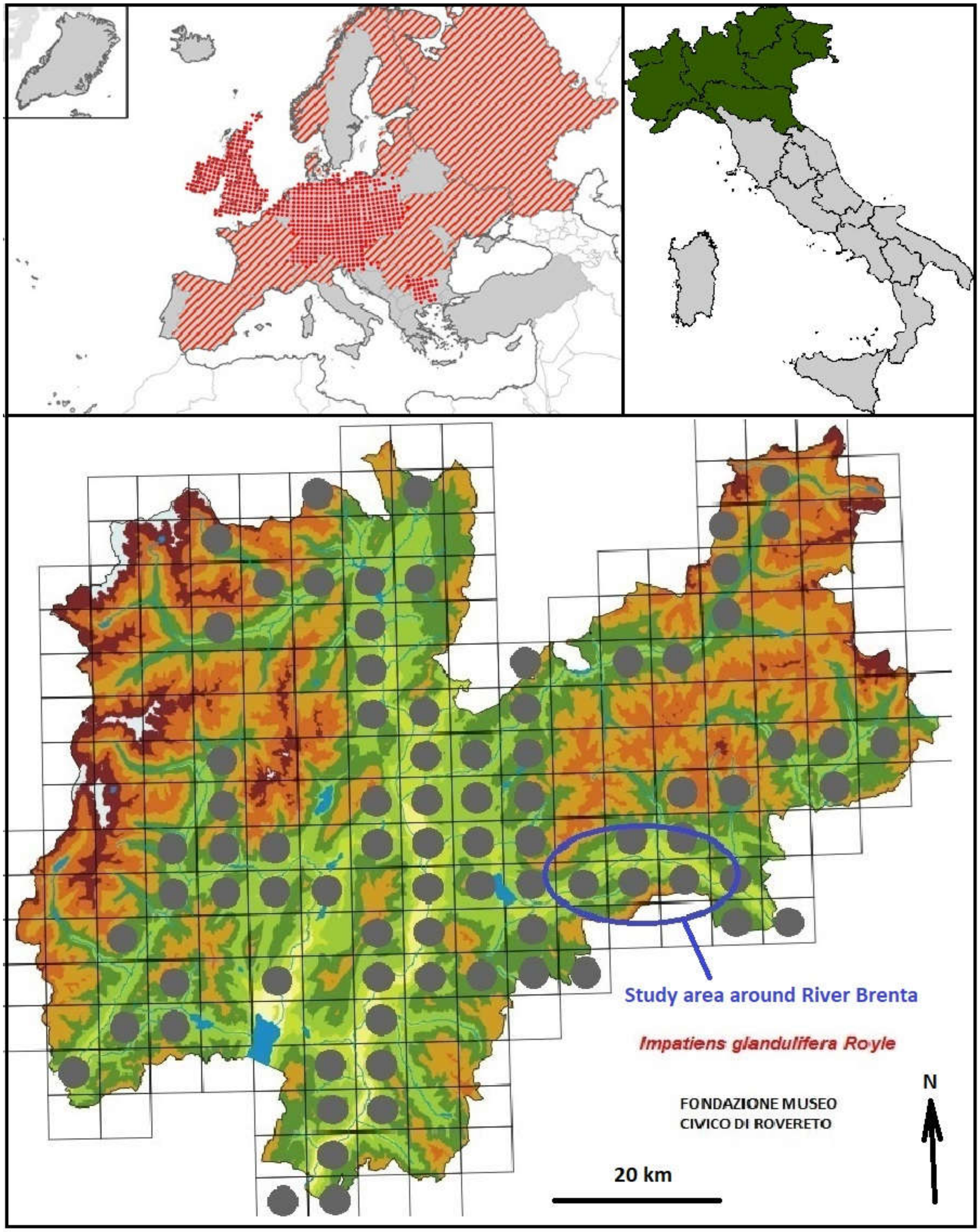


Figure 3.5 Distribution of Himalayan balsam in Europe, Italy and the Trentino region (Daisie database 2016; Flora Italiana 2016).

The River Brenta is a 174 km long river whose upstream section flows through the southeast of the Trentino region. Himalayan balsam is well-established along the Brenta. The upstream sections of the Brenta catchment are in the piedmont region of the Southern Alps and the river valley is used for intensive agriculture. The combination of these two features means that the river is representative of mountainous and agricultural regions exposed to considerable anthropological stress (Bozzola and Swanson, 2014).

The source of the river Brenta is in the south-east of the Trentino region and from there it flows to the south-east before it reaches the Adriatic Sea. The most notable feature of the upstream part of the Brenta catchment is the presence of lakes Caldonazzo (elevation 451 m asl) and Levico (elevation 440 m asl) which collect upstream headwaters and channel water through two outlets which join downstream after approximately 1.5 km and form the river Brenta. Most of the sediment originating in the headwaters is deposited in the lakes and therefore the upstream sections of the River Brenta have low suspended sediment concentrations. The amount of sediment increases in the downstream sections from tributaries that drain the hills surrounding the valley (Bertoldi, 2014). The study area is located within the upstream stretch of the River Brenta, that runs from the source of the Brenta river to the town of Primolano. During a preliminary survey undertaken in May 2014, continuous, dense stands of Himalayan balsam were recorded only in the middle section, between the towns of Borgo Valsugana and Grigno, and therefore this 15 km long stretch was selected as the focus of this study (Figure 3.6).

Figure 3.6 A 15 km long stretch of the River Brenta that is a focus of the Himalayan balsam survey. The location of the eight survey sites is indicated.

Following step in research design dealt with the choice of the number of field sites to survey. Richards (1996) outlined two contrasting approaches usually used in geomorphology, an extensive research based on a large number of samples and an intensive method based on a small number of case studies. While both approaches have their advantages, the preference to one of the two is given based on methodology and research questions (Hildrew, 1996). Due to the lack of detailed studies and knowledge regarding the role of Himalayan balsam as an ecosystem engineer and the fact that research design aims to answer three different research questions, an intensive approach was considered more fitting. Based on the experience of other studies (Greenwood and Kuhn, 2014, Henshaw et al. 2012), eight sites were considered an appropriate number of field sites.

The choice of sites was based on several factors. During the preliminary survey, no areas with exclusively native vegetation or Himalayan balsam were recorded. Vegetation was characterised by a gradient of areas with higher or lower relative abundance of Himalayan balsam. Therefore, in order to compare two types of vegetation, the first criterion for the choice of sites was the presence of patches dominated by Himalayan balsam and native vegetation in relative proximity to each other. Additionally, in order to ensure good representativeness of habitat heterogeneity, sites with different microhabitat characteristics were included (shade, slope and distance from water). On the basis of stated criteria, eight study sites were selected (Figure 3.6). The main characteristics of the studied sites are presented in Table 3.2, while the snapshots provide additional information on their overall characteristics (Figures 3.7, 3.8).

Table 3.2 Basic qualitative characteristics of the eight study sites on the River Brenta

Site	River	Flow type	Tree cover	Dominant bank sediment
1	Brenta	perennial	light	earth
2	Brenta	perennial	none	earth
3	Brenta	perennial	none	earth
4	Tributary	perennial	light	earth
5	Brenta	perennial	heavy	earth
6	Tributary	intermittent	light	earth
7	Brenta	intermittent	none	sand
8	Brenta	perennial	none	sand

Figure 3.7 Photographs of study sites 1 (top) to 4 (bottom). For each site, the photo on the left shows the river channel and the one on the right shows the riverbank.

Figure 3.8 Photographs of study sites 5 (top) to 8 (bottom). For each site, the photo on the left shows the river channel and the one on the right shows the riverbank.

3.5 Himalayan balsam study research design

Before discussing the details of the experimental design, it is necessary to define the concept of "native vegetation" for this survey. While Himalayan balsam is one species, native vegetation on the riverbank consists of hundreds of plant species (Hejda and Pyšek, 2006), which realistically cannot all be surveyed. Therefore, it was decided to focus on the dominant representatives of the native vegetation, the ones that cover the most surface area over all sites.

During the preliminary survey, five plant types were recorded as dominant in percentage cover: grasses (Poaceae), bramble (*Rubus* sp.), oxeye (*Buphthalmum* sp.), stinging nettle (*Urtica dioica*) and smartweed (*Polygonum* sp.). In addition to these, all other plants were grouped as either unspecified monocotyledons or unspecified dicotyledons. While grasses (Poaceae) is a family with numerous species in every river habitat, the relative similarity in their root system justified treating them as one group. Therefore, the survey focused on these seven types of native plants. These types are not at the same taxonomical level of identification, but they were appropriate for this survey on the basis of ease of identification in the field and dominance in all the sites.

In addition to plant type, the extent of the abundance of each group was assessed. This was done by using the modified DAFOR scale (Rich et al. 2005). The original DAFOR scale is based on the subjective assessment of the frequency and cover and is based on five classes, from dominant to rare, depending on the percentage of area covered by each plant. For the purpose of this survey, the same principle was used, but plant cover was simply assessed to the nearest 10 % vegetation coverage value. The relative abundance of the seven different native vegetation types and Himalayan balsam are shown in the Figure 3.9. This has enabled a good assessment of abundance for each plant type. These vegetation traits will be taken into account in the design of surveys for each separate chapter.

Three research questions explore differences between Himalayan balsam and native vegetation on different levels in relation to the position of the plant in the wider environment. In respect to that, research questions four and five both explore the plants directly within their natural environment through the use of transect surveys, while they only differ among themselves in the object of study (competition between plant species and different influence on the morphological activity). On the other hand, the research question six analyses differences between Himalayan balsam and native vegetation on the level of individual plant specimens.

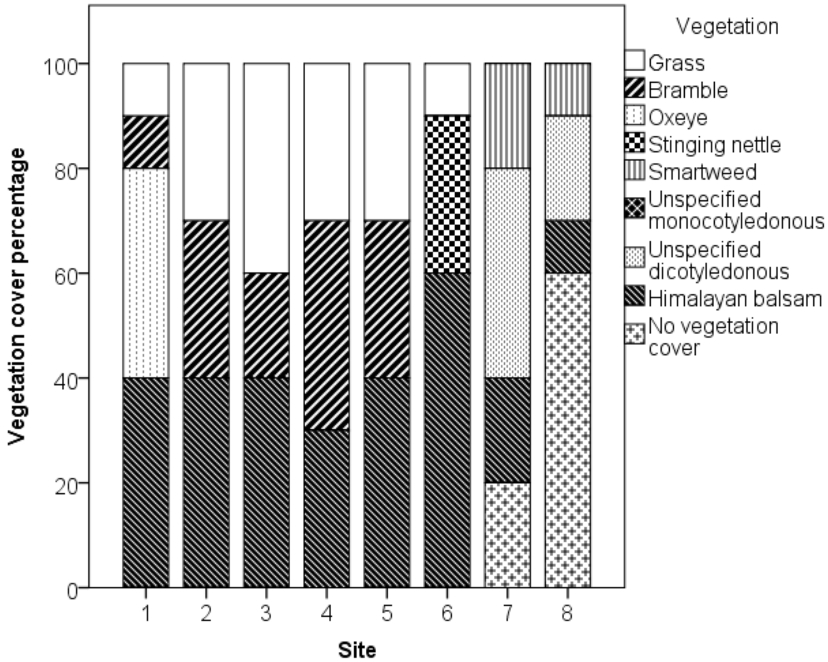


Figure 3.9 Percentage cover of the eight main vegetation types and no vegetation cover on eight study sites.

3.6 Data analysis

Prior to statistical analysis, the normality of the data set was assessed using the Kolmogorov Smirnov test. Since variables deviated from the normal distribution, non-parametric tests were used in further analyses. Correlations between biophysical habitat, burrowing and erosion variables were assessed using Spearman's Rank and statistically significant differences between groups were identified using Mann Whitney (2 groups) or Kruskal Wallis (>2 groups). In order to reduce the dimensionality of the large data set, Principal Components Analysis (PCA) was used. PCA is a linear ordination method which transforms original, correlated variables into uncorrelated principal components in order to maximise original variance. In all PCA analyses, a correlation matrix was used for extraction of factors, and the significant principal components were identified as those with eigenvalues greater than 1 and an inflexion point in the scree plot. Principal Components (PCs) were rotated using a varimax rotation to maximise interpretability. PC scores were obtained with the regression method and variable loadings were used to identify the dominant characteristics of the PCs.

3.7 Reframing research questions

While the literature review identified six research questions on the basis of knowledge gaps, in this chapter these research questions are placed in context of practical constraints. On that basis four main research aims are identified and each one will be answered with a respective research chapter:

1. What is the role of signal crayfish as ecosystem engineer at the bank section in reach spatial scale (Chapter 4)?
2. What is the role of signal crayfish as ecosystem engineer at the reach in catchment spatial scale (Chapter 5)?
3. What is the role of signal crayfish as ecosystem engineer at the bank section in catchment spatial scale (Chapter 6)?
4. What is the role of Himalayan balsam as an invasive ecosystem engineer (Chapter 7)?

CHAPTER 4: Signal crayfish as ecosystem engineer at the bank section in reach spatial scale

4.1 Introduction

Influence of ecosystem engineers is proportionate to their population density, the frequency of engineering activity and impact of that activity (Jones et al. 1994; Loades et al. 2010). For the purpose of this survey, those factors translate to study of crayfish population density, the frequency of occurrence of burrows and impact of burrows on erosion processes. Therefore a hierarchy of causality exists that will be followed throughout this chapter: ecosystem engineer (signal crayfish) causes a structural change (burrows) and those, in turn, lead to abiotic change (increase in erosion). Therefore, this chapter follows a modified Jones et al. (2010) model outlined in Chapter 3 and aims to explore the interaction between habitat characteristics, signal crayfish population density, the occurrence of burrows and river bank erosion that occurs at bank scale within a reach spatial scale.

The stated interactions between habitat characteristics, signal crayfish population density, burrows occurrence and erosion will be undertaken on the bank scale within a reach spatial scale. As elaborated in Chapter 3, following definition of Turner et al. (1989), this scale is defined by the pixel size of 10 m and extent size of few hundred meters. A ten meters bank scale is often used as a basic survey unit in analysis of river habitat characteristics (Frissell et al. 1986; Harvey et al. 2008; Raven et al. 2000), crayfish populations (Bubb et al. 2004; Faller et al. 2006, Wutz and Geist, 2013), ecosystem engineering effects (Siebert and Branch, 2006; Statzner and Sagnes 2008) as well as erosion (Davis and Harden, 2012). At the same time, a few hundred meters long river reach is one of the most often used spatial extents in the river science (Brierley et al. 2002; Parker et al. 2012; Maceda-Veiga et al. 2017). While river reach is a relatively small spatial extent in comparison to the river catchment (Charlton, 2008), it enables collection of detailed information about studied parameters and therefore it is considered appropriate for the first chapter addressing signal crayfish burrowing.

While the previous studies on signal crayfish burrowing (Guan, 1994; Stanton 2004; Roberts, 2012) provided initial insights into basic characteristics of signal crayfish burrows occurrence, the influence of habitat and impact of burrows on erosion, there are few critical aspects that remain to be addressed. The influence of signal crayfish population density on occurrence of burrows was addressed through a small-scale study by Guan (1994) however it remains a surprisingly understudied aspect, especially on the reach level. In a similar way, the presence of burrows is hypothesised to cause erosion (Harvey et al. 2011), however, this effect has remained largely untested in the field. In addition to the listed interactions, crayfish population density, burrowing occurrence and river bank erosion are all influenced by habitat characteristics and there is a significant discrepancy in the level of understanding of those three impacts. Influence of habitat on signal crayfish is relatively well studied on a variety of spatial scales (Holdich 2002; Souty-Grosset et al. 2006; Hudina et al. 2009). Similarly, erosion, as one of the central processes shaping river ecosystems, was studied in great detail for several decades (reviews of factors influencing erosion were given by Thorne, 1982; Rinaldi and Darby 2007 and Grabowski et al. 2011). Finally, the influence of habitat characteristics on crayfish burrows occurrence was addressed to some extent by Guan (1994), Stanton (2004) and Roberts (2012), but it remains understudied.

In addition to above-described analyses, one additional aspect of burrowing will be addressed. Signal crayfish create burrows bellow water line (Holdich 2002) and due to seasonal oscillation of the water stage (Charlton, 2008), some of those burrows, created during the high water levels are exposed during low water levels. Studies by Guan (1994) and Stanton (2004) were primarily based on records of burrows bellow water level, while Roberts (2012) based her broad-scale study primarily on the observation of burrows above the water line. However, currently, there is a lack of understanding about how good prediction about an overall number of burrows can be made on the basis of an information about burrows above the water line only. Since chapter 5 and 6 are heavily reliant on observation of burrows above the water line, this aspect of burrowing will be addressed in this chapter.

Following research aims will be addressed in this chapter:

1. What are the basic quantitative characteristics of signal crayfish population density, burrows occurrence and presence of erosion?
2. What is the influence of habitat characteristics on signal crayfish population density?
3. What is the influence of habitat characteristics and signal crayfish population density on signal crayfish burrows presence?
4. What is the influence of habitat characteristics and signal crayfish burrows on presence of erosion on river banks?
5. What is an interaction between number of burrows above and below the water line?

4.2 Methodology

4.2.1 Survey design

The survey reach is located on the River Windrush, near the town of Hardwick (UK National grid reference SP 38247 05990) and was chosen on the basis of presence of relatively high number of burrows in combination with the low likelihood of presence of water voles (the process of site selection is described in detail in Chapter 3). By use of standard measuring tape, the total length of 410 m was demarcated and divided into 41 ten metre long transects (Figure 4.1). Definition of transect was adjusted from the River Habitat Survey (Environment Agency, 2003) and slightly modified for the purpose of this research. Each transect encompasses a ten meter long stretch of the river including channel, both banks and riparian area up to 5 m distance from the water edge.

Figure 4.1 Typical river transects on the survey reach, the River Windrush.

On each transect, information was collected separately for left and right bank and channel area between them (Figure 4.2). It is known that many habitat characteristics, as well as the occurrence of signal crayfish burrows demonstrate different characteristics on the left and right bank of the same micro-location (Raven et al. 2000; Roberts, 2012). Therefore it was decided to treat left and right bank separately and use a ten metres long bank section as a main basis of analysis. In order to include channel information into this concept, each channel variable information was associated with both bank sections that surround it. This concept of bank section is used for answering research aims one to four and will also be applied in Chapter 6. In total, 41 transects were surveyed, generating a base data input for 82 ten metre long bank sections.

Four types of variables were collected for each bank section: crayfish population, burrows and erosion variables as well as habitat characteristics. Habitat, burrows and erosion variables are collected through direct observation. Crayfish population density information is obtained through trapping and therefore requires a more detailed explanation of the methodology used which will be presented in the following section. After that, the overall data collection protocol will be outlined.

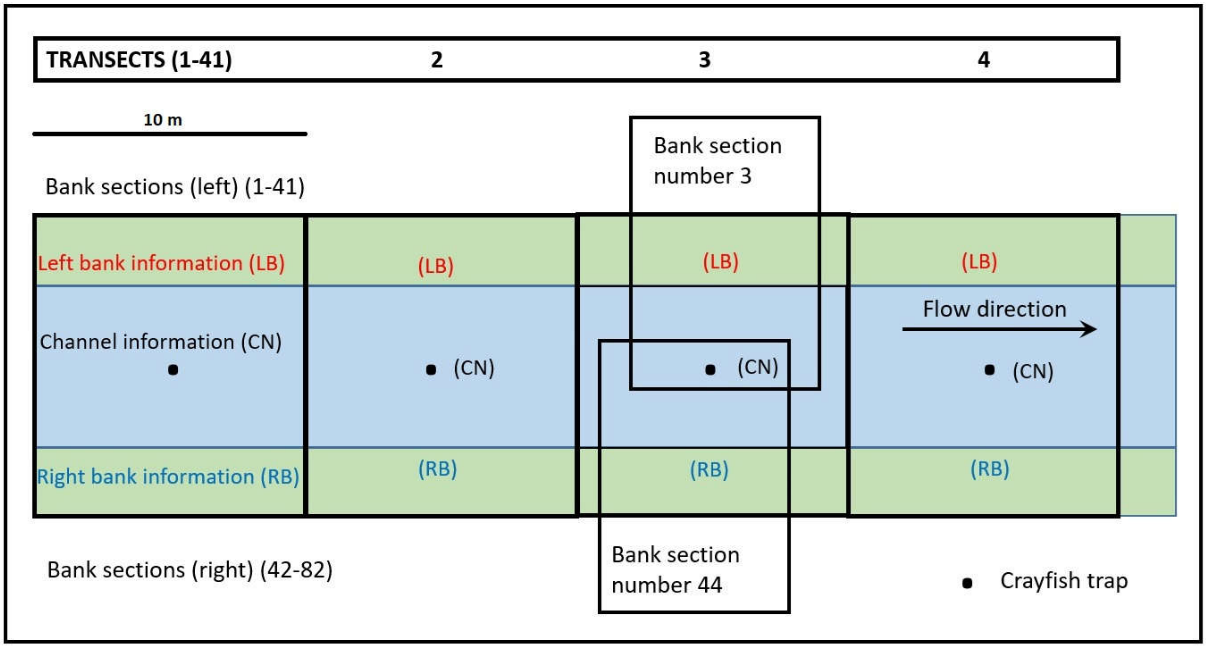


Figure 4.2 Relationship between river transect and bank sections. Bank section is a basic unit of analysis. An example of a combination of data from bank and channel variables is given for bank sections 3 and 44. Both of them are based on transect number 3, but bank section 3 combines data from left bank and channel while bank section 44 combines data from right bank and channel.

4.2.2 Trapping protocol and handling of crayfish

Crayfish trapping was undertaken during five consecutive days between 19th and 23rd September 2015. Traps were checked twice a day, in the morning and evening since that approach reduces the likelihood of crayfish leaving the trap before scheduled trap check. For the purpose of data analysis, morning and evening catch were grouped together, therefore generating five data points about a number of crayfish caught. Traps used were commercially available, cylindrical, plastic crayfish traps (Trappy™ crayfish trap, Virserum, Sweden). Each trap is 50 cm long and has a 20 cm diameter with a 25 x 35 mm mesh and a 51 mm diameter aperture, and fulfils requirements stated under Environment Agency licence used (Environment Agency, 2010). Traps were baited with commercially available frozen fish and rebaited twice a day, during each trap check. A total of 41 traps were used, and for each transect, one trap was placed in the middle of the river which resulted in an average distance of 10 m between traps. For each caught crayfish sex, total length and number of the trap in which it was caught were recorded. The total length was measured to the nearest 1 cm with a simple ruler. Following that, crayfish were placed in the moist mesh and at the end of each day killed by chilling in the air to -15 °C (RSPCA, 2003). All the dead crayfish were disposed of as a biological waste at the Queen Mary University London.

4.2.3 Survey variables

Variables collected for each bank section focused on four main areas: crayfish population, burrows, erosion and habitat characteristics. Information was collected by walking through the river channel in waders in the upstream direction in order to reduce the increase in turbidity caused by walking. Parts of the bank covered by riparian vegetation were closely inspected to check for the presence of burrows that would otherwise be obscured. This approach enabled detailed observation of each meter of the bank and accurate assessment of bank conditions.

Information regarding signal crayfish population is based on trapping. Catch per unit of effort (CPUE) is the most common way to establish a link between trapping results and assessment of local population density and is often used for assessment of relative population density of crayfish (Peay and Hiley 2004; Faller et al. 2006; Zimmerman and Palo, 2011). The method assumes that the same unit of effort (one trap) is applied to each survey location (transect) and that difference in catch is representative of the relative difference in population density. Therefore, it does not give an assessment of absolute population size, which is always several times bigger than the catch, but it gives a good assessment of local differences in population size (Hudina et al. 2009). Therefore, this method of signal crayfish population assessment is considered appropriate for the purpose of this study.

CPUE is recorded for each trap and each day for males and females separately, and these results are presented in order to enable comparison with other similar studies. However, for the majority of analysis and answering of the research aims, catch per unit of effort is expressed for all days and both gender together. Therefore, two variables are derived for the bank section analyses. Crayfish absence or presence in each transect implies whether at least one crayfish was caught during the five day period. Crayfish number indicates a total number of males and females caught during five day period (Table 4.1).

Table 4.1 Variables regarding crayfish population, burrows and erosion collected for each ten metres long bank section.

Variable	Description
Crayfish presence	Positive if at least one crayfish is present at the bank section
Crayfish number	Total number of crayfish caught (CPUE)
Burrows presence	Positive if at least one burrow is present at the bank section
Burrows number	Sum of burrows above and below water line
Erosion presence	Positive if at least one meter of bank length eroded
Eroded bank length (m)	Total length of the river bank impacted by visible signs of erosion on the basis of Thorne (1987)

Following part of the sampling protocol deals with records of burrows observation. There is currently no standard field method for detailed quantification of distribution of signal crayfish burrows. Therefore the approach to recording crayfish burrows used in this survey was devised on the basis of a modification of method used by Roberts (2012). Burrows observation was done by direct visual observation of the ten metre long bank sections. In comparison to the broad range, Thames catchment based survey undertaken by Roberts (2012), relatively small extent of this surveyed reach (820 m of total bank length) enabled much more detailed observations. The observations were done for burrows above as well as above water. Additionally, the ability to walk through the river channel enabled observation of the river bank in greater detail compared with observations from a distance by walking on top of the river bank. This resulted in burrows numbers that can reasonable be assumed to represent the majority of existing burrows. Burrows numbers above and below water line were recorded and analysed separately in section 4.5 of this chapter for the purpose of analysing their mutual interaction. However, for the majority of the analyses, burrows above and below water line were grouped together for each bank section. For the purpose of answering the stated research aims, burrows occurrence was expressed as burrows presence which indicates the presence of at least one burrow and burrows number, which stated the overall number of burrows on specific bank section (Table 4.1).

As with the rest of variables, erosion survey was undertaken during the same sampling period of several days. This meant that usual methods of erosion assessment, like erosion pins (Lawler et al. 1997), or repeated analysis of river bank images obtained either by remote sensing techniques for the large scale surveys (Marzolff and Poesen 2009) or structure from motion for the smaller scale (Rieke-Zapp and Nearing, 2005) could not be used. Therefore an approach described by Thorne (1998), the stream reconnaissance method was used.

The stream reconnaissance method (Thorne, 1998) relies on assessment of signs of erosion on the basis of direct observation. While this method does not give an exact quantitative estimate of the extent of erosion, it does enable a good differentiation of micro locations where erosion does and does not occur. While the original stream reconnaissance method analyses multiple aspects of erosion (type, length, extent on the reach, severity) for the purpose of this survey, only length of bank impacted by erosion was recorded. For each bank section, erosion was recorded as erosion presence or absence and as a total length of bank impacted by erosion (Table 4.1).

Habitat variables aim to characterise the nature of each bank section and are covering both, bank and channel characteristics. The basis for methodology of collecting information is the River Habitat Survey (RHS) (Environment Agency, 2003), Urban River Survey (Davenport et al. 2004) and River Styles Framework (Brierley and Fryirs, 2005), with addition of few extra variables that are considered important in order to better suit the specific requirements of this survey. As described in the section 4.2.1, on each transect, channel variables are associated with the left and right bank section in that transect. Total of 17 bank variables and eight channel variables are collected and two index variables are calculated (Table 4.2).

Table 4.2 Variables collected and indices calculated describing habitat characteristics of each ten metres long bank section.

<table>
<tr><th></th><th>Variable</th><th>Description or coding for PCA</th></tr>
<tr><td rowspan="17">Bank characteristics</td><td>Bank height (m)</td><td></td></tr>
<tr><td>Bank angle (degrees)</td><td></td></tr>
<tr><td>Bank material</td><td>1 – earth, 2 – sand 3 – gravel</td></tr>
<tr><td>Length of tree roots above water (m)</td><td></td></tr>
<tr><td>Length of tree roots bellow water (m)</td><td></td></tr>
<tr><td>Bank emergent broad leaved vegetation (coverage)</td><td rowspan="13">Modified DAFOR scale. Values from 0 to 10 are associated with each 10 % increment in surface coverage for selected vegetation type</td></tr>
<tr><td>Bank emergent narrow leaved vegetation (coverage)</td></tr>
<tr><td>Bank face bare (coverage)</td></tr>
<tr><td>Bank face grass (coverage)</td></tr>
<tr><td>Bank face herbs (coverage)</td></tr>
<tr><td>Bank face shrubs (coverage)</td></tr>
<tr><td>Bank face trees (coverage)</td></tr>
<tr><td>Bank top bare (coverage)</td></tr>
<tr><td>Bank top grass (coverage)</td></tr>
<tr><td>Bank top herbs (coverage)</td></tr>
<tr><td>Bank top shrubs (coverage)</td></tr>
<tr><td>Bank top trees (coverage)</td></tr>
<tr><td rowspan="8">Channel characteristics</td><td>Channel vegetation (coverage)</td></tr>
<tr><td>Channel flow</td><td>1 – smooth 2 - rippled</td></tr>
<tr><td>Water depth (m)</td><td></td></tr>
<tr><td>Water width (m)</td><td></td></tr>
<tr><td>Planar angle (degrees)</td><td></td></tr>
<tr><td>Channel material</td><td>1 – earth, 2 – sand 3 - gravel</td></tr>
<tr><td>Channel boulders (m^2)</td><td></td></tr>
<tr><td>Channel large wood (m)</td><td></td></tr>
<tr><td rowspan="2">Indices</td><td>Shelter availability index</td><td>= 1 + tree roots below water line + large wood + boulders + channel vegetation</td></tr>
<tr><td>Shelter pressure index</td><td>= number of crayfish / shelter availability index</td></tr>
</table>

Bank height and angle were measured using the meter pole and analogue hand inclinometer in order to provide a basic characterisation of the river bank. Bank material, as one of the key factors limiting burrowing (Holdich, 2002), was recorded as belonging to one of three ordinal variables (earth, sand, gravel). Tree roots, a major factor that represents crayfish shelter (Holdich, 2002) were expressed as the length of the bank covered by them (Table 4.2).

Different types of vegetation were quantified as coverage. Recording of the coverage of different vegetation types incorporates greater detail than traditional RHS surveys to address potential implications for bank stability. For example, grasses and herbs are grouped into a single category within RHS but can have different root structures (Zhongming et al. 2010), and the classification of vegetation structure into categories such as ‘simple’ and ‘complex’ may overlook specific elements of the understorey which may have implications for burrowing and erosion through providing cover or influencing bank structure (Gurnell, 2014). Therefore a modification of the DAFOR score system (Rich et al. 2005) is used for quantification of coverage of bare bank and four major vegetation groups (grass, herbaceous vegetation, shrubs and trees). DAFOR score is based on assigning a score based on the abundance of specific vegetation type and it was modified by assigning a score from 0 to 10 for each 10% increase in coverage for specific vegetation type (Table 4.2).

Eight additional variables describe channel characteristics. Channel vegetation coverage was assessed on the same modified DAFOR principle as bank vegetation. Channel surface flow type was marked as either rippled or smooth on the basis of modified RHS methodology. Channel dimensions (width and depth) were measured using a measuring pole. Planar angle represents approximate angle at which river curves when looked from above. It was designated as having a positive value for the outer and negative value for the inner meander bend. Channel material is classified into three ordinal groups, with an additional category added for the surface of channel boulders which represent an important shelter for crayfish (Holdich, 2002). Finally, the length of important shelter for crayfish, large wood (defined as each piece of wood longer than 1 m and thicker than 10 cm) is assessed for each transect (Table 4.2).

In addition to variables collected directly, two index variables were calculated in order to combine the effects required for answering research questions. Shelter availability index combines four variables that are known to provide shelter for crayfish. A value of one is added because it is assumed that minimum amount of shelter exist in each bank section and in order to enable calculation of the shelter pressure index for the bank sections where no obvious shelter is observed. Shelter pressure index compares a number of crayfish with available existing shelter in order to illustrate the pressure or incentive for crayfish to dig burrow as an additional shelter. When the ratio is high, there is a lot of competition between crayfish for existing shelter and therefore incentive to dig burrows is assumed to be higher (Table 4.2).

Daily flow rate on the River Windrush is shown in the Figure 4.3 and it is considered indicative of general seasonal trends regarding river flow. It is visible that around the end of September, the flow level is very low and therefore many of the burrows that were above water line would be submerged during the rest of the year.

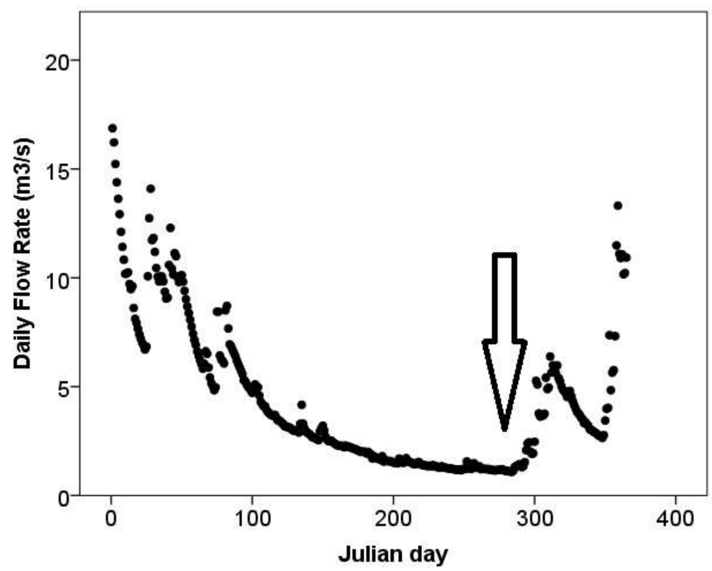


Figure 4.3 Daily flow rate on the River Windrush at Worsham (CEH, 2015). The arrow indicates approximate month of the field survey (September).

4.3 Results

4.3.1 Basic quantification of crayfish, burrows and erosion presence

In total, 41 transects were surveyed resulting in data for 82 bank sections (Table 4.3). Crayfish were caught in all but one trap, resulting in 80 bank sections with presence of crayfish (Figure 4.4, 4.6). Total of 576 crayfish were caught, with a mean value of 14, the median value of 8 and the maximum value of 64 crayfish per trap during the period of 5 trapping occasions. In general, more males were caught than females, but both sexes showed a reduction in a number of animals caught over the consecutive period. Burrows were present on 36 or less than half (44%) bank sections with a mean value of 2.43 and the maximum value of 30 burrows per bank section (Figure 4.5, 4.6). Burrows distribution had a strong positive skew, with only a smaller number of bank sections having more than six burrows. A total of 199 burrows were recorded, with 101 burrows above and 98 burrows below the water line. There was a strong, statistically significant correlation between a number of burrows below and above water line ($r = 0.747$, $p=0.000$). Erosion was recorded on 16 bank sections (19%) with a mean value of 0.72 m and the maximum value of 10 m, the whole length of the bank section showing signs of erosion (Figure 4.6).

Table 4.3 Descriptive statistics for crayfish, burrows and erosion related variables based on analysis of 82 surveyed bank sections.

Variable	Mean	Median	Std. Deviation	Minimum	Maximum	Sum
Crayfish presence	0.98	1	0.16	0	1	80
Crayfish number	14.05	8	12.60	0	64	576
Burrows presence	0.44	0	0.50	0	1	36
Burrows number	2.43	0	4.50	0	30	199
Erosion presence	0.20	0	0.40	0	1	16
Eroded bank length (m)	0.72	0	1.72	0	10	59

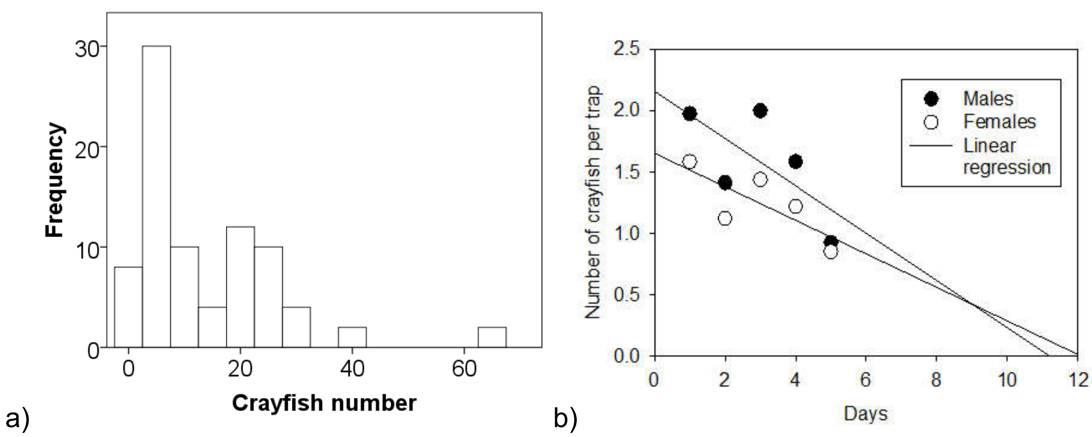


Figure 4.4 a) Frequency distribution for the number of crayfish caught over the five day survey period and b) number of male and female crayfish caught during each day of the trapping survey. Linear regression indicates a general reduction in a number of caught crayfish.

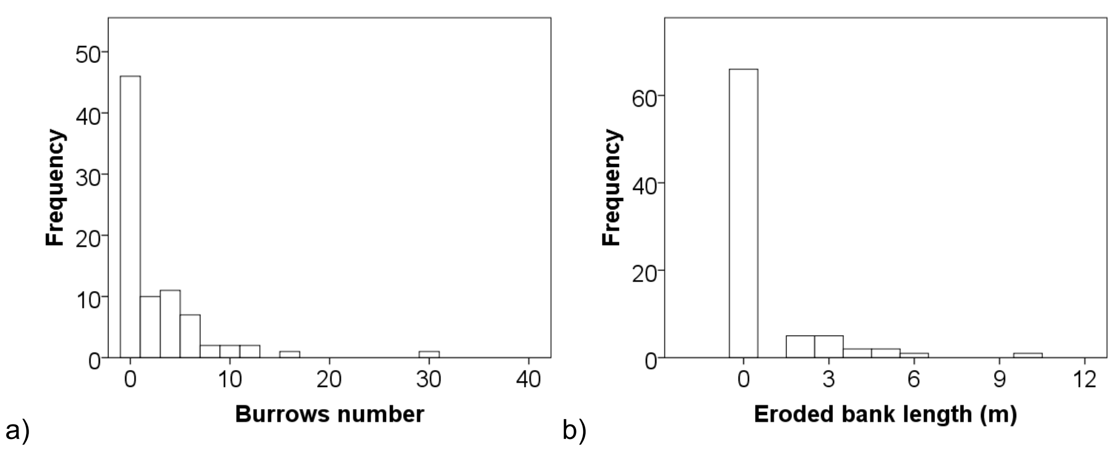


Figure 4.5 a) Frequency distribution for a number of burrows recorded (burrows above and below water line are grouped together) and b) frequency distribution of different eroded bank lengths recorded during the field survey.

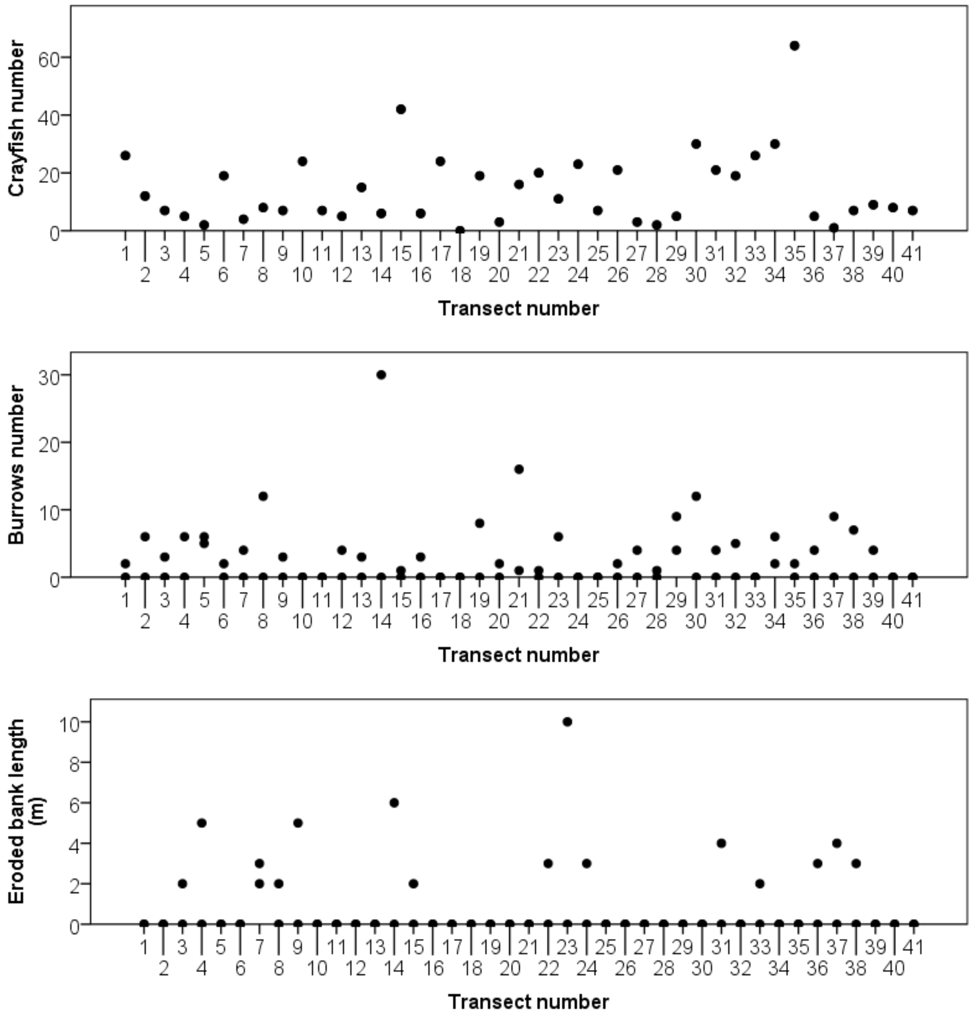


Figure 4.6 Variation in the crayfish number, burrows number and eroded bank length throughout 41 transect of the surveyed reach.

