# *Spatial patterns of habitat use by white clawed crayfish (Austropotamobius pallipes) on the River Wansbeck*

PEARSON, CAITLIN,ELIZABETH

PEARSON, CAITLIN,ELIZABETH (2011) *Spatial patterns of habitat use by white clawed crayfish (Austropotamobius pallipes) on the River Wansbeck*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/3203/

# Spatial patterns of habitat use by white clawed crayfish (*Austropotamobius pallipes*) on the River Wansbeck

## Caitlin Elizabeth Pearson

Thesis submitted for the degree of
Master of Science (by research)

Department of Geography and
School of Biological
and Biomedical sciences

Durham University

2011

# Abstract

The white clawed crayfish (*Austropotamobius pallipes*) is a freshwater crustacean at imminent risk of extinction, largely due to the introduction of American signal crayfish (*Pacifastacus leniusculus*) to Britain. With the purpose of determining how white clawed crayfish respond to habitat and spatial variables, this study correlated white clawed crayfish distribution over a 35 km length of the River Wansbeck, Northumberland, to physical variables at three-spatial scales. White clawed crayfish were present throughout the study area at an average density of 5.3 individuals per square metre. The realised niche of white clawed crayfish was very broad; the only available areas crayfish could not make use of were those with microhabitat scale $D_{50}$ smaller than 8 mm. Within their wide realised niche, crayfish showed significant responses to habitat. The strongest response was to grain size, with crayfish preferentially selecting cobbles as refuges. Distance downstream and lateral distance did not influence distribution or density of white clawed crayfish but crayfish were more abundant in the upstream half of the study area, reflecting the higher availability of favourable habitat in low order streams. Patchiness in distribution was only evident at the sub-metre scale, suggesting crayfish are only directly responding to microhabitat scale heterogeneity. Habitat based conservation actions should be conducted at this scale. However, habitat variables operating at the kilometre section and site scale (100 m) influenced the suitability of microhabitats. The abundant, dense population of white clawed crayfish on the River Wansbeck makes it a site of international importance. It is therefore recommended for designation as a Special Area of Conservation.

# Declaration of Copyright

I confirm that no part of the material presented in this thesis has previously been submitted by me or any other person for a degree in this or any other university. In all cases, where it is relevant, material from the work of others has been acknowledged.

Caitlin Elizabeth Pearson
Department of Geography
Durham University
December 2010

# Contents

# List of tables

# List of figures

Chapter 2 – Review of concepts

Chapter 3 - Overview of current knowledge of the white clawed crayfish

Chapter 4 - Methods

Chapter 5- Results

Chapter 6 - Interpretation and Discussion

# Acknowledgements

First and foremost, I would like to thank my supervisors, Dr. Patrice Carbonneau and Dr. Martyn Lucas for their support and guidance throughout this project. Their expert knowledge, advice and positive attitudes have been invaluable. I am sincerely grateful to ONE North East for their financial support, which made this project possible. Special thanks go to all staff and volunteers at the Northumberland Wildlife Trust, particularly Steve Lowe. Working with the Trust has been both immensely valuable and extremely enjoyable. Finally, I would like to thank everyone who assisted me with the field work for this project. I hope they enjoyed crayfishing as much as I did!

# Chapter 1- Introduction

## 1.1 Introduction and Rationale

Freshwater ecosystems are immensely valuable to human communities as they provide economical, cultural, scientific and intrinsic benefits (Dudgeon *et al.* 2005). The global value of ecosystem goods and services provided by inland freshwaters has been estimated at US $6579 billion per year (Constanza *et al.* 1997). This value exceeds the GDP of every country in the world apart from the USA and is greater than the combined value of all terrestrial systems (Constanza *et al.* 1997). The value of freshwaters is, in part, due to the number and diversity of species they contain. Whilst freshwaters account for only 0.8 % of the Earth's surface they support 6 % of all known species (Hawksworth & Kalin-Arroyo, 1995).

Consequently, freshwater ecosystems are often heavily exploited. Unsustainable use of these systems has led to severe degradation (Dudgeon *et al.* 2005), rapid declines in biodiversity (Sala *et al.* 2000) and accelerating extinction rates (Moyle and Leidy, 1992). Data on global extinction rates is sparse but the evidence collected thus far suggests that rates of decline in freshwater species richness and abundance are higher than rates of decline in terrestrial species (Sala *et al.* 2000; Millennium Ecosystems assessment, 2005). The causes of these declines can be categorised under four main headings: overexploitation, water pollution, habitat modification and introduction of invasive species (Dudgeon *et al.* 2005). These threats are briefly outlined below.

Unsustainable catch rates have resulted in severe depletion of many species harvested for food, including molluscs (*e.g.* Anthony and Downing, 2001), fish (*e.g.* Holmlund and Hammer, 1999) and crustaceans (*e.g.* Le Vay *et al.* 2001). Pollutants, encompassing a wide range of contaminants such as domestic and industrial effluent, agricultural runoff, siltation, endocrine disruptors and pathogens, may cause direct mortality in freshwater species or act as long-term stressors (Dudgeon *et al.* 2005). Large-scale alterations of freshwater systems are also widespread, primarily occurring in order to allow human exploitation of freshwater resources and to prevent flooding (Nilsson and Berggren, 2000). Indirect habitat modification due to changes within a catchment, such as deforestation, can also be detrimental to aquatic ecosystems (Dudgeon *et al.* 2005). Invasive non-native species can have negative impacts on native species, ecosystem functioning, economic activity and human health. Attempting to deal with invasive species costs £ 2 billion per year in the U.K. alone (DEFRA, 2008). Climate change and the resultant change in temperature and precipitation patterns are acting as additional stressors for many species and increasing the pervasiveness of invasive species (Vescovi *et al.* 2009). The combination of these threats has led to a global crisis in freshwater ecosystems but awareness of the need to conserve them is low (Dudgeon *et al.* 2005). Immediate action is needed to prevent irreversible losses of valuable freshwater species. Thus, conservation and management of freshwater biodiversity is a priority, in both the U.K. and worldwide (Dudgeon *et al.* 2005). Rivers, streams and standing waters are all recognised as priority habitats for conservation in the U.K. (U.K. Biodiversity Action Plan [BAP], 2007). Over forty species of recognised conservation importance in the U.K. are reliant on these habitats, including birds, fish, amphibians, crustaceans, molluscs, mammals and cnidarians (U.K. Biodiversity Action Plan, 2007). Many of these species are internationally threatened and rapidly declining in the U.K.

In order to maximise the effectiveness of conservation efforts with limited resources, conservationists must have a thorough understanding of the habitat requirements and preferences of a species (Simberloff, 1988). This understanding is necessary for assessing habitat quality, predicting distribution, maintaining and creating suitable habitat and identifying potential reintroduction sites (Smith *et al.* 1996). Habitat requirements and preferences can be determined by studying the distribution of populations in relation to the distribution of physical variables (Hirzel, 2002).

Previous studies have shown that the likelihood of riverine species being present in a given location changes with longitudinal and lateral position within the channel (*e.g.* Richardson and Mackay, 1991; Torgersen and Close, 2004). Thus, acknowledging spatial position as an explanatory variable is likely to improve predictions of a species distribution from physical variables (Thorp *et al.* 2006). Further, the hierarchically structured nature of river systems (Frissell *et al.* 1986) makes generally applicable habitat models difficult to obtain. This structure means that the observed patterns of environmental heterogeneity and conclusions on species-habitat relationships depend on the scale at which the system is viewed (Torgersen and Close, 2004). Previous studies have shown that different taxonomic groups respond to their environment at different scales (*e.g.* Townsend *et al.* 2003; Torgersen and Close, 2004). Habitat studies and management efforts should view river systems at the scale over which the focal species responds to environmental heterogeneity.

The white clawed crayfish (*Austropotamobius pallipes*) is an example of a freshwater species that is ecologically and economically valuable but is threatened both internationally and in the U.K. The white clawed crayfish (WCC) is a decapod crustacean (Groves, 1985) and the only crayfish species native to the U.K. (Holdich and Lowery, 1988). Crayfish, as omnivorous foragers and detrital feeders, are polytrophic and therefore play an important role in freshwater ecosystem functioning (Goddard and Hogger, 1986). This influence makes native crayfish key species in freshwater ecosystems, and as such, they help maintain populations of other species of cultural, ecological or economic importance (*e.g.* Statzner *et al.* 2000).

Like many freshwater species, crayfish are threatened by pollution, habitat degradation and introduction of non-native competitors (Crandall and Buhay, 2008). The major threat to WCC in Britain is competition from the North American signal crayfish (*Pacifastacus leniusculus*) which was introduced to Britain in the 1970s. Signal crayfish out-compete WCC for food and habitat and carry a fungal plague (*Aphanomyces astaci*), which is lethal to native crayfish (Holdich, 1988). Signal crayfish also cause broader negative consequences in river systems. They are a nuisance to anglers, their presence is detrimental to stream fish populations (Guan and Wiles, 1997) and they have been shown to exacerbate bank erosion through burrowing activity (Guan, 1994; Stancliffe-Vaughan, 2009). Due to the combined negative impacts of signal crayfish, habitat degradation, habitat modification and pollution (Holdich, 2003), the number of 10 km grid squares occupied by WCC in England and Wales declined by 20.3 % between 1997 and 2001 (Sibley *et al.* 2002). It is estimated that the number of white-clawed crayfish in the U.K. has declined by 60 % since 2000 (Holdich *et al.* 2009). At this rate of decline, WCC will be extinct in Britain by 2030 (Sibley *et al.* 2002).

Consequently, WCC are recognised as 'endangered' by the International Union for Conservation of Nature (IUCN) and listed as a priority species in the EC habitats directive (European Council Directive 92/43/EEC). Signatories to this directive are required to 'maintain and restore priority habitats and species at a favourable conservation status'. The directive specifies that conservation of WCC requires the designation of Special Areas of Conservation (SACs). In response to this, the U.K. has a Biodiversity Action Plan for WCC, which aims to maintain the present distribution of the species until 2013 (U.K.BAP, 1995). Maintaining biological diversity and protecting native species is also crucial in meeting the EU Water Framework Directive, the 15 year commitment made by EU member states in 2000 to bring freshwater systems back to good ecological, chemical and geomorphological quality (European parliament and council directive 2000/60/EC). Meeting these legislative aims and ensuring continued survival of WCC will require population monitoring, habitat management and increased public awareness (U.K. BAP, 1995). Application of conservation measures to prevent extinction of WCC is imperative, before the opportunity to act is lost.

Several authors have conducted studies of WCC habitat preferences (*e.g.* Smith, 1996; Naura and Robinson, 1998; Benvenuto *et al.* 2008) and as a result some aspects of WCC habitat use are well understood. It has been established that WCC; require stable refuges to shelter from predation and high flows during daylight, avoid fast flowing areas, and locate in proximity to in-channel vegetation (*e.g.* Reynolds 1998; Benvenuto *et al*. 2008). However, the findings of habitat studies for WCC are often inconsistent. Inconsistencies are evident in the literature on many aspects of WCC habitat use, including: physio-chemical requirements and tolerances, the size of refuge they require, the favourability of exposed roots, preferred bank profiles and maximum tolerable flow velocities. Several authors have attempted to create models allowing prediction of WCC distribution from physical variables (*e.g.* Smith *et al.* 1996; Naura and Robinson, 1998). However, each model has different conclusions suggesting models are not generally applicable across river systems.

This inconsistency in habitat models for WCC may be due to the lack of knowledge on the influence of spatial context and study scale. Failure to account for these factors may lead to flawed conclusions about species-habitat relationships and erroneous conservation actions (Thorp *et al*. 2006). To the author's knowledge, no study has examined the influence of spatial context and position in the channel on distribution patterns of WCC. Therefore, this study aims to address these gaps in current knowledge in order to improve predictive models of WCC distribution and habitat use and identify the scale at which management efforts should be focussed.

This study is a field-based survey of WCC over 35 km of the River Wansbeck, Northumberland. The River Wansbeck has been regarded as a site of international importance due to the size and density of the WCC population it supports and the absence of non-native crayfish species (Rogers, 2005). It has therefore been recommended as a SAC for WCC (Rogers, 2005) but has not been designated. In this study, habitat heterogeneity at three spatial scales will be correlated to daytime distribution of WCC with the aim to determine the pattern of habitat use in this river and the scale at which WCC are responding to their environment. Location within the channel will be included as an explanatory variable to determine if lateral and longitudinal positions consistently influence distribution of WCC.

This research is performed in conjunction with the Northumberland Wildlife Trust, a charity which aims to 'rebuild biodiversity' (Royal Society of Wildlife Trusts, 2010). In order to maintain and enhance WCC distribution with limited resources, the Northumberland Wildlife Trust requires accurate information on current distribution and species-habitat correlations. It is hoped that the results of this study will be a valuable resource for future WCC conservation efforts by the Northumberland Wildlife Trust.

## 1.2 Aims and Objectives

The main aims of this research are three-fold:

1. To determine the day-time response to habitat variables by WCC on the River Wansbeck
2. To determine whether distribution of WCC is influenced by position in the channel
3. To determine the spatial scale at which WCC are responding to their habitat

In order to achieve these aims, the following questions need to be addressed:

1a) How are WCC distributed on the River Wansbeck?
1b) What range of habitat variables are WCC making use of in daylight hours?
1c) Which habitat types are WCC selecting and avoiding in daylight hours?

2a) Does the likelihood of WCC being present change with longitudinal and lateral position?
2b) What is the explanatory power of river position on probability of finding WCC, independent of habitat quality and availability?
2c) Are there predictable trends in occurrence of favourable habitat with distance downstream?

3a) Over what scale do WCC respond to heterogeneity in habitat variables?
3b) What scales of habitat heterogeneity influence distribution of WCC?

## 1.3 Thesis outline

The following chapters present the context, methodology, results and discussion of the research outlined above. Chapter 2 reviews concepts and ideas in conservation and spatial ecology applicable to this study. Chapter 3 reviews current knowledge on the threats and conservation status of WCC and considers their ecology and habitat preferences in the wider framework of riverine spatial ecology, as discussed in chapter 2. An overview of the physical environment of the River Wansbeck and the field methodology used to obtain results are described in chapter 4. The statistical analyses undertaken are also outlined. In chapter 5 the data obtained from the field survey is presented and analysed. Chapter 6 discusses the results in the context of previous work and conservation management. The main conclusions of the work are presented in chapter 7.

## Chapter 2- Review of concepts

This chapter briefly outlines why conservation of threatened species is a priority in today's society and why an increased knowledge of species distribution and habitat use is crucial. Within this chapter, ecological concepts and methods used to determine species-habitat relationships are reviewed. Further, the principles of spatial ecology, concerned with spatial factors and scale, are outlined. The relevance of these principles to river systems and their implications for conservation of river species are then examined.

### 2.1 Conservation and ecology

Globally, biodiversity is declining at an unprecedented rate due to human-induced pressures on ecosystems and climate change (Sala *et al.* 2000). In 2010, 33 % of all assessed species were at risk of extinction (IUCN, 2010). Biodiversity loss has a major negative impact both economically and for human well-being due to loss of species and habitats resulting in loss of ecosystem services (Costanza *et al.* 1997). Recognising this, the Convention on Biodiversity, in 2002, set a target 'to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level'. The most recent publication of this convention, the 'Global Biodiversity Outlook 3' (Secretariat of the Convention on Biological Diversity, 2010), states that this target has not been met. The 'Global Biodiversity Outlook 3' report presents the findings that most endangered species are at increasing risk of extinction, the global threats to biodiversity are increasing and there is a continued decline in the range and quality of natural habitats. However, this publication suggests that conservation efforts over the last decade have had a positive impact on reducing biodiversity loss and that with an increase in the level of effort and resources dedicated to conservation globally, there is reason to be optimistic that the situation can improve.

An integrated approach of social sciences, economics, resource management and physical and biological sciences is required to improve the effectiveness of conservation efforts. Ecological studies will need to be a key component of any conservation strategy as a complete knowledge of the distribution of a species and its response to environmental variables is vital for a species protection and management (Simberloff, 1988). This understanding allows efforts to be targeted to areas where they will be most effective, helps identify threats and agents of decline, guides development of captive breeding programmes and is necessary for identifying suitable areas for reintroductions (Smith *et al.* 1996).

### 2.2 Describing the response of a species to physical variables

### 2.2.1 Habitat niche

Every species is able to tolerate a range of physical conditions, beyond the limits of which it is unable to survive (Blackman, 1905). The combination of a species' tolerances to multiple variables produces a multi-dimensional environmental space in which the species can exist in the absence of competitors. This is termed the fundamental habitat niche (Hutchinson, 1978) (fig. 2.1). At the broadest scale, physiological tolerances limit the habitat niche and hence, the distribution of a species (Lodge and Hill, 1994). The physiological capacity of an individual to endure variation in variables such as, light, temperature, moisture and pH determine the breadth of conditions over which it can survive. Organisms may require certain elements above a critical level for survival. Conversely, high concentrations of other elements may preclude the organism from inhabiting a given area. Within areas of suitable physiochemical parameters, resource requirements limit the area in which a species can exist (Lodge and Hill, 1994). Together, physiochemical tolerances and resource requirements dictate the multi-dimensional fundamental niche for a species. If any one of the requirements for survival and reproduction is not met, a species cannot persist in that area.

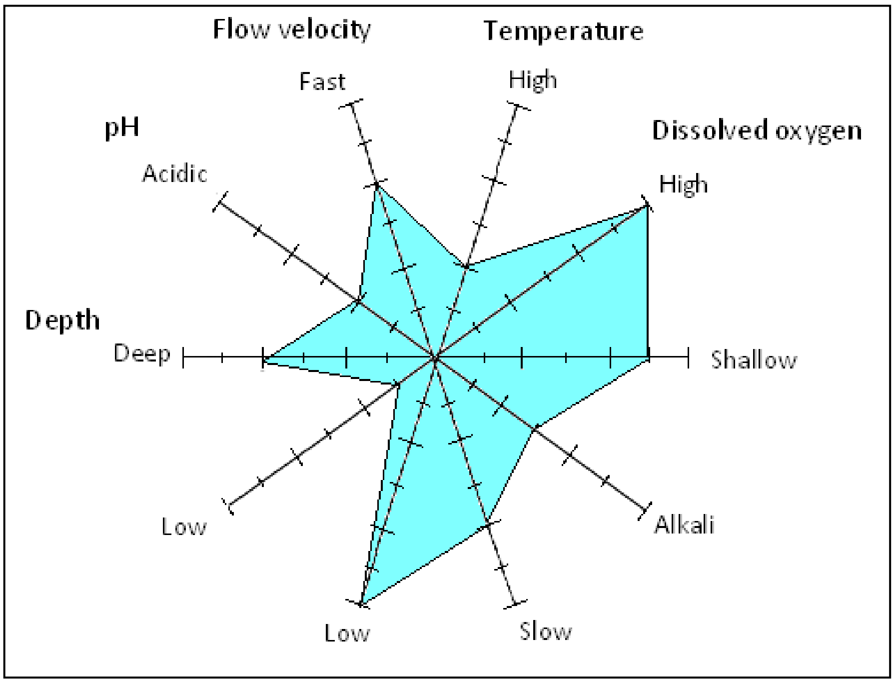

*Figure 2.1-An example of some of the key parameters of the fundamental niche space for a hypothetical aquatic species*

Understanding the fundamental niche of a species is vital for maintaining suitable habitat. Absolute physiological tolerance limits can only be precisely determined by controlled experiment but extensive study of the distribution of a species can define the range of conditions over which it occurs (Pearson and Dawkson, 2003). However, the conditions required for growth and reproduction, and hence the persistence of a population, are likely to be more specialised than the full range of conditions in which an individual can survive. Defining the range of conditions in which growth and reproduction occurs is more informative for conservation ecology (figure 2.2) (Shelford, 1913). To ensure conditions are favourable for reproduction, ecological studies need to be repeated throughout reproductive cycles or ensure there is evidence of breeding activity within the population. Biotic interactions and disturbances further restrict the area of the fundamental hyper-volume that is made use of (Hutchinson, 1978). Presence of predators and inter-specific competitors, particularly non-indigenous species, may preclude use of favourable physical areas due to the high mortality rates encountered in the presence of these pressures (Hutchinson, 1978). Thus, the actual areas over which a species is distributed is termed the realised niche and is the combined result of physiochemical tolerance, physical habitat requirements and biotic interactions (Lodge and Hill, 1994) (figure 2.3). The extent to which biotic interactions influence the distribution of a species varies spatially. Thus, transferring inferences of optimal habitat made in one system to other areas must be done with caution (*e.g.* Vanreusel *et al.* 2007).

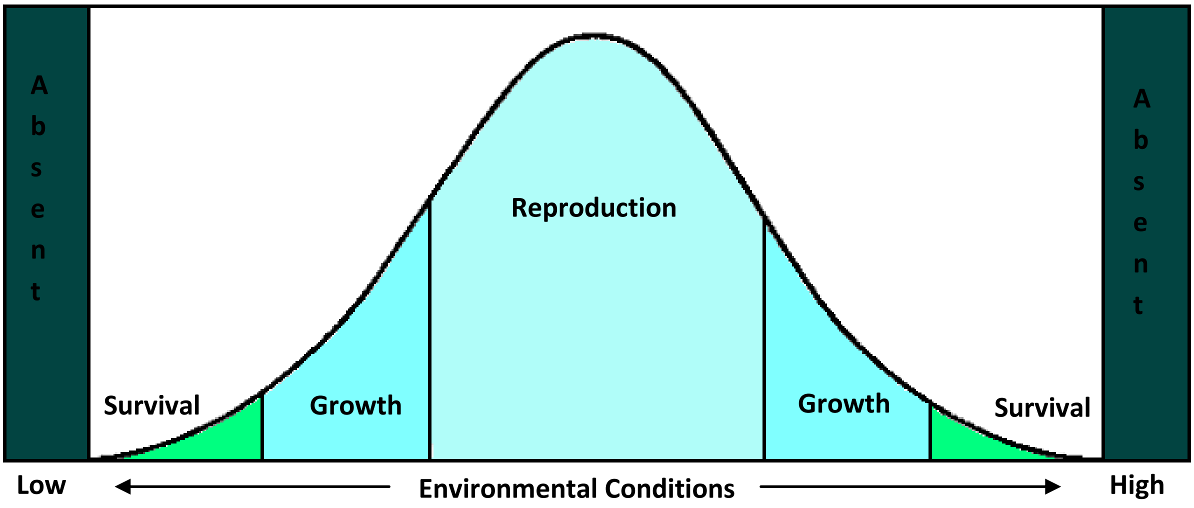

*Figure 2.2 – Idealised tolerance curve. A species can survive within a range of environmental conditions. Growth and reproduction will only occur in a subset of this range (redrawn from Smith and Smith, 2001)*

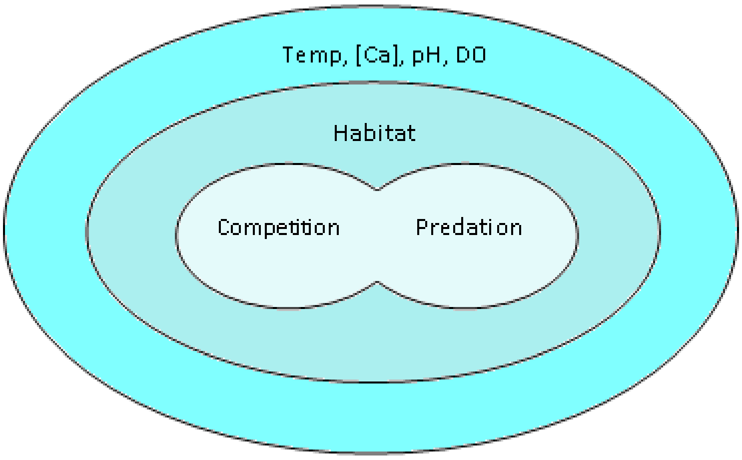

*Figure 2.3- Conceptual model of controls on the distribution of an animal species. Physiochemical parameters determine the large-scale areas in which the species can survive. Where physiochemical parameters are within a species' tolerated range, distribution is conditioned by refugia and food availability. Where these are limiting, populations experience competition and predation, which are interacting processes and ultimately determine population size (Lodge and Hill, 1994)*

Niche limits can be inferred from the range of conditions a species is found over. If certain habitat types are not made use of despite high availability, it is likely these are outside the niche space of the species. Krebs (1999) suggests that if a species is making use of less than 5 % of the available area of a given habitat type then that habitat type is outside the species' niche space. This gives a more conservative estimate of niche breadth than when considering complete absence and may be more informative for a single sample, as it accounts for biotic interactions or disturbance temporally forcing individuals into unfavourable habitat in which they could not persist for an extended time. This measure is therefore more likely to represent the niche space for growth and reproduction rather than just survival.

### 2.2.2 Habitat preferences

Within a species' realised niche, a subset of habitat types will give an individual the highest likelihood of surviving to reproductive age and maximise their production of viable offspring (Fretwell and Lucas, 1970). Thus, the fitness of an individual, defined as the 'genetic contribution by an individual's descendants to future generations' (Smith and Smith, 2001) is affected by the habitat in which it locates (Fretwell and Lucas, 1970). Mobile organisms will preferentially locate in areas with the conditions that result in the highest fitness gain (Cody, 1985). For conservation efforts, where the aim is to maintain viable populations, the combined response to habitat of whole populations is of interest (Pidgeon *et al.* 2006). To give the maximum gain to the focal population, conservation efforts should focus on the highest quality habitat, where the quality of a habitat type is a measure of the relative contribution to the next generation from individuals in that habitat type (Hall *et al.* 1997). Thus habitat quality is a measure of density of organisms that can persist in a given habitat type and the contribution they make to the next generation.

Active selection of high quality habitats often results in the majority of individuals using a more restricted range of conditions than that in which they could survive and reproduce. Thus, comparing the range of values of a given habitat variable within which the majority of a population is located to the total range of values available illustrates if the population is demonstrating a habitat preference (Hirzel, 2002) (fig 2.4). This measure is termed specialisation and illustrates whether the population is preferentially using a subset of the available range of a habitat variable (Hirzel, 2002). This may indicate niche limits but is also useful for identifying presence of habitat selection within a study area. Determination of the direction of habitat selection can be achieved by comparing the mean value of conditions used by a population and the mean value of conditions available. This measure is termed marginality (Hirzel, 2002) (fig. 2.4).

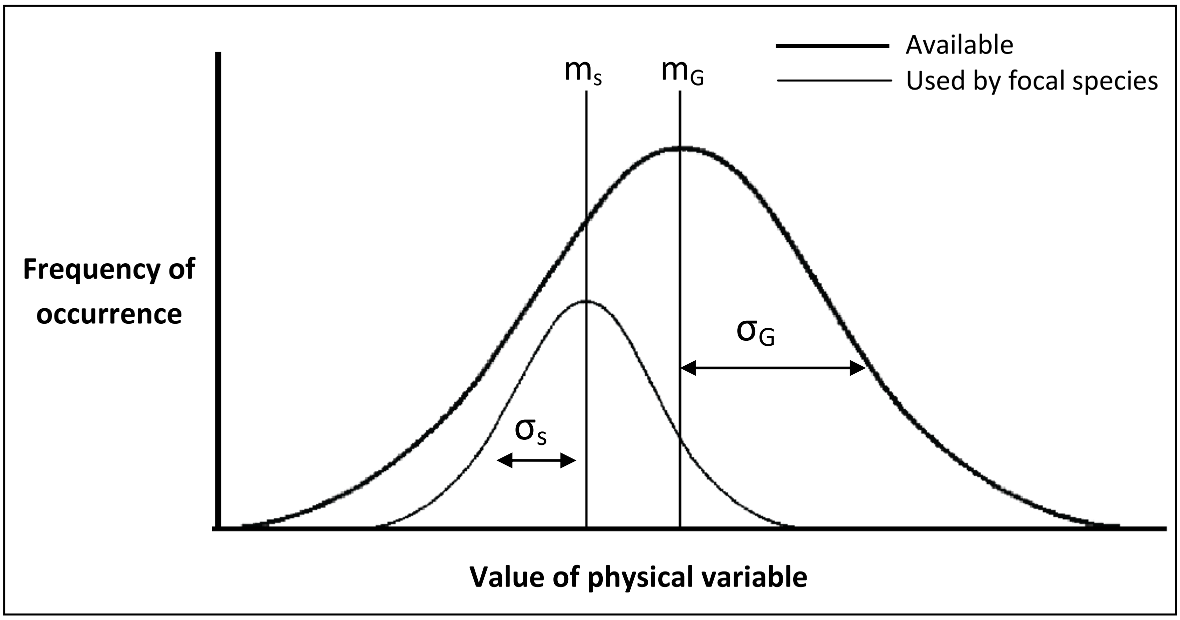

*Figure 2.4- Marginality and specialisation in distribution. Marginality is the difference between the mean value of all habitat variables ($m_G$) and the mean value of the habitat made use of by the population ($m_S$). Specialisation is the difference in the standard deviations of the used range ($\sigma_S$) and the available range ($\sigma_G$) (Redrawn from Hirzel, 2002)*

Because the distribution patterns of mobile species responding to habitat quality are a result of the distribution of heterogeneous physical variables, correlative approaches can be used to gain a detailed knowledge of habitat preferences (Johnson, 1980). There are three correlative methods for inferring habitat quality and hence habitat preferences of a species a) comparing use of different habitat types relative to their availability, b) correlating population density to habitat type and c) correlating condition of individuals to the physical variables of the area in which they are located (Johnson, 2007). The methods and advantages and disadvantages of each are briefly discussed below.

The first correlative method for inferring habitat quality compares use of habitat types to their availability and assumes that deviation from random use indicates selection or avoidance. Electivity index formulas consider relative use and availability of habitat types to output a numerical value, which can be interpreted as selection or avoidance of given habitat types (Jones, 2001). If a habitat type is used in excess of its availability it is assumed to have been selected due to its high quality (Jones, 2001). A wide variety of electivity indices have been developed, largely for studying selection of food types but can be applied to selection of habitat. The simplest index of selection is the forage ratio (Eq. 2.1) (Savage, 1931, in Krebs, 1999).

$$E_i = \frac{r_i}{p_i} \qquad \textit{(Eq. 2.1)}$$

Where $r_i$ is the proportion of habitat type *i* used by the individual (area of habitat type *i* used by the individual/total area of habitat type *i*), $p_i$ is the proportion of habitat type *i* in the whole study area (area of habitat type *i*/total area) and $E_i$ is the preference score and ranging from +1 to infinity for preferred items and 0 to 1 for avoided items. A value of 1 shows random use of habitat types.

Although widely used, this index is heavily influenced by the relative availability of different habitat types, particularly of the rarest habitat type. The maximum value the forage ratio can attain depends on the proportion of each habitat type available. This means deviation from random is not symmetrical for preference and avoidance and values obtained from different samples are not comparable (Lechowicz, 1982). Several authors have proposed variations on the forage ratio to overcome the dependence of the index on relative abundance of habitat types (Manly, 1971; Johnson, 1980). The most commonly used is Manly's α (Eq. 2.2) also referred to as Chesson's index and the standardized forage ratio.

$$\alpha_i = \frac{r_i}{p_i} / \sum \left(\frac{r_i}{p_i}\right) \qquad \textit{(Eq. 2.2)}$$

The value of α when habitat use is random is the reciprocal of the number of habitat types available. The index varies between 0 and +1 with values above *1/no. habitat types* showing selection and values below this value showing avoidance. Manly's alpha is recommended where there are large variations in the availability of habitat types, but the index is strongly affected by proportional use of rare resources (Krebs, 1999). In interpreting electivity index scores it must be recognised that selection also depends on the costs of finding and moving to given habitat types (Fretwell and Lucas, 1970) and accessibility of different habitat types to the focal organism (Jones, 2001). Further potential for inaccurate results with this correlative method occurs where a habitat type is extremely abundant and density-limiting biotic factors determine the maximum proportion of the habitat that can be made use of (Angermeier *et al.* 2002). To prevent erroneous conclusions being drawn, the adaptive significance of preferences should be considered when interpreting the outputs of selection indices (Jones, 2001).

Only recording presence in a given habitat type means proportional use indices can be skewed by 'false absences' where individual were present but undetected (Reese *et al.* 2005). Similarly, presence in a habitat does not necessarily demonstrate a preference, especially when sampling is only conducted once at each site. Individuals may be in transition between two areas of favourable habitat at the time of the survey or may have been forced into less favourable habitat due to disturbance or biotic interactions (Jones, 2001). These observations may be thought of as 'false positives'. These problems explain why the majority of preference studies use population density based methods to determine habitat preferences of a species (Johnson, 2007). Areas of high population density are assumed to have higher habitat quality, as more individuals are present to survive to maturity and produce viable offspring. Comparing average population density in different habitat types can therefore inform about a species' habitat preferences (Johnson, 2007). Failure to detect an individual is more likely in areas of low population density, thus 'false-absences' have less influence on results than when using proportional-use measures. However, whether population density accurately represents habitat quality depends on intra-specific competitive interactions. If individuals are not equal competitors, the despotic distribution model states that dominant individuals will monopolise high quality habitats forcing sub-dominants into sub-optimal habitat (Fretwell, 1972). Areas with lower fundamental habitat quality may support larger densities of individuals. Under these circumstances, population density will not accurately indicate habitat quality (Van-Horne, 1983). Prioritising habitats based on the density of individuals they support requires an understanding of the competitive interactions in the population.

The final method of assessing habitat quality considers the difference in condition of individuals residing in different habitat types. For this method to be informative the condition must be a consequence of the habitat *e.g.* due to lower food supply or increased predation risk (Johnson, 2007). Morphological indicators such as body mass are easier to assess than physiological indicators such as endocrinological signs of stress which require tissue samples. However, both methods are extremely time-consuming and are not suitable for assessing rapid changes in habitat conditions due to the lag time in response. Further, body condition may be the cause of differential habitat use. Habitat segregation may occur based on size or smaller individuals may be competitively inferior and thus forced into lower quality habitat. Thus, like measures of population density, this method requires knowledge of the competitive structure of the population (Johnson, 2007). The use of multiple indicators of habitat selection is recommended because conditions affecting survival, population density and reproduction may not be the same (Johnson, 2007). Obtaining consistent results from multiple approaches to defining habitat quality strengthens conclusions and reduces the effect of the weaknesses of each approach.

### 2.2.3 Predictive modelling

The findings from correlative approaches to habitat modelling can be used to produce empirical predictive models of habitat suitability. Using predictive models, rapid assessments of habitat suitability in unsurveyed areas can be made, allowing production of maps of potential habitat or predicted species distribution (Guisan and Zimmermann, 2000). Predictive models are increasingly being used as a conservation tool and have a number of useful applications. Firstly, predictive maps can be used to identify areas that require further survey resulting in optimal allocation of the limited resources conservation agencies have for field survey (Rodríguez *et al.* 2007). In areas where sampling is difficult or expensive, predicted habitat suitability may be the best substitute for field sampling (Rodríguez *et al.* 2007). The understanding of factors influencing a species distribution inherent in predictive models means they are capable of predicting impacts of land-use change or engineering. For endangered species, this understanding may aid in efforts to mitigate decline (Rushton *et al.* 2004). Perhaps the most useful application of predictive models to conservation efforts is identification of potential reintroduction sites and identification of areas of good habitat that should be conserved for future use (Engler *et al*. 2004; Angermeier *et al.* 2002). Predictive models can also be used to identify barriers to movement or areas that are unlikely to be colonised and predict the carrying capacity of an area. This permits a thorough evaluation of potential reintroductions (Rodríguez *et al.* 2007). Because empirical models do not describe cause and effect but only statistical correlates, the ecological relevance of model parameters of habitat models must be assessed before they are used to guide conservation measures (Guisan *et al.* 2000).

In order to be useful for the applications outlined above, a predictive model must perform well in areas other than that in which it was created. In creating a model, a trade-off is needed between the model being accurate and informative and being generally applicable across a range of locations (Guisan and Zimmerman, 2000). Overfitting the model to the data used to create it reduces the transferability of models between locations (Strauss and Biedermann, 2007). This is particularly problematic when the data set is small, and when conditions are present in new locations that were not present in the data set used to create the model (Vaughan and Ormerod, 2005). The species may have the potential to live in a wider range of habitats than those that were present in the test data. Therefore, models created in areas with a wide range of environmental conditions are likely to have the highest transferability (Angermeier *et al.* 2002).

Transferability of species-habitat models is likely to be higher for specialist species than for generalists and models will perform better in new areas that have similar landscapes and climatic regions to the area used to create the model (Angermeier *et al.* 2002).

The influence of biotic interactions on the distribution of a species varies spatially and therefore biotic interactions can reduce the generality of predictive habitat models (*e.g.* Vanreusel *et al.* 2007). These include differences in both intra and interspecific competitive interactions, differences in availability and types of food, differences in dispersal constraints, allee effects and differences in predation pressures. Anthropogenic effects and historical factors also vary spatially and may threaten the transferability of predictive habitat suitability models (Jiménez-Valverde *et al.* 2008). Few authors test the validity of their models in new locations. Generally applicable models have been created for fish species (*e.g.* Belaud *et al.* 1989) but most attempts do not transfer well between catchments (Leftwich and Angermeier, 1997).

### 2.3 Spatial ecology

Correlating spatial patterns of species distributions to environmental parameters in order to produce predictive models, as discussed above, is the premise of spatial ecology (Perry *et al.* 2002). Spatial ecology is a sub-discipline of ecology directly concerned with observed spatial patterns of ecological parameters and species (Perry *et al.* 2002). In spatial ecology, it is recognised that heterogeneity in physical variables is evident at multiple scales (Fortin *et al.* 2002) and therefore the pattern of distribution of a species and the observed response to physical variables is specific to a given scale (Bellier *et al.* 2007). Further, physical parameters may vary in consistent, identifiable patterns such as gradients or patches (Fortin *et al.* 2002) meaning the distribution of a species in an area may change in a predictable way with relative location in that area. Acknowledging the influence of location and scale in patterns of ecological variables is essential for gaining accurate understanding of species-habitat relationships and creating generally applicable habitat suitability models (Thorp *et al.* 2006).

### 2.4 Spatial ecology in river systems

River systems provide immense benefits to human communities and have potential to cause considerable damage to human developments. Therefore, river systems worldwide have been heavily exploited and altered, resulting in them experiencing rapid declines in biodiversity (Sala *et al.* 2000). Riverine species are therefore a global priority for conservation action. River systems possess certain key spatial characteristics that make concepts developed in spatially ecology particularly relevant to conservation efforts in these systems (Fausch *et al.* 2002). Firstly, river systems are hierarchically structured, meaning heterogeneity in physical variables occurs at multiple spatially nested scales. The pattern evident at each spatial scale is composed of interacting smaller scale components and is itself a component of a larger scale entity (O'Neill *et al.* 1989). This means variables operating at larger spatial scales constrain those at lower spatial scales (Frissell *et al.* 1986). Therefore, an integrated whole catchment approach is required for effective management of river systems (Thorp *et al.* 2006). Secondly, river systems are uniquely linear systems with unidirectional flow. At broad scales, there are consistent gradients in many hydrological and geomorphological features with distance downstream (Vannote *et al.* 1980). These characteristics and their implications for ecological studies and conservation management will be discussed in the following sections.

### 2.4.1 The hierarchical river system

The distinct hierarchy in physical variables in river systems is best conceptualised by the classification system of Frissell *et al.* (1986) (fig. 2.5). The entire network of surface water within a catchment makes up the broadest spatial scale, conditioned by large-scale variables of climate and geology. Controlling variables at this coarse scale usually change over geological time scales, for example climatic change, tectonic uplift or sea level change (Frissell *et al.* 1986). Within the catchment, the river network is composed of a number of stream segments 'portions of the stream flowing through a single bedrock type and bounded by tributary junctions, major waterfalls or abrupt transitions' (Frissell *et al.* 1986). A segment will have reasonably uniform slope, sediment and discharge patterns controlled by the drainage area, valley side slopes and position in the drainage network. Within a single segment, Frissell's (1986) hierarchy defines reaches as, 'lengths of stream segments lying between breaks in the channel slope, local side slopes, valley floor width and bank material', which range from ten metres to hundreds of metres depending on stream size. Within reaches of overall uniform bed material and flow velocity, pool and riffle systems are the next scale of heterogeneity. Pools are areas of deep, slow flowing water with finer sediment and riffles are the accumulation of coarse sediment producing shallower areas of faster flow (Richards, 1976). This scale of heterogeneity also includes cascades, rapids, runs, boils, glides and slack waters (Padmore, 1998). Pool and riffle systems are characterised by oscillations in bed topography and water velocity and are conditioned by the slope and sediment budget of the reach (Schuum and Lichty, 1965). The smallest hierarchical scale of heterogeneity recognised by Frissell *et al's* (1986) classification is microhabitat. Microhabitats are patches within pools or riffle that have homogenous substrate depth and velocity at the scale of centimetres to meters.

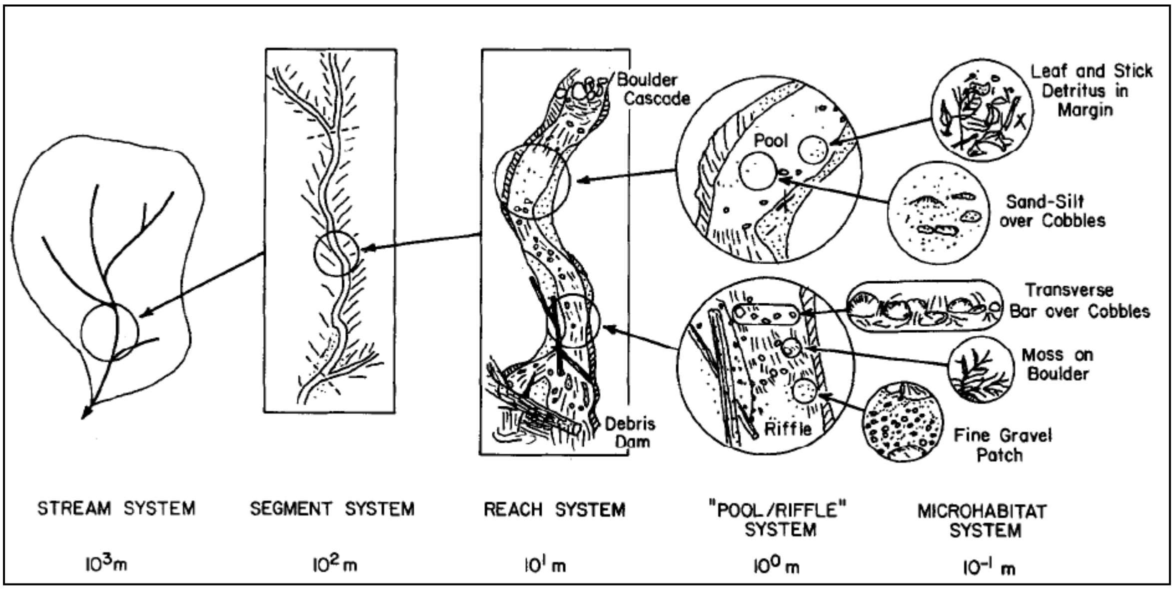

*Figure 2.5 - Hierarchical organisation of lotic systems. The spatial scales shown are average for a second or third order stream (Frissell et al. 1986)*

### 2.4.2 Implications of hierarchies for ecology and conservation

#### 2.4.2.1 The scale of active habitat selection

Individuals will respond to variation in habitat quality over a certain range of scales within the hierarchy depending on their perception of their environment (Kotliar and Wiens, 1990). The perception grain of an organism is the smallest scale at which it can differentiate between physical patch structure. At spatial scales finer than this grain, the organisms' behavioural and perceptual limits cause it to perceive the environment as homogenous and thus it no longer responds to variations in habitat quality (Kolasa, 1989). An organism's perception extent is the maximum range over which it interacts with its environment (Gustafson, 1998). Limits of perception depend on an organism's sensory capability, size, behaviour and mobility (Hildrew and Giller, 1994), and will differ between species and, to a lesser extent, between individuals within species due to size, age and behavioural differences (Wu and Loucks, 1995). It is vital to understand the scale at which a species is interacting with its environment so that management can be conducted at the relevant scale (Wiens *et al.* 1993; Fausch *et al.* 2002). Numerous studies have been performed to determine the scale of species-habitat relationships for riverine species. Robson and Chester (1999) conducted a two-tiered nested sampling design to determine the relative influence of pool-riffle scale and microhabitat scale physical variables on macro-invertebrate community structure. The results of this study indicated that microhabitat characteristics had a much more significant impact on macro-invertebrate community structure than riffle scale habitat. Similarly, Torgersen and Close (2004) sampled larval Pacific lamprey (*Lampetra tridentata*) over a 55km section of the Middle Fork John Day River, Oregon within 60 m sites and 1 m² quadrats, to determine whether the influence of habitat variables on larval abundance differed with spatial scale. Habitat variables were measured over the scale at which they showed variation (site or quadrat) *e.g.* depth, dominant substrate and velocity were measured in each quadrat whereas gradient, width, canopy closure, pH and temperature were measured once per site. Larval lamprey were mainly responding to variables operating at the microhabitat scale (Torgersen and Close, 2004). Fukushima (2001) found Sakhalin taimen (*Hucho perryi*), a Pacific salmonid, preferentially constructed redds (nests) in Japanese streams in highly sinuous areas when sinuousity was measured over 50 m but this correlation was not evident when sinuosity was measured over larger scales. This suggests Sakhalin taimen were only responding to variables operating over the local (50 m) scale. Conversely, increasing the scale over which variation in habitat variables was recorded from 50 m to 100 m to 200 m, increased the explanatory power of habitat on the distribution of Atlantic salmon parr (*Salmo salar*) within an 88 km stretch of the Sainte Margauerite River, Canada (Bouchard and Boisclair, 2008). Further, Hedger *et al.* (2006) demonstrated that measures of grain size in a 5 x 20 m area around juvenile Atlantic salmon had much greater explanatory power on their distribution than the grain size in the exact locality they were found. This suggests that juvenile Atlantic salmon, as mobile animals requiring multiple habitat types to complete their life cycle (*c.f.* Schlosser, 1991), respond to habitat suitability at a broader scale than that of the microhabitat. The variability of results of studies into the scale of responses of riverine species to physical variables demonstrates that identifying the appropriate scale to measure species-habitat relationships is complicated (Gido *et al.* 2006).

The perception grain and extent of an individual may encompass several scales within the hierarchy of habitat heterogeneity (Levin, 1992). Where an individual is capable of perceiving and responding to multiple scales of habitat heterogeneity, habitat will be selected at sequentially smaller hierarchical scales (Wiens, 1985). This has been shown for a variety of bird species (*e.g.* Barbaro *et al.* 2008) with individuals selecting broad scale habitat areas based on food availability and specific roosts within these area based on breeding requirements (Martinez and Zuberogoitia, 2004). Evidently, the scale of response to habitat heterogeneity is highly variable between species and locations. Identifying the scale of response to habitat is necessary to ensure habitat based conservation measures are relevant to the focal organism.

#### 2.4.2.2 Hierarchical filters

The scales of physical heterogeneity beyond the limits of an organism's perception are not irrelevant, despite the fact that individuals will be unable to respond to them directly (Wiens, 1985). In hierarchical systems, patterns and processes at coarse scales condition those occurring at smaller scales (Wiens, 1985). For a particular location to be suitable for a species, with values of all physical variables within the species' fundamental niche space, all broader scale constraints must also be suitable. This idea was formalized in Poff's 'landscape filter' model (1997) which says habitat selection is 'a sequence in which every category is included in the detail of the previous one' (Hilden, 1965) (fig 2.6). To occur at a given locale, a species must pass through broader scale filters. For example, although macro-invertebrates are unlikely to respond directly to catchment geology or land-use, these broad scale factors correlate to macro-invertebrate assemblage structure due to the fact they condition flow velocity and substrate at the microhabitat scale, which macro-invertebrates do respond to (Richards *et al.* 1996; Robson and Chester, 1999). The process of broad scale filters precluding use of certain areas can be thought of as passive habitat selection. Patterns of distribution are the result of the collective influence of all scales in the hierarchy (Torgersen and Close, 2004) and it is difficult to separate the relative influence of habitat heterogeneity at different scales on the distribution of a species (Gido *et al.* 2006). The linkages across hierarchical levels and constraints of broad scale processes on small-scale habitat features are not well-understood (Poff, 1997) but appreciation of the influence of all scales in the hierarchy is necessary for effective habitat management and creation.

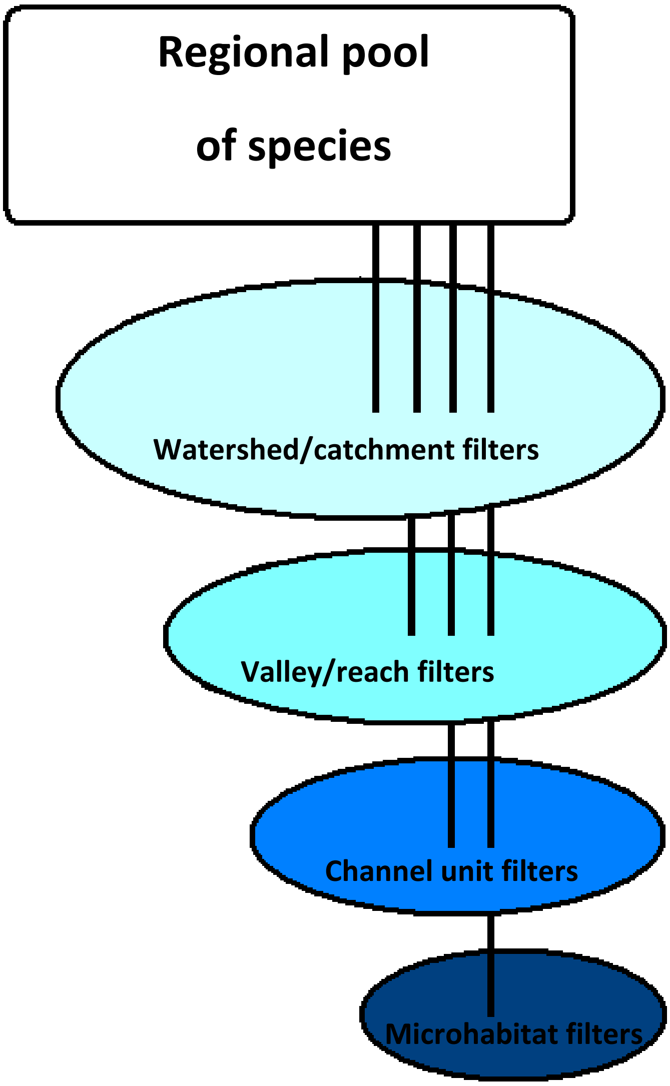

*Figure 2.6- Poff's (1997) landscape filter model*

### 2.4.3 Downstream trends

Rivers are unique linear systems with unidirectional flow. At broad scales, there are consistent trends in many hydrological and geomorphological features with distance downstream (Vannote *et al.* 1980). Altitude and slope decrease from source to mouth, discharge increases with the addition of water from more of the catchment and width and depth increase to accommodate increased discharge (Vannote *et al.* 1980). Traditionally, a downstream fining of grain size has also been asserted (*e.g.* Leopold, 1953) with a trend from boulders and large cobbles in headwaters to gravel and sands in lowland channels, because of selective transport and abrasion during transport. Recently, Petts *et al.* (2000), confirmed particle size decreased and heterogeneity of grain sizes increased with distance downstream although the scientific community now acknowledge that downstream fining is an oversimplified model (*e.g.* Rice and Church, 1996; Rice, 1998). Many authors have suggested predictable downstream trends in biological processes and community structure, as a response to these linear trends in physical variables. The River Continuum Concept (RCC) (Vannote *et al.* 1980) was the first model to explicitly detail a continuous downstream gradient of physical variables (depth, width, slope, velocity, discharge, temperature and entropy gain) and postulate the influence these gradients had on biological processes. The RCC recognises that the significance of autochthonous production varies with distance downstream. Photosynthesis is low in heavily shaded uplands, increases in the middle reaches of a river, because width increases more rapidly than depth with longitudinal distance resulting in greater light penetration, and decreases in large lowland channels due to depth and turbidity (Rice, 2001). The RCC proposes that in response to this, macro-invertebrate community structure, trait representation and biodiversity vary in a continuous gradient downstream such that stream order (*c.f.* Horton, 1945) is an accurate predictor of system characteristics. Work on the Salmon River, Idaho by Minshall *et al.* (1982) and Bruns *et al.* (1984) supported the claims of the RCC for macro-invertebrate functional feeding groups. Similarly, Culp and Davies (1982) showed a longitudinal zonation of macro-invertebrate communities in the Saskatchewan River, Canada with downstream changes in dominance of functional feeding guilds in agreement with the RCC.

Differences in physical variables in a longitudinal gradient may result in the probability of occurrence of a species changing with position within the channel due to changes in availability of habitat (Thorp *et al.*, 2006). For example, distribution and diversity of a variety of riverine fish species has been shown to vary with depth (Sheldon, 1968). Deeper areas become more common with distance downstream producing a longitudinal trend in species assemblage of fish (Sheldon, 1968; and Hocutt and Stauffer, 1975). Similarly, river channels exhibit largely predictable lateral gradations with channel margins generally having higher shade coverage, more backwaters, higher vegetation coverage and increased riparian debris than mid channel areas (Ward, 1989).

Torgersen and Close (2004) found abundance of larval lamprey to be significantly higher in channel margins than mid-channel.

However, the source to mouth gradients postulated by the RCC are disrupted by the presence of discontinuities such as tributary junctions (Benda *et al.* 2004), geological discontinuities, land use change and lakes (Sedell *et al.* 1989). These factors are system specific and result in disruption of predictable downstream changes (Statzner and Higler, 1985). For example, modified catchments may rapidly vary between open pasture and wooded river banks in an unpredictable downstream pattern. This will result in reach or multi-reach scale discontinuities in shading, allochthonous input and runoff characteristics and hence disruptions in patterns of species distribution. Similarly, catchment specific variability in soil type, geology, relief and basin shape will result in variable runoff patterns with distance downstream and modification of longitudinal trends in hydrology and habitat (Minshall *et al.* 1982).