Environmental parameters were within the values associated with other reaches of the River Windrush (presented in Chapter 5) (Table 4.4). Bank height was on average 0.8 m tall with an angle of 65 degrees. Bank material was dominated by earth on the majority of transects, while sand and gravel were dominant on a smaller number of transects (2 and 8 respectively). Tree roots covered on average one meter of each bank section above water and 2 m bellow water. Bank emergent vegetation was sparse with mean values of less than value 1 coverage, however, on few sites it reached higher values and covered almost the whole length of the bank section. Bank face was primarily covered with herbaceous vegetation (mean coverage value 7), followed by bare bank surface (mean coverage value 1.7). In comparison, bank top vas rarely bare and was dominated by herbaceous vegetation and grasses (mean values of coverage 9 and 1 respectively). Shrubs and trees had lower values, with trees occurring more often on bank top than bank face (mean values of coverage 1.1 and 0.7 respectively). Flow type was dominated by smooth flow and was rippled on 13 (32%) transects. Max water depth was on average 0.6 m, while width was 5.6 m. Planar angle ranged from 0 to 70 degrees indicating a corresponding variation in extent of the river channel meandering. Channel material was dominated by gravel, while sand was dominant at only 27 (33%) transects. Large boulders in the channel were mainly absent (total of 2 m^2), while a total of 80 m of length of large wood was recorded. Shelter availability index, had a mean value of 4 and maximum of 14, indicating the relatively good presence of shelter. The shelter pressure index had a mean value of 5 and the maximum value of 30 crayfish per unit of shelter indicating a high variability in a that variable.

Table 4.4 Descriptive statistics for habitat variables calculated for the 82 studied bank sections.

Variable	Mean	Median	Std. Dev	Min	Max	Sum
Bank height (m)	0.793	0.8	0.35	0.3	1.6	65
Bank angle (degrees)	65.37	65	20.50	20	100	5360
Bank material	1.22	1	0.61	1	3	100
Length of tree roots above water (m)	1.11	0	1.75	0	10	91
Length of tree roots bellow water (m)	1.98	1	2.51	0	8	162
Bank emergent broad leaved vegetation (coverage)	0.46	0	1.54	0	8	38
Bank emergent narrow leaved vegetation (coverage)	0.8	0	2.27	0	10	66
Bank face bare (coverage)	1.74	0	2.65	0	8	143
Bank face grass (coverage)	0.9	0	2.02	0	10	74
Bank face herbs (coverage)	7.26	8	3.01	0	10	595
Bank face shrubs (coverage)	0.34	0	1.08	0	8	28
Bank face trees (coverage)	0.74	0	1.28	0	6	61
Bank top bare (coverage)	0.07	0	0.38	0	2	6
Bank top grass (coverage)	1.09	0	2.39	0	10	89
Bank top herbs (coverage)	8.84	10	2.39	0	10	725
Bank top shrubs (coverage)	0.17	0	0.56	0	2	14
Bank top trees (coverage)	1.1	2	1.05	0	4	90
Channel vegetation (coverage)	0.39	0	0.86	0	3	32
Channel flow	1.32	1	0.47	1	2	108
Water depth (m)	0.637	0.5	0.31	0.2	1.4	52.2
Water width (m)	5.56	6	1.30	3	8	456
Planar angle (degrees)	0	0	22.50	-70	70	0
Channel material	2.68	3	0.47	2	3	220
Channel boulders (m^2)	0.02	0	0.16	0	1	2
Channel large wood (m)	0.98	0	1.87	0	8	80
Shelter availability index	4.37	4	3.15	1	14	358
Shelter pressure index	5.416	2.607	6.84	0	30	444.1

4.3.2 Factors influencing signal crayfish population density

The number of crayfish caught was statistically significantly influenced by five habitat variables (Table 4.5). Spearman correlation revealed that crayfish preferred habitat with more large wood and more overall shelter, deeper and wider parts of the river and smaller size of particles of channel material. However, correlations are relatively weak, with the strongest link being the one with the length of large wood (R=0.47).

Table 4.5 Spearman's rank correlations between crayfish number and habitat variables. Significant values ($p<0.05$) are indicated with *.

Spearman's rho	Crayfish number
Bank height (m)	-0.118
Bank angle (degrees)	0.14
Bank material	-0.182
Length of tree roots above water (m)	0.062
Length of tree roots bellow water (m)	0.056
Bank emergent broad leaved vegetation (coverage)	-0.166
Bank emergent narrow leaved vegetation (coverage)	0.059
Bank face bare (coverage)	-0.014
Bank face grass (coverage)	-0.153
Bank face herbs (coverage)	0.036
Bank face shrubs (coverage)	-0.117
Bank face trees (coverage)	-0.027
Bank top bare (coverage)	0.129
Bank top grass (coverage)	0.058
Bank top herbs (coverage)	-0.101
Bank top shrubs (coverage)	-0.12
Bank top trees (coverage)	0.058
Channel vegetation (coverage)	-0.016
Channel flow	-0.213
Water depth (m)	.358*
Water width (m)	.218*
Planar angle (degrees)	0
Channel material	-.218*
Channel boulders (m^2)	-0.188
Channel large wood (m)	.471*
Shelter availability index	.255*

4.3.3 Factors influencing signal crayfish burrows presence

A number of burrows recorded was statistically significantly influenced by ten habitat variables (Table 4.6). Spearman correlation revealed that burrows occurred on habitats with high bank height and steep bank angle, high planar angle, the small size of bank material particles, the high length of tree roots bellow and above water and high coverage of bare bank face. However, correlations are relatively weak, with the strongest link being the one with the bank angle and bare bank face (R=0.43 and 0.41 respectively). Shelter pressure index and crayfish numbers did not correlate statistically significantly with a number of burrows (R=-0.16, R=-0.10 respectively). Therefore, the presence of burrows cannot be explained by crayfish population density and pressure for natural shelter within this data set.

Table 4.6 Spearman's rank correlations between the number of burrows and factors that influence it: number of crayfish and habitat variables. Significant values ($p<0.05$) are indicated with *.

Spearman's rho	Burrows number
Crayfish number	-0.102
Bank height (m)	.334*
Bank angle (degrees)	.428*
Bank material	-.273*
Length of tree roots above water (m)	.283*
Length of tree roots bellow water (m)	.261*
Bank emergent broad leaved vegetation (coverage)	-0.18
Bank emergent narrow leaved vegetation (coverage)	-.223*
Bank face bare (coverage)	.414*
Bank face grass (coverage)	-.239*
Bank face herbs (coverage)	-.288*
Bank face shrubs (coverage)	-0.001
Bank face trees (coverage)	0.008
Bank top bare (coverage)	0.101
Bank top grass (coverage)	-0.109
Bank top herbs (coverage)	0.073
Bank top shrubs (coverage)	-0.031
Bank top trees (coverage)	-0.027
Channel vegetation (coverage)	-0.004
Channel flow	-0.191
Water depth (m)	0.041
Water width (m)	0.029
Planar angle (degrees)	.306*

Table 4.6 (continued)

Spearman's rho	Burrows number
Channel material	0.043
Channel boulders (m^2)	0.017
Channel large wood (m)	-0.043
Shelter availability index	0.168
Shelter pressure index	-0.164

In order to further investigate the multidimensionality of the influence of habitat characteristics, principal component analysis was performed on 28 variables including variables describing habitat characteristics, crayfish number and shelter pressure index. On the basis of scree plot and eigenvalues >1, six principal components were identified that cumulatively explain 57% of the variance in the data set (Table 4.7). Variable loadings are presented in the Table 4.8. Principal component 1 (PC1) defines a gradient from low coverage by herbaceous vegetation to high grass coverage, while the PC2 relates to the typical characteristics of the river bank at the outside bank of meander (high bank height, bank angle and planar angle as well as bare bank face). PC3 relates to presence shelter and, related to that low shelter pressure index. The PC4 is related to lentic character with deep water, small size of channel particles, smooth water flow and low. In addition to that it is characterised by high crayfish numbers and high shelter pressure index. PC5 strongly relates to presence of crayfish and shelter availability, while PC6 represents a gradient of increase in herbs coverage. Scatter plots and bi-plots for the six PCs illustrated the difference in PC scores between bank sections with and without burrows (Figure 4.7). Overall there is considerable overlap in PC scores between two types of bank sections. Spearman correlation has shown that signal crayfish number is statistically significantly positively correlated with PC2 and negatively with PC6 (Table 4.9). These two correlations translate into the trend of burrows occurrence on the bank sections with characteristics of the outside meander bend and low presence of herbs on the bank face.

Table 4.7 Eigenvalues and cumulative variance explained for Principal Component Analysis performed on the habitat variables and a number of crayfish.

Principal component	Eigenvalue	% of Variance	Cumulative%
PC 1	4.102	14.65	14.65
PC 2	4.017	14.346	28.996
PC 3	2.428	8.671	37.667
PC 4	2.234	7.977	45.644
PC 5	1.706	6.093	51.738
PC 6	1.612	5.757	57.494

Table 4.8 Principal component loadings for the variables and interpretation of the PCs for analysis of the influence of habitat and signal crayfish population density on a number of burrows.

Principal component	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Interpretation	Herbs to grass	Outside meander	Shelter presence	Lentic character	Crayfish presence	Herbs presence
Bank top grass (coverage)	0.935	0.127	-0.062	0.119	0.081	0.048
Bank top herbs (coverage)	-0.927	-0.158	0.078	-0.163	-0.077	-0.019
Bank face grass (coverage)	0.723	-0.491	-0.051	0.083	-0.103	-0.279
Bank emergent narrow leaved vegetation (coverage)	0.474	-0.463	-0.154	0.205	-0.179	-0.268
Bank height (m)	0.243	0.783	0.051	-0.113	-0.085	-0.103
Planar angle (degrees)	-0.064	0.706	0.098	0.069	-0.016	0.091
Bank angle (degrees)	0.055	0.668	0.120	0.171	0.073	-0.222
Bank face bare (coverage)	0.039	0.654	0.124	0.027	-0.058	-0.568
Length of tree roots bellow water (m)	-0.181	0.106	0.856	0.040	0.112	-0.047
Shelter availability index	-0.103	0.003	0.742	-0.067	0.592	-0.094
Length of tree roots above water (m)	0.053	0.302	0.714	0.102	-0.082	-0.119
Shelter pressure index	0.007	0.028	-0.590	0.435	0.104	0.166
Water depth (m)	0.297	-0.029	0.055	0.789	-0.026	-0.053
Channel material	-0.190	-0.067	0.026	-0.761	-0.019	-0.044
Channel flow	0.067	-0.008	0.003	-0.568	-0.052	0.413
Channel large wood (m)	0.124	-0.098	0.133	-0.126	0.835	-0.039
Crayfish number	-0.042	0.035	-0.093	0.411	0.768	-0.011
Water width (m)	-0.023	0.154	0.071	-0.153	0.446	-0.342
Bank face herbs (coverage)	-0.516	-0.235	-0.066	-0.078	0.076	0.709
Bank material	0.042	0.010	-0.214	0.013	-0.277	0.614
Channel vegetation (coverage)	-0.095	-0.084	-0.078	-0.127	0.052	-0.140
Bank top shrubs (coverage)	0.028	-0.044	0.023	-0.065	-0.167	0.058
Bank emergent broad leaved vegetation (coverage)	0.254	0.075	-0.226	-0.268	-0.050	0.376
Bank face shrubs (coverage)	-0.030	0.010	0.019	-0.039	0.025	-0.060
Channel boulders (m^2)	-0.125	-0.014	0.048	0.196	-0.118	0.102
Bank top trees (coverage)	-0.333	-0.018	0.238	-0.029	0.006	0.191
Bank face trees (coverage)	-0.086	-0.120	0.251	-0.056	0.068	0.074
Bank top bare (coverage)	-0.056	0.197	-0.097	0.275	-0.031	-0.183

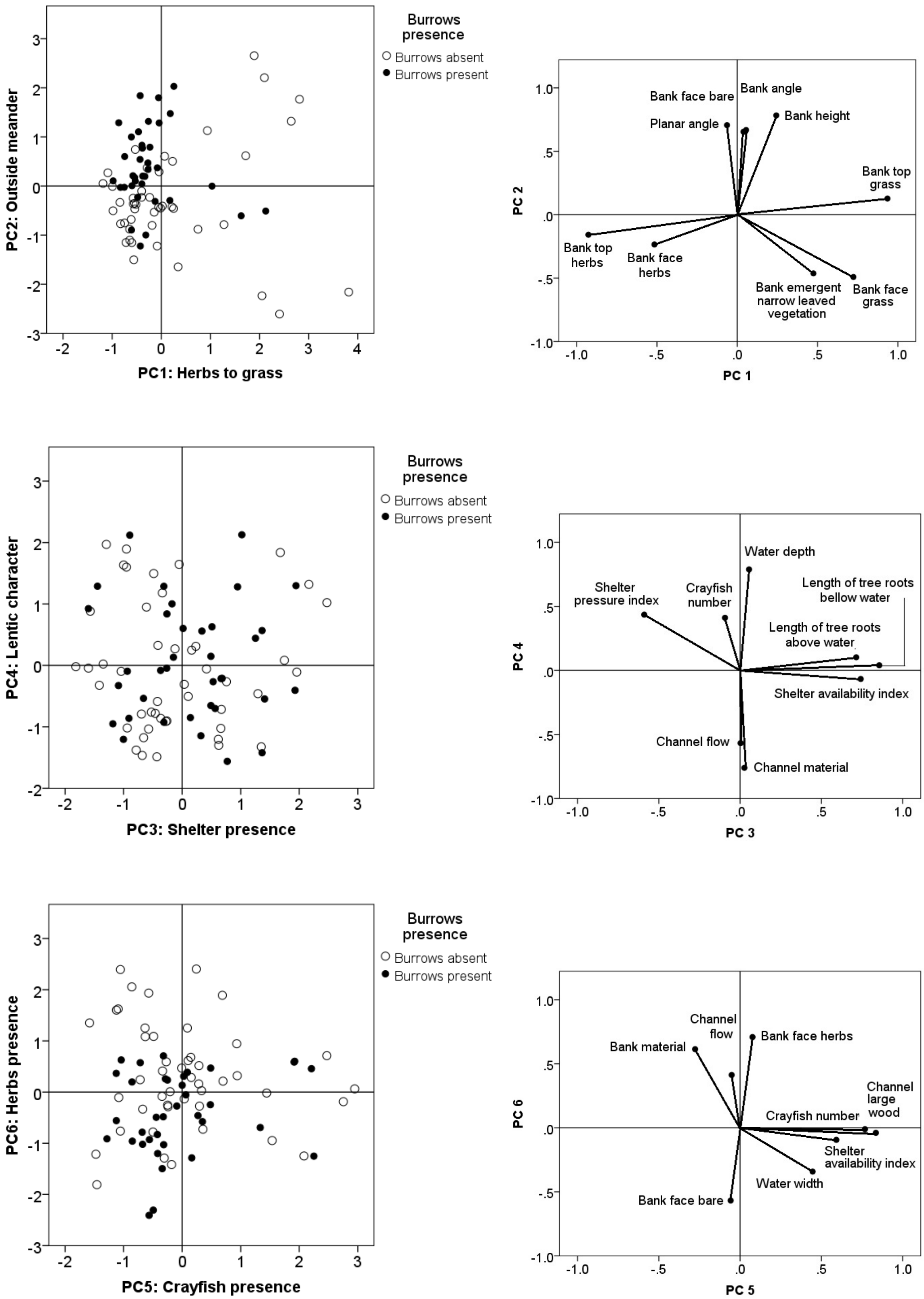


Figure 4.7 Scatterplots and biplots for principal component scores for sites with and without burrows presence.

Table 4.9 Spearman’s rank correlations between burrows number and principal component scores. Significant values (p<0.05) are indicated with *.

Spearman's rho	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Burrows number	-0.088	.409*	0.171	0.026	-0.103	-.351*
Sig. (2-tailed)	0.434	0	0.125	0.818	0.358	0.001
N	82	82	82	82	82	82

4.3.4 Factors influencing presence of erosion on river banks

The length of the eroded bank was correlated statistically significantly with seven habitat variables as well as with the number of burrows on bank sections (Table 4.10). Spearman correlation revealed that length of erosion was higher on bank sections with a high number of burrows, high bank height, steep bank angle, high coverage of bare banks and low coverage of herbs and trees. Channels with smooth flow and large surface covered with boulders also experienced higher rates of erosion. Again, correlations are relatively weak, the length of the eroded bank had the strongest correlation with bare bank face (R=0.496) and bank angle (R=0.477).

Table 4.10 Spearman’s rank correlations between length of eroded bank and factors that influence it: number of burrows, the number of crayfish and habitat variables. Significant values (p<0.05) are indicated with *.

Spearman's rho	Eroded bank length (m)
CPUE	-0.078
Burrows number	**.354***
Bank height (m)	**.361***
Bank angle (degrees)	**.477***
Bank material	-0.109
Length of tree roots above water (m)	0.19
Length of tree roots bellow water (m)	-0.001
Bank emergent broad leaved vegetation (coverage)	0.02
Bank emergent narrow leaved vegetation (coverage)	-0.202
Bank face bare (coverage)	**.496***
Bank face grass (coverage)	-0.123
Bank face herbs (coverage)	**-.351***
Bank face shrubs (coverage)	-0.105
Bank face trees (coverage)	-0.088
Bank top bare (coverage)	-0.095
Bank top grass (coverage)	0.039
Bank top herbs (coverage)	-0.002
Bank top shrubs (coverage)	-0.149

Table 4.10 (continued)

Spearman's rho	**Eroded bank length (m)**
Bank top trees (coverage)	**-.388***
Channel vegetation (coverage)	-0.006
Channel flow	**-.276***
Water depth (m)	0.118
Water width (m)	0.114
Planar angle (degrees)	0.189
Channel material	-0.005
Channel boulders (m^2)	**.290***
Channel large wood (m)	-0.028
Shelter availability index	0.022
Shelter pressure index	-0.118

However, since correlation does not automatically imply causation, it was important to test whether burrows and erosion simply both occur in the same conditions or presence of burrows genuinely contributes to erosion. Therefore three variables identified as positively correlated with occurrence of erosion are identified (bank height, bank angle, bare bank face) and bank sections which had all three values higher or equal to respective median (bank height >= 0.8 m; bank angle 65; bare bank face 0) were selected for analysis. This ensured that analysis is done for bank sections which already favoured erosion and therefore provide better insight into role of burrows. Spearman's correlation has shown that there is a positive correlation between burrows and erosion (R=0.385, p=0.05). This indicates that even on sites where erosion likelihood is high, presence of burrows increases likelihood of erosion. Figure 4.8 a) shows presence and absence of records of erosion on bank sections with and without burrows. While 2 out of 10 (20 %) of bank sections without burrows had records of erosion, presence of burrows raised that likelihood almost to 10 out of 18 (55 %). Mean erosion length on bank sections with no burrows is 0.80 m (median 0) while on sections with burrows is 2.22 m (median 2), however, that difference is not statistically significant. (p = 0.110) (Figure 4.8 b).

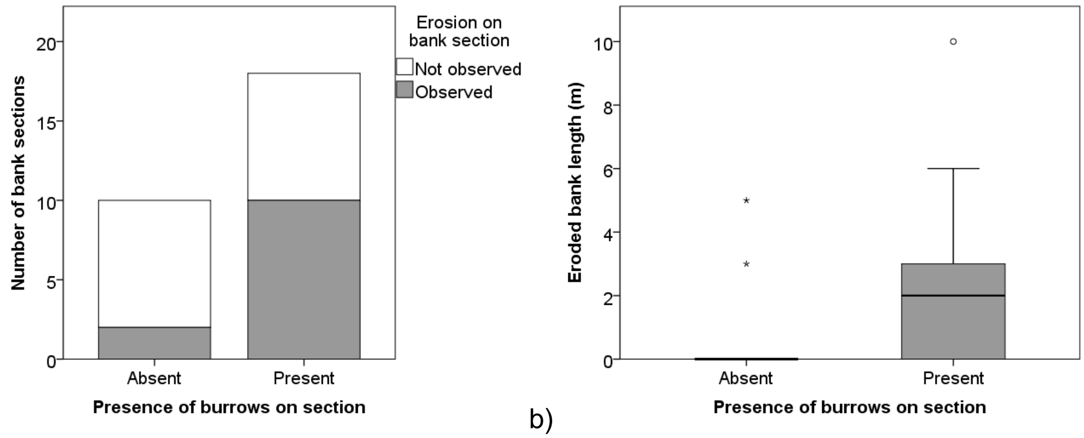


Figure 4.8 Illustration of relationship between crayfish burrows and eroded bank, done for 28 bank sections which had characteristics which lead to occurrence of river bank erosion (further clarified in text) a) Number of bank sections with and without erosion for bank sections with and without burrows. b) Boxplot for length of eroded bank shown for bank sections with and without burrows.

4.3.5 Interaction between burrows above and below water line

A total of 199 burrows were recorded and they were evenly distributed above (101 burrows) and below (98 burrows) water line (Figure 4.9). When analysed on the basis of individual bank sections, Spearman correlation revealed that number of burrows above and below water line was statistically significantly, positively correlated ($R=0.747$, $p=0.001$).

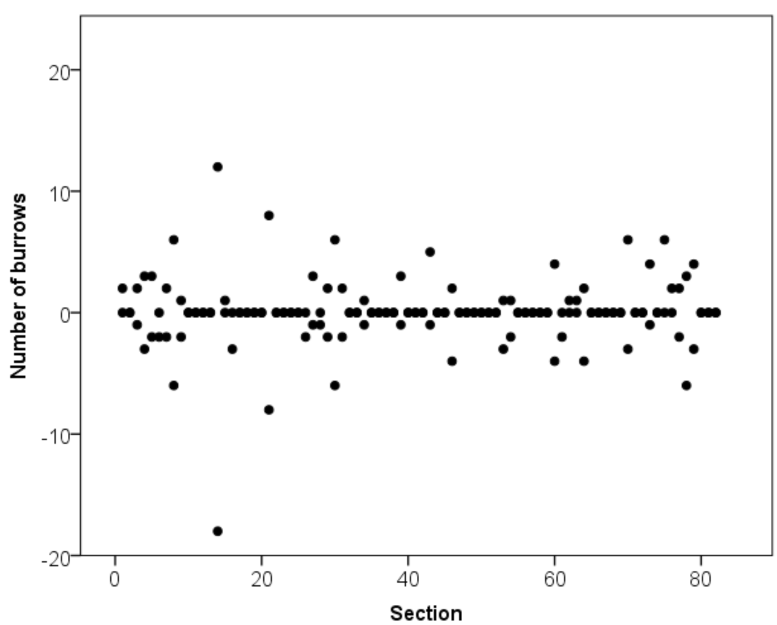


Figure 4.9 Number of burrows above and below water line along the 82 surveyed bank sections. For each bank section, positive values indicate a number of burrows above and negative ones a number of burrows below the water line.

4.4 Discussion

Presented results provide an important insight into ecosystem engineering impact of signal crayfish on river banks. In comparison with earlier studies with the same focus (Guan, 1994; Stanton, 2004; Roberts, 2012), this survey provides an additional insight due to several key aspects. Firstly, it is the first reach based survey that is based on reporting a number of burrows with clear reference to the length of bank surveyed. That enables interpretation of the results within the wider context of spatial scale analysis of river systems. Secondly, due to detailed observation procedure and records of burrows above and below water, a much more accurate assessment of burrows numbers is gained. Thirdly a small spatial extent of the survey in combination with detailed observation of habitat characteristics, crayfish population density, burrow occurrence and signs of erosion enabled a detailed assessment of the interaction between those factors. Finally, information on the correlation between burrows occurrence above and below the water line provided critical information on which analysis in following two chapters (Chapter 5 and 6) relies.

4.4.1 Exploratory analysis of variables

Crayfish were found on all, but one transect. However, even on that one transect, crayfish are likely present, but in a lower number. It is known that signal crayfish are adjustable to a wide range of habitat conditions (Naura and Robinson, 1998; Almeida et al. 2013; Wutz and Geist, 2013) and therefore, finding crayfish on all but one transect of the same river reach is expected. The total number of crayfish caught was 576, but it is important to keep in mind that this is only the number of caught animals. The linear regression in Figure 4.4 predicts that if trapping continued, by the end of day 12, no more crayfish would be caught. However, on the basis of several trapping reports (Peay, 2001; Hudina et al. 2009; Moorhouse et al. 2011; Moorhouse et al. 2014), that is not likely to occur. Due to the process known as “trap shyness”, and well known antagonistic interactions between individual crayfish (Figler et al. 1999; Alonso and Martínez, 2006; Hudina and Hock, 2012) crayfish avoid each other, and therefore the number of crayfish caught in the early days is limited. In addition to that, in the early days, it is usual that larger animals are caught first and due to the crayfish antagonistic interactions suppress capture of smaller animals. Since most crayfish populations fit the normal distribution of sizes (Holdich, 2002), smaller size classes usually have much higher numbers of animals. Therefore, a total number of crayfish present on the studied reach and individual transects, even with a conservative estimate is at least double that of crayfish caught during the five days period.

The crayfish population estimates are fairly consistent with other similar studies done on the basis of catch per unit of effort method. With similar trap density, Hudina et al. (2009) caught between 1 and 6 individuals, while Moorhouse et al. (2014) caught between 5 and 9 signal crayfish per trap per night. Pattern detected in results, characterised by relatively high variability in crayfish numbers within reach and coupled with a slightly higher number of caught males than females is also found by Wutz and Geist (2013). On the basis of comparison with stated studies, it can be said that results presented in this study fit into the current understanding of healthy signal crayfish population. This makes studied crayfish population a representative object for the study of the impact of the signal crayfish population density on its overall ecosystem engineering activity.

Signal crayfish burrows were found at 36 (44%) riverbank sections, indicating that on more than half bank sections signal crayfish were using other forms of shelter. Even more importantly, the number of burrows (199) is much lower than the number of signal crayfish (significantly more than 576). Therefore the ratio of crayfish per burrow is at least 1:3 and probably around 1:5 and possibly much higher. Therefore, this finding represents a first description of the ratio between signal crayfish population and burrow densities on the reach scale. Since there is sufficient space for digging extra burrows, such a disparity means that signal crayfish dig burrows only in specific circumstances.

Signal crayfish burrows density on the spatial scale of reach (0.24 burrows per metre of the bank) is much lower than density reported by Guan (1994) which ranged from 0.47 to 3.7 burrows per metre. Similarly, Stanton (2004) based his survey only on burrows below the water line and still reported higher burrow densities (2.4 burrows per m of the bank). However, these differences can be explained since both Guan (1994) and Stanton (2004) studies are focused on shorter stretches of river with high burrow densities, while reach used in this survey is longer and includes both areas of high and low burrows presence. Therefore the studied reach is more representative of the broader river length. Once this survey is analysed on the bank section level, mean values of 0.24 burrows per metre of the bank and maximum values of 3 burrows per metre of the bank are similar to the studies by Guan (1994) and Stanton (2004).

Erosion was found on 16 bank sections (20%) which indicates that a special set of conditions is required to trigger it. Due to lack of studies using the stream reconnaissance method (Thorne, 1998) it is hard to compare these numbers to other similar surveys. While visual assessment obtained in this survey cannot be translated into numerical values, comparison with studies using erosion pins offers the best alternative insight for contextualising these results. Results obtained by Henshaw et al. (2012) show that erosion above a certain threshold during the summer period occurs at approximately 20% of locations. While that threshold differed between years, it can be said that erosion is a process with a wide range of values and presence of erosion on 20% of bank sections is within normal erosion occurrence.

The habitat characteristics of studied reach are within the range of variables as reported by similar studies. Roberts (2012) study in the Thames river catchment covered similar types of lowland, low energy rivers, while a study by Harvey et al. (2008) identified lowland rivers as one of the main river types in the nationwide dataset. Additionally, high values of planar angle, as well as wide range of bank slope angles demonstrate that a natural meandering regime is underway (Charlton, 2008). Riparian vegetation with variety in the density of trees densities as well as alternating ground cover dominated by either grasses or herbs means that it is representative of the wide range of land uses. Therefore, it is concluded that studied reach is representative of typical lowland river in the UK.

4.4.2 Can crayfish occurrence be explained by habitat parameters?

The increase in crayfish population density was associated with pool sections with a lot of large wood and overall shelter. These findings are consistently confirmed by both correlations and PCA. These findings are in line with previous findings regarding crayfish in general and signal crayfish in specific micro habitat selection (Holdich, 2002).

Crayfish, especially larger individuals usually caught in traps are known to be more strongly associated with pool sections in natural rivers (Faller et al. 2006). The pool sections, primarily characterised by deep water, offer extra protection from avian predators (Holdich 2002; Souty-Grosset 2006) and are therefore favoured by crayfish. In addition to that, usually slower water movement in pools in combination with the concave shape of bed channel, favour deposition processes (Charlton, 2008). That means that organic material is more likely to aggregate in the pool sections, ranging from large wood which serves as crayfish shelter to organic matter of various types like detritus which represent crayfish food (Holdich, 2002; Souty-Grosset 2006). Due to those factors, pool sections are known to be a preferred habitat of crayfish and therefore it was expected to find elevated signal crayfish numbers in pool sections.

The shelter is often identified as one of the main factors influencing and limiting crayfish populations (Holdich 2002; Souty-Grosset 2006). Both types of specific shelter known from the literature to be used by crayfish (presence of large wood and boulders) show strong correlations with signal crayfish density. In addition, tree roots and channel vegetation which were not identified individually, but contribute to a shelter availability index are known to be the additional refuge of crayfish (Blake et al. 1994).

The interaction of a studied population of signal crayfish and habitat parameters is in line with current knowledge about signal crayfish habitat preferences (Souty-Grosset, 2006). The relatively high population density of crayfish in combination with a predictable response to habitat characteristics indicate that this signal crayfish population is a healthy one and therefore representative of expected signal crayfish population responses in relation to burrowing.

4.4.3 Can burrows occurrence be explained by habitat parameters and crayfish presence?

Riverbank sections with characteristics of the outside meander bend are the most strongly dominant driver of a number of signal crayfish burrows. Outside meander bend is a feature of the naturally functioning river, in general associated with faster flow and dominance of erosion as the main process involving sediment (Charlton, 2008). In addition, it is characterised by tall, steep banks and sparsity of vegetation. There are several implications of those conditions for the signal crayfish and their tendency to burrow.

Faster water flow and higher rates of erosion reduce the amount of material that is accumulated on the river bottom, for instance large wood. Another type of shelter, riverbank vegetation is also less likely to occur due to the rapidly changing surface of the bank face. Therefore the sparsity of natural shelter can increase the incentive for the signal crayfish burrowing. Another influence of the faster rates of flow in the outside meander bend leads to less sediment deposition in and around burrows. This is important since burrowing animals spend a significant effort on maintaining cleanliness of burrows. Therefore by creating a burrow in areas of faster flow, signal crayfish achieve easier maintenance. An additional positive aspect of higher rates of flow, the more rapid exchange of water in and out of burrows. The studied reach is positioned downstream from middle-sized town (Whitney, population 27,000) and also has a significant portion of catchment as an agricultural area, therefore an occasional lack of oxygen can occur. Since crayfish breathe through gills (Holdich, 2002) and depend on diffusion of oxygen from surrounding water, the increase in the supply of water can lead to more oxygen supply. Again, this means that positioning of burrows in the areas of outer meander bend makes it more likely for crayfish to weather occasional oxygen deficiencies.

An additional feature that correlated with an increase in a number of burrows was the presence of tree roots above and below water. This finding can seem contradictory since it is known that tree roots are often used as a shelter for crayfish (Souty-Grosset, 2006) and therefore there would be no need for crayfish to expand energy to dig additional burrows. However, when assessed from the point of view of crayfish population, a different perspective emerges. It can be argued that crayfish prefer the bank sections with tree roots since those provide an extra shelter. However, once that shelter becomes occupied with a high number of crayfish, due to antagonistic interactions between crayfish (Hudina and Hock, 2012) the incentive for individual crayfish to move and create an additional shelter nearby increases. Therefore this example shows that presence of shelter can have an affirmative effect on the creation of burrows since it attracts crayfish in the first place and leads to digging burrows in order to accommodate a growing population.

4.4.4 Can erosion occurrence be explained by habitat parameters, crayfish and burrows presence?

The length of the eroded bank was, similarly to the presence of burrows, associated with outer meander bend type of habitat. The presence of burrows also contributed to an increase in the length of erosion. In total, twelve variables statistically significantly impacted the length of erosion with six of them identified by both correlations and PCA. Outside meander is well known to be a micro location of the erosion in naturally meandering rivers (Thorne, 1982). The features identified in results are also well known in the literature to be associated with the outside meander bend: high bank height, steep bank angle, sharp planar angle, a high proportion of bare bank face and low coverage of vegetation, which primarily due to active erosion does not manage to establish itself. Due to the usually deeper water, the flow of water in the channel is smooth and not rippled as it was observed in the results. Therefore association of increased bank length influenced by erosion and variables that are usually associated with erosion prone areas is expected. Signal crayfish burrows are another factor that statistically significantly correlated with the increase in the length of erosion. It is known that change in the surface of the river bank influences near bank flow (Ozalp et al. 2010; Jackson et al. 2015) and can lead to mass failure (Fox and Wilson, 2010). Therefore there is a theoretical background that explains field observations presented in this chapter leading to the strong likelihood that presence of burrows contributes to river bank erosion.

4.4.5 Interaction between burrows above and below water line

The number of burrows above and below water line was almost identical and two types of burrows correlated statistically significantly. Roberts (2012) also recorded burrows above and below water and found mixed results, however, those results were aggregated per reach and no correlation on the same site was done. The presented results show that on the bank section scale, burrows above water line can be considered a relatively reliable predictor of the burrows numbers below the water line.

4.5 Conclusion

Signal crayfish were present at almost every bank section (98%). A total number of 576 crayfish caught on the 410 m long reach which corresponds to 1.4 crayfish per one meter of the river channel length. It is important to note that the number of crayfish is expressed as a catch per unit of effort which is good for comparing different bank sections, but overall represents an underestimation of the total crayfish number. This is an underestimation of a number of grown up crayfish and even more so for the total population. Signal crayfish numbers varied dramatically in a number of crayfish caught, from 0 to 64 caught (mean 14). The main microhabitat preference was toward bank sections with the presence of large wood and overall shelter in the channel, wider and deeper water, and fine sediment. These microhabitat preferences were in line with current understanding of the crayfish microhabitat selection. These findings imply that chosen reach was a good representation of the high population densities that are known to exist in many rivers in the UK.

Burrows were present on 36 out of 82 bank sections (44%). The total number of recorded burrows was 199, which put in the context of the length of the river bank surveyed corresponds with 2.4 burrows each ten meters of the bank. Both these numbers imply high burrow density on this site, which corresponds to some of the higher densities recorded and therefore provides a good context for studying burrows. A number of burrows per bank section varied greatly, ranging from 0 to 30 (mean 2.4). The prime drivers of burrow distribution were high bank angle and height, sharp planar angle, the presence of bare bank face and absence of different types of vegetation (grass, herbs) and presence of tree roots. These findings are comparable with previous studies of signal crayfish burrowing. Signal crayfish population density did not have a statistically significant impact on the presence of burrows. This can be attributed to the changing microhabitat in terms of vegetation in comparison with the relatively long duration of the burrows.

Erosion was recorded on 16 out of 82 (20%) bank sections. The total length of the eroded bank was 59 m, what on average equates to 0.7 m of each ten metres long bank section was influenced by erosion. Since not many studies have used similar methodology, these numbers cannot be readily compared to other rivers. However, since the same methodology was used on each bank section, it enables comparisons in context of this survey. The length of the eroded river bank varied between 0 and 10 m (mean value 0.72 m). Burrows number was statistically significantly positively correlated with the occurrence of erosion. The other contributing factors were high bank angle and height, the presence of bare bank face and absence of vegetation (herbs and trees), smooth channel flow and presence of boulders.

A number of burrows above and below waterline correlated statistically significantly. This enabled use of above waterline burrows observations as a reliable tool to assess burrows over a wide range, an approach that will be used in the following chapters. Still, due to the potential difference in signal crayfish burrowing behaviour in different habitats, this approach should be used with caution.

CHAPTER 5: Signal crayfish as ecosystem engineer at the reach in catchment scale

5.1 Introduction

This chapter aims to provide an insight into signal crayfish burrowing on the reach spatial scale. Signal crayfish burrowing in Europe was first reported by Guan (1994) who provided basic information about burrow dimensions and dynamics of burrowing at several sites on a single study reach. Stanton (2004) added additional insight by demonstrated an increase in burrow densities in the four year period at several dozen of sites on a single river, as well as illustrating the tendency of signal crayfish to burrow in banks with a high clay content. Roberts (2012) greatly expanded the knowledge about influence of habitat on burrows presence or absence on 24 sites in the Thames catchment by revealing a tendency of signal crayfish to burrow in the river banks with high variance in vegetation structure. However, the exact extent of signal crayfish burrowing in terms of proportion of the river bank that is impacted as well as habitat characteristics that lead to burrowing remained unexplained. Therefore, it can be said that extent of signal crayfish burrowing as well as factors influencing burrows still require clarification.

In addition to observance of burrows and conditions that lead to burrowing, all three previous crayfish burrowing studies also focused on the dimensions of burrows. Burrows dimensions reached up to 65 cm and in all three studies the majority of burrows had s single cylindrical shape (Guan, 1994; Stanton, 2004; Roberts, 2012). However, combining the information about burrows volume and their density in order to study the contribution to the sediment supply of the river remained unanswered.

The reach scale is one of the basic spatial scale units used in the river research (Charlton, 2008) and it is often described as a building block of the catchment network (Paz and Collischonn, 2007). Despite that, definition of the river reach is not consistent and existing definitions can broadly be divided as either operational or functional (Parker et al. 2012). Operational definitions describe the reach in terms of fixed spatial terms, mainly by river length (Raven et al. 1998) or number of river widths. Functionally reach is defined as stretch of river composed of homogeneous geomorphological units (Eyquem, 2007). In the case of monitoring of rivers in the UK, the most widely used survey, the River Habitat Survey defines a reach as a 500 m long stretch of the river (RHS, 2015). Following that definition, river reach is used as a basic spatial scale for a diverse set of studies covering influence of rock type on sedimentological and vegetation characteristics of the reach (Harvey et al. 2008), distribution of aquatic species (Naura and Robinson, 1998) and environmental assessment and catchment planning (Raven et al. 2000).

In addition to being an appropriate spatial scale to study geomorphological processes, a 500 m river reach is a meaningful scale to study signal crayfish. Signal crayfish migration rates vary significantly, Stanton (2004) detected the maximum movement of hundred meters over two years period, while Bubb et al. (2004) recorded higher migration rates of up to 790 m during a four months period. While those are the maximum values, both authors reported that most crayfish were much more sedentary, which means that it can be expected that single crayfish will spend significant periods of time within one reach. On the basis of the stated, river reach is the appropriate spatial scale to study signal crayfish burrowing.

On the basis of stated knowledge and knowledge gaps, following four research aims are identified:

1. To quantify the extent and main traits of burrowing on the reach scale in the Thames catchment.
2. To assess the spatial organisation and local intensity of signal crayfish burrowing within seven tributaries of the River Thames.
3. To explore relationships between crayfish burrow presence and extent and biophysical river habitat characteristics.
4. To estimate the volume of sediment excavated due to crayfish burrowing within the surveyed river stretches.

5.2 Methodology

5.2.1. Survey design

Unlike the previous chapter which was focused on individual reach, this chapter uses an extensive research design (Richards, 1996) using data from a large number of sites in order to identify general trends. It is focused on the Thames catchment and a total of 103 reaches are chosen following procedure described in the Chapter 3.

The main focus of this analysis is to evaluate the potential for using existing secondary data sources to explain and predict the occurrence and intensity of burrowing by signal crayfish at the reach scale of river systems. Therefore, for this analysis, the basis for the choice of sites was the Environment Agency's River Habitat Survey database (RHS, 2015). Reaches included in the RHS data base were selected using a stratified random sampling design in order to ensure representative longitudinal coverage along each tributary. RHS database provides an extensive source of data on physical habitat characteristics and that information was supplemented with map derived (Digimap 2015) and geological information (BGS 2015). Information from those three, publicly available sources was combined with visual observation of crayfish burrows along the selected river reaches. Finally, information regarding number of present burrows were coupled with the information on the volume of average burrow in order to assess the amount of sediment excavated and enable interpretation in the context of the studied river systems.

5.2.2 River Habitat Survey variables and derived indices

The Environment Agency's River Habitat Survey (RHS, 2015; Environment Agency, 2003) is the principal method for assessing and characterising river habitat in England and Wales. RHS provides a standard field method for recording the physical character of rivers along 500m 'reaches' through visual assessment and simple measurements of channel dimensions, supplemented by map-derived variables (e.g. slope). RHS was designed to provide a rapid and reproducible field method requiring minimal 'expert' training (Raven et al., 1998) and has been applied across the UK to produce a large database of biophysical river properties for over 20,000 surveyed reaches. The field survey methodology records observations of the channel and bank features at ten equally spaced 'spot-check' transects, together with a 'sweep-up' component designed to capture the general river characteristics and infrequent features not occurring at spot-checks (Environment Agency, 2003).

The RHS data set contains a large number of variables (> 100) reported in nominal, ordinal or ratio format. In order to summarise reach-scale biophysical properties and make effective use of categorical data, RHS-based indices have been used in previous research to explore catchment controls on sequences of geomorphic units (Emery et al. 2003), classify the biophysical characteristics of urban rivers (Davenport et al. 2004) and explore relationships between physical habitat and rock type (Harvey et al. 2008). This chapter uses a combination of raw variables and derived indices to represent key landscape-scale and reach-scale factors that may influence the occurrence of crayfish burrowing and stability of river banks.

Six landscape, eight reach scale and two habitat quality indices were derived from the RHS database (RHS, 2015) and Digimap online service (Digimap, 2015) following Davenport et al. (2004), Emery et al. (2003) and Harvey et al. (2008) (Tables 5.1, 5.2 and 5.3). Landscape scale indices provide information on the landscape-scale drivers influencing the reach: distance from source, source altitude, site altitude, slope, cross sectional area (CSA) and total stream power index (TSPI). Reach scale physical indices represent the unit stream power (USPI), and calibre of bed and bank material (SEDCAL and BANKCAL), while BANKPROF and FLOW indicate profile of the river bank and dominant type of flow. Reach scale vegetation indices represent the complexity of channel vegetation (INCHANVEG) and bank vegetation (BANKVEG) and riparian tree cover (TTS). Two summary indices are also calculated from RHS data: a Habitat Modification Score (HMS) which represents the level of anthropogenic disturbance to the river channel and surrounding corridor and a Habitat Quality Assessment (HQA) score based on features considered to be of importance to wildlife. In further text these 16 variables and indices are erred to as habitat variables. In addition, bedrock geology was extracted from the British Geological Survey online service (BGS, 2015) and grouped into following major groups: chalk, other limestone, sandstone and other sedimentary. Likewise superficial geology was divided into two groups: alluvium (clay, silt, sand and gravel type) and the other superficial deposits.

Table 5.1 Six landscape indices used to characterise reach sites.

	Variable / Index	Variable source, index calculation and key erences	Reason for inclusion in burrow analysis
Landscape indices	Distance from source / km	Read from Digimap (2016)	Position in catchment
	Source altitude / m	Read from Digimap (2016)	Reach-scale energy conditions, representing wider morphohydraulic environment
	Site altitude / m	Read from Digimap (2016)	
	Slope / m/km	Calculated from Digimap (2016) data as slope = y/x where y is vertical difference between two contour lines, x is horizontal distance between 2 points of intersection of river and contour line (EA Manual).	
	Cross sectional area (CSA) / m^2	Channel width multiplied by the sum of smaller between right and left bank top height and the water depth (Emery 2004)	Indicator of channel size
	Total stream power index (TSPI) / m^3km^{-1}	TSPI=CSA*slope (Emery 2004)	Indicator of stream power and hence hydraulic stress

Table 5.2 Five local, reach scale physical indices used to characterise reach sites.

	Variable / Index	Variable source, index calculation and key erences	Reason for inclusion in burrow analysis
Local-scale physical indices	Unit stream power index (USPI) / m^2km^{-1}	USPI=TSPI/river width (Emery 2004)	Scaled indicator of stream power and hence hydraulic stress (broad scale)
	Bed sediment calibre (SEDCAL)	SEDCAL = (-8*BO-7*CO-3.5*GP-1.5*SA+1.5*SI+9*CL) / (BO+CO+GP+SA+SI+CL) ; where boulders (BO), cobble (CO), gravel and pebble (GP), sand (SA), silt (SI) and clay (CL) represent number of transect profiles allocated to each sediment class (Emery 2004)	Indicates availability of larger clasts (shelter) and bed stability
	Bank sediment calibre (BANKCAL)	BANKCAL = (-8*BO-7*CO-1.5*GS+1.5*EA+9*CL) / (BO+CO+GS+EA+CL) ; where boulders (BO), cobble (CO), gravel and sand (GS), earth (EA) and clay (CL) represent number of transect profiles allocated to each sediment class (Emery 2004)	Indicates characteristics of bank material into which burrows are dug
	Bank profile (BANKPROF)	Left bank (S+V) + right bank (S+V); where Steep (>45^{o}) S = (1.5*P+3*E) Vertical V = (1.5*P+3*E)	Indicates the availability of steep/vertical bank faces for burrowing
	Flow type (FLOW)	FLOW = (1*NP+2*SM+3*UP+4*RP+5*UW+6*BW +7*CF+8*CH+9*FF) / (NP+SM+RP+UW+BW+CF+CH+FF) where no perceptible flow (NP), smooth flow (SM), upwelling (UP), unbroken standing waves (UW), broken standing waves (BW), chaotic flow (CF), chute flow (CH) and free fall (FF) represent the number of transects allocated to each flow type.	Indicates hydraulic environment (occurrence of smoother or rougher flow types throughout the reach) and hence hydraulic stress/ shelter requirements.

Table 5.3 Three vegetation and two overall indicators of habitat modification indices used to characterise reach sites.

	Variable / Index	Variable source, index calculation and key erences	Reason for inclusion in burrow analysis
Local scale vegetation indices	In channel vegetation index (INCHANVEG) absent (A), present (P), extensive (E) represent number of spot checks at which each vegetation type and abundance was recorded	INCHANVEG = EH+EM+SB+SF+SL+FA+RF ; where Emergent broad leaved EH=(0*A+1.5*P+3*E)/(A+P+E) Emergent reeds EM=(0*A+1.5*P+3*E)/(A+P+E) Submerged broad leaved SB=(0*A+1.5*P+3*E)/(A+P+E) Submerged fine leaved SF=(0*A+1.5*P+3*E)/(A+P+E) Submerged linear leaved SL=(0*A+1.5*P+3*E)/(A+P+E) Filamentous Algae FA=(0*A+1.5*P+3*E)/(A+P+E) Rooted floating leaves RF=(0*A+1.5*P+3*E)/(A+P+E) absent (A), present (P), extensive (E) represent number of spot checks at which each vegetation type and abundance was recorded	Indicates cover/complexity of instream vegetation types providing habitat diversity, food source, shelter.
	Bank vegetation index (BANKVEG)	BANKVEG = (0*B+1*U+2*S+3*C)/(B+U+S+C); where bare (B), uniform (U), simple (S) and complex (C) represent number of spot checks at which each vegetation type and abundance was recorded	Indicates complexity of bank vegetation and hence cover/accessibility at the bank face.
	Total tree score (TTS)	Left bank score + Right bank score; where No trees=0, Isolated=1, Regularly spaced=2, Occasional clumps=3, Semi-continuous=4, Continuous=5	Indicates complexity of the riparian zone and hence availability of cover/ allochthonous inputs.
Habitat quality	HMS	Habitat Modification Score (HMS) (EA 2015)	Indicates level of disturbance to river habitat by channel and bank modifications
	HQA	Habitat Quality Assessment (HQA) (EA 2015)	Indicates overall quality of habitat in the reach, including the presence of diverse habitat features.

5.2.3 Reach-scale survey of signal crayfish burrows

At each site identified from the RHS database, the presence and abundance of signal crayfish burrows was recorded. Sites were surveyed in either autumn 2013 or spring 2013, avoiding the summer period of highest vegetation cover that would have inhibited burrow observations. In terms of spatial scope, 103 sites that form a basis of this study offer an improvement in comparison with previous studies on crayfish burrowing (Guan, 1994; Stanton, 2004; Roberts, 2012) because of the higher number of sites included and their distribution between several different river catchments. The high number of sites and their balanced distribution between different tributaries ensured that findings are representative of the whole Thames catchment. At each studied reach, the aim was to record burrows along the 500 m RHS reach recorded in the RHS database. In practice, access limited the length of bank face along which burrows could be observed and hence the maximum bank length possible was surveyed for each reach. Taking the above into consideration, it is considered that this study provides a representative coverage of the Thames catchment basin.

Following the methodology used by Guan (1994) and Roberts (2012), observations were made by visual assessment from the channel or opposite bank with naked eye or binoculars in case of wider rivers. This method is considered appropriate, however, due to two issues, related to water transparency and terrain features must be observed. Due to water visibility issues, only burrows above water line were recorded (Figure 5.1). It is known that crayfish dig burrows only bellow water level (Holdich, 2002) and therefore burrows recorded above water line represent burrowing during high water level. However, for the purpose of this study it is assumed that burrows above water line are representative of overall burrowing activity. The second concern, the terrain features is considered to influence observation of burrows. For example, heavily vegetated banks often hide burrows, while steep, bare banks make burrow observation accessible. Due to the rapid nature of this study, bank vegetation was not disturbed in order to check for the presence of burrows behind the vegetation. Therefore due to the constraints caused by water turbidity on observations below the water line and the location of some burrows beneath vegetation, the number of burrows observed is almost certainly an underestimate of the total number of burrows present.

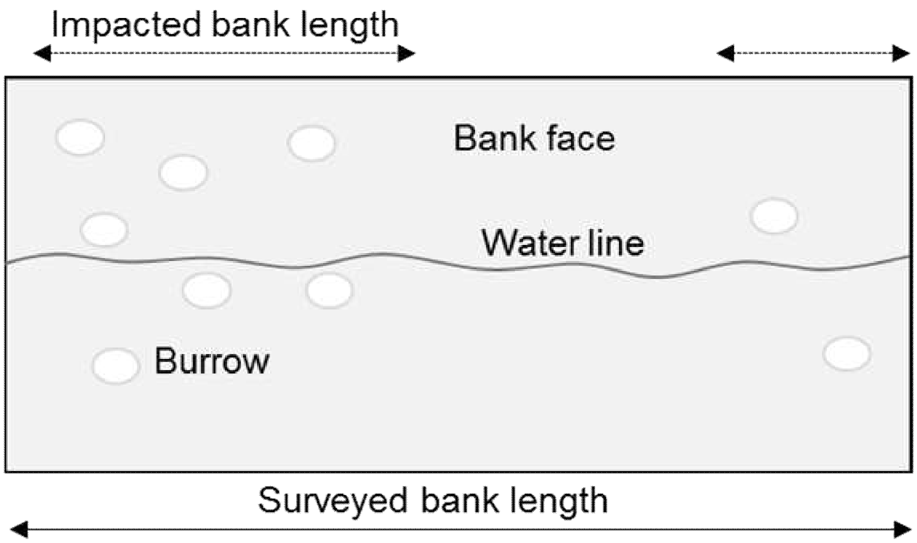


Figure 5.1 Diagram showing approach to the survey of signal crayfish burrows

While previous surveys on the extent of signal crayfish burrowing (Guan, 1994; Stanton, 2004; Roberts, 2012) recorded a number of burrows at a specific site, this survey aims to add an extra value by putting that information in context of the length of the surveyed bank (Table 5.4). Therefore during the field survey, four variables were collected: burrows presence or absence on site, the number of burrows, the length of the bank impacted by burrows and total surveyed bank length. All variables are expressed for the left and right bank combined. In order to put that information in context, from three variables collected in the field, three new variables that combined raw burrow information and site length were calculated: the proportion of bank length with burrows, burrows local density and burrows site density.

Therefore four metrics are used in further analyses and erred to as the burrowing metrics. Burrows presence and absence simply states whether at least one burrow was present on the studied reach. Burrow site density gives an overall status of burrowing over the length of whole reach, while the burrow local density indicates density on the impacted bank length. It is considered that number of burrows on site is more relevant for the assessment of sediment released by burrowing, while influence of burrowing on mass failure, which require a critical lack of stability is more influenced by localised burrowing density. During data analysis, for some analyses only reaches where at least one burrow is present are included, since burrows and crayfish can be absent from site because of the parameters that are not assessed in this study, for instance point pollution (Holdich 2002). The described field survey gave information on the total length of the bank surveyed at each reach and four variables related to burrowing (burrowing metrics).

Table 5.4 Variables collected on each reach during field survey

Variable	Description
Surveyed bank length (SBL) (m)	Total length surveyed on both river banks
Burrows presence / absence	Presence of only one burrow marked site as burrow positive
Length of bank with burrows (LBB) (m)	In case when distance between burrows is more than one metre, it is considered that each burrow impacts one metre of the bank
Total number of burrows recorded (NB)	Includes burrows above water level only
Proportion of bank length with burrows (%)	= LBB / SBL
Burrows local density (no. burrows per m of impacted bank length)	= NB / LBB
Burrows site density (no. burrows per km of surveyed bank)	= 1000 * NB / SBL

5.2.4 Estimation of volume of sediment excavated from burrows

The reach level information on crayfish burrow abundance was used to estimate the volume of material excavated from surveyed reaches. Previous research within the Thames catchment has identified average crayfish burrow lengths of 0.2 m, burrow entrance widths of 0.1 m and height of 0.08 m from simple measurements that assume a single chamber straight burrow (Roberts, 2012). Field observations confirmed that those values are also representative of burrows surveyed on studied sites. Burrow volume was calculated according to the volume of an elliptical cylinder, assuming a simple straight chamber with a single opening (Equation 1) in order to provide a conservative estimate of the volume of bank material excavated.

Burrow volume = $\pi ABL/4$

Where A = major axis (entrance width), B = minor axis (entrance height) and L = length.

Equation 1: Burrow volume calculation based on elliptical cylinder

5.3 Results

5.3.1 Extent of signal crayfish burrowing across surveyed sites

In total, 29 km of river bank were surveyed across 103 reaches on seven different tributaries of the River Thames. Frequency histograms (Figure 5.2) and descriptive statistics (Table 5.5) show the variability in length of bank surveyed and the extent of burrowing across the surveyed reaches. At no reach was it possible to accurately visually assess burrow presence along all 500m of left and right banks and therefore the length of bank surveyed varied between 70m and 800m, with a median bank length of 270 m. Signal crayfish burrows were recorded at 69 (67%) of the 103 surveyed reaches and following descriptive statistics of burrowing metrics is performed only for those 69 sites. In total, 917 m of bank length were impacted by burrows. This represents 3.15 % of the total surveyed bank length on all 103 sites (29,040 m) or 4.69 % of the surveyed bank length when only 69 sites with presence of burrows are considered (19,560 m). The length of impacted bank ranged from 1 to 50 m (median 8 m). The proportion of bank with observed burrows on individual reach ranged from 0.2% to 23.5% with a median of 3.2%. In total, 1,299 burrows were recorded, while the number of burrows recorded on individual reach ranged from 1 to 87 per reach (median 12). Burrows local density ranged from 1 to 3 burrows per m of impacted bank (median 1.3), while burrows site density ranged from 2 to 435 burrows per km of surveyed bank length (median 45). The frequency distributions for the length of impacted sections and burrow density show positively skewed distribution. This indicates that for the majority of reaches where burrows were observed, burrows were limited in number and spatial extent, but that there are is a small number of sites that appear to be more heavily impacted.

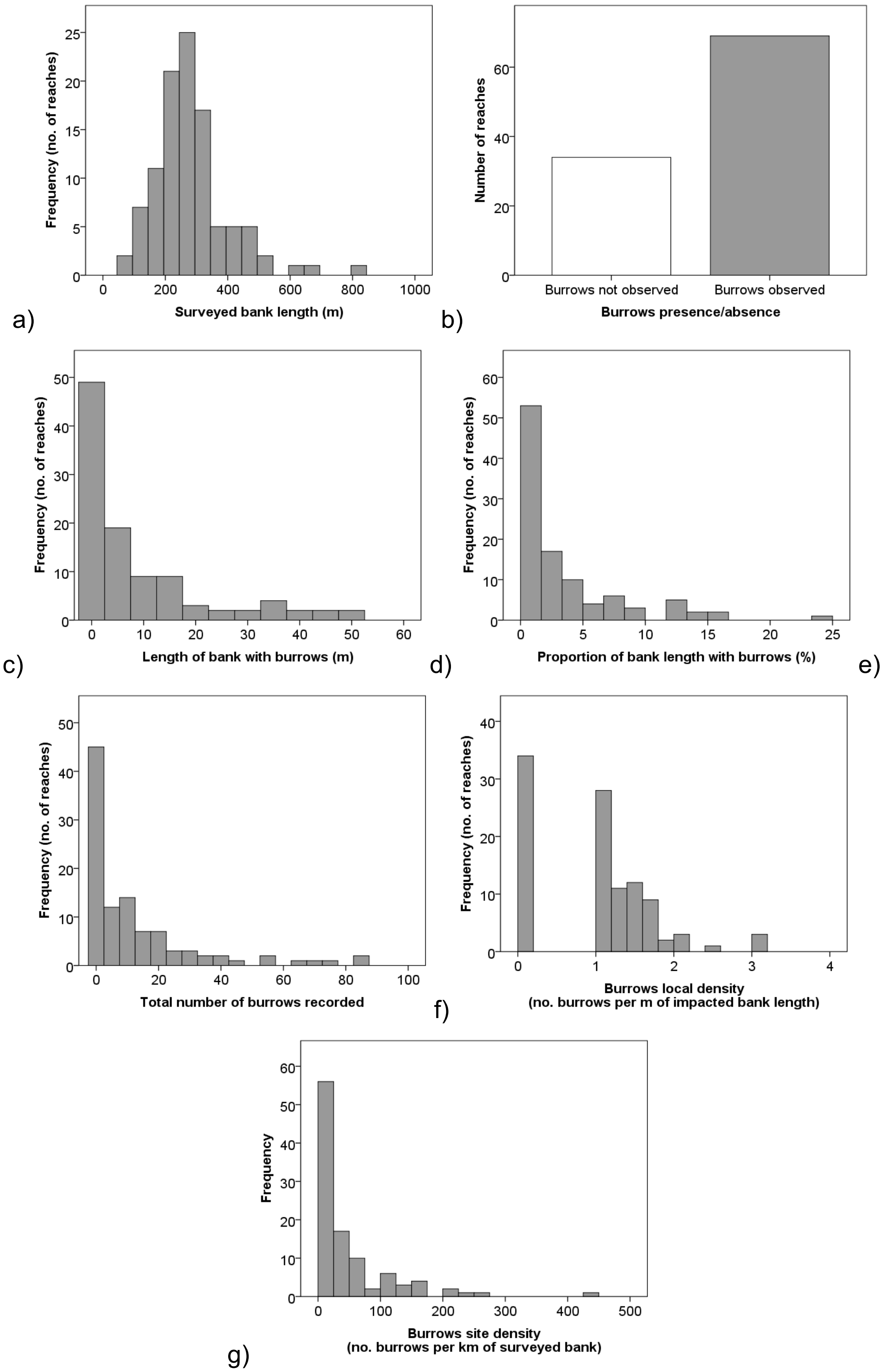


Figure 5.2 Frequency distribution for length of the bank surveyed (a) and burrow survey metrics (c-g) as well as number of reaches with and without burrows (b).

Table 5.5 Descriptive statistics for the length of surveyed bank and burrow survey metrics. Surveyed bank length is calculated for all 103 surveyed sites, while the rest of metrics only for 69 sites with the presence of burrows.

Variable	Mean	Percentile 25	Median	Percentile 75	Min	Max	Sum
Surveyed bank length (m)	282	200	270	320	70	800	29,040
Length of bank with burrows (m)	13.29	4	8	18	1	50	917
Proportion of bank length with burrows (%)	4.87	1	3.21	7	0.2	23.5	336
Total number of burrows recorded	18.83	4	12.00	24	1	87	1,299
Burrows local density (no. burrows per m of impacted bank length)	1.40	1	1.29	2	1	3	97
Burrows site density (no. burrows per km of surveyed bank)	68.77	17	45.45	100	2	435	4,745

5.3.2 Patterns of crayfish burrowing within and between tributaries

The general character of seven surveyed tributaries is presented in Figure 5.3. The reaches surveyed on tributaries across the Thames catchment capture stretches with elevations between 10 and 175 m a.s.l and low slope values between 0.3 and 5.5 m / km. The reaches can therefore all be considered as lowland, low energy stretches within the national (UK) context (Harvey et al. 2008) but cover a range of energy contexts within this class. The majority of reaches had channel cross sectional area smaller than 25 m^2, although larger channels up to 100 m^2 are included in the data set. Median stream power index (TSPI) is similar across the tributaries, but stream power values are low within the natural context (e.g. compared to ranges reported in Harvey et al., 2008). The median bed sediment calibre (SEDCAL) ranges from fine gravel (-3 phi) to medium sand (1.5 phi) but sites with finer sand, silt and clay (up to 10 phi) are also represented within the data set (Colne, Mole and Windrush). Bank material calibre (BANKCAL) was much less variable across the tributaries and individual reaches, with the vast majority of sites characterised by earth banks. The Windrush and Mole have the most variability in bank sediment calibre, with the latter including a range from clay to sand. Bedrock geology was identified as either chalk (35 reaches), sandstone (10), limestone (6) or other sedimentary rock types (52) and superficial geology was almost exclusively alluvium (98% of reaches).

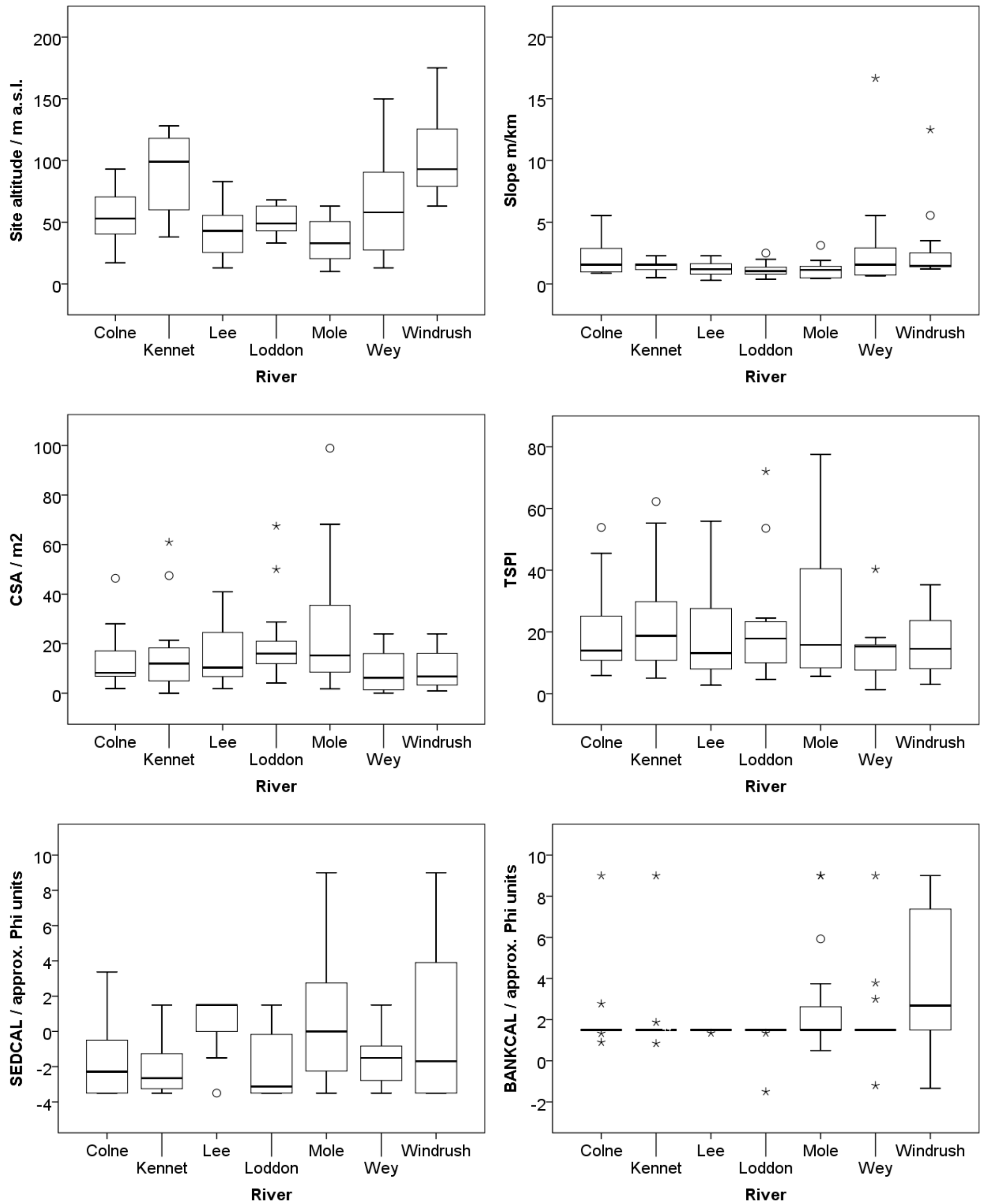
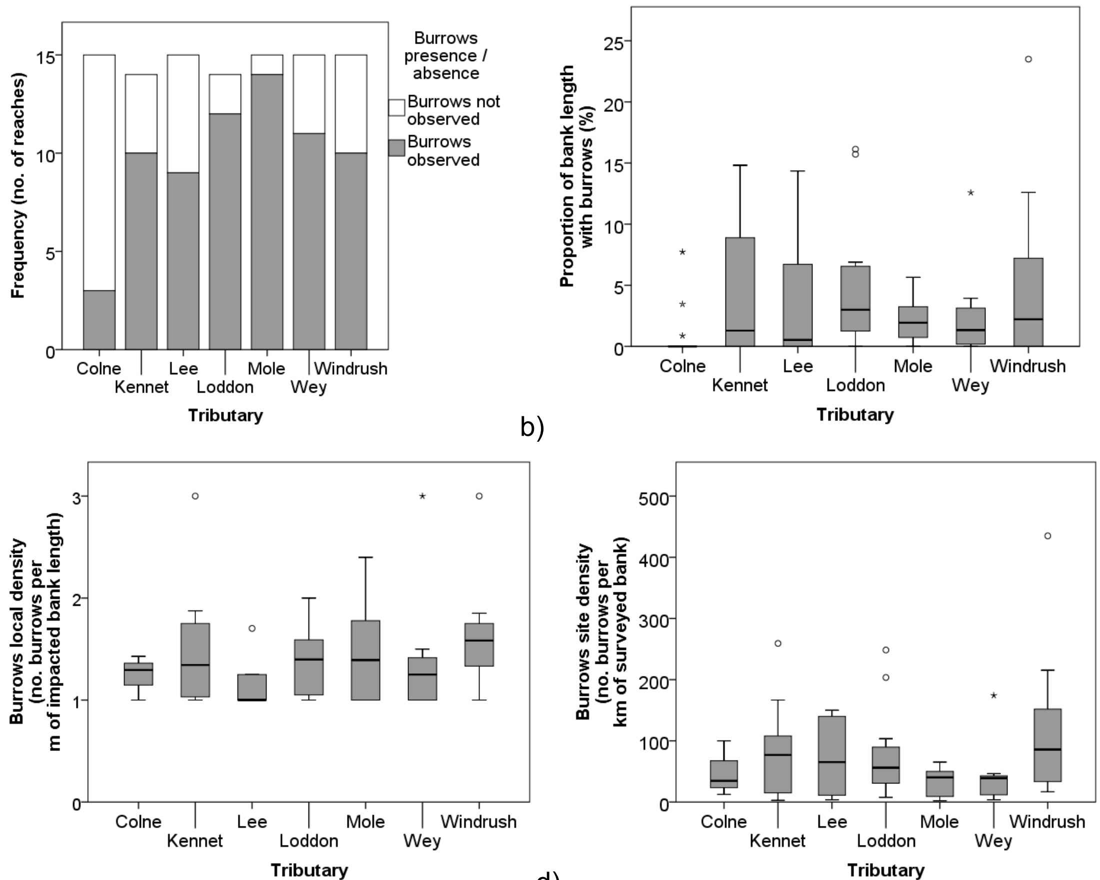


Figure 5.3 Boxplots showing a range of site energy and sediment characteristics in the surveyed tributaries of the River Thames.

Comparison of tributaries along four burrowing metrics is illustrated in the Figure 5.4. Signal crayfish burrows were observed on the majority (60-93%) of reaches for all tributaries except the River Colne which had the lowest number of reaches with observed burrows (3 out of 15 reaches; (Figure 5.4). The River Mole had the highest number of reaches with burrows (14 reaches out of 15 surveyed), followed by the Loddon with 12 out of 14. The remaining tributaries (Kennet, Lee, Wey, Windrush) had a similar proportion of burrowed reaches (between 9 and 11). Kruskal-Wallis tests showed that differences between tributaries in burrows presence and absence were statistically significant (p = 0.001) and post hoc pairwise comparisons shown that the River Colne had statistically significantly lower values than rivers Loddon, Mole and Wey (Figure 5.4 a).

Differences in the remaining three burrowing metrics are illustrated with boxplots (Figure 5.4 b-d). The proportion of bank length impacted by burrows was more variable on the Kennet, Lee and Windrush, suggesting high variability in burrowing on a reach basis including some heavily impacted sites (with more than 15 % impacted bank length). The highest median impacted length was observed on the Loddon followed by the Windrush while the Lee and Wey had lower median values. Kruskal-Wallis test showed that differences between tributaries in proportion of bank with burrows differed statistically significantly between tributaries (p = 0.035) and post hoc pairwise comparisons shown that River Colne had statistically significantly lower values than River Loddon. Local burrow density was the highest and most variable on the Windrush, Mole, Loddon and Kennet, with the Wey, Colne and Lee were characterised by lower median densities and narrower ranges. Kruskal-Wallis test showed that differences between tributaries in burrows local density differed statistically significantly between tributaries (p = 0.001) and post hoc pairwise comparisons shown that River Colne had lower values than rivers Loddon, Mole and Windrush. Site burrow density was the highest and most variable on the rivers Windrush, Kennet and Lee, while the Colne, Mole and Wey had low values. Kruskal-Wallis test showed that differences between tributaries in burrows site density differed statistically significantly between tributaries (p=0.013) and post hoc pairwise comparisons shown that Colne had lower values than Loddon.

Downstream trends in impacted bank length and local burrow density on each tributary are presented in Figures 5.5 and 5.6 respectively. There are no clear trends between distance downstream and occurrence of burrows. This was confirmed by Spearman correlation which showed that distance from source did not correlate statistically significantly with proportion of bank impacted by burrowing (R=0.062, p=0.537), local burrow density (R=-0.1, p=0.314) or site burrows density (R=0.04, p=0.685). Despite that, for some sites the higher proportions of impacted lengths tend to be concentrated in either the upper (Colne, Wey) or lower (Windrush) stretches of the surveyed tributary. For the remaining tributaries, impacted bank length is variable downstream with no clear trend. A similar pattern is noted for local burrow density which shows some clustering of higher densities in the upper (Loddon, Mole) or lower (Windrush) stretches of some tributaries, but with most showing no clear downstream trend.



a) b) c) d)

Figure 5.4 Burrows presence/absence across the studied tributaries of the River Thames (a). Boxplots indicating differences in burrowing metrics across the tributaries of the River Thames (proportion of the bank length with burrows (b) is calculated all 103 sites, while burrow density metrics (c and d) are calculated for sites with burrows only.

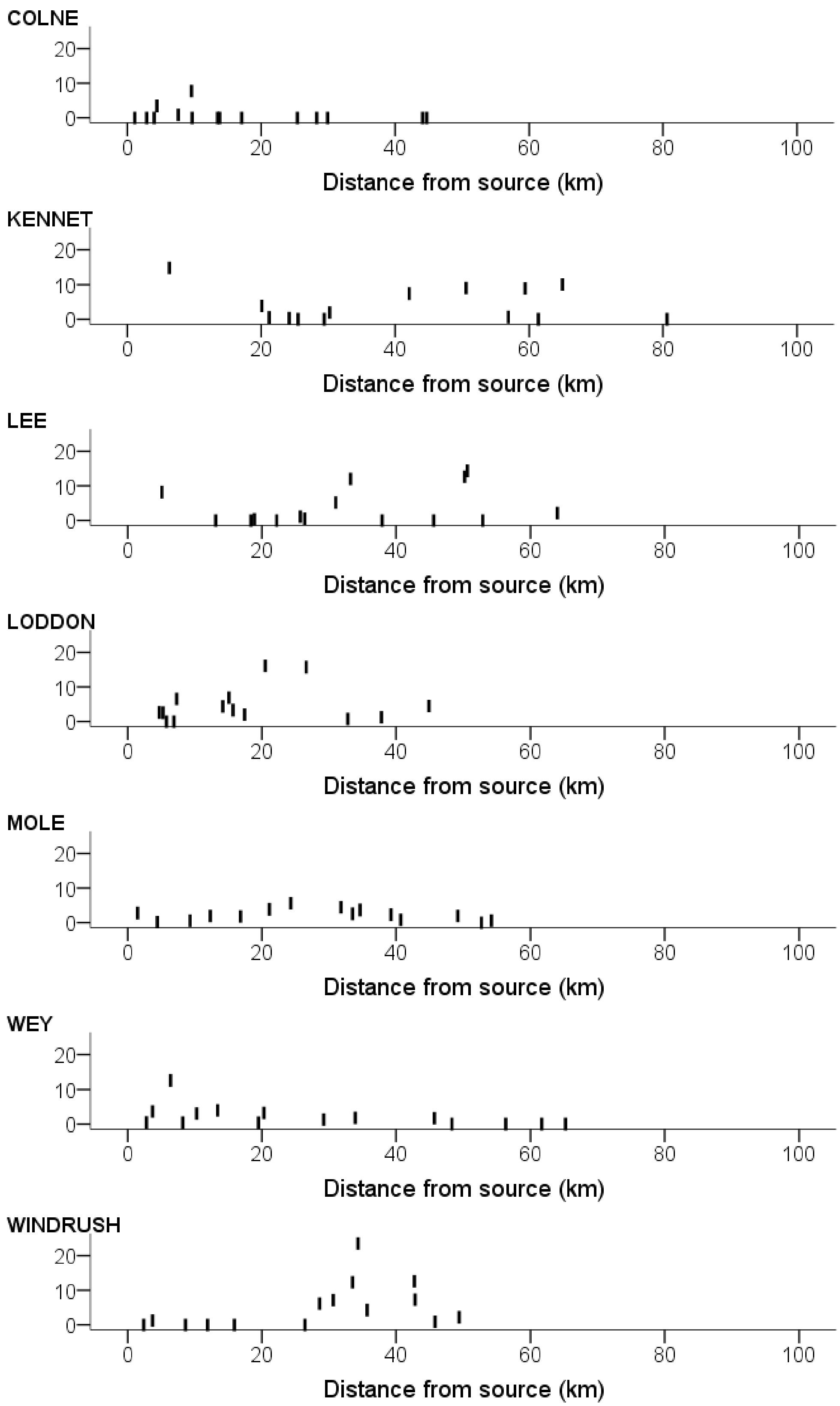


Figure 5.5 Downstream trend in proportion of bank length impacted by burrows (%) for seven studied tributaries.

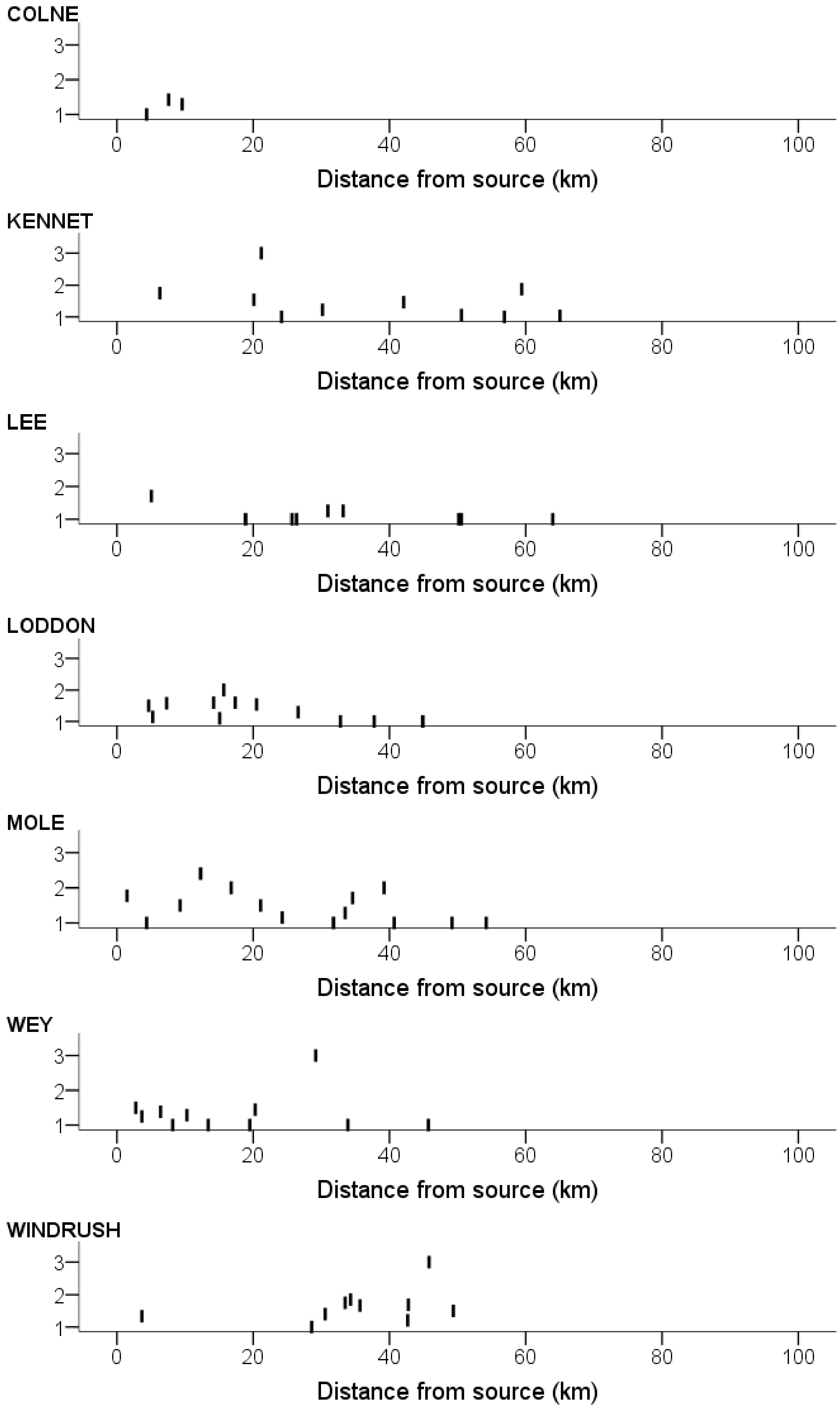


Figure 5.6 Downstream trend in burrows local density for seven studied tributaries.

5.3.3 Relationships between burrowing and RHS-derived indices

All habitat variables show considerable overlap in their ranges for sites with and without burrows, although some broad trends are observed (Figure 5.7, 5.8 and 5.9, Table 5.6). Sites where burrows were observed show a tendency for a higher river source and site altitude, CSA, TSPI, USPI, SEDCAL, BANKCAL, BANKPROF, pool and riffle spacing, pools and riffles number, bank vegetation, total tree score and HQA while at the same time displaying a lower values of distance from source, slope, channel vegetation cover/complexity and HMS index. These trends are subtle, and only CSA, BANKPROF and HQA were significantly different between burrowed and non-burrowed sites (Mann Whitney U, P<0.001) (Table 5.6).

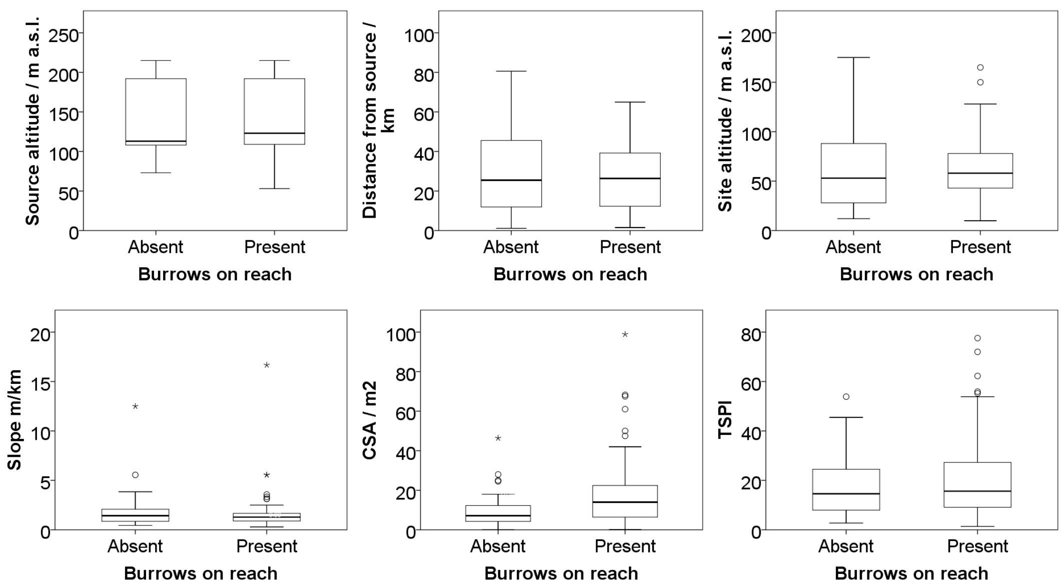


Figure 5.7 Landscape-scale energy conditions/channel dimensions.

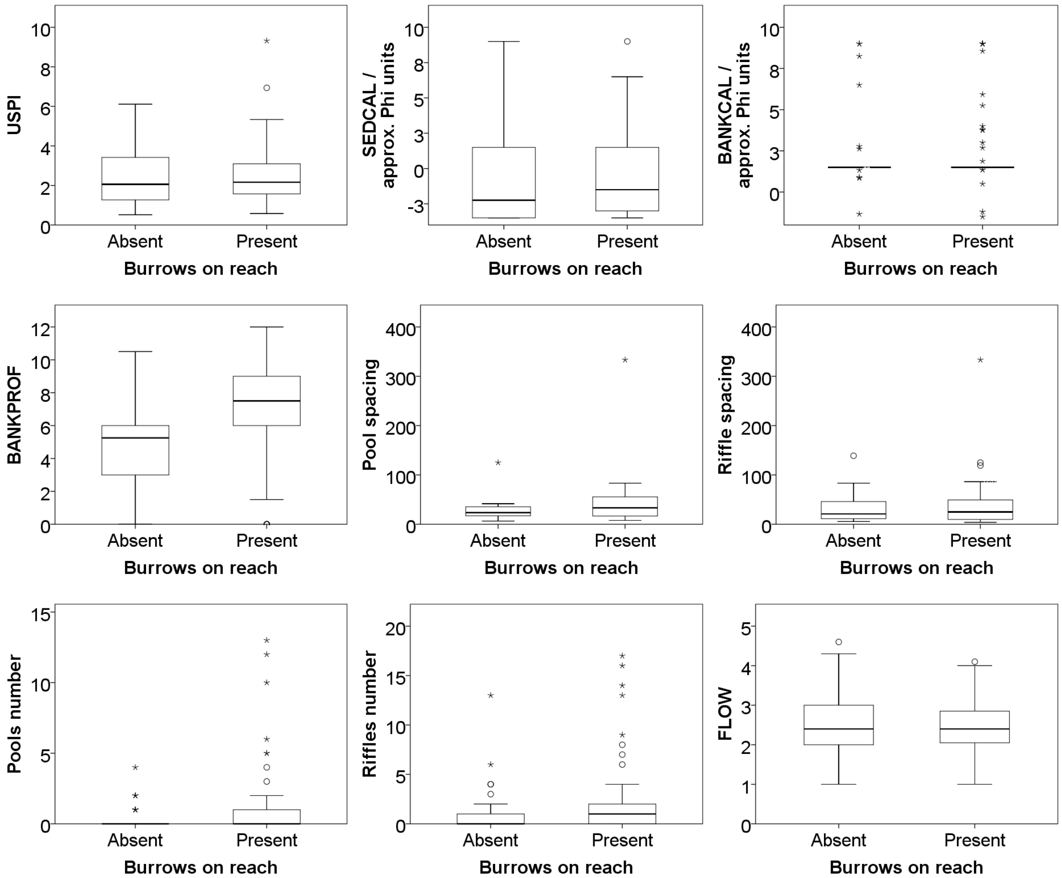


Figure 5.8 Local scale physical indices

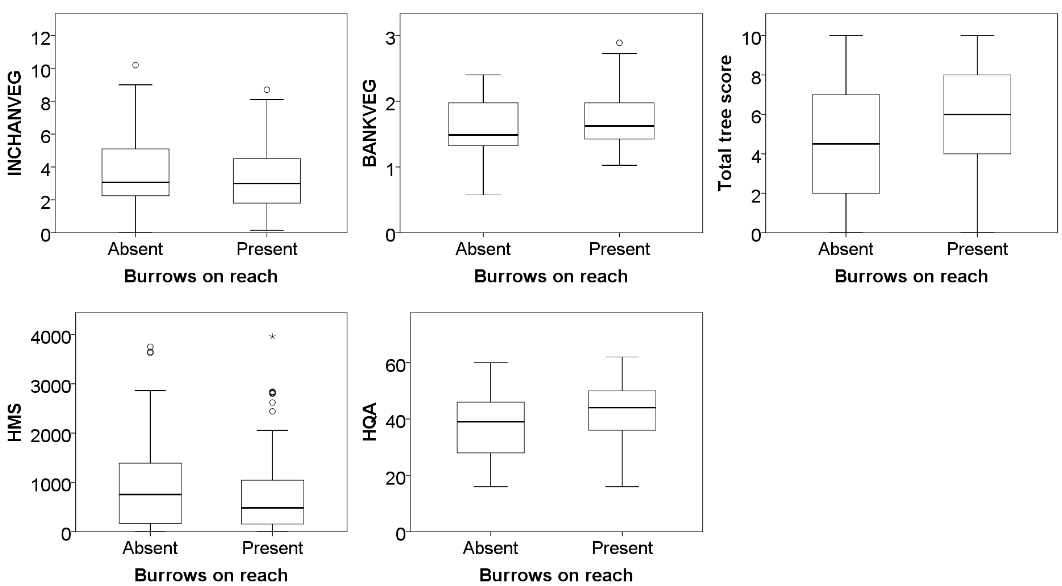


Figure 5.9 Local scale vegetation indices and reach habitat quality and modification scores.