Tributary confluences are a major disruption to longitudinal trends in river systems. Tributaries input large volumes of water and sediment that can be characteristically distinct from that of the main channel. Not all tributaries will influence the characteristics of the main channel. The magnitude and characteristics of the water and sediment added determine which characteristics of the main river are altered and the extent to which they are changed (Rice, 1998). This is dependent on the size, land-use, lithology and geomorphology of the tributary's sub-basin (Rice, 1998). Influential confluences often cause adjustments in slope, depth, width, flow velocity, shear stress and riparian shade cover of the main channel (Naiman *et al.* 1987; Rice, 1998) resulting in marked discontinuities in downstream trends (Rice, 1998). Inputs of coarse sediment produce step-changes in mean substrate size, substrate heterogeneity and substrate angularity (fig 2.7) (Rice, 2001). If there is sufficient distance between adjacent significant tributaries a fining trend may be seen due to sorting, and possibly abrasion (Rice, 1998). The resultant pattern in substrate size is a saw-tooth of gradual fining punctuated by sudden increases in grain sizes (fig 2.7) (Rice, 2001). Each length of downstream fining, separated by abrupt discontinuities in grain size, is termed a sedimentary link.

Many of the variables influenced by confluences are responded to by riverine species and thus the arrangement of tributaries is likely to be an important control on the longitudinal distribution of populations. Studies have shown tributary confluences to result in discontinuities in community structure of benthic fauna (Illies, 1953; in Rice, 2001; Bruns *et al.* 1984) and fish (Osbourne and Wiley, 1992). For lithophilous species, the largest impact of tributaries on habitat quality and availability is likely to be the change in grain size. Thus, there is likely to be greater availability of habitat for lithophilous species immediately downstream of confluences where larger refuges are more abundant and refuges are more angular and thus more stable in high flows. The influence of the sedimentary link structure on grain size in the St. Marguerite River, Canada, was strong enough to result in a predictable spatial pattern in presence of grains suitable for salmon spawning. Hence, Davey and Lapointe (2007) were able to predict the distribution of Atlantic salmon (*Salmo salar*) spawning sites from the position of tributaries in this low gradient gravel-bed river.

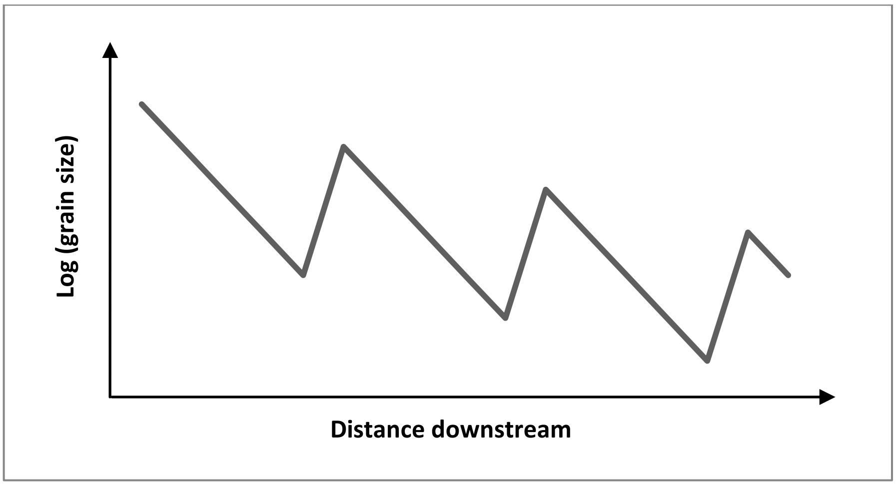

*Figure 2.7- Stylised trend in grain size with distance downstream. An overall fining trend is punctuated by inputs of coarser material where significant tributaries enter the channel. Fining occurs between adjacent confluences forming sedimentary link. Redrawn from Rice et al. (2001)*

Most habitat variables, including depth, substrate size, flow velocity and food availability are heterogeneous at multiple scales (Frissell *et al.* 1986). The continuous downstream trends discussed above are often evident at the catchment scale. At intermediate scales discontinuities such as lakes, land-use modifications and tributaries result in inconsistent downstream patterns. When the system is viewed at this segment scale, predictable longitudinal gradients may be evident but discontinuities cause these to be zonal rather than clinal (Ward, 1992). At the microhabitat scale parameters vary as seemingly stochastic patchiness (Rice, 2001) (fig 2.8). Duncan and Kubecka (1996) demonstrated, using acoustic echo integration, that the longitudinal density of fish in the River Thames is patchy at multiple scales. If organisms respond to habitat at the microhabitat scale there is unlikely to be predictable downstream trends (Wiens, 1989). Naiman *et al.* (1987) found no pattern in benthic macro-invertebrate richness or diversity with distance downstream and concluded the community was influenced by microhabitat and local-scale factors that were highly heterogeneous. Differences in the scale of response and the scale at which lateral and longitudinal gradients are evident is also likely to account for the lack of influence of spatial position on distribution of Atlantic salmon parr in a study by Bouchard and Bosclair (2008). The explanatory power of eighteen variables accounting for spatial position, both as an absolute measure within the system and as a relative distance to other habitat types such as thermal refugia, spawning sites, over-wintering habitat and tributary junctions was low compared to that of local scale habitat variables.

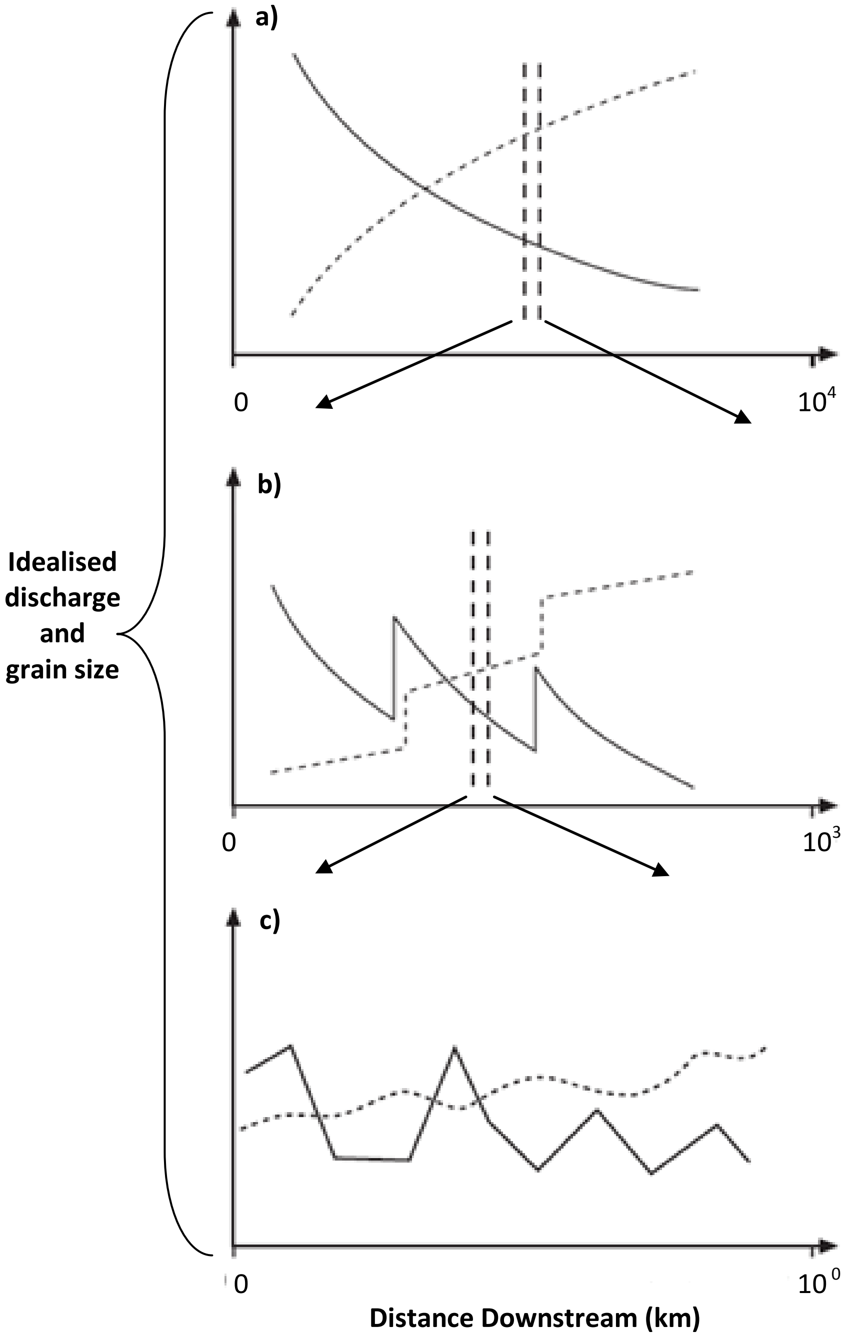

*Figure 2.8- Idealised downstream changes in discharge (dashed line) and grain size (solid line) viewed at the spatial scales of a) the entire drainage basin b) a river segment and c) pools and riffles within a link. Vertical dashed lines show a snapshot area expanded in the next graph. Patterns of longitudinal variation in grain size and discharge change with the scale of observation (Rice et al. 2001)*

Downstream trends may be a response to neither continuous nor discontinuous changes in physical parameters but may reflect the 'spatial context of biological factors' (Rice, 2001), such that locational variables are a seemingly independent predictor of distribution (Torgersen and Close, 2004). Variability in community composition, predators and competitors are examples of these factors and are likely to be system specific. Historic distribution and dispersal ability will also determine the area over which a species is currently located. Barriers to connectivity of movement may preclude use of otherwise favourable areas (Fahrig and Merriam, 1985). Analysis of locational variables is necessary to highlight system complexities.

It is important for managers to understand whether likelihood of a species being present, or the habitat types selected by that species, vary with position within the channel in order to target conservation efforts with limited resources (Torgersen and Close, 2004). It is therefore useful to study the influence of spatial factors on distribution of species of conservation priority to inform future conservation efforts.

### 2.4.4 Sampling techniques to account for hierarchical, longitudinal systems

Traditionally, studies of species-habitat relationships have been conducted over short lengths of river at a single scale, generally that which is most easily conceptualised and most convenient for the surveyor, rather than that which is relevant to the organism (Wu and Qi, 2000; Fausch *et al.* 2002). Wheatley and Johnson (2009) reviewed 79 peer-reviewed papers which considered species-habitat relationships at multiple scales. Seventy percent of these papers made observations at arbitrary scales with no biological relevance. The hierarchical nature of river systems is rarely acknowledged when presenting results; surveyors fail to recognise that presence within the sample site already indicates a passive or active selection of physical variables that show variation at the site scale (Wu and Loucks, 1995). Single scale studies over short reaches are therefore likely to miss key influences on species distribution patterns because species distribution may be a response to habitat heterogeneity at scales of the hierarchy that are not perceived by the surveyor (Orians and Wittenberger, 1991). The potential to miss influences on distribution with traditional sampling designs was demonstrated by a multi-scale study of Bull charr (*Salvelinus confluentus*) distribution in a Montana mountain river. Bull charr were found to be preferentially constructing redds in low-gradient bounded alluvial valley segments (BAVS) where thermal conditions for egg incubation were favourable due to upwelling groundwater. BAVS occurred at intervals of 5-10km down the channel and thus this association between Bull char distribution and physical conditions would not have been detected by traditional sampling over short reaches (Baxter and Hauer, 2000).

Another problem with single scale studies is that the scale chosen for study determines the conclusions drawn on the distribution of species and availability of habitat (Kotliar and Wiens, 1990). In a survey performed over a 55 km section of the Middle Fork John Day River, Oregon larval lamprey were present in 93% of 60 m sampling sites but quadrat scale distribution was highly heterogeneous (Torgersen and Close, 2004). Thus, conclusions drawn on the frequency of occurrence of suitable habitat would have been different at different scales of observation. This is formally known as the Modifiable areal unit problem (MAUP). The MAUP recognises that arbitrarily selected scales of study produce scale specific and arbitrary results preventing complete understanding of ecosystem functioning (Openshaw, 1983), which could result in inappropriate conservation actions (Talley, 2007). The problem was neatly summarised by Wiens (1999) 'We can no longer…cling to the belief that the scale on which we view systems does not affect what we see'. The ecological community needs to understand and appreciate the MAUP in order to produce relevant results appropriate for conservation decisions (Jelinski and Wu, 1996).

Nested sampling is a rapid, cost-effective method to sample hierarchical systems at multiple scales over long lengths of the river. In nested sampling, the total sampling area is divided into primary sampling units which are sub divided into secondary sampling units, which are further subdivided into tertiary sampling units (Bellehumeur and Legendre, 1998) (fig 2.9). At each sampling scale, habitat variables that show variation over that scale are analysed. This design integrates fine-scale variability with the broad-scale processes that condition it (Hewitt *et al.* 2002). Nested sampling can prevent scale-specific results but has not been widely used in lotic systems (Cooper *et al.* 1997). The collection of multiple samples within each site increases both the ability to discern habitat suitability and the reproducibility of the results (Southwood and Henderson, 2000). Further, because detailed fine scaled analyses are conducted within larger primary sampling units, a long length of river can be surveyed in a realistic time span. Nested sampling is therefore suitable for discerning longitudinal changes in habitat availability, species distribution and habitat use (Armitage and Cannan, 1998). The notion that physical variables and community structure have corresponding spatial hierarchies in rivers (Frissell *et al.* 1986) allows nested sampling designs to utilise watershed, reach, biotope and microhabitat scales (fig 2.9).

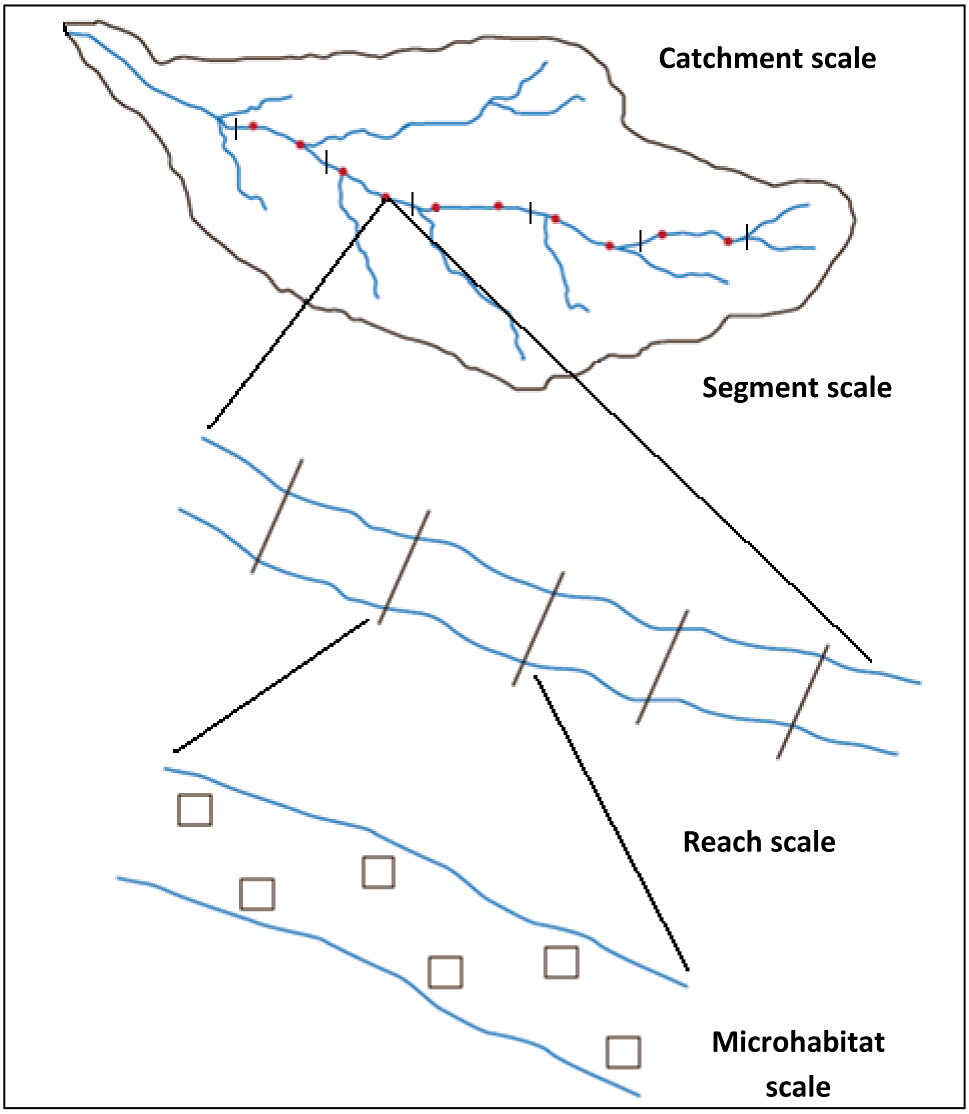

*Figure 2.9- Nested sampling design. Sampling is carried out in progressively smaller scale units nested within larger spatial units (adapted from Peay, 2003)*

Many authors have shown nested sampling to increase explanatory power of habitat models (Hewitt *et al.* 2002) without increasing sampling density and field work (Thrush *et al.* 2000). A multi-scale nested study of fish densities in Hungarian rivers demonstrated the improvement in predictive ability gained by considering multiple scales (Poizat and Pont, 1996). Point abundances of fish, found by electro-fishing, were related to habitat variability at three spatial scales. The largest scale considered was the difference between the main channel and 'dyked side channels'; areas partially enclosed by an artificial embankment. Within each of the channel types the same five bank types were present. Within each of the bank types, in both main and dyked channels, microhabitat variables of bank slope, depth, substratum, current velocity, turbidity, shelter, filamentous algae cover and shade were measured. Microhabitat variables alone accounted for only 23% of total variation in fish distribution and when considered in isolation resulted in incorrect associations between species distribution and habitat variables. Including multiple scales improved the ability to predict fish densities by 21% (Poizat and Pont, 1996).

### 2.5 Combining riverine spatial ecology concepts with predictive modelling

In recent decades the need to communicate effectively about rivers, compare sites and predict how a river system will respond to perturbation or management, has increased (Newson *et al.* 1998a). In response to the need for a holistic, objective and statistically robust method of characterizing rivers, the River Habitat Survey (RHS) was developed (Raven *et al.* 2000). The RHS involves recording features in the channel, marginal area, bank and a 50 m riparian corridor along a 500 m site (Newson *et al.* 1998b). Ten spot checks are performed per 500 m site to eliminate the subjectivity inherent in trying to estimate percentage abundance of cover of different habitat types. At each spot check variables such as substrate type, aquatic vegetation, depth and complexity of bank vegetation are recorded (Raven *et al.* 1997). To capture rare features or those which occur between spot check locations, a 'sweep up' survey is also performed. The 'sweep up' records information such as flow type boundaries, bankfull and water width, valley form, adjacent land use, planform, extent of channel shading, extent of vegetation types. It is necessary to estimate the percentage cover of certain features but to reduce inaccuracy, a simple three point scale; absent, present (<33%) and extensive (>33%), is used (Raven *et al.* 1997).

The RHS provides a standardized and efficient method of characterising lotic systems. Many of the variables recorded in the RHS are ecologically relevant (Jeffers, 1998), thus RHS criteria can be made use of in habitat studies to make results comparable and reproducible. Further, the distribution of species can be predicted from RHS criteria if the species habitat requirements are understood (*e.g.* Naura and Robinson 1998; Buckton and Ormerod, 1997). Buckton and Ormerod (1997) used correlative approaches to determine which variables recorded in the RHS influence the likelihood of presence of five species of riverine birds (dipper *Cinclus cinclus*, grey wagtail *Motacilla cinerea*, common sandpiper *Actitis hypoleucos*, goosander *Mergus merganser* and mallard *Anas platyrhynchos*) at 74 upland river sites. The results of this study showed the RHS to be a useful tool for predicting distribution of these species. Similarly, Naura and Robinson (1998) created a predictive model for WCC distribution using RHS criteria.

An analogous predictive modelling technique is that of HABSCORE. HABSCORE is an established method of assessing habitat suitability for riverine species, particularly game fish. To conduct HABSCORE, a surveyor visually assesses a variety of criteria and scores them as optimal, sub-optimal, marginal or poor for biota. These criteria include: biotope variability, embeddedness of substrate, bank stability, sediment deposition, riparian vegetation, channel alteration and availability of refuges (Parsons *et al.* 2002). The total score gained for each site is compared to an optimal reference condition to determine suitability for a species.

Both RHS and HABSCORE record the average conditions over a 500 m stretch of river. This single-scale data is unlikely to correspond to the scale at which riverine species are responding to habitat variables and is subject to missing variables that influence species distribution. Failure to consider all spatial scales relevant to the focal species is likely to weaken the predictive power and transferability of habitat suitability models based on RHS data (Guisan and Thuiller, 2005). Broad scale RHS cannot be extrapolated to finer scales because different processes are prevail at finer scales (Thrush *et al.* 1997a; Guisan and Thuiller, 2005). Thus, to improve predictive power of habitat suitability modelling from RHS data observations from all scales relevant to the focal species need to be incorporated (Leftwich and Angermeier, 1997). RHS criteria could be adapted into a nested sampling design to produce findings on species-habitat relationships that are not scale specific.

# Chapter 3- Overview of current knowledge of the white clawed crayfish

In this chapter the ecology and life history of the white clawed crayfish is outlined. The threats to the continued survival of the species and the current conservation actions and legislations aimed at preventing it from extinction are discussed. Literature on habitat requirements and preferences of the white clawed crayfish is reviewed with the aim of identifying gaps in current knowledge and areas of debate. Finally, the need for application of principles of spatial ecology to conservation of white clawed crayfish is established.

## 3.1 Introduction to white clawed crayfish

### 3.1.1 Classification and distribution

White clawed crayfish are freshwater crustaceans of the order Decapoda and family Astacidae. The range of the WCC extends from 56 ˚N in Britain to 38˚S in Spain and from 8˚W in Ireland to 16˚E in the former Yugoslavia (Laurent, 1988). They are the only species of crayfish native to Britain (Holdich and Lowery, 1988). WCC are typically a benthic, lithophilous species and can inhabit both lotic and lentic freshwater environments. Populations are found throughout England and Wales, confined to areas of base-rich substrate due to their requirement of calcium to harden their exoskeleton (Holdich, 1991).

### 3.1.2 Anatomy and life cycle

White clawed crayfish are the largest mobile, native freshwater invertebrate in the U.K., reaching lengths up to 12 cm (Reynolds, 1998). Crayfish have a segmented typical arthropod body plan, composed of the cephalothorax and abdomen, covered by a protective calcified exoskeleton known as the carapace (Groves, 1985) (fig. 3.1). The most anterior of their five pairs of perepods (*i.e.* legs) supports enlarged 'claws', termed chelae, which are used for manipulating food, in aggressive display and in mating by males (Mason, 1974). The other four pairs are walking legs used for movement across substrate. They can also make rapid backward movements through the water column using their tail fan (Mason, 1974) (fig. 3.1). Crayfish have two ocular peduncles for vision and sensory antennae for touch, smell and taste (Groves, 1985). At a species level, WCC are identifiable by their whitish ventral side compared to their brown body (Goddard and Hogger, 1986); the presence of spikes along the cervical grove and the single post-orbital ridge behind each eye, terminating in a spine (Freshwater Invertebrate Survey of Suffolk, 2010).

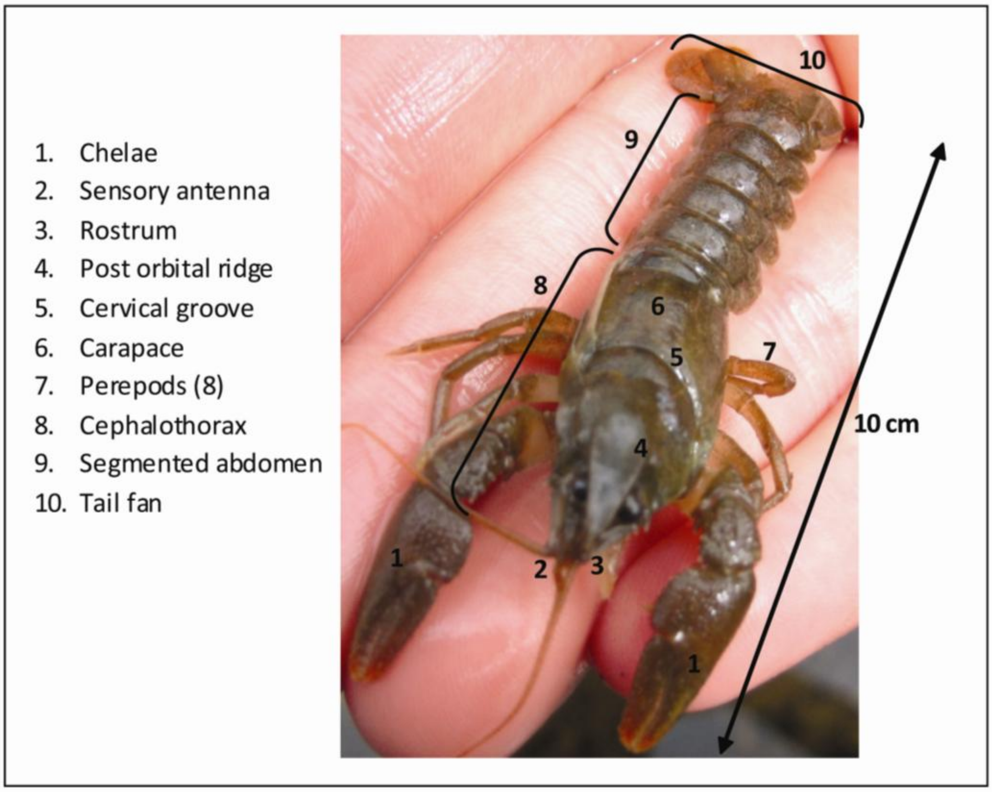

*Figure 3.1- Basic external anatomy of an adult white clawed crayfish*

The lifespan of WCC can exceed 10 years (Brewis and Bowler, 1982) with sexual maturity occurring in Britain at three to four years, dependent on local environmental conditions with some variability between populations (Reynolds, 1998). Brewis and Bowler (1982; 1985) found females reach sexual maturity between 22 and 27 mm carapace length (CL) and males can reach sexual maturity at even smaller sizes (Brown and Bowler, 1977; Thomas and Ingle, 1987). Natural England use a guideline figure of 25 mm for both males and females (Peay, 2000). After sexual maturity is reached, moult frequency varies between the sexes leading to sexual dimorphism. Males moult more frequently and grow faster than females and have proportionally larger chelae (Reynolds, 2002).

White clawed crayfish are poikilothermic and their annual cycle of growth and reproduction is conditioned by seasonal changes in temperature and day-length (Brown and Bowler, 1977). When water temperatures drop below 10˚C, usually in October or November but variable between rivers, males establish and aggressively defend territories to compete for mates. Reynolds (2002) examination of male WCC vas deferens suggested that some males copulate with multiple females and some males do not mate at all. This indicates a dominance hierarchy is present in WCC mating (Reynolds, 2002). Males fertilise eggs by the transfer of a spermatophore by the gonads onto the underside of the female (Reynolds, 1998). Six days after fertilisation, the female lays eggs into a viscous matter called glair, which then attaches to the underside of her abdomen (Brown and Bowler, 1977). The average number of eggs is between sixty and eighty but is dependent on the size of the female (Reynolds *et al.* 1992). The female carries the egg clutch beneath her tail for seven to ten months and in this state is described as ‘berried’. This is an iteroparous reproductive strategy, since it is repeated over a number of years, with high investment in relatively few eggs (Holdich and Lowery, 1988). Whilst berried, females are relatively inactive and migrate to deep waters to incubate the eggs. Eggs hatch on the female between late June and August depending on water temperature (Hogger, 1988). Hatching is likely to occur later in Northern or upland populations due to lower temperatures (Brewis and Bowler, 1985). The young remain attached to the female for one to two weeks before they become independent, leaving the female entirely by their third moult (Lowery, 1988). After the release of young, activity rates by females are much higher as they forage to increase resources ready for fertilisation (Mason, 1974).

In order to grow, WCC moult their calcareous exoskeleton. Absorption of calcium from the water is necessary to harden the new exoskeleton, restricting WCC to calcium rich rivers (Lowery, 1988). Young of the year have rapid growth rates moulting seven or eight times within the first year (Holdich and Lowery, 1988). The number of moults decreases each year until, at sexual maturity (3 to 4 years) adult females moult once per year in August and adult males moult twice per year when water temperatures exceed 10˚C, usually in July and September (Pratten, 1980). Loss of the protective exoskeleton makes crayfish susceptible to predation and cannibalism during moult (Brewis and Bowler, 1982). A strong tendency to synchronise moulting is demonstrated by WCC, which is thought to be an adaptation to reduce susceptibility predation and cannibalism (Lowery, 1988).

### 3.1.3 Diet and role in the ecosystem

The WCC is an omnivorous forager with a diverse diet including worms, insect larvae, snails, small fish (Reynolds, 1979), a wide variety of aquatic plants and detrital material (Mason, 1974). Foraging activity largely occurs nocturnally when risk of predation is lower (Gheradi, 2002). Juveniles are more carnivorous than adults are, preferentially feeding on nymphs and larvae (Reynolds, 1998). This is due to their requirement for protein to increase growth rates in order to decrease the length of time during which they are vulnerable to cannibalism and gape limited fish predators (Reynolds, 1998). Analysis of WCC gut contents reveals them to be opportunistic feeders (Gheradi *et al.* 2004). Detritus is consumed in the highest proportion in autumn when leaf litter is abundant and insects are consumed in the highest proportion in spring (Gheradi *et al.* 2004).

The range of food sources used by freshwater crayfish means they cannot be assigned to a trophic level, instead filling multiple trophic roles (Momot *et al.* 1978). This polytrophic position of WCC in freshwater food webs means they can contribute significantly to energy flow in freshwater systems (Momot *et al.* 1978) and have strong impacts on aquatic community dynamics. By grazing on macrophytes WCC reduce excessive weed growth (Goddard and Hogger, 1986) and influence the assemblage of benthic invertebrates (Nyström and Strand, 1996). Their ability to ingest detrital material, such as wood and leaves, and convert it into fine particulate organic matter means WCC significantly increase community productivity (Momot *et al.* 1978) and slow eutrophication rates (Hogger, 1984). White clawed crayfish also provide a prey source for species of economical and conservation importance, such as trout (*Salmo trutta*), pike (*Esox spp.*), perch (*Perca fluviatilis*), kingfishers (*Alcedo atthis*) and otters (*Lutra lutra*) (Smith *et al.* 1996). Inter-specific competition occurs between WCC and other fish species for food and refuges, such as bullheads (*Cothus gobio*) (Bubb *et al*. 2009). The importance of crayfish in influencing community structure and ecosystem functioning is disproportionate to their biomass making them key species in aquatic systems (Hogger, 1988).

Crayfish are also ‘ecosystem engineers’ due to their alteration of physical habitats by bioturbation of fine substrates (Statzner *et al.* 2000). Most notably, the walking motion of crayfish reduces sand content among gravels, which increases the survival of salmonid eggs (Statzner *et al.* 2000) and increases the abundance of macro-invertebrates reliant on interstitial spaces (Brown and Lawson, 2010). Overall, native crayfish have an important role in structuring riverine communities and a positive impact on river ecosystem health and biodiversity (Englund and Krupa, 2000). Conservation of WCC will bring wider ecological and economical benefits.

### 3.2 Threats to the white clawed crayfish

Despite recognition of the importance of WCC, the species has declined rapidly over the last three decades in England and Wales (Sibley, 2003). At the current rate of decline, WCC will be extinct in mainland Britain by 2030 (Sibley *et al.* 2002). The main cause of this decline has been the introduction of non-indigenous signal crayfish (*Pacifastacus leniusculus*) (Smith *et al.* 1996). North American signal crayfish were introduced to Britain in the 1970s to be commercially farmed for food but escaped into natural river courses (Holdich *et al.* 1995). They are larger, more aggressive, have higher growth rates and higher fecundity than WCC (Holdich, 1988; Nyström, 2002) and therefore out-compete WCC for food and refuges. This leads to increased WCC mortality and lower recruitment (Holdich, 1988). Inter-specific mating further reduces WCC reproductive success (Lodge *et al.* 2000). Signal crayfish can spread rapidly throughout river systems moving, on average, more than twice the distance moved by WCC per day (Bubb *et al*. 2006). Although mainly found in the south of England, populations of signal crayfish are rapidly spreading north. Introduction of signal crayfish has invariably led to local extinction of WCC, with no record of coexistence for more than nine years (Holdich, 2003). The ability of signal crayfish to colonise new areas has resulted in them becoming more abundant in Britain than native crayfish (Sibley *et al.* 2002). Five other species of non-native crayfish are also present in the U.K. (Holdich *et al.* 2009). These are the noble crayfish (*Astacus astacus*), the Turkish or narrow-clawed crayfish (*Astacus leptodactylusi*), the red swamp crayfish (*Procambarus clarkii*), the virile crayfish (*Orconectes virilise*) and the calico crayfish (*Orconectes immunis*). The number of 10 km grid squares in Britain occupied by invasive crayfish increased by 43 % between 1997 and 2001 (Sibley *et al.* 2002). Correspondingly, WCC declined by 20 % over the same period. In 2001, only 13 river catchments containing native crayfish remained free of invasive crayfish species (Sibley *et al.* 2002). Since then, it is estimated that the number of WCC in the U.K. has declined by 60 % (Holdich *et al.* 2009).

Signal crayfish also have a negative influence on the broader river ecosystem. They are less susceptible to predation than WCC and thus contribute less to the transfer of energy across trophic levels and to the diet of other species of conservation importance (Lodge *et al.* 2000). Signal crayfish have been shown to cause a reduction in abundance and diversity of macrophytes (Nyström and Strand, 1996), macro-invertebrates (Stenroth and Nyström, 2003) and fish (Guan and Wiles, 1997). In addition to this, the negative impacts of signal crayfish are economically costly. Their presence is a nuisance to anglers and a threat to fisheries productivity as they consume fish eggs and small fish (Guan and Wiles, 1997) and outcompete Atlantic salmon (*Salmo salar*) and benthic fish for food and refuges (Griffiths *et al.* 2004; Bubb *et al.* 2009). Further, signal crayfish can burrow into soft riverbanks exacerbating bank erosion (Guan, 1994; Stancliffe-Vaughan, 2009) which has deleterious effects on fish and is costly for landowners. Eliminating signal crayfish populations is essential not only for conservation of native crayfish but also for maintaining healthy, productive river systems as a whole.

A further threat to WCC is crayfish plague, a lethal oomycete fungus (*Aphanomyces astaci*), which causes behavioural abnormalities, impairs mobility and results in 100 % mortality in an infected population (Oidtmann, 2000). Once infected WCC usually survive for less than two weeks (Smith and Söderhall, 1986). The fungus is carried by signal crayfish, red swamp crayfish and spiny cheeked crayfish, which are resistant the disease. Crayfish plague can also be transferred on damp surfaces, such as boats or fishing tackle (Holdich, 1991; Palmer, 1994; Holdich *et al.* 2004). Consequently, crayfish plague has spread rapidly throughout the U.K. (Alderman, 1993). Most outbreaks of the disease have occurred in Southern England and Wales but the plague is spreading north. Disinfection and thorough drying of equipment can prevent spread of the plague

(Peay, 2000) but increased public awareness is necessary to ensure river users take these precautions (Reynolds, 1997).

Even in catchments free from invasive crayfish and crayfish plague, WCC are at threat from human modification to river systems (Reynolds, 1998). Due to slow movement rates (Bubb *et al.* 2008) and dependence on refugia, WCC are highly sensitive to changes in their physical habitat (Westman, 1985). Human alteration of river systems destroys and fragments habitat. Dredging, bank stabilisation and canalisation result in loss of refuges leading to increased mortality from disturbance and predation (Schulz and Schulz, 2004). Construction of flood prevention schemes, such as culverts and weirs, may introduce barriers to upstream movement of WCC. This causes fragmentation of populations leading to reduced genetic diversity and a higher probability of stochastic extinction (Peay, 2002). Construction activities may increase sedimentation, as does removal of riparian vegetation and bank poaching by livestock (Brusconi *et al.* 2008). Sedimentation degrades refuges and reduces oxygen content in the substrate interstices WCC use as refuges (Slater and House, 2001). These non-lethal habitat modifications may increase stress on individuals resulting in increased susceptibility to disease. White clawed crayfish are affected by porcelain disease caused by the protozoan *Thelohaniasis conjeanil*. When highly prevalent, porcelain disease can cause significant crashes of WCC populations (Souty-Grosset *et al.* 2006).

Crayfish have specific water chemistry requirements and are therefore sensitive to chemical pollution (Laurent, 1988). Many pollutants, including pesticides and fertilisers, permethrin-type sheep dip, alkalis leached from concrete construction and industrial chemical effluent have been found to have significant detrimental effects on WCC (Schulz and Schulz, 2004). When subjected to ammonia concentrations typical of farm effluent (5-7mg/L of ammonium chloride) mortality rates of WCC significantly increased above areas with no added ammonia within 24 hours (Foster and Turner, 1993). Nutrient enrichment leading to enhanced macrophyte growth, high turbidity and night-time oxygen deficit is particularly threatening to WCC (Reynolds, 1998).

As for many species, climate change poses an additional threat to WCC. The predicted changes in precipitation patterns may result in more frequent and severe flood events (IPCC, 2007). Flood events can cause substantial mortality of WCC, either directly through the impact of high velocity flows, or indirectly by increasing sedimentation and by depositing individuals onto floodplains who become stranded and are unable to move back to the channel when floodwaters recede (Lewis and Morris, 2008). Further, as the need for flood prevention increases, detrimental river engineering works are becoming more widespread.

### 3.3 Conservation of white clawed crayfish

The rate of decline and threats to WCC populations have led to the International Union for the Conservation of Nature and Natural Resources (IUCN) classifying WCC as ‘endangered’. This classification recognises WCC as a globally threatened species that has a very high chance of extinction in the near future if its circumstances do not improve. White clawed crayfish have been recognised in U.K. legislation since 1981. They are protected under schedule five of the Wildlife and Countryside Act (1981), appendix III of the Bern Convention (Council decision, 1982), the Town and Country Planning Act (1990) and the Water Resources Act (1991) (Sibley, 2003). However, only with the signing of the Convention on Biological Diversity at the Earth Summit in Rio de Janeiro, 1992, did the need for active conservation of this species become recognised in legislation. The 1992 Convention on Biological Diversity led to the creation of the EU habitats directive (European council directive, 92/43/CEE) which listed WCC under annex II as ‘a species of community interest whose conservation requires the designation of Special Areas of Conservation (SACs)’ and annex V, ‘a species of European interest whose capture and trade are to be submitted to management measures’.

The U.K. Biodiversity Action Plan (UKBAP) was developed in response to the EU habitats directive with the objective to ‘conserve, and where practicable enhance, the overall populations and natural ranges of native species and the quality and range of wildlife habitats.’ White clawed crayfish were acknowledged as a priority species in the UKBAP and an action plan was developed for the species with the aim to maintain their current distribution. Population monitoring, habitat management, designation of SACs and public awareness were recognised as vital for meeting this aim (UK BAP, 1995). Thus far, seven areas of high quality habitat have been designated as SACs for WCC in England and Wales, in line with Annex II of the EU habitat directive (fig. 3.2). Although this network will contribute considerably to conservation efforts, it is important to recognise the range of habitats which WCC can utilise and protect all significant populations.

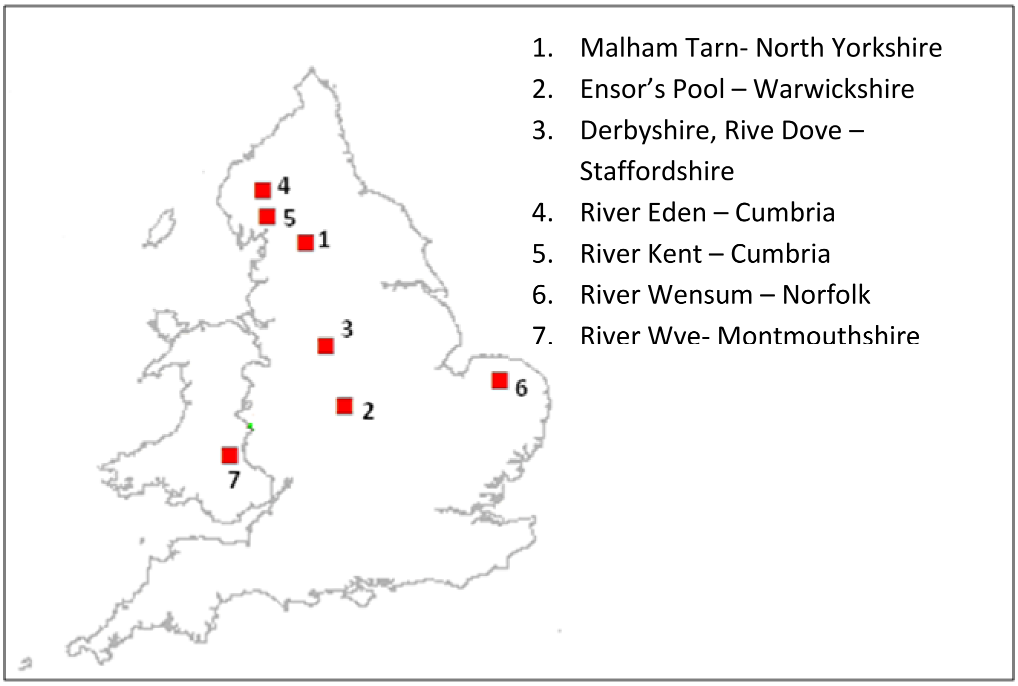

*Figure 3.2 - Location of Special Areas of Conservation for white clawed crayfish in England and Wales ( jncc.gov.uk [26/01/10])*

The Water Framework directive (European Parliament and Council Directive 2000/60/EG), implemented in 2000, requires all surface water to be of good ecological, chemical and geomorphological status by 2015. The preservation of biodiversity, and hence maintenance of WCC populations, is a key requirement of the WFD. New legislation concerning river environments continue to incorporate the WCC, for example the 2006 Natural Environment and Rural Communities Act listed WCC as a species of principal importance. This demonstrates the necessity of, and commitment to, conserving WCC in Britain.

A range of conservation initiatives for WCC have been implemented throughout Britain. Thus far, no effective method of eradicating signal crayfish has been found. Consequently, current conservation efforts are focussed on introducing WCC populations to isolated waters, free of invasive crayfish, known as ark sites (Rogers and Watson, 2007). For ark sites to safeguard the population against extinction, they need to contain suitable, sustainable habitat for WCC and must be free from the threat of colonisation by non-native crayfish (Whitehouse, 2010). Therefore, most ark sites are isolated ponds or former gravel extraction sites. Although ark sites form an essential part of preventing extinction of the WCC, they should not replace wild populations (Synder *et al.* 1996). It is also essential that favourable natural habitat conditions for native crayfish are protected and maintained (Synder *et al.* 1996). Areas of suitable habitat exist that are not currently occupied by WCC. Introduction to establish new populations is another conservation strategy (Schulz *et al.* 2002; Edsman and Smietana, 2004) and has been successful in

Ireland (Schulz *et al.* 2002). Identifying suitable introduction sites and evaluating the suitability of natural areas requires predictive habitat suitability models based a thorough understanding of WCC habitat requirements.

Preventing the spread of non-native crayfish into currently unaffected systems and reintroduction sites is vital for the continued existence of this species in the wild. Increased public involvement is necessary in order to; raise awareness of the detrimental impact of signal crayfish, encourage disinfection in order to reduce spread of crayfish plague and foster community ownership of local rivers. Although legislation implemented over the last two decades has slowed the decline of WCC (Holdich and Pockl, 2005), the species is still vulnerable.

At a regional scale, the Northumberland Biodiversity Action Plan aims to maintain the range of WCC in the region at the eleven 10 km squares that were occupied in 2000 (Jaggs, 2009). The plan of action between 2008 and 2012 contains a wide range of conservation approaches to both maintain and increase populations in the wild and create safe-haven ark sites. Attempts to safeguard existing populations have included campaigns with farmers to address diffuse pollution issues; raising awareness among anglers in order to reduce inadvertent spread of crayfish plague; and habitat improvement projects. Identifying reintroduction sites and potential ark sites are the key aims over the next two years. Ongoing monitoring of both WCC and signals is recognised as key (Jaggs, 2009).

## 3.4 Habitat use by white clawed crayfish

The effort dedicated to conservation of WCC has led to a large number of studies being conducted on their habitat requirements and physiological tolerance. Many different techniques have been used to study tolerances and preferences including laboratory based analyses (*e.g.* Gheradi *et al.* 2004), correlation of habitat to distribution and population density (*e.g.* Smith *et al.* 1996; Armitage, 2001), radio-tracking (Bubb *et al.* 2006) and correlation of WCC distribution to RHS criteria (Naura and Robinson, 1998). From this work, a good level of understanding has emerged but disagreements and gaps in knowledge are evident. These are reviewed in the following sections.

### 3.4.1 Physiological tolerances of white clawed crayfish

The most widely cited requirement of white clawed crayfish is that for dissolved calcium to replace their exoskeleton after moulting. The minimum concentration of calcium in which WCC can survive is widely cited as 5 mg $l^{-1}$ (*e.g.* Jay and Holdich, 1981) but other authors have found presence of WCC in water with just 1 mg $l^{-1}$ of calcium (Trouilhe *et al.* 2007). Magnesium ions are also required for exoskeleton development (Trouilhe *et al.* 2007). These requirements mean that

WCC generally inhabit slightly alkali waters but experimental evidence has revealed WCC can inhabit areas with pH between 6.8 and 8.2 (Jay and Holdich, 1976). Evidence suggests WCC can survive for several weeks in a salinity of 21g $l^{-1}$ (Holdich *et al.* 1997) but salinities exceeding 7 g $l^{-1}$ disrupt growth and reproduction (Nyström, 2002). Failure in body salt regulation causes death in unsuitable salinities or pH (Jay and Holdich, 1976). Specifically, potassium and sodium are required for body salt regulation (Trouilhe *et al.* 2007). For most ions, the threshold concentration required is not agreed upon in the literature but the study of Smith *et al.* (1996), which compares the range of concentrations available in the study area with the range of concentrations over which WCC were found, gives a good indication of the concentrations required for survival. These findings suggest minimum tolerated concentrations are 0.8 mg $l^{-1}$ potassium, 3 mg $l^{-1}$ magnesium and 5.7 mg $l^{-1}$ sodium. Conversely, crayfish are unable to tolerate concentrations of some ions above a critical threshold (Trouilhe *et al.* 2007). The maximum tolerated concentrations found by Smith *et al.* (1996) and Trouhile *et al.* (2007) are shown below (table 3.1) but the full range of concentrations over which WCC can survive has not been clearly defined (Lyons and Kelly-Quinn, 2003).

*Table 3.1- Estimated chemical tolerance limits for white clawed crayfish, from Smith et al. (1996)and Trouilhe et al. (2007)*

| **Chemical** | **Max. tolerated concentration (mg $l^{-1}$)** |
|---|---|
| Nitrate | 4.2 |
| Sulphate | 23.6 |
| Phosphate | 0.22 |
| Ammonia | 0.148 |
| Chloride | 23 |

It has been extensively documented that WCC require very high water quality, making them bioindicators of river health (*e.g.* Jay and Holdich, 1981). However, crayfish have been found to inhabit streams with a wider range of water chemistry and quality than previously thought (*e.g.* Trouilhe *et al*. 2007), persisting in moderately polluted waters and tolerating short term acute pollution (Demers and Reynolds, 2002). Within the wide variety of water parameters that are suitable for survival, exact mineral concentrations have not been found to influence distribution or abundance (Foster and Turner, 1993). Concentration of organic matter, however, has been shown to discriminate presence and absence of WCC (Trouilhe *et al.* 2003; Trouilhe *et al.* 2007). Areas with high organic matter concentrations tend to have low dissolved oxygen and are therefore usually unsuitable for WCC. WCC experience oxygen stress when oxygen concentration falls below 5 mg $l^{-1}$ (Westman, 1985) and BOD levels exceed 18 mg $l^{-1}$ $O_2$ (Lyons and Kelly-Quinn, 2003). Oxygen levels decrease with increasing temperature and the combination of these stresses results in death due to physiological damage when water temperatures exceed 28˚C (Whiteley and Taylor, 1993), or remain above 18˚C for an extended period of weeks to months (Reynolds, 1979; Grandjean *et al.* 2001). However, by making use of shaded areas and cool burrows WCC may be able to persist in areas with higher surface temperatures (*c.f.* Payette and McGaw, 2003). Although, WCC can survive temperatures lower than 1˚C, mortality in winter is higher than other seasons, suggesting low temperature acts as a stressor (Brewis and Bowler, 1983). Growth and reproduction only occurs when temperatures exceed 10˚C, restricting the realised niche of the species and placing a limit on the northerly latitude of the species' distribution (Pratten, 1980).

### 3.4.2 Physical requirements and the fundamental niche of white clawed crayfish

Within tolerated limits, water chemistry has very little influence on the distribution or abundance of crayfish (Smith *et al.* 1996) and the physical structure of habitat determines distribution (Lodge and Hill, 1994). Physical variables therefore have more explanatory power on the distribution of WCC than physiochemical parameters (Broquet *et al.* 2002). However, several authors have found that habitat is not a strong nor consistent discriminator of crayfish presence (*e.g.* Armitage, 2001) due to WCC having a wide habitat niche in both lentic and lotic systems.

Suitability of an area for WCC is primarily determined by permanence of the water and the availability of stable refuges, which crayfish require to shelter from predators and high flows (Reynolds, 1998). Refuges must be large enough to cover an individual and be stable in high flows (Foster, 1993). Thus, the presence of WCC has largely been found to correlate with presence and abundance of boulders and cobbles and other stable refuges such as water saturated logs, bedrock crevices, tree roots, man-made debris and crevices in banks (*e.g.* Naura and Robinson, 1998; Armitage, 2001; Broquet *et al.* 2002; Bubb *et al.* 2006). Until recently, it was thought that crayfish avoided all areas of fine substrate such as gravel, sand or mud (Holdich, 2003), yet several recent studies have found WCC thriving in areas of fine substrate. Peay *et al.* (2006) found WCC in microhabitats dominated by silt in the River Ivel, south-east England. Despite an overall finding that the probability of WCC presence was increased by the presence of small cobbles (64 – 128 mm grain diameter) and reduced by presence of gravel, sand and silt, Ream (2010) found WCC of all age groups to be present in areas where gravels (8 – 16 mm) were the largest grains. Young of the year (less than 9.4 mm CL) were found in microhabitats where the substrate was entirely sand. Similarly, a recent survey on the Darnford brook, a tributary of the River Severn, Shropshire found crayfish to be abundant in areas of deep, anoxic and unvegetated mud (Holdich *et al.* 2006). Dewatering Darnford brook revealed up to 50 crayfish per square meter burrowed into mud in areas with organic silt and twigs present (Holdich *et al*. 2006). White clawed crayfish were observed emerging from beneath the surface of the mud in areas without burrows leading the authors to discover than WCC can overcome problems of gill clogging by reversing the flow of water through their gill chambers (Holdich *et al.* 2006). Further, WCC are able to forage on the surface of mud, which can be a rich source of macroinvertebrates and decaying vegetation. The authors suggest that it is stability that determines suitability of a refuge and very dense mud, particularly that stabilised by twigs, can provide such stability (Holdich *et al.* 2006). The results of these studies suggest WCC can locate in any substrate that provides stable refuges and larger individuals may be able to burrow into fine substrate for refuge. White clawed crayfish tend to avoid areas of frequently shifting fine sediment with low stability where there are no stable refuges present in the banks and no suitable artificial or vegetative refuges (Smith *et al.* 1996).

Where suitable refuges are present, WCC can tolerate a wide range of channel structures and depths, existing in lakes, ponds, canals, major rivers and narrow, shallow drainage ditches (Grandjean *et al.* 2000). Although Broquet *et al.* (2002) found the presence of crayfish to be unrelated to depth, low flows over extended periods dramatically increase susceptibility to terrestrial predators, meaning at least 5 cm of water is required to support a population of WCC (Rogers and Holdich, 1995a). However, individuals, especially juveniles, can locate in areas less than 1 cm deep (Ream, 2010).

The requirement for dissolved oxygen by WCC means they are unable to tolerate stagnant water (Westman, 1985; Reynolds, 1998). As long as water is not stagnant, there is no minimum flow velocity required by crayfish. Maximum tolerable flow velocity is determined by the size and stability of available refuges (Demers *et al.* 2003). High flow speeds cause downstream movement of refuges and may damage crayfish directly. Foster (1995) claimed that WCC do not live in high velocity, turbulent flows and Ream (2010) found a negative correlation between flow velocity and presence of WCC. Benvenuto *et al.* (2008) found avoidance by WCC of areas with flow velocities exceeding 0.1 $ms^{-1}$ and Bohl (1989b; in Renz and Breithaupt, 2000) estimated the closely related *Austropotamobius torrentium* could not tolerate flow velocities exceeding 0.3 $ms^{-1}$. Absolute tolerances are, however, likely to vary between locations depending on the refuges available.

The wide range of food types consumed by WCC means nutritional requirements do not significantly restrict their distribution but WCC must locate in proximity to areas containing detritus or vegetation such as blanketweed (*Cladophora* spp.) moss or submerged vascular plants such as water crowfoot *(Ranunculus aquatilis)* (Gallagher *et al.* 2006). Individuals have been shown to move up to 34 m per day, with an average movement of 4.2 m per day for males and 1.7 m per day for females in summer (Robinson *et al.* 2000) and 0.233 m per day when averaged over the whole year (Bubb *et al.* 2008). Therefore, food sources are not necessarily a requirement in an individual’s immediate locale.

### 3.4.3 Habitat preferences of white clawed crayfish in lotic systems

Within areas containing suitable chemical and physical conditions, crayfish have been shown to demonstrate active preferences, selecting certain habitat types and showing relative avoidance of others (Armitage, 2001). Therefore, habitat is a better predictor of population density than of presence/absence of WCC (Armitage, 2001). The response by WCC to numerous habitat variables has been consistent between studies and consensus has emerged on their favourability to WCC. The influence of other physical variables on habitat suitability for WCC has, however, been disputed, with different studies drawing different conclusions. The discrepancies in findings may be due to location specific interactions and system functioning or may be a product of the different approaches used. Gaining a full understanding of habitat preferences in rivers, and how this varies between systems, is required to inform conservation measures.