Table 5.6 Mean values for the habitat variables shown separately for reaches where burrows are absent (34 sites) and present (69 sites) and Mann Whitney U significance of difference.

Variable	Mean		Significance
Burrows	Absent	Present	p
Source altitude / m a.s.l.	138	141	0.680
Distance from source / km	29	27	0.922
Site altitude / m a.s.l.	62	63	0.510
Slope m/km	2.0	1.7	0.449
CSA / m2	11	19	0.032*
TSPI / m2	18	22	0.644
USPI / m	2.3	2.6	0.584
SEDCAL	-0.9	-0.7	0.392
BANKCAL	2.2	2.3	0.530
BANKPROF	4.7	6.7	0.002*
Pool spacing	35	47	0.550
Riffle spacing	36	43	0.845
Pools number	0.4	1.2	0.194
Riffles number	1.2	2.1	0.143
FLOW	2.6	2.6	0.673
INCHANVEG	3.6	3.3	0.560
BANKVEG	1.6	1.7	0.140
Total tree score	4.8	5.8	0.059
HMS	1,092	834	0.358
HQA	38	43	0.020*

Spearmans correlations were conducted to explore relationships between the habitat variables and burrowing metrics (proportion of impacted bank length, local and site burrow density) on 69 sites with burrows presence only (Table 5.7). In general correlations are weak ($R < 0.4$ for positive correlations and 2.69 for negative ones). Statistically significant positive correlations were identified between burrows local density and BANKCAL, BANKPROF, site altitude and HQA score suggesting that higher density of burrows on impacted bank are weakly associated with higher altitude sites, finer bank material and higher overall habitat quality. A weak but statistically significant, negative relationship was identified between burrow local density and CSA, suggesting that higher density of burrows on impacted bank are weakly associated with smaller channels. Burrows site density is statistically significantly positively correlated with in channel vegetation.

Table 5.7 Spearman's rank correlations between burrow survey metrics and the landscape and local scale physical habitat indices. Statistically significant values are marked with ** for significance at p = 0.01 level and * for significance at p = 0.05 level.

Spearman's rho	Proportion of bank length with burrows (%)	Burrows local density (no. burrows per m of impacted bank length)	Burrows site density (no. burrows per km of surveyed bank)
Source altitude / m a.s.l.	0.046	0.047	0.063
Distance from source / km	0.165	-0.208	0.118
Site altitude / m a.s.l.	0.048	**.270***	0.084
Slope m/km	-0.092	0.18	-0.063
CSA / m^2	0.092	**-.269***	0.031
TSPI / m^2	0.103	-0.255	0.032
USPI / m	0.016	-0.064	-0.015
SEDCAL	-0.193	-0.198	-0.181
BANKCAL	-0.014	**.367****	0.07
BANKPROF	0.006	**.343****	0.097
Pool spacing	-0.184	0.288	-0.161
Riffle spacing	-0.142	0.265	-0.073
Pools number	0.124	0.141	0.131
Riffles number	0.167	0.059	0.149
FLOW	0.212	0.029	0.184
INCHANVEG	0.216	0.091	**.238***
BANKVEG	-0.219	0.111	-0.153
Total tree score	-0.015	0.112	0.022
HMS	0.048	-0.155	-0.017
HQA	0.17	**.257***	0.218

Principal components analysis (PCA) was performed on 16 RHS-derived variables using a Spearmans rank correlation matrix and varimax rotation. Six principal components had eigenvalues >1 and cumulatively explained 73 % of the variance in the data set (Table 5.8). Variable loadings on individual PCs are presented in Table 5.9.

Table 5.8 Eigenvalues and cumulative variance explained for PCA performed on the sixteen habitat variables.

Principal component	Eigenvalues	% of Variance	Cumulative %
PC1	3.404	21.273	21.273
PC2	2.257	14.107	35.38
PC3	1.897	11.855	47.235
PC4	1.724	10.774	58.009
PC5	1.238	7.738	65.746
PC6	1.165	7.281	73.028

Principal component 1 (PC1) defines a gradient of position of reaches in the catchment, while the PC2 relates to the stream power and size. PC3 represents a gradient of site energy and habitat quality and PC4 defines a gradient of bed and bank material calibre. PC5 relates to habitat modification and bank vegetation, while PC6 represents tree cover and channel vegetation. Bi-plots for the six PCs illustrated the difference in PC scores between sites with and without burrows (Figure 5.10). Overall there is considerable overlap in PC scores among the tributaries which generally show a range of values for each PC and hence a range of biophysical habitat conditions at the reach scale. Mann Whitney U test has shown that difference between sites with and without burrows is only significant along the PC3 (sites with burrows had statistically significantly higher scores, $p = 0.013$). In addition, Spearman correlation has shown that the only statistically significant correlation is positive link between burrows local density and PC5 ($R = 0.290$) (Table 5.10).

Table 5.9 Principal component loadings for the variables and interpretation of the PCs.

	Component					
	1	2	3	4	5	6
Interpretation	Position in catchment	Stream power and size	Site energy and habitat quality	Bed and bank material calibre	Habitat modification and bank vegetation	Tree cover and channel vegetation
Distance from source / km	**-0.82***	0.33	0.19	0.00	-0.23	0.05
USPI / m	**0.79***	**0.45***	-0.04	0.04	0.02	0.12
Slope m/km	**0.70***	-0.14	0.35	-0.18	0.07	0.17
TSPI / m2	0.10	**0.94***	-0.07	0.08	-0.06	-0.02
CSA / m2	-0.31	**0.87***	-0.11	0.03	-0.05	0.09
Source altitude / m a.s.l.	-0.11	-0.08	**0.88***	0.24	-0.18	-0.02
Site altitude / m a.s.l.	**0.59***	-0.30	**0.63***	0.11	-0.06	-0.01
FLOW	0.32	-0.09	**0.59***	**-0.41***	0.19	-0.37
SEDCAL	0.02	0.05	-0.01	**0.87***	-0.02	-0.08
BANKCAL	-0.05	0.03	0.12	**0.76***	0.12	0.16
HMS	-0.06	0.19	0.00	0.05	**-0.74***	0.25
BANKVEG	0.12	0.15	-0.28	0.10	**0.67***	0.20
HQA	0.06	0.04	**0.49***	-0.07	**0.51***	0.35
BANKPROF	0.05	-0.34	0.22	0.29	**0.46***	0.16
Total tree score	0.10	0.11	-0.04	0.13	0.28	**0.76***
INCHANVEG	-0.04	0.05	0.00	0.01	0.13	**-0.70***

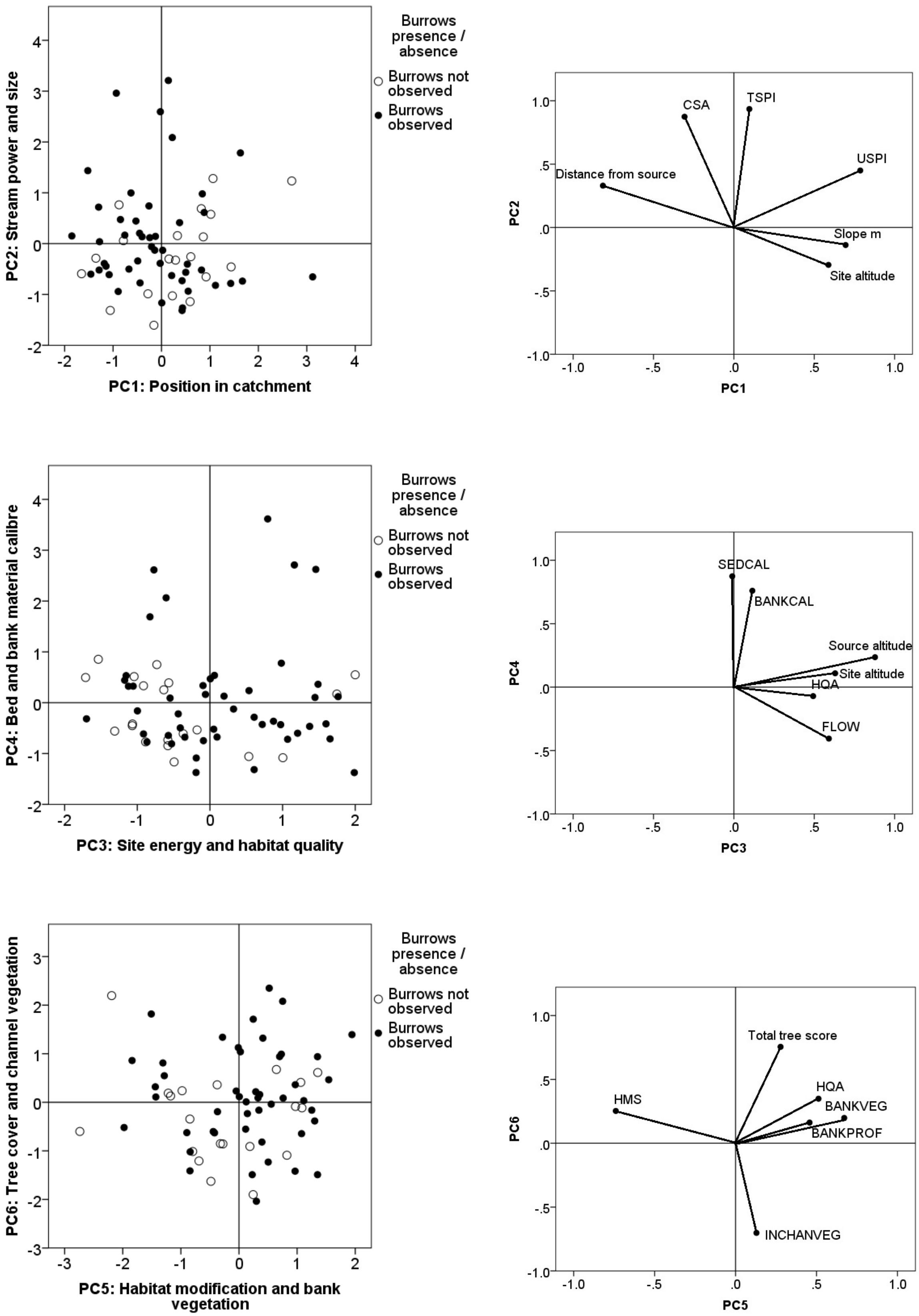


Figure 5.10 Scatterplots and biplots for principal component scores for sites with and without burrows presence.

Table 5.10 Correlation between principal component scores and three burrowing metrics done for 69 sites with burrows presence only.

Spearman's rho	Proportion of bank length with burrows (%)	Burrows local density (no. burrows per m of impacted bank length)	Burrows site density (no. burrows per km of surveyed bank)
PC1: Position in catchment	-0.023	0.039	-0.036
PC2: Stream power and size	0.158	-0.226	0.1
PC3: Site energy and habitat quality	0.134	0.001	0.131
PC4: Bed and bank material calibre	-0.169	0.12	-0.099
PC5: Habitat modification and bank vegetation	-0.099	.290*	0.025
PC6: Tree cover and channel vegetation	-0.061	0.135	-0.051

5.3.4 Estimation of volume of sediment excavated from burrows

The reach level information of crayfish burrow abundance and the volume of average burrow (Equation 1) were used to estimate the volume of material excavated from surveyed reaches (Figure 5.11, Table 5.11). In total, signal crayfish burrowing has delivered a minimum of 1,876 L of bank material from the 29 km of surveyed river stretches. The amount of material excavated from individual tributaries ranged from 59 L on the River Colne to 446 L on the River Windrush. When these numbers are put in context of the bank length across the seven tributaries, those number correspond with an average of 2 L of sediment excavated per metre of impacted bank length or 67 L per km of surveyed bank length.

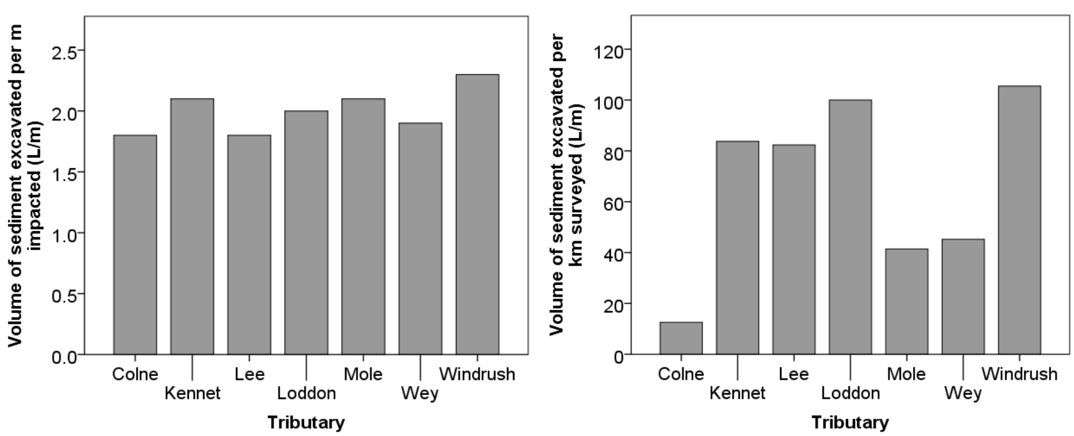


Figure 5.11 Estimates of volume of bank material excavated by crayfish burrowing across the seven tributaries based on field survey (grey bars).

Table 5.11 Estimated volume of sediment excavated by crayfish burrowing based on field survey

Tributary	No Burrows	Surveyed bank length (m)	Length impacted (m)	Total volume excavated (L)	Volume of sediment excavated per impacted bank (L/m)	Volume of sediment excavated per surveyed bank (L/km)
Colne	41	4,710	33	59.2	1.8	13
Kennet	229	3,950	159	330.8	2.1	84
Lee	187	3,280	149	270.1	1.8	82
Loddon	259	3,740	184	374.1	2.0	100
Mole	129	4,500	87	186.3	2.1	41
Wey	145	4,630	109	209.4	1.9	45
Windrush	309	4,230	196	446.3	2.3	105
Mean	186	4,149	131	268	2.0	67
Total	1,299	29,040	917	1,876.3		

On the basis of presented information, it is visible that the River Windrush has the highest density of burrows. In combination with the fact that it also has the smallest catchment area of seven studied tributaries, it is assumed that the impact of burrows on suspended sediment in rivers is the most pronounced.

5.4 Discussion

Presented results provide an important insight into ecosystem engineering impact of signal crayfish on river banks. In comparison with the other studies of the same topic (Guan, 1994; Stanton, 2004; Roberts, 2012), this study improved both the scope and methodological approach to quantifying burrows. Obtained results need to be interpreted with limitations described in the Methodology sections in mind, which primarily imply that an observed number of burrows is likely a great underestimation of the real numbers. This applies to all results presented here since it is a general limitation of the method and will not be repeatedly emphasized. However, this means that all stated interpretations have to be taken cautiously since effects are probably stronger. Overall, this approach enabled surveying on the wide geographical area and gaining a basic insight into signal crayfish burrowing in the multi catchment river system.

5.4.1 Spatial organisation and local intensity of signal crayfish burrowing in the Thames catchment

The first main finding is that crayfish burrows were observed on the majority (67 %) of surveyed reaches. That is significantly higher than the previous study of signal crayfish burrowing in the Thames catchment found (Roberts, 2012). While a similar methodology was used, burrows were detected on only 38 % of sites. This difference is even more pronounced since the sites in Roberts (2012) were not randomly chosen, but focused on reaches with known well-established populations of crayfish (as informed by the UK Environment Agency). However, the higher percentage of burrow records in this study could be a consequence of observation during early spring and late autumn, when vegetation did not obscure the view of the river bank in comparison to the previous study that was undertaken during summer.

The high percentage of sites with records of burrows can be explained by a combination of two principles. Firstly, it can be reasonably assumed that crayfish are present on each studied site, as elaborated in detail in Chapter 3. Secondly, it is well known that a shelter is one of the key habitat requirements for crayfish (Holdich, 2002) and that due to the high population densities often achieved by crayfish (Hudina et al. 2009; Moorhouse and Macdonald 2011), all natural shelter can be expected to be occupied. Therefore a combination of crayfish wide range distribution and ubiquity of burrows as a survival requirement leads to the high proportion of sites with records of burrowing.

The second main finding is that on the sites where burrows are present, they are recorded in relatively small numbers. This is represented by low values of the proportion of bank length with burrows (median value of 3 %) as well as a number of burrows per kilometre of the surveyed bank (median value 45). This result is unexpected since it is well known that signal crayfish population densities reach high values of up to few thousand individuals per kilometre of the river (extrapolated from Moorhouse and Macdonald, 2011) and even more importantly, crayfish are relatively uniformly present across sites (Hudina et al. 2009). Therefore a small number of burrows on individual sites is the result of two potential scenarios. First one is based on the notion that, as already mentioned in the methodology section, the number of burrows is probably much higher than recorded by the field observation. The second possibility is based on assumption that signal crayfish burrowing is triggered by very localised, microhabitat characteristics. It is known that crayfish population density does oscillate with habitat quality (Hudina et al. 2009; Moorhouse and Macdonald 2011) and therefore interaction between microhabitat and burrow presence is to be explored further.

The third main finding is that local density of burrows is mainly low (median value 1.3 burrows per m of impacted bank), but occasionally reached higher values (3 burrows per m of impacted bank), meaning that burrowing differed between different parts of the reach. In a similar manner to burrows site density, this can be explained by an impact of microhabitat characteristics.

5.4.2 Differences between tributaries

This survey was performed on the tributaries of the Thames catchment and as such, it is not representative of the full range of river types across the UK and Europe. When compared with a survey on the national data set (Harvey et al. 2008), studied rivers had a gentler slope due to predominantly lowland character. Overall, seven studied tributaries shown similarity in their physical properties, however, since they are all primarily lowland rivers in the same region of UK that type of similarity is expected. This similarity between tributaries is reflected in crayfish burrowing patterns. Burrows are present on approximately two-thirds of the surveyed sites on all tributaries, with the River Colne as the only exception as a river with a lower occurrence of burrows. Analysis of habitat characteristics did not enable explanation of special case of the river Colne. Therefore it can be concluded that local habitat is the primary determinant of burrows presence while differences between tributaries are not so significant.

Almost all processes in rivers are influenced by downstream gradient (Charlton, 2008), however, burrows occurrence did not demonstrate a similar pattern (Figures 5.5 and 5.6). There are two potential explanations for this. On the one hand, the need for shelter is universal for crayfish and position in the catchment is not known to influence that requirement (Holdich, 2002). Alternatively, due to the primary lowland character of the studied reaches (there were only a few typical headwaters sites sampled), it can be argued that there was not a significant difference in habitat characteristics between upstream and downstream parts of rivers. Therefore factors like local conditions are a more important predictor of the burrows occurrence.

5.4.3 Relationships between crayfish burrow occurrence and biophysical river habitat characteristics

Influence of habitat characteristics on crayfish burrowing at the reach scale revealed that there is a lot of overlap in studied habitat variables between burrowed and non-burrowed sites. This is evident in the comparison between sites with and without burrows that statistically significantly differed in only three indices. The correlation analysis confirmed this tendency with low coefficients of correlation, even in cases when the correlation was statistically significant. Lack of definitive habitat influence on all four burrowing metrics can be explained in two ways. The first one is that the number and even more importantly, patterns of burrows distribution recorded in this survey are not representative of overall burrowing distribution. The second possibility is that burrowing is influenced by factors not included in this survey. For instance, predator density is known to influence crayfish behaviour, especially in respect to shelter use (Figler et al. 1999), while point source pollution is known to completely eradicate populations of crayfish (Holdich, 2002) or have a negative effect on the metabolism of living organisms (Owens et al. 2005). Therefore, these results are similar to findings by Roberts (2012) who also did not find a definite conclusion about factors that lead to burrowing.

Despite the lack of definitive influence of habitat, several habitat indices do show a statistically significant impact on the burrows. While different analytical approaches used identified different habitat indices as significant, there is a general trend, identified across different analytical approaches that identify high bank angle and good habitat quality as parameters conducive to burrowing. These findings are different from a study by Roberts (2012) who identified complex flow types and vegetation properties as main parameters that could be linked with burrowing preferences.

High bank angle has two types of implications for burrowing. Firstly, since banks with high angle are usually on the outer bank of the river meander, they are often bare and therefore burrows are more visible. Therefore the characteristics of habitat might lead to burrows being more visible and therefore recorded more frequently. Secondly, high bank angle, associated with the outer banks of the river meander are also conducive to higher levels of erosion (Thorne et al. 1985) and therefore it can be assumed that availability of natural shelter is lower in such microhabitats and therefore there is more incentive for crayfish to dig burrows there.

While the previously presented findings partially explain direct link between habitat characteristics and burrows occurrence, an indirect impact is also worth considering. Habitat quality can have an impact on burrowing through influence on the crayfish population size. Diverse, high-quality habitats are known to support greater biodiversity of organisms which in turn have a greater biomass than more uniform, poorer habitats (Wetzl, 2001). Since crayfish are omnivores which feed on wide range of food (Ahvenharju and Ruohonen, 2006), from plant to invertebrates and detritus, their population density is often limited by food supply (Almeida et al. 2013). Therefore on the diverse habitats, a higher population density can be expected. A higher number of crayfish is more likely to occupy all available shelter and therefore there is a higher incentive for the remaining crayfish to dig burrows.

5.4.4 Volume of sediment excavated due to crayfish burrowing within surveyed rivers

This survey represents the first attempt to use information about average burrow size and put it in context of burrows density on the river banks. Since the same volume of burrows is used, the differences between tributaries in the volume of sediment reflects the previously addressed differences in burrows local density and burrows site density. The results, 2 L of sediment per m of impacted bank length or the equivalent of 67 L per kilometre of the surveyed bank, have to be taken into account with few considerations in mind. Firstly, those values are almost are almost certainly an underestimation, since it is based only on burrows above the water line. Secondly, the influence of signal crayfish burrowing must also include the effects of burrows on increase likelihood of mass failure erosion since the stability of the river bank is compromised by burrowing (Simon et al. 2000) as well as mobilisation of sediment on the bottom by walking (Harvey et al. 2014).

Thirdly, the lack of time component in this survey prevents the ability to put the stated volume of sediment in context of annual sediment budgets. Despite not being able to quantify the amount of sediment properly, due to seasonal effects, sediment released by signal crayfish burrowing might have a disproportionate effect on river ecosystem.
It is known that most erosion usually happens during autumn and winter (Charlton, 2008), while crayfish activity is correlated with temperature and peaks during summer (Holdich, 2002). Therefore supply of sediment by crayfish can occur during the period when there is usually less sediment supply to rivers. Also, summer is the period of the highest biological activity and especially important for photosynthesizing organisms like macrophytes which are known to be negatively impacted by turbidity (Wetzl, 2001). Therefore, since river ecosystems are a complex system with several thresholds of tolerance (Bedoya et al. 2011), the stated contribution of sediment by signal crayfish burrowing might have a significant effect.

5.5 Conclusion

Signal crayfish burrowing on the reach in catchment spatial scale was undertaken on 103 sites in the River Thames catchment, all of which were presumed to be exposed to signal crayfish presence.

Signal crayfish burrowing was present on 69 out of 103 of the sites (67%). This corresponds well with the wide distribution of crayfish in the Thames catchment and the general understanding that crayfish do regularly burrow on a wide range of micro habitats. Total of 1,299 burrows were observed which put in the context of the length of the river bank surveyed corresponds with 44.7 burrows per km of the river bank. The total length of 917 meters was impacted by burrowing, which put in the context of the length of the river bank surveyed corresponds with 31.5 m of impacted bank per km of the river bank. Therefore it can be concluded that signal crayfish burrowing is a wide spread phenomenon in the Thames catchment.

However, once burrowing was observed on 69 reaches with burrows presence, the presence of burrows along all burrowing metrics was low. The proportion of the bank with burrows ranged from 0.2% to 23% (mean 4.87%) for 69 sites with burrows. The density of burrows on 69 sites ranged from 2 to 435 per km (mean 69). Burrow local density on 69 sites ranged from 1 to 3 per m of the impacted bank (mean 1.4). The low sparse occurrence of burrows is an indication that burrowing is a facultative activity for signal crayfish.

Habitat influence on burrows presence or absence can be primarily described with a big overlap in almost every measured trait between reaches with and without burrows. However, the reaches with burrows did have statistically significantly higher cross sectional channel area (CSA), steep bank profile and higher habitat quality (HQA).

Impact of burrowing on erosion was calculated by use of information about a number of burrows per km of the surveyed bank and the average volume of an individual burrow. A number of burrows gave the opportunity to express it per km length of the river.

The volume of the sediment excavated by signal crayfish burrowing was relatively high when considered per length of the burrow impacted bank, averaging 2 L per metre. This value was fairly consistent between seven tributaries, ranging from 1.8 to 2.3 L per metre. However, when the volume of sediment was expressed with a more objective measure of mean volume per length of the surveyed bank, the average value was much lower, 67 L per kilometre. This value varied much more, primarily due to a big difference in the overall density of burrows on seven tributaries, ranging from 13 L / km on the River Colne to 105 L / km on the River Windrush. The significance of these numbers is hard to put in context since no information on the time period required for burrowing was collected.

CHAPTER 6: Signal crayfish as ecosystem engineer at the bank section in catchment scale

6.1 Introduction

This chapter explores the relationships between crayfish burrowing, biophysical river habitat characteristics and the occurrence of bank erosion on the bank section spatial scale. In the previous chapter (Chapter 5), investigation on the reach scale implied that signal crayfish burrowing might be better described with very local habitat traits. In addition to that, three previous studies on signal crayfish burrowing (Guan, 1994; Stanton, 2004; Roberts, 2012), did not explore burrowing on this scale. In addition to that, a survey on this scale enabled observation of signs of erosion by following the procedure described by Thorne (1998).

The bank sections scale is often used in geomorphological studies. In the RHS methodology (RHS, 2015), two bank sections form a transect, a basic unit of data collection for a range of habitat variables. This spatial level is on the same order of magnitude as meander bed defined by Charlton (2008). As such this spatial scale is important since it captures local heterogeneity in habitat, primarily differences between riffle and pool sequences, but also random disturbances like large wood which dominate the local hydrology and refugia creation in rivers (Clifford et al. 2006).

In addition to this, bank section scale is a good basis for any crayfish based survey. While signal crayfish are known to migrate significantly along the river (Bubb et al. 2004), it is recognised that signal crayfish are primarily linked to a specific location which is used as shelter during the day and immediate surrounding explored during the night. This immediate surrounding is often based on the level of bank section (Wutz and Geist, 2013). Therefore it can be said that bank section is appropriate for studies of signal crayfish burrowing, especially since it is known that creation of burrows takes place in the relatively short span of time (Johnson et al. 2010).

On the basis of stated knowledge and knowledge gaps, following five research aims are identified:

1. To quantify the extent and main characteristics of signal crayfish burrowing and river bank erosion on the bank section scale in the Thames catchment.
2. To assess the spatial organisation and local intensity of signal crayfish burrowing and river bank erosion within seven tributaries of the River Thames.
3. To explore relationships between crayfish burrow presence and extent and biophysical river habitat characteristics.
4. To explore relationships between river bank erosion and biophysical river habitat characteristics.
5. To estimate relationships between burrowing, local habitat variables and erosion patterns.

6.2 Methodology

6.2.1 Survey design

This chapter is based on analysis of the same sites as the ones selected in Chapter 5, however basic unit (pixel) of analysis is individual bank section and not the reach. In addition to that, in order to address the specific concerns related to the different spatial scale of this analysis, few additional differences are applied, primarily regarding the choice of sites included into the survey and main methods of obtaining data regarding habitat parameters.

Field surveys were undertaken at the 69 sites on seven tributaries of the River Thames where at least one burrow was recorded (see Chapter 3: Research Design). The exclusion of the 34 sites without any burrow present was done in order to eliminate the “false negative records” from further analysis. This was undertaken since signal crayfish burrows can be absent from a specific reach for a variety of reasons not included in this survey, for instance, point source pollution or habitat fragmentation (Holdich, 2002). Since one of the main as aims of analysis is an assessment of the influence of habitat on presence and absence of signal crayfish burrowing inclusion of bank sections which are placed on reaches where crayfish are completely absent would lead toward a bias.

On the basis of the described elimination of the reaches, the data set includes 69 reaches where at least one burrow is present. Out of those, on 63 sites ten transects are surveyed, while on the remaining six, due to the access or visibility issues, between four and nine transects were surveyed. However, since for some transects both bank sides could be observed, this resulted in a total of 768 bank sections sampled across the tributaries. Non-burrowed ‘intervening’ sections were ideally spaced around 50 m apart but that distance varied according to the site length. At some sites, access was limited and shorter stretches with fewer bank sections (minimum four) were sampled.

Additional, the main difference in respect to the previous chapter is that habitat variables were recorded directly in the field for each bank section, therefore enabling the study of habitat characteristics and burrow occurrence on the more direct level. In addition, direct observation of the river bank enabled recording of signs of erosion, therefore putting crayfish burrowing in a new context. For each transect, the GPS position, water transparency and side of the bank from which survey was undertaken were noted.

The definition of bank section and its relationship with river transect is the same as the one used in

Chapter 4. At each transect, a range of variables were recorded through visual observation from either the channel or bank. Given uncertainties associated with making accurate observations of the bank on which the observer is located, data on both banks was included only when a good view of both bank faces was possible by accessing the river channel. For sites where observations were made from the bank, data on the opposite bank only was included. The basic sampling unit for this survey is therefore one “bank section” containing burrowing, habitat and bank erosion data observed on the bank and associated habitat information for the channel.

6.2.2 Survey variables

To meet the need for extensive spatial coverage across seven tributaries, it was necessary to devise a method to enable rapid and standardised collection of information. Principles from other rapid field survey methods were incorporated, in particular, River Habitat Survey (RHS, 2015), Urban River Survey (Davenport et al. 2004), River Styles (Brierley and Fryirs, 2005) and Stream Reconnaissance (Thorne, 1998). The variables used to describe habitat characteristics on each studied bank section are listed in Table 6.1 and 6.2.

Table 6.1 Overview of variables collected during field survey. Bank – physical characteristics and vegetation.

Variable name	Variable description (units/categories)
Bank material	Bank material (artificial (1), non-cohesive (2), cohesive (3))
Bank angle (degrees)	Bank angle (degrees)
Bank height (m)	Bank height (m)as measured from the water surface to the bank top
Planar angle (degrees)	Curvature of river meander (degrees) defined between observation point and points on the same bank approximately five river widths upstream and downstream. For each bank, planar angle is defined as positive for the bank on the outside of meander and negative for the bank on the inside of meander.
Tree roots (m)	Length of bank with tree roots (m)
Bank emergent broad leaved vegetation (coverage)	% cover of vegetation immediately adjacent to the bank toe.
Bank emergent narrow leaved vegetation (coverage)	% cover of vegetation immediately adjacent to the bank toe. Includes Reeds, sedges, rushes, grasses, horsetails
Bank face bare (coverage)	% cover of bare bank face
Bank face grass (coverage)	% cover of all monocotyledon vegetation (includes tails and sedges) on the bank face
Bank face herbs (coverage)	% cover of all dycotiledon vegetation on the bank face
Bank face shrubs (coverage)	% cover on the bank face
Bank face trees (coverage)	% cover on the bank face
Bank top bare (coverage)	% cover on the top of the bank (within 5 m from the bank)
Bank top grass (coverage)	% cover on the top of the bank (within 5 m from the bank)
Bank top herbs (coverage)	% cover on the top of the bank (within 5 m from the bank)
Bank top shrubs (coverage)	% cover on the top of the bank (within 5 m from the bank)
Bank top trees (coverage)	% cover on the top of the bank (within 5 m from the bank)

Table 6.2 Overview of variables collected during field survey. Channel – physical characteristics and vegetation.

Variable name	Variable description (units/categories)
Water width (m)	Channel width at water surface level (m)
Water depth (m)	Estimated addtotext Channel water depth (m)
Channel flow	Flow type (smooth 1, rippled 2)
Channel material	Channel substrate (artificial (1), cobble (2), gravel (3), sand (4), cohesive material (5))
Channel boulders (square m)	Surface area of boulders in the channel (m^2)
Channel large wood (m)	Length (m) of large wood (>10cm diameter and >1m length)
Channel emergent broad leaved macrophytes (p/a)	Presence / absence
Channel emergent narrow leaved macrophytes (p/a)	Presence / absence
Channel submerged broad leaved macrophytes (p/a)	Presence / absence
Channel submerged fine leaved macrophytes (p/a)	Presence / absence
Channel submerged linear leaved macrophytes (p/a)	Presence / absence
Channel filamentous algae (p/a)	Presence / absence
Channel rooted floating leaved macrophytes (p/a)	Presence / absence
Channel number of vegetation types	number

There is currently no standard field method for detailed quantification of the distribution of signal crayfish burrows and the approach to recording crayfish burrows used in this survey was therefore devised on the basis of preliminary field observations. Three variables were recorded in the field for each bank section: burrow presence/absence, the total number of burrows and the length of bank impacted by burrows (Table 6.3). The number of burrows includes only those burrows above the water surface at the time of survey since high turbidity levels at the majority of transects prevented accurate observations of submerged burrows. The number of burrows recorded may therefore underestimate the total number of burrows present. Impacted bank length refers to the approximate length of bank impacted by burrows (to the nearest 1 m). Burrow density was then computed as number of burrows divided by the impacted bank length.

Three burrow variables were recorded for each bank section: burrow presence/absence, the total number of burrows (above the water surface) and the length of bank impacted by burrows (to the nearest 1m). A linear burrow density was then calculated as the number of burrows divided by the impacted bank length.

Table 6.3 Variables collected during the field survey to illustrate burrows presence and bank erosion.

Variable name	Variable description (units/categories)
Burrows on site	Presence of burrows on site
Burrows on section	Presence of burrows on section
Number of burrows per bank section	Total number of burrows observed on bank section above the water surface
Burrow-impacted bank length (m)	Length of bank impacted by burrows (m) within the 10m transect
Burrow density (burrows per m)	Impacted bank length/ number of burrows
Erosion-impacted bank length (m)	Length of bank with erosion features (m)

In order to make rapid visual assessments of erosion types and extent across multiple sites, the length of bank impacted by three primary erosion types (fluvial, mass failure and artificial) was recorded at each bank section following Thorne (1998) (Table 6.3; Figure 6.1). Fluvial bank erosion is caused directly by the energy of river flow and is indicated by features such as undercut bank and exposed roots (Figure 1a). Mass failure refers to amounts of material falling into the river and is indicated by features such as the presence of cracks and blocks of failed material at the bank toe (Figure 1b). Artificial erosion is used as group term for bank erosion caused by humans or domestic animals, usually related to access to river (Figure 1c). The presence and length of the impacted bank were recorded for each of these three primary types of bank erosion. The main limitation was that the method relied on simple visual identification of erosion and no data on levels of activity/erosion rates were collected.

Figure 6.1. Examples of three types of erosion: (a) fluvial erosion (5 m long, River Mole), (b) mass failure erosion (2 m long River Mole), (c) artificial erosion (2 m long, River Colne).

6.3 Results

6.3.1. Extent of signal crayfish burrowing and erosion across surveyed sites

This survey is based on 69 sites with burrows presence and out of total of 768 bank sections surveyed, 245 (32 %) had records of burrows and 261 (34 %) recorded signs of erosion. Frequency histograms (Figure 6.2) and descriptive statistics (Table 6.4) show the variability in burrowing metrics and the extent of erosion records across the surveyed reaches. A total of 881 burrows was recorded, ranging between 1 and 16 burrows per bank section (median 3). The total length of bank impacted within the burrowed bank sections was 578 m which represents 24% of the length of transects (2,450 m) where burrows were recorded. On each individual section, length of bank impacted by burrows ranged from 1 to 10 m with median value of 2 m. Burrow density varied between 1 and 6 burrows per metre of impacted bank (median 1 burrow per m). The erosion impacted bank length totalled 786 m and ranged from 1 to 10 m of the river bank (median 2 m). There was a positive correlation between the number of burrows and erosion impacted bank length which was confirmed by Spearman's Rank ($r = 0.872$; $p < 0.05$). The frequency distributions of all three burrowing metrics had a strong positive skew (Figure 6.2) illustrating that high values of all three burrowing metrics and erosion records were rare. Overall, the median value for bank sections with burrows was to have less than 3 burrows per bank section, less than 2 m of impacted bank length and a density of 1 burrows per m length of bank, with a small minority of transects associated with higher burrow densities of up to a maximum of 6 burrows per m of impacted bank length.

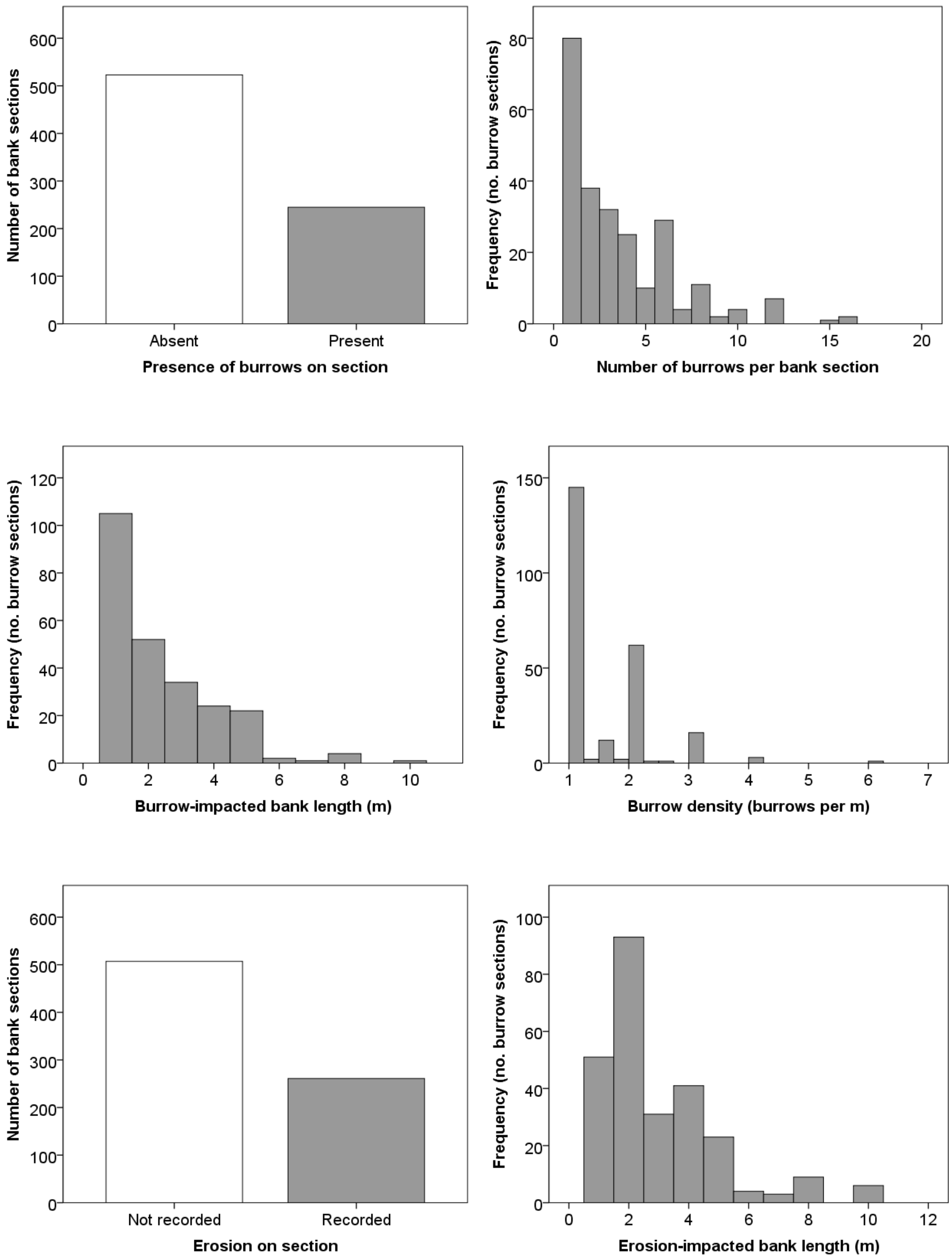


Figure 6.2 Frequency distribution for burrowing metrics (n = 245 bank sections) and erosion (n = 261 bank sections).

Table 6.4. Descriptive statistics for three burrowing metrics (n = 245 sections)

	Number of burrows per bank section	Burrow-impacted bank length (m)	Burrow density (burrows per m)	Erosion-impacted bank length (m)
Valid N	245	245	245	261
Mean	3.6	2.36	1.491	3.01
Median	3	2	1	2
Mode	1	1	1	2
Std. Deviation	3.039	1.653	0.724	1.993
Minimum	1	1	1	1
Maximum	16	10	6	10
Sum	881	578	365.3	786
Percentiles 25	1	1	1	2
Percentiles 75	5	3	2	4

6.3.2 Patterns of crayfish burrowing within and between tributaries

The seven tributaries revealed differences in the three burrowing metrics (Figure 6.3, Table 6.5). Overall there was a statistically significantly higher numbers of burrows and longer impacted lengths on the river Windrush, compared with lower numbers of burrows and shorter impacted lengths on the rivers Mole, Loddon and Wey (Kruskall Wallis $p < 0.05$). The distribution of burrow densities showed greater similarity across the tributaries although the Windrush (median value 2 burrows per m) was associated with a statistically significantly higher (Kruskall Wallis $p < 0.05$) and the Lee, Wey and Loddon (median value 1 burrows per m) showed narrower ranges of and lower density values compared to the other tributaries.

Table 6.5 Significance of difference in burrowing and erosion related variables between studied tributaries of the Thames.

Variable	p	Pairwise comparisons
Number of burrows per bank section	0.001	Wey, Loddon, Mole < Windrush
Burrow-impacted bank length (m)	0.001	Wey, Loddon, Mole < Windrush
Burrow density (burrows per m)	0.002	Lee, Wey, Loddon < Windrush
Erosion-impacted bank length (m)	0.739	Not significant

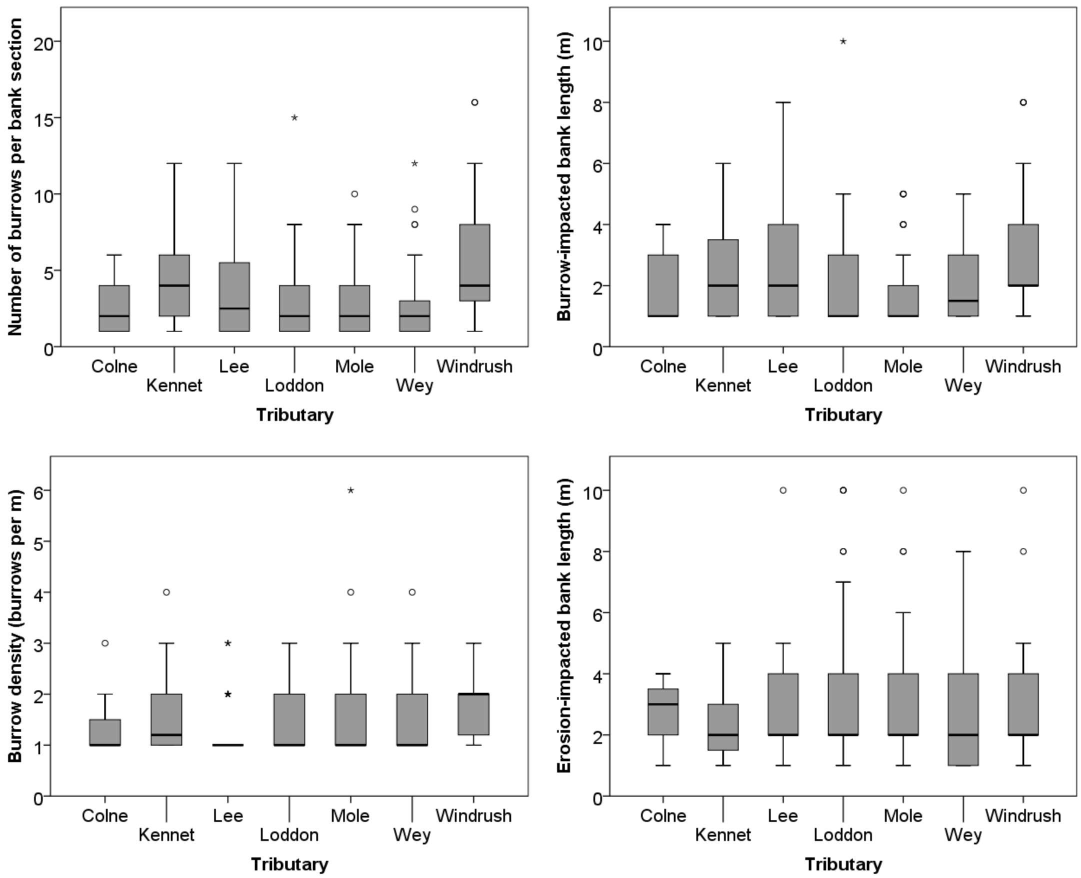


Figure 6.3 Burrowing metrics across the tributaries (n = 245 bank sections)

6.3.3 Relationships between burrowing and biophysical river habitat characteristics

The distribution of biophysical habitat characteristics for bank sections with and without burrows are shown (Figures 6.4 and 6.5) and Mann Whitney U tests were performed to explore whether differences between the two groups were statistically significant. (Table 6.6). Nine of the 31 variables revealed statistically significant differences between bank sections with and without burrows. Burrows were not found in the banks with artificial material. Cohesive bank material was recorded on the majority of bank sections (743) and out of those a 243 (33%) had burrows. Non cohesive material was recorded on much smaller number of bank sections (19) and only one bank section (6%) had burrows present. Therefore it is evident that burrowing occurs more than five times more frequently on banks with cohesive sediment than other sediment types. Burrowed sections were also associated with higher bank angles and larger areas of bare bank face and wider channels and lower coverage of emergent broad and narrow leaved vegetation, lower coverage of grass and trees on the bank face and lower coverage of submerged fine leaved macrophytes in the channel ($P<0.05$).

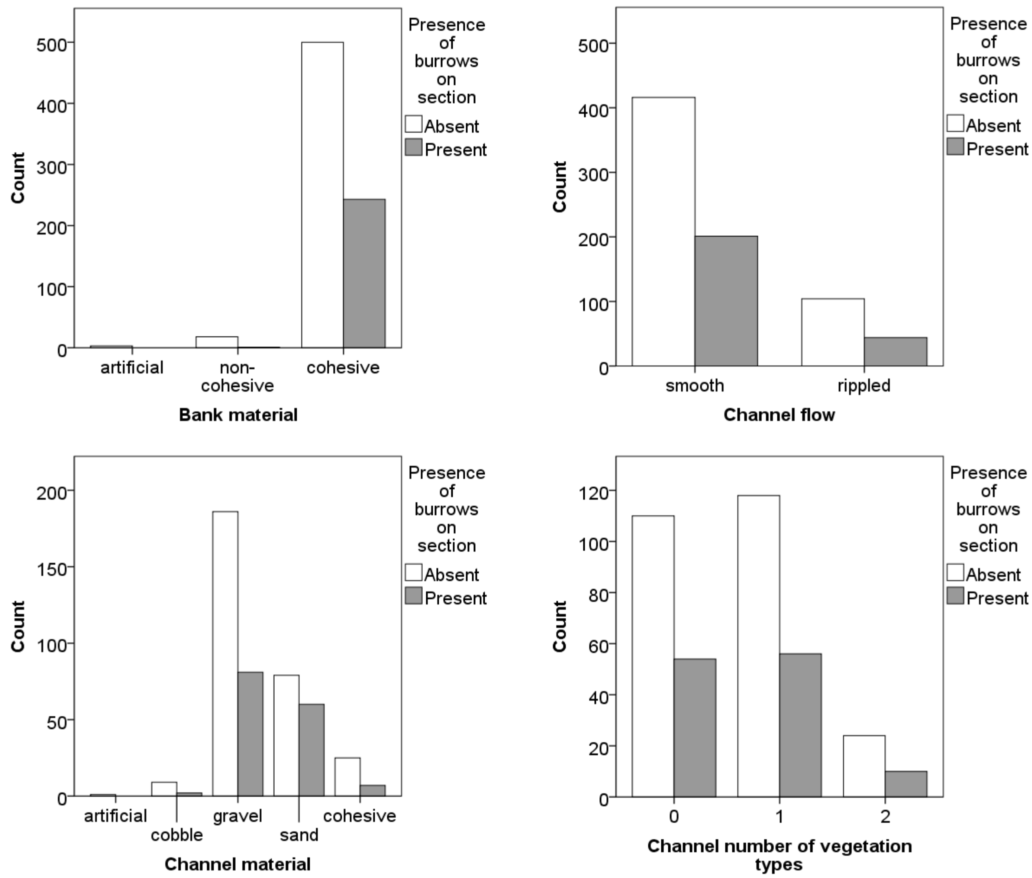


Figure 6.4 Frequency distribution of habitat variables for bank sections with and without burrows (calculated for all 768 bank sections).

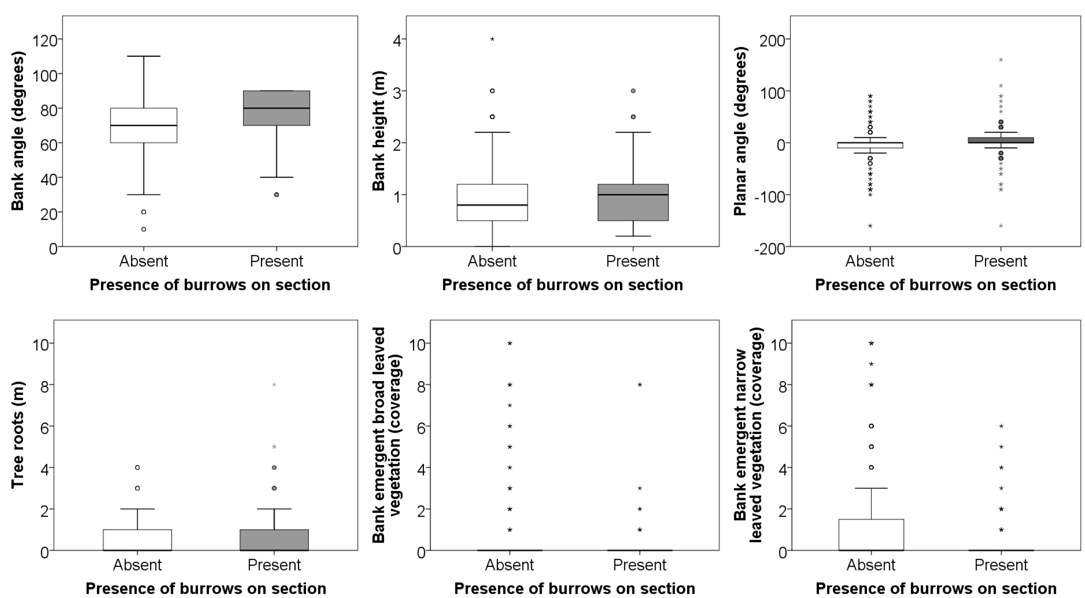


Figure 6.5 Boxplots for 31 habitat variable for bank sections without and with burrows presence (calculated for all 768 bank sections).

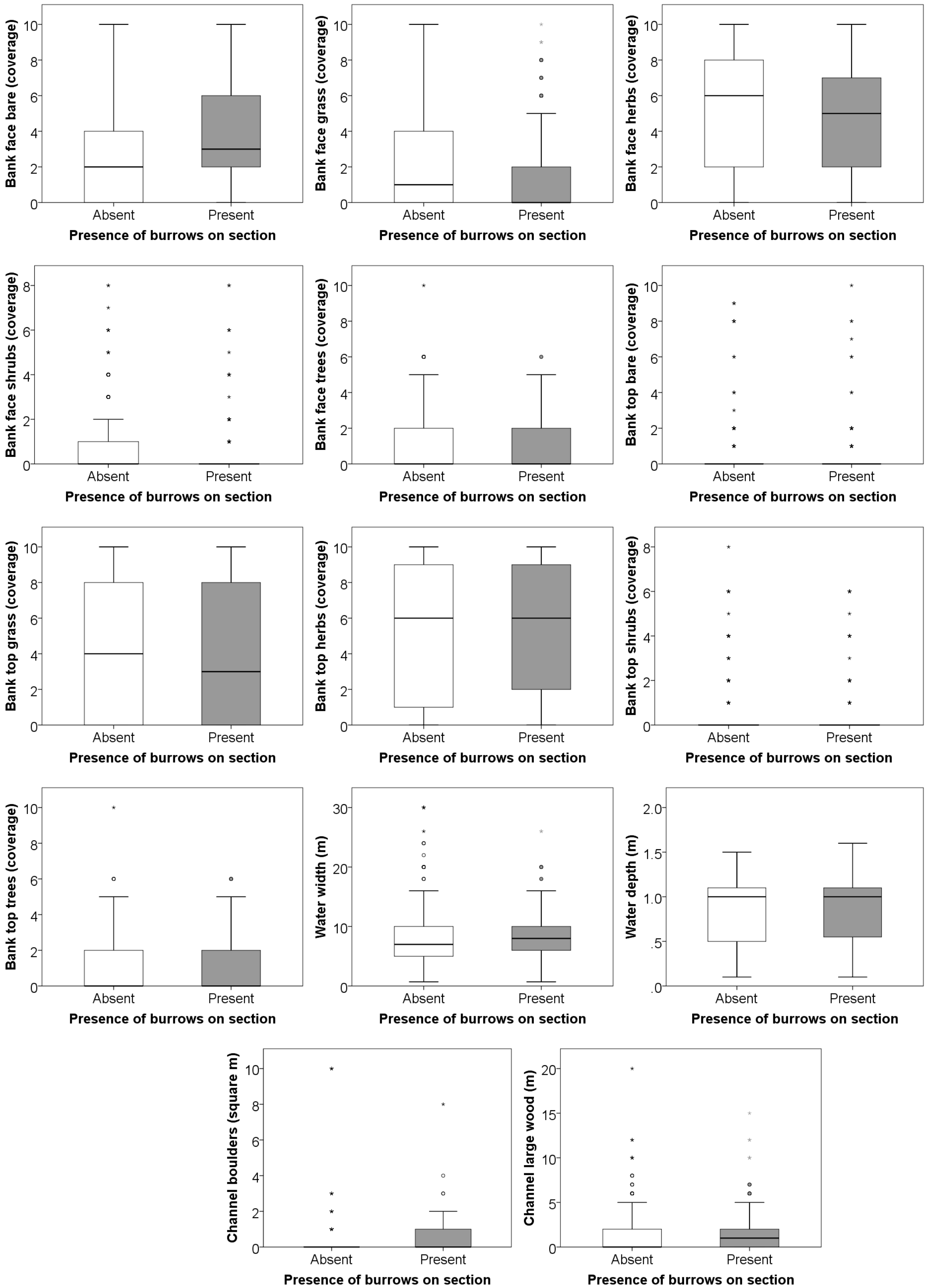


Figure 6.5 (continued)

Table 6.6 Comparison between bank sections without and with burrows.

	N	Mean	Mean	Asymp. Sig. (2-tailed)
Burrows present		no	yes	
Bank material	521	2.95	3.00	0.005*
Bank angle (degrees)	512	66.70	77.55	0.000*
Bank height (m)	523	0.93	0.93	0.272
Planar angle (degrees)	523	-3.37	-0.08	0.057
Tree roots (m)	515	0.51	0.48	0.648
Bank emergent broad leaved vegetation (coverage)	518	0.36	0.11	0.028*
Bank emergent narrow leaved vegetation (coverage)	504	1.62	0.18	0.000*
Bank face bare (coverage)	499	2.27	3.84	0.000*
Bank face grass (coverage)	497	2.68	1.38	0.000*
Bank face herbs (coverage)	497	5.00	4.79	0.328
Bank face shrubs (coverage)	505	0.65	0.57	0.379
Bank face trees (coverage)	505	1.19	0.85	0.011*
Bank top bare (coverage)	481	0.43	0.48	0.194
Bank top grass (coverage)	481	4.44	4.25	0.34
Bank top herbs (coverage)	481	5.09	5.26	0.304
Bank top shrubs (coverage)	506	0.56	0.46	0.081
Bank top trees (coverage)	506	1.25	1.25	0.873
Water width (m)	520	7.77	8.10	0.028*
Water depth (m)	519	0.78	0.84	0.125
Channel flow	520	1.20	1.18	0.505
Channel material	300	3.39	3.48	0.078
Channel boulders (square m)	221	0.54	0.46	0.625
Channel large wood (m)	317	1.46	1.69	0.381
Channel emergent broad leaved macrophytes (p/a)	252	0.04	0.06	0.421
Channel emergent narrow leaved macrophytes (p/a)	252	0.00	0.00	0.49
Channel submerged broad leaved macrophytes (p/a)	252	0.04	0.08	0.122
Channel submerged fine leaved macrophytes (p/a)	252	0.21	0.11	0.020*
Channel submerged linear leaved macrophytes (p/a)	252	0.11	0.14	0.399
Channel filamentous algae (p/a)	252	0.24	0.22	0.647
Channel rooted floating leaved macrophytes (p/a)	252	0.02	0.03	0.545
Channel number of vegetation types	252	0.66	0.63	0.743

Spearman correlations analysis was run for 245 bank sections with presence of burrows (Table 6.7). Correlation between burrow metrics and individual habitat characteristics were weak ($r<0.3$) although burrows occurrence correlated statistically significantly ($p<0.05$) with eight variables. Positive correlation was recorded for the bank angle, coverage of bare bank face and bank top trees, presence of rippled flow, while negative one was observed for the bank emergent broad leaved vegetation, bank top grass coverage, water width and depth, channel cohesive material and channel submerged broad leaved material and number of channel vegetation types.

Table 6.7 Spearman correlations for 245 bank sections.

Spearman's rho	Number of burrows per bank section	Burrow-impacted bank length (m)	Burrow density (burrows per m)	Erosion-impacted bank length (m)
Bank material	0.021	-0.008	0.053	0.068
Bank angle (degrees)	.149*	.143*	0.109	.312**
Bank height (m)	-0.018	-0.052	0.012	0.001
Planar angle (degrees)	0.017	-0.032	0.061	-0.019
Tree roots (m)	0.022	0.027	0.001	-0.021
Bank emergent broad leaved vegetation (coverage)	-0.122	-.139*	-0.045	-0.043
Bank emergent narrow leaved vegetation (coverage)	0.072	0.031	0.105	-0.008
Bank face bare (coverage)	.229**	.183**	.178**	.271**
Bank face grass (coverage)	-0.119	-0.115	-0.058	0.02
Bank face herbs (coverage)	-0.076	-0.05	-0.075	-.246**
Bank face shrubs (coverage)	-0.059	-0.097	0.037	-.191**
Bank face trees (coverage)	-0.031	0.011	-0.081	-0.09
Bank top bare (coverage)	0.026	-0.033	0.073	0.025
Bank top grass (coverage)	-.133*	-0.108	-0.08	.207**
Bank top herbs (coverage)	0.097	0.098	0.028	-.229**
Bank top shrubs (coverage)	0.109	0.103	0.07	-0.042
Bank top trees (coverage)	.148*	0.06	.199**	-0.106
Water width (m)	-0.099	0.028	-.241**	.138*
Water depth (m)	-.139*	-0.093	-.166**	0.083
Channel flow	0.107	0.051	.150*	-0.072
Channel material	-.182*	-0.13	-.181*	.188*
Channel boulders (square m)	0.031	-0.033	0.108	0.003
Channel large wood (m)	-0.072	-0.033	-0.113	0.001
Channel emergent broad leaved macrophytes (p/a)	0.125	0.096	0.133	0.078
Channel emergent narrow leaved macrophytes (p/a)	.	.	.	.
Channel submerged broad leaved macrophytes (p/a)	-.209*	-0.179	-0.16	-0.149

Table 6.7 (continued)

Spearman's rho	Number of burrows per bank section	Burrow-impacted bank length (m)	Burrow density (burrows per m)	Erosion-impacted bank length (m)
Channel submerged fine leaved macrophytes (p/a)	-0.079	-0.071	-0.03	-0.018
Channel submerged linear leaved macrophytes (p/a)	-0.078	-0.037	-0.129	0.166
Channel filamentous algae (p/a)	-0.155	-0.125	-0.144	0.011
Channel rooted floating leaved macrophytes (p/a)	-0.005	0.027	-0.055	-0.015
Channel number of vegetation types	-.220*	-0.159	-.215*	0.052

A PCA was performed on 20 variables and data for 768 bank sections included. Given the difficulties identifying channel substrate and submerged vegetation types at many sites due to high turbidity levels, and the fact that the Mann Whitney U and Spearmans Rank analyses identified bank physical and vegetation properties as the key variables that differed between burrowed and non-burrowed bank sections, the PCA analysis focused on a more conservative range of bank-related variables. Still due to missing data the final data set consisted of 466 bank sections.

Six principal components had eigenvalues >1 and cumulatively explained 56 % of the variance in the data set (Table 6.8). Variable loadings on individual PCs are presented in Table 6.9. The PC loadings were used to interpret the gradients represented by the PCs. Principal component 1 (PC1) defines a gradient of increasing coverage of herbs on the banks, while the PC2 relates to the channel size. PC3 represents a gradient of bank angle and coverage of bare bank and PC4 defines a gradient of bare bank. PC5 relates to trees presence, while PC6 represents shrubs coverage.

Table 6.8 Eigenvalues and cumulative variance explained for PCA performed on the sixteen habitat variables.

PC	Total	% of Variance	Cumulative %
1	3.078	15.39	15.39
2	2.249	11.245	26.635
3	1.986	9.932	36.567
4	1.466	7.331	43.898
5	1.34	6.699	50.597
6	1.152	5.761	56.358

Bi-plots for the six PCs illustrated the difference in PC scores between bank sections with and without burrows (Figure 6.6). Overall there is considerable overlap in PC scores among the bank sections which generally show a range of values for each PC and hence a range of biophysical habitat conditions at the section scale. Mann Whitney U test has shown that difference between sections with and without burrows is significant for four PCs ($p < 0.05$). Sections with burrows had higher scores along the PC3, PC4, and lower scores along the PC5 and PC6. That implies a tendency of crayfish to dig burrows on the bare banks with high bank angle with low presence of shrubs and trees.

Spearman's Rank correlations were performed between the three burrowing metrics and the six PCs for 245 bank sections where burrows were observed (Table 6.10). Two statistically significant correlations are revealed. Firstly there is a positive link between number of burrows per bank section and PC4 ($r = 0.18$) implying a tendency to for burrowing on the bare banks. Secondly, burrows density is correlated negatively with PC2 ($r = -0.16$) and positively with PC4 ($r = 0.23$) implying a tendency of crayfish to dig burrows in bare bank sections associated with narrower channel size.

Table 6.9 Principal component loadings for the variables and interpretation of the PCs.

Component	1	2	3	4	5	6
Interpretation	Herbs on banks	Channel size	Bank angle and bare bank	Proportion of bare bank	Trees presence	Shrubs coverage
Bank top herbs (coverage)	**0.91**	0.06	-0.02	-0.04	-0.03	-0.02
Bank top grass (coverage)	**-0.91**	-0.01	-0.01	-0.20	0.05	0.01
Bank face herbs (coverage)	**0.64**	0.05	0.23	**-0.46**	0.12	0.32
Bank top trees (coverage)	**0.46**	-0.10	-0.15	0.39	0.11	0.01
Water depth (m)	-0.01	**0.83**	0.15	-0.04	0.16	-0.01
Water width (m)	0.06	**0.75**	0.03	-0.03	0.15	0.11
Channel flow	-0.04	**-0.69**	0.09	0.00	0.12	0.10
Bank angle (degrees)	-0.08	0.15	**0.69**	-0.09	-0.19	-0.08
Bank emergent narrow leaved vegetation (coverage)	-0.09	0.19	**-0.68**	-0.13	-0.29	-0.07
Bank face grass (coverage)	**-0.57**	-0.09	**-0.67**	-0.14	-0.15	-0.04
Bank top bare (coverage)	0.05	-0.06	0.05	**0.73**	-0.02	0.04
Bank face bare (coverage)	-0.11	0.08	**0.46**	**0.68**	0.03	-0.32
Bank top shrubs (coverage)	0.27	-0.01	-0.08	**0.48**	-0.01	0.34
Tree roots (m)	0.01	0.04	0.06	0.03	**0.80**	-0.06
Bank face trees (coverage)	0.01	0.13	0.03	-0.07	**0.79**	0.07
Bank face shrubs (coverage)	0.02	0.06	0.04	0.06	0.11	**0.69**
Bank emergent broad leaved vegetation (coverage)	0.05	-0.14	-0.10	-0.11	-0.20	**0.50**
Bank height (m)	-0.12	0.25	0.33	0.09	0.14	0.38
Bank material	-0.01	0.19	-0.10	-0.09	-0.02	0.03
Planar angle (degrees)	-0.05	-0.09	0.29	-0.01	-0.03	0.02

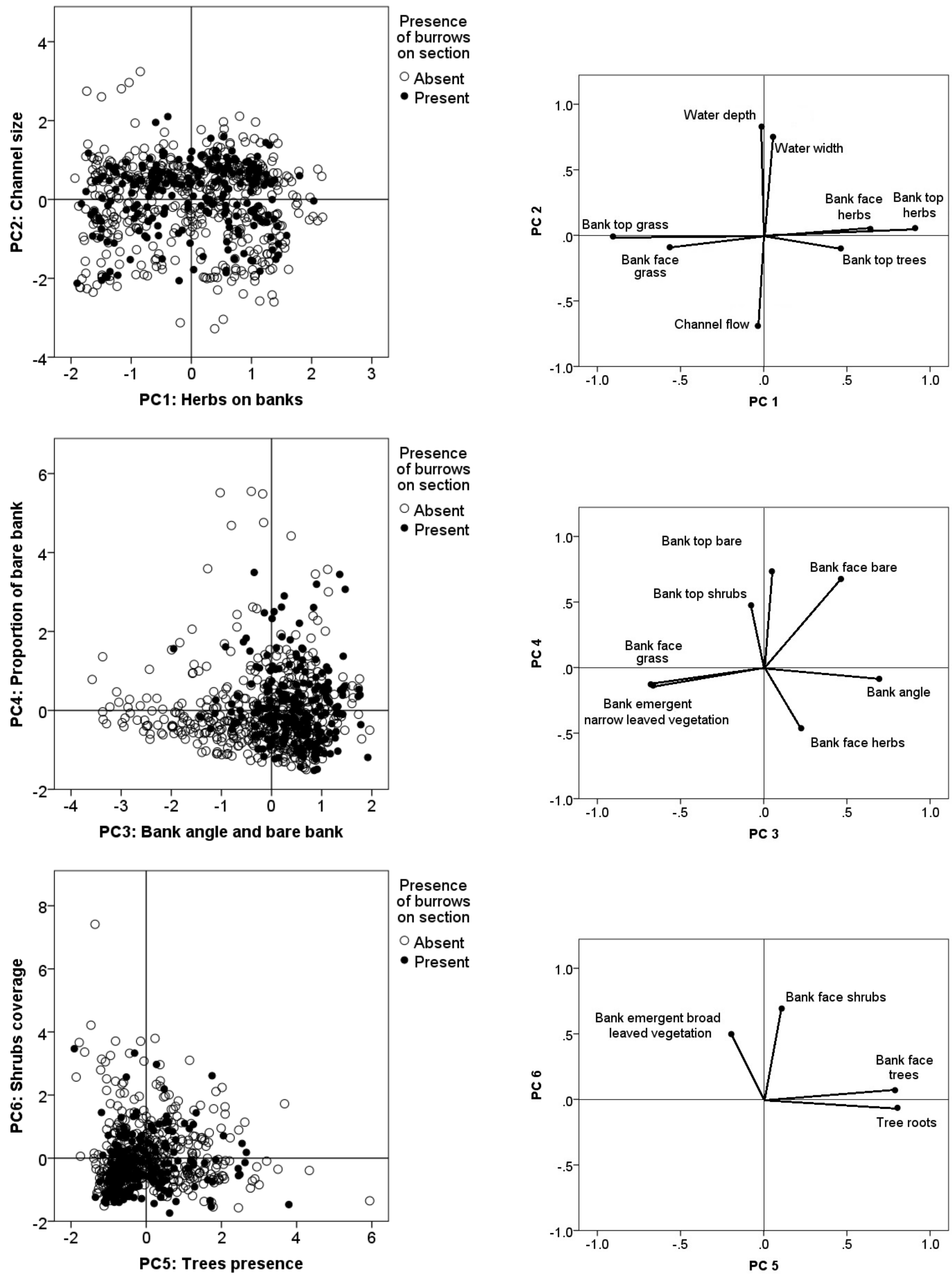


Figure 6.6 Scatterplots and biplots for principal component scores for sites with and without burrows presence.

Table 6.10 Correlation between principal components and burrowing metrics for 245 bank sections.

Spearman's rho	Number of burrows per bank section	Burrow-impacted bank length (m)	Burrow density (burrows per m)
PC1: Herbs on banks	0.066	0.073	0.011
PC2: Channel size	-0.091	-0.025	-.164*
PC3: Bank angle and bare bank	0.066	0.061	0.031
PC4: Proportion of bare bank	.184**	0.09	.232**
PC5: Trees presence	-0.055	-0.056	-0.018
PC6: Shrubs coverage	-0.085	-0.101	-0.019

6.3.4 Relationships between bank erosion and biophysical river habitat characteristics

The Mann Whitney U tests were performed to explore whether differences between the two groups (bank sections with and without erosion) were statistically significant. (Table 6.11). A total of 15 out of the 31 variables revealed statistically significant differences between bank sections with and without records of erosion. Sections with records of erosion were associated with steeper and higher banks, higher planar angle, coverage of bare bank face, coverage of grass on the bank top, water depth, more cohesive channel material and higher presence of linear leaved macrophytes in the channel. They also had a lower coverage of bank emergent broad and narrow leaved macrophytes, bank face coverage of grass, herbs and shrubs, as well as bank top coverage of herbs and presence of fine leaved macrophytes in the channel ($P<0.05$).

Table 6.11 Comparison between bank sections without and with signs of erosion present.

Group Statistics	N	Mean no erosion	Mean erosion	Asymp. Sig. (2-tailed)
Bank material	504	2.96	2.98	0.108
Bank angle (degrees)	496	65.47	79.21	**0.000***
Bank height (m)	507	0.897	0.997	**0.001***
Planar angle (degrees)	507	-3.94	0.84	**0.034***
Tree roots (m)	499	0.46	0.58	0.384
Bank emergent broad leaved vegetation (coverage)	497	0.38	0.09	**0.001***
Bank emergent narrow leaved vegetation (coverage)	481	1.67	0.21	**0.000***
Bank face bare (coverage)	476	2.05	4.1	**0.000***
Bank face grass (coverage)	474	2.68	1.49	**0.000***
Bank face herbs (coverage)	474	5.22	4.41	**0.000***
Bank face shrubs (coverage)	482	0.79	0.32	**0.000***
Bank face trees (coverage)	482	1.15	0.95	0.418
Bank top bare (coverage)	453	0.43	0.48	0.169
Bank top grass (coverage)	453	4.11	4.84	**0.027***
Bank top herbs (coverage)	453	5.41	4.67	**0.018***
Bank top shrubs (coverage)	482	0.6	0.4	0.114
Bank top trees (coverage)	482	1.3	1.16	0.215
Water width (m)	503	7.84	7.95	0.434
Water depth (m)	503	0.773	0.847	**0.011***
Channel flow	504	1.2	1.18	0.386
Channel material	305	3.36	3.56	**0.000***
Channel boulders (square m)	229	0.58	0.37	0.311
Channel large wood (m)	319	1.43	1.76	0.063
Channel emergent broad leaved macrophytes (p/a)	264	0.05	0.05	0.972
Channel emergent narrow leaved macrophytes (p/a)	264	0	0	0.522
Channel submerged broad leaved macrophytes (p/a)	264	0.06	0.05	0.588
Channel submerged fine leaved macrophytes (p/a)	264	0.21	0.09	**0.008***
Channel submerged linear leaved macrophytes (p/a)	264	0.08	0.21	**0.001***
Channel filamentous algae (p/a)	264	0.22	0.27	0.275
Channel rooted floating leaved macrophytes (p/a)	264	0.02	0.03	0.417
Channel number of vegetation types	264	0.63	0.69	0.530

Spearman correlations analysis was run for 261 bank sections with presence of burrows (Table 6.12). Correlation between presence of erosion and individual habitat characteristics were weak ($r<0.3$) although erosion occurrence correlated statistically significantly ($p<0.05$) with four variables. Positive correlation was recorded for the bank angle, coverage of bare bank face and water width, while negative one was observed for the bank face herbs coverage.

Table 6.12 Correlation between habitat variables and length of eroded bank, only for 261 eroded sections on sites with burrows

Spearman's rho	Erosion-impacted bank length (m)
Bank material	-0.112
Bank angle (degrees)	**.200****
Bank height (m)	-0.035
Planar angle (degrees)	0.025
Tree roots (m)	-0.055
Bank emergent broad leaved vegetation (coverage)	-0.12
Bank emergent narrow leaved vegetation (coverage)	-0.099
Bank face bare (coverage)	**.271****
Bank face grass (coverage)	-0.075
Bank face herbs (coverage)	**-.156***
Bank face shrubs (coverage)	0.007
Bank face trees (coverage)	-0.095
Bank top bare (coverage)	0.017
Bank top grass (coverage)	0.061
Bank top herbs (coverage)	-0.086
Bank top shrubs (coverage)	-0.026
Bank top trees (coverage)	-0.023
Water width (m)	**.141***
Water depth (m)	0.098
Channel flow	-0.008
Channel material	0.116
Channel boulders (square m)	-0.01
Channel large wood (m)	0.157
Channel emergent broad leaved macrophytes (p/a)	0.013
Channel emergent narrow leaved macrophytes (p/a)	.
Channel submerged broad leaved macrophytes (p/a)	0.013
Channel submerged fine leaved macrophytes (p/a)	0.089
Channel submerged linear leaved macrophytes (p/a)	-0.111
Channel filamentous algae (p/a)	-0.124
Channel rooted floating leaved macrophytes (p/a)	-0.061
Channel number of vegetation types	-0.097

PCA analysis on the basis of same variables as in the previous section (Section 6.3.3) (Tables 6.8; 6.9) was run in order to test for differences between bank sections with and without erosion. Biplots for the six PCs illustrated the difference in PC scores between bank sections with and without records of erosion (Figure 6.7). Overall there is considerable overlap in PC scores among the bank sections with and without records of erosion. Mann Whitney U test has shown that difference between sections with and without burrows is significant for four PCs ($p < 0.05$). Sections with records of erosion had higher scores along the PC3, PC4, and lower scores along the PC1 and PC6. That implies a tendency for erosion to occur on the steep, bare banks (Table 6.13).

Spearman's Rank correlations were performed between length of erosion and the six PCs for 261 bank sections where erosion was observed (Table 6.14). Three statistically significant correlations are revealed. There is a positive link between length of erosion per bank section and PC3 and PC4 ($r = 0.244$ and 0.215 respectively) and negative link with PC6. That implies that erosion occurs on bank sections with bare surface and high bank angle.

Table 6.13 Difference in PC scores between bank sections with and without presence of erosion.

		Erosion		
	N	Absent	Present	p
PC1: Herbs on banks	436	0.09	-0.16	0.002*
PC2: Channel size	436	-0.03	0.05	0.566
PC3: Bank angle and bare bank	436	-0.30	0.51	0.000*
PC4: Proportion of bare bank	436	-0.08	0.13	0.000*
PC5: Trees presence	436	0.04	-0.07	0.117
PC6: Shrubs coverage	436	0.16	-0.27	0.000*

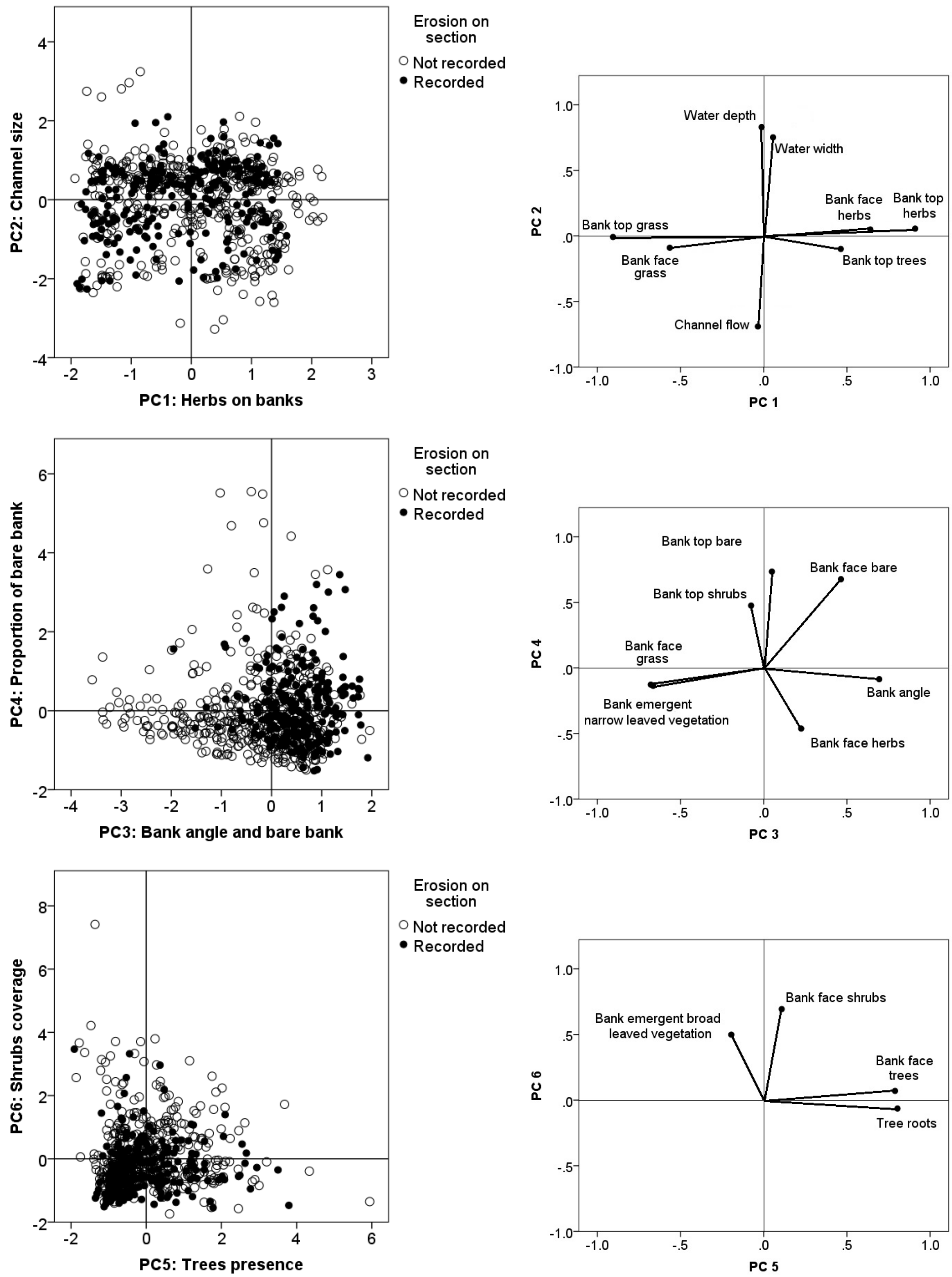


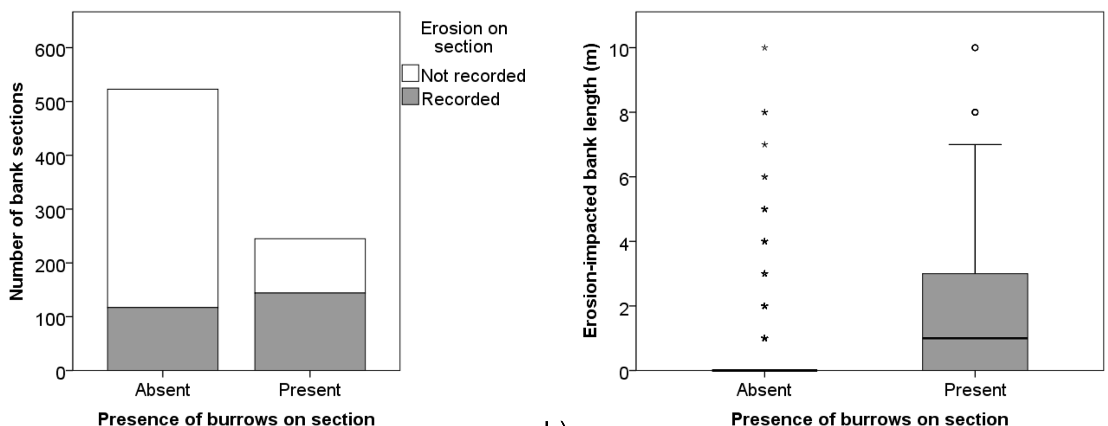
Figure 6.7 Scatterplots and biplots for principal component scores for sites with and without erosion presence.

Table 6.14 Correlation between principal components scores and erosion presented for 261 bank sections.

Spearman's rho	PC1: Herbs on banks	PC2: Channel size	PC3: Bank angle and bare bank	PC4: Proportion of bare bank	PC5: Trees presence	PC6: Shrubs coverage
Erosion-impacted bank length (m)	-0.088	0.098	.244**	.215**	-0.103	-.141*

6.3.5 Relationships between burrowing, local habitat variables and erosion patterns

In this section the relationship between burrowing, local habitat variables and erosion patterns will be explored by analysis of presence and absence of records of erosion on bank sections with and without burrows (Figure 6.8; Table 6.16). Mean erosion length on bank sections with no burrows is 0.62 m (median 0) while on sections with burrows is 1.88 m (median 1), that difference is statistically significant (p = 0.000). While only 22 % of bank sections without burrows recorded erosion, presence of burrows raised the likelihood of erosion by almost three times (59%).



a) b)

Figure 6.8 a) Frequency distribution illustrating number of bank sections with and without records of erosion depending on whether burrows are present or not on the respective bank section. b) Boxplot illustrating difference in length of impacted river bank depending on whether signal crayfish burrows are absent or present on the respective bank section.

Table 6.16 Number of bank sections with and without records of erosion depending on whether burrows are present or not on the respective bank section.

		Erosion on section		%	Total
		Not recorded	Recorded		
Presence of burrows on section	Absent	406	117	22	523
	Present	101	144	59	245
Total		507	261		768

PCA was undertaken on 245 bank sections with burrows only included in order to investigate in which circumstances presence of burrows is more likely to lead to erosion (Figure 6.9). Out of those 245 bank sections, 141 (57%) had presence of erosion. Mann Whitney U test has shown that difference between sections with and without records of erosion is significant for three PCs ($p < 0.05$) (Table 6.17). Sections with erosion had higher scores along the PC3, lower scores along the PC1 and PC6 implying a tendency of crayfish burrows to contribute to erosion in cases when bank where they burrowed is also a bank with high bank angle with no herbs and shrubs.

Table 6.17 Difference in PC scores between bank sections with and without presence of erosion.