Although crayfish can make use of a range of refuge types (Holdich *et al.* 2006), the proportion of studies that have found WCC in cobbles and boulders compared to pebble or mud suggests that crayfish ‘prefer’ these coarse substrates (*e.g.* Foster, 1993; Naura and Robinson, 1998; Armitage, 2001; Broquet *et al.* 2002; Ream, 2010). There is disagreement in published literature, with Naura and Robinson (1998) and Foster (1993) claiming cobbles do not provide a stable enough refuge for adult WCC but Armitage (2001) and Demers *et al.* (2003) finding adult WCC preferentially selecting cobbles as refuges. The inconsistency between these studies may be due to differences in flow velocity in the study areas. High flow velocity and discharge decrease the favourability of small and less stable refuges. Alternatively, this difference could be due to differences in the size of individuals in the study, as smaller individuals require smaller refuges (Foster, 1993; Ream, 2010). This explanation is supported by the results of Brusconi *et al.* (2008) which showed increasing percentage cover of cobbles increased abundance of young of the year and 1 + crayfish but decreased the abundance of older age classes. Similarly, Ream (2010) found pebbles were made use of by young of the year and 1 + WCC (up to 16.5 mm CL), cobbles were preferred by 2 + WCC (16.5 – 30.5 mm CL) and boulders were selected by 3+ individuals (30.5 + mm CL). These results suggest substrate heterogeneity is necessary to provide suitable habitat for all age groups.

There are also differences in findings on the favourability of bedrock. Where bedrock lacks crevices it has a negative association with crayfish distribution and population density (Armitage, 2001; Ream, 2010) but where bedrock crevices are present crayfish preferentially make use of them (Gallagher *et al.* 2006; Englund and Krupa, 2000). Bedrock crevices are particularly favourable due to the reduced flow turbulence over smooth bedrock surfaces. Slow, smooth flows allow individuals to maintain their position in the water column with low energetic expenditure (Gallagher *et al.* 2006), meaning glides are likely to be the preferred hydraulic biotope of WCC. However, Reynolds (1998) found shallow riffles to be the preferred habitat when large rocks were present. Turbulent areas increase dissolved oxygen concentrations and are therefore likely to be favourable where the impact of the high flow velocity is not detrimental. Benvenuto *et al.* (2008) found WCC to avoid areas with flow velocity exceeding $0.1 ms^{-1}$. Peay (2000) claims, without reference to field data, that WCC prefer areas with flow velocity less than $0.1 \ m \ s^{-1}$ and avoid areas with flow velocity exceeding $0.2 \ ms^{-1}$. The flow velocity WCC preferentially use will depend on the size of the individual (Ream, 2010) and the size and stability of available refuges. As WCC increase in size, they are able to maintain their position in the water column against higher flow velocities (Ream, 2010). Gallagher *et al.* (2006) found flow type in isolation had no effect on the distribution of crayfish.

Consistently studies of crayfish habitat use have found preferences for areas with in-channel vegetation. Laboratory based preference tests showed moss to be the preferred food source due to the fungi, microbes and metazoan hosted on moss plants (Gherardi *et al.* 2004). This preference has been reflected in field-based habitat studies. For example, Gallagher *et al.* (2006) found presence of crayfish could be predicted from distribution of moss and bedrock with 100 % accuracy and Ream (2010) found moss to increase likelihood of crayfish presence, particularly of larger individuals (greater than 16.5 mm CL). Conversely, liverworts and blanketweed have been shown to have a negative association with WCC presence (Naura and Robinson, 1998). Areas with submerged macrophytes, such as water crowfoot (*Ranunculus* spp.) and watercress (*Rorippa nasturtium-aquaticum*) are selected by WCC due to the shelter and food they provide (Demers *et al.* 2003; Holdich *et al.* 2006). Submerged macrophytes can support high densities of crayfish in the absence of substrate refuges (Reynolds *et al.* 2002). However, macrophytes can be unfavourable to WCC where they are so dense they impede movement (Peay *et al.* 2006).

Responses to riparian vegetation by WCC have also been demonstrated. Many studies have found areas with overhanging bank-side vegetation and overhanging boughs to be preferentially used by WCC (Foster, 1995; Smith, 1996; Naura and Robinson, 1998; Armitage, 2001; Ream, 2010). Riparian vegetation and canopy cover increase habitat favourability by providing food in the form of leaf detritus and insects and by shading the river, preventing high water temperatures (Brusconi *et al.* 2008). Further, canopy cover can reduce predation pressures from terrestrial predators (Ream, 2010). However, too much shading from trees may decrease the growth of photosynthetic macrophytes and actually reduce food sources for WCC (Peay *et al.* 2006). An intermediate extent of canopy cover is likely to be optimal.

Roots of riparian trees protruding into the channel have been cited as an important refuge for crayfish and also trap leaf litter, a primary food source (Smith *et al.*, 1996; Nyström, 2002). The structural complexity provided by exposed tree roots is important as protection for juveniles against high flows (Benveuto *et al.* 2008). However, Naura and Robinson (1998) found no correlation between WCC presence and tree roots. They suggest exposed roots may offer refuges to predators such as mink (*Neovison vison*) and otters and can indicate bank erosion and therefore are not always favourable refuges. Crevices in the banks themselves from soil cavities and vegetation are utilised by WCC (Holdich *et al.* 2006). Bank refuges offer added protection from predators and high flows (Groves, 1985; Holdich *et al.* 2006). Therefore, earth and boulder banks with natural crevices are preferred by WCC and bedrock banks or artificial concrete banks are avoided (Naura and Robinson, 1998; Armitage, 2001). Undercut and overhanging banks can offer natural refuges (Schulz and Schulz, 2004) but may indicate erosion, which has been found to be detrimental to crayfish by increasing turbidity and sedimentation of substrate refuges (Foster, 1995; Naura and Robinson, 1998).

The majority of studies on WCC habitat have focussed on day-time refuges but a complete understanding of WCC habitat needs requires information on night-time foraging habitat. Clavero *et al.* (2009) used electivity indices to evaluate night-time habitat preferences. The surveyors used torches to conduct a hand-search after dark. A metal disk was placed where each crayfish was found and habitat variables in each location measured the flowing morning. Significant selections were evident, with crayfish making use of pools with fine, silty substrate in excess of their proportional availability. Adult crayfish show strong night-time preferences for deeper areas (Clavero *et al.* 2009), with high proportions of organic carbon and nitrogen from plant detritus (Gheradi *et al.* 2001). These differences between preferred resting and foraging habitat suggest that, at the scale of WCC's daily movements, optimal WCC habitat should contain a heterogeneous mix of substrate sizes (Grandjean *et al.* 2003; Clavero *et al.* 2009) and flow types (Holdich, 2003) to enable them to collect food and return to refuges (Sáez-Royuela *et al.*, 2001).

Several authors have attempted to create generally applicable models of habitat quality for WCC. Creation of predictive models that perform satisfactorily across a range of sites would permit rapid, cost-effective assessment of habitat quality in un-sampled areas. This would allow prediction of WCC distribution and would enable identification of potential lotic ark sites and suitable reintroduction sites for WCC. Smith *et al.* (1996) used multiple regression analysis to correlate field obtained population density estimates to physical habitat to create a predictive model of habitat quality for WCC. Their model showed that percentage of vertical bank, percentage of channel with overhanging bank-side vegetation and percentage of exposed roots explained 71 % of variation in crayfish abundance. A different predictive model was created by Naura and Robinson (1998) by correlating River Habitat Survey (RHS) data to crayfish presence and absence at a coarser scale. In this model, crayfish presence could be predicted from presence of overhanging boughs, extensive steep banks, presence of submerged vegetation, boulder/cobbles as a bank substrate and tree shading. Variables associated with crayfish absence were; eroding cliff banks poached by cattle, bank substrates of gravel, pebble or sand, and artificially reinforced banks. However, the model did not perform well at predicting WCC absence and was not tested on any data other than that used to create the model. Using Naura and Robinson's (1998) model, Peay (2002b) predicted that WCC would be absent at four sites in the Eden catchment. Yet sampling found crayfish to be present at all four of these sites. This suggests low generality in the model. This may be due to overfitting of the model, unique conditions in the Eden, or differences in predation and competition pressures between the two systems.

Further, Naura and Robinson (1998) asserted that crayfish presence could be predicted from altitude, slope and distance from the source. This finding was not supported by Gallagher *et al.* (2006) who showed that when sites have low variability in these parameters they cannot satisfactorily predict WCC distribution. These variables do not have biological relevance to WCC and are likely to be correlated to different micro-scale habitat variables in different systems (Randin *et al.* 2006). In order for predictive models of WCC distribution to perform satisfactorily in different catchments, relevant habitat variables should be measured over an appropriate scale (Leftwich and Angermeier, 1997) and should only be transferred between similar systems (Angermeier *et al.* 2002). For example, predictive models of habitat suitability for WCC created in upland gravel-bed rivers are unlikely to perform well in lowland chalk streams. Further, distribution of non-indigenous crayfish and crayfish plague are major determinants on the suitability of areas for WCC. Evaluation of current or potential biotic threats need to be incorporated into predictive models of habitat suitability for WCC (Jiménez-Valverde *et al.* 2008).

### 3.4.4 Confounding influences on crayfish habitat relationships

White clawed crayfish distribution patterns and habitat use are likely to be specific to a given location due to differences in population structure and biotic influences. Biotic interactions may explain the results of recent studies that have not found significant correlations between physical habitat and crayfish presence (*e.g.* Armitage, 2001; Lyons and Kelly-Quinn, 2003).

Aggressive intra-specific interactions have been observed in WCC populations. Male WCC defend territories in the mating season, remaining in one location for several days and displaying aggressive behaviour towards other WCC (Mason, 1974; Robinson *et al.* 2000; Bubb *et al.* 2008). WCC also cannibalise juveniles (Mason, 1974). These behaviours suggest intra-specific competition for refuges and food occurs, which may limit population density, influence distribution and result in segregation of larger dominant and smaller subordinate individuals (Lodge and Hill, 1994). The strength of competition is likely to depend on availability of food and refuges compared to the population size (Lodge and Hill, 1994).

Intra-specific competitive interactions may explain the observed habitat segregation between age classes (*e.g.* Foster, 1993; Smith *et al.* 1996; Ream, 2010). Competition and cannibalism by dominant individuals may force smaller individuals into less favourable substrates. To the author's knowledge, no study has conclusively shown competitive exclusion resulting in sub-dominants being forced into habitat areas that result in slower growth rates or lower survival. If this does occur, WCC would conform to the despotic distribution model (*c.f.* Fretwell, 1972) meaning density may not always accurately represent habitat quality (Van Horne, 1983).

However, segregation of age classes may be explained by differences in age-specific food preferences. Smith *et al.* (1996) and Ream (2010) found juveniles to preferentially use shallow channel margins and Demers *et al.* (2003) confirmed juveniles select areas with finer substrates and more leaf litter as refuges than adults. Size related differences also occur in depth preferences with juveniles selecting shallower areas than adults do, particularly during foraging (Clavero *et al.* 2009; Ream, 2010). Deeper areas are correlated with increased plant debris, preferred by adult crayfish (Clavero *et al.* 2009) and shallower channel margins have a higher abundance of insect larvae, favoured by juveniles (Reynolds and O'Keefe, 2005). Further, differential predation pressure changes realised habitat quality and can result in differences in habitat use between different sized individuals and between sampling locations. Where the major predation pressure is from terrestrial predators, such as heron (*Ardea cinerea*), kingfisher, otter and mink, the realised habitat quality of shallower areas is reduced. Larger WCC are preferentially selected by terrestrial predators and therefore utilise larger refuges in deeper areas and avoid shallow stream margins (Clavero *et al.* 2009). However, aquatic predators, such as eel (*Anguilla anguilla*), salmonids, perch and pike, may also be present. Due to limits on gape size, aquatic predators predate on small prey. Shallow channel margins, which are difficult for fish to access, are more therefore favourable for small WCC (Englund and Krupa, 2000). Variations in type, number and distribution of predators will alter the distribution and habitat use by WCC.

### 3.5 Sampling techniques

Several sampling techniques are used to monitor and assess crayfish populations. Different techniques are suited to different survey objectives. July to September is the optimal survey period for assessing population size and condition. Sampling in this period results in minimal disturbance to breeding activity as young crayfish are released from females between May and mid July and mating has not yet begun (Moriaty, 1972). Further, the summer months provide optimal conditions for survey and greatest sampling efficiency, as rivers have low flows and clear waters and crayfish are more active due to higher water temperatures.

The standard method for assessing crayfish populations is to identify the five patches containing the most optimal WCC habitat in the survey reach and to hand search ten refuges in each (Peay, 2003). Manual searching in this way is the most time and cost efficient method for obtaining baseline data and monitoring populations but is unsuitable for detailed studies on habitat use and population structure as it is biased towards large individuals, misrepresents juveniles and only samples favourable habitat (Rabeni *et al.* 1997; Ream, 2010). Fixed area sampling gives better estimates of local population density and population structure and can be used to study response to habitat variables (Rabeni *et al.* 1997; Peay, 2003). A surber sampler can increase the efficiency of fixed-area searches. Surbers are cuboid metal frames with three sides covered with netting and weighted at the bottom to prevent crayfish escaping (Surber, 1936). The fourth side, which is positioned downstream, has a large net attached to catch individuals washed downstream (fig 3.3). Dorn *et al.* (2005) demonstrated that surber sampling gives accurate estimates of population density, size distributions, and sex ratios for slough crayfish (*Procambarus fallax*). By stocking seven enclosures with a known number of crayfish Dorn *et al.* (2005) were able to evaluate the efficiency of sampling techniques. Surber sampling had an 88 % efficiency rate. Efficiency did not differ with vegetation cover or with absolute density. The size distribution and sex ratio of crayfish caught did not differ significantly from that of the stocked population. However, small crayfish were captured at a slightly lower relative frequency than larger individuals suggesting a slight size bias. These results provide a strong indication that surber sampling is an efficient method and gives more accurate estimates of population size than night-viewing counts, refuge hand searches or trapping. Efficiency of trapping varies with the number of natural refuges within the channel and is highly biased towards large active males (Hogger, 1988; Byrne *et al.* 1999). Further, traps are expensive, prone to vandalism and can harm water voles (*Arvicola amphibious*) and shrews (*Sorex araneus*). All techniques are biased towards catching large individuals but the inclusion of all substrate sizes in surber sampling means this bias is significantly less using this method than in manual searches or trapping (Rabeni *et al.* 1997).

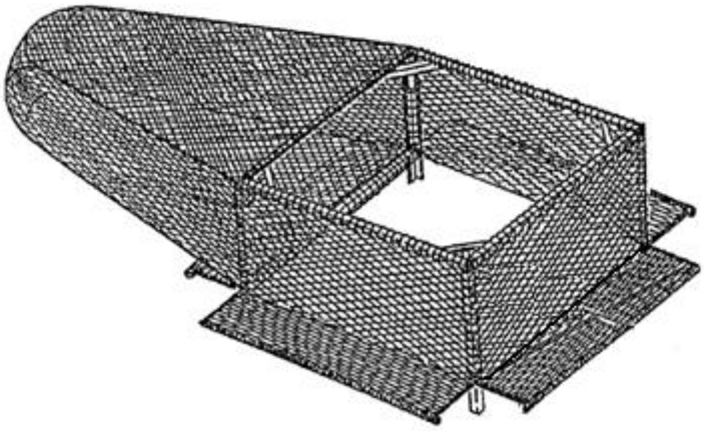

*Figure 3.3 – Drawing of a surber sampler (Di Stefano et al. 2003).*

### 3.6 White clawed crayfish on the River Wansbeck

Previous WCC surveys performed in the Wansbeck catchment show that the river contains a 'dense and thriving' population of WCC (Armitage, 2001; Rogers, 2005). Rogers (2005) claimed the River Wansbeck probably contained the largest dense population of WCC in England and as such was a site of global importance. The report recommended that the River Wansbeck was designated as a SAC for WCC but this has not occurred. Currently, the River Wansbeck is not protected as a conservation site by any statutory or non-statutory designation, though all crayfish are protected under the Wildlife and Countryside Act (1981).

The results of previous published surveys on the Wansbeck found the WCC population to be patchily distributed with high abundance in some areas and absence in others (Douglas, 1993; Rogers, 2005). In 2005, David Rogers Associates conducted a WCC survey at eight locations on the River Wansbeck. At each site, a hand-search of fifty potential refuges was conducted and ten baited traps were set overnight. Of the eight locations successfully surveyed, crayfish were absent at two, Low Angerton, 27 km downstream of the source (NZ 09302 84310) and Meldon Bridge, 31 km downstream of the source (NZ 120 851) due to siltation from stock grazing and poor water quality from road runoff respectively. The survey location at Meldon Bridge was very close to the location of survey by Douglas (1993) which found a high abundance. This suggests a deterioration of habitat quality at this location over the decade.

A major pollution incident occurred in the lower reaches of the Hart Burn, a major tributary of the River Wansbeck, in May 2004. Almost the entire population of WCC on the Hart Burn, downstream of the pollution source, was wiped out by this event. Sampling of WCC and analysis of macro-invertebrate assemblages in the week subsequent to the incident showed no impact on the River Wansbeck (M. Lucas, unpublished data).

Between 5th – 8th September 2008, the Wansbeck experienced a 1 in 150 year flood event with river levels at Mitford 3 m higher than average for the time of year (Environment Agency, 2010). Lewis and Morris reported that 20 000 WCC had been stranded by the flood and the EA estimated total mortality from flood flows or subsequent stranding of individuals on surrounding land to be 10 300 individuals (Ream, 2010). However, a survey conducted throughout summer/early autumn 2009 showed no significant difference between population density before and after the flood at Mitford (Ream, 2010). A redistribution of WCC was evident after the flood event with higher maximum number of individuals per square meter and higher heterogeneity in number of WCC per surber area after the flood (Ream, 2010). The flood flows had reduced the area containing suitable WCC habitat by depositing mounds of gravel or removing larger substrate from areas underlain with bedrock, resulting in higher densities of WCC locating in the remaining suitable habitat (Ream, 2010). A further result of the flood event was a reduction in the number of larger crayfish (greater than 16.5 mm CL). Larger WCC are unable to utilise small crevices and are more likely to be injured if their larger refuge shifts. Larger WCC will also suffer higher mortality rates than juveniles when stranded due to lower survival rates in shallow pools of standing water. This event could have had a lasting impact on population abundance as population growth rates in WCC are limited by slow maturation (Mason, 1974).

### 3.7 Summary of study context and rationale

The discussion in this and the preceding chapter has placed this research in context and confirmed the need for this study. White clawed crayfish are a threatened native species that have important positive impacts on wider river ecosystems (Momot *et al.* 1978; Sibley 2003). Despite much legislation existing to protect and conserve them, the distribution of WCC in Britain continues to decline (Holdich and Sibley, 2009). In order to manage a species effectively, conservationists must have a thorough understanding of habitat requirements and preferences (Edsman and Smietana, 2004). This review has highlighted disparity in findings of previous studies on the range of conditions WCC can make use of and the conditions they find preferable.

The easiest and most widely achievable method to obtain information on species response to their environment is by correlating current distribution to environmental parameters (Jones, 2001). Inclusion of location within the channel as a parameter may increase the accuracy of predictive models (Perry *et al.* 2002). However, conclusions drawn depend on the scale at which the study is conducted (Wiens, 1999). The most relevant conclusions will be from studies conducted at the same spatial scale the focal organisms is responding to. Previous studies have shown various taxonomic groups to respond to their environment at different scales but this has not been determined for WCC. The constraints imposed on distribution by broad scale processes, as discussed in Poff's landscape filter, must be determined. Failure to acknowledge the potential influence of these large-scale constraints may result in erroneous conclusions about habitat suitability (Jelinski and Wu, 1996). To the authors knowledge a multi-scale habitat study for WCC has not been conducted. Schulz and Schulz (2004) found that landscape scale land-use influenced the distribution of European indigenous crayfish species. This suggests that broad scale variation in physical variables may be relevant to WCC and that habitat studies should include variables operating at a landscape scale. Identifying the scale of WCC response to habitat is crucial for maintaining and improving WCC habitat, a key aim in their Biodiversity Action Plan.

# Chapter 4- Methods

## 4.1 Characteristics of the River Wansbeck, Northumberland

The River Wansbeck, Northumberland (fig.4.1) is a gravel bed river with a catchment of 331 km² (EA, 2005). The source of the River Wansbeck is in the marshy grassland of Four Laws hilltop (NY 913 829) at 345 m a.s.l. (EA, 2005). From the source, the river flows eastwards, passing through a stocked fishing lake called Sweethope Lough at 2 km downstream and continuing for approximately 60 km before discharging into the North Sea. The Wansbeck has two main tributaries, the Hart Burn, which joins from the north bank at 32 km downstream, and the River Font, which drains the Simonside Hills, and also joins from the north, at 43 km downstream (fig. 4.1). The upstream 20 km of the river have an underlying geology of carboniferous limestone. Downstream of this the river is underlain by millstone grit, which was deposited during the Carboniferous age (Abesser *et al.* 2005). Most of the catchment is covered by glacial till, which is clayey and largely impermeable (EA, 2005). Hence, the catchment has flashy flood hydrographs, dominated by surface runoff, (EA, 2005) and frequently experiences major flood events.

The Wansbeck catchment contains a number of land-uses. The headwater area is largely heather moorland with wet mires and extensive areas of afforestation. Downstream of Sweethope Lough, land-use is agriculturally managed, improved/semi improved grass or arable land, interspersed with small settlements and mixed woodland. Bankside vegetation is mainly tall grasses including canary grass (*Phalaris arundinaceai*), branched bur reeds (*Sparganium erectum*) and butterbar (*Petasites hybridus*). After 45 km the river flows through Morpeth, a small market town with a population of nearly 14 000 (Office for National Statistics, 2001). For 10 km downstream of Morpeth surrounding land use continues to be agricultural with wide riparian buffers, composed mainly of alder species, present on both sides of the channel. The river then flows through the larger town of Ashington (population approx. 28 000, Office for National Statistics, 2001) before widening into a sand based estuary at North Seaton.

Environment Agency records from Middleton (approximately 22 km downstream), Mitford (approximately 40 km downstream) and the River Font and Hart Burn confluences show very high water quality, between 2000 and 2008 (Environment Agency, 2009). All sites are consistently classified as ‘very good’, both chemically and biologically with a pH between 7 and 8 (variables recorded are macro-invertebrate community structure, dissolved oxygen, ammonia, phosphate, nitrates, pH, copper, zinc and calcium carbonate). Downstream of Morpeth, water quality is variable. Although concentration of dissolved oxygen remains high, concentrations of phosphates are consistently classified as ‘high’ or ‘very high’.

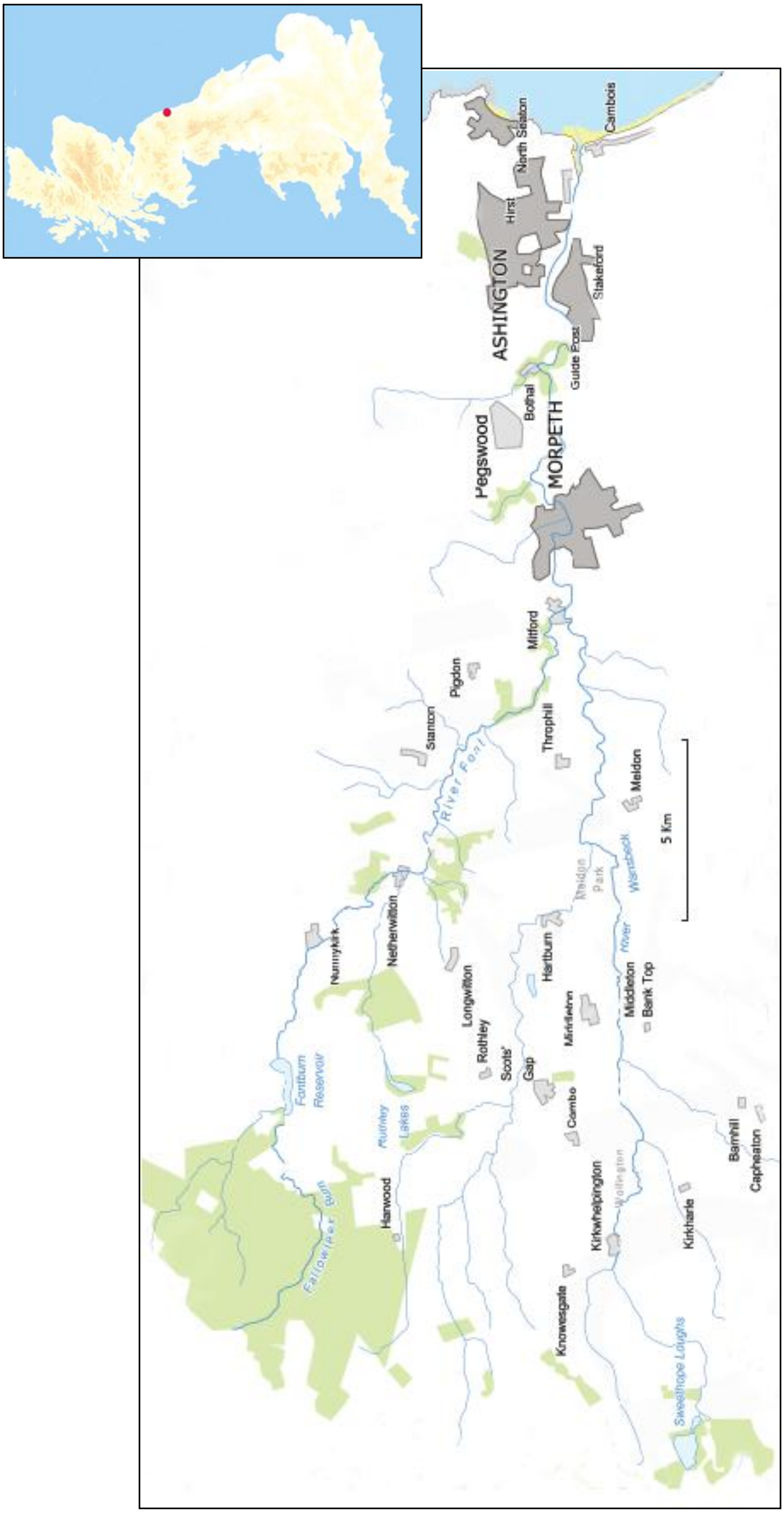

*Figure 4.1 – Location map of the Wansbeck catchment*

### 4.2 Creating a frame of reference for the channel

The aim of this study is to investigate spatial patterns in WCC distribution and habitat use over several tens of kilometres of the River Wansbeck. To extract spatially explicit information from river systems, it is necessary to have a frame of reference relevant to the channel, such that distance downstream is measured as perceived by aquatic organisms (Legleiter and Kyriakidis, 2006). A curvilinear river coordinate system has been developed which transforms [x,y] Cartesian coordinates into [s,n] river coordinates with s being distance downstream on the streamwise axis and n being distance from the centre line (Smith and McLean, 1984) (figure 4.2). Dugdale and Carbonneau (in review) have developed a Fluvial Information System (FIS) as a tool for riverine scientists and managers with need for spatially explicit, high resolution data over large scales. The FIS is a Matlab-based tool which is capable of automatic mapping of riverine habitats from high resolution aerial imagery of rivers (Dugdale and Carbonneau, in review). The FIS is capable of delimiting the river channel in images by classifying images into a predefined number of groups using statistical clustering of pixels groups with similar attributes (Dugdale and Carbonneau, in review). Algorithms implemented the FIS can then transform the [x,y] Cartesian coordinates of the river centreline into [s,n] river coordinates to produce a river coordinate system which can be used to accurately measure longitudinal and lateral distances. The FIS promises to be a vital tool in developing spatially explicit understanding of species-habitat relationships and was employed in this study to create a river coordinate system for the River Wansbeck so that longitudinal trends and spatial patterns in WCC and their habitat could be analysed.

Twenty-five centimetre resolution, fully geo-referenced, aerial imagery of the river corridor was purchased from the Infoterra Geostore. These images were cropped in Erdas, an image analysis software, into areas of equal pixel number and entered into the Fluvial Information System (FIS). Because the FIS is not designed for 25 cm resolution imagery, the river could not be accurately classified straight from the Infoterra images. To overcome this problem, the river channel on each image was accurately traced in bright red in Adobe Photoshop. The FIS classification could then easily and accurately distinguish between the channel and surrounding land, allowing production of a digitised vector centreline and a river coordinate system. This was used to determine distance downstream for all analyses and allowed Cartesian coordinates and measurements obtained in the field to be transformed to accurate distances downstream.

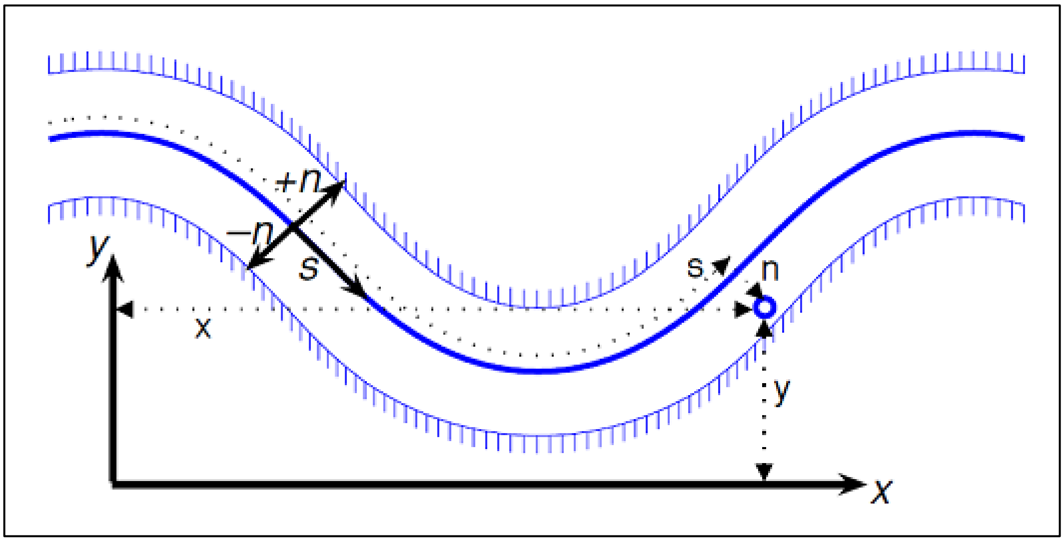

*Figure 4.2- Transformation between Cartesian (x, y) and channel-cantered curvilinear (s, n) coordinate systems. Flow is from left to right such that s is distance downstream, +n is deviation from the centre line towards the left bank and –n towards the right bank. The dashed lines show the co-ordinates for the circled points in the two co-ordinate systems (Legleiter and Kyriakidis, 2006)*

### 4.3 Nested sampling design and site selection

As well as investigating influence of locational factors on WCC, this study also aimed to identify the scale of interaction between WCC and their habitat. It was therefore necessary to conduct a multi-scale study. A three scale spatially nested sampling design was employed with a primary sampling unit of one kilometre river lengths. Within each kilometre section a secondary sampling unit of 100 m, herein referred to as a site, was selected, and within each site ten 0.49 $m^2$ tertiary units were sampled. Habitat variables were recorded over the scale at which they showed variability (see 4.6) and crayfish were sampled in each of the tertiary units (see 4.4). Due to time constraints, it was estimated that thirty-five kilometre sections was the maximum number that could be sampled. To determine which 35 km section of river to study and identify suitable sites within kilometre sections, a walkover survey was performed between the River Wansbeck's source and the town of Morpeth, during October 2009. The purpose of this was to determine access, gain landowner permission and identify features that would prevent safe and accurate sampling. General characteristics of the channel and valley were recorded over 500 m areas. This information provided a comprehensive, spatially continuous context for selecting the study area and sample sites. Based on access and suitability for survey, the length of river from the 7th to the 42nd kilometre downstream (Crook Dean to Lowford Bridge) was identified as the optimal study area.

The river coordinate system was used to delimit kilometres from the starting point of the survey. Two kilometre sections spanned major tributary junctions and were thus considered to be in different river segments. These sections were shortened to ensure the whole channel length of each section had the same stream order (*c.f* Frissell *et al.* 1986). Where possible the central 100 m of each kilometre section was selected as the sample site. However, this was constrained by physical access, landowner permission and suitability for surber crayfish sampling, which requires average depth to be less than 0.5 m and width to be greater than 0.5 m. Where the central 100 m was deemed unsuitable the neighbouring areas were assessed until a suitable site was found. Two kilometre sections had no suitable areas for survey due to extremely steep valley sides making entering the channel very dangerous. This resulted in thirty-three sample sites an average of 1.06 km apart (fig 4.3). The Cartesian coordinates of the upstream and downstream extents of the sample sites were obtained from the FIS allowing them to be located in the field using a handheld GPS. The ten tertiary sampling units in each site were arranged in pairs, separated by 22.5 m in the downstream direction. Their location alternated between channel margins (1/5 and 4/5 of wetted channel width) and either side of the channel midline (figure 4.4). The position of the tertiary sampling units within the catchment was identified by finding the coordinates of the downstream boundary of the site using a handheld Etrex GPS and then using a simple tape measure to establish the positions of the surbers within the site according to the layout shown in figure 4.4.

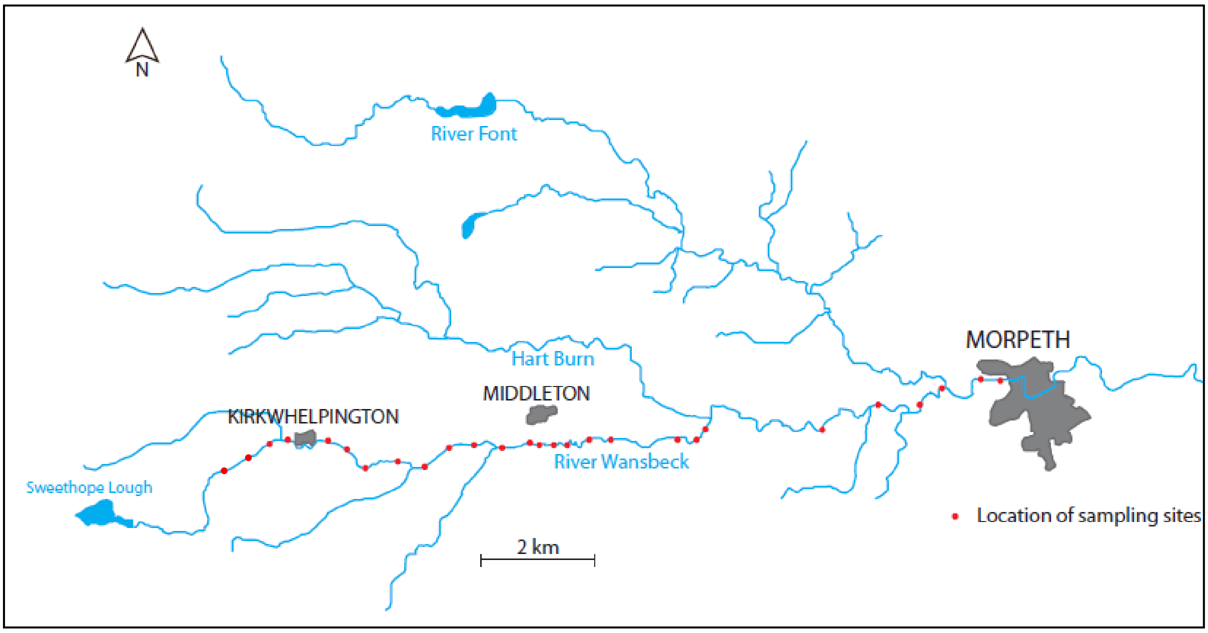

*Figure 4.3 – Location of sampling sites. See appendix 1 for site names, numbers and co-ordinates. NB/ Permission was not granted to share results at six of the sites surveyed. Data from these sites was used in analysis but is not shown in maps or appendix.*

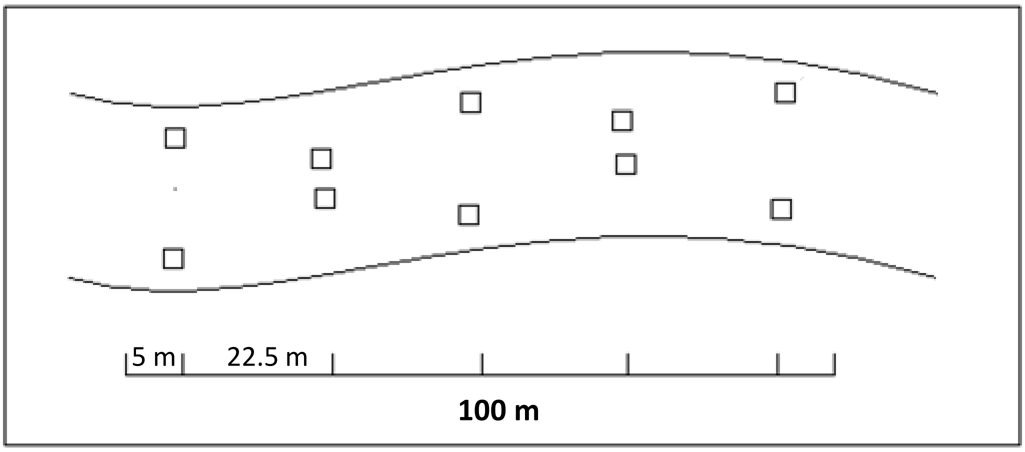

*Figure 4.4- Layout of tertiary sampling units within each site*

### 4.4 Crayfish sampling

Crayfish surveys were carried out between 15th June and 18th August 2010. To prevent transference of disease between river systems all equipment was disinfected using a weak bleach solution and left to dry in sunlight before and after sampling. Sampling was only conducted on dry days with low wind when the river was at a low stage and substrate was visible at a depth of 50 cm. Data on crayfish was obtained as an abundance per tertiary sampling area. A surber was used for each sample in order to increase efficiency. The surber used for each sample was 0.7 x 0.7 m, and therefore enclosed an area of 0.49 $m^2$, with a height of 0.5 m. Three-millimetre netting was used for the side netting and skirt. In each tertiary sampling location, the surber was carefully placed on the riverbed and pushed into the substrate to prevent crayfish escaping. Where areas were too deep or too turbid for accurate crayfish sampling, or substrate was too large to be lifted, the surber was moved to the nearest suitable location, which was accurately measured and recorded.

The most downstream surber areas were sampled first and sampling proceeded in an upstream direction to avoid disturbance of subsequent sampling areas. All substrate that could be lifted was systematically removed from within the surber. Each refuge was overturned in a downstream direction so that disturbed sediment flowed away from the site. Once sediment had settled crayfish were picked up or captured in a hand-net. A wetted, Perspex viewing chamber was used to improve sampling efficiency. Small, loose substrate was then disturbed by a glove-protected hand to dislodge remaining crayfish (Armitage, 2001). Individuals trapped in the surber netting were retrieved at the end of sampling. Root systems and vegetation were also sampled. There was no time limit on this but average search time was approximately 25 minutes per surber. Stones were replaced as near as possible to the position in which they had been found to minimise disruption to the habitat.

All captured crayfish were immediately placed in a bucket containing water and a few cobbles or some vegetative matter until sampling of the surber pair was complete. Each crayfish was measured to the nearest millimetre using vernier callipers from the tip of the rostum to the posterior tip of the telson, the hind-most extension of the tail fan, with the tail fully extended on a flat surface (*c.f.* Smith *et al.* 1996). For a subsample of individuals, measures of carapace length, from the tip of the rostum to the posterior median edge of the cephalothorax, were also obtained in order to derive a conversion between total length and carapace length. Individuals were also sexed. For individuals less than 20 mm total length sex was not distinguishable in the field.

### 4.5 Measurement of habitat variables

A broad range of habitat variables were recorded in this study. Each variable was recorded at the scale of the nested sampling design at which it showed variation (table 4.1). The definitions used to classify features were largely based on those used in the RHS (*c.f.* Environment Agency, RHS manual 2003). Largely, it was felt the recording format and definitions used the RHS was sufficient to obtain data relevant to crayfish and had the advantage of been tested and reproducible. For a few variables it was felt that more detail was required to be relevant to crayfish and additional detail was recorded. Conversely, for other variables the level of detail in the RHS was deemed unnecessary after an extensive literature review on crayfish ecology and habitat preference. For these variables, which included bank features, flow type, bank side land-use, bank profile and vegetation types, the level of detail recorded was reduced. Some variables included in RHS, for example artificial features, were not present at any of the sites and therefore were not considered in analysis.

*Table 4.1- Habitat variables recorded at each spatial scale, defined according to River Habitat Survey Manual (Environment Agency, 2003)*

| **Habitat variable** | **Classes and Units** |
|---|---|
| **Variables recorded at the scale of kilometre sections** | |
| Water chemistry | Temperature (°C), dissolved oxygen (%), conductivity (mS/cm), pH, concentration of anions and cations (mg/l) |
| Stream order and distance from source | After Shreve (1966) and in kilometers |
| Gradient | In degrees |
| Sinuosity | |
| Predominant valley form | Flat |
| | Shallow V |
| | Deep V |
| | U-shaped |
| | Asymmetric |
| **Variables recorded at the site-scale** | |
| Predominant Land-use (5 m and 50 m from the channel) | Deciduous/mixed woodland |
| | Park/garden |
| | Urban/suburban development |
| | Scrub/shrub |
| | Grassland/arable |
| Bank poaching | Present/Absent |
| Total distance of bank erosion | In meters |
| Width | In meters |
| Sinuosity | |
| Predominant bank profile/s | Undercut |
| | Vertical |
| | Steeper than 45 ˚ |
| | Shallower than 45 ˚ |
| Predominant bank material/s | Earth |
| | Bedrock |
| | Boulder/cobble |
| | Clay/fines |
| Vegetation | Mosses, algae and liverworts (Absent/< 33 %/ > 33%) |
| | Submerged vascular macrophytes (Absent/< 33 %/ > 33%) |
| | Emergent vascular macrophytes (Absent/< 33 %/ > 33%) |
| Shade and overhanging boughs | Absent/< 33 %/ > 33% |
| Exposed roots | Absent/< 33 %/ > 33% |
| Average substrate size | $D_{95}$, $D_{84}$, $D_{50}$, $D_{16}$, $D_5$ (mm) |
| Hydraulic biotope | Percentage category of Pool, Glide, Run and Riffle (Absent, 1-20 %, 21-40 %, 41-60 %, 61-80%, 81-100 %) |
| **Variables recorded at the surber-scale** | |
| Depth | In meters |
| Substrate size | As above |
| Flow velocity | At 60 % depth and at substrate boundary (m/s) |
| Overhanging boughs and shade | Present/Absent |
| Exposed roots | Present/Absent |
| Predominant bank material | As above |
| Predominant bank profile | As above |
| Bank erosion | Absent, slow or fast |
| Substrate type (measurements are Wentworth, 1922 classifications and refer to the diameter of a single grain) | Bedrock |
| | Boulders (> 256 mm) |
| | Cobbles (> 64 mm) |
| | Pebbles (> 4 mm) |
| | Gravel (> 2 mm) |
| | Sand/silt (< 2 mm) |
| Vegetation | As above |

### 4.5.1 Habitat recording at the kilometre scale

Water chemistry in each kilometre section was analysed in autumn 2009. Using a YSi meter, temperature (˚C), conductivity (mS/cm), salinity, total dissolved solids (g/L), pH and dissolved oxygen (% and mg/L) were recorded. The YSi measurement was taken three times in the nearest riffle to the downstream boundary of each kilometre section and the average value used in analysis. Following standardized water sampling protocol (Nearhoof, 1995) a vial of water was collected at the same location as the YSi recording. The vials were frozen as soon as possible. Concentrations of nitrate, bromide, phosphate, ammonia, chloride, calcium, magnesium, potassium and sodium, were analysed in the lab using a Dionex ion chromatography machine. Recorded values were compared to established crayfish tolerance limits derived from Smith *et al.* (1996) and Trouilhe *et al.* (2007).

The stream order of each kilometre section was counted from a 1:25 000 OS map according to Shreve (1966). Altitude of the upstream and downstream extent of each kilometre section was obtained from Google Earth allowing calculation of gradient. Sinuosity was measured as channel length divided by the straight-line distance between the upstream and downstream extent of the kilometre section, which was measured on Google Earth. Valley-form was classified according to RHS criteria, using Google Earth measurements of change in altitude with lateral distance from the channel and observations from the walkover survey. The categories were reduced to shallow V, deep V, bowl shaped, flat and asymmetric (Environment Agency, RHS manual, 2003).

### 4.5.2 Habitat recording at the site-scale

Land-use within 5 m and 50 m of the riverbanks over each 100 m site length was classified according to the categories shown in table 4.1. Because phosphate and nitrate concentrations are continually low throughout the river (Environment Agency, 2009) it was not considered necessary to further classify agricultural type. Predominant bank material was classified, following definitions in the RHS (Environment Agency, RHS manual, 2003), into the categories shown in table 4.1 for the bank immediately adjacent to the current water level.

Bank poaching by cattle was recorded as present or absent regardless of its abundance. Width was measured across the five transects of the locations of the surber pairs. The average width was used in analysis. Sinuosity was calculated by dividing 100 m by the straight-line distance between the upstream and downstream extent of the site, which was found using Google Earth. Due to the difficulty of accurately estimating percentage coverage over such a large area a simple three-point scale of 'absent', 'less than 33 %' and 'greater than 33 %' was used for vegetation characteristics. Three categories of vegetation were recorded: mosses, liverworts and filamentous algae; submerged vascular plants; and emergent vascular plants. Vegetation was assessed based on the habitat structure they were providing at the time of survey, not on their mature character. Due to the prevalence of mosses and algae, an additional category of 'greater than 66%' was added. Exposed roots and overhanging boughs were also recorded on this three-point scale. Shade was recorded separately as continuous, semi-continuous, isolated/scattered or absent.

Percentage cover of the hydraulic biotopes: pool, glide, run and riffle were recorded on a six-point scale; absent, rare (1-20%), occasional (21-40%), frequent (41-60%), abundant (61-80%) and dominant (81-100%) (*c.f.* Gurnell *et al.* 1996). This classification retained the maximum information on flow type whilst being reproducible and spatially consistent. The following descriptors were used to distinguish between biotopes, based on definitions from the National Rivers Authority (1992): Riffle- shallow water flowing over coarse unconsolidated substrate with higher velocity, turbulent flows, often with unbroken standing waves; Runs - continuously rippled surface, moderate to fast velocity but lower turbulence than riffles; Glides- smooth flow with low but visible velocity, generally deeper than 30 cm; Pools- areas deeper than 30 cm with smooth surfaces, no perceptible flow, characterised by finer substrate and shallow gradient.

Finally, it was necessary to obtain accurate measures of grain size at the site-scale, as grain size is a major control on the distribution of WCC (*e.g*. Smith *et al.* 1996). However, field based Wolman counts (Wolman, 1954) and percentage cover estimates of substrate have been shown to be non-reproducible (Kondolf, 1997), biased towards large particles (Whitman, 2003) and prohibitively time consuming over large areas (Marcus, 2002). Thus, terrestrial remote sensing methods were used in this study to accurately measure grain size over large areas, as relevant to WCC.

Vertical photographs were obtained using an off-the-shelf digital camera, of either five or eight megapixels, attached to a platform atop an extendable pole. The surveyor faced upstream positioned 2 m downstream of the area to be photographed. The bottom of the pole was placed on the riverbed, secured under the surveyor's foot (fig 4.5). When a field assistant was present, the camera pole, extended to 6 m length, was lowered to the assistant who pressed the trigger with a ten-second delay. The pole was then elevated to a 60˚ angle, measured by an attached clinometre, so that the camera was parallel to the riverbed when the photograph was taken (fig 4.5). When a single surveyor was present, the surveyor pressed the trigger and fed the pole forward until the end was secured under their foot, before elevating the pole to a 60˚ angle. A pole length of 4 m was the maximum manageable by a single surveyor. With the pole extended to 6 m each image covered a ground area of 5.2 m x 3.6 m. A pole length of 4 m gave an image extent of 3.45 m x 2.4 m. A white rectangular object of known size was placed on the riverbed in the frame of each photograph so the scale of the image was known. The imagery was obtained at high sun elevation (10:00 to 16:00 British summer time) to reduce sun glint and shadow from riparian vegetation.

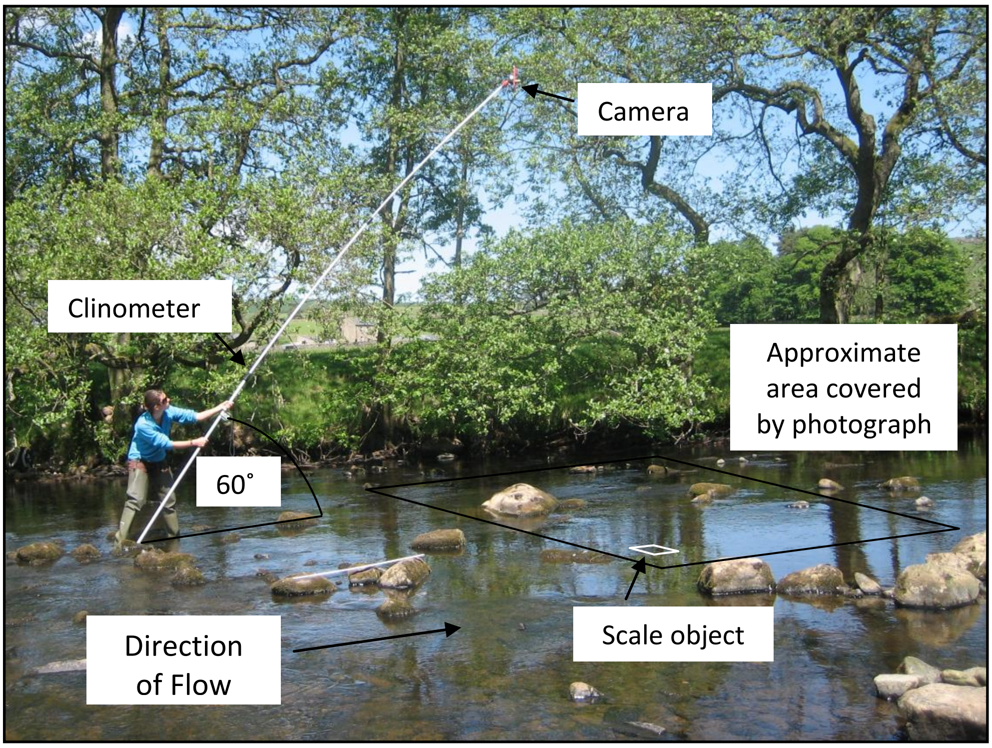

*Figure 4.5 – Stylised diagram of image acquisition (not to scale)*

On arrival at a site the positions of the surber samples were determined (see section 4.3) and their midpoints marked. Transects of images were taken across the full channel width at the location of each surber pair before crayfish sampling was conducted. Because the surveyor stood 2 m downstream of the sample site, disturbance of the surber locations was minimal. The transect always began from the left bank. After each photograph the surveyor moved towards the right bank by 3 m when using a 4 m pole and 5 m when using a 6 m pole. This ensured the whole channel width was covered with minimal overlap. This gave coverage of complete width for 20 m, one fifth of the site. In most circumstances, image acquisition and crayfish sampling occurred on the same day. However, the shortage of days with favourable light conditions during the short time span available for the study meant images were obtained for as many sites as possible when light conditions were favourable. Therefore, for some sites crayfish sampling was conducted on separate days to image acquisition. Between image acquisition and crayfish sampling there was no prolonged rainfall and the river level did not fluctuate more than 5 cm according to Environment Agency electronic sensor measurements (Environment Agency, 2010). Markers left in the locations of the surbers ensured that location of images and crayfish sampling coincided.

Individual grains significantly larger than the pixel resolution were distinguishable in the imagery due to their variations in image brightness (fig. 4.6). The images obtained had pixel sizes between

1.03 mm and 1.93 mm depending on the camera resolution and the height from which the image was obtained. This allowed individual particles down to 2-3 mm (coarse sand after Wentworth, 1922) to be differentiated by eye at the on-screen computer display resolution. The images were manually photo-sieved using a graphical user interface programmed in MATLAB (fig. 4.6). Using this programme, the sides of the scale object were identified using a cross-hair and its known length was entered to calibrate the pixel resolution. The programme superimposed a unitless 7x8 square grid over the image and the user clicked on each side of the grain below each intersect, using the minor axis for ellipsoid grains (fig 4.6). In areas of shadow and glare the nearest visible grain was measured. Where several intersects fell on vegetation or bank, measurements of random grains were made. Where grains were less than 2 mm in diameter (sand, silt or bedrock) the cross hair was not moved between the clicks defining each side of the grain. In each picture, 56 grains were measured, from which the programme calculated percentiles of grain diameter: $D_{5}$, $D_{16}$, $D_{50}$, $D_{84}$ and $D_{95}$. Overall, between ten and thirty-five pictures were taken and measured per site depending on channel width. This gave sample sizes of 560 to 19, 600 particles. The average of the outputs of $D_x$ for all pictures were calculated and used as the estimate of site-scale grain size.