Group Statistics	Erosion		
	Absent	Present	p
PC1: Herbs on banks	0.26	-0.13	0.002*
PC2: Channel size	0.01	0.13	0.542
PC3: Bank angle and bare bank	0.28	0.53	0.009*
PC4: Proportion of bare bank	-0.03	0.18	0.12
PC5: Trees presence	-0.09	-0.18	0.279
PC6: Shrubs coverage	-0.08	-0.32	0.044*

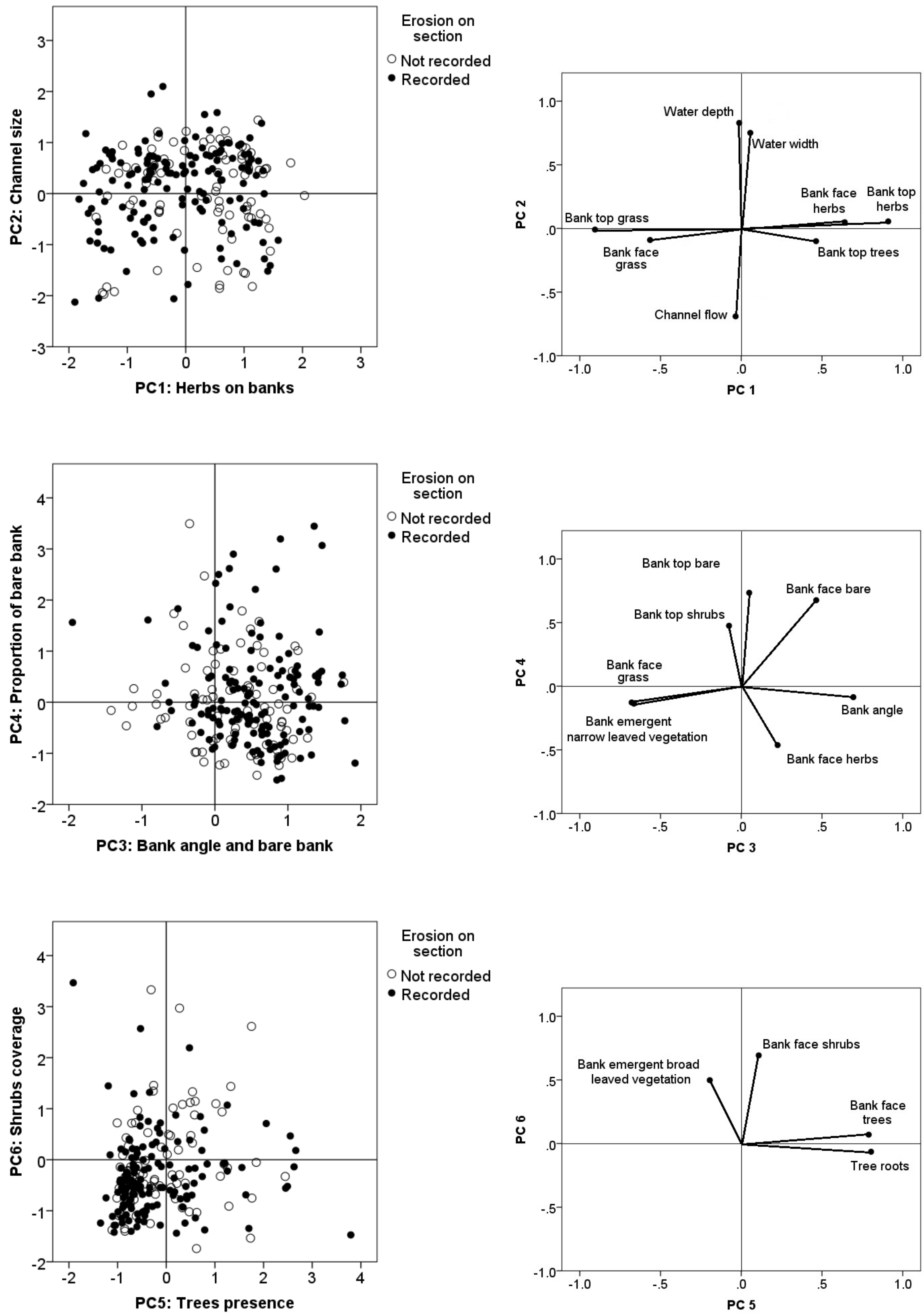


Figure 6.9 Scatterplots and biplots for principal component scores for sites with and without erosion presence.

Spearman’s Rank correlations were performed between the three burrowing metrics and the six PCs for 144 bank sections where burrows were observed (Table 6.18). Two statistically significant correlations are revealed. Firstly there is a positive link between length of bank impacted by erosion and PC3 (r = 0.321) implying a tendency for erosion to occur on steep, bare banks. Secondly, there is a negative correlation with PC1 (r = -0.200) implying a tendency of erosion to occur on bank sections with less herbs on the river bank. The Chi-square statistic is significant at the 0.01 level confirming indicating that there is a significant association in the co-occurrence of burrows features indicative of fluvial bank erosion or mass failure.

Table 6.18 Correlation between principal components scores and erosion presented for 144 bank sections.

Spearman's rho	PC1: Herbs on banks	PC2: Channel size	PC3: Bank angle and bare bank	PC4: Proportion of bare bank	PC5: Trees presence	PC6: Shrubs coverage
Erosion-impacted bank length (m)	-.200*	0.103	.321**	0.162	-0.152	-0.089

6.4. Discussion

In comparison with previous studies (Guan, 1994; Stanton, 2004; Roberts, 2012), presented results represent the first insight into the interaction between river habitat characteristics, the occurrence of crayfish burrows and signs of erosion on the bank section spatial scale. Same methodology, observation from the river bank, was used as in Chapter 4, and therefore presented results are subject to certain limitations. Primarily, a number of burrows is an underestimation and may not be representative of the patterns bellow water.

6.4.1. Extent of signal crayfish burrowing and erosion across surveyed sites

The first main finding is that on the sites where signal crayfish burrows were present, burrows are observed at only 32 % of river bank sections. This finding is consistent with findings from the previous chapter that indicated that signal crayfish burrows are concentrated in small areas within the reach. It contrasts findings from the previous chapter where burrows were found at a majority of the surveyed reaches. However, it also implies that as the spatial scale changes, from reach to bank section, on the same sites, the percentage of burrows presence at a unit of spatial scale falls down. Similar cases when a change in scale influenced the conclusion reached were described by Levin (1989).

The second main finding is that majority of banks had low length impacted by burrows and also by a small number, however, on rare occasions, these impacts were higher. This is manifested in both lengths of bank impacted as well as burrows density. This is similar to finding from the previous chapter which found that on the reach scale, only small lengths are impacted and this is confirmed on a smaller scale too. This finding reinforces the explanation made in Chapter four, made on the well-known tendency of crayfish to select certain micro habitats (Hudina et al. 2009), that localised changes in habitat conditions can cause the occurrence of burrows.

The third main finding is related to erosion, firstly only 34% of bank sections had records of erosion and even on those sections, the length of erosion was low (median value 2 m). Since no other studies are done using this methodology, it is not possible to put those results in context as absolute values, but only use them as comparison between different bank sections in this study.

6.4.2 Patterns of crayfish burrowing within and between tributaries

There were no significant differences in the number of burrows and impacted length between tributaries, although the river Windrush was dominant. Burrowing was variable across tributaries with significantly higher densities and impacted bank length on the River Windrush. This is similar to the pattern observed on the reach scale, where the fact that all rivers are a low land tributaries of Thames and as such represent only a subset of the national dataset as described by Harvey et al. (2008). Therefore differences in burrowing are not attributed to characteristics of individual tributaries and the causalities will be explored through analysis of the direct influence of habitat characteristics.

6.4.3 Relationships between burrowing and biophysical river habitat characteristics

Influence of habitat characteristics on burrows presence on the bank section scale revealed that there is a lot of overlap between bank sections with and without burrows which is similar to findings on the reach scale. However, the explanatory power is better than on the reach scale with 9 variables demonstrating statistically significant differences between burrowed and non-burrowed sites. The improved link between habitat and burrows can primarily be attributed to change in methodology as compared to the reach scale since both presence of burrows and habitat traits were observed on same transects. Secondly, this implies that microhabitat changes, on the level of bank section, are more significant than the reach level differences.

6.4.4 Relationships between bank erosion and biophysical river habitat characteristics

Influence of habitat characteristics on records of erosion showed a significant overlap between bank sections with and without records of erosion, but also a higher number, a total of 15 variables demonstrated a statistically significant differences between two groups of bank sections. The variables identified to correspond to erosion records, high, steep banks, on the outside of the river meander, with less vegetation fit into the current understanding of erosion causes.

6.4.5 Relationships between burrowing, local habitat variables and erosion patterns

In this final section, an attempt was made to answer whether burrows presence increases the likelihood of erosion records occurrence. Firstly, the presence of burrows increased the likelihood of erosion by almost three times and erosion was significantly longer on bank sections with burrows. Burrows undermine the structural integrity of the bank and therefore promote mass failure, while their presence in the river bank causes local eddies in flow which contribute to fluvial erosion. Therefore two main types of erosion are directly promoted by burrowing.

In the next step of the analysis, the aim was to identify whether burrowing promotes erosion in specific types of conditions. Out of bank sections with burrows, the ones with higher bank angle and a lower proportion of vegetation like herbs and shrubs had more frequent records of erosion. While these results are in line with already identified parameters, it is worth noting that burrows do not cause new pathways for erosion mechanism, just reinforce factors already causing erosion.

6.5 Conclusion

The research presented in Chapter 6 revisits the 69 sites with burrows only but analyses them on the level of the individual, ten metres long bank sections. The change in spatial scale in comparison to the previous chapter revealed new findings.

Signal crayfish burrows are present at 245 out of 768 bank sections (32%) of river bank sections. This spatial scale reveals a new insight. It shows that while crayfish burrowing is omnipresent on the catchment level, on the level of reach, even where some crayfish are burrowing, actually only one-third of bank sections are influenced by burrows.

A number of burrows per bank section ranged from 1 to 16 (mean value of 3.6) and covered a length ranging from 1 to 10 m of (mean 2.4 m). These two numbers indicate that even on the bank sections influenced by burrow, not many of them occur and usually only short distance is impacted. This is further confirmed by burrow density ranging from 1 to 6 values which (mean 1.5).

Habitat characteristics differed between burrowed and non-burrowed bank sections, with the dominant trend was the overlap in traits between the two. However, the reaches with burrows did have a statistically significant tendency toward the cohesive material, higher bank angles, less vegetation and more bare bank face, wider water width.

Presence of burrows increased the likelihood of erosion by approximately three times. Non impacted bank sections had records of erosion in 22% cases, while the presence of burrows increased that likelihood to 59%. However, this result should be interpreted as a strong suggestion but not a proof that signal crayfish burrowing contributes to river bank erosion.

CHAPTER 7: Himalayan balsam as an invasive ecosystem engineer

7.1 Introduction

The role of vegetation as an ecosystem engineer on river banks is well recognised and it occurs throughout wide variety of processes and over range of spatial scales (Gurnell, 2014). One of the main impacts of vegetation is its influence on erosion and deposition (Osterkamp and Hupp, 2010) and therefore an overall morphological activity, the term that encompasses the joint effect of those two processes (Henshaw et al. 2012). While the role of vegetation changes throughout the catchment (Abernethy and Rutherfurd, 1998), it is a complex process depending on interaction between hydrology, habitat characteristics and traits of plant communities that inhabit river banks (Curran and Hession, 2013).

River banks are a highly heterogeneous habitats, consisted of relatively small patches with unique combination of environmental conditions and that results in wide variety of microhabitats (Bryant and Gilvear, 1999). Composition of plant community on river banks is defined by presence and relative abundance of individual species (Gimeno et al. 2006). Interactions between species are primarily influenced by their competition (Bennet et al. 2012) and differential ability to utilise available resources and those interactions are the basis of a concept of an ecological niche (Pocheville, 2015). In case of invasive species, the ecological niche is wider, meaning that they are more competitive under wider range of conditions and that results in occupation of more diverse microhabitats than native species (Ehrenfeld, 2010). Depending on the stage of invasion and competiveness between native and invasive species (Vaclavik and Meentemeyer, 2012), river bank will be dominated by native or invasive plants to different extent. Therefore habitat heterogeneity in combination with competitive traits of native and invasive species define which plant species will dominate specific riverbank.

The composition of species and their relative density are a prime determinant of an ecosystem engineering effect of the overall plant community (Gurnell et al. 2012). Plant density directly influences reinforcement of soil by roots (Loades et al. 2010). In addition to this, since different plants have different types of roots or soil reinforcement properties (Pollen-Bankhead et al. 2009), plant community type influences erosion processes (Zhongming et al. 2010). It can be said therefore that the presence of different types of vegetation and their density can have a profound impact on hydrogeomorphic processes (Stoffel and Wilford, 2012). Therefore a complex interaction between habitat characteristics, plant community structure and ecosystem engineering traits of individual species results in overall ecosystem engineering characteristics caused by vegetation on river banks.

There are numerous traits of plant species that impact their ecosystem engineering role (Simon and Collison, 2002). While the role of trees is well recognised (Šamonil et al. 2010), influence of different elements of riparian vegetation (Wynn and Mostaghimi, 2006) as well as in channel vegetation (Gurnell et al. 2010) are emerging as important. One of the key traits determining the role of individual plants is its resistance to pull force (Stokes et al. 2009; Liffen et al. 2011). In addition to this, the ability of roots to bind the soil and increase cohesion (Adhikari et al. 2013) as well as reinforce it against tension (Pollen-Bankhead and Simon, 2010) are well studied. Finally, traits of shoot (above ground part of plant) are also important since it influences the drag force applied to plant and contributes to surface roughness of the river bank during floods (Cantalice et al. 2015). Therefore, understanding of specific traits of individual plants is important for understanding the role of vegetation as ecosystem engineers.

Himalayan balsam is an invasive annual plant (Beerling and Perrins, 1993) widely distributed across Europe (DAISIE, 2016). Invasiveness of Himalayan balsam is well documented (Dawson and Holland, 1999), however its invasion dynamics (Pyšek and Prach 1995; Schmitz and Dericks, 2010) and competition with native vegetation (Tickner et al. 2001; Hejda and Pyšek, 2006) are mainly focused on large scale or mesocosm studies. While some studies are done on the limits to its spread caused by temperature (Willis and Hulme, 2002), the extent of dominance of Himalayan balsam over different native plant species at microhabitat scale is relatively unknown.

The role of Himalayan balsam in protection of soil against erosion has been hypothesized to be different and weaker than the one of respective native vegetation (Dawson and Holland, 1999). However, the first attempt to quantify this in the field was not undertaken until work by Greenwood and Kuhn (2014). They concluded that transects of river bank covered by Himalayan balsam do experience higher rates of erosion. However, few factors known to be important in studies of morphological activity like basing a study period on full annual season of measurements (Henshaw et al. 2012), accounting for the influence of microhabitat characteristics (Lawler et al. 1997) and characterisation of biological traits of native and invasive plant communities (Gurnell et al. 2012), were not addressed and therefore those results are inconclusive.

Himalayan balsam differs from the native riparian vegetation in Europe in several important traits and those are recognised to have a strong influence on its role as an ecosystem engineer. (Dawson and Holland, 1999). Those traits are mainly linked to its unusual morphology, characterised by tall shoots and weak roots which results in high shoot to root ratio. In addition the low content of dry matter leads to weaker strength of individual plants. The implications of those traits were tendency of plant to uproot and weak overall reinforcement of soil. In addition to that a special trait of Himalayan balsam is a “winter die back”, described by Dawson and Holland (1999), which refers to tendency of Himalayan balsam, as an annual plant to die in winter. Therefore, multiple traits of Himalayan balsam have been hypothesized to cause a weaker reinforcement of soil than native vegetation, however, none of these have been specifically studied.

On the basis of presented points of interest and knowledge gaps, three research aims are identified:

1. What is the extent of Himalayan balsam dominance over native vegetation?
2. What is difference in morphological activity (Hjulström, 1935) on parts of river banks dominated by native vegetation and Himalayan balsam?
3. What is difference between several representatives of native vegetation and Himalayan balsam in characteristics of individual plants relevant for their ecosystem engineer role?

7.2 Methodology

The field survey was undertaken on the River Brenta, Italy, at eight sites which were chosen on the basis of principles described in the Chapter 3 (Figure 7.1). Methodology consists of two main components: survey on the basis of transects and survey of individual plants. The transect based survey serves as a basis for description of habitat and answering the first two research aims, and it is therefore focused on analysis of vegetation structure and morphological activity. Survey of individual plants is focused on addressing the third research aim. Specific methodology used is outlined in the following sections.

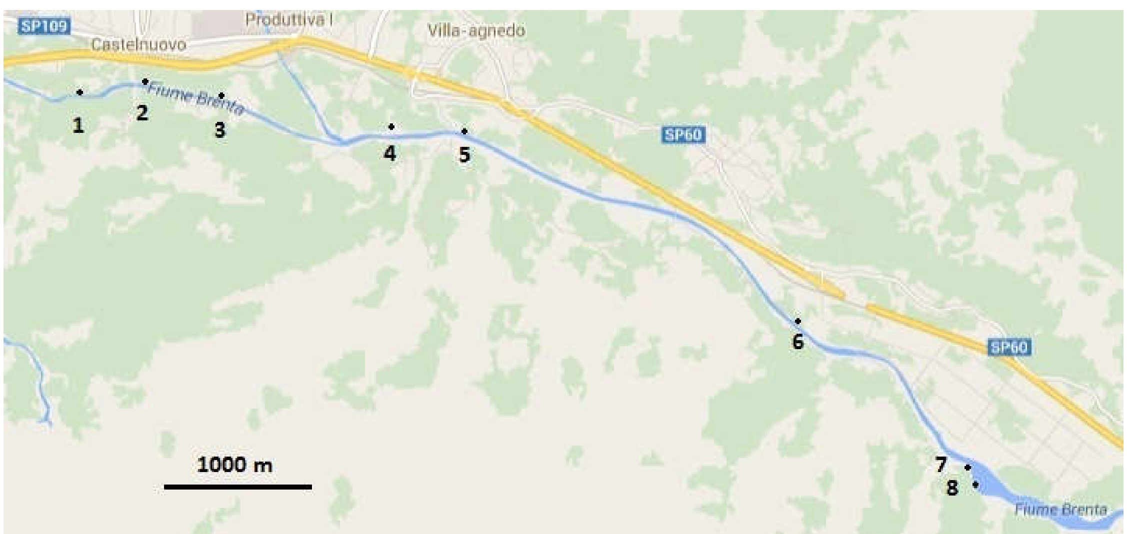


Figure 7.1 A 15 km long stretch of the River Brenta that is a focus of the Himalayan balsam survey. The location of the eight survey sites is indicated.

Data for the Himalayan balsam survey were collected during four sampling periods: summer 2014, autumn 2014, spring 2015 and summer 2015. The winter period was omitted due to difficulty in sampling and the fact that Himalayan balsam is known to die back during winter. Despite effort done in order to choose sites that will enable sampling throughout the whole year, not all sites remained undisturbed during the sampling period. Site 8 was destroyed in the major flood in the November 2014, while sites 1 and 5 where partially disturbed during a riverbank management programme in spring 2015. This loss of data for some sites and periods influenced data analysis process and will be addressed during the analysis.

7.2.1 Transect based survey

The survey design for research aims one and two is based on transects. Methodology for the transect based survey consisted of several distinct processes, which will be explained in separate subsections. Firstly, principles for positioning transects will be explained in the section 7.2.1.1. After that, procedure for use of the erosion bridge, a key element that enabled collection of data will be described in section 7.2.1.2. Erosion bridge is the improvement of the classical erosion pins method described in details by Shakesby (1993). In the following two sections, procedure for collection of vegetation information and morphological activity will be described. Finally, habitat characterisation of transects will be covered in section 7.2.1.5.

7.2.1.1 Positioning of transects

Transects are often used in vegetation studies as a mean to define a study area in a complex environment and enable quantification of factors like density and size of plants (Doulatyari et al. 2014). In geomorphology, erosion pins, a classical method used in erosion research (Lawler, 2005; Henshaw et al. 2012) can be modified for use in transect setting by application of erosion bridge (Shakesby, 1993; Shakesby et al. 2002). Therefore transect based survey can offer a realistic insight into the influence of Himalayan balsam on both vegetation structure and morphological activity. However, two important considerations had to be addressed when choosing transects. The first one is related to patterns of plant distribution on the local scale, while the second one dealt with isolating the influence of vegetation from other environmental factors. These will be discussed below.

Patterns of plant distribution had a major influence on the choice of specific locations for transects on each surveyed site. On a given habitat different plant species occupy different microhabitats, based on difference in their competitive advantage under different conditions (Bedoya et al. 2011). Therefore on heterogeneous habitats like river banks, this results in formation of mix of patches dominated by different vegetation. This theoretical aspect was confirmed by the observations in the field, where distinct patches of land were dominated either by native vegetation or Himalayan balsam. Following this, choice of transect locations was based on finding distinct pairs of patches dominated with native vegetation and Himalayan balsam that were close to each other (within 10 to 50 m) and also similar in character (with respect to slope, shade, horizontal and vertical distance from water edge). Such couples of transects would mean that all difference in morphological activity rates could be attributed to different vegetation cover and provide adequate answers to research questions stated. This is an approach similar to the one used by Greenwood and Kuhn (2014).

However, once in the field, such perfect couples of patches could not be established. This is primarily because the distribution of each plant is defined by it a competitive advantage over other plants in relation to a range of environmental parameters (soil moisture, slope, shade, competition with other plants) (Vaclavik and Meentemeyer, 2012). Therefore, patches of soil with Himalayan balsam and native vegetation are certain to differ in the range of environmental parameters. What is important is that the same parameters that influence plant competitiveness also influence erosion and deposition (Thorne, 1990; Gurnell, 2014). In order to account for that, an effort was taken to record differences in physical parameters between transects taken in native vegetation and Himalayan balsam patches. Therefore, the final design of the transect survey was based on a comparison of patches with native vegetation and Himalayan balsam; however these patches were never identical in the range of environmental parameters.

The second challenge in the choice of location for transects was how to separate the influence of vegetation from other factors influencing erosion. Soil erosion is known to be impacted by many factors: flooding regime, soil moisture, slope, soil type, the density of tree cover (Lawler et al. 1997; Rinaldi and Darby 2007; Grabowski et al. 2011). However, these same factors are known to influence competitiveness and therefore the distribution of native and invasive plant species (Bradford et al. 2007). The implications of this for a hypothetical study will be illustrated bellow.

In a hypothetical setting, one type of vegetation can have a preference for moist habitat and therefore grow closer to the water line, while other is more competitive in drier soil and therefore is positioned further away from the river bank. If this hypothetical setting resulted in first transect experiencing higher erosion rates compared to the second one, it could not be possible to distinguish whether that occurred because of the difference in vegetation or because the proximity to river bank makes fluvial erosion more likely. Therefore, the key problem is that the studied process (morphological activity) and factors influencing it (types of vegetation) are both influenced by very similar environmental parameters. Therefore, comparing vegetated transects only would not enable distinction in influence of plants on morphological activity between different types of vegetation.

In order to address the problems described above, a combination of vegetated and cleared –

control sites was chosen for this study (Figure 7.2), an approach similar to the one used by Truscott et al. (2008) in a study of impact of invasive species on species composition and soil properties. For the field survey, on each site, two patches were defined: one with native vegetation and one with Himalayan balsam. Patches were usually between 5 and 20 m apart from each other. On each patch, two parallel transects were selected. One of the two transects was cleared of all vegetation at the beginning of the survey, while the other one was left intact. Initial clearing process undoubtly disturbed the soil surface, however an effort was made to minimise the effect of that action. The cleared transect provided a reference point that enabled recording of morphological activity that would occur without protective effect of vegetation. It could be expected that in the control (i.e., cleared) transects, erosion depends mainly on physical parameters like soil type, slope, horizontal and vertical distance from the river. Hence, the measurements taken on the vegetated transects would demonstrate the impact of vegetation. Therefore transect survey on each site was based on four transects, two of which are cleared and two of which are intact and split between native vegetation and Himalayan balsam patches.

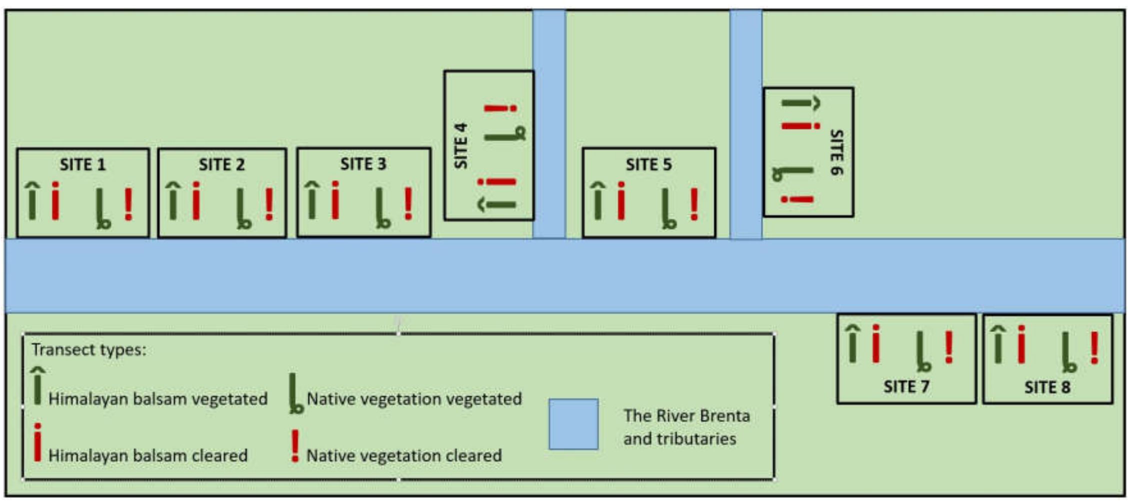
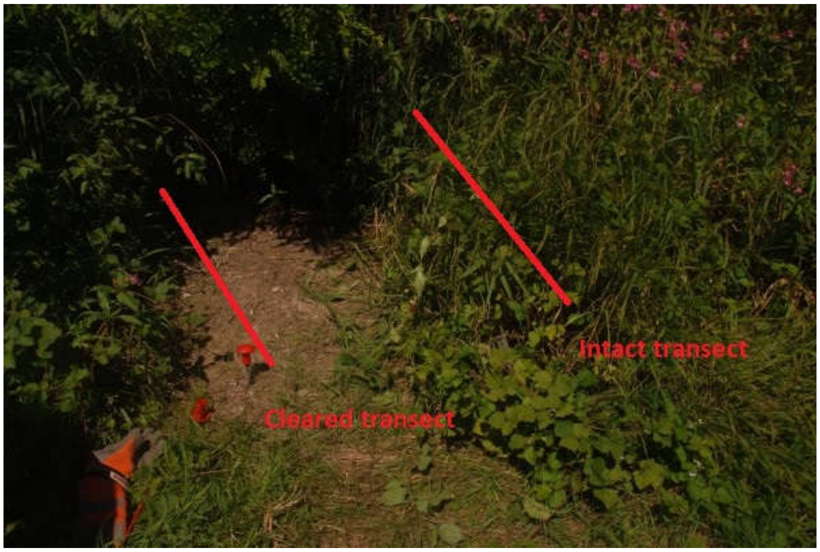


Figure 7.2 The sampling pattern for the research aims 1 and 2.

Each transect was positioned in a perpendicular (at a 90° angle) direction to the river bank (Figure 7.3). Once patches of native vegetation and Himalayan balsam were chosen, the position of the two paired transects was defined for Himalayan balsam and native vegetation, for a total of four transects at each of the eight sites. The distance between paired transects was always between one and two meters apart while the transects themselves were 120 cm long. At the end of each transect, one 80 cm long metal pin was hammered into the soil leaving a 15 cm section protruding. Those two pins were used to position the erosion bridge (Shakesby, 1993), a device that enabled collection of vegetation and morphological activity data and which will be further explained in section 7.2.1.3. Out of the two transects, on a random basis, one was designated as a vegetated transect and another one as a control. The vegetated transect was left intact, while the control one was cleared of all vegetation.



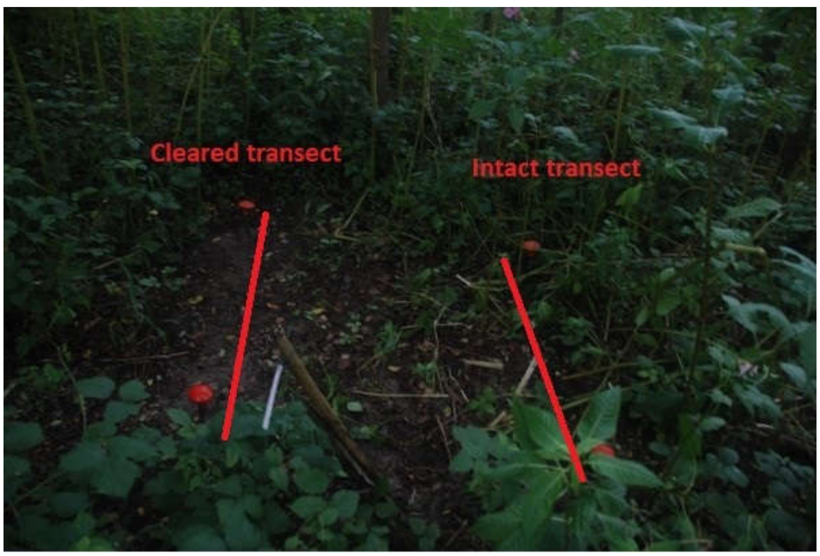


Figure 7.3 Example of transect setup. Top photograph shows cleared and intact native vegetation transect on the site 2. Bottom photograph shows cleared and intact Himalayan balsam transect on the site 5.

7.2.1.3 Erosion bridge, the basis for field measurement of transects based surveys

Field measurements undertaken as part of the transect based survey were based on use of the erosion bridge (adapted from Shakesby, 1993 and Greenwood and Kuhn, 2014). An erosion bridge was made from a hollow piece of aluminium with square cross section (20 x 20 mm) (Figure 7.4). Twenty three 5 mm holes were drilled into the bridge in order to enable insertion of a measuring rod. Meassuring rod is a piece of wood with a millimetre scale that enabled measuring of distance between soil surface and reference point. Once the measurement rod hit the soil, point impact area was visually defined.

The point impact area is 5 cm long (in the direction of the erosion bridge) and 10 cm wide (5 cm on each side of the point of impact) area of the soil surface. Therefore a surface area of 50 cm^2 was visually defined and assessed each time a measuring rod hit the ground. On each point, measuring rod was inserted through the holes in an erosion bridge until it hit the soil surface. In case there was any debris above the soil, it was carefully removed and after measurement placed back. The erosion bridge created a semi-permanent reference point from which multiple measurements of vegetation structure and morphological activity were taken. In addition to that, each one of 23 holes in erosion bridge defined a point impact area, a 5 x 10 cm area that was used for quantification of vegetation (Figure 7.5). Measurement process was repeated on each point (from 1 to 23). Details regarding exact use of measuring rod will be described in Section 7.2.1.5.

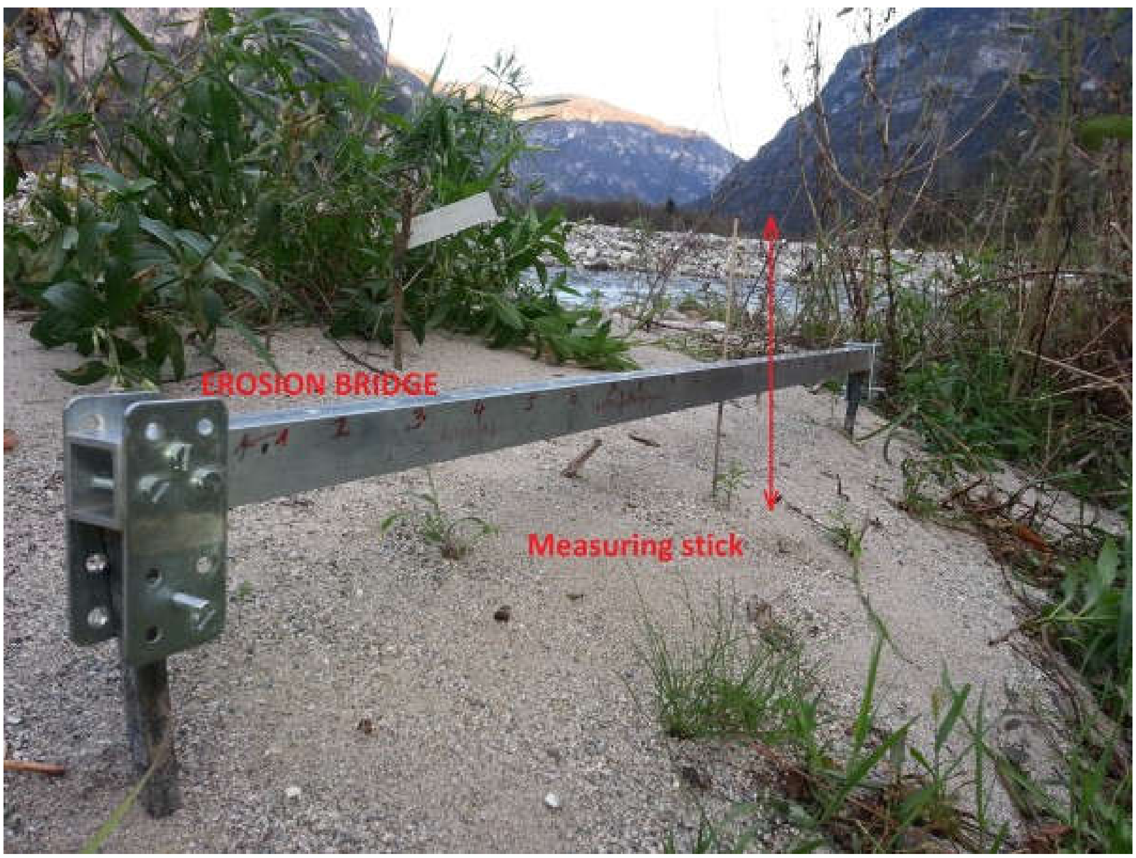


Figure 7.4 Photograph of the erosion bridge and measuring rod (used for measurement of elevation).

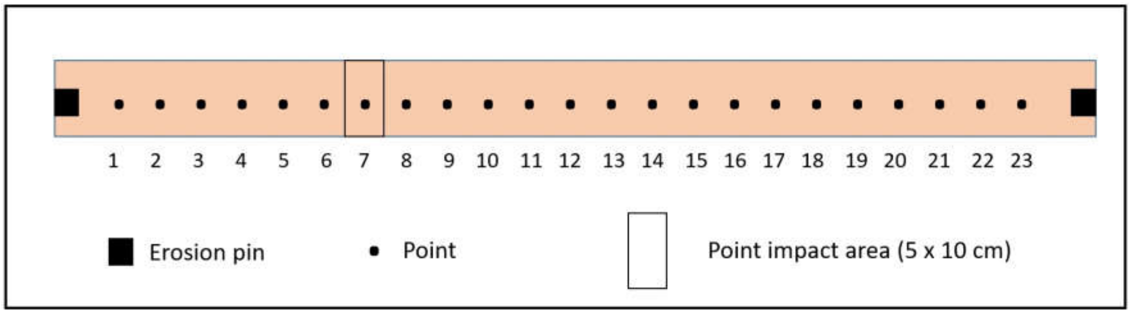


Figure 7.5 Scheme of the erosion bridge survey technique

In a similar study, Greenwood and Kuhn (2014) used a vernier calliper for the same function. However, when tested, such approach was found not to be appropriate in this case. Vernier caliper is heavy and operating it in order to touch the delicate soil surface often resulted in disturbance of soil. Instead a wooden rod with one millimetre demarcations was used. Since a wooden rod is much lighter and can be slipped until it hits the surface, it did not disturb the soil surface. Therefore wooden rod provided results with a resolution of 1 mm. The possible lack of resolution caused by using the wooden rod instead of a calliper (which can measure to tenth parts of millimetre) was considered insignificant since the main challenge in measurement was to not disturb the soil surface, a task which very light wooden rod performed much better. Measurement were taken at each of the 23 points by inserting the measurement rod until it reached the soil and recording the distance to the top of the erosion bridge.

Therefore measuring was performed on four occasions. Erosion bridge was positioned on top of two erosion pins and fixed by use of metal plates and screws. Measuring was undertaken by positioning the measuring rod on top of the erosion bridge and lowering it to the soil surface through drilled holes. Once the measuring rod hit the soil surface, information regarding vegetation abundance and morphological activity were collected, as described in the sections 7.2.1.4 and 7.2.1.5 respectively. The same procedure was repeated for all 23 points on the erosion bridge.

7.2.1.4 Plant abundance measurements

While the previous section described the overall procedure for positioning of transects and use of measuring rod, in this section, the procedure for assessment of plant abundance is described. Plant abundance is often expressed in terms of surface coverage (Rich et al. 2005; Truscott et al. 2008), but in this survey, due to short length of individual transects (1.2 m), a variation of those methods is used. The method was primarily based on counting number of plants and their diameter in each point impact area (illustrated in the Figure 7.5). Within the point impact area, a number, plant type and diameter of major plant types were recorded (Table 7.1). From those field records, the sum of stem diameters was calculated for each native vegetation type independently and

Himalayan balsam. This procedure was repeated for all studied transects.

Table 7.1 Variables collected at each point impact area. Plant type being: oxeye, grasses, bramble, stinging nettle, smartweed, unspecified monocotyledon, unspecified dicotyledon, Himalayan balsam.

Variable	Description or unit
Point	1-23
Individual plant type is present	y/n
Number of individuals of plant type	Number of plants (recorded for each plant type separately)
Sum of stem diameters (plant)	mm (calculated for each of eight plant types)
Sum of stem diameters (vegetation)	mm (calculated native vegetation and Himalayan balsam separately)

On the basis of the information about number and diameter of plants collected for each one of 23 point impact areas, a sum was calculated for each transect. In order to enable comparison of abundance of two types of vegetation on two types of transects, sums scores were calculated for native vegetation and Himalayan balsam separately (Table 7.2). Therefore four abundance indices or "sums of sums" of diameters were calculated: nv1, hb1, nv2, hb2. These four indices described absolute values of abundance of native vegetation and Himalayan balsam.

Table 7.2 Variables collected for each vegetated transect. Basic types of grouping used for calculation of native vegetation reduction and Himalayan balsam dominance indices are described.

Transect	Vegetation type	Index	Description
Native vegetation transect	Native vegetation	nv1	Sum of diameters of all native vegetation plants present on native vegetation transect
	Himalayan balsam	hb1	Sum of diameters of all Himalayan balsam plants present on native vegetation transect
Himalayan balsam transect	Native vegetation	nv2	Sum of diameters of all native vegetation plants present on Himalayan balsam transect
	Himalayan balsam	hb2	Sum of diameters of all Himalayan balsam plants present on Himalayan balsam transect

The following step was to quantify the extent to which invasive species reduces the abundance of the native ones. While this is a well recognised effect of inavasive species (Hejda and Pyšek, 2006; Bennet et al. 2012; Vaclavik and Meentemeyer 2012), two methods of quantifying this effect were undertaken. On the basis of previous four indices, it was possible to create two new indicators of change caused by invasive species: native vegetation reduction index and Himalayan balsam dominance index.

Native vegetation reduction index (NVRI) was based on premise that native vegetation abundance will be reduced on transects with Himalayan balsam presence. Therefore it compares abundance of native vegetation on native and on Himalayan balsam transect:

NVRI = nv1 / nv2 (for Himalayan balsam transect)

The result is a number that represents a multiplication factor – how many times is native vegetation less abundant on the Himalayan balsam transect compared to native vegetation transect. Native vegetation transects are assumed not to experience any reduction in native vegetation abundance and therefore for the purpose of following analyses, native vegetation transects are assigned a value of 1 for the NVRI. Therefore, NVRI is calculated for the Himalayan balsam transect only.

On the other hand, Himalayan balsam dominance index (HBDI) is simply comparing abundance of native vegetation and Himalayan balsam one for each vegetated transect. Therefore it is expressed as:

HBDI = hb1 / nv1 (for native vegetation transect)
HBDI = hb2 / nv2 (for Himalayan balsam transect)

The result is again a multiplication factor. However, it can be directly calculated for both types of transects. These two types of indices enable a good quantification of interaction between two plant types.

7.2.1.5 Morphological activity measurement

Morphological activity (combined activity of erosion and deposition) was expressed as a difference in soil elevation between two sampling occasions. Elevation was meassured in relation to the erosion bridge, which was used as a semi-permanent reference point. Therefore the methodology was similar to the one used by Greenwood and Kuhn (2014), but with a notable exception that in this study, an measuring rod was used instead of Vernier caliper. Measuring rod was used instead of Vernier calliper (used in the Greenwood and Kuhn (2014) study) since it was lighter and therefore it did not disturb the soil surface as much. The distance from the top of the bridge to the soil surface is recorded as elevation (E). Due to nature of the experimental setting, which was based on reference point above the soil surface, points that are positioned higher had lower values of elevation and reverse. For each point, morphological activity (MA) was defined as a difference between elevations recorded during two sampling occasions (E1 – first elevation record, E2 – end elevation record): MA = E1 – E2 and treated as erosion for negative values and deposition for positive values. Since data were collected on four occasions, morphological activity is defined for three seasons: Summer, combined period of Autumn and Winter and Spring. Described in this way, each value of morphological activity is calculated per time interval or season, between two sampling occasions. Since sampling seasons are of different length, all values of morphological activity are also recalculated as a morphological activity per month (MAm) (Table 7.3).

Table 7.3 Variables recorded during each measuring season and additional variables calculated on the basis of those data.

Variable	Description or unit
Values collected on each sampling occasion	
Point	1-23
Elevation (E)	mm
Values calculated for the season between two sampling occasions	
Morphological activity per season (MAs)	MAs = E1 – E2
Morphological activity per month (MAm)	MAm = MAs / number of months

The only exception to the above-described measurement procedure is related to an extreme flood event that occurred during November 2014 which completely flushed out the whole mid channel bar on which site 8 was positioned. From the comparison of photographs before and after the flood event, it is visible that at least one meter of sediment was eroded. In order to include that information in the data analysis, an arbitrary morphological activity value of -10,000 mm was allocated to points on that site and season.

The above described event on the site 8 was considered a mass failure due to the sheer volume of sediment involved. Also the configuration of the terrain indicates that a mass failure of non cohesive sediment bank, described by Thorne (1982), could occur in that situation. In addition to the described mass failure event, the extreme flood event left a major impact on the site 1 and site 7. Since those sites were visited directly after the flood, it was visible from the direction of vegetation and left over debris that water level has risen to respective sites. Therefore erosion observed on site 1 is classified as a fluvial erosion, while deposition on the site 7 is classified as fluvial deposition. Therefore three extreme events that could be directly traced to a cause are treated separately during analyses. In addition to that, in cases when point is impacted by animal ecosystem engineer, for instance earthworm mounds or mole excavations, those processes are marked as invertebrate or vertebrate ecosystem engineer activity. All other changes are marked as subaerial processes.

7.2.1.2 Transect characterisation data

In order to enable better contextualization of vegetation and erosion data, information regarding the character of individual transects was collected. The main guidance for the choice of variables for the characterisation of habitat as the River Habitat Survey (RHS) (Environment Agency, 2003) and similar surveys regarding vegetation and erosion (Gurnell, 2014). On each site, intact and cleared transect were in close proximity of each other (between 1 m and 2 m) and therefore considered to be on the same microhabitat. For each of the 32 transects, nine variables were measured (Table 7.4).

Table 7.4 Variables describing habitat characteristics, calculated for each of the 32 transects.