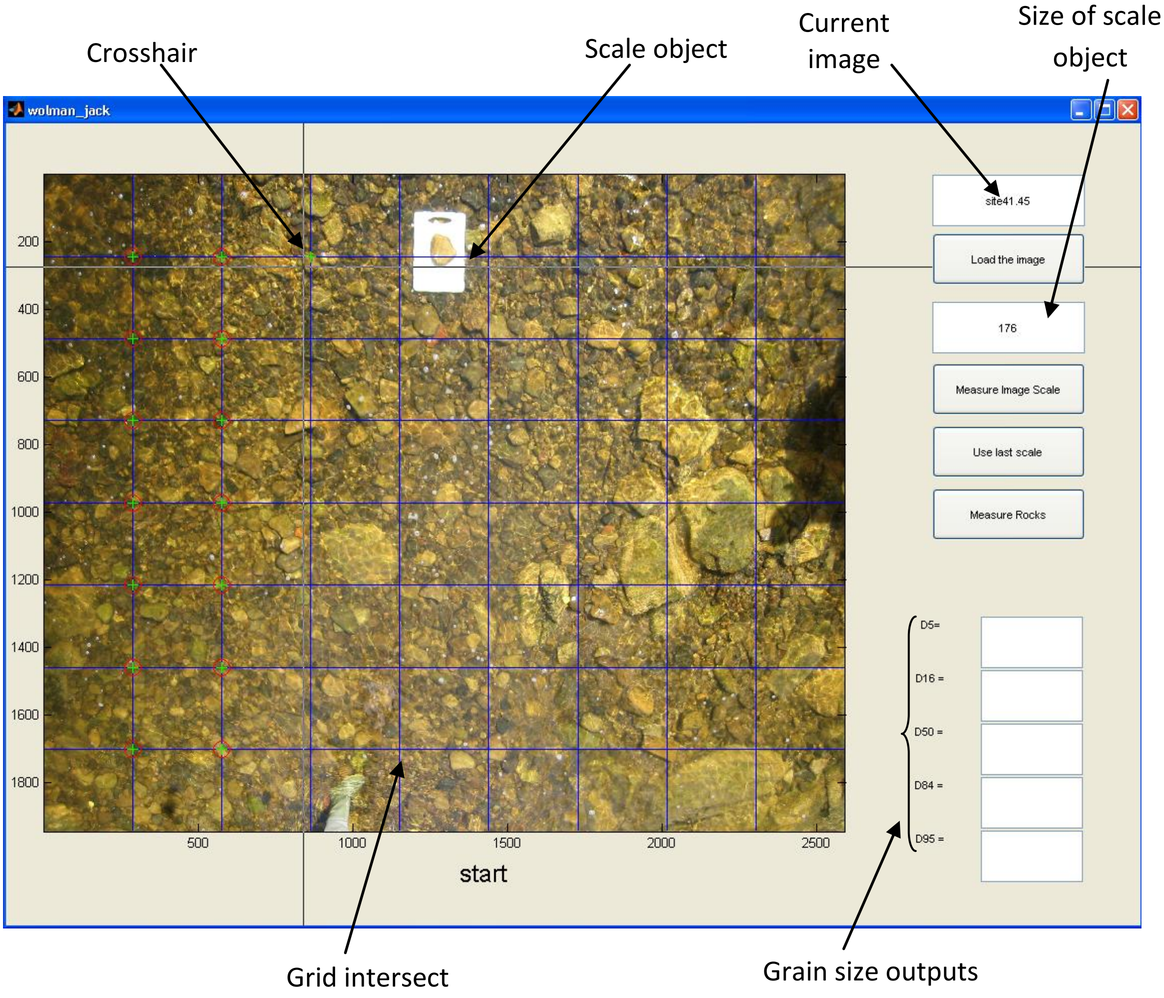

*Figure 4.6 – MATLAB user interface for manual photo-sieving. Actual dimensions of scale object were 176 mm length x 129 mm width*

### 4.5.3 Habitat recording at the surber-scale

To measure grain size at the surber-scale, vertical images of grains within surbers were taken from a height of 1 m, when light conditions permitted (fig. 4.7). These images were loaded into the MATLAB user interface and grain sizes were measured, as described above. The location of surbers was identifiable on larger scale photographs from the markers. Where aerial photographs of individual surbers were not possible, grain size at the surber-scale was therefore measureable by re-loading images containing markers into the MATLAB programme and measuring only the particles in the 0.5 m² area around the marker.

*Figure 4.7 – Vertical photograph of a surber area used to measure grain size by manual photo-sieving*

Other microhabitat scale variables were recorded within surber areas immediately after crayfish sampling and returning of substrate. The exact distance of the surber from the bank was recorded to allow lateral distance to be calculated from the transect width. Depth was recorded to the nearest centimetre, using a meter stick, in all four corners of the surber area and in the centre. Depth was taken to the top layer of base substrate in interstices between cobbles, not resting on the top of large substrates. After the surber frame had been removed, flow velocity was recorded using an electromagnetic flow metre in corners and the centre of the surber area at both 60% depth and the substrate boundary in the exact location of the surber sample.

Overhanging boughs, shade and exposed roots were recorded as present or absent. A visual estimate of the percentage cover of each of moss/algae, submerged vegetation and emergent vegetation was made for each surber area in the categories: absent, less than 20%, 21-40%, 41-

60%, 61-80% and greater than 80%. The characteristics of the bank closest to the surber over the 0.7 m length of the surber, were recorded according to the material and profile criteria outlined above. Bank erosion at this scale was classified as, not eroding; slow erosion, as evidenced by undercut banks and cliffs; or fast erosion, such as slumps, poaching or unstable cliffs. A record was made for each surber area of presence of bedrock, silt/sand, gravel, pebbles, cobbles and boulders classified according to Wentworth (1922) and whether or not grains were embedded (see table 4.1 for definitions).

### 4.6 Preparation of crayfish records for data analysis

#### 4.6.1 Conversion to carapace lengths

To be comparable to previous studies, total lengths of WCC needed to be converted to carapace length. Total length and carapace length were measured on seventy-two crayfish (twenty-eight females, forty males and four too small to be sexed) ranging from 11 to 92 mm total length. Linear regression equations were calculated for the relationship between total and carapace length for each of males, females and individuals too small to sex and the recorded data converted according to these equations.

#### 4.6.2 Elimination of young of the year

The study period encompassed the release of young of the year causing inconsistency in the total number of crayfish caught per site. To prevent bias, young of the year were identified and removed from further analysis. Size-frequency plots were drawn to discern what sized individuals were young of the year. The percentage of females with young attached and the percentage of individuals identified as young of the year were plotted against sample date to verify individuals of this size were not present throughout the study period.

### 4.7 Statistical analyses

#### 4.7.1 Measuring aggregation

Analyses to determine whether distribution of crayfish was random or aggregated were performed using the frequency distribution of number of crayfish per surber area. The index of dispersion was calculated according to equation 4.1. An index of dispersion greater than one shows an aggregated distribution (Krebs, 1999).

$$I = \frac{s^2}{\bar{x}} \qquad \textit{Eq.4.1}$$

Where $s^2$ is the variance in number of crayfish per surber and $\bar{x}$ is the mean number of crayfish per surber area. The observed frequency distribution was then compared to expected frequency distributions under Poisson and negative binomial models. If the data fits a Poisson distribution, it can be inferred that individuals are randomly located. If the data fits a negative binomial distribution, aggregation is evident. The negative binomial exponent was found by solving equation 4.2, which is known as the maximum likelihood method (Krebs, 1999).

$$(N)log_e\left(1+\frac{\bar{x}}{\hat{k}}\right) = \sum_{i=0}^{\infty}\left(\frac{A_x}{\hat{K}+x}\right) \qquad \textit{Eq. 4.2}$$

Where, N is the total number of surbers, $\hat{\mathrm{k}}$ is the estimate of the negative binomial exponent, $\bar{x}$ is the sample mean, $x$ is the number of crayfish in a surber and $A_x$ is calculated according to equation 4.3.

$$A_x = \sum_{j=x+1}^{\infty}(f_j) = f_{x+1} + f_{x+2} + f_{x+3} \qquad \textit{Eq 4.3}$$

Where $i$ is a counter (0,1,2,3 …), $j$ is $i+1$ and $f_x$ is the number of surbers containing $x$ individuals (Krebs, 1999). A chi-squared goodness-of-fit test was used to assess how well the Poisson distribution matched the observed values. The U-statistic was used to test the adequacy of the negative binomial distribution as a description of observed counts (Evans, 1953). This was shown to be the most efficient test for the given mean and *k* exponent (Krebs, 1999). If the output of the U statistic is less than two times the standard error of the data then the observed data is not significantly different from the negative binomial distribution. If the data does fit the negative binomial model the formula below can be used to determine whether this aggregation is due to variability in the environment (Blackith cited in Southwood and Henderson, 2000). If the mean size of an aggregation, as calculated by equation 4.4, is less than two then aggregation is due to an environmental effect and is not an active behavioural process.

$$\lambda = \frac{\bar{x}}{2k}\,v \qquad \textit{Eq. 4.4}$$

Where λ is the mean number of individuals in a clump, *k* is the the negative binomial exponent and *v* is the critical value of a chi-squared distribution with 2*k* degrees of freedom at *P* = 0.5

### 4.7.2 Measuring niche breadth

A preliminary analysis to determine which continuous variables crayfish were showing a response to was conducted by calculating marginality and specialisation according to the equations 4.5 and 4.6 (Hirzel, 2002).

$$S = \frac{s_t}{s_c} \qquad \textit{Eq. 4.5}$$

Where $S$ is the specialisation value for the focal habitat variable, $s_t$ is the standard deviation of values of the focal habitat variable in all surber areas and $s_c$ is the standard deviation of values of the focal habitat variable only in surber areas containing crayfish.

$$M = \frac{|\bar{x} - \bar{x}_c|}{1.96 \times s_t} \qquad \textit{Eq. 4.6}$$

Where $M$ is the marginality value for the focal habitat variable, $\bar{x}$ is the mean value of the focal habitat variable in all surbenr areas and $\bar{x}_c$ is the mean of values of the focal habitat variable only in surber areas containing crayfish. A specialisation value greater than 1 shows the niche width is narrower than the range of conditions available. Marginality is usually between 0 and 1. The closer the marginality value is to one, the larger the difference between the mean of the habitat used by crayfish and the mean of all available habitat (Hirzel, 2002). Only variables showing marginality values exceeding 0.5 or specialisation values exceeding one were used in further analysis, apart from in the logistic regression analysis for which all variables were considered.

For all categorical variables, it was determined whether crayfish were making use of each habitat type. For the continuous variables where either specialisation or marginalisation was evident, it was determined whether crayfish were making use of the maximum and minimum available values. If a population is making use of all habitat types surveyed then no niche limits can be specified. Krebs (1999) suggests less than 5% use of an available habitat type suggests it is outside the niche space. Proportional use was calculated for each categorical variable and for broad groupings of continuous variables. For classes where less than 50 % of the available habitat in that class was used by WCC, the class was subdivided to identify any range with less than 5% use, maintaining at least ten observations per group.

Smith's (1982) measure of niche breadth (equation 4.7) was calculated for all variables for which the range of conditions made use of was narrower than the range of conditions available. This measure (*FT*) ranges from 0 to 1, with higher values indicating a broader niche, and provides a standardized measure of niche breadth for comparison between locations and habitat parameters.

$$FT = \sum\left(\sqrt{a_j p_j}\right) \qquad \textit{Eq. 4.7}$$

Where, $FT$ is Smith's measure of niche breadth, $p_j$ is the proportion of individuals using habitat type *j* and $a_j$ is the proportion of total habitat accounted for by type *j* (Smith, 1982).

### 4.7.3 Logistic regression

A single logistic regression model was created in Stata to describe the relationship between presence/absence of crayfish in surber areas and the habitat variables shown in table 4.1 for all three spatial scales. Logistic regression was the most suitable method for analysing influence of habitat parameters on probability of WCC presence in this study as it does not assume normality and homoscedasticity (Trexler and Travis, 1993) and is able to cope with continuous, binary and categorical independent variables. All recorded habitat variables were assessed for utility in the model. For depth, boundary flow velocity, flow velocity at 60 % depth and coefficient of variation flow velocity a median value was calculated for each surber area and entered into the logistic regression model. The midpoints of the percentage categories of biotope cover and surber algae/moss were used (0, 10, 30, 50, 70 or 90%). Pool was then removed due to pool, glide, run and riffle creating a near constant sum. Due to low numbers of positive observations, percentage coverage of emergent and submerged vegetation at the surber-scale were amalgamated into present/absent for emergent and absent, less than 20 % and greater than 20 % for submerged. For categorical data, dummy variables were created. Locational variables of distance downstream and lateral sample position were also entered into the model.

It was necessary to remove some variables due to the presence of multicollinearity. Multicollinearity violates the assumption of logistic regression that predictor variables are independent, resulting in increased standard error, wider confidence intervals, reduced statistical significance and erratically acting coefficients (Allison, 1999). A tolerance of 0.2 was used in this study. Using Stata, the pair wise correlations between all predictor variables were calculated to identify multicollinearity. Any correlation between variables with an $R^2 > |0.8|$ were considered to present a serious collinearity problem (Allison, 1999). Collinearity was dealt with by removing the correlated variable least relevant to crayfish. Although variable exclusion risks bias and a loss of explanatory power (Menard, 2002), it was felt that all correlations between habitat variables with $R^2 > |0.8|$ highlighted genuine repetition in recording of an ecologically relevant parameter. Therefore, the variable that was least relevant to crayfish, based on previous knowledge of their ecology, was removed from the model.

A logistic regression was run with all remaining variables. The least significant variable (highest *P* value) was removed from the model and the logistic regression run again. This process was repeated, systematically removing the least significant variable one at a time, until all the variables in the model were significant at the 5% level ($P < 0.05$). For the variables remaining at a 5 % significance level, Akaike's information criterion (Akaike, 1973) was calculated for every combination of these variables to determine the most parsimonious model. The most parsimonious model was the final logistic regression output. To obtain actual probabilities of finding crayfish in a given surber area the values of the predictor variables were substituted into the final model and the probability calculated according to equation 4.8.

$$P = [Exp\ (model)]/[\ 1 + Exp\ (model)] \qquad \textit{Eq. 4.8}$$

Where *P* is the probability of crayfish being present in a surber and $model$ is the output value from the model when the observed values for a given surber area are inputted.

The odds ratios of each predictor variable is the exponential of its coefficient in the logistic model and shows the predicted increase in the odds of finding crayfish for every one unit increase in that predictor variable, holding all other variables constant. Hence, for binary and categorical variables the odds ratio gives the increase in the odds of finding crayfish when these variables are present compared to when they are absent. The logistic regression outputs a *Z* value for each variable in the logistic regression. The *Z* value is the variable's logistic regression coefficient divided by the standard error. This value shows the relative importance of each predictor variable compared to others in the model.

The strength of the model was evaluated using goodness-of-fit tests. The likelihood ratio chi-square value compares predictions made using the model to expected results with no predictor variables to see if the whole model is statistically significant (Trexler and Travis, 1993). The pseudo R-squared value was not considered in this study due to the variety of possible techniques used to derive the value and the lack of agreement between them. Twenty surbers, selected using a random number generator were omitted from analysis and were used to assess the predictive performance of the model. It was ensured the twenty validation surber areas were not clustered in position, grain size, depth or flow velocity. The reliability of the model was calculated by comparing the number of surber areas predicted to have a probability greater than 50 % of having crayfish to the number of surber areas in which crayfish were actually observed (*c.f.* Naura and Robinson, 1998). The ability of the model to discriminate between occupied and unoccupied surbers (Pearce and Ferrier, 2000) was calculated as omission and commission error. Omission error was calculated as the number of surber areas in which WCC were caught when the model predicted less than 20 % probability of crayfish being present (Boone and Krohn, 2000). Commission error was calculated as the number of surbers in which crayfish were not observed when the model had predicted a greater than 80 % chance of crayfish being present.

#### 4.7.4 Measuring habitat preferences

#### 4.7.4.1 Proportional use

Preferences for categorical habitat variables were analysed using a chi-squared test to determine if observed usage of different habitat types was significantly different from that expected if habitat use were random. Where analyses had one degree of freedom Yates's correction was applied to make the Chi-squared estimate more conservative (Eq. 4.9). The null hypothesis is that habitat types are used in proportion to their availability. The null hypothesis was rejected at the 5 % significance level. For each habitat variable for which the chi-squared tests showed a significant result, the actual use of each habitat category/class by WCC was graphically compared to the expected use if WCC were randomly distributed, to determine the direction and strength of the response to the habitat variable by WCC in the study area.

$$\chi^2 = \sum \frac{(|O-E|-0.5)^2}{E} \qquad \textit{Eq. 4.9}$$

Where $\chi^2$ is the chi squared value, $O$ is the observed number in each class and $E$ is the number expected in each class is habitat type had no influence on the proportion used.

Continuous habitat variables were separated into intervals and proportional use of surbers within each class was calculated according to Manly's alpha (eq. 4.10), which was found from preliminary analyses to be the most representative preference index. To normalize the values, *1/total number of habitat classes* was subtracted from the values of Manly's alpha. Positive values showed selection and negative values showed avoidance.

$$Manly's\ \alpha_i = \frac{r_i}{p_i}\left(\frac{1}{\sum r_j/p_j}\right) \qquad \textit{Eq. 4.10}$$

Where, $r_{i,}$, $r_j$ is the proportion of habitat type $i$ or $j$ used by the individual and $p_i$ , $p_j$is the proportion of habitat type  type $i$ or $j$ or  in the whole study area (Krebs, 1999).

Preliminary analysis showed preference indices to be highly sensitive to variations in number of observations per class. Class widths were therefore selected with the aim to maintain a constant number of observations per class, as this gave the best representation of the trends evident in the data and prevented the result being strongly affected by rare habitat types. Due to variability in the frequency of observed values, with multiple observations often having the same value, some irregular class widths were necessary. Different numbers of classes were systematically trialled and the final number of classes chosen to minimise noise and ensure classes did not span large gaps in magnitudes of observations whilst maintaining roughly the same number of observations per class. Preference values were plotted to aid identification of trends.

#### 4.7.4.2 Analysis of crayfish population density

Habitat preferences of WCC were also analysed based on population density of WCC in different habitat types. Analyses used the number of crayfish per surber area, including surber areas in which no WCC were caught. A Kolmogorov-Smirnoff test was used, in conjunction with the results from the goodness-of-fit to Poisson and negative binomial distributions, to determine if the data was normally distributed. This test compares the distribution of an observed sample to the normal distribution with the null hypothesis that the distributions are the same. A 5 % significance level was used. Levene's tests were also performed for each habitat variable to determine the homogeneity of variances of observations in different categories. Again, the null was that all categories have equal variances and a 5 % significance level was used. Preliminary analysis showed the distribution of the number of crayfish per surber was not normal and variances were largely homogeneous. Therefore, non-parametric tests were used.

A Kruskal-Wallis test was performed in Stata for each habitat variable. The test determines whether the observations in different categories are from the same population, with the null hypothesis that the probability of a random observation from one category exceeding a random observation from another category is 0.5 (MacDonald, 2009). All observations of the dependent variable are ranked from the smallest to the largest value. In this case, the number of crayfish per surber was ranked from 1 to 328 using the average rank for tied data. After ranking all observations, the test is performed according to equation 4.11. To determine the influence of habitat variables measured as continuous data, observations were split into classes based on the magnitude of the measured habitat variable. Because this analysis is less sensitive to sample size than preference indices, even class widths could be used. Even class widths give results that are more ecologically relevant and easier to interpret. Ultimately, class widths were selected to minimise noise, to ensure classes did not span large gaps in magnitude of the habitat variable and to retain at least ten observations per class.

$$H = \left(\frac{12}{N(N+1)}\sum_{i-1}^{k}\frac{{R_i}^2}{n_i}\right) - 3\,(N+1) \qquad \textit{Eq. 4.11}$$

Where *H* is the Kruskal-Wallis output value, showing the variance of the ranks among categories, $R_i$ is the sum of ranks in category *i*, $n_i$ is the number of observations in category *i* and *N* is the total number of observations. An adjustment was made when ties were present in the ranks of the dependent variable by dividing *H* by the output of equation 4.12. This increases the statistical power of the test (Rogerson, 2006).

$$1 - \frac{\sum_i({t_i}^3 - t_i)}{N^3 - N} \qquad \textit{Eq. 4.12}$$

Where *t* is the number of observations tied at rank *i* and the sum is over all sets of tied ranks (Rogerson, 2006). Because *H* is approximately a chi-squared distribution the probability of obtaining a particular value of *H* by chance if the null were true can be determined from a chi-squared distribution table, using the number of groups minus one as the degrees of freedom. The null was rejected at the 5 % significance level.

For the variables with significant Kruskal-Wallis outputs, box plots for each category/class were plotted to allow visual comparison of the differences in number of crayfish per surber in different categories/classes. Further, Mann-Whitney U tests were performed in Stata to compare all possible pair-wise combinations of categories/classes. Essentially, the Mann-Whitney U test determines whether there is a significant difference between the medians of two groups. The null hypothesis is that the distributions of both groups are equal such that the probability of a random observation from the first group exceeding a random observation from the second group is 0.5 (Aitken and Taroni, 2004). This test also ranks all observations and is calculated according to equations 4.13 and 4.14.

$$U_1 = R_1 - \frac{n_1(n_1+1)}{2} \qquad \textit{Eq. 4.13}$$

$$U = \frac{U_1}{n_1 n_2} \qquad \textit{Eq. 4.14}$$

Where $|U|$ is the Mann-Whitney output value, $R_1$ is the sum of ranks of observations in one of the categories, $n_1$ is the number of observations in this category and $n_2$ is the number of observations in the other category. The significance of $|U|$ is automatically outputted in Stata. Because multiple pair-wise comparisons were made, Bonferroni corrections were applied. Bonferroni corrections adjust the significance level at which the null hypothesis is rejected, to account for the increased probability of type 1 errors (significant differences occurring by chance) when multiple independent comparisons are made (Aitken and Taroni, 2004). To maintain a type 1 error probability of 5 %, the values at which differences between groups were considered significant is reduced to $0.05/p$ where $p$ is the number of pair-wise comparisons made. However, application of Bonferroni corrections risks omitting significant differences due to the reduction in the accepted significance level being overly conservative. To account for this, Holm's sequential Bonferroni corrections (Holm, 1979) were used in this study. In Holm's method the alpha value at which a difference is considered significant varies depending on the rank of the *U* value for each pair-wise comparison. For the pair-wise comparison with the highest *U* value to be significant the alpha value must be below that calculated in the Bonferroni correction. For subsequent comparisons the significant alpha value decreases, according to equation 4.15. The significance values for different numbers of categories/classes after applying Holm's sequential Bonferroni corrections are shown in table 4.2.

$$\frac{\alpha}{(n-r)+1} \qquad \textit{Eq. 4.15}$$

$\alpha$ is the target significance level, in this study 0.05; n is the number of pair-wise comparisons and $r$ is the rank number when all paired comparisons are ranked 1 to $n$ in ascending order of $|U|$.

*Table 4.2 – Holm's sequential Bonferroni correction values. Adjusted significance values to maintain a type 1 error probability of 0.05 when conducting multiple pair-wise comparisons.*

| **Number of different classes/categories** | **Number of pair-wise comparisons made** | **$\lvert U \rvert$ Rank** | **Bonferroni corrected significance value for $\alpha = 0.05$** |
|---|---|---|---|
| 3 | 3 | 1 | 0.017 |
| | | 2 | 0.025 |
| | | 3 | 0.05 |
| 4 | 6 | 1 | 0.0083 |
| | | 2 | 0.01 |
| | | 3 | 0.0125 |
| | | 4 | 0.017 |
| | | 5 … | 0.025 |
| 5 | 10 | 1 | 0.005 |
| | | 2 | 0.005556 |
| | | 3 | 0.00625 |
| | | 4 | 0.007143 |
| | | 5 … | 0.008333 |
| 6 | 15 | 1 | 0.0033 |
| | | 2 | 0.003571 |
| | | 3 | 0.003846 |
| | | 4 | 0.004167 |
| | | 5 … | 0.004545 |
| 7 | 21 | 1 | 0.0024 |
| | | 2 | 0.0025 |
| | | 3 | 0.002632 |
| | | 4 | 0.002778 |
| | | 5 … | 0.002941 |
| 8 | 28 | 1 | 0.0018 |
| | | 2 | 0.001852 |
| | | 3 | 0.001923 |
| | | 4 | 0.002 |
| | | 5 … | 0.002083 |

### 4.7.5 Influence of river position

The influence of lateral position within the channel on WCC was analysed in three ways. Firstly, the number of crayfish in a surber area was correlated against lateral distance of the surber using Spearman's rank (eq. 4.16), due to preliminary analysis showing a non-linear relationship between these data sets. Secondly, the significance of the difference between observed and expected proportional use of lateral and medial surbers was calculated using a Chi-squared test and then visualised as a box-plot (eq. 4.9). Finally, the average number of crayfish in lateral and medial surbers was compared using a Mann-Whitney U test (eqs. 4.13 and 4.14).

$$r_s = 1 - \frac{6 \sum D^2}{n(n^2 - 1)} \qquad \textit{Eq. 4.16}$$

Where $r_s$ is the spearman's rank correlation, $D$ is the difference in the rank between the dependent variable, in this instance number of crayfish, and the independent variable, lateral distance in this case, and $n$ is the number of observations.

Total numbers of crayfish found per site (in all ten surbers) and the proportion of surber areas in each site that were occupied by WCC were plotted against distance downstream to determine if a longitudinal pattern in WCC distribution was evident. Spearman's rank tests (eq. 4.16) were performed to test the significance of these relationships. Separate Spearman's rank tests were conducted to compare number of WCC in each surber area with its distance downstream, number of crayfish caught at a site with its distance downstream and number of surber areas within each site that were occupied by WCC with distance downstream.

The significance of the difference between observed site totals and site totals expected if all sites were used equally was found using a chi-squared test (eq. 4.9). The results were then split into the upstream half of the study area (6.6 – 23.5 km downstream) and the downstream half of the study area (23.6 – 44.6 km downstream). A chi-squared test (eq. 4.9) was performed to determine whether the proportional use of surber areas by WCC in the upstream and downstream halves differed from that expected by random. A Mann-Whitney U-test (eqs. 4.13 and 4.14) was performed to determine whether the number of WCC in occupied surbers differed between the upstream and downstream halves of the study area. All statistical tests were considered significant at a 5 % significance level.

Analyses were conducted to determine if the longitudinal pattern of crayfish distribution was solely attributable to variations in habitat quality and to determine the cause of any differences between WCC distribution in the upstream and downstream halves of the study site. All habitat variables for which previous analyses had revealed WCC to have strong consistent responses to were considered. Preferred ranges of continuous variables were determined from examining and combining the results of all analyses conducted. For surber-scale variables, the proportion of surber areas within preferred habitat categories/classes in each site was used in analysis. To examine longitudinal influences, the number of crayfish caught per site was plotted against each significant habitat variable and Spearman's rank was performed (eq. 4.16) to determine the strength and significance of the correlation. To determine the cause of differences in the upstream and downstream half of the study site, chi squared tests (eq. 4.9) were performed to compare the proportion of surbers in a given habitat type to the proportion expected if habitat types were present in equal amounts in upstream and downstream sections. This analysis indicated whether certain habitat types that WCC were responding to were more common in one half of the study reach.

The final analysis was performed to determine whether the location of confluences influenced the longitudinal distribution of substrate sizes and hence the distribution of WCC in the study area. Identifying which tributaries influence the characteristics of the main channel can only be done by considering the effect each tributary has on the grain size, channel form and discharge (Rice and Church, 1996). The position of all tributaries were identified on line graphs of the longitudinal trends in average site width, a proxy for discharge (average width x average flow velocity x maximum recorded depth) and site-scale $D_{50}$, for which a $\log_2$ y-axis scale was used (Rice, 1998). Ray Burn, Swilder Burn, Hart Burn and the River Font were identified as the tributaries that resulted in discontinuities or step changes in the downstream pattern of these variables in the main channel. Rice and Church (1996) acknowledge that 'recognising trends is seldom straightforward and a significant degree of judgement is usually required.'

Site-scale $D_{50}$ for each site was plotted, on a $\log_2$ scale, against distance downstream on a scatter graph, using a separate series for each inter-tributary length. The distance between the upstream end of each site and closest upstream influential tributary was calculated. This was not possible for sites in the most upstream sedimentary link as the location of the nearest upstream influential tributary was unknown. This left 29 data points. To test whether site-scale $D_{50}$ decreased with distance downstream from an influential tributary a one-tailed Pearson's correlation coefficient was calculated ($\alpha = 0.05$).

To determine if the pattern of WCC distribution was attributable to the sedimentary link substrate pattern, and hence could be predicted from the location of influential tributaries, the number of WCC caught per site was plotted onto the scatter graph showing sedimentary links, using the same x-axis to allow comparison of downstream trends. The correlation between the distance downstream of an influential tributary and number of WCC caught per site was calculated using Pearson's correlation coefficient ($\alpha = 0.05$).

# 5. Results

## 5.1 Preliminary results

### 5.1.1 Converting total lengths to carapace lengths

Strong linear correlations between total length and carapace length (CL) were evident for all demographic groups of WCC. The $R^2$ values were 0.9942, 0.9941 and 0.9996 for males, females and individuals too small to be sexed respectively (fig. 5.1).

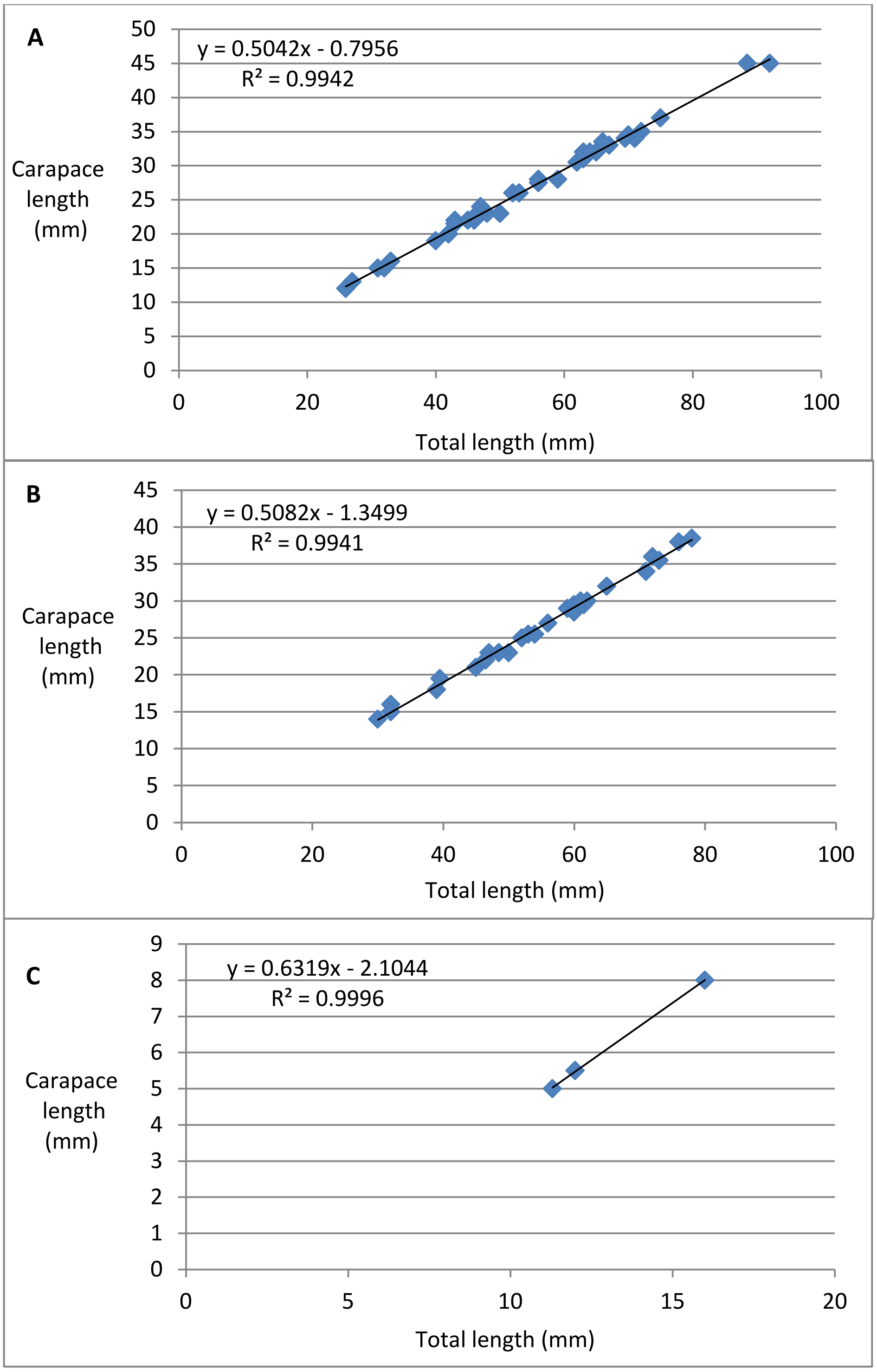

*Figure 5.1- Correlations between total length and carapace length for a) Males b) Females and c) Individuals too small to be sexed (<21 mm total length)*

### 5.1.2 Eliminating young of the year

Size frequency plots showed distinct grouping in the data (fig.5.2). No captured crayfish measured between 13 and 15 mm total length (TL) (6-7.5 mm CL) but smaller and larger individuals were present. This is interpreted as the distinction between young of the year and age 1+ crayfish.

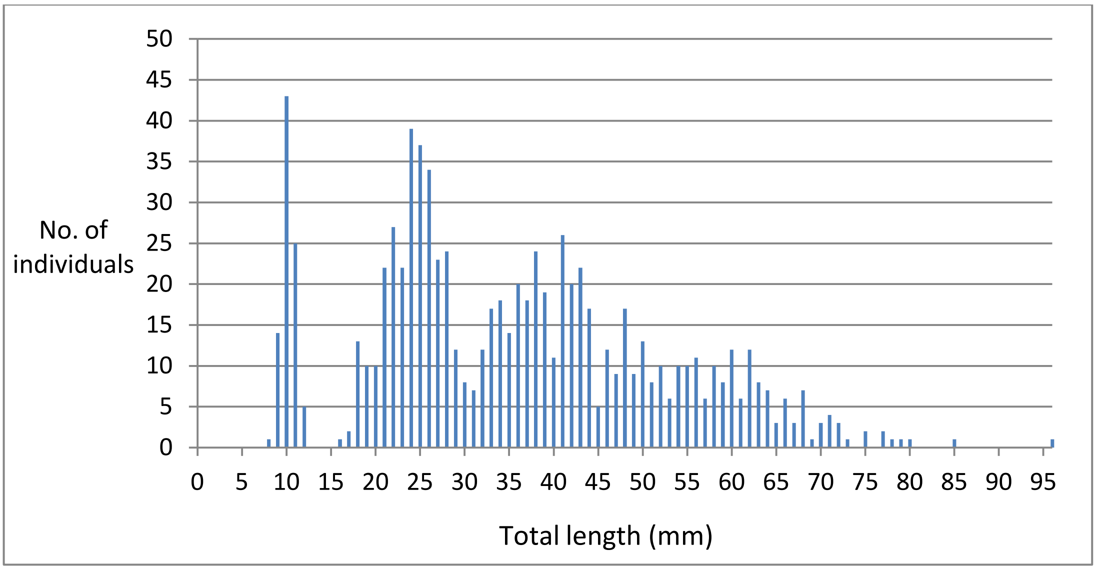

*Figure 5.2- A size frequency plot using total length of all individuals caught in the survey*

Plotting the number of individuals smaller than 13 mm total length per site against sample date showed individuals of this size were only captured after 19th July (fig 5.3). Before this date, berried females were present. The percentage of the total number of crayfish caught in each site accounted for by individuals of less than 13 mm total length increased throughout July, peaked in early August and declined thereafter (fig 5.3).

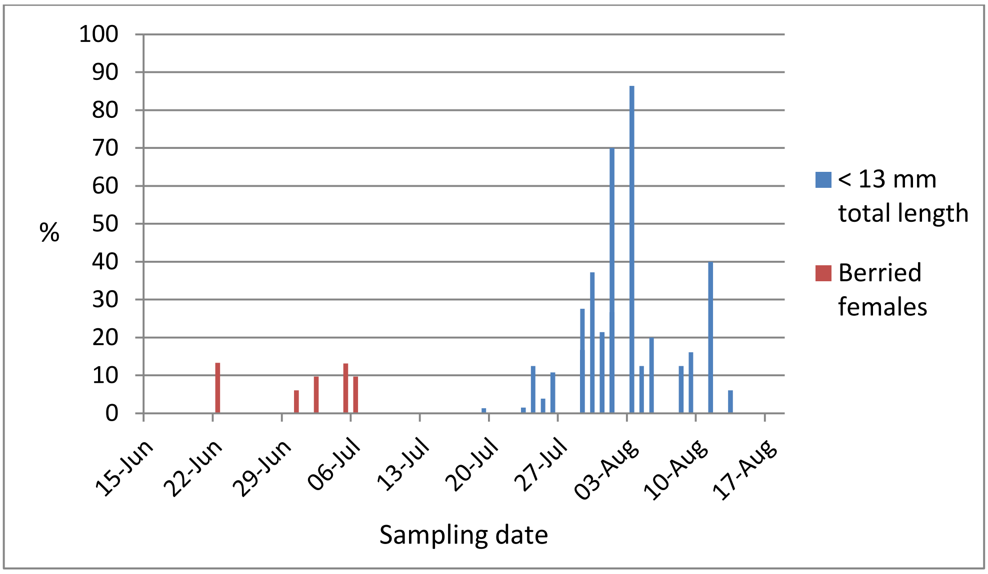

*Figure 5.3- Change over sampling period in the percentage of individuals recorded per site accounted for by berried females (red) and individuals less than 13 mm total length (blue)*

## 5.2 Distribution of crayfish on the River Wansbeck

All crayfish captured were WCC. WCC were present at all 27 sites for which permission was granted to share results. The total number of crayfish found at each site varied from 4 to 73 individuals or 4 to 57 with young of the year removed. The ten surber areas sampled in each site covered a total area of 4.9 $m^2$, therefore it could be calculated that the overall mean number of crayfish per sampled square meter was 5.3 for all individuals or 4.7 with young of the year removed. At the site-scale the number of crayfish caught per sampled square meter ranged from 0.8 to 14.9 individuals, with a median of 4.2 crayfish per square meter (fig 5.4a). Of the 328 surber areas sampled in total, 229 contained crayfish. Extrapolating the number of crayfish found in each 0.49 $m^2$ surber area to number per square metre gave estimated densities over a smaller scale. These ranged from zero to 24.5 crayfish per square metre with a median of 4.1 (fig 5.4b).

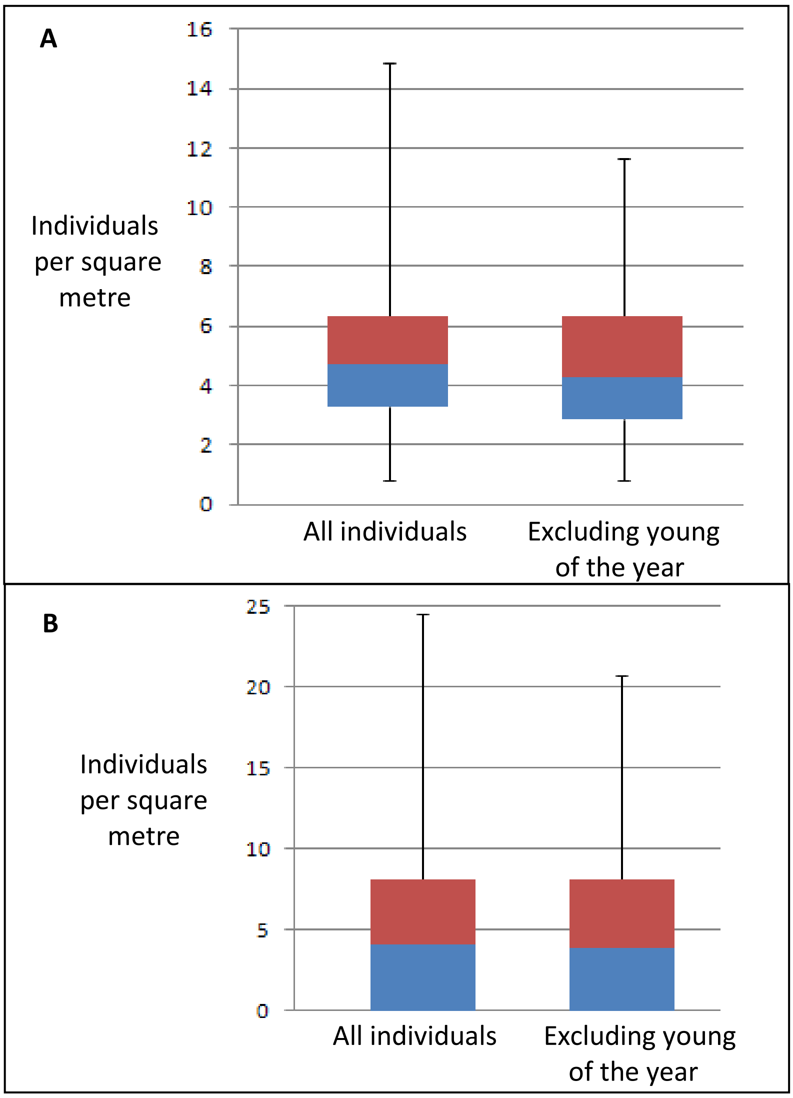

*Figure 5.4 - Box plots showing number of crayfish per square metre a) at the site-scale (total number of crayfish caught per site divided by 4.9) and b) at the surber-scale (number of crayfish per surber area x 2.041). Colour change shows the median value, blue area shows lower quartile, red area shows upper quartile and bars extend to maximum and minimum.*

The index of dispersion value (Eq. 4.1) was 2.2. The observed frequency distribution of crayfish in all surber areas did not fit the Poisson model (fig 5.5) but showed a good fit to the expected frequencies of the negative binomial distribution (fig 5.6). A chi-squared goodness-of–fit test showed that the observed distribution was significantly different to that expected by the Poisson model at the 5 % significance level (table 5.1). The U-statistic for the negative binomial model is considerably less than twice the standard error and therefore the binomial model adequately describes the observed data (table 5.1). The mean size of an aggregation, as described by equation 4.4, was 1.67.

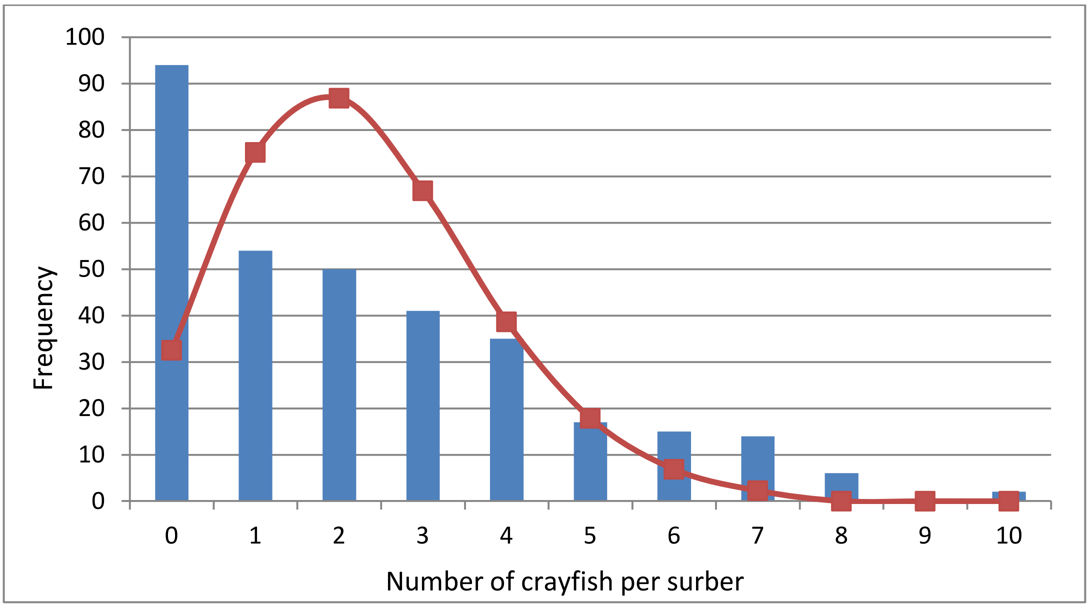

*Figure 5.5- Comparison of observed frequency distribution of 1+ crayfish in all surber areas (columns) to expected frequencies according to Poisson distribution (squares)*

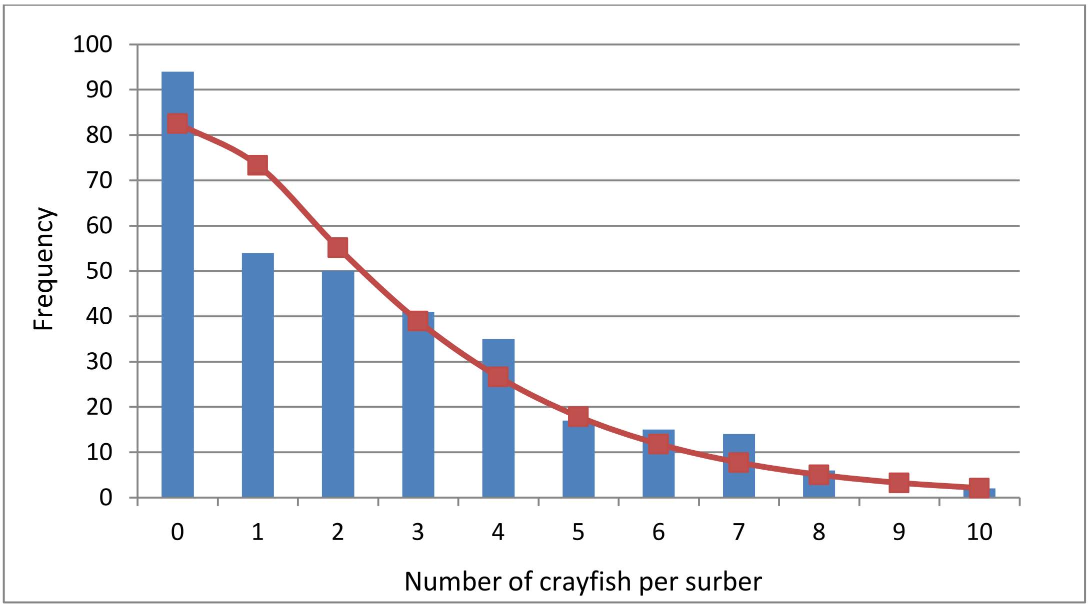

*Figure 5.6- Comparison of observed frequency distribution of 1+ crayfish in all surber areas (columns) to expected frequencies according to the negative binomial distribution (squares)*

*Table 5.1- Statistics generated by fitting Poisson and negative binomial distribution models to observed frequency distribution and testing their adequacy. Methods follow Krebs (1999)*

| **Poisson Distribution** | | **Negative binomial distribution** | |
|---|---|---|---|
| **Mean** | 2.31 | **Mean** | 2.31 |
| **Variance** | 5.10 | **Variance** | 5.10 |
| **Index of dispersion** | 2.20 | **K value** | 1.44 |
| **Chi-squared goodness of fit** | 21926.87 | **U- statistic for goodness-of-fit** | -0.916 |
| **Significance (*P*)** | < 0.0001 | **Standard error** | 0.564 |

Figure 5.7 shows the percentage of the total number of age 1+ crayfish recorded in the study that were found at each site, excluding sites where permission to report was not granted. The sites between 9 and 13, inclusive, accounted for a very high percentage of the total catch. Each site represented 3 % of the total number of samples but sites 9 to 13 each contained more than 5 % of the total number of crayfish caught. Sites 2, 17, 20, 29 and 31 also had relatively high total numbers of crayfish (see appendix table 1, where a break-down of site totals and population structure is presented).

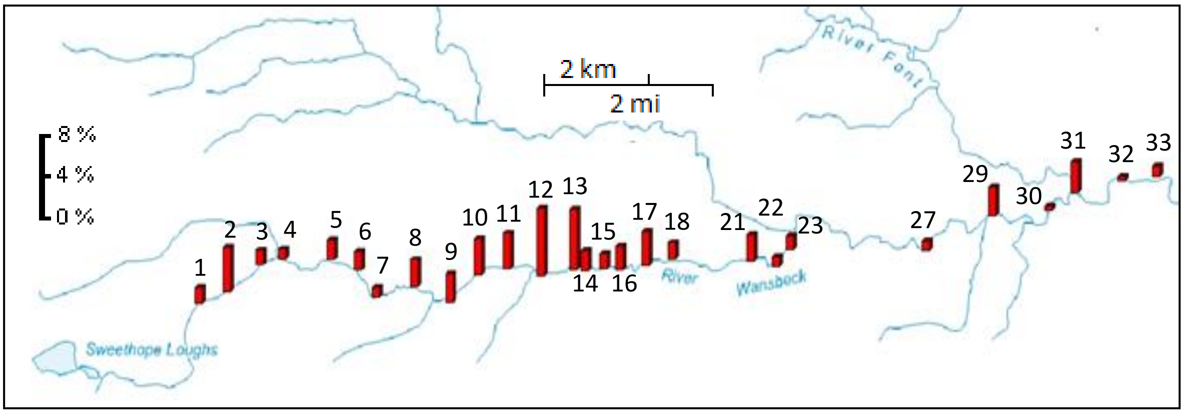

*Figure 5.7- Relative distribution of white clawed crayfish in study sites. Height of red bars shows the percentage of all crayfish caught in the study found at each sample site on the River Wansbeck, omitting sites where permission to report findings was not granted by landowner. Numbers show site labels names*

### 5.3 Niche breadth of white clawed crayfish on the River Wansbeck

### 5.3.1 Water quality parameters

Concentrations of nitrite (as N), bromide and phosphate at all sample sites were below the detection limits of the Dionex ion chromatography machine. The ranges of concentrations of other ions relevant to crayfish in the study area are shown in figures 5.8 and 5.9. pH and dissolved oxygen concentration were within required ranges for WCC at all sites (fig 5.10) (Trouhile *et al.* 2007).

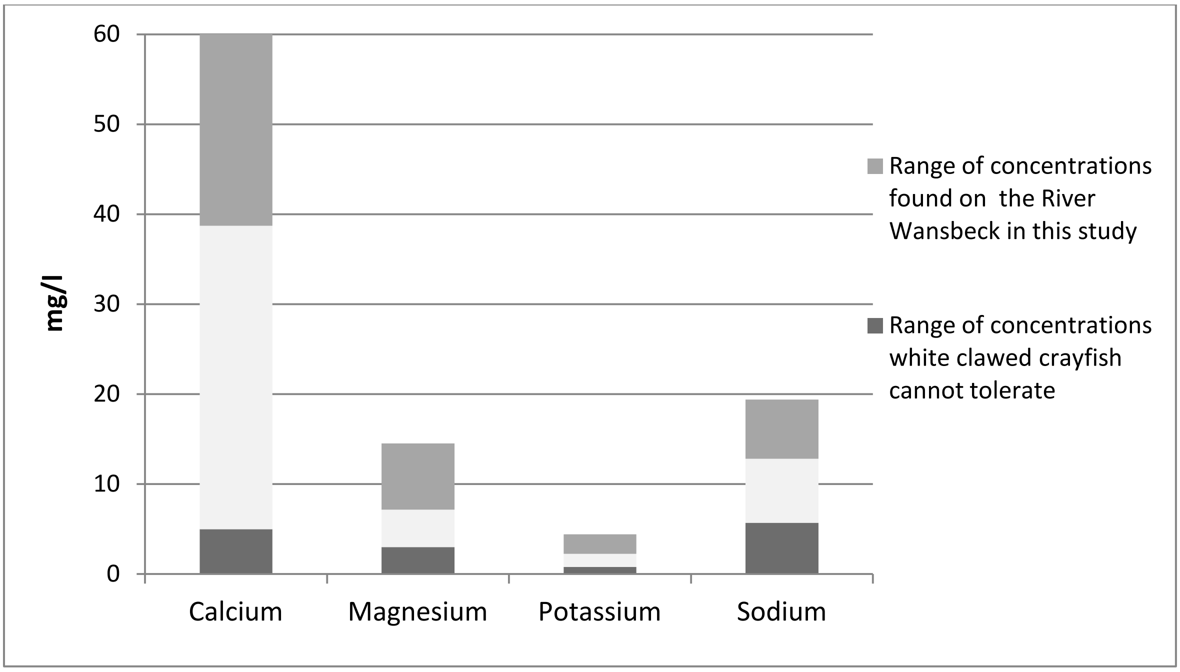

*Figure 5.8- Recorded concentrations for ions that white clawed crayfish require for survival. Tolerance limits derived from Jay and Holdich (1981) Smith et al. (1996) and Trouilhe et al. (2007) (see section 3.4.1).*

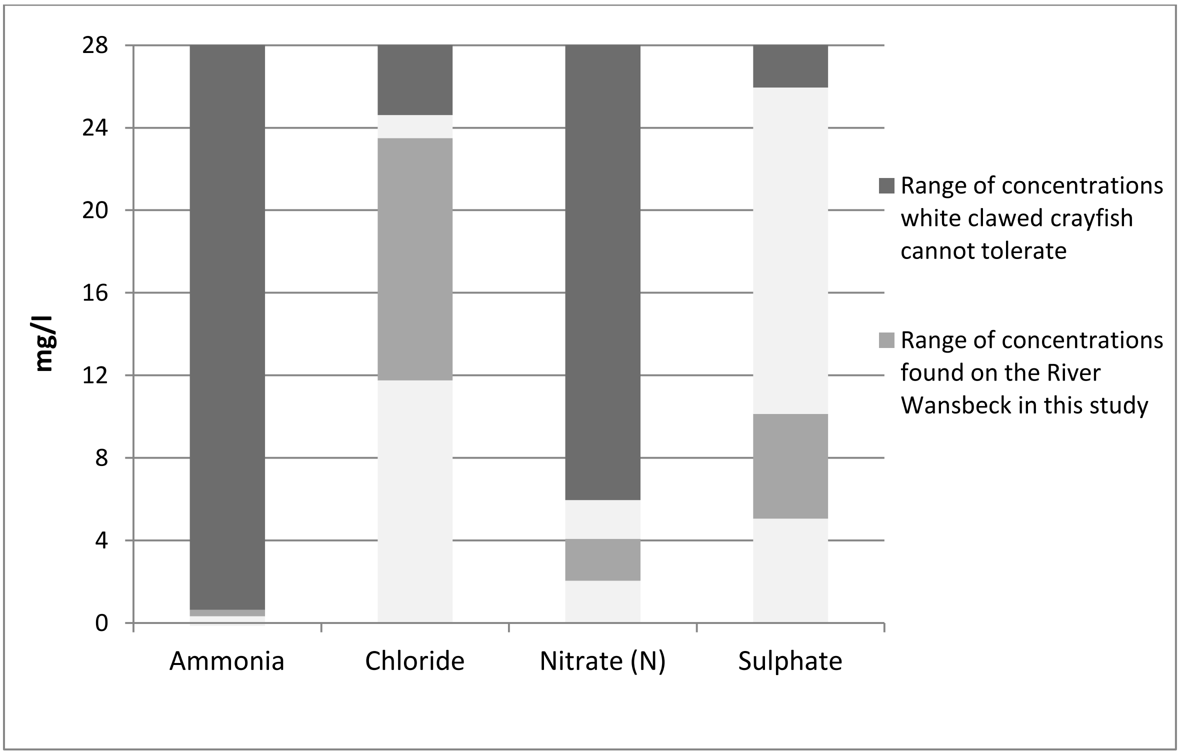

*Figure 5.9- Recorded concentrations for ions that white clawed crayfish cannot tolerate above a certain concentration. Tolerance limits derived from Smith et al. (1996) and Trouilhe et al. (2007) (see section 3.4.1)*

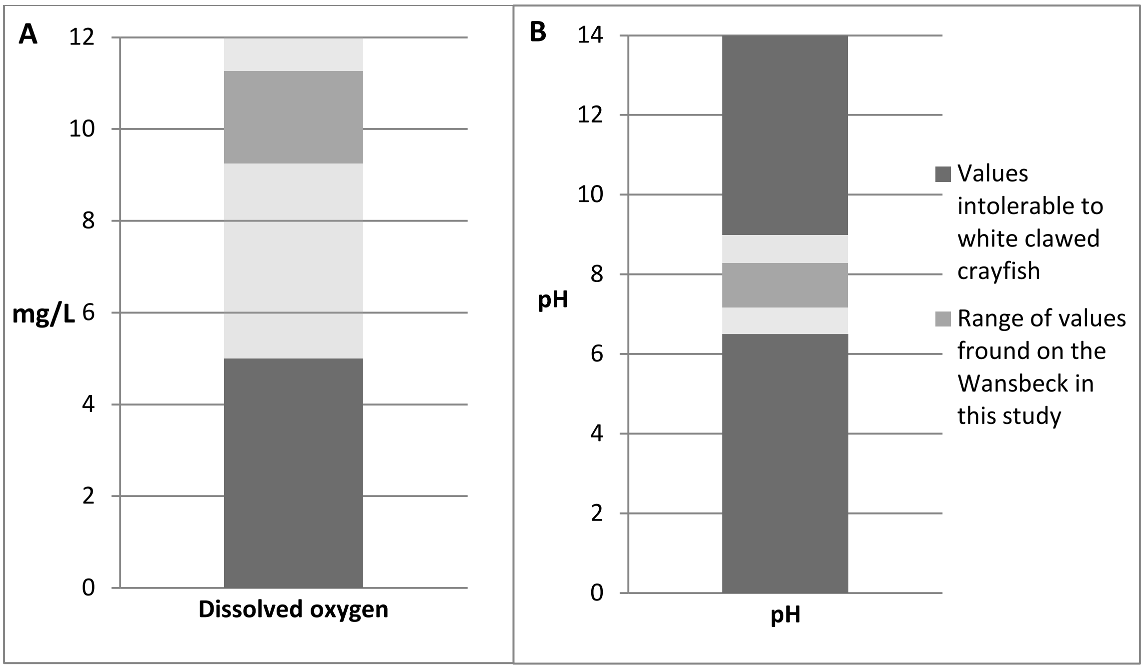

*Figure 5.10- a) Concentrations of dissolved oxygen and b) pH values. Tolerance limits derived from Jay and Holdich (1976) and Lyons and Kelly-Quinn (2003) (see section 3.4.1).*

### 5.3.2 Physical variables

There was no evidence of marginality in the use of continuously measured habitat variables by WCC but the use of several habitat variables was specialised to some degree (table 5.2). No response to boundary flow velocity coefficient of variation or $D_5$ at site or surber-scale was evident. Depth, $D_{50}$ and $D_{95}$ at both site and surber-scale showed the greatest specialisation.