Variable	Description
Trees and shrubs cover (%)	
Horizontal distance from river edge (m)	
Vertical distance from river edge (m)	
Transect slope (degrees)	
Surface sediment (silt or sand)	Ordinal variable, in later analyses silt is coded as 1 and sand as 2
Soil percentage water content (%)	
Soil percentage organic matter (%)	percentage of dried soil mass, not the total mass
Dominant soil particle size smaller than (mm)	
Soil shear vane (MPa)	

All transect based variables were assessed during a full growing season in August 2014. Trees and shrubs coverage was visually assessed and expressed as a percentage of cover that shaded the surface. Horizontal and vertical distance from the river were measured using a meter tape during summer base flow. Transect slope was measured with a simple mechanical angle meter. Surface sediment was assessed visually for each transect and classified as either silt or sand.

Three soil variables are based on 10 cm deep soil profile sample taken approximately 30 cm away (in upstream or downstream direction) from the respective transects. Soil samples were processed as follows: a subsample of soil was weighted with an analytical scale and dried in an oven at 80°C for 20 hours in order to remove water. The dried subsample was subsequently weighted and the percentage of water calculated from the difference in weights. Following that, a subsample of the dried sample was weighted and dried for additional 20 hours at 400°C in order to burn all the organic matter, following methodological approach described by Schumacher (2002). After that, it was weighted again and percentage of organic matter calculated from the difference in weights.

The dominant soil particle was analysed with separation sieves and an automatic shaker. Each sample was ran through series of sieves with progressively smaller openings (4 mm, 2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, 0.075 mm). Mass of residue that remained in each sieve was weighted with an analytical scales and the particle size with the highest mass designated as the dominant soil particle size. Soil shear vane was measured with a hand held soil shear vane device (NZGSI, 2001). This procedure enabled a good characterisation of all 32 transects.

7.2.2 Individual plant based survey

7.2.2.1 Basic considerations

The research design for research aim 3 (What is a difference in characteristics of individual plants?) was strongly influenced by the vegetation structure on individual sites as presented in the Chapter 3 (Figure 3.9). Firstly, out of seven plant types of native vegetation, five represent a huge majority of coverage, while unspecified monocotyledonous or unspecified dicotyledonous covered minute surface and were not covered in this survey. Therefore the focus was on five native vegetation plant types: oxeye, grasses, bramble, stinging nettle and smartweed. These five, again differ in terms of their presence on sites. For instance some plant types dominate only on specific sites like oxeye (site 1), stinging nettle (site 6) and smartweed (sites 7 and 8) while grasses and bramble were present at almost every site. Therefore grasses and bramble were studied in more detail in relation to complexity of tree cover since that is one of the main aspects influencing ground vegetation (Hejda and Pyšek, 2006). Therefore, grasses and bramble were studied in two distinct habitats in relation to the complexity of tree cover: open space with no tree cover (site 2) and shaded space underneath tree canopy (site 5) (Figure 7.6). Therefore, sampling seven native plant types on the basis of their dominance is considered a well-representative sample of the native vegetation and a good basis for comparison with the Himalayan balsam.

The survey design is outlined in Figure 7.6. On each site a coupled sample of dominant native plant and Himalayan balsam was taken (between five and ten individual plants on each sampling occasion). Plants were chosen from the patches of uniform vegetation that were in proximity to transects.

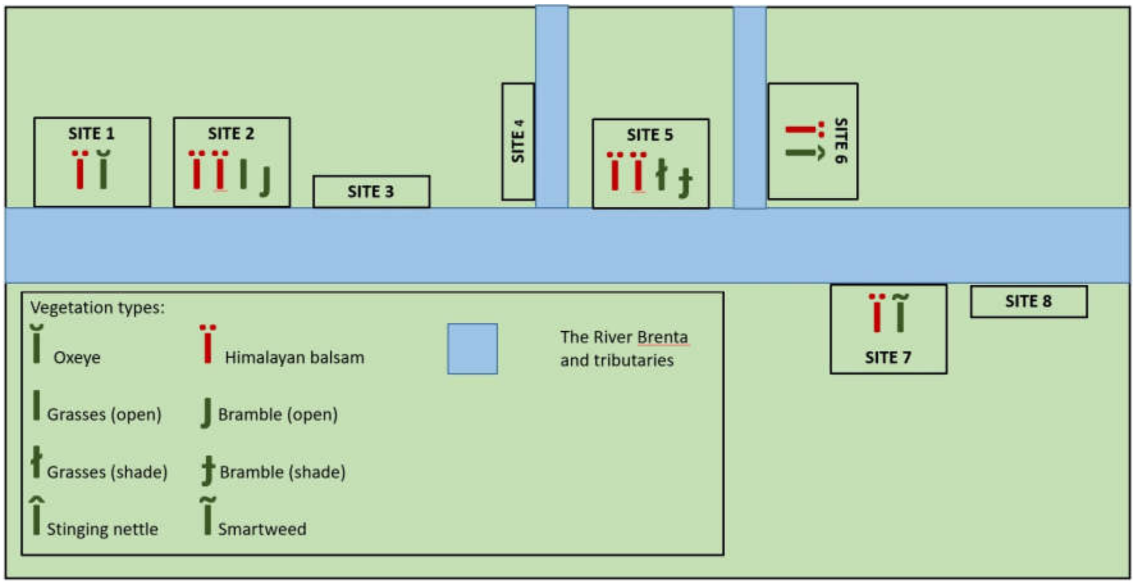


Figure 7.6 The sampling pattern for research aim 1. Each symbol represents ten individual plants of respective plant type. (Distances are not to scale, refer to Figure 7.1 for the exact location of sites.)

All sampling was done on same sites on four occasions: summer (August 2014), autumn (October 2014), spring (March 2015) and summer (July 2015). It is important to note that during spring sampling occasion, measurements were done on plants that remained from the previous vegetation season and not the young shoots of the year. In the case of native vegetation, that did not make a big change since all five plant types are perennial plants. However, in the case of the Himalayan balsam, an annual plant, that meant that specimens collected were remains of the plants that died in autumn and were decomposing throughout winter. This approach was chosen because it captured a representative situation in the field during the winter period. In the following section, methodology for actual measurements is described.

7.2.2.2 Plant measures and investigative design

All data were collected using the same sampling procedure. Plants were collected in the same area during each sampling occasion. Pull strength was measured directly in the field, and after that, plant was marked and placed in a bag for laboratory measurements. The plant specimen was transported to the laboratory for measurement of morphological characteristics. After that, a coupling Himalayan balsam plant was sampled the same way. This process was repeated ten times for each couple as indicated in Figure 7.7.

Measurement of individual plants was done in the field and a laboratory. Pull strength was measured directly in the field by pulling the plant out of the soil with a digital dynamometer (Figure

7.7.). An improvised gripper was attached at the base of the plant and maximum force achieved during the pullout process was recorded (the weight of the gripper was accounted for). In the laboratory, length and diameter of shoot and root were measured using metering tape. Shoot width was measured at the internode section, at the lower end of the stem. In the case of grasses which grow in the bushy form, it was not possible to isolate individual plants, so the whole bush was pulled out and diameter was measured for whole stem and root sections. Similarly, smartweed stem is branching at very low height into multiple stem, however only diameter of one main stem was recorded. Root width was measured at the widest point. Root length measurements are complicated since main body of root was often short, while extra-long root was measured in length. Therefore, wet mass is considered the most objective measure of the size of both stem and root. Wet mass of stem and root were measured independently using analytical weighting scale. After that, stem and root were separately dried on 80°C for 20 hours in order to remove moisture from the plant tissue. Dry mass was measured on the same weighting scale as the wet mass. Therefore for each sampled plant specimen, nine variables were directly recorded (Table 7.5).

Figure 7.7 Measuring pull strength of grass (left) and Himalayan balsam (right).

Out of all potential metrics that could be generated from the described measurement procedure, on the basis of similar studies on the influence of plant morphology on river bank processes (Liffen et al. 2011), four variables are chosen for further analyses (Table 7.5). Pull strength gives basic context for the strength of individual plant. However, due to the well known differences in size of individual plants as well as their density, pull strength had to be put in context of plant size. Pull strength in comparison to root size, the most reliably expressed through root diameter, indicates strength of the roots in binding to the soil. Pull strength in relation to shoot biomass gives best indicator of pull force that will be applied to plant during flood. Finally, percentage of dry mass is an often used indicator of plant health and strength. Plants resistance to pull is directly linked to the plant size (Liffen et al. 2011), and therefore should be put in context to enable comparison between individuals of different species and size.

Table 7.5 List of variables collected for each individual plant.

Variable	Unit	Description
Variables measured for each plant specimen		
Root diameter	mm	
Root wet mass	g	
Root dry mass	g	
Shoot wet mass	g	
Shoot dry mass	g	
Pull strength	N	
Variables calculated for each plant specimen on the basis of measured variables		
Pull strength to root diameter ratio	N/mm	= Pull strength / Root diameter
Pull strength to shoot wet mass ratio	N/cm	= Pull strength / Shoot wet mass
Percentage dry mass whole plant	%	= (Shoot dry mass + Root dry mass) * 100 / (Shoot wet mass + Root wet mass)

7.3 Results

Data were sampled on four sampling occasions across eight sites, each with two transects (Table 7.6). In ideal conditions, this would yield data for 64 transects. However, due to the destruction of sites 1, 5 and 8 during the survey period, a total of 56 valid transect data sets were collected. Therefore a total number of 1235 valid points data were obtained (each transect had information about either 22 or 23 points). It is important to note that this section is focused on all individual plants (native vegetation and Himalayan balsam) that are present on either type of transect. Data were collected during four occasions, generating information on morphological activity for three distinct seasons. However, data were not collected for all sites. During Season 1, a large flood event caused mass deposition on sites 7 and mass erosion on site 8. In addition to that, sites 1 and 5 were destroyed as part of regular river maintenance. Therefore, main analysis is done on four sites with complete records (sites 2, 3, 4 and 6).

Table 7.6 of ability to collect data on respective sites and sampling occasions. Data were collected fully (+), partially (x).

Site	Aug	Oct	Mar	Jul
1	+	+	+	x
2	+	+	+	+
3	+	+	+	+
4	+	+	+	+
5	+	+	+	x
6	+	+	+	+
7	+	+	+	+
8	+	x	x	x

7.3.1 Differences in habitat traits between native vegetation and Himalayan balsam transects

Despite close distance between native vegetation and Himalayan balsam transects, they demonstrated important differnces in meassured variables. A series of boxplots visualised these differences (Figures 7.8; 7.9) while mean values and significance of difference between native vegetation and Himalayan balsam transects are presented in the Table 7.7. Himalayan balsam transects differed from native ones in statistically significantly higher horizontal and vertical distance from water edge, more frequent occurrence on the sites with sand as a surface sediment as opposed to silt, and sites with higher water and organic matter percentage.

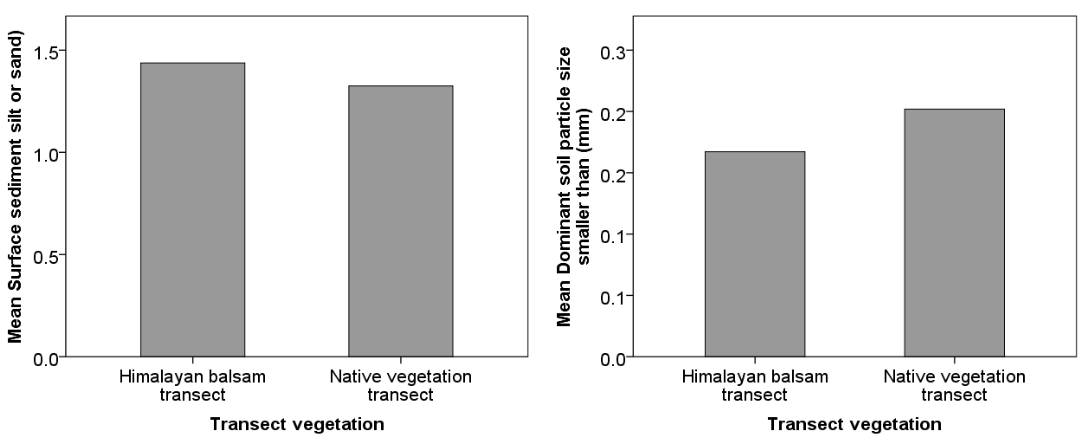


Figure 7.8 Charts illustrating difference between Himalayan balsam and native vegetation transects on the studied sites.

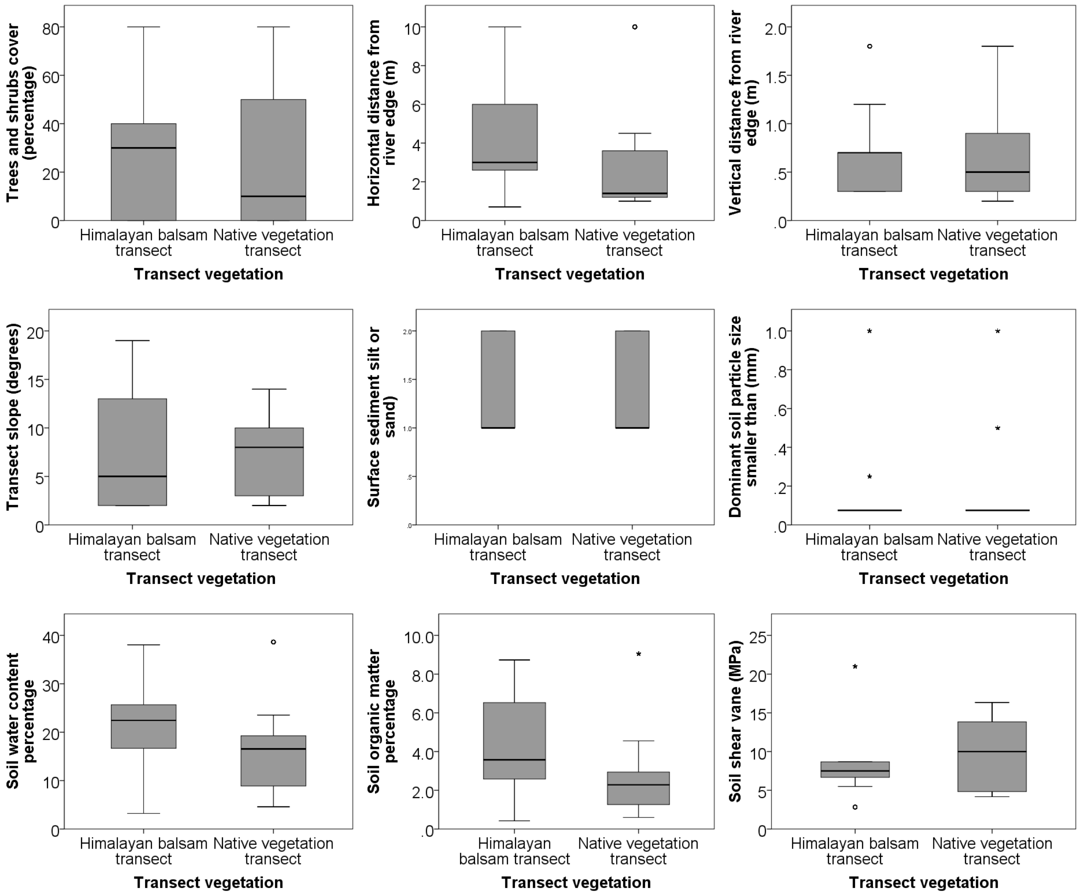


Figure 7.9 Difference between Himalayan balsam and native vegetation transects on the studied sites.

Table 7.7 Mean values and statistical significance of difference (Mann Whitney test) performed on nine variables describing transect characteristics.

Variable	Mean value		p
	Native vegetation transect	Himalayan balsam transect	
Trees and shrubs cover (percentage)	25.13	28.94	0.107
Horizontal distance from river edge (m)	3.22	4.22	0.000*
Vertical distance from river edge (m)	0.682	0.706	0.002*
Transect slope (degrees)	7.35	7.88	0.275
Surface sediment silt or sand	1.32	1.44	0.000*
Dominant soil particle size (mm)	0.202	0.167	0.445
Soil water content percentage	17.13	21.56	0.000*
Soil organic matter percentage	3.01	4.05	0.000*
Soil shear vane (MPa)	9.29	8.73	0.535

7.3.2 Relationship between native vegetation and Himalayan balsam abundance

7.3.2.1 Comparison of vegetation on native vegetation and Himalayan balsam transects

In order to investigate abundance of different plant types, a detailed analysis of vegetation structure was undertaken for each transect. Data are collected only for the intact transects. In this section focus will be on analyses of differences between native vegetation transects and Himalayan balsam transects on the point impact scale. Since vegetation is at its fullest during summer, and since data for all sites exist only for the first summer sampling occasion, data collected in August 2014 will be analysed. Also cleared transects are devoid of vegetation, so focus is on the analysis of intact transects only. However, it is important to note that both native vegetation transects and Himalayan balsam transects have a mix of both vegetation types. Therefore, total of 400 points collected on eight Himalayan balsam and native vegetation intact transects were analysed.

Overall, native vegetation transects had a higher mean number of plant individuals per point (1.71) than Himalayan balsam transects (0.81) and that difference is statistically significant (p=0.000) (Figure 7.10). However, the sum of stem diameters per point is similar, native vegetation having only slightly higher mean value (2.35 mm) than the Himalayan balsam (2.25 mm) and that difference is not statistically significant (p=0.128).

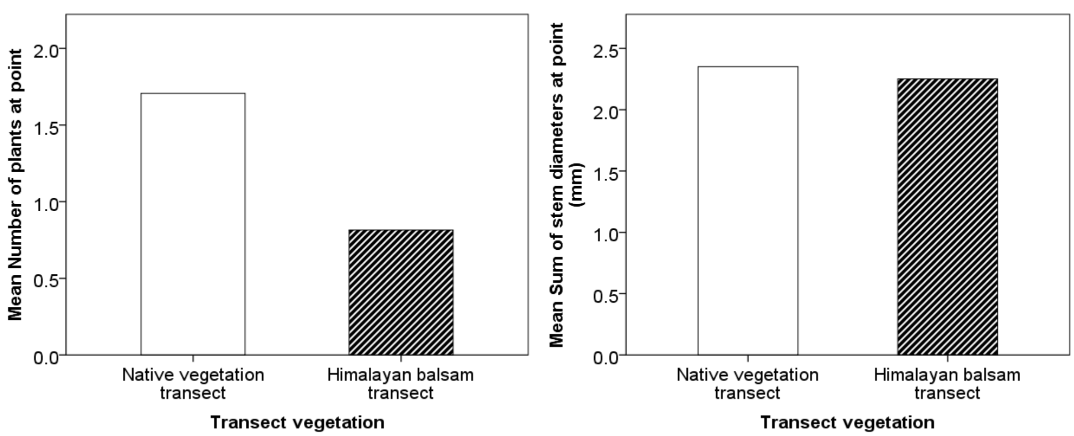


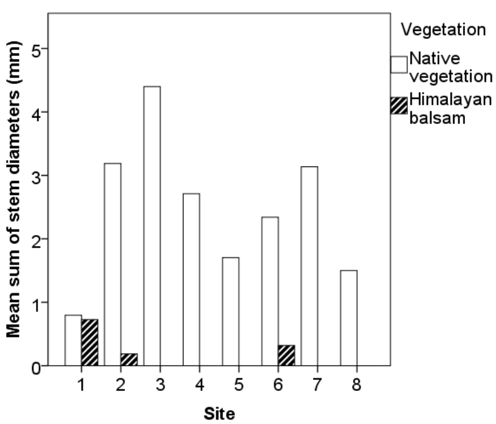
Figure 7.10 Difference between native vegetation and Himalayan balsam transects in vegetation abundance measured by two different metrics.

Since number of plant types and sum of diameters are shown to strongly correlated (spearman rho = 0.9). While for some analysis (influence of vegetation on morphological activity, Section 7.3.2) both number of plants and sum of stem diameters will be used, due to the strong correlation of the two variables, for the sake of simplicity, analysis will be done only on the basis of sum of diameters.

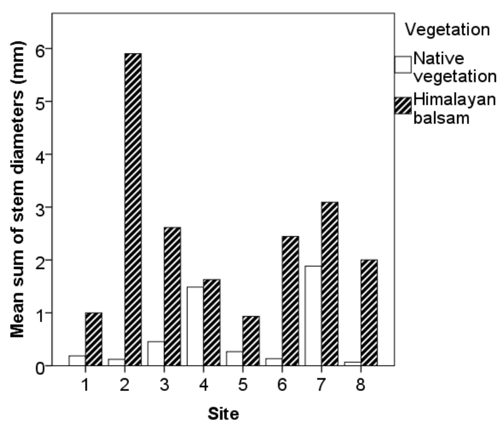
Native transects and Himalayan balsam transects are not different in amount of shading they receive and it can be assumed that they receive the same amount of light. It is known that plant abundance is directly proportional to the amount of sunlight. Therefore, while certain differences in efficiency of turning light into biomass exist, the abundance on two types of transects can be considered the same. With that in mind, sum of stem diameters is much better metric of plant abundance than number of plants. On the basis of that, future analyses will be done on sum of stem diameters.

7.3.2.2 Comparison of abundance of native vegetation and Himalayan balsam

Two types of vegetation, native one and Himalayan balsam occur on both types of transects and Figure 7.11 illustrates these differences. Native vegetation transects are dominated by native vegetation plants and contain very low abundance of Himalayan balsam (mean sum of stem diameters is 2.48 and 0.15 respectively). This implies that native vegetation dominates Hiamalyan balsam by factor of 16 and that difference is statistically significant (p=0.000). Invaded transects, although dominated by the Himalayan balsam (p=0.018) still contain significant presence of native vegetation plant types (mean sum of stem diameters is 2.42 and 0.57 respectively), translating into dominance by factor of four.



a)



b)

Figure 7.11 Difference between a) native vegetation and Himalayan balsam transects in vegetation abundance measured by two different metrics.

Further, the difference in abundance on two types of transects for the eight plant types is illustrated in the Figure 7.12 and Table 7.8. For seven native vegetation plant types, two types of interactions can be identified. In first group, there is a strong, statistically significant difference in abundance of plant types on native vegetation and Himalayan balsam transect. In this group are oxeye, grasses, stinging nettle and smartweed. Out of the four, only grasses maintain similar abundance on the

Himalayan balsam transects, while the remaining three plant types are almost absent on transects dominated by Himalayan balsam. Second group consists of bramble and dicotyledons which have similar abundance on native vegetation and Himalayan balsam transects. For both plant types actually, their abundance is slightly higher on the Himalayan balsam than native vegetation, implying that competition with native vegetation supress them more than Himalayan balsam does.

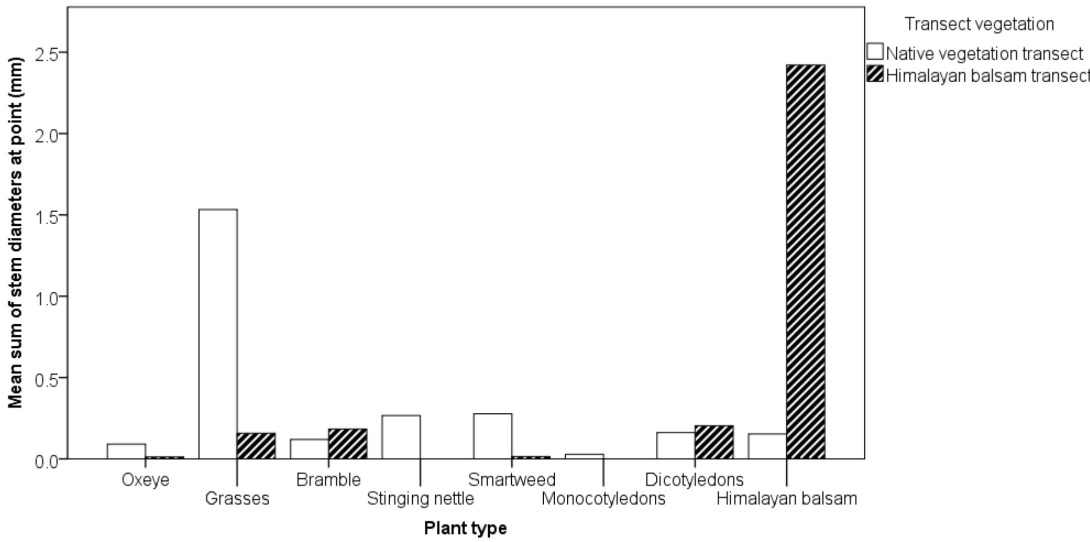


Figure 7.12 Difference between native vegetation and Himalayan balsam transects in abundance for individual plant types.

Table 7.8 Mean values and statistical significance of difference (Mann Whitney test) performed on nine variables describing differences between abundance of plant types on native vegetation and Himalayan balsam transects.

Statistics	Mean		p
Variable	Native vegetation transect	Himalayan balsam transect	
1 Oxeye	0.09	0.01	0.007*
2 Grasses	1.53	0.16	0.000*
3 Bramble	0.12	0.18	0.350
4 Stinging nettle	0.27	0.00	0.000*
5 Smartweed	0.28	0.01	0.000*
6 Monocotyledons	0.03	0.00	0.320
7 Dinocotyledons	0.16	0.20	0.748
8 Himalayan balsam	0.15	2.42	0.000*

7.3.2.3 Impact of Himalayan balsam on native vegetation

While Figure 7.13 and Table 7.9 illustrate general occurrence of plant types on two types of transects, they do little to illustrate differences on individual couples of Himalayan balsam and native vegetation transects. In order to quantify these interactions, NVR index and HBD index are calculated (Table 7.9). While on native vegetation transects, native vegetation reduction index is arbitrarily set to 1, on the invaded transects it varies a lot. On sites 4 and 7 native vegetation is only reduced in half, while on sites 2, 6 and 8 reduction is really strong with around 20 times less native vegetation on Himalayan balsam transects than native vegetation transects (Figure 7.13). Himalayan balsam dominance index also demonstrates stark difference between two types of transects. On native vegetation transects, only on sites one the value is 1, representing parity between native vegetation and Himalayan balsam, while in other sites the value is 0, representing minute presence of Himalayan balsam. However on invaded transects, Himalayan balsam is less than ten times more dominant on sites 1, 3, 4, 5 and 2, while on sites 2, 6 and 8 dominance of Himalayan balsam plants rises to 47, 18 and 30 times compared to native vegetation.

Table 7.9 Decrease in native vegetation abundance and extent of Himalayan balsam dominance expressed for native vegetation and Himalayan balsam transects. The results presented in this table are used as input for analysis in the section 7.3.2

	Decrease in native vegetation abundance		Himalayan balsam dominance	
Site	Native vegetation transect	Himalayan balsam transect	Native vegetation transect	Himalayan balsam transect
1	1	4	1	6
2	1	24	0.05	47
3	1	10	0	6
4	1	2	0	1
5	1	7	0	4
6	1	18	0.14	18
7	1	2	0	2
8	1	22	0	30

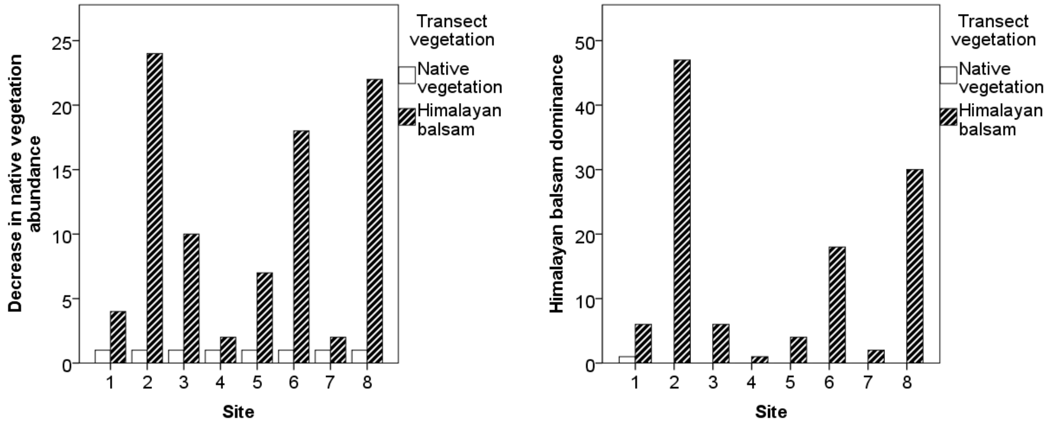


Figure 7.13 Decrease in native vegetation abundance and extent of Himalayan balsam dominance expressed for native vegetation and Himalayan balsam transects.

7.3.3 Variability in morphological activity between seasons, sites and process types

Data were collected on four occasion, providing information for morphological activity during three distinct seasons (summer; autumn and winter; spring). However, two events had a major impact on the sampling scheme. Firstly in November 2014 a major flood event occurred. This had a strong impact on sites 7 and 8. On site 7 it caused a significant deposition of sediment. However, it was possible to find the erosion pins and continue measuring. On the site 8, it caused a massive erosion and the whole bar positioned in the middle of the river channel was eroded. Secondly, during late March, a river bank management programme completely cleared sites 1 and 5.

7.3.3.1 Exploratory analysis of morphological activity data

Data were sampled on four sampling occasions across eight sites, each with two transects. In ideal conditions, this would yield data for 64 transects. However, due to the destruction of sites 1 and 5 and extreme changes at the sites 7 and 8 during the survey period, a total of 80 valid transect data sets (20 seasons x 4 transects on each site) were collected. Therefore a total number of 1,868 valid points data were obtained (each transect had information on between 22 and 25 points). It is important to note that this section is focused on all individual plants (native vegetation and Himalayan balsam) that are present on either type of transect. These data are shown in Figure 7.14 and Table 7.10.

Morphological activity per season and per month showed similar trends. Table 7.10 shows basic information about the data collected. Due to different length of seasons (1.86, 4.80 and 4.10 months), data for future analyses are expressed per month. A measure of central tendency, a median, indicates that a lot of points had no morphological activity, however, mean is influenced by the extreme events and its negative values indicates the overall dominance of erosion processes. The value of -10,000 mm or -1 m is assigned to all points on the site 8 since 1 m was the conservative estimate of the erosion that happen on that place. However, since it is an estimate it is not included in the further analyses. Maximum values (249 mm), indicating maximum deposition occurred on site 7 during season 2 (autumn and winter).

Morphological activity per month differed between sites and seasons (Figure 7.14). The most extreme values of both erosion and deposition were recorded during season 2, during autumn and winter, with the most extreme values on sites 8 and 7. Except for these two examples, the rest of the seasons and sites were fairly similar without clear trends.

Table 7.10 Morphological activity per season and per month, including all eight sites

Statistics	Morphological activity per season (mm)	Morphological activity per month (mm)
Valid N	1868	1868
Mean	-489.77	-101.913
Median	0	0
Std. Deviation	2271.53	473.20
Minimum	-10,000*	-2083*
Maximum	1196	249

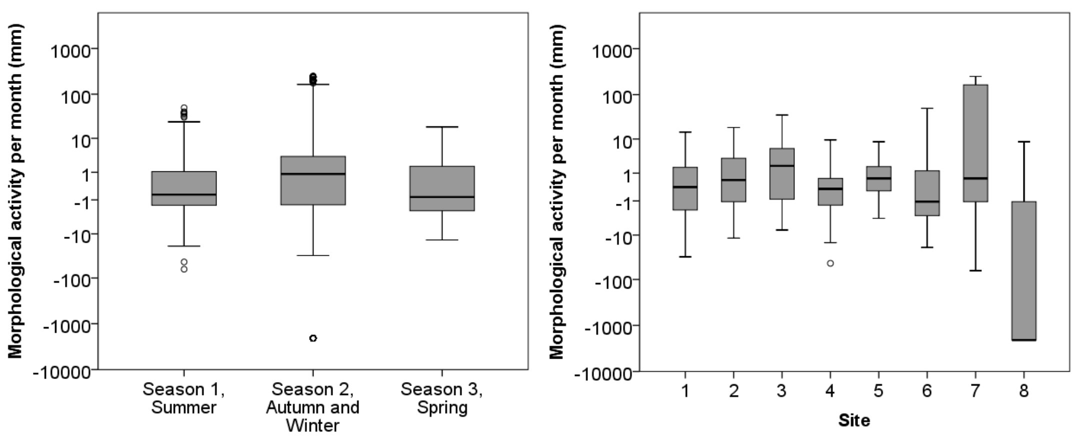


Figure 7.14 Boxplots illustrating differences in morphological activity between individual seasons and sites.

Due to described data collection disturbances, analyses will be organised in the following way. Firstly, two extreme events (deposition on site 7 and erosion on site 8) will be shortly examined to see what was the influence of vegetation in those cases (Section 7.3.3.2), but will be excluded from the remainder of the analyses. The same was done for two sites (1 and 5) which were influenced by river bank management, excluded. Therefore, main body of analyses is done for the sites that had a full data set for all three seasons (sites 2,3,4 and 6) and those results are presented in the sections 7.3.3.3-5.

7.3.3.2 Special case of vegetation impacts during extreme erosion and deposition events

Mass failure erosion event is recorded on the site 8 during season 2. As previously stated, extreme flood event in November 2014 completely changed the local landscape. The photos taken few days after the flood indicate that location of transects is completely eroded (Figure 7.15) and subsequent visits during low flow did not manage to locate the erosion pins. On the basis of terrain configuration and photographs, it is concluded that at least one meter of sediment was eroded. Differences between transects in terms of habitat characteristics and vegetation did not seem to influence the outcome of the morphological change.

Figure 7.15 Site eight after a major flood event. Left photo shows the top of the mid channel bar. The red line in the right photo indicates original position of bank and transects.

Fluvial deposition event occurred at all four transects on the site 7 following the extreme flood event in November 2014. The position of vegetation and debris clearly indicate that river flow was going on top of the site (Figure 7.16). Approximately 10 cm of sediment was deposited, however, location of all pins was successfully located.

Figure 7.16 . Site seven after a major flood event.

Despite the overall magnitude of the deposition event, there is a statistically significant difference in the morphological activity between transects (Figure 7.17). Morphological activity is measured during the March of the next year. However it can safely be assumed that the most of the activity happen during that one event, and therefore morphological activity is expressed per season, not a month. Both cleared transects experienced similar amounts of deposition (around 950 mm), while native vegetation intact transect had higher values (1150 mm), and Himalayan balsam intact transect had lower values of mean deposition (716 mm). Statistical difference between four transects is significant (p=0.000). While this can be related to the abundance of native vegetation on each transect, no clear links can be made between the amount of deposition and presence of vegetation.

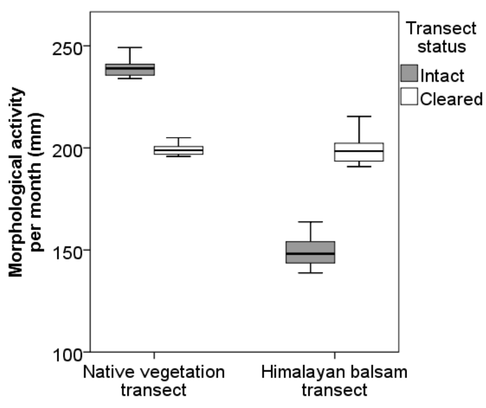


Figure 7.17 Comparison of morphological activity on four transects at site 7 only, since it was the only site directly affected by a flood that still enabled data collection.

7.3.3.3 Has vegetation protected vegetated transect in comparison to cleared ones?

On average, cleared transects had lower rates of morphological activity than vegetated ones (Figures 7.18; 7.19). That difference was statistically significant for the whole sampling period, for both native vegetation and Himalayan balsam (Table 7.11). In case of native vegetation, cleared transects had a mean value of morphological activity of 0.72 mm, compared with 1.45 mm on vegetated transects, while difference during each season was not statistically significant (Table 7.12). Similarly, Himalayan balsam had positive values of morphological activity (deposition) on vegetated transects (1.11 mm), while negative (erosion) on cleared ones (-0.15 mm). Therefore, both types of vegetation caused positive values of morphological activity in comparison to cleared transects.

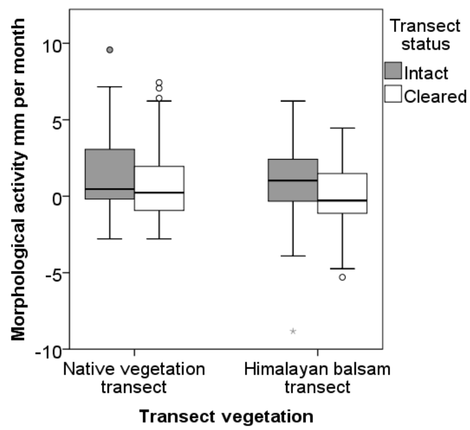


Figure 7.18 Boxplots showing difference in morphological activity between cleared and intact transects for the whole survey period.

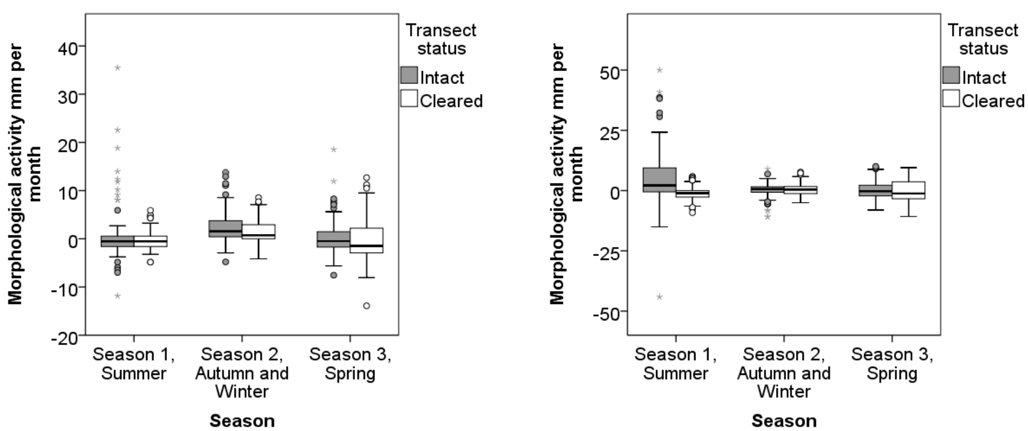


Figure 7.19 Boxplots showing difference in morphological activity between cleared and intact transects for each of survey seasons.

Table 7.11 Descriptive statistics showing difference in morphological activity between cleared and intact transects for native vegetation transects.

	mean	mean	
Transect type	Intact transect	Cleared transect	Significance of difference
All seasons	1.45	0.72	0.022*
Season 1	0.87	0.23	0.696
Season 2	2.61	1.74	0.055
Season 3	0.35	-0.24	0.104

Table 7.12 Descriptive statistics showing difference in morphological activity between cleared and intact transects for Himalayan balsam transects.

	mean	mean	
Transect type	Intact transect	Cleared transect	Significance of difference
All seasons	1.11	-0.15	0.000*
Season 1	5.60	-1.27	0.000*
Season 2	0.06	0.39	0.951
Season 3	0.30	-0.28	0.256

7.3.3.4 What is a difference in morphological activity between native vegetation and Himalayan vegetation transects?

Following previous analysis, aim is to see whether there is a difference in morphological activity between transects with Himalayan balsam and native vegetation (Figure 7.20; Table 7.13). When the whole survey period is assessed, there is no significant difference between transects with native vegetation and Himalayan balsam, however, analysis of individual seasons reveals differences between two vegetation types. During season 1 (between summer and autumn), values of morphological activity were higher on the Himalayan balsam transects (5.60 mm) than transects with native vegetation (0.87 mm). However, during season 2 (between autumn and spring) values of morphological activity were higher on transects with native vegetation (2.61 mm) in comparison to the ones with Himalayan balsam (0.65 mm). Therefore there is no conclusive difference in impact on morphological activity between two vegetation types.

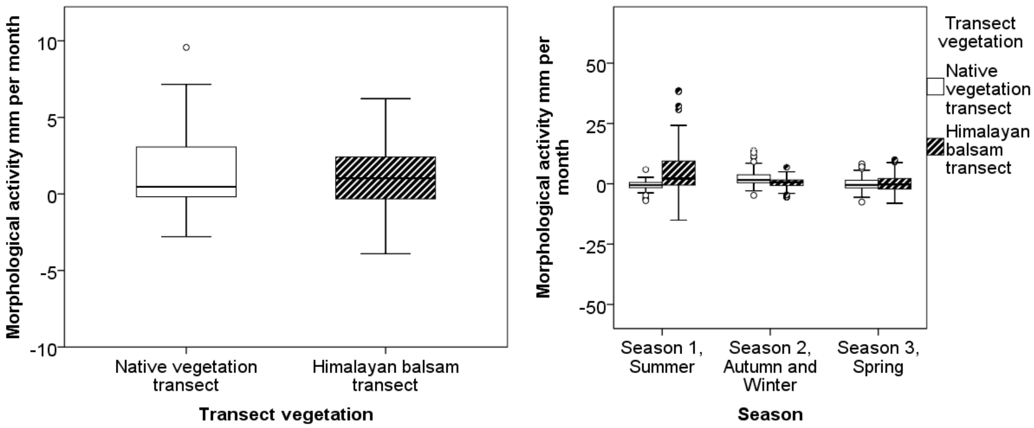


Figure 7.20 Boxplots showing difference in morphological activity between native vegetation and Himalayan balsam transects for all seasons together and individual seasons.

Table 7.13 Difference in morphological activity between native vegetation and Himalayan balsam transects for all seasons together and individual seasons.

	mean	Mean	
Transect type	Native vegetation	Himalayan balsam	Significance of difference
All seasons	1.45	1.11	0.939
Season 1	0.87	5.60	0.000
Season 2	2.61	0.65	0.000
Season 3	0.35	0.30	0.976

7.3.3.5 Influence of plant dominance through vegetation indices

In the final stage of analysis, habitat characteristics as well as properties of vegetation for all transects are analysed in context of observed morphological activity and distinguished between parameters that lead to increase in erosion and deposition (Table 7.14). Erosion (negative values of morphological activity) was statistically significantly correlated with increase in trees and shrubs coverage and high soil water and organic matter content. On the other side, deposition (positive value of morphological activity) was statistically significantly correlated with horizontal distance from the river edge, number and sum of stem diamaters of Himalayan balsam, number of native vegetation plants as well as total vegetation presence.

Table 7.14 Correlations between characteristics of transects and morphological activity, analysed for all surveyed transects together. Significan correlations (p<0.05) are marked with *.

Spearman's rho	Morphological activity mm per month
Trees and shrubs cover (percentage)	-.491*
Horizontal distance from river edge (m)	.193*
Vertical distance from river edge (m)	0.123
Transect slope (degrees)	0.09
Surface sediment silt or sand)	
Dominant soil particle size smaller than (mm)	
Soil percentage water content	-.208*
Soil percentage organic matter	-.208*
Soil shear vane (MPa)	0.133
Native vegetation reduction index	0.016
Himalayan balsam dominance index	0.016
Himalayan balsam number of plants at point	.198*
Himalayan balsam sum of stem diameters (mm)	.163*
Native vegetation number of plants at point	.162*
Native vegetation sum of stem diameters (mm)	0.088
Total vegetation number of plants at point	.316*
Total vegetation sum of stem diameters at point (mm)	.251*

7.3.4 What is difference between native vegetation and Himalayan balsam in characteristics of individual plants?

In this section, a general comparison of Himalayan balsam and native vegetation will be done on the basis of four morphological variables. In order to examine differences between native and invasive plants, 246 individuals belonging to seven native plant types are grouped together as native vegetation and compared with 246 specimens of Himalayan balsam.