*Table 5.2- Marginality and specialisation values for selection of focal habitat variables by white clawed crayfish. Habitat selection was considered to be evident when marginality values exceeded 0.5 and specialisation values exceed 1, see 4.7.2 for full details.*

| **Habitat variable** | **Marginality value** | **Specialisation value** | **Interpretation** |
|---|---|---|---|
| Sinuosity | 0.0062 | 0.983 | Neither |
| Gradient | 0.0443 | 1.01 | Neither |
| Width | 0.0643 | 1.16 | Specialisation |
| Site sinuosity | 0.0236 | 1.12 | Specialisation |
| Depth | 0.0612 | 1.13 | Specialisation |
| Boundary flow velocity | 0.0437 | 1.03 | Weak specialisation |
| Boundary flow coeff. variation | 0.00287 | 0.689 | Neither |
| 60 % flow velocity | 0.0125 | 1.033 | Weak specialisation |
| Site $D_5$ | 0.0666 | 0.948 | Neither |
| Site $D_{50}$ | 0.106 | 1.13 | Specialisation |
| Site $D_{95}$ | 0.0536 | 1.11 | Specialisation |
| Surber$D_5$ | 0.0666 | 0.948 | Neither |
| Surber$D_{50}$ | 0.106 | 1.13 | Specialisation |
| Surber$D_{95}$ | 0.0792 | 1.16 | Specialisation |

Every category of the habitat variables categorised qualitatively, e.g. bank material, included surber areas that contained multiple WCC. This showed that none of these habitat categories were intolerable to WCC. Considerably more than 5 % of surber areas in each habitat category were made use of by WCC. Crayfish were present in surber areas with the maximum and minimum values of boundary flow velocity, flow velocity at 60 % depth and surber $D_{50}$ and $D_{95}$. Crayfish were not present in surber areas with the maximum values for depth, or the minimum values for surber-scale $D_{50}$ and surber-scale $D_{95}$. Although no crayfish were found in the surber area with the highest median depth, multiple crayfish were present in the surber areas with the next highest median depth. This single surber area does not give enough evidence to infer a niche limit for depth. The thirty-five surber areas with $D_{50}$ less than 8 mm and the nineteen surber areas with $D_{95}$ less than 10 mm never supported multiple crayfish. A single crayfish was present in one surber area with these grain sizes but the surveyor's observations was that this crayfish was transitory at the time of the sample. When the niche space was considered as the habitat types that WCC used more than 5 % of (*c.f.* Krebs, 1999), the range of grain sizes within the niche of WCC was slightly narrower than that found using total absence. Surber areas with $D_{95}$ less than 50 mm and $D_{50}$ less than 8 mm were not part of the niche space. Applying Smith's (1982) measure of niche breadth to surber-scale $D_{50}$ and $D_{95}$ gave values of 0.94 and 0.9 respectively.

## 5.4 Predicting distribution

Multicollinearity was found to be present among habitat variables. Table 5.3 shows for each pair of variables correlated with an $R^2$ value exceeding |0.8| which variable was retained and which was removed from the logistic regression. After performing logistic regression analysis with all remaining variables, the final logistic regression model, based on 295 observations, contained nine variables significant at $P = 0.05$.

*Table 5.3- Habitat variables removed from logistic regression analysis due to collinearity with other habitat variables ($R^2 > |0.8|$)*

| **Variable removed** | **Colinear with** | **$R^2$** |
|---|---|---|
| Stream Order | Average width | 0.841 |
| Surber $D_{16}$ | Surber $D_{50}$ | 0.8703 |
| Surber $D_{84}$ | Surber $D_{50}$ | 0.8188 |
| Average width | Distance downstream | 0.8888 |
| Site-scale shade | Site-scale overhanging boughs | 0.8672 |
| Surber-scale shading | Surber-scale overhanging boughs | 0.8990 |
| Site $D_{84}$ | Site $D_{50}$ | 0.8235 |
| Site $D_{16}$ | Site $D_{50}$ | 0.8614 |

Applying Akaike's information criterion (Akaike, 1973) to all combinations of these variables showed that the optimum model contained five predictor variables (Eq. 5.1 and table 5.4). Three of these variables, $D_{50}$ within the surber area, presence of cobbles in a surber area and presence of pebbles within a surber area increased the likelihood of the surber area containing crayfish. The other variables, wood or shrub as a land-use within 50 m of the channel, decreased this chance. None of the remaining explanatory variables was significantly collinear with each other ($R^2 < 0.4$).

$$Log\left(\frac{P}{1-P}\right) = -0.9198065 - (1.361704w) - (0.9287149s) + (1.993771c) + (0.6766072p) + (0.0150951sbD_{50}) \qquad Eq.\ 5.1$$

Where *P* is the probability of crayfish being present in a given surber area, *w* is the binary presence/absence of woodland as a land-use within 50 m of the channel, *s* is the binary presence/absence of shrub as a land-use within 50 m of the channel, *c* is the binary presence/absence of cobbles within the surber area, *p* is the binary presence/absence of pebbles within the surber and $sb\ D_{50}$ is the $D_{50}$ in millimetres of the grains within the surber area.

In surber areas containing only sand, silt or bedrock and located in sites where surrounding land-use is not wood or shrub, the output of the equation 5.1 is – 0.9198. This translates to a probability of finding a WCC in a surber sample under these conditions of 28.5 %. Where woodland is the dominant land-use within 50 m of the channel, this probability is decreased by a factor of 3.91. Presence of shrub within 50 m of the channel decreases the probability of crayfish being present by a factor of 2.53. Presence of cobbles in a surber area make it 7.34 times more likely to contain crayfish and presence of pebbles in a surber area make it 1.97 times more likely to contain crayfish. The calculated *Z* values (table 5.4) show that cobbles have the greatest relative importance in this model. $D_{50}$ within the surber area also has a significant influence with each one millimetre increase in surber-scale $D_{50}$ increasing the likelihood of the surber area containing crayfish by a factor of 1.015. Surber-scale $D_{50}$ in the sampled data range from 0 to 150 mm. Thus, the odds of crayfish being present are 9.46 times higher in surber areas with the largest observed $D_{50}$ than in surber areas where $D_{50}$ is sand, silt or bedrock. Within the range of habitat variables recorded in the study site, the model predicts probabilities of crayfish presence between 3.88 and 93.4 %.

*Table 5.4- Outputs of the logistic regression. Standard error and confidence intervals associated with odds ratio (to 3 d.p)*

| Variable | Coeff. | Odds ratio | Standard error | Z | P \|z\| | 95 % C.I. | |
|---|---|---|---|---|---|---|---|
| Surber$D_{50}$ | 0.015095 | 1.01 | 0.006 | 2.50 | 0.01 | 1.00 | 1.027 |
| Cobbles | 1.993771 | 7.34 | 2.925 | 5.01 | 0.00 | 3.36 | 16.028 |
| Pebbles | 0.676607 | 1.96 | 0.598 | 2.23 | 0.02 | 1.08 | 3.569 |
| Shrub as 50 m land-use | -0.928715 | 0.39 | 0.177 | -2.08 | 0.03 | 0.16 | 0.949 |
| Woodland 50 m land-use | -1.361704 | 0.25 | 0.089 | -3.93 | 0.00 | 0.13 | 0.505 |

The likelihood ratio chi-square test was 100 % significant. This is a rare occurrence and shows that there is no chance that the likelihood ratio chi-square value could be obtained if the independent variables had no affect on the likelihood of finding crayfish. The model performs well at predicting presence of crayfish in the twenty surber areas omitted from model creation. The model predicts that eighteen of the twenty observations have more than a 50 % chance of containing crayfish. Sixteen of these surber areas actually contained crayfish. Thus, the reliability of the model is 89 %. Of the two surber areas the model predicts to have less than a 20 % chance of containing crayfish, both were absent of crayfish. The model predicts eleven surber areas to have more than an 80% chance of having crayfish. All of these surber areas did contain crayfish. For this sample, the model does not have any omission or commission error at this accuracy level.

## 5.5 Habitat preferences by proportional use

### 5.5.1 Categorical variables

The results of the chi-squared tests for preference of categorical habitat types are shown in table 5.5. The categories used are shown in table 4.1. Distribution of crayfish in areas with different valley forms and bank profiles was not significantly different from that expected if habitat use were random. Only land-use within 5 m of the channel influenced distribution, despite land-use within 50 m of the channel emerging as a predictor variable in the logistic regression output. The presence of exposed roots, submerged macrophytes or emergent vascular macrophytes did not influence the distribution of WCC at either site or surber scale. However, differences in the abundance of moss/algae in both sites and surbers did result in a pattern of proportional use significantly different from that expected if distribution were random. The presence of overhanging boughs above a surber area did not significantly affect the distribution of crayfish but the proportion of overhanging boughs within the site did have a significant influence on WCC distribution within the study area. Despite the proportion of run, glide and riffle at a site influencing proportional use by WCC, no significant response to the percentage of the site containing pool biotope was evident. Due to a small number of observations in which substrate within a surber area was armoured or embedded (n = 7), no significant influence of this on WCC distribution was found. However, a smaller proportion of surber areas with armoured/embedded substrate contained crayfish than surber areas without armoured/embedded substrate (43 % compared to 72 %). Surber areas containing boulders were not made use of by WCC any more or less frequently than would be expected if habitat use were random.

For all other habitat variables, the proportional use by WCC of different categories was significantly different from that which would be expected if habitat use were random. Graphs of observed frequency of presence of WCC in each habitat category compared to the expected frequency if habitat selection were random reveal the direction and strength of habitat preferences by WCC.

*Table 5.5 - Habitat preferences for categorical habitat types as shown by chi-squared test analysis. Categories used are shown in table 4.1. n = 327 or 328*

| **Habitat variable** | **Chi squared value ($\chi^2$)** | **Significance** | **Significant at α = 0.05** |
|---|---|---|---|
| Valley form | 7.724 | 0.052 | No |
| Land-use 50 m from channel | 6.787 | 0.079 | No |
| Land-use 5 m from channel | 6.347 | 0.042 | Yes |
| Site-scale bank material | 23.896 | 0.000006 | Yes |
| Site-scale bank profile | 1.799 | 0.615 | No |
| Site-scale overhanging | 6.208 | 0.0449 | Yes |
| Site-scale exposed roots | 0.923 | 0.337 | No |
| Site-scale moss/algae cover | 9.691 | 0.0079 | Yes |
| Site-scale submerged vascular macrophytes | 2.496 | 0.287 | No |
| Site-scale emergent vascular macrophytes | 0.635 | 0.426 | No |
| Cattle poaching | 9.724 | 0.00182 | Yes |
| Surber-scale bank material | 45.946 | < 0.000001 | Yes |
| Surber-scale bank profile | 2.202 | 0.531 | No |
| Surber-scale overhanging | 0.487 | 0.485 | No |
| Surber-scale exposed roots | 0.154 | 0.694 | No |
| Surber-scale moss/algae | 26.8301 | 0.000062 | Yes |
| Surber-scale submerged vascular macrophytes | 0.519 | 0.771 | No |
| Surber-scale emergent | 0.155 | 0.694 | No |
| Surber-scale erosion | 7.532 | 0.0231 | Yes |
| Pool | 3.231 | 0.357 | No |
| Glide | 7.944 | 0.0472 | Yes |
| Run | 8.140 | 0.0432 | Yes |
| Riffle | 11.639 | 0.0202 | Yes |
| Substrate armouring/embedding | 1.593 | 0.207 | No |
| Bedrock | 16.728 | 0.000043 | Yes |
| Boulder | 1.349 | 0.246 | No |
| Boulder and/or cobble | 48.465 | < 0.000001 | Yes |
| Boulder, cobble and/or pebble | 48.019 | < 0.000001 | Yes |

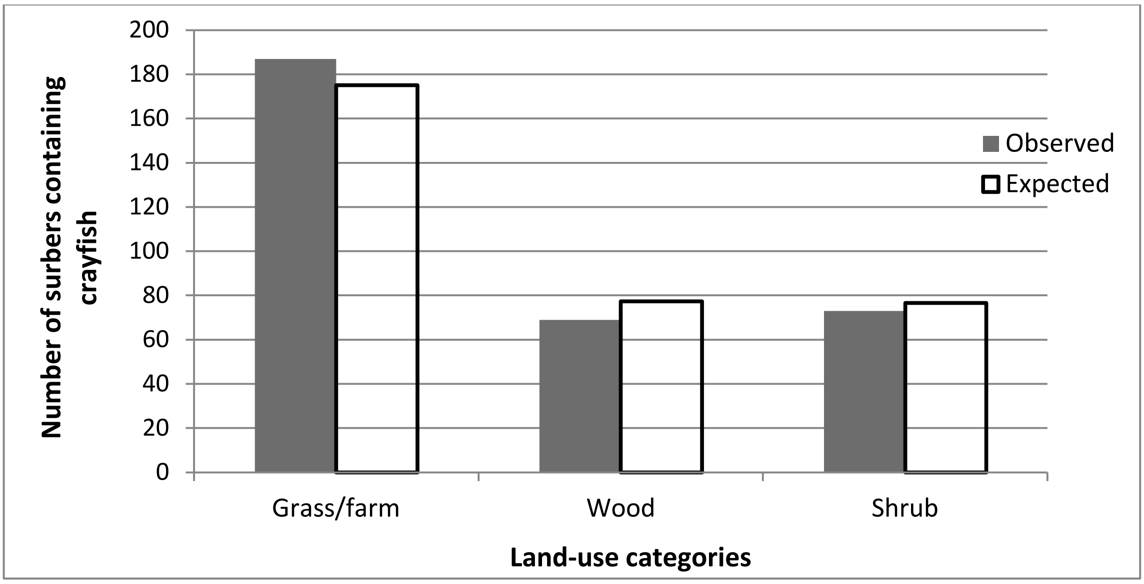

*Figure 5.11- Observed and expected numbers of surber areas containing crayfish in different categories of land-use within 5 m of the channel. Expected values based on random habitat use*

Areas with grassland/arable farmland with 5 m of the channel are used by WCC more frequently than expected whereas areas where wood and shrub are predominant within 5 m of the channel are used less frequently than expected (fig. 5.11). Similar patterns of preference for bank material were seen at the site and surber-scale (figs. 5.12 and 5.13). Areas with earth banks were used by WCC in a higher proportion and areas with bedrock banks used in a lower proportion than expected at random. At the surber-scale areas with boulders/cobbles as bank material were relatively avoided by WCC in the study area. This is the opposite result to boulders at the site-scale, which were preferred.

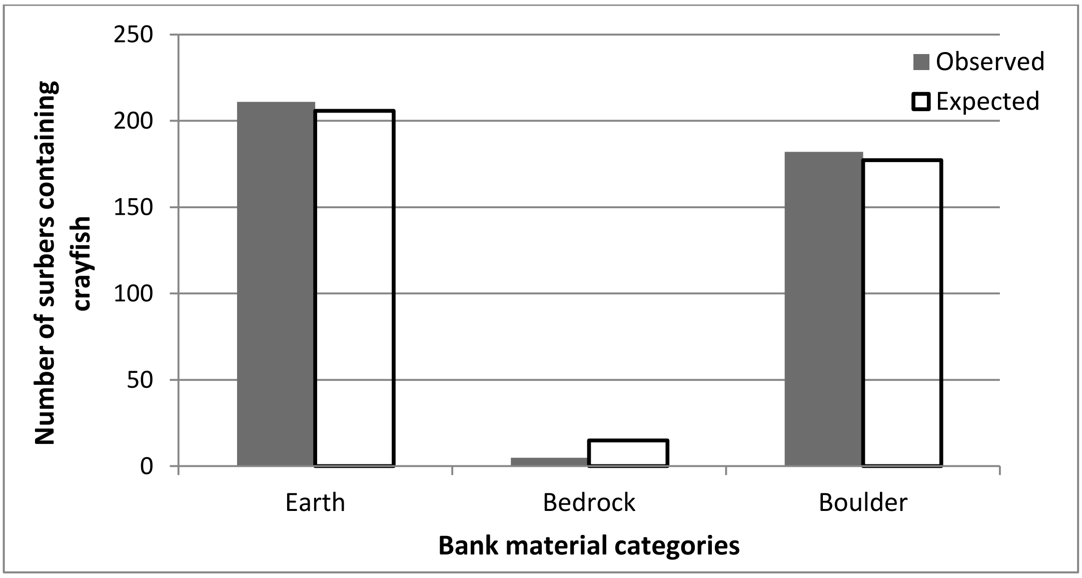

*Figure 5.12- Observed and expected numbers of surber areas containing crayfish in different categories of bank material recorded at the site-scale. Expected values based on random habitat use*

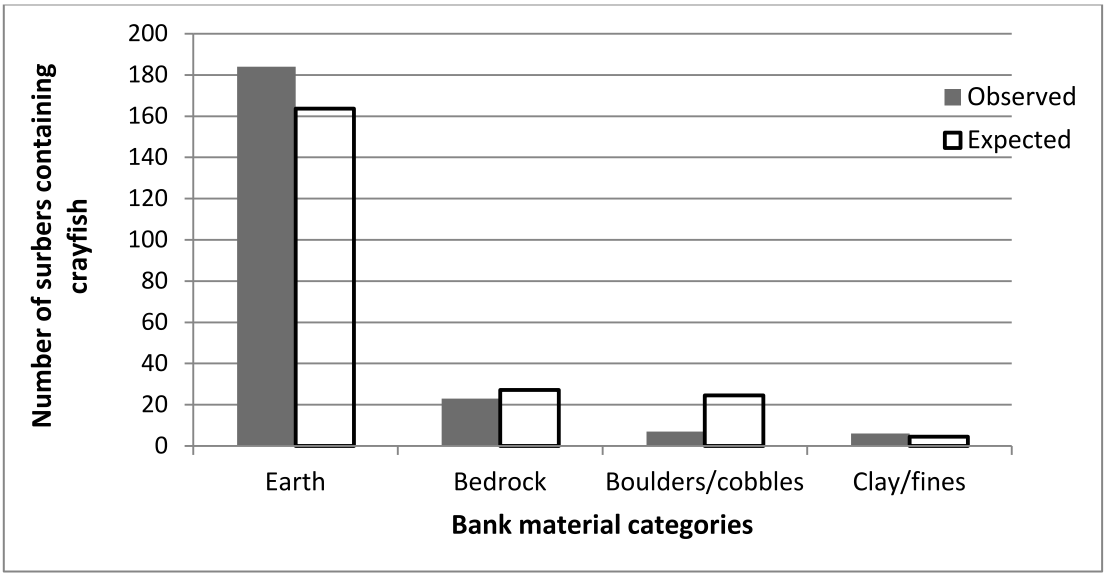

*Figure 5.13- Observed and expected numbers of surber areas containing crayfish in different categories of bank material recorded at the surber-scale. Expected values based on random habitat use*

Areas where cattle poaching of the riverbank had occurred were used by WCC in a higher proportion than expected at random (fig. 5.14a). Similarly, areas where rapid erosion was evident at the surber-scale in the form of poaching, slumps or unstable cliffs were used in a higher proportion than expected (fig. 5.14b). Conversely, surber areas adjacent to banks showing signs of slow erosion, such as undercut banks, were used by WCC less frequently than would be expected if habitat use were random.

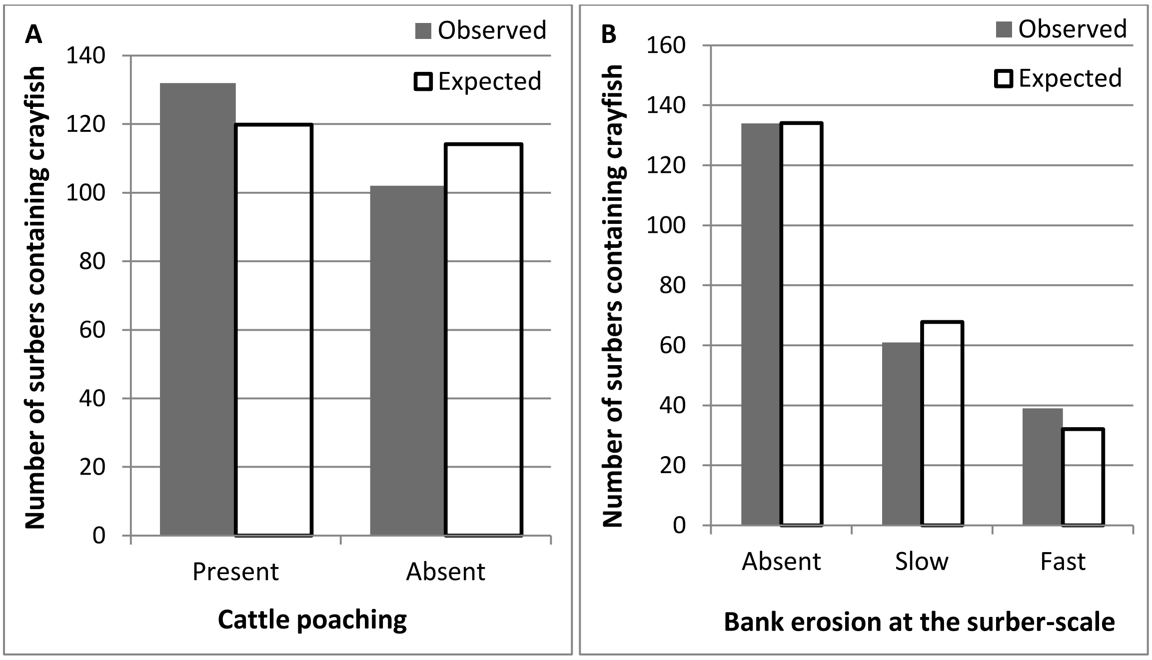

*Figure 5.14- Observed and expected numbers of surber areas containing WCC in a) sites with bank poaching present and absent and b) areas of different speeds of bank erosion adjacent to the surber. Expected values based on random habitat use*

Moss/ algae was the only vegetation type that influenced distribution of WCC in the study area. At the site-scale, areas with low moss/algae cover (less than 33 % of the site) were relatively avoided. Areas with intermediate coverage (between 33 and 66 % of the site) were used more frequently than expected at random and no deviation from the expected proportional use was evident for sites with very high coverage of moss (fig. 5.15). A similar pattern was evident at the surber-scale. Surber areas that did not contain moss/algae were used considerably less and surber areas with 1 – 20 % coverage of moss/algae marginally less than would be expected at random. Surber areas with 21 -80 % moss/algae cover were used more frequently than expected at random. No response by WCC to high abundances (more than 80 % coverage) of moss/algae was evident (fig. 5.16). Surber areas in sites where overhanging boughs were abundant (covered more than 33 % of the site) had lower occupancy rates than expected at random whilst surber areas in sites with less than 33 % cover by overhanging boughs or no boughs at all had slightly higher occupancy than expected at random (fig. 5.17).

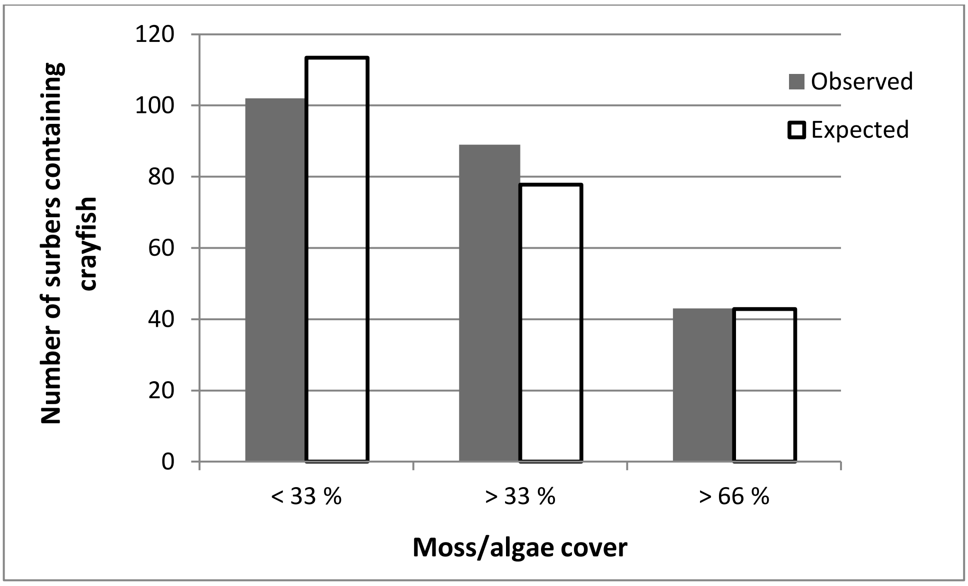

*Figure 5.15- Observed and expected numbers of surber areas containing crayfish in sites with different percentage cover of moss/algae. Expected values based on random habitat use*

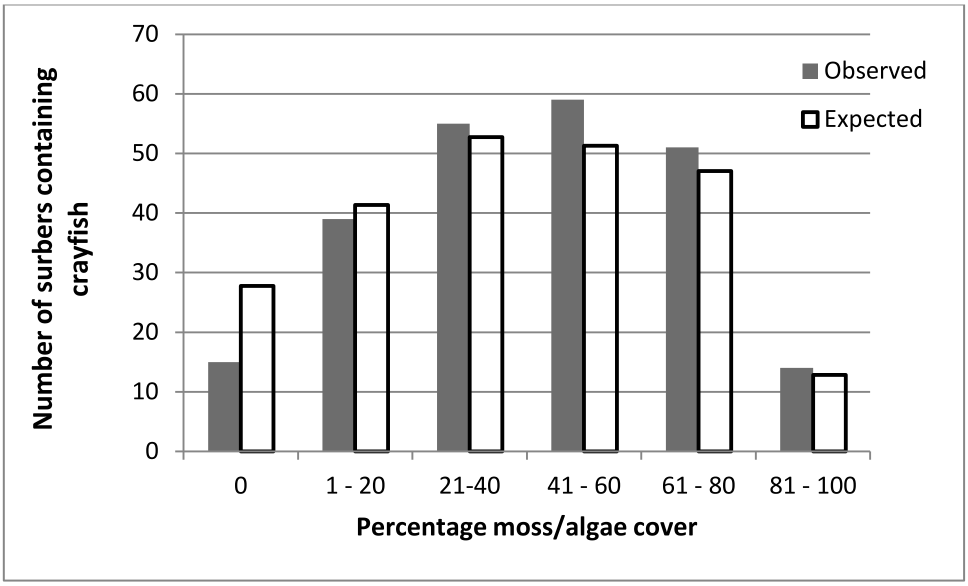

*Figure 5.16- Observed and expected numbers of surber areas containing crayfish in different categories of percentage cover of moss/algae. Expected values based on random habitat use*

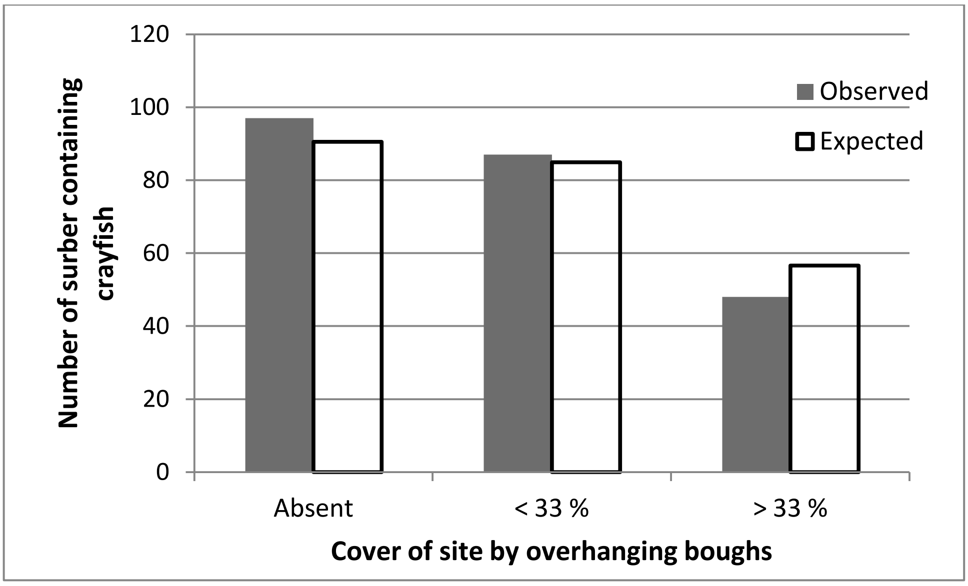

*Figure 5.17- Observed and expected numbers of surber areas containing crayfish in sites with differing percentage cover by overhanging boughs. Expected values based on random habitat use*

Surber areas in sites where glide biotopes accounted for more than 20 % of the site area were occupied by WCC marginally more frequently than would be expected at random, particularly those in sites with more than 40 % cover by glide biotope. Surber areas in sites with low proportions of glide (less than 20 %) were used in a lower proportion than would be expected at random (fig. 5.18). A complex pattern of proportional use in sites with differing proportions of run biotope was found in the study area. Surber areas in sites without any run biotope and in sites in which run biotope accounted for 21 – 40 % of the site area were occupied by WCC slightly more frequently than expected if habitat use were random (fig. 5.19). However, surber areas in sites in which run biotope accounted for 1 – 20 % or 61 – 80 % of the site area were occupied by WCC slightly less frequently than expected (fig. 5.19). Surber areas in sites with intermediate proportions (1 – 40 %) of riffle biotope were preferred by WCC in the study area. Surber areas in sites where riffle biotope was absent or where riffle accounted for more than 40 % of the site area were relatively avoided by WCC in this study (fig. 5.20).

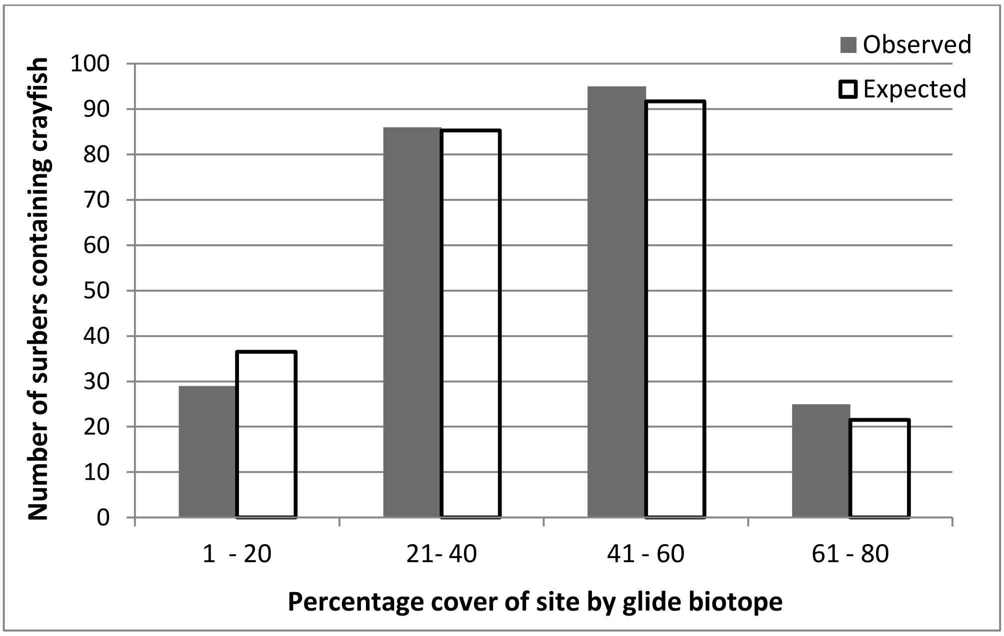

*Figure 5.18- Observed and expected numbers of surveyed surber areas containing crayfish in sites with differing percentage cover of glide biotope. Expected values based on random habitat use*

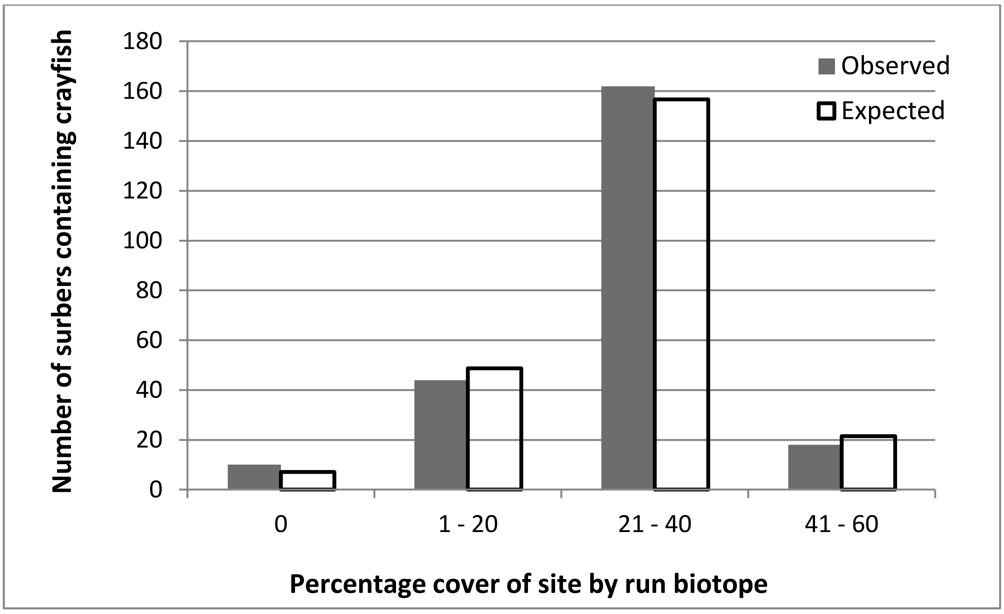

*Figure 5.19- Observed and expected numbers of surveyed surber areas containing crayfish in sites with differing percentage cover of run biotope. Expected values based on random habitat use*

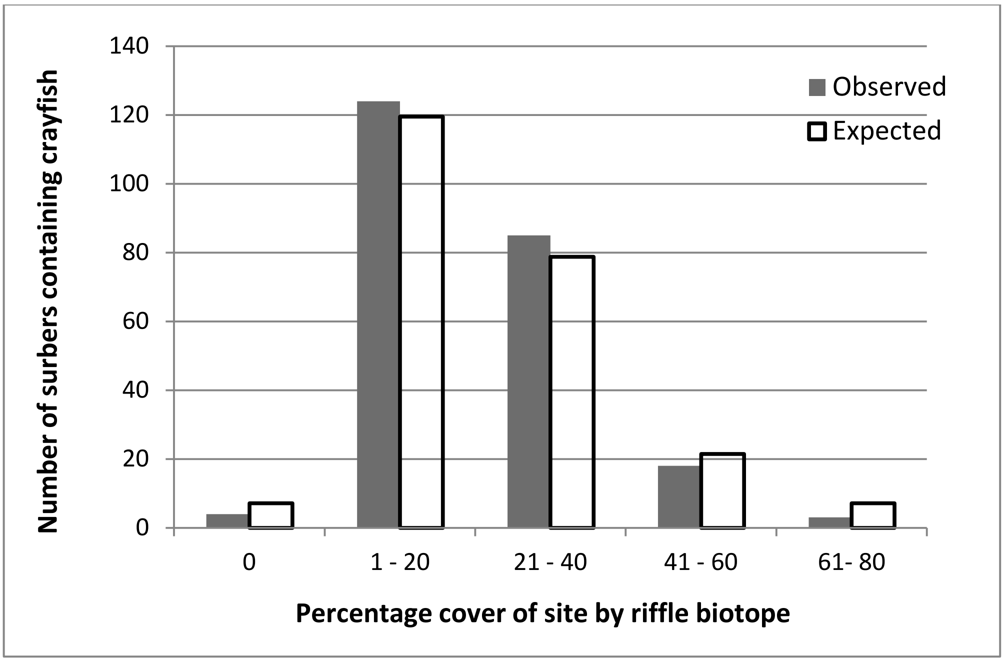

*Figure 5.20- Observed and expected numbers of surveyed surber areas containing crayfish in sites with differing percentage cover of riffle biotope. Expected values based on random habitat use*

Considerable differences between observed and expected proportional use by WCC of surber areas containing different substrate types were found. Surber areas containing bedrock were occupied less frequently than expected (fig. 5.21). Surber areas without boulders or cobbles were used by WCC less frequently than if habitat use were random (fig. 5.22). This difference was even more significant for surber areas than did not contain boulder, cobbles or pebbles. Only one such surber area was occupied meaning the observed value was considerably lower than the expected (fig. 5.23).

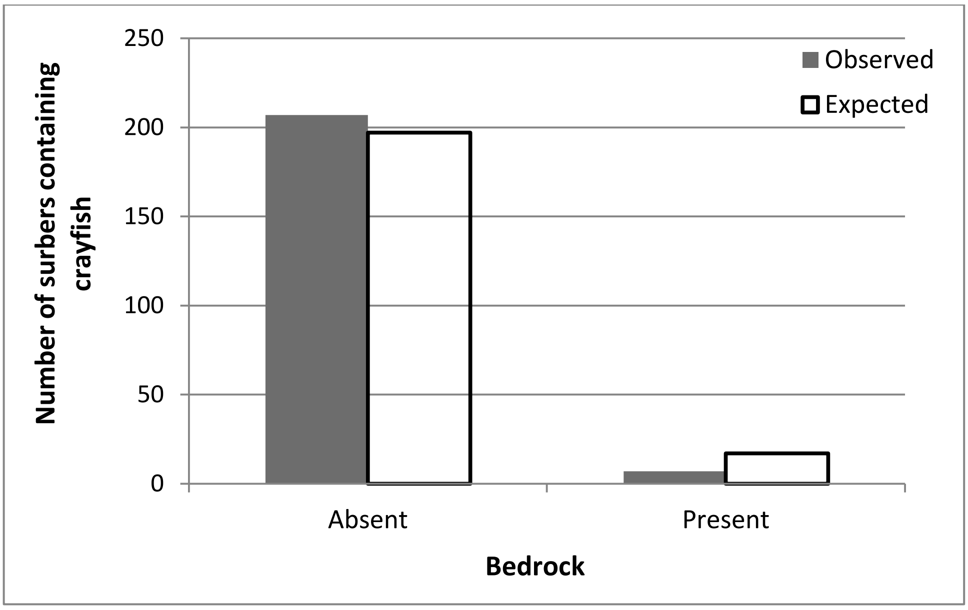

*Figure 5.21- Observed and expected numbers of surveyed surber areas containing crayfish when bedrock was and was not present. Expected values based on random habitat use*

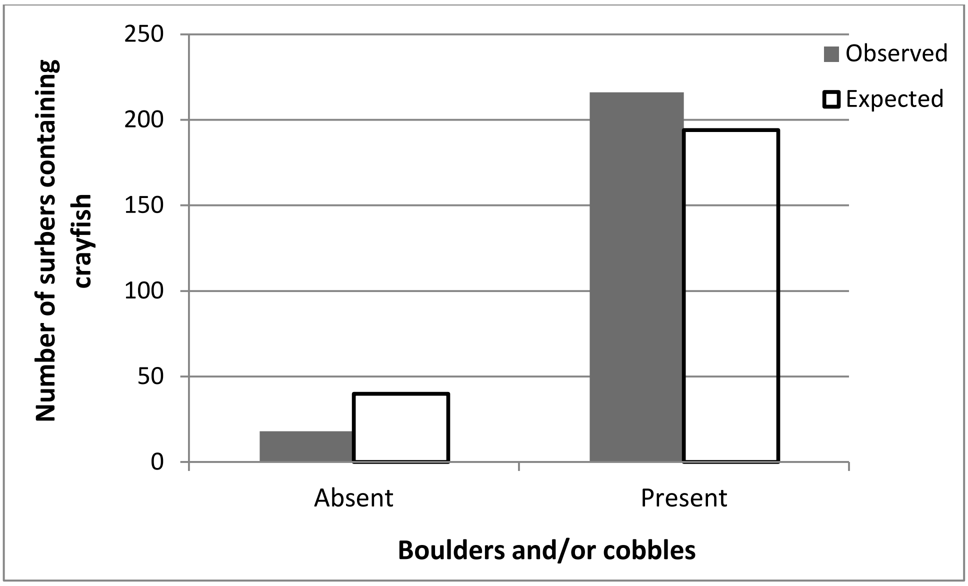

*Figure 5.22- Observed and expected numbers of surveyed surber areas containing crayfish when boulders and/or cobble were and were not present. Expected values based on random habitat use*

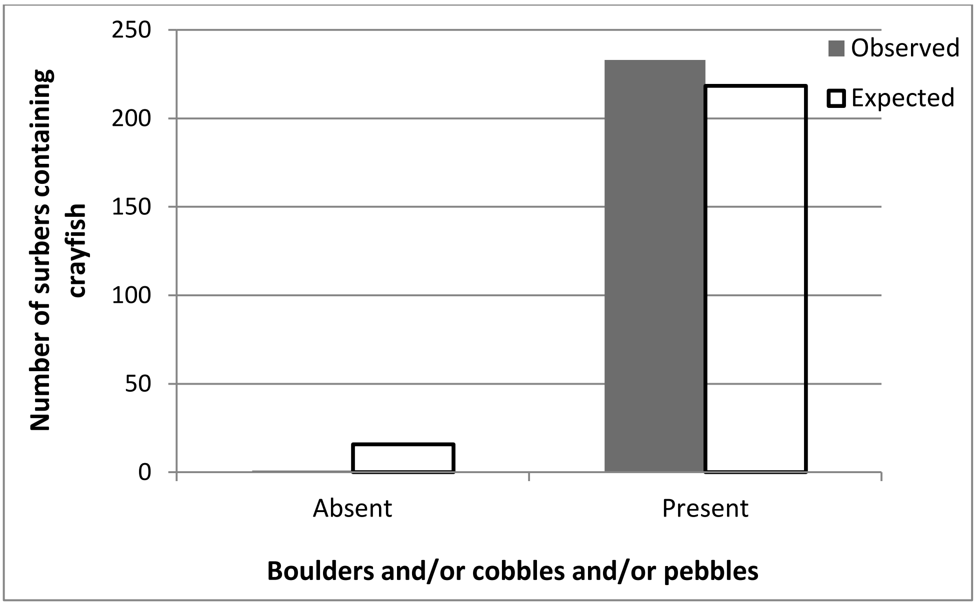

*Figure 5.23- Observed and expected numbers of surveyed surber areas containing crayfish when boulders and/or cobble and/or pebbles were and were not present. Expected values based on random habitat use*

### 5.5.2 Continuous variables

No trend was evident in the preference for surber areas in sites with differing average width but trends were evident for all other continuous variables for which specialisation had been found. For median depth, this trend was an intermediate peak. Surber areas with median depths between 16 and 20 cm were preferred and surber areas shallower than 16 cm and deeper than 30 cm were relatively underused (fig. 5.24). Regardless of the groupings used, there was noise in the pattern of depth preference.

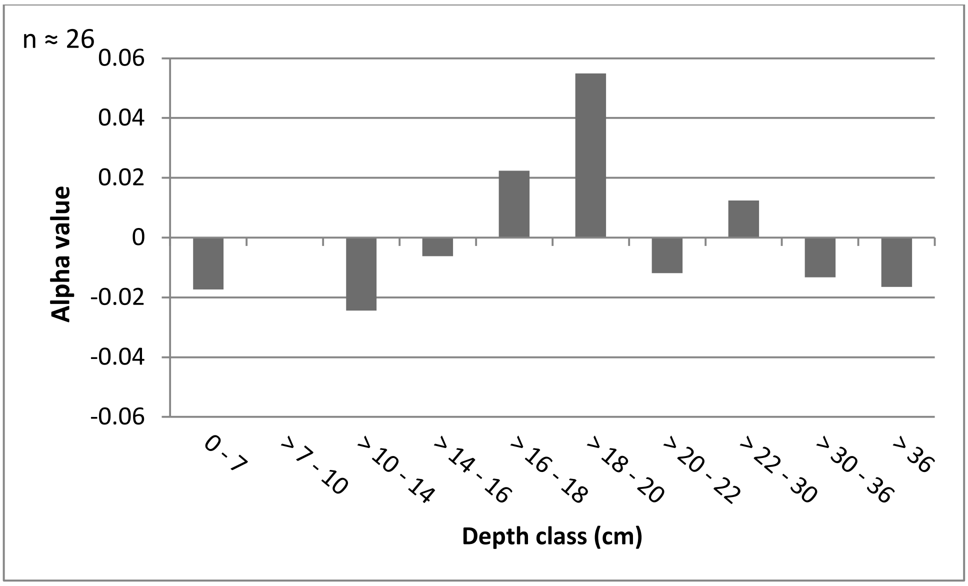

*Figure 5.24- Preferences by white clawed crayfish for different depth classes, as calculated by Manly's alpha. n is the approximate number of observations per group*

A preferences for intermediate values of flow velocities relative to the recorded range was demonstrated by WCC. Areas with flow velocity between 0.05 ms$^{-1}$ and 0.16 ms$^{-1}$ at 60 % depth and between 0.02 ms$^{-1}$ and 0.12 ms$^{-1}$ at the river bed were preferred (fig. 5.25 and 5.26). Slower and faster flowing areas were relatively avoided, particularly when considering boundary flow.

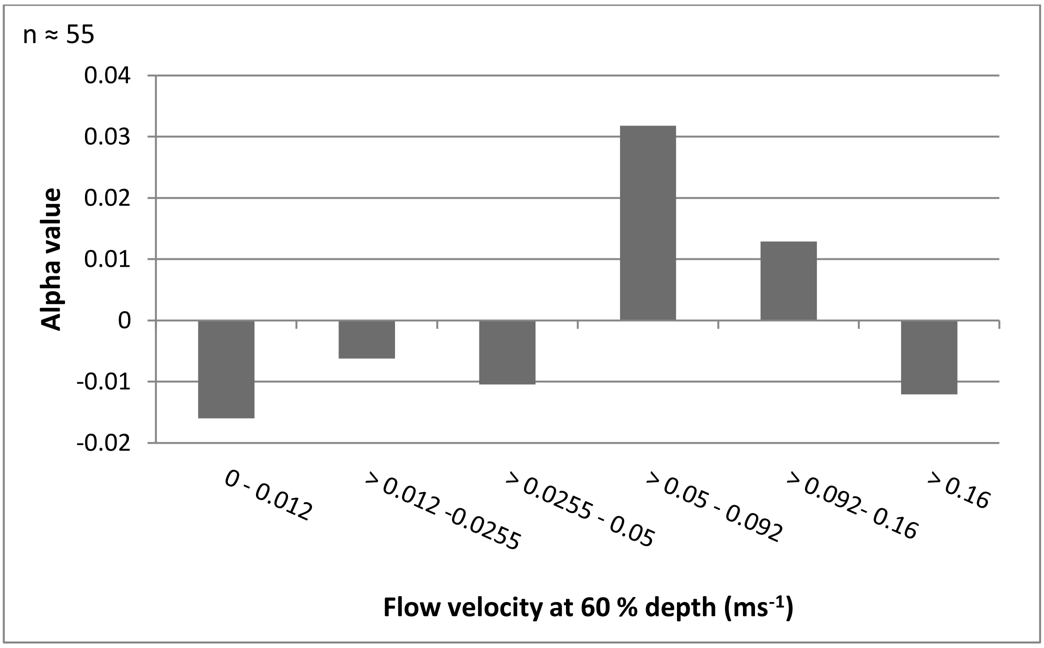

*Figure 5.25- Preferences by white clawed crayfish for different flow velocities at 60 % depth, as calculated by Manly's alpha. n is the approximate number of observations per group*

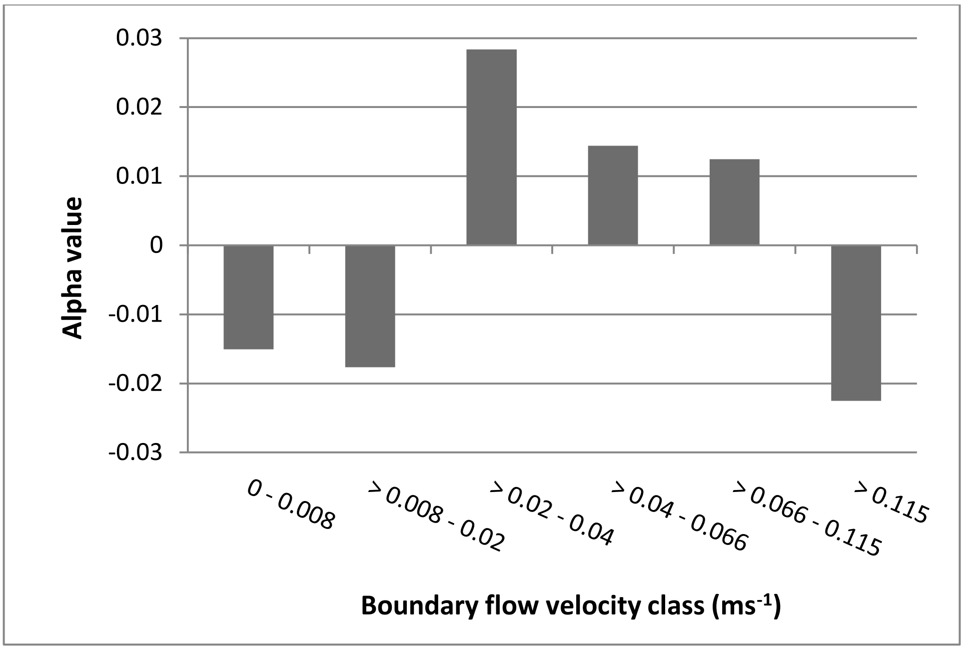

*Figure 5.26- Preferences by white clawed crayfish for different boundary flow velocity classes, as calculated by Manly's alpha. n is the number of observations per group*

Selection for grain size was evident at both the site and surber scale but alpha values are higher and trends more consistent at the surber-scale than at the site-scale. There was strong avoidance of surber areas with $D_{50}$ less than 8 mm and $D_{95}$ less than 50 mm. Intermediate $D_{50}$ values were preferred; strong selection was evident for surber areas with $D_{50}$ values between 35 and 77.5 mm (fig. 5.27). Selection for surber-scale $D_{95}$ was less specific, with all $D_{95}$ values above 92 mm being selected for equally (fig. 5.28). Similar trends were evident at the site-scale. Surber areas in sites with average $D_{50}$ less than 10 mm were avoided and site-scale average $D_{50}$ greater than 53 mm was selected for (fig. 5.29). Surber areas in sites with average $D_{95}$ less than 100 mm were avoided and surber areas in sites with average $D_{95}$ greater than 215 mm were preferred. Between these grain sizes there was noise in the data set and alpha values were small (fig. 5.30).

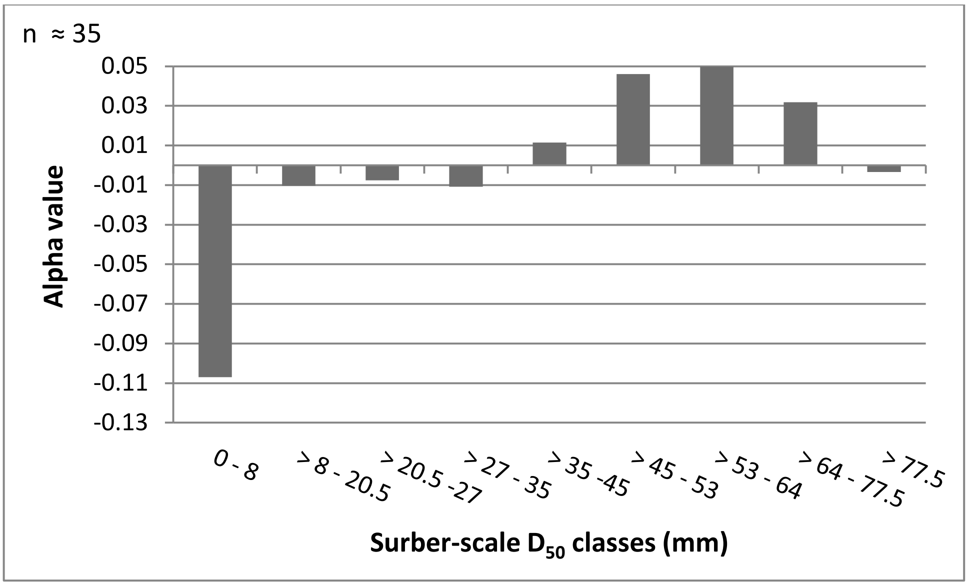

*Figure 5.27- Preferences by white clawed crayfish for different classes of $D_{50}$ value in surber areas, as calculated by Manly's alpha. n is the approximate number of observations per group*

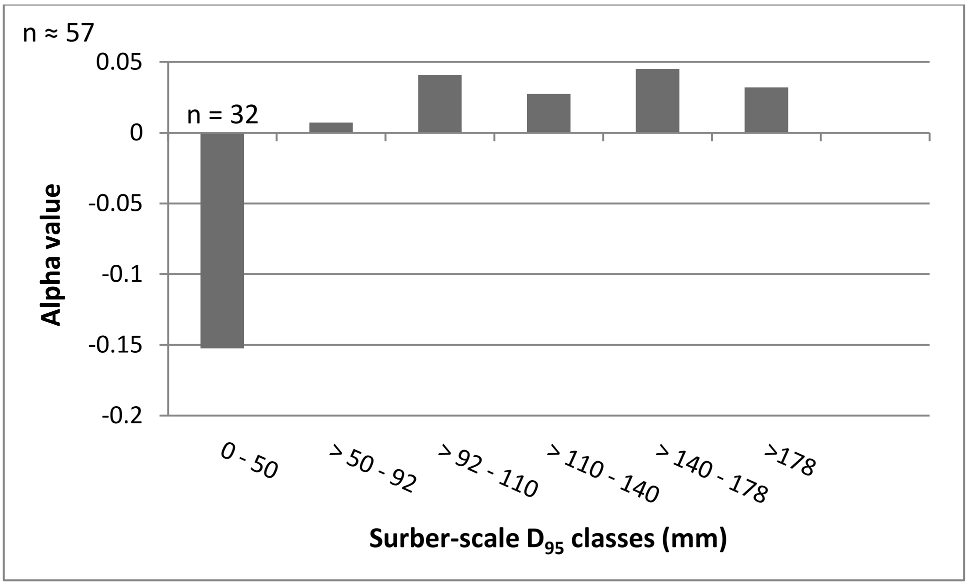

*Figure 5.28- Preferences by white clawed crayfish for different classes of average $D_{95}$ values in surber areas, as calculated by Manly's alpha. n is the approximate number of observations per group*

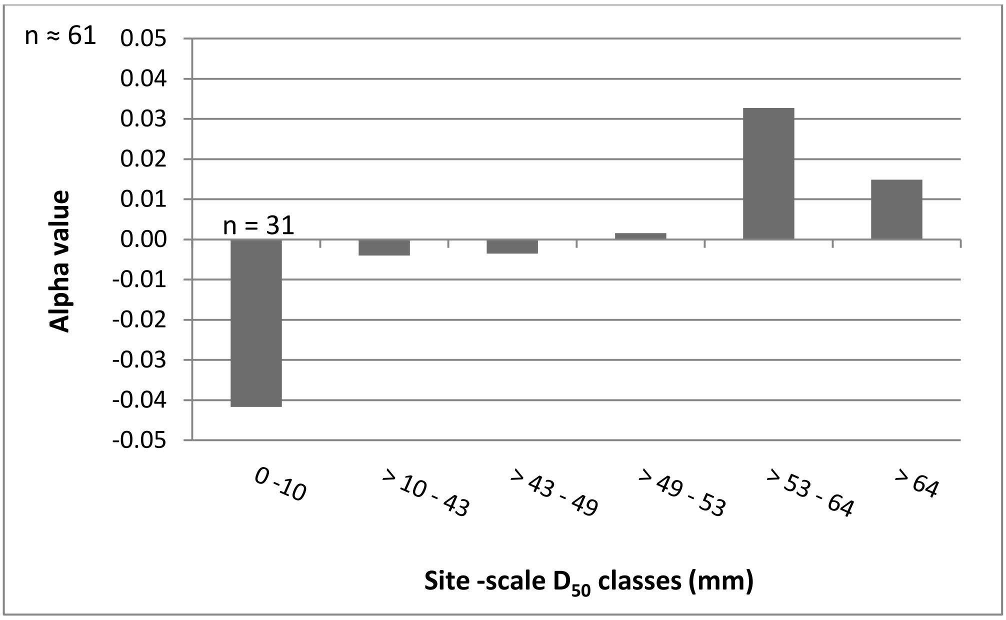

*Figure 5.29- Preferences by white clawed crayfish for different classes of average $D_{50}$ values in sites, as calculated by Manly's alpha. n is the approximate number of observations per group*

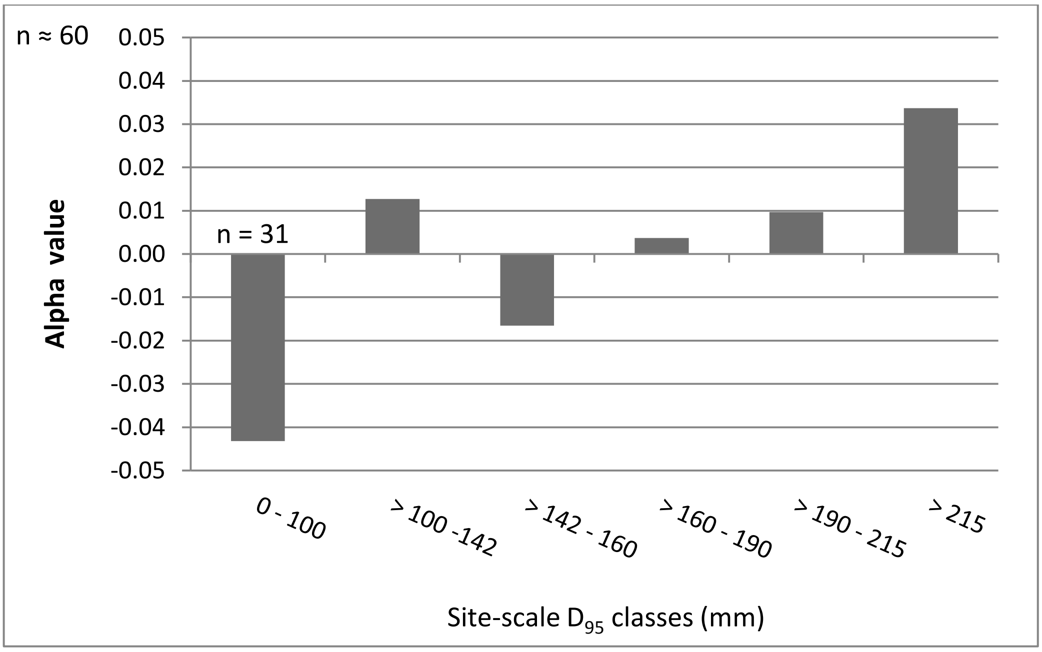

*Figure 5.30- Preferences by white clawed crayfish for different classes of average $D_{95}$ values, in sites as calculated by Manly's alpha. n is the approximate number of observations per group*

### 5.6 Analysis of crayfish population density

The good fit of the observed frequency distribution of number of crayfish per surber area to the negative binomial distribution shows that the observed data is not normally distributed. This was supported by the significance of the Kolmogorov-Smirnoff test ($K$ = 0.171; $P$ < 0.0001) and the result that 0.61 % of observations exceeded three standard deviations of the mean. The significance of the results of Levene's tests for each habitat variable were varied. For most variables, the statistic was insignificant meaning the samples had equal variances. However, the output of Levene's tests for valley-form and all biotope types were significant at the 5 % significance level, meaning observations in categories of these variables had unequal variances. Overall, non-parametric tests were deemed suitable for analysis of WCC population density.

### 5.6.1 Categorical variables

From Kruskal-Wallis tests it can be seen that the number of crayfish per surber area was not influenced by valley-form, bank profile at both site and surber scale, exposed roots at both scales, submerged and emergent vascular macrophytes at both scales, overhanging boughs at the surber-scale or presence of boulders in a surber area (table 5.6). For all other measured categorical habitat variables the sampled densities of WCC in different categories were from significantly different populations.

*Table 5.6 – Results of Kruskal-Wallis tests performed on categorical habitat variables. Differences are considered significant at an α value of 0.05. See table 4.1 for categories*

| Habitat variable | Kruskal-Wallis value | Significance | Significant at |
|---|---|---|---|
| Valley form | 7.717 | 0.051 | No |
| Land-use 50 m from channel | 6.617 | 0.0366 | Yes |
| Land-use 5 m from channel | 23.339 | 0.0001 | Yes |
| Site-scale bank material | 22.184 | 0.0001 | Yes |
| Site-scale bank profile | 0.3 | 0.8609 | No |
| Site-scale overhanging boughs | 11.270 | 0.0036 | Yes |
| Site-scale exposed roots | 1.697 | 0.1927 | No |
| Site-scale moss/algae cover | 19.423 | 0.0001 | Yes |
| Site-scale submerged vascular | 4.201 | 0.1224 | No |
| Site-scale emergent vascular | 1.340 | 0.2471 | No |
| Cattle poaching | 11. 056 | 0.0009 | Yes |
| Surber-scale bank material | 9.038 | 0.0288 | Yes |
| Surber-scale bank profile | 0.858 | 0.8355 | No |
| Surber-scale overhanging boughs | 0 | 1 | No |
| Surber-scale exposed roots | 1.412 | 0.2347 | No |
| Surber-scale moss/algae cover | 22.740 | 0.0004 | Yes |
| Surber-scale submerged vascular | 3.455 | 0.6301 | No |
| Surber-scale emergent vascular | 0.272 | 0.6023 | No |
| Surber-scale erosion | 13.206 | 0.0014 | Yes |
| Pool | 8.620 | 0.0348 | Yes |
| Glide | 14.41 | 0.0027 | Yes |
| Run | 23.878 | 0.0001 | Yes |
| Riffle | 23.209 | 0.0001 | Yes |
| Substrate armouring/embedding | 3.369 | 0.0664 | No |
| Bedrock | 22.939 | 0.0001 | Yes |
| Boulder | 1.984 | 0.1590 | No |
| Boulder and/or cobble | 41.460 | 0.0001 | Yes |
| Boulder, cobble and/or pebble | 35.092 | 0.0001 | Yes |

Areas with grass or farmland within 5 m of the channel had significantly higher densities of WCC than other land-uses (fig. 5.31a and table 5.7). Similarly, areas with grass or farmland within 50 m of the channel had significantly higher densities of crayfish than areas of woodland (figure 5.31b and table 5.7). There was no significant differences in density of crayfish in areas of the channel with a surrounding land-use of woodland compared to areas with a surrounding land-use of shrubs.

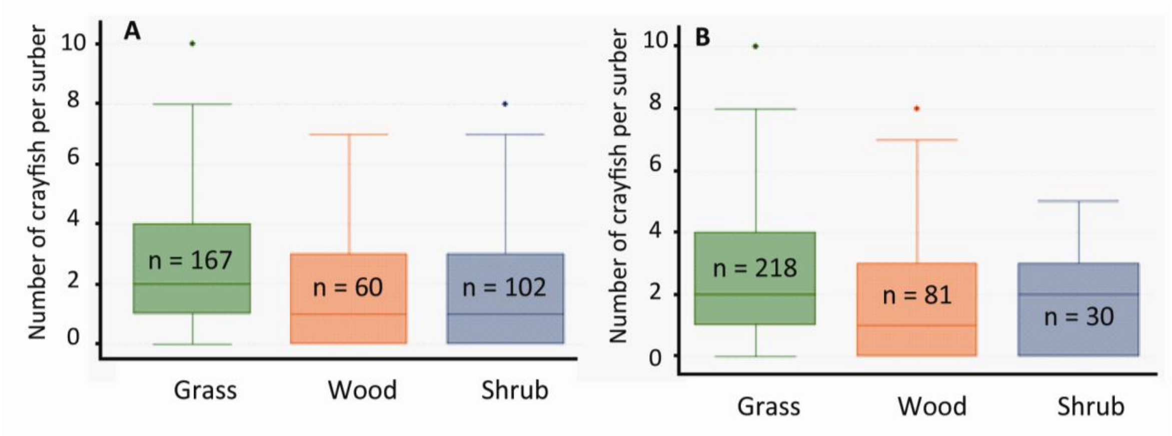

*Figure 5. 31 - Box plots, showing minimum, lower quartile , median, upper quartile, maximum and outliers of the number of crayfish per surber area in areas of differing land-use within a) 5 m and b) 50 m of the channel. n is the number of surber areas sampled in each category*

*Table 5.7 – Significance P values of Mann-Whitney U tests for paired comparisons of white clawed crayfish density in different land-use categories. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Land use 5 m** | Grass/arable | Woodland | Shrub |
|---|---|---|---|
| Grass/arable | | | |
| Woodland | 0.0008 | | |
| Shrub | 0 | 0.6537 | |

| **Land use 50 m** | Grass/arable | Woodland | Shrub |
|---|---|---|---|
| Grass/arable | | | |
| Woodland | 0.0133 | | |
| Shrub | 0.2562 | 0.6604 | |

Sites where the predominant bank material was bedrock had significantly lower densities of WCC than sites with a predominant bank material of earth or boulder/cobble (fig. 5.32a and table 5.8). There was no significant difference between WCC densities in areas of different bank material when viewed at the surber-scale. Despite surber areas adjacent to banks composed of clay or fines containing a much lower median density of crayfish than all other bank materials, this difference was not significant due to the low number of observations in this category (fig. 5. 32b and table 5.8).

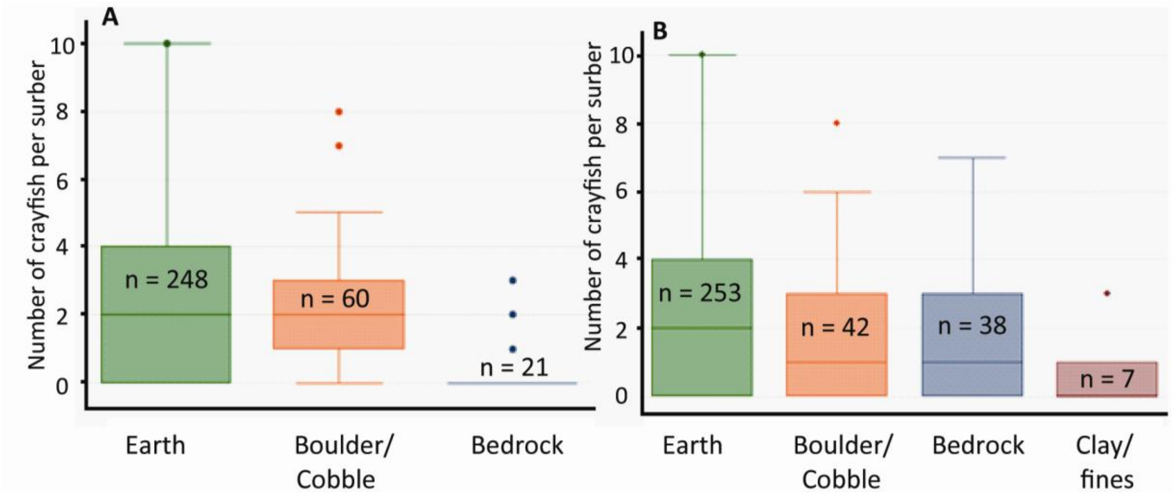

*Figure 5.32 - Box plots, showing minimum, lower quartile , median, upper quartile, maximum and outliers of the number of crayfish per surber area in areas of differing bank material over a) site-scale and b) surber-scale. n is the number of surber areas sampled in each category*

*Table 5.8 – Significance P values of Mann-Whitney U tests for paired comparisons of white clawed crayfish density in different bank material categories. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Site- scale bank material** | Earth | Boulder/Cobble | Bedrock |
|---|---|---|---|
| Earth | | | |
| Boulder/cobble | 0.6583 | | |
| Bedrock | 0 | 0 | |

| **Surber bank material** | Earth | Boulder/cobble | Bedrock | Clay/fines |
|---|---|---|---|---|
| Earth | | | | |
| Boulder/cobble | 0.0312 | | | |
| Bedrock | 0.4064 | 0.9378 | | |
| Clay/fines | 0.0329 | 0.1099 | 0.2311 | |

Sites with evidence of cattle poaching contained significantly higher densities of crayfish than sites where cattle poaching was not evident (fig. 5.33b and table 5.9). Similarly, surber areas adjacent to banks showing rapid erosion (slumps, poaching or unstable cliffs) contained significantly higher densities of crayfish than surber areas next to banks that were not eroding or were showing signs of slow erosion (fig. 5.33a and table 5.9).

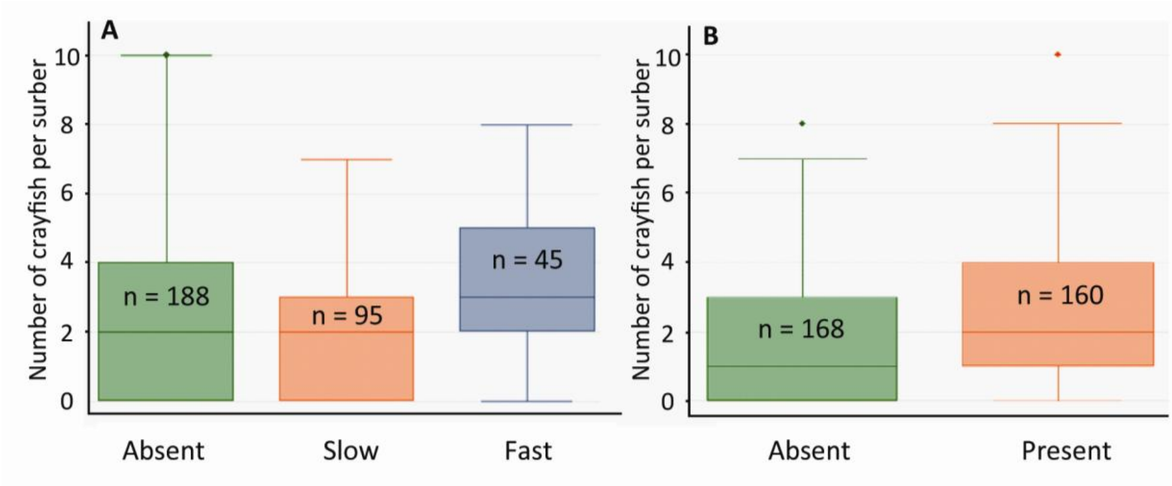

*Figure 5.33 - Box plots, showing minimum, lower quartile , median, upper quartile, maximum and outliers of the number of crayfish per surber area in areas of differing in a) speeds of erosion at the surber-scale and b) presence of cattle poaching at the site-scale. n is the number of surber areas sampled in each category*

*Table 5.9 – Significance P value of Mann-Whitney U tests for paired comparisons of white clawed crayfish density in different erosion and cattle poaching categories. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Cattle Poaching** | Present | Absent |
|---|---|---|
| Present | | |
| Absent | 0.0009 | |

| **Erosion** | Absent | Slow | Fast |
|---|---|---|---|
| Absent | | | |
| Slow | 0.3654 | | |
| Fast | 0.0016 | 0.0004 | |

Population density of WCC was significantly lower in sites where more than two thirds of the channel was covered by overhanging boughs than in sites where overhanging boughs covered less of the channel or were absent (fig. 5.34a and table 5.10). Despite this, overhanging boughs had no influence on WCC population density at the surber-scale.

At both site and surber-scale, abundance of moss/algae influenced average population density of WCC. Sites with less than a third of the substrate covered in moss/algae had significantly lower densities of crayfish than sites with 33 – 66 % coverage by moss/algae. No significant difference was evident between sites with more than 66 % moss/algae cover and all other sites . An intermediate coverage by moss/algae gives resulted in the highest densities of WCC (fig. 5.34b and table 5.10). Surber areas in which more than 20 % of substrate was covered by moss/algae has higher median WCC densities than surber areas with less than 20 % or no moss/algae present (fig. 5.35). However, the only significant difference was that surber areas without any moss/algae contained lower numbers of WCC than surber areas where 21- 80 % of substrate was covered by moss/algae (table 5.11).

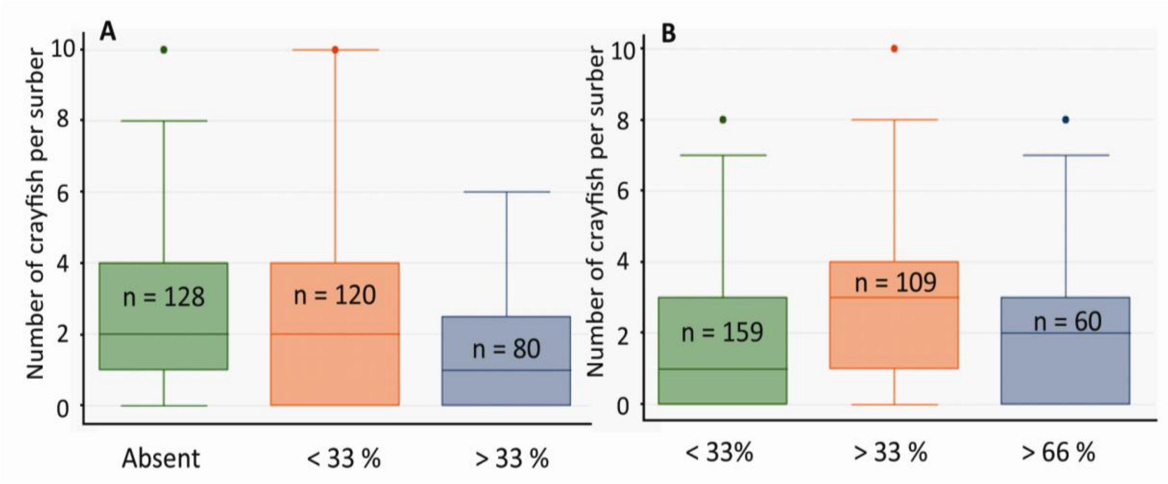

*Figure 5.34 - Box plots, showing minimum, lower quartile, median, upper quartile, maximum and outliers of the number of crayfish per surber area in sites with different percentage coverage of a) overhanging boughs and b) moss/algae. n is the number of surber areas sampled in each category*

*Table 5.10 – Significance P value of Mann-Whitney U tests for paired comparisons of white clawed crayfish density in different* site-scale *overhanging boughs and moss/algae percentage cover* categories*. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Site overhanging boughs** | Absent | < 33 % | > 33 % |
|---|---|---|---|
| Absent | | | |
| < 33 % | 0.7993 | | |
| > 33 % | 0.0032 | 0.0021 | |

| **Site moss/algae cover** | < 33 % | > 33 % | > 66 % |
|---|---|---|---|
| < 33 % | | | |
| > 33 % | 0 | | |
| > 66 % | 0.1445 | 0.0309 | |

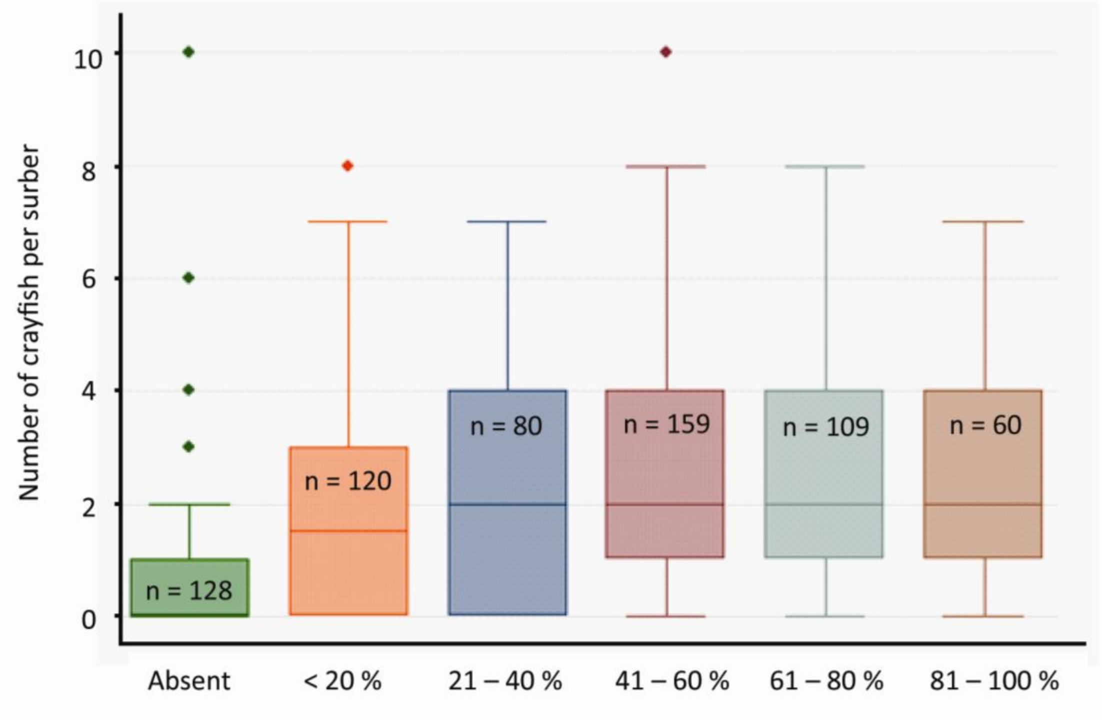

*Figure 5.35 - Box plots, showing minimum, lower quartile, median, upper quartile, maximum and outliers of the number of crayfish per surber area in surbers with different percentage coverage of moss/algae. n is the number of surber areas sampled in each category*

*Table 5.11 – Significance P value of Mann-Whitney U tests for paired comparisons of white clawed crayfish density in different surber- scale moss/algae percentage cover categories. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Surber-scale moss/algae cover** | Absent | 1 - 20 % | 21 - 40 % | 41 - 60 % | 61- 80 % | 81 - 100 % |
|---|---|---|---|---|---|---|
| Absent | | | | | | |
| 1 - 20 % | 0.0075 | | | | | |
| 21 - 40 % | 0.0004 | 0.3417 | | | | |
| 41 -60 % | 0 | 0.0319 | 0.2033 | | | |
| 61 - 80 % | 0.0001 | 0.1536 | 0.6024 | 0.4581 | | |
| 81 - 100 % | 0.0062 | 0.3926 | 0.8104 | 0.5646 | 0.912 | |

Average population density of WCC varied in response to differences in the proportional cover of different hydraulic biotopes. Average number of crayfish per surber area was significantly lower in sites where pool accounted for 21-40 % of the channel area than all other sites (fig. 5.36a and table 5.12). Surber areas in sites with high proportions of glide (more than 60 %) had significantly higher densities of crayfish than surber areas in sites with less 60 % glide. Below 60 % proportional cover of glide had no influence on average population density of crayfish per surber area (fig. 5.36b and table 5.12). Number of crayfish per surber area peaked in sites in which riffle covered 21 – 40 %. However, the only significant difference between WCC population density in areas of differing proportion of riffle was that sites where riffle covered more than 60 % of the site area had significantly lower densities of WCC than sites with 0 to 60 % cover by riffle biotope (fig 5.37a and table 5.13). Surber areas in sites which contained no run biotopes had significantly higher densities of WCC than sites where run was present (fig 5.37b and table 5.13). The response by WCC to percentage cover by run was complex with sites in which run accounted for 1 – 20 % of the site area having significantly lower densities of crayfish than sites in which run accounted for 21 – 40 % of the site area.

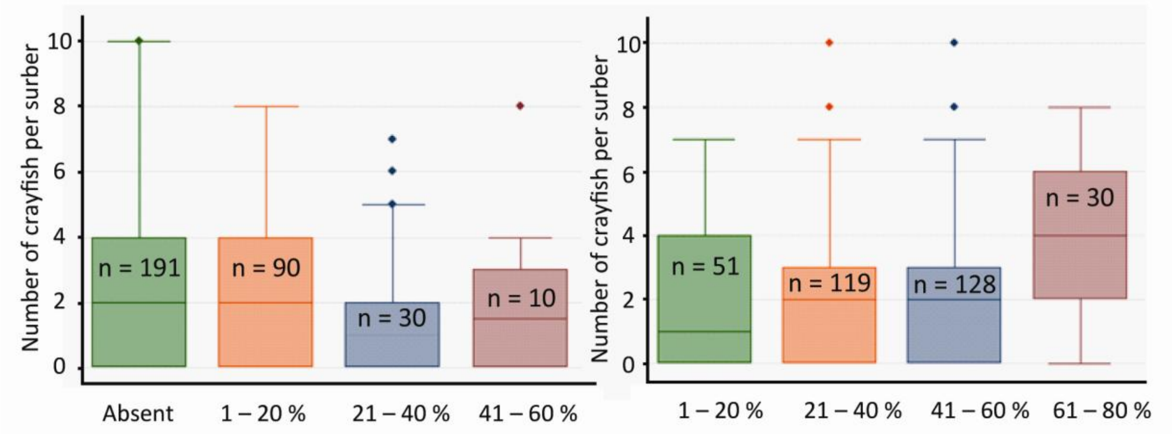

*Figure 5.36 - Box plots, showing minimum, lower quartile , median, upper quartile, maximum and outliers of the number of crayfish per surber area in sites with different percentage coverage of a) pool and b) glide. n is the number of surber areas sampled in each category*

*Table 5.12 – Significance P value of Mann-Whitney U tests for paired comparisons of crayfish density in different pool and glide percentage cover categories. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Pool** | Absent | 1 - 20 % | 21 - 40 % | 41 - 60 % |
|---|---|---|---|---|
| Absent | | | | |
| 1 - 20 % | 0.4636 | | | |
| 21 - 40 % | 0.0037 | 0.0287 | | |
| 41 -60 % | 0.5095 | 0.7089 | 0.3554 | |

| **Glide** | 1 - 20 % | 21 - 40 % | 41 - 60 % | 61- 80 % |
|---|---|---|---|---|
| 1 - 20 % | | | | |
| 21 - 40 % | 0.5572 | | | |
| 41 -60 % | 0.4837 | 0.9927 | | |
| 61 - 80 % | 0.0015 | 0.0005 | 0.0007 | |

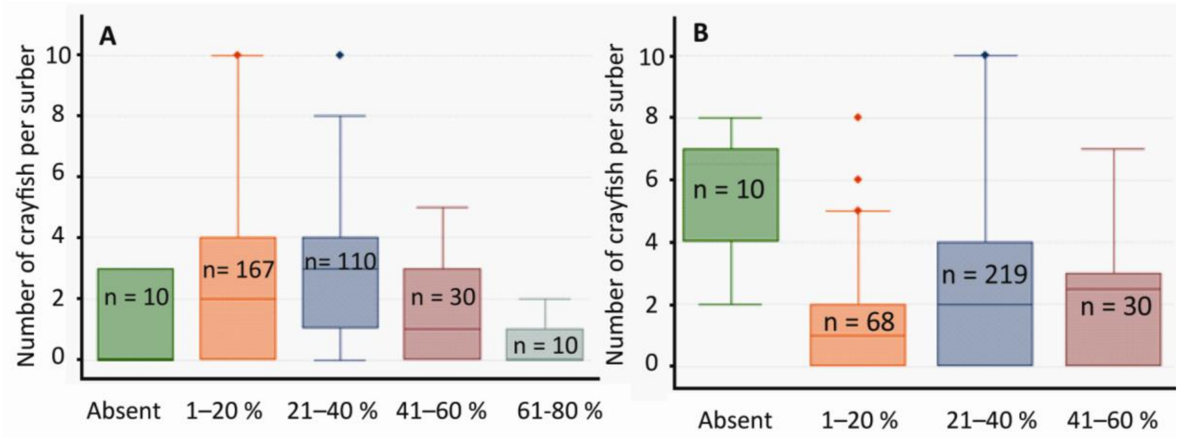

*Figure 5.37 - Box plots, showing minimum, lower quartile , median, upper quartile, maximum and outliers of the number of crayfish per surber area in sites with different percentage coverage of a) riffle and b) run. n is the number of surber areas sampled in each category*

*Table 5.13 – Significance P value of Mann-Whitney U tests for paired comparisons of crayfish density in different riffle and run percentage cover categories. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Riffle** | Absent | 1 - 20 % | 21 - 40 % | 41 - 60 % | 61- 80 % |
|---|---|---|---|---|---|
| Absent | | | | | |
| 1 - 20 % | 0.0494 | | | | |
| 21 - 40 % | 0.0127 | 0.0501 | | | |
| 41 -60 % | 0.3073 | 0.1495 | 0.0108 | | |
| 61 - 80 % | 0.3543 | 0.0011 | 0.0002 | 0.0267 | |

| **Run** | Absent | 1 - 20 % | 21 - 40 % | 41 - 60 % |
|---|---|---|---|---|
| Absent | | | | |
| 1 - 20 % | 0 | | | |
| 21 - 40 % | 0.0001 | 0.0101 | | |
| 41 -60 % | 0.0004 | 0.2864 | 0.5863 | |

Surber areas with armoured substrate contained considerably lower crayfish densities than surber areas where grains were not embedded. However, there were too few positive observations for this difference to be significant. Densities of WCC were significantly lower in surber areas that contained bedrock than those that did not (fig. 5.38a and table 5.14). There was no significant difference in the average population density of WCC in surber areas with or without boulders but surber areas with cobbles or boulders contained significantly more crayfish than surber areas without (fig. 5.38b and table 5.14). The difference between WCC population density in surber areas containing at least one of boulders, cobbles or pebbles and those without boulder, pebble or cobble was highly significant (fig. 5.38c and table 5.14). Only one crayfish was found in the twenty-two surber areas containing only gravel, fines or bedrock. The surveyor observed that this crayfish was moving between refuges at the time of survey. Population density in areas of gravel, fines and bedrock was effectively zero.

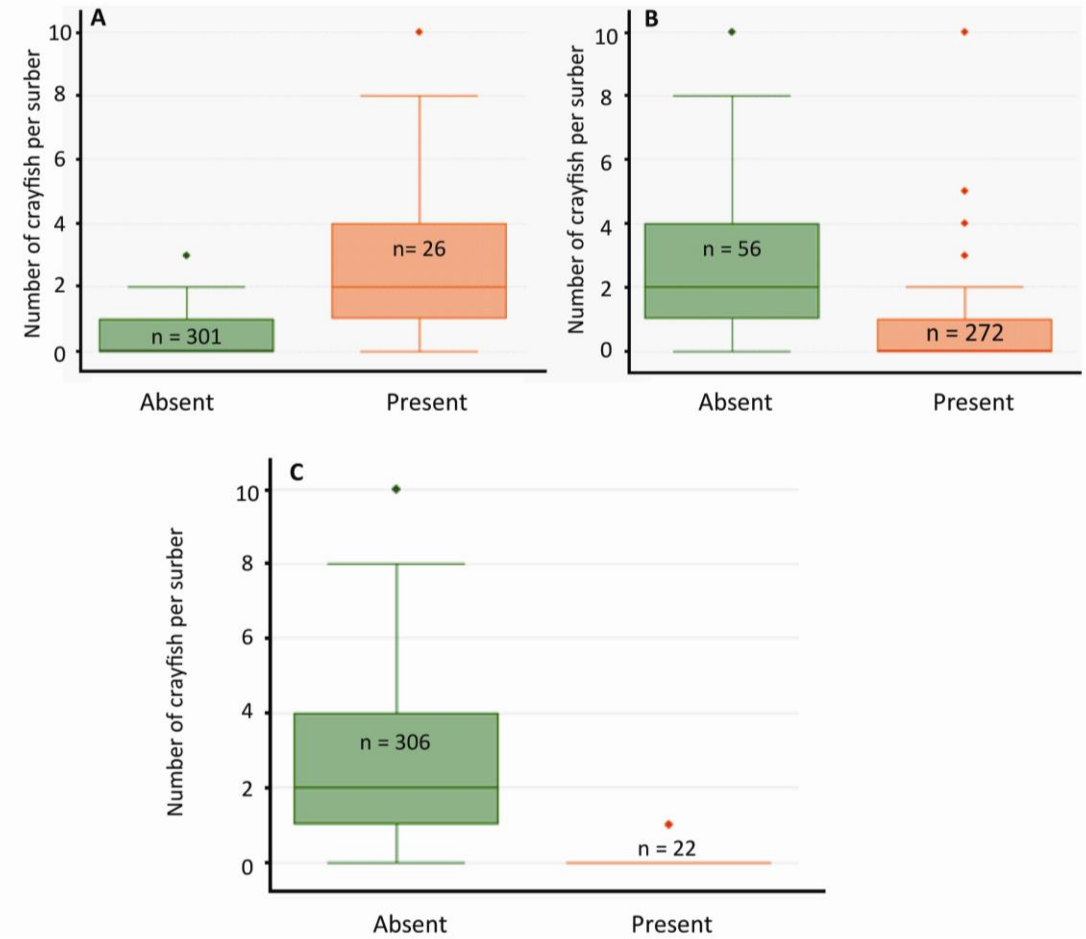

*Figure 5.38 - Box plots, showing minimum, lower quartile , median, upper quartile, maximum and outliers of the number of crayfish per surber area in surbers with and without a) bedrock, b) boulders and/or cobbles and c) boulders and/or cobbles and/or pebbles. n is the number of surber areas sampled in each category*

*Table 5.14 – Significance P value of Mann-Whitney U tests for paired comparisons of crayfish density in surber areas with and without different substrate categories. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Bedrock** | Present | Absent |
|---|---|---|
| Present | | |
| Absent | 0 | |

| **Boulders and/or cobbles** | Present | Absent |
|---|---|---|
| Present | | |
| Absent | 0 | |

| **Boulders, cobbles and or pebbles** | Present | Absent |
|---|---|---|
| Present | | |
| Absent | 0 | |

### 5.6.2 Continuous variables

From Kruskal-Wallis tests it can be seen that the number of WCC per surber area varied significantly between classes of all continuous variables apart from flow velocity at 60 % depth (table 5.15). Box plots and Mann-Whitney U tests show which categories have significantly different densities of WCC.

*Table 5.15 – Results of Kruskal-Wallis tests performed on classes of habitat variables measured continuously. Differences are considered significant at an α value of 0.05*

| **Habitat variable** | **Classes** | **Kruskal-Wallis value (*H*)** | **Significance** | **Significant at α = 0.05** |
|---|---|---|---|---|
| Depth | 0 – 10 cm, 11 – 20 cm, 20- 30 cm, 31 – 40 cm, 41 – 50 cm, 50 + cm | 20.558 | 0.001 | Yes |
| Boundary flow velocity | 0 – 0.005 $ms^{-1}$, > 0.005 – 0.02 $ms^{-1}$, > 0.02 – 0.1 $ms^{-1}$, > 0.1 – 0.2 $ms^{-1}$, > 0.2 $ms^{-1}$ | 12.131 | 0.0164 | Yes |
| Flow velocity at 60 % depth | 0 – 0.005 $ms^{-1}$, > 0.005 – 0.02 $ms^{-1}$, > 0.02 – 0.1 $ms^{-1}$, > 0.1 – 0.2 $ms^{-1}$, > 0.2 $ms^{-1}$ | 4.599 | 0.331 | No |
| Site-scale $D_5$ | 1 – 2 mm, > 2 – 4 mm, > 4 - 6 mm, > 6 – 8 mm, > 8 – 10 mm, > 10 - 12 mm, > 12 mm | 37.425 | 0.0001 | Yes |
| Site-scale $D_{50}$ | 1 – 10 mm, > 10 – 20 mm, > 20 -30 mm, > 30 – 40mm, > 40 – 50 mm, > 50 -60 mm, >60 – 70 mm, > 70 -80 mm, > 80 mm | 32.535 | 0.0001 | Yes |
| Site-scale $D_{95}$ | 0 – 100 mm, > 100 – 130 mm, > 130 – 160 mm, > 160 – 190 mm, > 190 – 220 mm, > 220 mm | 32.870 | 0.0001 | Yes |
| Surber-scale $D_5$ | 0 – 1 mm, > 1 – 6 mm, > 6 - 12 mm, >12 – 18 mm, > 18 – 24 mm, >24 mm | 25.594 | 0.0001 | Yes |
| Surber-scale $D_{50}$ | 0 – 8 mm, > 8 – 20 mm, > 20 - 40 mm, > 40 – 60 mm, > 60 – 80 mm, > 80 - 100 mm, > 100 mm | 83.169 | 0.0001 | Yes |
| Surber-scale $D_{95}$ | 0 – 50 mm, > 50 – 100 mm, > 100 - 150 mm, > 150 – 200 mm, > 200 – 250 mm, > 250 - 300 mm, > 300mm | 56.843 | 0.0001 | Yes |

Highest median densities of WCC were found in surber areas with intermediate values of both depth and boundary flow velocity relative to the sampled range. Shallow areas (< 10 cm depth) had significantly fewer crayfish than surber areas in which water depth was between 11 and 20 cm (fig. 5.39a). Although very deep areas (> 50 cm depth) had low densities of crayfish, fewer than one crayfish per surber area on average, this difference was not significant due to the low number of observations in this class (table 5.16). A highly skewed distribution in observed flow velocities meant analysis of average population density using even class widths was uninformative. Surber areas with boundary flow velocity between 0.02 and 0.1 ms$^{-1}$ contained the highest crayfish densities (fig 5.39b). However, the broad range of WCC densities found in surber areas with these flow velocities mean there is no significant difference between crayfish densities in any of the flow categories when considered using separate Mann-Whitney U tests with bonferroni corrections (table 5.17).

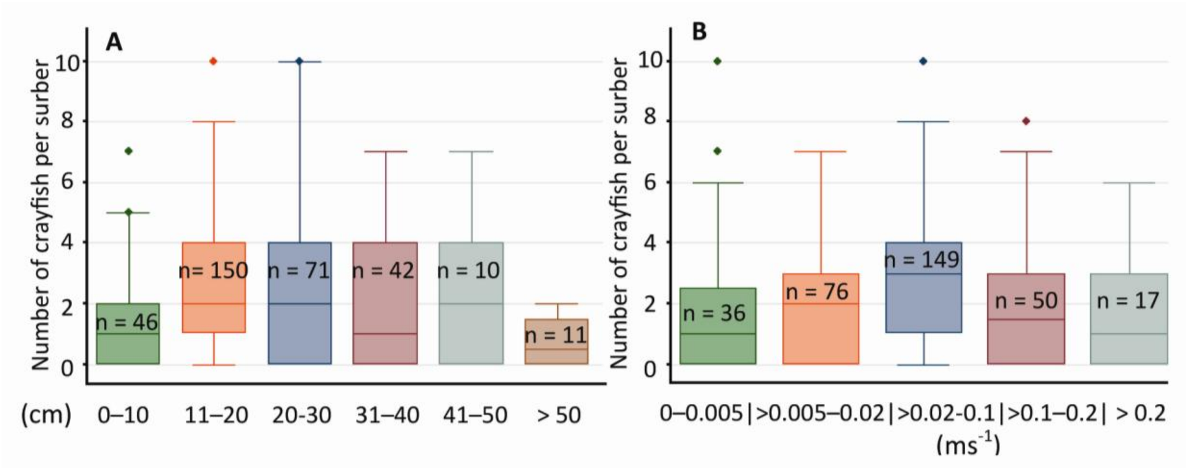

*Figure 5.39 - Box plots, showing minimum, lower quartile , median, upper quartile, maximum and outliers of the number of crayfish per surber area in surbers with differing a) depth and b) boundary flow velocity. n is the number of surber areas sampled in each category*

*Table 5.16 – Significance P value of Mann-Whitney U tests for paired comparisons of crayfish density in different depth classes. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Depth (cm)** | 0 - 10 | > 10 - 20 | > 20 - 30 | > 30 - 40 | > 40 - 50 | > 50 |
|---|---|---|---|---|---|---|
| 0 - 10 | | | | | | |
| > 10 - 20 | 0.0001 | | | | | |
| > 20 -30 | 0.006 | 0.5257 | | | | |
| > 30 - 40 | 0.3122 | 0.027 | 0.1534 | | | |
| > 40 -50 | 0.3645 | 0.5323 | 0.7476 | 0.7556 | | |
| > 50 | 0.4227 | 0.0114 | 0.0312 | 0.2069 | 0.2252 | |

*Table 5.17 – Significance P value of Mann-Whitney U tests for paired comparisons of crayfish density in different boundary flow velocity classes. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Boundary flow velocity (m/s)** | 0 - 0.005 | > 0.005 - 0.02 | > 0.02 -0.1 | > 0.1 - 0.2 | > 0.2 |
|---|---|---|---|---|---|
| 0 - 0.005 | | | | | |
| > 0.005 - 0.02 | 0.5327 | | | | |
| > 0.02 - 0.1 | 0.0323 | 0.0271 | | | |
| > 0.1 - 0.2 | 0.7828 | 0.6843 | 0.019 | | |
| > 0.2 | 0.7224 | 0.3648 | 0.0358 | 0.5981 | |

Strong responses to substrate size were evident in patterns of WCC density. WCC were present in significantly lower densities in sites with $D_5$ less than 2 mm than in all other sites (fig. 5.40a and table 5.18). A similar trend was seen at the surber-scale with surber areas containing substrate with a $D_5$ value less than or equal to 1 mm having significantly lower densities of crayfish than surber areas in which substrate $D_5$ was between 1 and 12 mm but this difference was not sustained as $D_5$ class values increased (fig. 5.40b and table 5.18). Similarly, areas in the smallest class of $D_{95}$ supported significantly fewer crayfish at both the site and surber-scale but further increases in $D_{95}$ had no consistent influence on WCC density (fig. 5.41 and table 5.19). Only one surber area with $D_{95}$ less than 50 mm contained a crayfish.

There were also significantly fewer crayfish in surber areas with $D_{50}$ less than 8 mm and in surber areas within sites where average $D_{50}$ was less than 10 mm (table 5.20). Only one surber area with $D_{50}$ less than 8 mm contained a crayfish. At the site-scale, average $D_{50}$ of 50 to 60 mm had the highest median density of crayfish but this difference was only significant when compared to areas with $D_{50}$ 30 to 40 mm, which contained relatively few crayfish (fig 5.42a and table 5.20). A stronger trend was evident at the surber-scale (fig. 5.42b). Box plots show an increase of median number of crayfish per surber area as grain size classes increases from 0 - 8 to 60 - 80 mm and a decline thereafter. Crayfish population density is significantly higher in surber areas with $D_{50}$ between 40 and 80 mm than surber areas with smaller $D_{50}$ values. Surber areas with $D_{50}$ between 60 and 80 mm have significantly higher densities of crayfish than surber areas with $D_{50}$ between 0 and 40 mm but the difference with surber areas with $D_{50}$ between 40 and 60 mm is not significant (table 5.19). The range of surber-scale $D_{50}$ most heavily selected for by WCC in the study area can be clearly defined as greater than 40 mm, although there is suggestion that 40 – 80 mm is the preferred range (fig 5.41b).