Pull strength resistance was statistically significantly stronger for the native vegetation than the Himalayan balsam for all nine related variables (Figure 7.21, Table 7.15). In absolute value, that difference was three times higher, but when pull strength was compared with dimensions of respective shoots and roots, the difference rose to up to twenty times higher when compared to surface of root or stem. For each vegetation type, all pull resistance related variables showed a strong, statistically significant correlation ($p<0.05$) (Table 9.14) and therefore only pull resistance in relation to root and shoot diameter are used in further analyses. Percentage of dry mass is higher in native vegetation than Himalayan balsam for both roots and shoots separately and the whole plant. These differences are statistically significant for all three variables. Since whole mass of plant is mainly influenced by shoot diameter, it will be omitted, while shoot and root variable will be shown separately.

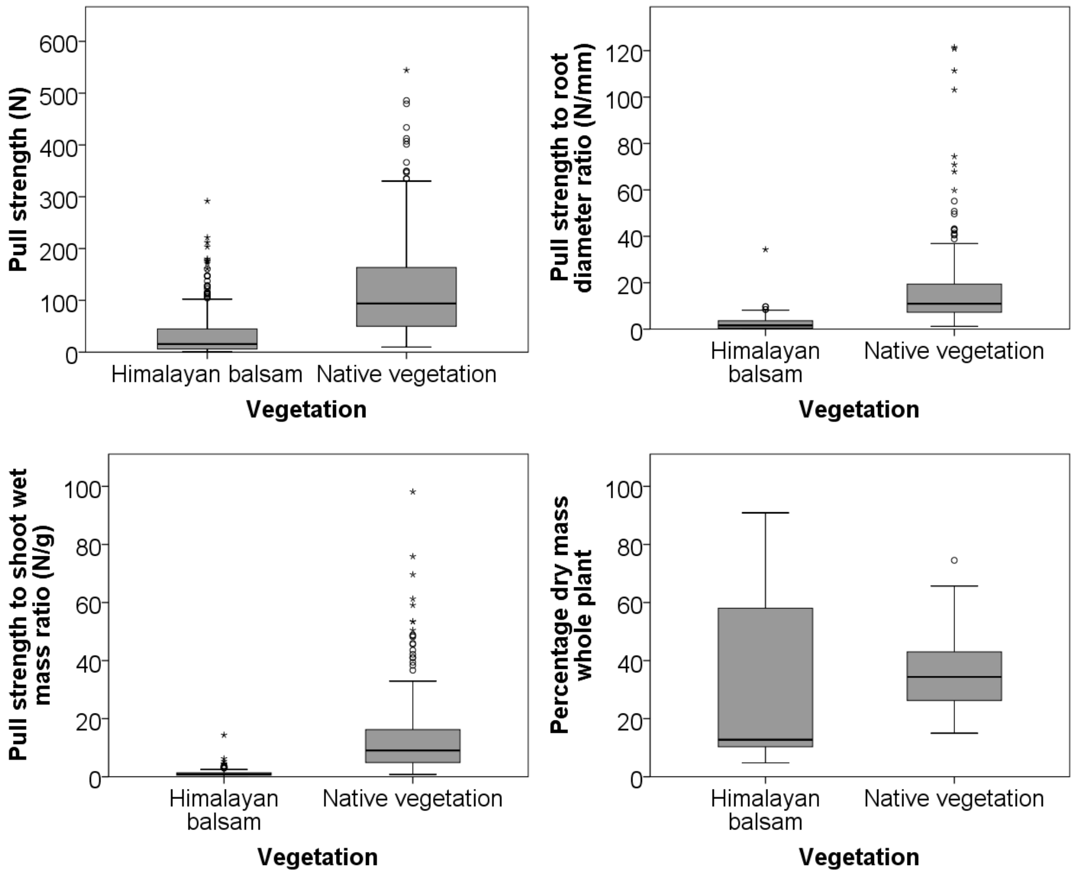


Figure 7.21 Boxplots for variables related to pull strength demonstrating the difference between Himalayan balsam and native vegetation.

Table 7.15 Descriptive statistics and significance of the difference between native vegetation and Himalayan balsam for variables related to pull strength.

Variable	Mean		Median		p
Type of vegetation	NV	HB	NV	HB	
Pull strength (N)	121.75	37.25	93.88	15.65	0.00
Pull strength to root diameter ratio (N/mm)	17.10	2.40	10.96	1.60	0.00
Pull strength to shoot wet mass ratio (N/g)	13.50	1.13	9.06	0.85	0.00
Percentage dry mass whole plant	34.81	30.96	34.38	12.75	0.00

Further, it is important to note that above presented differences displayed a seasonal dynamics (Figure 7.22). That is the most strongly visible observation that is made in spring 2015. Pull strength of Himalayan balsam was statistically significantly lower in comparison to native vegetation ($p<0.05$) during that same period. Additionally, Himlayan balsam pull strength was also statistically significantly lower during spring in comparison to autumn period ($p<0.05$).

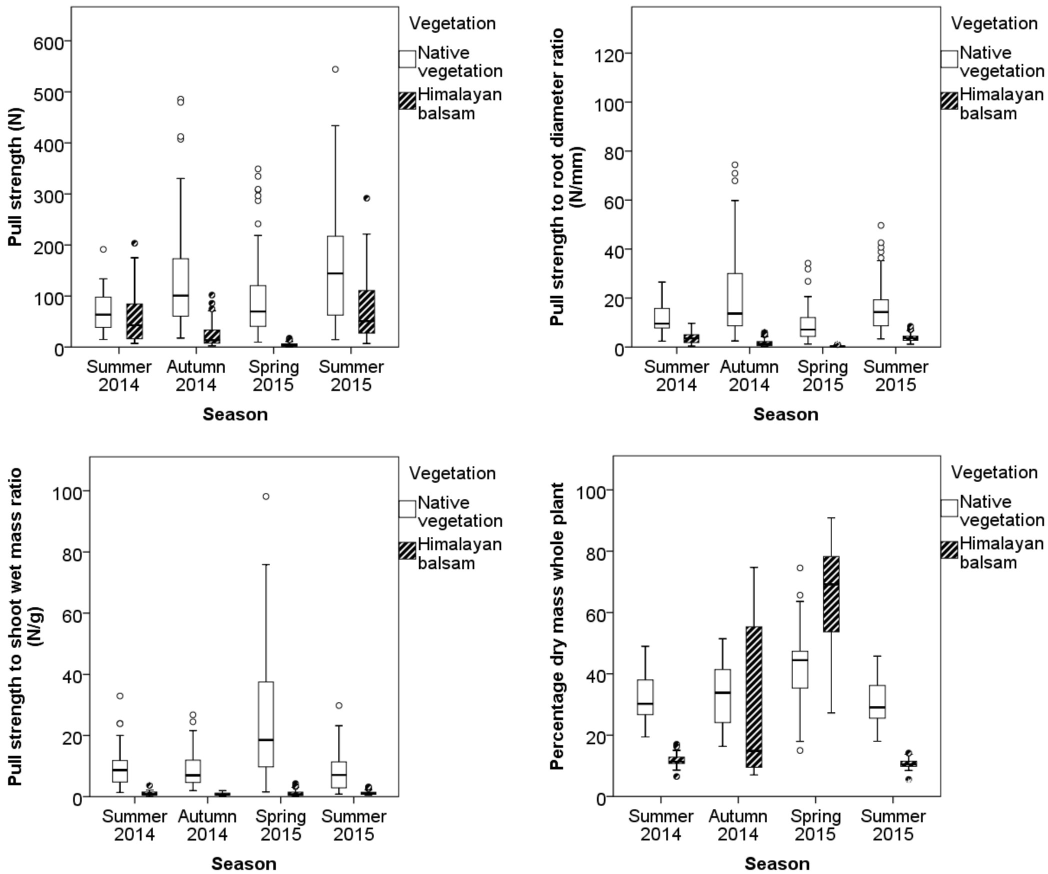


Figure 7.22 Boxplots indicating differences between native vegetation and Himalayan balsam over the course of four survey seasons.

7.4 Discussion

The presented results offer a unique insight into influence of Himalayan balsam on riparian vegetation as well as physical processes on the river banks. While the original study design envisioned continuous data sampling on eight sites, natural and man made disturbances caused a significant loss of data points. Still, due to wide range of aspects analysed, starting with microhabitat preferences of Himalayan balsam, quantification of competitive interaction between native vegetation and Himalayan balsam, in situ measurement of realised change in morphological activity and finally comparison of differences between individual plants belonging to two vegetation types, this study offers a novel insight that will be further interpreted below.

Comparison of difference in habitat preferences between native vegetation and Himalayan balsam in this study is characterized by two main points. Finding that six out of nine variables showed significant differences indicate that chosen variables were good in capturing the differences in environmental parameters between native vegetation and Himalayan balsam transects. Himalayan balsam transects were further away from the water edge than native vegetation ones. This might seems counterintuitive, since the current knowledge is that the Himalayan balsam is associated with riparian habitats (Pyšek and Prach, 1995). Additionally, Himalayan balsam transects were based on soil with higher water and organic matter content than the native vegetation ones and that is in line findings by Tickner et al. (2001).

The comparison of abundance of two types of vegetation was undertaken by recording two related variables. While native vegetation and Himalayan balsam transects do not different in amount of shading it can be assumed that they receive the same amount of light. It is known that plant abundance is directly proportional to the amount of sunlight (Koller, 2000). Therefore, while certain differences in efficiency of turning light into biomass exist, it can be assumed that overall the abundance on two types of transects should be the same. On the basis of this criteria, and the results presented in the Figure 7.10, sum of stem diameters is a better metric of plant abundance than number of plants.

Native plants respond to presence of Himalayan balsam in two distinct patterns. While grasses and bramble both are able to coexist with Himalayan balsam to some extent, oxeye, stinging nettle and smartweed are completely excluded from the Himalayan balsam transects. That means that their niche requirements are very similar and Himalayan balsam out competes them completely. Therefore, river banks dominated by those three groups of plants will be much more vulnerable to negative effects of Himalayan balsam invasion. Two indices aimed to quantify the extent of Himalayan balsam dominance over native vegetation both demonstrate a big difference between eight studied sites, ranging from partial to overwhelming dominance. Therefore it can be argued that on the spatial scale of this study, Himalayan balsam has a significant impact on native vegetation. This is in line with findings by Tickner et al. (2001), and Tanner and Gange (2013), stating that on the very local level Himalayan balsam outcompetes native vegetation. However, this explanation is in contrast to conclusion by Hejda and Pyšek (2006) who state that Himalayan balsam has negligible effects on the riparian communities, however they base that claim only on presence and absence of species and not on their relative abundances. Therefoer it can be concluded that Himalayan balsam did have a significant impact on native vegetatin and therefore changed overall structure of riparian vegetation.

Overall difference in morphological activity between native vegetation and Himalayan balsam is not statistically significant for the overall period of survey. However due to the mentioned disturbance of half sites, only four out of original eight sites were included in the analysis and that potentially contributed to lack of conclusiveness in results. However, it is statistically significant for two out of three seasons of the year. This implies that caution has to be used when interpreting results from incomplete annual measurements (Greenwood and Kuhn, 2014).

Direct measurements of differences in plant traits revealed a statistically significant difference between native vegetation and Himalayan balsam in all four studied variables. Pull strength was more than three times weaker for the Himalayan balsam than native vegetation. Since pull strength is the most important trait that indicates the overall resistance of plant to uprooting (Liffen et al. 2013), it is indicative that Himalayan balsam has weaker role in support of the soil in comparison to native vegetation. However, since Himalayan balsam plants are on average bigger and less numerous than native vegetation (Beerling and Perrins, 1993), the relative strength of the plant as measured by following two metrics is even more important (Loades et al. 2010).

Pull strength to root diameter is seven times stronger for native vegetation than Himalayan balsam. This is important, since diameter of roots approximately defines the area that plant occupies and therefore it is a better indicator of overall support a certain vegetation type provides to the soil (Thomas and Pollen-Bankhead, 2010). Pull strength to shoot wet mass ratio is twelve times stronger for native vegetation than Himalayan balsam. That is important since shoot biomass and overall surface are linked to the hydraulic drag forces that act on plants when they are submerged, which can happen during flood events in case of riparian vegetation (Sand-Jensen, 2008; Schutten and Davy, 2000). Therefore it can be argued that in two important characteristics, reinforcement of soil by roots and resistance to uprooting during extreme flood events Himalayan balsam is several times weaker than native vegetation.

7.5. Conclusion

Himalayan balsam dominance over native vegetation depended on local environmental parameters, with Himalayan balsam transects occupying areas of river bank that were horizontally and vertically further away from the river edge and soil that had a higher percentage of water and organic matter.

Himalayan balsam did not completely displace native vegetation, it achieved a range of dominance factors going from 1 to 47 more abundance and reducing native vegetation by factors of 2 till 24. Therefore it can be said that eight studied sites covered a wide range of gradients of Himalayan balsam invasion success. Out of seven types of native vegetation, oxeye, grasses, stinging nettle and smartweed experienced marked a reduction in their abundance, while bramble and remaining dicotyledons were not impacted.

The difference in morphological activity between native vegetation and Himalayan balsam transects was not conclusive. However, the measurement of the difference in morphological activity between native vegetation and Himalayan balsam transects was heavily impacted by natural and man-made incidents, which caused loss of half (4) survey sites.

The difference in characteristics of individual plants showed statistically significant differences between native vegetation and Himalayan balsam. Pull strength was three times stronger for native vegetation than Himalayan balsam (mean values 122 N and 37 N respectively). This is a good indicator of the general strength of the roots, which are much more powerful for the native vegetation. Pull strength to root diameter ratio was seven times stronger for native vegetation than Himalayan balsam (mean values 17.1 N/mm and 2.4 N/mm respectively). This metric is important because it puts strength in the context of root strength, which is directly linked with soil reinforcement and resistance to uprooting. Pull strength to shoot wet mass ratio was twelve times stronger for native vegetation than Himalayan balsam (mean values 13.5 N/mm and 1.1 N/mm respectively). This metric is important because it puts strength in the context of shoot mass, which is a key component that influences drag forces acting on plants in case of flooding. Percentage dry mass whole plant was more than two times higher for native vegetation than Himalayan balsam (median values 34% and 13% respectively). This metric is important because dry mass is proportionate to overall strength and makes plants more resistant during the winter season. Therefore, on the basis of traits of individual plants, it can be expected that Himalayan balsam is much weaker in the role of river bank protection from erosion than local native species.

CHAPTER 8: Conclusions

8.1 Introduction

In this chapter key findings from previous chapters are summarised and their implications on the science of invasive ecosystem engineers and management of river systems are further discussed. The main results of each section are summarised and cross-referenced in section 8.2. Following that is a discussion of methodological strengths and weaknesses of the methodology used in order to guide future research efforts in section 8.3. Afterwards, implications of the findings for the habitat conservation and river management are discussed in section 8.4. Finally, recommendations for the future research in the general field of invasive ecosystem engineers are presented in section 8.5.

8.2 Key findings

The original research questions identified at the end of the literature review (Chapter 2) were reframed during research design (Chapter 3) in order to address practical challenges of the research design. Therefore, the summary will follow the four key research themes as identified at the end of the research design chapter (Chapter 3):

1. Assessment of the signal crayfish burrowing on the bank section in reach scale (Chapter 4)
2. Assessment of the signal crayfish burrowing on the reach in catchment scale (Chapter 5)
3. Assessment of the signal crayfish burrowing on the bank section in catchment scale (Chapter 6)
4. Assessment of the Himalayan balsam ecosystem engineering effect (Chapter 7)

The summary of the answers is given in sections 8.2.1-8.2.4.

8.2.1. Signal crayfish burrowing on the bank section in reach scale

The research presented in Chapter 4 provided an insight into signal crayfish burrowing on the bank section in reach scale. The chosen survey site was chosen to be a representative of the river reach heavily impacted by burrowing. Therefore, this part of the survey was done on the river Windrush, the river with one of the most adverse impact of burrows, as indicated by Roberts (2012) and confirmed in Chapter 5. In order to further focus the study on the maximum impact of burrowing, one of the reaches with the highest presence of burrows on the River Windrush was chosen as a study site. This approach enabled an insight into signal crayfish burrowing on the site of their maximum impact that can reasonably be expected in the lowland river in the UK. At this site, a complex interaction between the occurrence of burrows, crayfish population density, records of erosion and influence of habitat characteristics was recorded and will be further discussed below.

Trapping part of the survey revealed that crayfish population density is high on the level of the whole reach, but also varies significantly between individual river sections. A number of crayfish caught (576 crayfish per 410 meters reach during five days of trapping) was similar to other studies of heavily impacted crayfish sites (Moorhouse and Macdonald, 2011; Moorhouse et al. 2014). On the basis of studies that assessed population structure in more detail (Peay, 2001; Wutz and Geist, 2013) it can be concluded that a total number of adult (trappable) crayfish as well as the overall number, including juveniles, is much higher. Except by high overall numbers, the studied reach was also characterised by high variability in a number of crayfish caught on different sections (ranging between 0 and 64 per bank section). This variability was mainly explained by the preference of crayfish for lentic microhabitats, a finding that is similar to established knowledge regarding crayfish habitat preferences (Souty-Grosset et al. 2006). Therefore two key findings related to signal crayfish population density, their total number and variability between microhabitats are in line with the general understanding of signal crayfish population dynamics (Holdich, 2002) and therefore the selected site is well representative of the river reach with a high density of signal crayfish in lowland British river.

The overall number of burrows was relatively high, with approximately one burrow for every four metres of the river bank (199 burrows per 820 metres of bank length). Since this study is the first one to systematically express a number of burrows per length of the riverbank surveyed, it is hard to compare the results recorded with other studies. However, it can be concluded, in context of results obtained by Guan (1994) and Roberts (2012) that the chosen reach is a good representation of the river highly impacted by signal crayfish burrowing.

A number of burrows oscillated between individual bank sections (ranging between zero and 30 per bank section) with a high number of burrows being associated with habitat characteristics like high banks and sharp bank angle as well as lack of vegetation on the bank face. This is similar to findings by Guan (1994) and Roberts (2012). Interestingly, both crayfish and burrows numbers achieved high values, however, those peaks did not occur on the same bank sections. This shift is likely explained by the changing nature of the river habitat (Crouzy et al. 2013) to which crayfish responded by migrating to another bank sections, as it is elaborated in Chapter 4. Additionally, detailed observation of burrows from the channel enabled observation of the burrows below and above the water line which enabled an informed development of the rapid survey assessment in the later chapters. Therefore it can be concluded that signal crayfish burrowing on highly impacted sites varied between individual bank sections and was influenced by local habitat variables.

The most important finding for the general interpretation of the influence of signal crayfish number on river bank erosion is the overall number of burrows. Less than two hundred burrows were recorded in comparison with at least five-fold number of crayfish present. This ratio implies that burrowing is a facultative behaviour, since not all crayfish dug a burrow as a shelter. There are two main implications of this result. The first one is that number of burrows could rapidly increase if conditions and drivers causing burrows change. The second implication is that burrowing might be of secondary importance as a signal crayfish ecosystem engineering activity. As shown by Harvey et al. (2012), general activities of crayfish, like walking and fighting could, due to high biomass and around the year activity of can cause significant disturbance of the river channel sediment. These findings imply that signal crayfish burrowing is facultative behaviour and that potential impact of signal crayfish as ecosystem engineers could be higher than previously anticipated.

Signs of erosion of the river bank were observed from the river channel and recorded on one-fifth of the bank sections. Erosion was primarily associated with habitat characteristics like the high angle of the bank and lack of vegetation. In addition to that, the presence of signal crayfish burrows was statistically significantly correlated with the occurrence of erosion.

8.2.2. Signal crayfish burrowing on the reach in catchment scale

The research presented in Chapter 5 provides a systematic insight into signal crayfish burrowing on the river reach in catchment scale. The choice of 103 reaches on seven tributaries of the River Thames, a river with a heavy presence of signal crayfish throughout the whole catchment, make this the most detailed and wide-ranging survey of signal crayfish burrowing. The use of rapid survey assessment enabled quantification of the extent of burrowing as well as identification of the habitat factors that lead to burrowing as well as implications of burrowing on erosion on the large scale.

Signal crayfish burrowing was spread widely throughout catchment, but in most cases, it covered low proportion of river bank. Two thirds (67%) of the reaches had the presence of burrows recorded, however, on the reaches with burrows, less than 5% of the river bank length was covered with burrows. However, the maximum percentage of the impacted bank, recorded on few locations, reached almost a quarter of river bank length, meaning that occasionally, there were high impact locations. These trends were similar for six tributaries of the Thames, while only River Colne had lower values. Therefore, signal crayfish burrowing is characterised by wide spread distribution, but mainly localised effects.

Habitat influence on signal crayfish burrowing was characterised by the strong overlap in the characteristics of reaches with and without burrows. However, river reaches with higher cross-sectional channel area, steep bank profile and higher habitat quality were more likely to be impacted by burrows. Since crayfish generally prefer high-quality habitats (Souty-Grosset et al. 2006), increase in burrow numbers could be attributed to a higher population densities on reaches with diverse habitats. Therefore, while certain habitat characteristics certainly promote the occurrence of burrows, high overlap in characteristics of reaches with and without burrows imply that other factors contribute to the creation of burrows.

Signal crayfish burrowing displaced a significant amount of sediment. On the basis of the average volume of burrows and burrow numbers, it was possible to assess the volume of sediment excavated by signal crayfish. On average, signal crayfish excavated a mean value of 67 Litres of sediment per kilometre of the bank, ranging from 13 L per km on the River Colne to 105 L per km on the Windrush. When the same approach is applied only on the bank impacted by burrowing, the values have a mean value of 2 L per m. However, both of these numbers provide a general idea regarding the volume of burrows, but they are impacted by two factors. Firstly, those numbers are based on the observation of burrows above the waterline, while more burrows are present below the water line and despite the work presented in chapter 4, the ratio of those two types of burrowing cannot be assessed over wide spatial ranges. Secondly, the volume of sediment cannot be put in the context of the annual sediment budget since the rate of burrowing per year is not yet known and was not covered in this or any other study. Therefore, signal crayfish excavate a significant amount of sediment through their burrowing activity, but the overall impact of those activities cannot be properly assessed.

8.2.3. Signal crayfish burrowing on the bank section in catchment scale

The research presented in Chapter 6 is based on 69 sites with the presence of burrows but analyses them on the level of the individual, ten metres long bank sections. This change in spatial scale revealed new findings, primarily regarding the influence of habitat characteristics on burrowing and impact of burrows on erosion.

Signal crayfish burrowing occurred on the one-third of the bank sections covered in this study. However, it is important to note that due to change in scale (focus on much shorter lengths as the main unit) and site selection (not a random selection of sites), this number is not representative of the general distribution of burrows. This finding does reinforce the results from the previous section and Chapter 5, stating that signal crayfish burrowing is widespread, but even on sites where it is recorded, it covers short lengths of the river bank.

In comparison with the previous chapter, direct, simultaneous field observation of all studied variables employed in this chapter, lead to improvement in understanding of the influence of habitat on the occurrence of burrows. While an overall similarity between bank sections with and without burrows was recorded for a range of habitat characteristics, few key elements were identified. Signal crayfish burrows were more likely to occur on bank sections with the cohesive material, higher bank angles, less vegetation, a higher proportion of bare bank face and wider water width. Due to the smaller basic unit of assessment and the fact that habitat and burrow information was collected at the same time, this finding represents the most detailed assessment of the influence of habitat. This type of classification is more specific than the one offered for the reach scale, primarily since the unit of length sampled is shorter. Therefore it can be concluded that signal crayfish burrowing has a tendency to occur on specific habitat types.

Signal crayfish burrowing presence was associated with an increase in the likelihood of erosion occurrence. While bank sections with no burrows had erosion in 22% of cases, in the case when burrows were present, that likelihood rose to 59%. While this is not a firm proof, it is a strong indication that signal crayfish burrowing should be included in the discussion related to river bank erosion. Erosion is influenced by many factors (Rinaldi and Darby, 2007), but current models of bank stability, like BSTEM (Simon et al. 2000; Midgley et al. 2012), do not enable quantification of the effect that burrowing has on the bank stability. However, it is known that cavities, like burrows, influence hydrology near the bank (Ozalp et al. 2010; Jackson et al. 2015) and related change in flow is known to contribute to the mass failure of the bank (Fox and Wilson, 2010). Therefore, on the basis of field observations and existing knowledge about factors leading to burrowing, there are indicators that signal crayfish burrowing could be contributing to river bank erosion.

8.2.4. Himalayan balsam

The research presented in Chapter 7 gives an overview of impacts of Himalayan balsam on native vegetation and physical processes on banks of the River Brenta. The specific methodology was used to explore each main area of interest. The use of transects enabled characterisation of difference in habitat characteristics occupied by native vegetation and Himalayan balsam as well as quantification of the extent of Himalayan balsam dominance over native vegetation. However, use of this method for the assessment of the difference in the ability of vegetation to influence morphological activity remained inconclusive. On the other side, the study of morphological differences between individual plants revealed stark differences between native vegetation and Himalayan balsam, but the question remains about extent and conditions under which these differences translate to change in the natural setting. All of those aspects will be reviewed and discussed below.

Native vegetation and Himalayan balsam inhabited different microhabitats along the river Brenta. Himalayan balsam transects occupied areas that were horizontally and vertically further away from the river edge and soil had a higher percentage of water and organic matter. These findings represent first insight of knowledge regarding Himalayan balsam microhabitat preferences. Those findings differ from the current studies (Pyšek and Prach, 1995; Tickner et al. 2001; Hejda and Pyšek, 2006), but those differences can be explained due to the difference in the spatial scale used and comparison with different sets of native vegetation, as elaborated in Chapter 7. Overall, the survey was based on a combination of transects that enabled the good combination of native vegetation and Himalayan balsam sampling sites.

Himalayan balsam partially displaced native vegetation on invaded transects. Its abundance was between one and 47 times higher than that of the native vegetation and it reduced the abundance of native vegetation between two and 24 times. Such a wide range of dominance of invasive plant over the native vegetation is typical for the newly established invader (Bennett et al. 2012). Therefore, it can be said that due to the great range in the level of dominance of the Himalayan balsam over native vegetation, this study covers a representative range of sites. The influence of different vegetation on morphological activity will be reviewed, separately for influence during the extreme flood events and the baseline seasonal morphological activity in following two paragraphs.

In case of two sites primarily influenced by the extreme flood events, the difference in morphological activity could not be attributed to different vegetation types. While there were statistically significant changes between individual points since only one site was hit by extreme erosion and one by extreme deposition no firm conclusions could be made. This is in line with the current understanding that states that non tree riparian vegetation (Gurnell, 2014), has limited effect in preventing extreme events, especially when those occur on river banks dominated by non-cohesive sediment. Therefore, this study did not answer the question of the impact of two types of plants in case of extreme events.

The main focus of the transect study, the four sites with continuous records of morphological activity throughout the year, demonstrated the similar influence of two types of vegetation studied. Presence of both, native vegetation and Himalayan balsam increased deposition on vegetated transects in comparison to the cleared ones. While this is the result based on the whole research period, for the native vegetation the most of that difference occurred during autumn and winter, while for the Himalayan balsam most of those impacts happen during summer. It is well established that erosion and deposition vary throughout the year (Henshaw et al. 2012) and are influenced by multiple factors (Lawler et al. 1997; Simon et al. 2000; Hooke, 1979). Therefore relatively short observation period in combination with a small number of sites did not manage to identify long-term trends.

The survey based on analyses of differences in morphology of individual plants found major differences between native vegetation and Himalayan balsam. All four studied metrics showed that native vegetation is multiple times stronger in all relevant traits. General resistance to uprooting and water content are known to improve the role of plants as soil reinforcement (Liffen et al. 2013). Even more important are relative measures of strength. In comparison to the diameter of roots, native vegetation is much stronger, meaning that with the same biomass it reinforces soil more strongly (Thomas and Pollen-Bankhead, 2010). The weak ratio of shoot mass to root strength indicates that high shoot of Himalayan balsam is more likely to cause a strong drag force during flood events and contribute to the uprooting of the whole plant (Sand-Jensen, 2008). Therefore, four studied metrics demonstrate that on the level of individual plants, in key parameters for plant reinforcement of soil, Himalayan balsam is much weaker than the native vegetation.

The presented results emphasize three main aspects of the interaction between native vegetation and Himalayan balsam from the perspective of invasive ecosystem engineers. The first set of findings, regarding the dominance of Himalayan balsam over native vegetation, provide context for the following two since the difference between two types of vegetation is only as important as a function of their respective presence on the river banks. The second set of findings, based on direct, real-time measurements in the field, did not provide conclusive results, but that is mainly due to methodological constraints. However, the third one, study of individual plants clearly demonstrates that there is a significant difference between two types of vegetation in key features that influence the main role of the vegetation as ecosystem engineer, reinforcement of the river banks. Therefore, it can be concluded that invasion of the Himalayan balsam of the river banks does cause significant changes in the river system, which is likely dependant on the rate of invasion success.

8.3 Implication of methodological improvements for future work

Throughout this thesis, a range of different methods were used across a wide range of spatial and temporal scales. The general survey design was based on the current state of knowledge in the respective fields and further shaped to enable addressing research questions in practical terms. However, throughout the work, several areas of potential improvement as well as important principles were identified. Those will be addressed separately for signal crayfish and Himalayan balsam and followed by a more general discussion of methodology in studying invasive ecosystem engineers.

8.3.1. Signal crayfish survey methodology or how to sample burrows

The research presented in this thesis is the most comprehensive survey of signal crayfish burrowing undertaken by now. It combined a focused, detailed study (Chapter 4) and a wide range surveys (Chapters 5 and 6). This methodological approach combined rapid assessment survey methodology that covered a wide area and detailed, in site observations which enabled calibration of previous results. Since all three main research questions were answered with this approach, it serves as a good basis for future studies of the same topic. Key recommendations that were recognised as important when designing a signal crayfish burrowing survey will be discussed below.

The first recommendation deals with the relationship between choice of sites for the survey and type of answers the survey provides. The assessment of signal crayfish burrowing covered three levels of spatial scale and was based on the combination of rapid assessment surveys applied over the large spatial extent and a focused, detailed study. However, the three chapters, focusing on three different spatial scales each have their unique set of answers they provide. One of the goals of the focused survey (Chapter 4), was to assess the "worst" case scenario by exploring the interaction between habitat, burrows and erosion. Therefore, the field site choice was on the river Windrush (the most heavily impacted out of seven studied tributaries) and further the reach chosen had some of the heaviest burrow load. Therefore, the results obtained provide a useful information about the "worst case" scenario, but cannot be extrapolated to a wider area (the rest of Thames catchment). On the other side, the aim of the wide range survey (Chapters 5), was to give an objective assessment of the extent of burrowing over the wide spatial scale. Therefore, sites (103 reaches) were chosen randomly. This procedure enabled objective assessment of the extent of signal crayfish burrowing in the Thames catchment. Finally, Chapter 6 was a mix of two approaches, designed in order to enable the best coupling of habitat, burrowing and erosion information and explain their interaction. While all three approaches are valid, it is important to adjust sampling design to the research questions asked. Therefore, in order to provide an objective quantification of the phenomenon on the large scale, a survey of random sites should be used, while exploration of specific questions can be done on a more focused selection of sites.

The second recommendation deals with the general context of sampling design. Two main approaches to quantification of burrows, used in previous signal crayfish burrowing studies (Guan, 1994; Roberts, 2012) were based on the records of the length of the impacted bank and number of burrows. However, the key improvement applied in this study was to keep track of the length of the bank surveyed. Therefore, quantification of burrows should always include a relation to the length of the bank surveyed and using variables like: number of burrows per metre and percentage of the total surveyed length that was impacted by burrows. This principle enables proper quantification of burrows and contextualisation of the obtained data.

The third important aspect is to consider challenges related to the use of the rapid reconnaissance survey. Downs and Thorne (1996) addressed the advantages and disadvantages of the reconnaissance surveys and emphasized that while they can never be as objective as detailed studies, that limitation is offset by the ability to provide an initial assessment of the studied topic. In this thesis, two key challenges were encountered due to the rapid survey of the river banks. Firstly, burrows were primarily observed above the water line, while burrowing is overall an underwater phenomenon. This issue was discussed in detail in Chapter 5 and the calibration process based on the observations made in Chapter 4 justified that approach. Secondly, an effort has to be made to distinguish between habitat traits that lead to some features and features themselves. For instance, both burrowing and erosion were strongly correlated with bare bank face, but at the same time, bare bank face enables better observation of burrows. Therefore, rapid surveys as used in this thesis can be a valuable tool in providing an initial assessment of complex phenomenon especially when the focused effort is done to identify and address key weaknesses in data collection and interpretation.

Finally, as recommended by Downs and Thorne (1996), research design survey has to be adjusted to the research questions. This was done by using a “modular approach” by which for each one of three research questions, information for the three main groups of variables surveyed (habitat, burrows and erosion) were collected in different ways. Already existing approaches were used and slightly adjusted like reach level indices in Chapter 5. Established methods were modified to suit current requirements, like in the case of the RHS survey methodology (Environment Agency, 2003) and Stream Reconnaissance (Thorne, 1998). Finally, newly developed modules were developed, like the procedure for recording burrow impact which emphasized requirement to put a number of burrows in context of the length of bank surveyed. In each of those cases, an informed judgement about the best approach to adjust the method was applied. The way of designing those methodological modules was primarily adjusted to suit the practical constraints of data collection and requirements of research questions

8.3.2. Himalayan balsam methodology or how to measure difference in influence of the morphological activity between different vegetation types

The impact of Himalayan balsam on the morphological activity on the river banks was assessed by a combination of two distinct methodological approaches which resulted in two distinct interpretations. One set of results (transect survey) produced an inconclusive result, while the other one (direct measurement of plant morphology) showed great differences between two studied types of vegetation. Therefore, these two interpretations indicate the urge to use a combination of methodological approaches to analysing complex environmental questions. Since direct measurements of plant morphology produced good results, that method is considered adequate for the research questions established. Therefore, aspects that limited the success of the transect based survey will be analysed in more details.

The first aspect of methodology that should be improved is that time span was relatively short for this type of process. Similar surveys based on monitoring of morphological activity via erosion pins (Henshaw et al. 2012) were based on the period of two years or more. Therefore, a longer timeframe would provide more information into a different impact of two types of vegetation. Another factor that impacted transect based survey was that due to the relatively high work requirement to collect the data, a small number of sites were established. This was further exuberated by the unpredicted destruction of few sites throughout the year and resulted in the small dataset. Since the morphological change was similar on each transect, improvement would be to reduce the number of points collected. Therefore, a survey design covering more sites with less sampling points spread over longer observation period would be beneficial. However, all three improvements are relatively small in comparison with the general change in methodology that occurred in recent years with the advent of digital methods. Therefore, an application of new modern methods would be best suited to answer research question related to change in morphological activity caused by different types of vegetation in the field and in real time. Since these methods represent a drastic diversion from the methods used, they will be discussed under directions for future work (Section 8.5.)

8.4 Implications of findings for the habitat conservation and system management

Both invasive ecosystem engineers covered in this study are widespread throughout Europe and their areal and presence within areal are both increasing. Current agreement in environmental science is that such successful invaders cannot be removed on the large scale and therefore are likely to cause a significant effect on the river ecosystems in the future (Vaclavik and Meentemeyer, 2012). In the case of signal crayfish and Himalayan balsam, due to their synergistic impact on invasive species and ecosystem engineers assessing their impact on river systems is a complex task. In order to address it, firstly the overview of the current status of habitat conservation and river system management will be given.

Current discourse regarding river systems management revolves around balancing the requirements of conservation of ecosystem and public use of the water resource (Costanza et al. 1997). This challenge is increasing in part due to the constantly increasing qualitative and quantitative uses of water on one side and multiple anthropogenic stressors that effect river ecosystems, like climate change, pollution, habitat fragmentation and invasive species. In order to integrate these findings and the role of individual species in this mess, it is important to analyse a general role of individual species in the ecosystem.

The role of individual species within an ecosystem can be assessed from two standpoints: as a net contributor to biodiversity and through the functional role it plays in the ecosystem (Coux et al.

2016). Detrimental influence of invasive species on biodiversity is well recorded for both, signal crayfish and Himalayan balsam. However, due to nature of this thesis focus on ecosystem engineering, it is the functional role that will be explored in more detail.

Two ecosystem engineers have complex trophic and ecological roles as functional species. The functional role of signal crayfish has a role as an omnivore macrozoobenthos has on the transfer of organic matter within the trophic chain and impact on macrophytes are the most well-known (Holdich, 2002). The functional role of Himalayan balsam is that it differs from the native riparian vegetation in a range of ecological and morphological traits (Beerling and Perrins, 1993). Despite the previously discussed ecological roles of both species covered in this thesis, throughout the thesis and literature, it is obvious that the most important aspect of the functional role is the contribution of both species to sediment dynamics in rivers.

While the impact of each species differs in parts of sediment pathways they impact, it is generally agreed that both species contribute to increase in erosion (Statzner 2012; Greenwood and Kuhn, 2014; Harvey et al. 2014). However, in both cases that effect is hard to quantify.

The vulnerability of river systems to increase in erosion and sedimentation depends primarily on the river system in question. Presence of macrophytes, a key functional group in river systems makes an ecosystem more vulnerable to increase in suspended sediment (Kohler et al. 2010). Trout fisheries, an important recreational industry in the UK, is also known to be negatively influenced by the increase in sediment suspension (Wood and Armitage, 1997).Finally, increase in sediment directly impacts the human use of water resource from either recreational or water supply perspective (Owens et al. 2005). Therefore all of those aspects have to be taken into account during management of river systems.

Habitat management in the modern world is a constant balance between conservational and management perspectives and involves multiple stakeholders (Palmer et al. 2003). Therefore, a river that is impacted by either signal crayfish or Himalayan balsam is additionally vulnerable to the increase in erosion and that effect can be classified as an extra risk that has to be quantified and taken into account (Haimes, 2009). From that perspective, practical implications of the impact of invasive ecosystem engineers will be interpreted through the general risk assessment framework and it will require additional awareness in decision making.

8.5 Recommendations for further research ecosystem engineers

This thesis explored several aspects of the understanding of ecosystem engineering impacts on the environment. In doing so, the potential for improvement became visible in few key areas of methodology. Therefore, recommendations for the potential future research of signal crayfish burrowing and Himalayan balsam impacts on erosion and deposition will be reviewed.

8.5.1. Future research of signal crayfish burrowing

Survey of signal crayfish burrowing revealed key insights into distribution and occurrence of burrows on three different scales in the Thames catchment. Throughout this work, three additional areas emerged that would improve current understanding and contextualisation of the signal crayfish burrowing phenomenon: analysis of the temporal component of burrowing, exploration of additional parameters leading to burrowing and assessment of the relative importance of burrows in relation to other forms of signal crayfish impacts. Those three topics will be elaborated below.

The analysis of the temporal component of burrowing remains the one component with the greatest potential to improve the assessment of burrowing impact on the overall sediment dynamics in the river systems. This survey provided a detailed information regarding the density of burrows on different spatial scales. However, since each site was visited only once, the rate of burrowing within specific time frame was not assessed. Currently, this lack of temporal information is the key element lacking in order to assess the impact of burrowing on sediment budget. In order to explore the temporal dynamics of burrowing, a monitoring survey should be undertaken with a preferred time frame between one and two years. The survey should follow the occurrence of new burrows as well as changes in erosion caused by burrowing. The recommended spatial scale for that monitoring survey should be bank section within reach scale, undertaken on a reach with a confirmed high activity of burrowing (similar to work described in Chapter 4). This type of survey would enable contextualisation of burrow density results in the annual sediment budgets (Collins and Anthony 2008).

The exploration of additional parameters leading to burrowing is the second important issue that warrants further research. One of the main features regarding signal crayfish burrowing is that, despite few general tendencies, there is a major overlap in characteristics of many habitat parameters between sites and bank section with and without burrows. This was observed on all three spatial scales and indicates that additional factors, the ones not covered by this survey can have a major impact on signal crayfish burrowing.

One of the main factors that was not explored was the presence of predators, primarily fish, which are known to influence crayfish behaviour (Souty-Grosset et al. 2006). Since crayfish burrows are primarily a shelter, the presence of predators increases the incentive of an individual animal to burrow. In addition to that, signal crayfish population density was studied only on one reach. Therefore, explanation of burrowing on the broader terms of crayfish population density in the river catchment could offer additional insights. While physical habitat was in majority of cases suitable for crayfish, other factors known to influence crayfish population densities like pollution and presence of predators were not accounted for. Therefore, it would be meaningful to explore additional factors leading to burrowing.

The third main recommendation is the assessment of the relative importance of burrowing in relation to other forms of ecosystem engineering activity performed by signal crayfish. This is primarily based on the findings from the Chapter 4, stating that a number of burrows is small, compared to the number of crayfish (a conservative assessment is a fivefold difference). Based on an overview of potential impacts by aquatic animals (Statzner, 2012), a general activity of crayfish that includes walking and fighting could be a significant contributor to the overall ecosystem engineering performed by signal crayfish. Impact of signal crayfish activity was confirmed by Harvey et al. (2014), however further studies are required to fully understand the impact of crayfish activity across a range of spatial scales and river styles.

8.5.2. Future research of Himalayan balsam impacts

Study of Himalayan balsam impacts was marked by the interplay between the role of Himalayan balsam as an invasive species and its ecosystem engineering activity which differed from the role of native vegetation. Two main guidelines for future work will be explored below.

Survey of the extent of dominance of invasive species is as important as the difference in their functional roles. Results of this thesis demonstrated that Himalayan balsam has a weaker root structure in comparison with native vegetation, but failed to prove consequence of that difference in real time measurement. On the other side, Greenwood and Kuhn (2014) found that erosion is higher on river banks covered with Himalayan balsam than native vegetation. However, they did not quantify the extent of dominance by invasive species and overall plant density on two types of sites. Therefore, to fully understand the impact of invasive plants on ecosystem engineering processes, coupled studies that should be designed.

The second recommendation for future work deals with methodology and use of novel methods. The method used in this survey is an adaptation of classical geomorphic method (Lawler et al. 1997) and it had obvious limitations in spatial and temporal extent of use. However, use of novel methods like infrared laser scans for quantification of vegetation (Baltensweiler et al. 2017) and structure from motion for monitoring of topography (Westoby et al. 2012) would rapidly increase spatial resolution and extent of coverage as well as the frequency of observations.

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