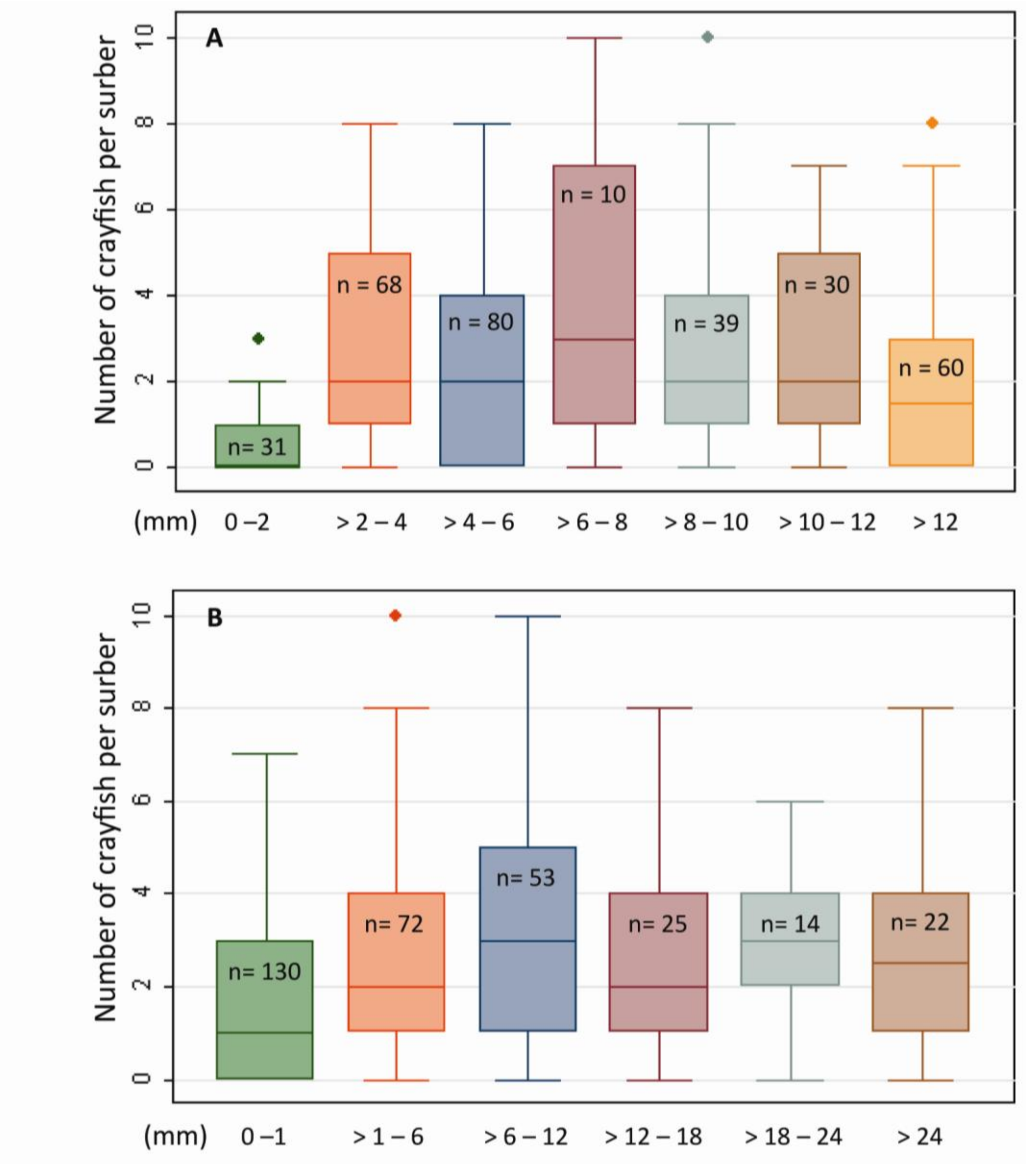

*Figure 5.40 - Box plots, showing minimum, lower quartile, median, upper quartile, maximum and outliers of the number of crayfish per surber area in surbers with differing $D_5$ values at a) site-scale and b) surber-scale. n is the number of surber areas sampled in each category*

*Table 5.18 – Significance P value of Mann-Whitney U tests for paired comparisons of crayfish density in different $D_5$ classes. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Site $D_5$ (mm)** | 0 - 2 | > 2 - 4 | > 4 - 6 | > 6 - 8 | > 8 - 10 | > 10 -12 | > 12 |
|---|---|---|---|---|---|---|---|
| 0 - 2 | | | | | | | |
| > 2 - 4 | 0 | | | | | | |
| > 4 - 6 | 0 | 0.7125 | | | | | |
| > 6 - 8 | 0.0002 | 0.2035 | 0.1695 | | | | |
| > 8 - 10 | 0 | 0.7681 | 0.5952 | 0.322 | | | |
| > 10 - 12 | 0 | 0.9253 | 0.5088 | 0.2627 | 0.8735 | | |
| > 12 | 0.0003 | 0.1063 | 0.1256 | 0.0471 | 0.0611 | 0.1185 | |

*Table 5.18 – Significance P value of Mann-Whitney U tests for paired comparisons of crayfish density in different $D_5$ classes. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Surber $D_5$ (mm)** | 0 - 1 | *> 1 - 6* | > 6 - 12 | > 12 - 18 | > 18 - 24 | > 24 |
|---|---|---|---|---|---|---|
| 0 - 1 | | | | | | |
| > 1 - 6 | 0.0029 | | | | | |
| > 6 - 12 | 0 | *0.1604* | | | | |
| > 12 - 18 | 0.0163 | *0.8248* | 0.3716 | | | |
| > 18 - 24 | 0.0117 | *0.4344* | 0.779 | 0.5523 | | |
| > 24 | 0.0068 | *0.464* | 0.7377 | 0.6659 | 0.8693 | |

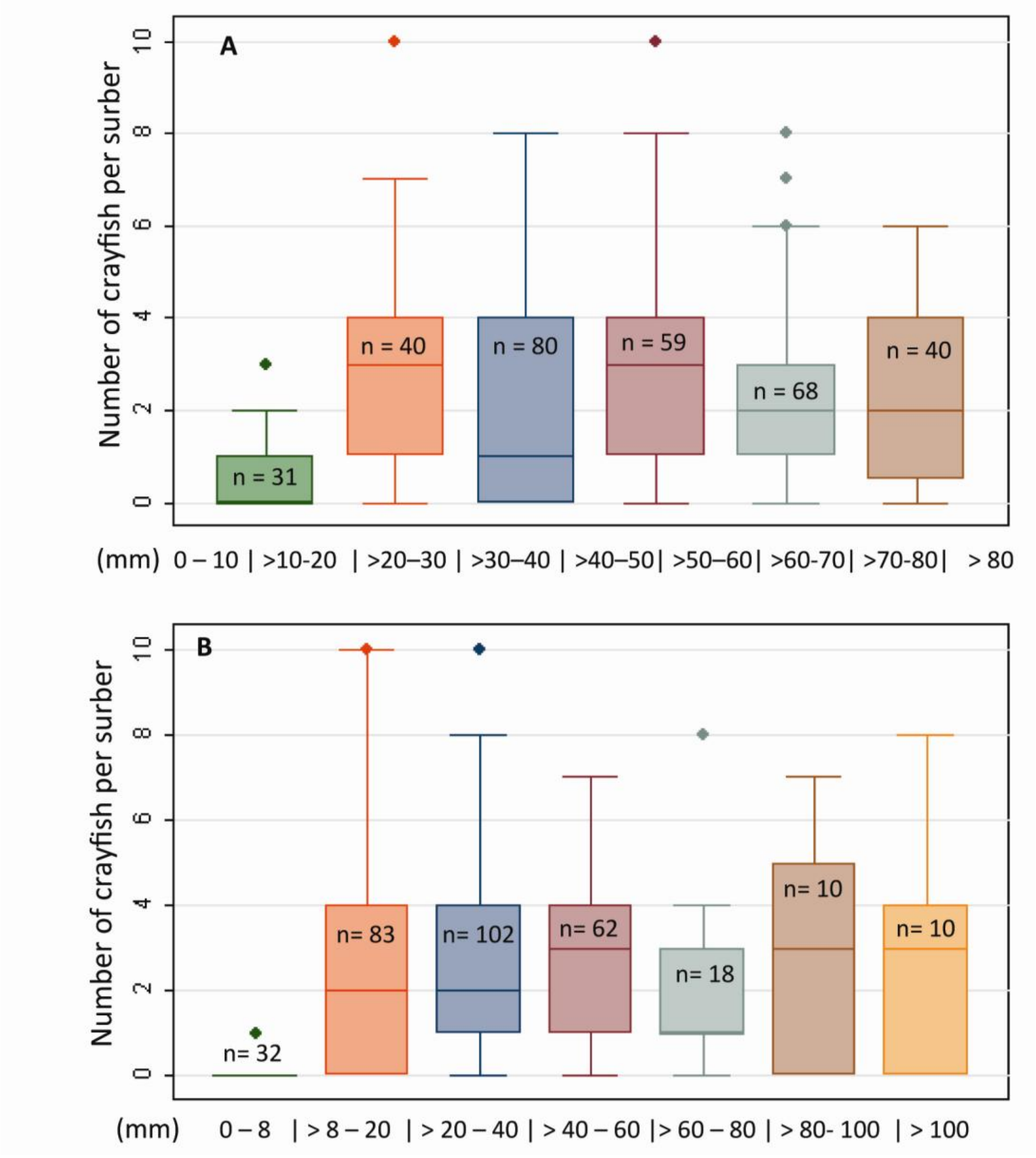

*Figure 5.41 - Box plots, showing minimum, lower quartile, median, upper quartile, maximum and outliers of the number of crayfish per surber area in surbers with differing $D_{95}$ values at a) site-scale and b) surber-scale. n is the number of surber areas sampled in each category.*

*Table 5.19 – Significance P value of Mann-Whitney U tests for paired comparisons of crayfish density in different $D_{95}$ classes. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Site $D_{95}$ (mm)** | 0 - 100 | > 100 - 150 | > 150 - 200 | > 200 - 250 | > 250 - 300 | > 300 |
|---|---|---|---|---|---|---|
| 0 - 100 | | | | | | |
| > 100 - 150 | 0 | | | | | |
| > 150 - 200 | 0.0001 | 0.0391 | | | | |
| > 200 - 250 | 0 | 0.8146 | 0.0974 | | | |
| > 250 - 300 | 0 | 0.0721 | 0.5075 | 0.1222 | | |
| > 300 | 0 | 0.2974 | 0.3995 | 0.3955 | 0.5532 | |

| **Surber $D_{95}$** | 0 - 50 | > 50 -100 | > 100 - 150 | > 150 -200 | > 200 - 250 | > 250 -300 | > 300 |
|---|---|---|---|---|---|---|---|
| 0 - 50 | | | | | | | |
| > 50 - 100 | 0 | | | | | | |
| > 100 - 150 | 0 | 0.3783 | | | | | |
| > 150 - 200 | 0 | 0.0112 | 0.0724 | | | | |
| > 200 - 250 | 0 | 0.6451 | 0.3418 | 0.0298 | | | |
| > 250 - 300 | 0 | 0.4802 | 0.7761 | 0.8051 | 0.4065 | | |
| > 300 | 0.0001 | 0.3924 | 0.5767 | 0.9721 | 0.3321 | 1 | |

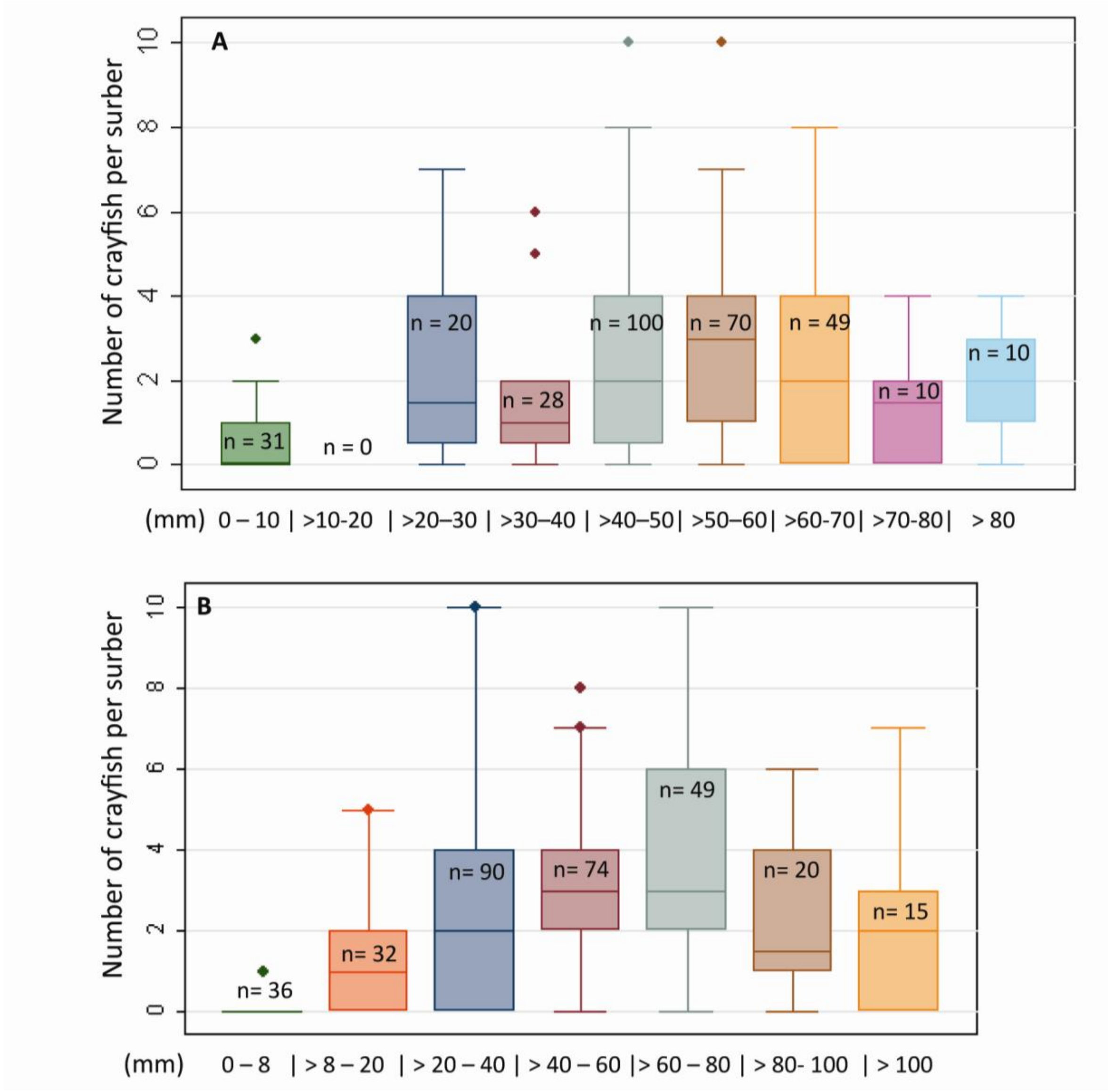

*Figure 5.42 - Box plots, showing minimum, lower quartile, median, upper quartile, maximum and outliers of the number of crayfish per surber area in surbers with differing $D_{50}$ values at a) site-scale and b) surber area-scale. n is the number of surber areas sampled in each category.*

*Table 5.20 – Significance P value of Mann-Whitney U tests for paired comparisons of crayfish density in different $D_{50}$ classes. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Site $D_{50}$** | 0 -10 | > 10 - | > 20 - | > 30 - | > 40 - | > 50 - | > 60 - | > 70 - | > 80 |
|---|---|---|---|---|---|---|---|---|---|
| 0 - 10 | | | | | | | | | |
| > 10 - 20 | / | | | | | | | | |
| > 20 -30 | 0.0005 | / | | | | | | | |
| > 30 - 40 | 0.0024 | / | 0.216 | | | | | | |
| > 40 - 50 | 0 | / | 0.7562 | 0.0184 | | | | | |
| > 50 - 60 | 0 | / | 0.3537 | 0.0015 | 0.2934 | | | | |
| > 60 - 70 | 0 | / | 0.8932 | 0.0761 | 0.7868 | 0.2689 | | | |
| > 70 - 80 | 0.0641 | / | 0.2713 | 0.9312 | 0.1246 | 0.0366 | 0.2247 | | |
| > 80 | 0.0034 | / | 0.7546 | 0.1379 | 0.4998 | 0.176 | 0.7504 | 0.3878 | |

*Table 5.20 cont. – Significance P value of Mann-Whitney U tests for paired comparisons of crayfish density in different* $D_{50}$ *classes. Yellow shows significant differences after application of Holm's sequential Bonferroni corrections*

| **Surber $D_{50}$ (mm)** | 0 - 8 | > 8 - 20 | > 20 - 40 | > 40 - 60 | > 60 - 80 | > 80 - 100 | > 100 |
|---|---|---|---|---|---|---|---|
| 0 - 8 | | | | | | | |
| > 8 - 20 | 0 | | | | | | |
| > 20 - 40 | 0 | 0.0412 | | | | | |
| > 40 - 60 | 0 | 0 | 0.0128 | | | | |
| > 60 - 80 | 0 | 0 | 0.00385 | 0.3518 | | | |
| > 80 - 100 | 0 | 0.1147 | 0.9027 | 0.1234 | 0.0513 | | |
| > 100 | 0 | 0.2081 | 0.7907 | 0.0817 | 0.0414 | 0.7991 | |

### 5.7 Influence of river position

Distribution of WCC in the study area was not influenced by lateral channel position. No relationship was found between lateral distance and number of WCC per surber area ($r_s = 0.056$, d.f. = 328, $P = 0.3121$). Further, laterally positioned surber areas were not occupied by WCC in a higher proportion than medially positioned surber areas ($\chi^2 = 1.025$, d.f.= 1, $P = 0.311$), nor was there a greater density of WCC in lateral surber areas than medial surber areas (U = 1.012 d.f. = 1, $P = 0.3114$). It can be seen from figure 5.43 that medial and lateral surber areas had the same lower quartile, median and maximum values for number of crayfish per surber area. Although crayfish population density in medial surber areas has a slightly negative skew, this difference is not significant (fig. 5.43).

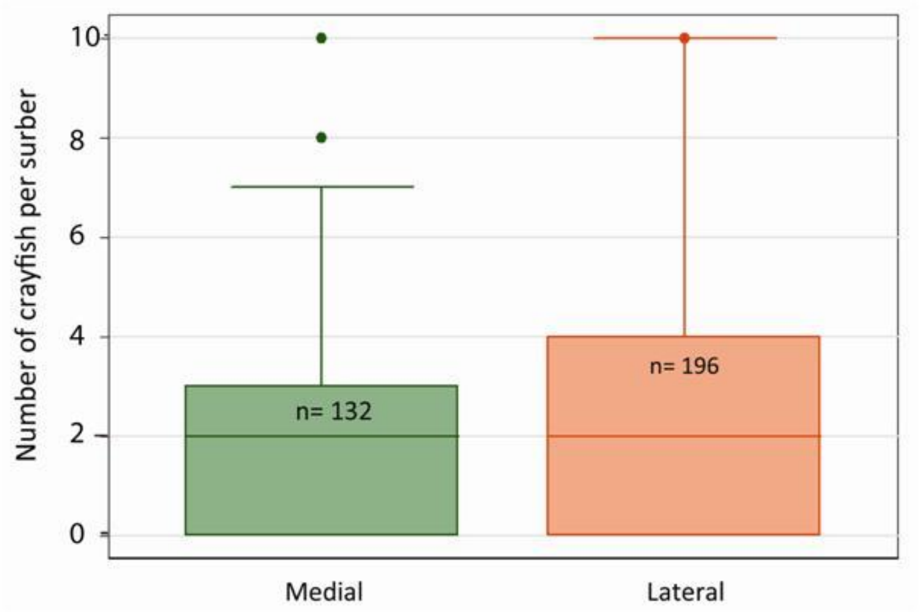

*Figure 5.43 - Box plots, showing minimum, lower quartile, median, upper quartile, maximum and outliers of the number of crayfish per surber area in laterally and medially positioned surbers. n is the number of surber areas sampled in each category*

A chi-squared test showed that there was significant variation in total numbers of crayfish found at each site ($\chi^2 = 232.8$, d.f. 32 $P = < 0.000001$). Consistently higher densities of WCC were found between 14 and 19.5 km downstream. Other 'hotspots' were found at single sites rather than continuous stretches. Although some sites had significantly higher densities than others, it can be seen from figure 5.44 that no consistent longitudinal trend in number of WCC caught per site nor the proportional use of surber areas in a site by WCC was evident. Spearman's rank tests confirmed that there was no correlation between total numbers of WCC found at a site and the distance downstream ($r_s = -0.3$, d.f. = 31, $P = 0.3$), nor between proportion of surber areas occupied by WCC caught per site and distance downstream ($r_s = -0.3$, d.f. = 31, $P = 0.2$). However, due to the larger sample size a weak but significant correlation between distance downstream and WCC at the surber-scale is evident ($r_s = -0.2$, d.f. = 326, $P = 0.003$). There is a weak trend of decreasing number of WCC per surber area with increasing distance downstream within the study area. This is further supported by significant differences between the upstream and downstream halves of the study area in terms of both proportional use of surber areas and median population density. Surber areas in the downstream half of the study site were used less frequently than expected at random and surber areas in the upstream half of the study site more frequently ($\chi^2 = 5.1$, d.f. 1 $P = < 0.02$). In addition, occupied surber areas in the upstream half of the study area contained a median of three WCC which was significantly more than occupied surber areas in the downstream half of the study area (U = 2.3 d.f. 1, $P = 0.02$) which contained a median of two WCC (fig. 5.45).

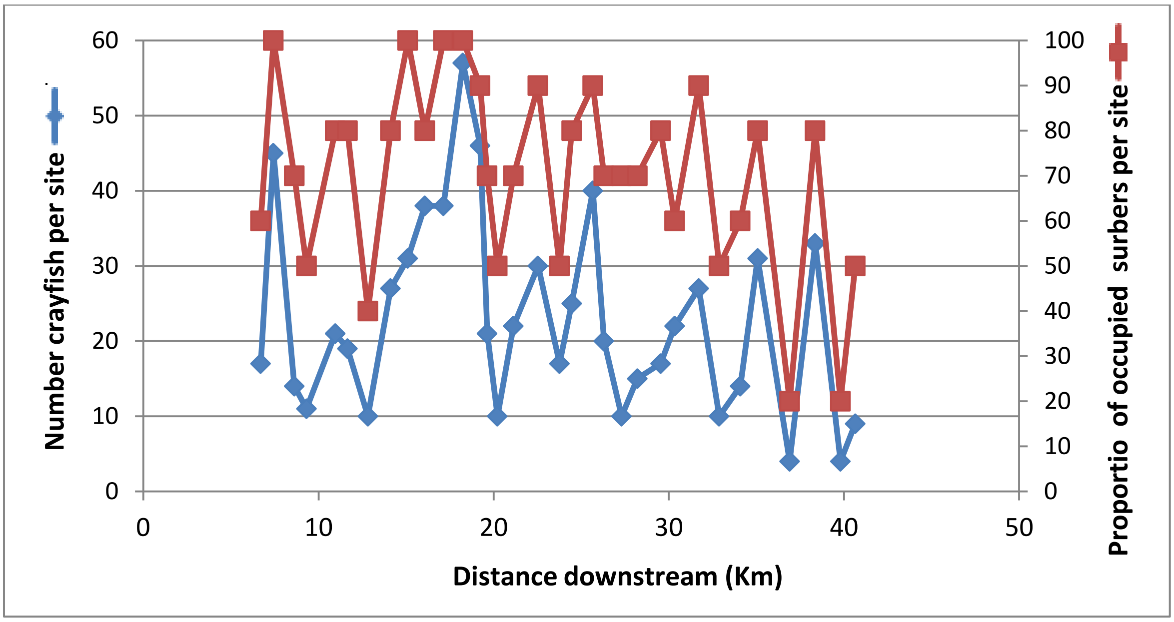

*Figure 5.44- Relationships between white clawed crayfish population density and distance downstream and proportional use of surber areas and distance downstream. Blue line shows number of white clawed crayfish collected per site (ten surber areas). Red line shows proportion of the ten surber areas sampled in each site that were occupied by white clawed crayfish*

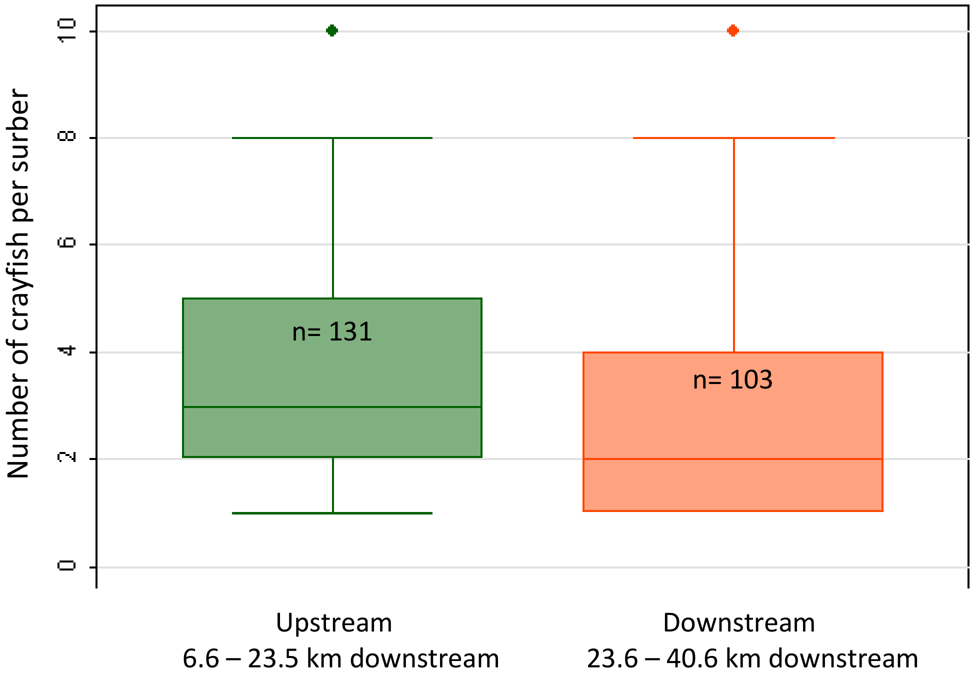

*Figure 5.45 - Box plots, showing minimum, lower quartile, median, upper quartile, maximum and outliers of the number of crayfish per surber area in the upstream half (6.6 – 23.5 km downstream) and the downstream half (23.6 – 40.6 km downstream) of the study area. n is the number of surber areas sampled in each category*

The results of this study reveal significant habitat preferences by WCC. The habitat variables significantly affecting crayfish population density and distribution were identified to allow analysis of longitudinal trends in habitat quality. The habitat variable with the biggest influence on WCC population density and distribution was substrate size. Surber areas containing only bedrock, sand/silt or gravel were avoided. This translated to avoidance of surber areas with $D_{50}$ less than 8 mm and sites with $D_{50}$ less than 10 mm. Site-scale $D_{50}$ in the range of 50 to 70 mm was selected for by WCC in the study area (figs. 5.29 and 5.41a and table 5.19). A clear preference for $D_{50}$ at the surber-scale between 40 to 80 mm was identified from figures 5.27 and 5.42b and table 5.20. Other significant responses to habitat by WCC found in this study were: a preference for areas with grass/arable land surrounding the channel (figs. 5.11 and 5.31 and table 5.7), avoidance of sites and surber areas with bedrock banks (figs. 5.12, 5.13 and 5.32 and table 5.8), a preference for surber areas between 15 and 23 cm deep (figs. 5.24 and 5.39 and table 5.16), a preference for surber areas with 20 -80 % moss/algae cover (figs. 5.16 and 5.35 and table 5.11) and avoidance of sites with less than 33 % moss/algae cover (5.15 and 5.34b and table 5.10).

Comparing the downstream pattern of number of crayfish caught per site to the downstream pattern of these habitat variables showed habitat fully accounted for the observed longitudinal distribution of crayfish at the site-scale. Most notably was the strong significant positive correlation ($r_s$ = 0.6264, d.f = 32, $P$ = 0.0001) between proportion of surber areas at a site with favourable surber-scale $D_{50}$ (40-80 mm) and the number of crayfish at a site (fig. 5.46). The longitudinal pattern in number of crayfish caught per site is largely attributable to variations in substrate size. All sites where this correspondence was low had less than 33 % coverage of moss/algae, which has been shown to be unfavourable for WCC in the study area (table 5.10, figs. 5.15 and 5.34b).

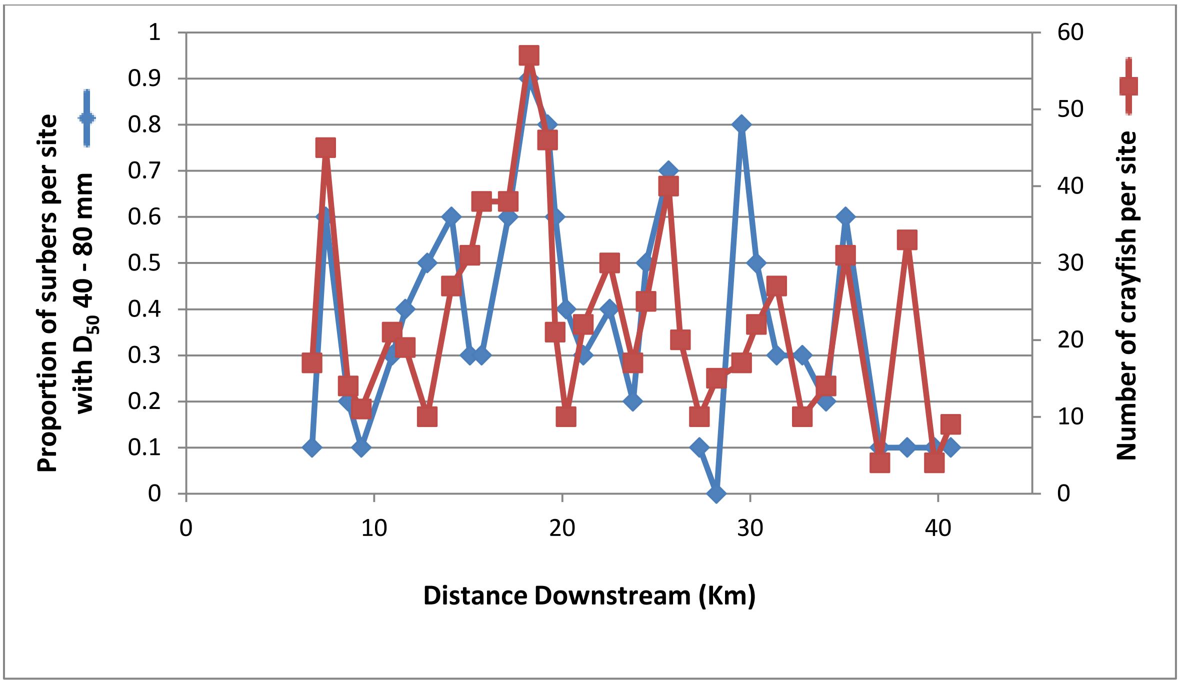

*Figure 5.46- Downstream trends in availability of surber areas with favoured grain sizes (proportion of surber areas containing substrate $D_{50}$ 40-80 mm per site) and total number of crayfish found per site (in ten surber areas)*

The frequency of occurrence of different habitat types varied between the upstream and downstream halves of the study site. Chi-squared tests to determine whether there were significant differences in the occurrence of different habitat categories in the upstream and downstream half of the study area revealed that grain size, land-use within 5 m of the channel and bank material accounted for the higher favourability of the upstream half of the study site for WCC (table 5.21). Sites with grass/arable land within 5 m of the channel were significantly more frequent in the upstream section than the downstream section. Despite having significantly more sites with grass/arable land within 50 m of the channel, the downstream half of the study area had higher frequency of wood/shrub within 5 m of the channel, which had been shown to be unfavourable to WCC in the study area (figs. 5.11 and 5.31 and table 5.7). Areas with bedrock banks, which were relatively avoided by WCC (figs. 5.12, 5.13 and 5.32 and table 5.8), were present in a significantly higher proportion in the downstream half of the site. The presence of moss, bedrock or preferred depths (10 – 23 cm; figs. 5.24 and 5.39a and table 5.16) was not significantly different between upstream and downstream halves of the study area and therefore did not account for the difference in WCC distribution or population density. Despite there being no significant difference in the occurrence of surber areas with boulders and/or cobbles and/or pebble in the upstream and downstream sections, the upstream section had a significantly higher occurrence of sites and surber areas within the preferred $D_{50}$ range and fewer sites with $D_{50}$ sizes that were avoided by WCC.

*Table 5.21 –Results of chi squared tests to compare occurrence of habitat types white clawed crayfish have been shown to be responding to in the upstream and downstream halves of the study area. 'Affect' indicates whether crayfish were found to be using the given habitat category more (positive) or less (negative) frequently than expected at random in the whole study area. Significance considered at P = 0.05*

| **Habitat variable** | **Categories considered** | **Affect on WCC** | **No. of observations** | **Chi-squared** | **Signifi-cance** | **Interpretation** |
|---|---|---|---|---|---|---|
| Land use within 50 m | Grass/arable | Positive | 328 | 9.854 | 0.00170 | Downstream favourable |
| Land use with 5 m | Grass/arable | Positive | 328 | 8.004 | 0.00467 | Upstream favourable |
| Bank material | Bedrock | Negative | 326 | 28.189 | 0.000001 | Upstream favourable |
| Moss (site) | < 33 | Negative | 328 | 0.221 | 0.639 | Not significant |
| Moss (surber) | 20 – 80 % | Positive | 327 | 0.645 | 0.422 | Not significant |
| Depth | 10 – 23 cm | Positive | 328 | 0.524 | 0.469 | Not significant |
| Substrate | Bedrock | Negative | 327 | 2.00 | 0.157 | Not significant |
|  | Boulder/cobble/pebbles | Positive | 328 | 0.271 | 0.602 | Not significant |
| Site-scale $D_{50}$ | < 10 mm | Negative | 318 | 5.380 | 0.0204 | Upstream favourable |
|  | 50 – 70 mm | Positive | 318 | 6.407 | 0.0114 |  |
| Surber-scale $D_{50}$ | < 8 mm | Negative | 316 | 0.188 | 0.665 | Not significant |
|  | 40 – 80 mm | Positive | 316 | 6.037 | 0.0140 | Upstream favourable |

### 5.7.1 Influence of tributary confluences

Site-scale $D_{50}$ showed the clearest pattern of a downstream gradient punctuated by tributaries. Average site $D_{50}$ decreased between each tributary showing downstream fining and abruptly increased at each influential confluence, producing a saw-tooth pattern (fig. 5.47). The two sites downstream of the River Font (blue stars on fig. 5.47) did not fit the pattern of sedimentary links due to the dominance of bedrock at the most upstream of these sites. This suggests four sedimentary links were present within the study site. The correlation between distance downstream of an influential tributary and site-scale $D_{50}$ was just insignificant when considering sites 5 to 33 (r = -0.2359 d.f. = 27 *P* = 0.109) but was significant if the two sites downstream of the

River Font, which did not fit the sedimentary link structure, were removed from analysis (r = -0.386 d.f. = 25 *P* = 0.0232).

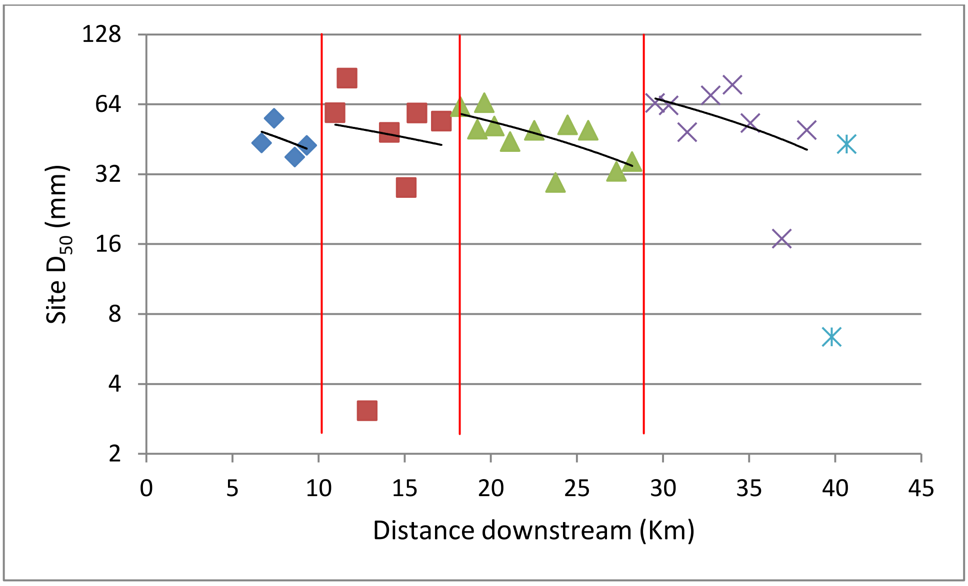

*Figure 5.47- Change in grain size with distance downstream, separated into lengths between influential tributaries. Different symbols indicate different inter-tributary lengths. Vertical lines show distance downstream of influential confluences*

Comparison of the sedimentary link structure with the longitudinal pattern of number of crayfish caught per site revealed that peaks and troughs in site totals did not correspond to the distribution of confluences (fig. 5.48). The correlation between distance from an influential tributary and the number of WCC found at a site was insignificant both with (r = 0.05276, d.f = 27, *P*= 0.393) and without inclusion of the most downstream two sites (r = 0.15538, d.f = 25, *P*= 0.219). Although sites at the downstream end of sedimentary links had smaller grain sizes and are thus more likely to have grain sizes below the range shown to be preferred by WCC in the study reach, this did not have a significant influence on distribution. The longitudinal pattern of WCC distribution could not be predicted from sedimentary link structure.

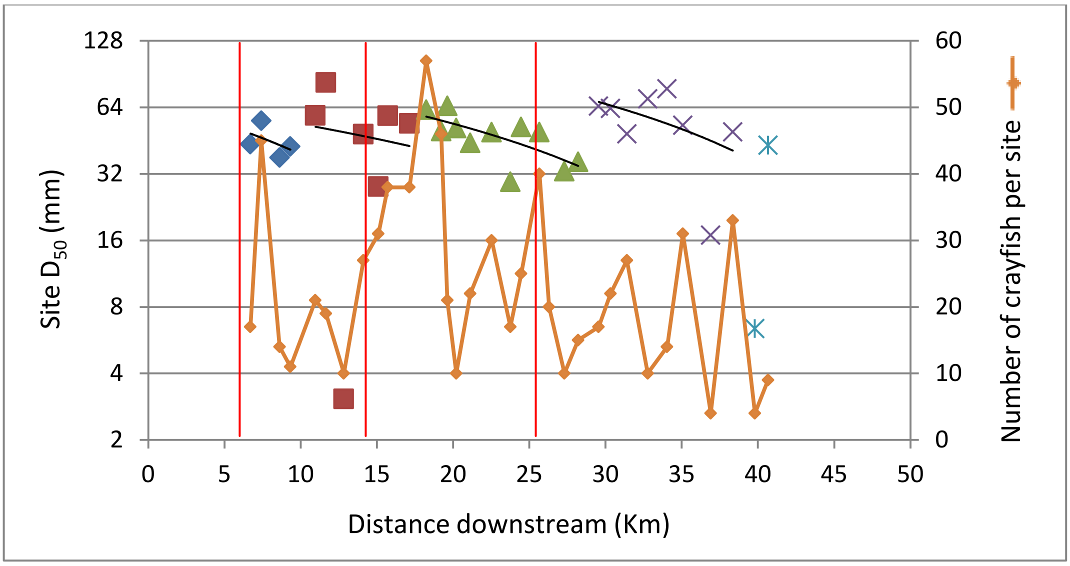

*Figure 5.48- Comparison of sedimentary link structure and the number of crayfish caught per site. Different symbol show site-scale $D_{50}$ in different sedimentary links. Orange line shows number of crayfish caught per site (caught in ten surber areas)*

## 6. Interpretation and Discussion

### 6.1 Distribution of crayfish on the River Wansbeck

An abundant and dense population of WCC was present in the study area with crayfish present at every site and in 68 % of surber areas. The average density of crayfish caught was 5.3 individuals per square metre sampled. The prevalence of crayfish at all sites suggests there is a continuous dense population of WCC throughout the entire study reach. The presence of either young of the year or berried females at twenty-three sites shows that the population of WCC on the Wansbeck is healthy and current conditions are favourable. The recorded data on young of the year suggests a release of the young from their mothers began on the 19th July. This is slightly later than the release data found by a survey conducted on the River Wansbeck the previous year, which found all juveniles to be released by mid-July (Ream, 2010). Relative abundance of young of the year increased rapidly after this date and then declined, probably due to high mortality rates of young of the year from predation and cannibalism (*c.f.* Brewis and Bowler, 1982). Large, mature adults were also present at the majority of sites showing conditions are suitable for long-term survival. A growth curve produced by Brown and Bowler (1978) in a similar temperature regime to the Wansbeck suggests the largest individual found in the present study (45 mm CL) was at least 11 years old.

Placing these results in a national context requires comparison with previous studies. Differences in survey techniques, distribution of samples and timing of surveys causes variations in reported densities of WCC for reasons unrelated to habitat quality. This means comparisons must be made with caution. Natural England provides a tentative grading of abundance for sampling in fixed areas surrounded by netting (Peay, 2003) (table 6.1), based on studies on a variety of rivers. It is likely that search efficiency in surber samplers in the present study was greater than the average for fixed area studies, particularly for juveniles. Nevertheless, this grading allows broad conclusions on relative abundances to be drawn.

*Table 6.1- Natural England classification for densities of white clawed crayfish found by fixed area sampling as given by Natural England (Peay, 2003)*

| **Average number per 1 m²** | **Population abundance** |
|---|---|
| > 5 | Very high |
| ≥2 - ≤5 | High |
| ≥0.2 - <2 | Moderate |
| < 0.2 | Low |
| 0 | Absent/undetected |

Average population density for twenty-five of the twenty-seven sites surveyed in this study for which results can be discussed is classified as ‘high’ or ‘very high’ by this grading system. This suggests that the population of WCC on the River Wansbeck is highly significant in a national context. Two sites, twelve and thirteen (NZ 05063 84210; NZ 05727 84282) had more than double the number of crayfish classified as a ‘very high’ population by Natural England. It is likely that these are some of the densest populations in England. This assertion is supported by comparison to other published studies. A review of scientific literature on crayfish published in 1988, found the highest recorded density of WCC in England to be 4.45 individuals per square metre (Hogger, 1988). This same review asserted that artificially enhanced habitat on the River Leen, Nottinghamshire, only supported densities up to 3.6 individuals per square metre (Hogger, 1988).

The densities of crayfish found in the present survey are highly comparable to a survey conducted on the River Wansbeck between the Hart Burn confluence and Mitford village in the summers of 2008 and 2009 (Ream, 2010). Using the same sampling technique as that used in the present study, Ream (2010) found density of WCC to be 5.3 individual per square metre before the September 2009 flood event and 5.7 individuals per square metre after the flood event. The similarity of this result to the 5.3 WCC caught per sampled square metre in the present study suggests the 2008 flood event has not had a lasting influence on population size.

Comparing these results to earlier surveys suggests density of WCC in the River Wansbeck has increased over the last decade. In 2005, David Rogers Associates conducted a WCC survey at eight locations on the River Wansbeck. The results are not directly comparable to the present study due to the different sampling methods used but general comparisons are informative. Of the eight locations surveyed in 2005, crayfish were absent at two, Low Angerton (NZ 09302 84310, site twenty) and Meldon Bridge (NZ 11960 85066, site twenty-five). This was interpreted by the study authors as being due to siltation from stock grazing and poor water quality from road runoff respectively. In this survey, permission was not granted to publish results from either of these locations but upstream and downstream sites had high population densities suggesting crayfish have recolonised these areas. Areas close to Lowford Bridge (NZ 18933 86119, site thirty-three) and Mitford Castle (NZ 17050 85619, site thirty-one) were sampled in both surveys. In 2005, both had low population densities according to Natural England categories for standard hand-searches. In the present survey, Lowford Bridge contained a ‘high’ and Mitford castle a ‘very high’ population density according to Natural England categories for fixed-area searches. Despite differences in methods, it is fair to say population density in these areas has increased since 2005. A longer-term increase in population density is demonstrated by comparing the results of the current survey to those of a study conducted over the area between sites 4 and 13 in 1997 and

1998 (Armitage, 2001). Like the current survey, Armitage (2001) used exhaustive surber sampling. In 1997 and 1998 average population densities found were 4.6 and 3.8 WCC per square metre respectively (Armitage, 2001) compared to an average of 5.6 WCC per square metre in the same stretch of river in this study. Overall, it would seem that the abundance of WCC on the River Wansbeck has increased markedly in the last 15 years and their distribution has become more uniform along the length of the river (see appendix table 1). It is not known whether this increase in abundance is due to improved habitat quality, reduction in predators or represents an intrinsic population cycle in WCC.

At the microhabitat scale, WCC had an aggregated pattern of distribution in the study area as shown by the index of dispersion and the fact that the observed frequency distribution did not differ significantly from the frequencies expected in a negative binomial model. The wide range of number of individuals caught per surber area suggests variation in the resources surber areas contain and a response to this by crayfish. This is supported by a value of mean size of an aggregation, according to equation 4.4, of 1.67 individuals. As this value is smaller than two, it can be concluded that the aggregated distribution of WCC on the River Wansbeck is a response to variation in environmental parameters and not an active behavioural process (Blackith cited in Southwood and Henderson, 2000). This is likely to be a response to physical habitat but may also be due to food availability, predation patterns or impacts of past flood events (*c.f.* Ream, 2010). Presence at every sampling site shows there was no heterogeneity in distribution at the site-scale in this study.

### 6.2 Habitat requirements of white clawed crayfish on the River Wansbeck

Crayfish were present in every kilometre section of the study site and were therefore able to tolerate the full range of water chemistry present. All water chemistry parameters, apart from ammonia, were within the range cited by Smith *et al.* (1996) or Trouilhe *et al.* (2007) as being tolerable to crayfish. In one kilometre section, concentration of ammonia exceeded the tolerance level cited in Trouilhe *et al.* (2007). Because water chemistry was not measured synchronously with crayfish sampling, it cannot be firmly concluded that WCC were present at the location of this high concentration of ammonia but populations must have persisted in close proximity. This supports the recent findings by Demers and Reynolds (2002) that WCC can tolerate moderately polluted waters although the single set of water chemistry samples obtained in this study does not allow determination of the duration of the high concentration of ammonia. Chronic pollution has been shown to have more severe impacts on populations than short-lived pollution events (Holdich and Reeve, 1991; Laurent, 1988). Due to crayfish being present in every kilometre section, no niche limits can be inferred for water chemistry parameters. Within tolerable limits, water chemistry has not been found to influence the distribution of individuals (Lodge and Hill, 1994; Smith *et al.* 1996) and was therefore not considered in further analysis.

The only physical variable that crayfish were not using the full available measured range of was grain size at the surber-scale. Analysis of substrate descriptions showed that, in this study, WCC were not making use of surber areas that contained only gravel, sand, silt or bedrock. When grain sizes were measured from photo-sieving, the smallest average ($D_{50}$) grain size crayfish were making use of in surber areas was 8 mm. Measurements of $D_{95}$ showed that this translated to all areas with $D_{95}$ less than 50 mm being outside the niche space of WCC in the Wansbeck. These results suggests that as well as areas containing only gravels and fines, areas containing only small pebbles are outside the realised niche of WCC.

These results agree with much of the previously published literature on WCC habitat preferences (*e.g.* Smith *et al.* 1996; Benvenuto *et al.* 2008). Recent studies that have found WCC in fine substrate (Peay *et al.* 2006; Holdich *et al.* 2006) have been conducted in areas of organic silt and mud which is stable enough for WCC to create burrow refuges. The fine sediment experienced in this study was shifting silt and sand, not stable mud or organic silt. Although Ream (2010) found WCC present in unstable sand and gravel only young of the year were present in areas where the substrate was entirely sand and this age class was not considered in the present study. Ream (2010) modified the Wentworth categories and classified gravel as grains of 8 to 16 mm diameter. Therefore, the finding of the present study that 1+ crayfish require grains larger than 8 mm is comparable to the results of Ream (2010). Avoidance of bedrock was also evident in this study. Gallagher *et al.* (2006) and Englund and Krupa (2000) showed bedrock crevices to be preferentially used by WCC whereas Armitage (2001) and Ream (2010) found crayfish in the Wansbeck to avoid bedrock areas. The bedrock sheets present in the study area have very few crevices suitable as refuges. The results of the present study confirm that the presence of stable refuges is the major determinant of WCC distribution.

The results of the logistic regression model confirmed the findings of niche breadth analysis. Grain size, in terms of both surber-scale $D_{50}$ and presence of cobbles, were the variables with the most influence on likelihood of crayfish occurrence. Pebbles were also shown to have a positive influence on the probability of finding crayfish, suggesting cobble on a base substrate of pebble was optimal habitat. This would provide interstice refuges for all sizes of crayfish (*c.f.* Nyström, 2002). The logistic regression model showed that land-use within 50 m of the channel influenced the likelihood of crayfish presence, with the presence of woodland and shrub having a negative influence on the probability of finding crayfish. Very few studies have been conducted on the influence of surrounding land-use on distribution of WCC (Schulz and Schulz, 2004). Shading from bank-side trees may result in reduced macrophyte growth (Peay *et al.* 2006) but the lack of correlation with land-use and in-channel vegetation parameters suggests this is not the cause of the negative association between WCC and woodland land-use. It is possible that predation from terrestrial predators, particularly from otter and mink that are abundant in the Wansbeck catchment (Armitage, 2001), is higher in areas with shrub and woodland surrounding the channel than in open grass/farmland areas. Evidently, further work is needed to determine the response of crayfish to land-use in rivers.

In disagreement with the present study, Smith *et al.* (1996) did not find grain size to be a significant predictor of WCC distribution when using logistic regression analysis. Smith *et al.'s* (1996) study found that the presence of WCC could be predicted from the presence of tree roots, overhanging boughs and vertical banks. None of these variables were significant predictors of presence/absence in the present study. Similarly, Naura and Robinson (1998) found overhanging boughs, bank substrate, erosion and presence of tree roots to be the most influential variables for WCC presence, but none of these variables influenced the likelihood of crayfish presence in the present study. Several authors have found crayfish unable to tolerate flow velocity exceeding 0.2 $ms^{-1}$ (*e.g*. Foster, 1995; Benvenuto *et al.,* 2008) but this study found multiple crayfish in areas with boundary flow velocity as high as 0.5 $ms^{-1}$. The results of the present study suggest that crayfish can tolerate and prosper in a much wider range of habitat variables than previously documented.

Although the logistic regression model performed well, as shown by a high reliability, low commission and omission errors and a highly significant likelihood ratio, absences were under-estimated. According to the model, based on a sub-set of all data, there was a 28.5 % chance of finding crayfish in areas of sand, silt or bedrock substrate without shrub or wood within 50 m of the channel. However, the data from all surber areas showed that only a 5.5 % chance of finding crayfish in these substrates, regardless of surrounding land-use types. When extrapolated to new areas the model performed less well and overestimated the frequency of crayfish occurrence. The density of WCC on the River Wansbeck is exceptional compared to other British rivers. For rivers containing small populations of WCC, individuals may not be present even in 'optimal' habitat as defined by the model presented here. For rivers with dense macrophyte growth, such as lowland chalk streams, substrate size may be less relevant than in the current system. The model could be of value to WCC conservation in all systems but has highest utility for predicting habitat suitability in upland gravel-bed rivers, where invasive competitors are not present.

In summary, WCC on the River Wansbeck are able to make use of a wide range of habitat types and have a broad realised niche. Even for the habitat variables for which crayfish could not make use of the full available range, surber-scale $D_{50}$ and $D_{95}$, Smith's (1982) measure of niche breadth shows the realised niche to be very wide. Habitat variables are not particularly strong discriminators of WCC presence in the River Wansbeck due to the large size of the WCC population and prevalence of individuals in a variety of habitat types. Thus, the ability to predict the presence of WCC from the habitat variables investigated is low. The only firm prediction that can be made is that WCC will be absent in microhabitat areas where the substrate is mobile small pebbles, gravel, fines, or bedrock.

## 6.3 Habitat preference of white clawed crayfish on the River Wansbeck

Despite being able to use the full available range of most habitat variables, the majority of crayfish located in a narrower range of habitat types than was available. This indicated that WCC were showing preferences for some habitat variables. Largely, analyses of proportional use and average density of WCC in different habitat types produced the same conclusions about habitat preferences by WCC. The fact that crayfish distribution and population density were exhibiting a similar response to habitat strengthens the conclusions drawn from this study.

No preferences were evident for sinuosity, width, gradient or valley form. This was expected as there is no evidence in previous literature of these parameters affecting WCC. No response to bank profile was evident but crayfish showed significant preferences for bank material. Earth banks were selected for and bedrock banks were avoided at both the site and surber scales. Earth banks offer additional refuges and protection from predation and high flows, as crayfish can make use of natural crevices in the bank and associated vegetation (Holdich *et al.* 2006). This explains why bedrock banks, which offered no refuges, were relatively avoided. The response to boulder/cobble banks was less clear. Proportional use analyses showed boulder banks at the site-scale to be preferred by WCC but boulder/cobble banks at the surber-scale to be relatively avoided by WCC in the study area. Boulder banks have crevices that offer refuges and were found to be strongly preferred by WCC in a study by Naura and Robinson (1998). Surber-scale boulder and cobble were amalgamated in this study due to the low number of observations in each class. The results suggest that boulders are preferred habitat and cobbles unfavourable for WCC. This may be due to high flows that occur on the River Wansbeck causing cobble banks to shift.

Previous studies have found vertical and overhanging banks to be favoured by WCC (Smith *et al.* 1996; Schulz and Schulz, 2004) but other authors have suggested that overhangs are indicative of erosion and are therefore avoided by crayfish due to the detrimental impact of increased turbidity and sedimentation (Naura and Robinson, 1998). In this study, crayfish avoided areas of slow erosion. The positive influence of refuges provided by stable overhanging banks combined with the negative influence of actively eroding overhanging banks may have resulted in the overall lack of significant response to bank profile found in this study. The analyses suggested that crayfish were selecting areas with rapidly eroding banks or cattle poaching but previous studies have shown both these factors to have a negative impact on WCC (Foster, 1995; Armitage, 2001). It is likely that the apparent positive influence of high erosion rates is an artefact of the correlation between erosion/poaching and earth banks. Some areas with signs of poaching and erosion will not currently be inputting enough sediment into the system to be detrimental to crayfish and will therefore have no influence on crayfish distribution. The positive effect of refuge provision in earth banks may override the negative influence of their propensity to erode.

Many previous studies have found WCC to respond to abundance and type of vegetation both within the channel and along the banks (*e.g*. Brown and Bowler, 1977; Armitage, 2001; Gallagher *et al.* 2006). Vegetation provides food directly and by hosting a range of invertebrate species, fungi and periphyton (Gallagher *et al.* 2006). Further, vegetation provides shelter and protection from high flows and predators (Reynolds *et al.* 2002). Thus, it would be expected that areas with in-channel vegetation would be preferentially used by WCC in high densities. However, no response to submerged or emergent vascular macrophytes was evident in this study at site or surber scale. The low number of positive observations for emergent vascular plants may account for the lack of significant response, yet the same lack of response to submerged vegetation was evident despite submerged macrophytes being present in over 40 % of samples.

The only response to in-channel vegetation was to abundance of moss/algae. White clawed crayfish avoided sites with less than 33 % moss/algae cover and surber areas without any moss/algae and selected surber areas with intermediate cover (40-80 %) of moss/algae. There was suggestion that sites with intermediate cover of moss/algae (33 – 66 %) were also preferred. The selection of intermediate cover of moss/algae may be due to high densities of moss impeding movement of WCC (Peay *et al.* 2006) or because high moss cover tends to occur on stable substrate such as bedrock or embedded boulders, which are not likely to offer refuges for crayfish (*c.f.* Gallagher *et al.* 2006). Moss has been shown to be preferred as a food source over macrophytes due to the fungi, microbes and metazoan its hosts (Gherardi *et al.* 2004) but algae and liverworts have a negative association with WCC (Gallagher *et al.* 2006; Naura and Robinson, 1998). The distinction between liverworts, algae and moss was not made in this study but the strength of preference for moss/algae suggests either liverworts and algae were not abundant in the study area or that crayfish were not avoiding them. The lack of response to submerged and emergent macrophytes may be due to the prevalence of moss in the study reach. If dietary requirements were met by moss, it would not be necessary for crayfish to seek out other vegetation types. In a spate river such as the Wansbeck, vegetation stands may provide insufficient protection to be used by WCC as refuges. This assertion is supported by the findings of a study by Demers *et al.* (2003) which showed that macrophytes support large numbers of crayfish in areas of slow moving current but contain few individuals in areas of higher flow velocities.

An additional source of food for WCC is leaf litter from overhanging boughs (Naura and Robinson, 1998). The shade provided by overhanging boughs also prevents high water temperatures, which can be detrimental to crayfish (Brusconi *et al.* 2008). Therefore, overhanging boughs have been widely cited as being preferentially used by WCC (*e.g*. Foster, 1995; Smith, 1996). In this study, presence of overhanging boughs had no influence on the density of WCC and high coverage of a site by overhanging boughs was actually unfavourable to WCC. This negative influence of overhanging boughs may be because the shade they create reduces growth of photosynthetic moss/algae, which was found to be favourable for WCC. Additionally, because the Wansbeck is towards the northerly limit of WCC's range, temperature stress is unlikely meaning shading will offer little or no benefit.

There has been debate in the literature about the favourability of exposed roots for WCC. Several authors have found exposed roots to be selected by crayfish due to the refuges they provide, particularly from high flows which may move substrate refuges, and their propensity to trap food in the form of leaf litter (Smith *et al.* 1996; Benvenuto *et al.* 2008; Ream, 2010). However, exposed tree roots indicate bank erosion, which is detrimental to crayfish, and may provide refuges for predators of crayfish such as mink and otters (Naura and Robinson, 1998), both of which are present on the Wansbeck (Armitage, 2001). In this study, no significant selection or avoidance of exposed tree roots was evident. This may be due to the combined positive and negative influences of the factors discussed above.

Distribution of predators can also influence depth selection by WCC (Clavero *et al.* 2009). In shallow areas, crayfish are at higher risk from terrestrial predators. Otters particularly are active predators of WCC on the River Wansbeck (personal observations) and herons, mink and kingfishers are also likely to consume crayfish. Large fish were absent from most of the study site due to the stream being small and shallow. Differential predation risk therefore adequately explains the avoidance of areas shallower than ~ 10 cm. Overall, analyses suggested that depths between 15 and 23 cm were preferred by WCC. The relative avoidance of deeper areas found in this study may be due to lower search efficiency in deeper areas or may be due to deeper pool areas generally having fine substrates and few refuges.

Substrate size was the habitat variable to which WCC in the study area were exhibiting the strongest response in terms of both proportional use and population density. This was expected as refuges to protect against predation, cannibalism and high flows are the major habitat requirement of WCC (Holdich, 2003). Brusconi *et al.* (2008) found substrate size to be the only variable with an influence on crayfish abundance, demonstrating its significance in determining habitat quality. The preference analysis confirmed the earlier findings on grain size tolerance limits and revealed a preferred range of grain sizes. Substrate of small pebbles, gravel, fines or bedrock were not made use of by WCC in the study area. This translated to avoidance of areas with site-scale $D_{50}$ less than 10 mm, site-scale $D_{95}$ less than 100 mm , surber-scale $D_{50}$ less than 8 mm and surber-scale $D_{95}$ less than 50 mm. There was also suggestion of avoidance of areas with armoured or embedded substrate and avoidance of areas with the lowest recorded $D_5$ values but this was not consistent or particularly informative.

A preference for intermediate grain sizes relative to those recorded in the study reach was evident when considering $D_{50}$ at both the site and surber-scale. The strength of response by WCC to substrate size was greater at the surber-scale than at the site-scale. White clawed crayfish showed relative avoidance of surber areas with substrate $D_{50}$ less than 35 mm and a preference for substrate $D_{50}$ between 40 and 80 mm. Similar trends were evident at the site-scale, with WCC preferentially using areas with $D_{50}$ exceeding 53 mm and using areas with $D_{50}$ between 50 and 60 mm in the highest density. These measurements correspond to large pebbles and small cobbles. No previous studies of crayfish have measured grain size in terms of $D_{50}$, making comparisons difficult. The photo-sieving method employed in this study measured all grains including fine grains between the substrate WCC were selecting as refuges. Therefore, the grains crayfish were selecting as refuges probably correspond to large cobbles. The finding that WCC were preferentially locating in areas with site-scale $D_{95}$ exceeding 190 mm, which also corresponds to cobbles, supports this assertion.

Analysis of recorded presence/absence of each substrate type supported the conclusion that cobbles were the preferred substrate of WCC in this study. White clawed crayfish did not use areas containing boulders more frequently or in higher densities than areas containing cobbles but areas of boulder and/or cobble were preferentially used over areas where pebble was the biggest grain size. This result agrees with both Armitage (2001) who found WCC on the Wansbeck to actively select cobbles and small boulders and Ream (2010) who found a preference for small cobbles by WCC on the Wansbeck. Demers *et al.* (2003) also found WCC to prefer cobbles in a study of Irish streams but Naura and Robinson (1998) and Foster (1993) both claimed that cobbles do not provide a stable enough refuge. The discrepancy between these studies may be due to differences in the size of crayfish studied, as smaller crayfish require smaller refuges (Foster, 1993). The prevalence of juveniles in this study, as reflecting the natural population, may account for the preferred grain size being smaller than that found in some previous studies. Further, the favourability of different refuge sizes differs depending on flow velocity.

Proportional use analyses suggested WCC preferred intermediate flow velocities relative to the range recorded in this study. Avoidance of very slow flows (less than 0.02 $ms^{-1}$) is likely to be due to the low levels of dissolved oxygen in these areas. The upper limit to the preferred range of boundary flow velocity was 0.12 $ms^{-1}$. Fast flows are unfavourable to WCC due to the increased energy expenditure required to maintain position in the water column (Gallagher *et al.* 2006). No response to flow velocity was evident when WCC densities were analysed. The discrepancy between these results is likely due to the distribution of refuges, as preferred water velocity depends on the size and stability of available refuges. Most areas with boundary flow velocity exceeding 0.12 $ms^{-1}$ could not be made use of by WCC but where these areas contained stable refuges, high densities of WCC were able to locate there. The combined influence of substrate and flow velocity was also evident in a study by Gallagher *et al.* (2006) who found flow velocity considered in isolation had no effect on the distribution of crayfish.

Descriptions of hydraulic biotopes combine flow velocity and substrate and are therefore likely to be more relevant to crayfish. Significant responses to biotopes were evident in this study. White clawed crayfish were preferentially using sites with intermediate proportions of riffle. Turbulent riffle flows oxygenate the water and can provide favourable habitat when stable refuges are present (Reynolds, 1998). However, if substrate pariticles in a riffle are small and unstable in the high flow velocities WCC will be unable to locate in them. This explains why presence of riffles in a site was favourable but sites with very high proportional cover of riffle biotope were relatively avoided. The lack of a consistent response to proportion of run may reflect the fact that this broad habitat category encompasses a wide range of substrate sizes and flow velocities. There was no consistent significant response to proportional cover of a site by pool biotope but a preference by WCC for sites with a high proportion of glide biotope was evident. White clawed crayfish showed avoidance of surber areas in sites with less than 20 % cover by glide biotope and used surber areas in sites with more than 60 % cover by glide biotope in high densities. Glide biotopes are likely to have suitable flow speeds and may provide both daytime resting and night-time foraging habitat (Clavero *et al.* 2009). Overall, sites with heterogeneous flow patterns, particularly sites containing both glide and riffle, appeared to be preferred by WCC in the study area.

Finally, there was evidence of a response to land-use within 5 m and 50 m of the channel. Areas of grass and farmland were selected for at both scales. In agreement with the logistic regression output, areas of the channel surrounded by wood or shrub were relatively avoided by WCC. This response was strongest when considering land use with 5 m of the channel. Because water chemistry/quality was not influencing distribution, it is difficult to perceive a mechanism by which land-use directly influences favourability of habitat. It is likely that the responses of WCC to land-use found in this study are due to associations between land-use and other habitat variables such as bank material, vegetation and overhanging boughs. No strong correlations were evident but areas of grass/arable land were more likely to have earth banks, which WCC were selecting, and less likely to have high coverage by overhanging boughs, which WCC were avoiding in the study area.

In summary, the distribution of WCC was a result of active responses to habitat variables. Within a wide realised niche crayfish demonstrated strong preferences for certain habitat types. Average substrate size was the most influential habitat parameter; it was the only variable to limit niche breadth in the study area and the variable to which WCC were exhibiting the strongest preferences. WCC were also showing significant responses to depth, flow velocity, hydraulic biotope type, abundance of moss/algae, surrounding land-use and bank material. Predictions of distribution and habitat quality would be possible from measures of these variables.

### 6.4 The scale of white clawed crayfish response to habitat

An aim of this study was to determine the spatial scale at which WCC were responding to and were affected by their environment. Like all river systems, the River Wansbeck is a hierarchically structured system with heterogeneity in physical variables evident at each of the three spatial scales of the study (Frissell *et al.* 1986). The presence of WCC at every site demonstrates that all variables operating at the scale of kilometre sections and site were tolerable to WCC. The wide range of kilometre section and site scale habitat types present in the study area suggests that sensitivity of WCC to these broader scale controls is very low, but it is impossible to draw firm conclusions about this due to the absence of unsuitable sites in this study area. Presence of WCC in all primary sampling units (kilometre sections) and secondary sampling units (100 m sites) but not all tertiary sampling units (surber areas) shows patchiness in distribution occurred only at the sub-metre scale. This suggests, for the range of scales considered in this study, WCC were only directly responding to microhabitat scale heterogeneity in physical variables. The findings of niche and preference analyses confirm that microhabitat scale variables had the most explanatory power on the distribution of WCC on the River Wansbeck. The primary control on WCC distribution was the occurrence of suitable refuges at the microhabitat scale. These findings agree with previous studies that found microhabitat scale variation to have the biggest influence on distribution of aquatic organisms (*e.g.* Poizat and Pont, 1996 ; Robson and Chester, 1999).

Although microhabitat scale heterogeneity had the most significant influence on WCC distribution in the study area, heterogeneity in kilometre sections and site scale variables did influence the distribution of WCC to some degree. Some of the apparent influences of variables operating at the kilometre section and site scale variables on WCC distribution were due to these broad-scale variables being correlated to microhabitat scale variables, as was found by Gido *et al.* (2006) in a multi-scale study of fish distribution in prairie streams. The higher the proportion of the site covered by a given habitat category, the more surber areas are likely to fall in that habitat type. For example, bank material and moss cover at the site and surber scales were correlated ($R^2 > 0.5$ and $R^2 > 0.4$ respectively) and the influence of the variables on crayfish was the same at both scales. Therefore, site-scale responses to bank material and abundance of moss/algae are manifestations of micro-scale responses repeated across surber areas. Similarly, the same trends in grain size preferences were evident at site and surber scales but responses to grain size were less distinct at the site-scale. The apparent response to site-scale average grain size is a result of the fact that sites with optimal average grain sizes are more likely to contain surber areas with optimal grain sizes. Because crayfish have been shown to require fine substrates for foraging (Clavero *et al.* 2009), a strong independent influence of site-scale grain size could have been expected in this study. A mixture of coarse and fine sediment within the ‘home-range’ has been cited as optimal for WCC (Nyström, 2002; Clavero *et al.* 2009) and thus it would be expected that optimal average grain size at the site-scale would be lower than optimal grain size in day-time microhabitat in surber areas. This response was found by Hedger *et al.* (2006) who showed that average grain size over 50 m river length had higher explanatory power on the distribution of juvenile salmon than the grain size at the in the actual location an individual was found. The requirement for multiple habitat types and the ability to move between them made larger-scale heterogeneity relevant to juvenile salmon. This has not been found in this study; WCC did not exhibit an independent response to site-scale grain size. Similarly, the mobility of WCC means food substances are not a necessity within their immediate locale. It could therefore have been expected that presence of vegetation would be selected for more strongly at the site-scale than at the surber-scale. Again, an independent site-scale response was not evident.

However, other habitat parameters operating at the kilometre and site scale were genuinely acting as filters on the microhabitat scale distribution of WCC, as in Poff's (1997) model of hierarchical habitat suitability. A response to proportional cover of hydraulic biotopes at the site-scale was evident, particularly for riffles. Turbulent areas increase the oxygen concentration of the water and in doing so increase favourability of the whole site (Reynolds, 1998). It is likely that the positive influence of riffle in a site is due to riffles increasing the likelihood of downstream microhabitat areas having sufficient dissolved oxygen, to which WCC respond. Thus, proportion of flow types in a site is a filter, conditioning suitability of microhabitats. Similarly, over-hanging boughs at the site-scale influence the amount of moss/algae at the surber-scale and is thus a broad scale filter on microhabitat suitability. The influence of land-use on WCC distribution is likely to be a result of its influence on vegetation parameters, sediment input, erosion and possibly depth and grain sizes, which influence WCC directly at the microhabitat scale.

The hierarchical nature of environmental heterogeneity and species response in the study area means that the observed distribution pattern was dependent on the scale of observation. Viewing the system at different spatial scales would have led to different conclusions on the distribution and response to habitat by WCC in this river. If this study had been conducted only at the scale of the site, it would have been concluded that all habitat types were suitable for WCC and important causes of variation would have been missed. This was also the case in a multi-scale study of larval lamprey by Torgersen and Close (2004). Only by conducting multi-scale studies did the importance of micro-scale habitat emerge in both Torgersen and Close's work and the present study. The modifiable areal unit problem is relevant to crayfish conservation: arbitrarily selected scales of study will produce scale specific arbitrary results (Openshaw, 1983), which will result in inappropriate conservation actions.

This study has shown that crayfish primarily respond to microhabitat scale variation in their environment. Habitat based conservation actions should be conducted over this scale to provide the greatest benefit to WCC (Wiens *et al.* 1993). Further work on species-habitat correlations should be conducted at this scale to give comparable and relevant results. However, this study has suggested that processes operating at coarser scales than that which WCC respond to directly still influence WCC distribution through their impact on finer scale processes (Wiens, 1985). The favourability of conditions on the River Wansbeck has meant this study was unable to discern the extent of the influence of broader scale habitat variables but future conservation actions should not ignore the wider spatial context of the system.

### 6.5 Influence of river position on distribution of crayfish

Distribution of WCC in the study area was not influenced by lateral channel position. There was significant variation in total number of WCC caught between sites but the lack of correlation between number of WCC and distance downstream suggests longitudinal position was not the cause of this variation.  At the surber-scale, a weak trend of decreasing number of WCC per surber area with increasing distance downstream was evident within the study area. This suggests that favourability for WCC decreases with distance downstream and is supported by the finding that proportional use of surber areas and population density in occupied surber areas was higher in the upstream half of the study area (6.6 – 23.5 km downstream) than the downstream half (23.5 - 23.6 – 40.6). The aim was therefore to determine whether these observed longitudinal patterns could be fully accounted for by habitat quality and availability or whether longitudinal position had some independent explanatory power on WCC distribution. Comparisons of the longitudinal pattern of total numbers of crayfish per site and longitudinal patterns of habitat parameters WCC had been found to be responding to showed that the differences in number of crayfish per site was fully accounted for by differences in grain size and abundance of moss/algae. The difference in WCC distribution in the upstream and downstream halves of the study site could also be accounted for by habitat variables. The upstream half of the study site had less wood/shrub surrounding the channel, which had been unfavourable to WCC, significantly higher occurrence of sites and surber areas within the preferred $D_{50}$ range and fewer sites with $D_{50}$ sizes that were avoided by WCC.

Continuous downstream trends in habitat variables are disrupted by tributary confluences (*e.g.* Rice, 1998). In the study reach, tributary confluences significantly influenced the downstream pattern of grain size. Four sedimentary links of downstream fining punctuated by abrupt coarsening were present. This sedimentary link structure influenced the availability of optimal substrate to some degree but the strength of this influence was too weak for distance from an influential tributary to account for the longitudinal pattern in number of crayfish per site. WCC distribution could not be predicted from sedimentary link structure.

Overall, river position had low explanatory power on the distribution of WCC in the study reach, confirmed by the insignificance of both lateral distance and distance downstream in the logistic regression.  There were no influence of longitudinal position on WCC distribution independent of habitat quality. Naura and Robinson (1998) claimed that likelihood of WCC presence could be predicted from altitude, slope and distance from the source. These variables are likely to be correlated, meaning the authors found a predictable downstream trend in WCC distribution. This has not been found in this study perhaps due to this study concentrating on a shorter study reach at a finer spatial scale than the data used by Naura and Robinson (1998). As discussed in section 6.4, the distribution of crayfish was conditioned by local-scale factors that were highly heterogeneous (Naiman *et al.* 1987). However, the physical conditions required by crayfish are evidently more common at certain distances downstream due to the geology, pedology and fluvial dynamics of the catchment. In this study there was indication that preferred WCC habitat is more common in low order streams. Further work is needed to discern whether this finding is system specific or applicable to all upland gravel-bed rivers. Overall, the distribution of WCC on the River Wansbeck could not be accurately predicted from any absolute spatial factor.

In a similar investigation on larval lamprey, Torgersen and Close (2004) found distance downstream to have significant explanatory power on distribution of individuals at multiple spatial scales. This explanatory power was not fully explained by the downstream pattern of habitat variables. Spatial context had an independent influence, which the author's suggest was attributable to the distribution of spawning adults. No such spatial biological process is evident for WCC on the River Wansbeck. Therefore, a non-spatially explicit approach may be adopted in habitat management for WCC within a catchment but different biotic pressures, flow regimes and available habitat means findings will not necessarily apply to across catchments.

It must be noted that there is a possibility that a tendency to locate at certain distances downstream has caused the habitat variables associated with these distances downstream to emerge as predictors of habitat quality. The lack of consistent longitudinal trends and sporadic high abundances in crayfish suggests this is not the case. Further, the ecological relevance of influential habitat variables suggests the correlation between WCC and physical parameters illustrate a true response to habitat quality.

### 6.6 Limitations and future research

Significant and informative results have emerged from this investigation. However, sources of error and limitations on general applicability were present in this study. In this section, potential errors in the methods used and the influence of these on overall conclusions is considered. Potentially confounding factors are then identified and the scope for future study on these is discussed.

A limitation on the applicability of the terrestrial remote sensing technique used in this study is the requirement of favourable weather conditions. The major barrier to obtaining decent images was glare on the water surface (fig 6.1a), which occurred on bright days with clouds. This restricted image collection to days with bright sunshine and low cloud cover or dark days with high cloud cover where the flash could be used to obtain satisfactory images (fig 6.1b). However, the ease and speed at which images can be obtained in favourable weather conditions does not preclude this from being a feasible technique of grain size mapping in this climate. Like field-based grain size measures, the technique employed in this study was confined to unconsolidated, open network bedding surfaces (Rice and Church, 1996; Carbonneau *et al.* 2005). Turbid water and areas deeper than 50 cm were not suitable for photo-sieving or surber crayfish sampling. Thus, the image acquisition technique was suitable for all areas where crayfish could be sampled. The resolution limits of the imagery meant sand and silt were not distinguished in this study. This did not influence the results as WCC were avoiding all grain sizes smaller than pebbles in this study area. Within the study area there was no fine but firm substrate, such as mud, which could have been used as refuges (Holdich *et al.* 2006).

Error will be present in imagery due to imbrications, (Carbonneau *et al.* 2004), slight image blur, minor deviation from plan view (Dugdale *et al.* 2010) presence of white water surfaces, overhead canopies (6.1c), river debris, shadow, sun-glint (fig 6.1c) and thick vegetation on the substrate (6.1d). Despite these issues, it was felt that the grains visible in each image were representative of the substrate over the whole picture extent. Using an extendable pole to obtain aerial imagery is a new method but similar image acquisition techniques combined with manual photo-sieving have been shown to have low error margins (*e.g.* Dugdale *et al.* 2010; Ibbeken and Schleyer, 1986). Photo-sieving of aerial imagery with 3 cm resolution using the same photo-sieving user interface employed in this study showed $D_{50}$ estimates to have a residual error of 0.5 to 3.5 mm compared to field datasets (Dugdale *et al.* 2010). The resolution of images in this study is an order of magnitude higher than imagery obtained by Dugdale *et al.* (2010). Using close range images of riverbeds, Adams (1979) achieved strong agreement (correlation coefficient = 0.94) between grain size found by manual photo-sieving of the images and grain size found by sieving in the field. There was a slight bias introduced by photo-sieving, which the author suggested could be rectified by multiplying $D_{50}$ by 1.07. Thus, for grain sizes around the 8 mm tolerance threshold of crayfish, the bias present in a photo-sieved $D_{50}$ measurement is 0.56 mm and the maximum error for grain sizes in the study area is 10 mm. These results suggest that the maximum error present in the current study is likely to be less than one centimetre and the error for smaller grains is likely to be less than a millimetre. This error does not influence the conclusions drawn from this study.

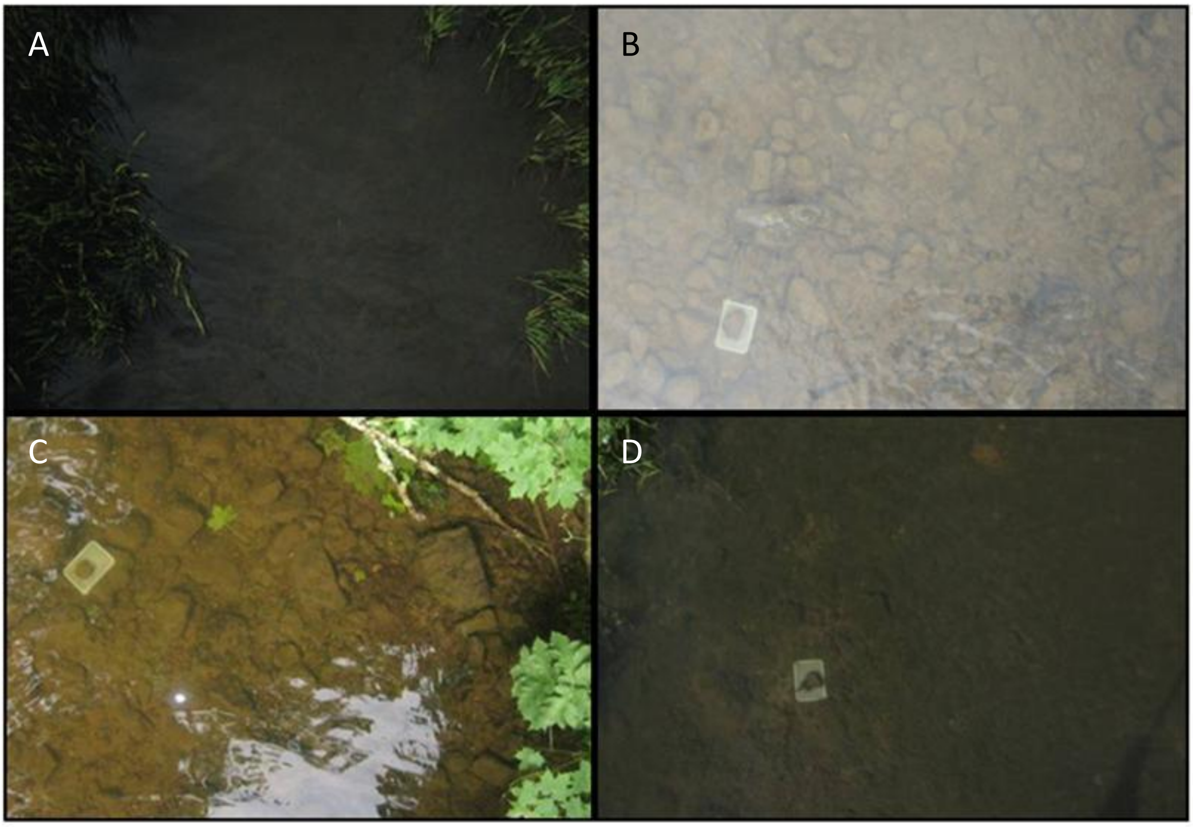

*Figure 6.1 – Sources of error and differing quality of aerial photographs. a) Cloud cover resulting in glarey images where substrate could not be seen b) Image quality obtained using flash photography c) Problems of overhanging canopies and sun-glint glare d) Lack of contrast between grains due to vegetation cover*

Unlike the method of image acquisition, the method of crayfish sampling used in this study is well established. Surber sampling has been shown to be the technique that gives the best estimates of local population density (Dorn *et al.* 2005). However, the aggregated distribution of WCC in this system means results are specific to the sampled areas (Peay, 2000) and cannot be extrapolated for the whole channel (Byrne *et al.* 1999). Repetition of a standardized sampling technique is needed to establish the population size and identify changes over time.

The generality of the results of this study to other catchments has not been tested. The logisitic regression model performed well at predicting distribution for the test data. The model was based on a large data set containing a diverse range of habitat types. Because the model contains few parameters and all modelled variables are ecologically relevant it is unlikely to be overfitted (*c.f.* Vaughan and Ormerod, 2005). The general findings from this study, such as the importance of different physical variables in discerning habitat quality and the scale at which WCC are responding to their habitat, are likely to be transferable between catchments, particularly other upland, gravel bed rivers, in Northern England where invasive species are absent. Therefore, the general findings from this study are likely to be of utility for informing future conservation efforts in the region. However, the specific findings, such as the exact tolerance limits and strength of WCC responses to habitat variables will only apply to the study reach as distribution and habitat selection are influenced by location-specific biotic interactions (Angermeier *et al.* 2002), the availability of different habitat types and the costs of finding and moving to certain habitat types (Fretwell and Lucas, 1970).

A biotic influence that will differ between catchments is the type and strength of predation pressures on WCC. Although predation is not an influential control on population size (Brewis and Bowler, 1983) differential predation pressures can influence realised habitat quality and can therefore determine habitat selection (Englund and Krupa, 2000). Where terrestrial predators are dominant, crayfish are likely to preferentially select deeper habitat, whereas in areas where fish predators are dominant, crayfish will use shallower areas (Clavero *et al.* 2009). Responses to predation may result in segregation by size, as juveniles are more susceptible to fish predators and adults to terrestrial predators (Englund and Krupa, 2000). Conservationists must consider predation pressures before deciding what constitutes optimal habitat in different systems.

Predation interacts with intra-specific competition to determine the size of the population (Lodge and Hill, 1994). The strength of competition depends on the availability of food and refuges and will therefore differ spatially and temporally (Lodge and Hill, 1994). Inter-specific competition will also differ between locations depending on the community structure. Presence of potential competitors, particularly non-indigenous crayfish species, will affect the distribution and habitat use of WCC (*c.f.* Hutchinson, 1978). Further work is needed to determine the influence of biotic interactions on habitat use and, from this knowledge, increase the applicability of findings to new areas.

A final limitation of this study was that it was restricted to daytime habitat use. Previous studies have shown preferred night-time foraging habitats differs from that used as daytime refuges (Clavero *et al.* 2009) but this has not been demonstrated on the River Wansbeck. Suitability of an area for crayfish should not be generalised from daytime studies without consideration of the availability of foraging habitat and the ability of WCC to move between required habitat types (Angermeier *et al.* 2002).

## 6.7 Implications of results for conservation measures in the Wansbeck catchment

The results of this study agree with Rogers (2005) that the Wansbeck probably contains the largest dense population of WCC in England. The river is therefore a stronghold for this endangered species and is of national and international importance. Strategic management and conservation efforts are essential to sustain favourable habitat on this river over long time scales.

Designating the River Wansbeck as an SAC would assist in doing this and would contribute to national conservation efforts, to meeting the requirements of the EU habitats directive and to fulfilling the U.K. Biodiversity Action Plan. The criteria for designation of an SAC for a species are: large population size and high population density; high quality habitat (including possibilities for restoration) and; low degree of isolation of the population from the species natural range (JNCC, 2010b). The River Wansbeck satisfies all these criteria. It is therefore reasserted that the Wansbeck should be put forward for designation as an SAC, as suggested by Rogers (2005).

The findings of habitat requirements and preferences found in this study are informative for identifying high-quality reintroduction sites and creating suitable habitat in lotic ark sites, both of which are identified as priority actions in the Northumberland Biodiversity Action Plan (Jaggs, 2009). Further, the results will be informative for the planned habitat improvement work, having identified what constitutes optimal habitat and ascertained that habitat creation should focus at the microhabitat scale. Overall, however, this study suggests that lack of physical habitat is not a major threat for WCC due to their tolerance of a wide range of habitat types. It is therefore recommended that to maintain populations in the wild the limited resources available for conservation should be directed towards maintaining suitable water quality and preventing the spread of non-native crayfish into currently unaffected systems. Since the development of the Northumberland Biodiversity Action Plan for WCC in 2000, signal crayfish have been introduced to the nearby Blyth catchment (Rogers, 2005) and the River Coquet (personal conversation, with Steve Lowe Northumberland Wildlife Trust, February 2010). This has increased the importance of the Wansbeck as a stronghold for the species and made efforts to prevent the spread of signal crayfish into this system a more vital need. Continued public awareness on the negative impact of signal crayfish and the need for disinfection to prevent the spread of crayfish plague is essential.

## Chapter 7- Conclusion

An abundant, dense and healthy population of white clawed crayfish (WCC) is present on the River Wansbeck. Average density of WCC per surveyed square metre was 5.3 individuals and in some areas density reached 24.5 individuals per square metre. Comparison to previous studies and Natural England guidelines shows this is a very dense population of national importance. The suitability of chemical and physical habitat for WCC along the entire length of the study reach suggests that, at the site-scale, there is a continuous distribution of crayfish between 8 km and 42 km downstream. Comparisons to previous published work on this river show the population size within this area is increasing. At the microhabitat scale, the distribution of crayfish was aggregated in response to heterogeneity in environmental parameters.

White clawed crayfish have a broad realised niche on the River Wansbeck and can tolerate and prosper in a wide range of habitat types. According to this study, the only available habitats they could not make use of during day-light were areas where the largest substrate was small pebbles, gravel, fines or bedrock. Absence could therefore be determined from $D_{50}$, $D_{95}$ or substrate descriptions. Presence/absence at the microhabitat scale could be satisfactorily predicted from surber-scale $D_{50}$, presence of cobbles and pebbles in a surber area and presence of wood and shrub within 50 m of the channel, but extrapolating these results to systems with less abundant populations is not likely to yield good results. Within their wide realised niche, crayfish appear to be actively responding to physical variables, showing strong selection and avoidance of different habitat types.

The strongest day-time response to a physical variable by WCC was to substrate size. White clawed crayfish were selecting microhabitats with an average grain size between 40 and 80 mm, which corresponds to cobbles. This requirement for coarse substrate agrees with the findings of previous studies (*e.g.*Foster, 1993; Brusconi *et al.* 2008) and was expected, as crayfish require refuges to protect against predation and high flows. Some authors have claimed that cobbles do not provide stable enough refuges for WCC (Naura and Robinson, 1998; Foster, 1993) but they were clearly adequate in the study area. A strong response to bank material was also evident with WCC selecting areas with earth banks and avoiding areas with bedrock banks. This response is likely to be caused by differing refuge provision in these materials and has been found by many authors (*e.g.* Holdich *et al.* 2006). Surprisingly, the day-time distribution of crayfish was not responding to the distribution of submerged or emergent macrophytes. Most previous studies have found preference for areas containing these vegetation types due to the food and shelter they provide (*e.g.* Brown and Bowler, 1977; Gallagher *et al.* 2006). However, crayfish were selecting areas where moss/algae was abundant. Where food requirements are met by moss and leaf litter, submerged and emergent macrophytes may not be required. Crayfish were also exhibiting a significant response to depth and flow velocity in the study area. Areas with an average depth of 15 to 25 cm and average boundary flow velocity between 0.05 and 0.16 m $s^{-1}$ were preferred. These findings are likely to be specific to the study area due to the influence of predation and refuge availability on response by WCC to these variables. A more widely applicable result is the preference of WCC for areas with heterogeneous flow patterns. Sites containing both riffles and glides were preferentially used, probably due to these sites having adequate dissolved oxygen and providing both resting and foraging habitat (Clavero *et al.* 2009).

There was no predictable spatial pattern in distribution of WCC in the study reach although the upstream half of the study reach had higher densities of WCC. The longitudinal pattern of WCC distribution could be fully explained by differences in habitat quality; there was no independent affect of river position on WCC distribution. The upstream half of the study reach had a higher abundance of favourable habitat for WCC indicating that WCC are more likely to be present in low order streams. The applicability of this finding to other catchments needs to be tested. If this finding is generally applicable, reintroductions and habitat improvement efforts should concentrate in low order streams to increase their success rates and cost-effectiveness. At the site and surber scale, WCC distribution could not be predicted from any spatial variable meaning inclusion of spatial factors will not improve the performance of predictive models.

Patchiness in the distribution of WCC was only evident at the sub-metre scale. If this study had been conducted only at the site-scale, different, and erroneous, conclusions about distribution and habitat preferences would have been drawn. The scale of patchiness in distribution suggests crayfish are only directly responding to microhabitat scale heterogeneity in physical variables. In this study, sensitivity to broad scale habitat variables was low but kilometre section and site-scale habitat heterogeneity did influence the distribution of crayfish to some degree by acting as filters on microhabitat-scale habitat suitability (*c.f.* Poff, 1997). Habitat based conservation actions should be conducted at the microhabitat scale to provide greatest benefit to WCC. However, broader scale influences on the suitability of microhabitats such as water chemistry, land-use and flow patterns should not be ignored.

The River Wansbeck is in a favourable conservation status for WCC, with a large, dense population and no imminent threats. The size and density of the population of WCC on the River Wansbeck make it a stronghold for the species and a site of national and international importance (Rogers, 2005). The study site meets all criteria for a Special Area of Conservation (SAC) for WCC and it is therefore recommended that the River Wansbeck be proposed for designation. Designating the

River Wansbeck as a SAC would contribute to conservation efforts and the meeting of legislation at regional and national levels. As SAC designation is a lengthy process, non-statutory designation as a local wildlife site may contribute to conservation of this endangered species in the interim.

The findings of this study are a valuable addition to the growing knowledge on the response of WCC to habitat. Further research is required in order to better understand the influences of biotic interactions on WCC-habitat relationships and to determine whether the findings of this study are applicable to different river catchments. The implications for conservation of the WCC emerging from this study is that  lack of suitable physical habitat does not appear to be a major threat to this species due to their tolerance of a wide range of habitat types. Therefore, conservation efforts should focus on maintaining favourable water chemistry at the landscape-level and preventing spread of invasive species and crayfish plague into currently unaffected systems. The most effective way of implementing this would be through public awareness campaigns that highlight the negative impact of signal crayfish and the need for disinfection to prevent the spread of crayfish plague.

# Appendix

*Appendix table 1- River Wansbeck survey site locations, details and population abundances*

| Site code | Site name | Landowner | Downstream coordinates | Upstream coordinates | Total cray-fish |
|---|---|---|---|---|---|
| **1** | Crook dean | Cornfields farm | NY 97362 83576 | NY 97309 83496 | 17 |
| **2** | Kirkwhelpington quarry | | NY 97986 83810 | NY 97914 83847 | 48 |
| **3** | Horncastle | Horncastle farm and The Shield | NY 98736 84350 | NY 98696 84274 | 16 |
| **4** | Kirkwhelpington bridge | | NY 99244 84464 | NY 99174 84466 | 11 |
| **5** | Ivy crag | Mr. Anderson Littleharle | NZ 00339 84457 | NZ 00246 84462 | 21 |
| **6** | Dean house | | NZ 00953 84246 | NZ 00855 84256 | 20 |
| **7** | Littleharle nature reserve | | NZ 01359 83706 | NZ 01429 83670 | 10 |
| **8** | Greave's dean | | NZ 02224 83918 | NZ 02146 83899 | 29 |
| **9** | Wallington woods | National Trust warden, Richard Dickinson | NZ 03021 83592 | NZ 02932 83567 | 31 |
| **10** | Wallington stepping stones | | NZ 03674 84155 | NZ 03614 84090 | 39 |
| **11** | Scarlett Hall | Scarlett Hall | NZ 04315 84283 | NZ 04343 84236 | 38 |
| **12** | Middleton bridge | Middleton Mill and Highlaws | NZ 05077 84138 | NZ 05063 84210 | 73 |
| **13** | Middleton mill | | NZ 05822 84261 | NZ 05727 84282 | 65 |
| **14** | Middleton mill 2 | | NZ 06072 84242 | NZ 06064 84310 | 21 |
| **15** | Middleton meanders | | NZ 06501 84280 | NZ 06489 84323 | 16 |
| **16** | Middleton meanders 2 | | NZ 06859 84246 | NZ 06798 84282 | 26 |
| **17** | Highlaws bridge | | NZ 07461 84335 | NZ 07364 84356 | 37 |
| **18** | West Marlish | Elizabeth Walton | NZ 08043 84461 | NZ 08012 84439 | 18 |
| **21** | Broome house cops | Broome House Allan Thompson Angerton Steads Mrs. Fenwick | NZ 09830 84429 | NZ 09761 84427 | 28 |
| **22** | Howlett hall bridge | | NZ 10402 84324 | NZ 10319 84280 | 10 |
| **23** | Broome house | | NZ 10712 84656 | NZ 10680 84569 | 15 |
| **27** | Rivergreen Mill | Rivergreen Mill | NZ 13783 84646 | NZ 13735 84729 | 10 |
| **29** | West scroggs stepping stones | Mitford Hall game keeper, Joe Pellegrino | NZ 15282 85336 | NZ 15200 85276 | 31 |
| **30** | Mitford hall | | NZ 16700 85371 | NZ 16674 85282 | 5 |
| **31** | Mitford | | NZ 17320 85901 | NZ 17223 85899 | 33 |
| **32** | Highford bridge | Highford bridge | NZ 18210 86040 | NZ 18138 85980 | 4 |
| **33** | Lowford bridge | | NZ 18993 86120 | NZ 18905 86093 | 11 |

*Appendix Table 2- Population structure analyses for River Wansbeck sites*

| Site | Largest individual CL (mm) | Smallest individual CL (mm) | Percent male | Percent female | Percent juveniles (CL < 25 mm) | Percent juveniles excluding yearlings |
|---|---|---|---|---|---|---|
| **1** | 27 | 9 | 66 | 33 | 87.5 | 88.2 |
| **2** | 27 | 5 | 53 | 47 | 98 | 97.8 |
| **3** | 23 | 5 | 67 | 33 | 100 | 100 |
| **4** | 23 | 7 | 13 | 88 | 100 | 100 |
| **5** | 34 | 8 | 61 | 39 | 66.7 | 66.7 |
| **6** | 35 | 5 | 60 | 40 | 70 | 90 |
| **7** | 47.5 | 11 | 50 | 50 | 90 | 90 |
| **8** | 32 | 4 | 55 | 45 | 79.3 | 77.8 |
| **9** | 33 | 8 | 52 | 48 | 67.7 | 67.7 |
| **10** | 31 | 5 | 67 | 33 | 81.6 | 89.5 |
| **11** | 38 | 9 | 55 | 45 | 81.6 | 81.6 |
| **12** | 42 | 5 | 39 | 61 | 87.7 | 86 |
| **13** | 34 | 4 | 48 | 52 | 95.3 | 93.5 |
| **14** | 30 | 11 | 43 | 57 | 95.2 | 95.2 |
| **15** | 33 | 4 | 40 | 60 | 81.3 | 70 |
| **16** | 29 | 5 | 36 | 64 | 80.8 | 84.6 |
| **17** | 38 | 4 | 47 | 53 | 94.9 | 73.3 |
| **18** | 38 | 5 | 33 | 67 | 83.3 | 82.4 |
| **21** | 25 | 4 | 49 | 51 | 96.4 | 95 |
| **22** | 24 | 8 | 43 | 57 | 100 | 100 |
| **23** | 30 | 8 | 31 | 69 | 73.3 | 73.3 |
| **27** | 34 | 12 | 80 | 20 | 50 | 50 |
| **29** | 32 | 8 | 60 | 40 | 77.4 | 77.4 |
| **30** | 25 | 8 | 0 | 100 | 75 | 100 |
| **31** | 28 | 8 | 52 | 48 | 78.8 | 78.8 |
| **32** | 39 | 11 | 100 | 0 | 50 | 50 |
| **33** | 27 | 5 | 56 | 44 | 91 | 77.8 |
| **Total** | 47.5 | 4 | 49 | 51 | 81.5 | 79.3 |

# References

Abesser C., Shand P. and Ingram J. (2005) Baseline report series: 18. The millstone grit of Northern England. *British geological survey commissioned report No. CR/05/015N*

Adams J. (1979) Gravel size analysis from photographs. *American society of civil engineers: journal of the hydraulics division*, 105, pp. 1247-1255

Aitken C.G.G. and Taroni F. (2004) *Statistics and the evaluation of evidence for forensic scientists.* Chichester: Wiley

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In B. N. Petrov and F. Csaki (Eds.) *Second international symposium on information theory*, Budpest: Academiai Kiado, pp. 267-281

Alderman D.J. (1993) Crayfish plague in Britain, the first twelve years. *Freshwater crayfish*, 9, pp. 266-272

Allison P. D. (1999) *Logistic regression using the SAS system: theory and application*. Cary N.C.: SAS institute Inc.

Angermeier P.L., Krueger K.L. and Dolloff C.A. (2002) Discontinuity in stream-fish distributions: implications for assessing and predicting species occurrence. In: J. M. Scott, P. J. Heglund, M. L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall and F.B. Samson (Eds) *Predicting species occurrences: issues of accuracy and scale*, Washington D.C.: Island Press, , pp. 519-527

Anthony J.L. and Downing J.A. (2001) Exploitation trajectory of a declining fauna: a century of freshwater mussel fisheries in North America. *Canadian journal of fisheries and aquatic* science, 58, pp. 2071-2090

Armitage V.L. (2001) *Influence of habitat and mammal predation on the spatial distribution of the Atlantic white clawed crayfish (Austropotamobius pallipes* L.*)* Ph.D. University of Newcastle upon Tyne

Armitage P.D. and Cannan C.E. (1998) nested multi-scale surveys in lotic systems- tools for management. In: G. Bretschko and J. Helesic (Eds.) *Advances in river bottom ecology*, Leiden, The Netherlands: Backhuys Publishers, pp. 293-314

Barbaro L., Couzi L., Bretagnolle V., Nezan J. and Vetillard F. (2008) Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (*Upupa epops*) in pine plantations. *Biodiversity conservation*, 17, pp. 1073-1087

Baxter C.V. and Hauer R.F. (2000) Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). *Canadian journal of fisheries and aquatic science*, 57, pp. 1470-1481

Belaud A., Chaveroche P., Lim P. and Sabaton C. (1989) Probability-of-use curves applied to brown trout (*Salmo trutta fario* L.) in rivers of southern France. *Regulated rivers: research and management*, 3, pp. 321-336

Bellehumeur C. and Legendre P. (1998) Multiscale sources of variation in ecological variables: modelling spatial dispersal, elaborating sampling designs. *Landscape ecology*, 13, pp. 15-25

Bellier E., Monestiez P., Durbec J-P. and Candau J.N. (2007) Identifying spatial relationships at multiple scales: principal coordinates of neighbour matrices (PCNM) and geostatistical approaches. *Ecography*, 30, pp. 385-399

Benda L., Poff N.L., Miller D., Dunne T., Reeves G., Pess G. and Pollock M. (2004) The network dynamics hypothesis: how channel networks structure riverine habitats. *Bioscience*, 54, pp. 413-427

Benvenuto C., Gherardi F. and Ilheu M. (2008) Microhabitat use by the white-clawed crayfish in a Tuscan stream. *Journal of natural history*, 42, pp. 21-33

Blackman F.F. (1905) Optima and limiting factors. *Annals of botany*, 19, pp. 281-298

Boone R.B. and Krohn W.B. (2000) Predicting broad-scale occurrences of vertebrates in patchy landscapes. *Landscape ecology*, 15, pp. 63-74

Bouchard, J. and Boisclair D. (2008) The relative importance of local, lateral, and longitudinal variables on the development of habitat quality models for a river. *Canadian Journal of fisheries and aquatic sciences*, 65, pp. 61-73

Brewis J.M. and Bowler K. (1982) The growth of the freshwater crayfish *Austropotamobius pallipes* in Northumbria. *Freshwater Biology*, 12, pp. 187-200

Brewis J. M. and Bowler K. (1983) A study of the dynamics of a natural population of the freshwater crayfish, *Austropotamobius pallipes*. *Freshwater Biology*, 13, pp. 443-452

Brewis J.M. and Bowler K. (1985) A study of reproductive females of the freshwater crayfish *A. pallipes*. *Hydrobiologia*, 121, pp. 145-149

Broquet T., Thibault M. and Neveu A. (2002) Distribution and habitat requirements of the white clawed crayfish*, Austropotamobius pallipes*, in a stream from the Pays de Loire region, France: an experimental and descriptive study. *Bulletin Français de la pêche et de la pisciculture*, 367, pp. 717-728

Brown D.J. and Bowler K. (1977) A population study of the British freshwater crayfish *Austropotamobius pallipes* (Lereboullet). *Freshwater crayfish*, 3, pp. 33-49

Brown D. J. and Bowler K. (1978) The relationship between size and age through the life cycle in *A. pallipes*. *Freshwater crayfish*, 4, pp. 35-42

Brown B.L. and Lawson R.L. (2010) Habitat heterogeneity and activity of an omnivorous ecosystem engineer control stream community dynamics. *Ecology*, 91, pp. 1799-1810

Bruns D.A., Minshall G.W., Cushing C.E., Cummins K.W., Brock J.T. and Vannote R.L. (1984) Tributaries as modifiers of the River Continuum Concept: analysis by polar ordination and regression models. *Archiv für hydrobiologie*, 99, pp. 208-220

Brusconi S., Bertocchi S., Barbara R., Massimiliano S., Souty-Grosset C. and Gherardi F. (2008) Conserving indigenous crayfish: stock assessment and habitat requirements in the threatened *Austropotamobius italicus. Aquatic Conservation - marine and freshwater ecosystems,* 18, pp. 1227-1239

Bubb D.H., Thom T.J. and Lucas M.C. (2006) Movement, dispersal and refuge use of co-occurring introduced and native crayfish. *Freshwater Biology*, 51, pp. 1359-1368

Bubb D.H., Thom T.J. and Lucas M.C. (2008) Spatial ecology of the white-clawed crayfish in an upland stream and implications for the conservation of this endangered species. *Aquatic conservation: marine and freshwater ecosystems*, 18, 647-657

Bubb D.H., O'Malley O.J., Gooderham A.C. and Lucas M.C. (2009) Relative impacts of native and non-native crayfish on shelter use by an indigenous benthic fish. *Aquatic conservation: marine and freshwater ecosystems*, 19, pp. 448-455

Buckton S.T. and Ormerod S.J. (1997) Use of a new standardized habitat survey for assessing the habitat preferences and distribution of upland river birds. *Bird Study*, 44, pp. 327-337

Byrne C.F., Lunch J.M. and Bracken J.J. (1999) A sampling strategy for stream populations of white clawed crayfish, *Austropotamobius pallipes* (Lereboullet) (Crustacea, Astacidae). *Biology and Environment*: *Proceedings of the Royal Irish Academy,* 99B, pp. 89-94

Carbonneau P.E., Bergeron N. and Lane S.N. (2005) Automated grain size measurements from airborne remote sensing for long profile measurements of fluvial grain sizes. *Water resources research*, 41, W11426 doi: 10.1029/2005WR003994 [Online] Available at: dro.dur.ac.uk/1159/1/1159.pdf?DDD14+dgg0pc+dgg0cnm [Accessed 12/12/10]

Carbonneau P.E., Lane S.N. and Bergeron N.E. (2004) Catchment-scale mapping of surface grain size in gravel-bed rivers using airborne digital imagery. *Water resources research*, 40, [Online] Available at: dro.dur.ac.uk/1160/1/1160.pdf [Accessed 12/12/10]

Clavero M., Benejam L. and Seglar A. (2009) Microhabitat use by foraging white clawed crayfish (*Austropotamobius pallipes*) in stream pools in the NE Iberian Peninsula. *Ecological Research*, 24, pp. 771-779

Cody M. L. (1985) *Habitat selection in birds*. Orlando, Florida: Academic press

Cooper S.D., Barmuta L. Sarnelle O., Kratz K. and Diehl S. (1997) Quantifying spatial heterogeneity in streams. *Journal of the North American benthological society*, 16, pp. 174-188

Costanza R., d'Arge R., de Groot R., Farber S., Grass M., Hannon B., Limburg K., Naeem S., O'Neill R.V., Paruelo J., Raskin R.G., Sutton P. and van den Belt M. (1997) The value of the world's ecosystem services and natural capital. *Nature*, 387, pp. 252-260

Council Decision 82/72/EEC of 3 December 1982 concerning the conclusion of the Convention on the conservation of European wildlife and natural habitats (Bern Convention)

Crandall K.A. and Buhay J.E. (2008) Global diversity of crayfish (Astacidae, Cambaridae, and Parastacidae—Decapoda) in freshwater. *Hydrobiologia*, 595, pp. 295-301

Culp J.M. and Davies R.W. (1982) Analysis of longitudinal zonation and the river continuum concept in the Oldman-South Saskatchewan river system. *Canadian journal of fisheries and aquatic science*, 39, pp. 1258-1266

Davey C. and Lapointe M. (2007) Sedimentary links and the spatial organization of Atlantic salmon (*Salmo salar*) spawning habitat in a Canadian Shield River. *Geomorphology*, 83, pp. 82–96

Demers A. and Reynolds J.D. (2002) A survey of the white-clawed crayfish, *Austropotamobius pallipes* (Lereboullet) and of water quality in two catchments of Eastern Ireland. , 367, pp. 729-740

Demers A., Reynolds J.D. and Cioni A. (2003) Habitat preference of different size classes of *Austropotamobius pallipes* in an Irish river. *Bulletin Français de la pêche et de la pisciculture*, 370-371, pp. 127-137

Department for Environment, Food and Rural affairs (DEFRA) (2008) *Non-native species* [Online] (2010) Available at: www.defra.gov.uk/wildlife-pets/wildlife/management/non-native/about.htm [Accessed 12/11/10]

DiStefano R.J., Gale C.M., Wagner B.A. and Zweifel D. (2003) A sampling method to assess lotic crayfish communities. *Journal of crustacean biology*, 23, pp. 678 - 690

Dorn N.J., Urgelles R. and Trexler J.C. (2005) Evaluating active and passive sampling methods to quantify crayfish density in a freshwater wetland. *Journal of the North American benthological society*, 24, pp. 346-356

Douglas C. (1993) *Distribution of crayfish on the rivers Wansbeck, Blyth and Pont*. Unpublished report to Environment Agency

Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z-I., Knowler D.J., Lévêque C., Naiman R.J., Prieur-Richard A-H., Soto D., Stiassny M.L.J. and Sullivan C.A. (2005) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, 81, pp. 163-182

Dugdale S.J., Carbonneau P.E. and Campbell D. (2010) Aerial photosieving of exposed gravel bars for the rapid calibration of airborne grain size maps. *Earth surface processes and landforms*, 35, pp. 627-639

Dugdale S.J Carbonneau P.E. and Clough S. (in review) The fluvial information system

Duncan A. and Kubecka J. (1996) Patchiness of longitudinal fish distributions in river as revealed by continuous hydroacoustic survey. *ICES Journal of marine science*, 53, pp. 161-165

Edsman L. and Smietana P. (2004) Exploitation, conservation and legislation. *Bulletin Français de la pêche et de la pisciculture,* 372-373, pp. 457-464

Engler R., Guisan A. and Rechsteiner L. (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of applied ecology*, 41, pp. 263-274

Englund G. and Krupa J.J. (2000) Habitat use by crayfish in stream pools: influence of predators, depth and body size. *Freshwater biology*, 43, pp. 75-83

Environment Agency (2003) *River Habitat Survey in Britain and Ireland: Field Survey Guidance Manual.* River Habitat Survey Manual: 2003 version, 136 pp.

Environment Agency (2005) *Wansbeck and Blyth Catchement Flood Mangement plan* [Online] Available at: www.environment-agency.gov.uk/static/documents/Research/section_1_1215463.pdf [Accessed on 19/07/09]

Environment Agency (2009) *River quality* [Online] Available at: www.environment-agency.gov.uk/homeandleisure/37811.aspx [Accessed 12/11/09]

Environment Agency (2010) *River levels: River Wansbeck at Mitford*. [Online] Available at: environment-agency.gov.uk/homeandleisure/floods/riverlevels/120694.aspx?stationId=8139 [Accessed 09/08/10]

European Council Directive 92/43/EEC of 21st May 1992 on the conservation of natural habitats and of wild fauna and flora

European Parliament and Council Directive 2000/60/EC of 23rd October 2000 on establishing a framework for the community action in the field of water policy, the EU Water Framework Directive

Evans D.A. (1953) Experimental evidence concerning contagious distributions in ecology. *Biometrika*, 40, pp. 186-211

Fahrig L. and Merriam G. (1985) Habitat patch connectivity and population survival. *Ecology*, 66, pp. 1762-1768

Fausch K.D., Torgersen C.E., Baxter C.V. and Hiram L.W. (2002) Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *Bioscience* 52, pp. 483-498

Fortin M.J., Dale M.R.T. and ver Hoef J. (2002) Spatial analysis in ecology. *Encyclopedia of environmetrics*, 4, pp. 2051-2058

Foster J. (1993) The relationship between refuge size and body size in the crayfish *Austropotamobius pallipes* (Lereboullet). *Freshwater crayfish*, 9, pp. 345-349

Foster J. (1995) Factors influencing the distribution and abundance of the crayfish *Austropotamobius pallipes* (Lereboullet) in Wales and the Marches, UK. *Freshwater crayfish*, 8, pp. 78-98

Foster J. and Turner C. (1993) Toxicity and field simulated farm waste episodes to the crayfish *Austropotamobius pallipes* (Lereboullet): elevated ammonia and reduced dissolved oxygen concentrations. *Freshwater crayfish*, 9, pp. 249-258

Freshwater Invertebrate Survey of Suffolk (2010) *Suffolk crayfish, native and alien species: a photographic guide to identification for the amateur naturalist*, [Online] Available at: www.boxvalley.co.uk/nature/fiss/General/crayfish.asp [Accessed: 19/01/11]

Fretwell S.D. (1972) Populations in a seasonal environment. *Monographs in population biology*, vol. 5. Princeton: Princeton University press

Fretwell S.D. and Lucas H.L. Jr. (1970) On territorial behaviour and other factors influencing distribution of birds, vol. 1. Theoretical development. *Acta biotheoretica*, 19, pp. 16–36

Frissell C.A., Liss W.J., Warren C.E. and Hurley M.D. (1986) A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental management*, 10, pp.199-214

Fukushima M. (2001) Salmonid habitat-geomorphology relationships in low-gradient streams. *Ecology*, 82, pp. 1238-1246

Gallagher M.B., Dick J.T.A. and Elwood R.W. (2006) Riverine habitat requirements of the white clawed crayfish, *Austropotamobius pallipes*. *Biology and environment*, 106 B, pp. 1-8

Gheradi F. (2002) Behaviour. In: D. Holdich (Ed) *Biology of freshwater* crayfish, Oxford:Blackwell sciences Ltd., pp. 258-290

Gherardi F., Acquistapace P. and Santini G. (2001) Foraging by a threatened species - the white clawed crayfish, *Austropotamobius pallipe. Archiv für hydrobiologie*, 152, pp. 339-351

Gheradi F. and Acquistapace P. and Santini G. (2004) Food selection in freshwater omnivores: a case study of crayfish *Austropotamobius pallipes*. *Archiv für hydrobiologie*, 159, pp. 357-376

Gido K.B., Falke J.A. and Oakes R.M. (2006) Fish habitat relations across spatial scales in prairie streams. *American fisheries society symposium*, 48, pp. 265-285

Goddard J.S. and Hogger J.B. (1986) The current status and distribution of freshwater crayfish in Britain. *Field studies*, 6, pp. 383-396

Grandjean F., Cornuault B., Archambault S., Bramard M. and Otrebsky G. (2000) Life history and population biology of the white-clawed crayfish, *Austropotamobius pallipes*, in a brook from the Poitou-Charentes region (France). *Bulletin Français de la pêche et de la pisciculture*, 356, pp. 55-70

Grandjean F., Jouteux R., Ropiquet A., Bachelier E. and Bramard M. (2001) Biological water quality assessments in running water sites harbouring the endangered crayfish, *Austropotamobius pallipes* based on macroinvertebrates and its potential in habitat selection for restocking. *Freshwater crayfish*, 13, pp. 338-348

Grandjean F., Momon J. and Bramard M. (2003) Biological water quality assessment of the white clawed crayfishes habitat based on macro-invertebrate communities: usefulness for its conservation. *Bulletin Français de la pêche et de la pisciculture*, 370-371, pp. 115-125

Griffiths S.W., Collen P. and Armstrong J.D. (2004) Competition for shelter among over-wintering signal crayfish and juvenile Atlantic salmon. *Journal of fish biology*, 65, pp. 436-447

Groves R. E. (1985) *The crayfish: its nature and nurture*. Surrey: Fishing news books

Guan R-Z. (1994) Burrowing behaviour of signal crayfish, *Pacifastacus leniusculus* (Dana), in the River Great Ouse, England. *Freshwater* forum, 4, pp. 155-168

Guan R. and Wiles P.R. (1997) Ecological impact of introduced crayfish on benthic fishes in a British lowland river. *Conservation biology*, 11, pp. 641-647

Guisan A. and Zimmermann N.E. (2000) Predictive habitat distribution models in ecology. *Ecological modelling*, 135, pp.147-186

Guisan A. and Thuiller W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology letters*, 8, pp. 993-1109

Gurnell A.M., Angold P.G. and Edwards P.J. (1996) Extracting information from river corridor surveys. *Applied Geomorphology*, 16, pp. 1-19

Gustafson E.J. (1998) Minireview: Quantifying landscape spatial pattern: what is the state of the Art? *Ecosystems*, 1, pp. 143-156

Hall L.S., Krausman P.R. and Morrison M.L. (1997) The habitat concept and a plea for standard terminology. *Wildlife society bulletin*, 25, pp. 171-182

Hawksworth D.L. and Kalin-Arroyo M.T. (1995) Magnitude and distribution of biodiversity. In: V.H. Heywood and R.T. Watson (Eds) *Global biodiversity assessment*, Cambridge: United Nations environment programme and Cambridge University press, pp. 107-191

Hedger R.D., Dobson J.J., Bourque J.F. and Bergeron N.E. and Carbonneau P.E. (2006) Improving models of juvenile Atlantic salmon habitat use through high resolution remote sensing. *Ecological modelling*, 197, pp. 505-511

Hewitt J., Legendre P., Thrush S., Cummings V. and Norkko A. (2002) Integrating results from different scales: a multi-resolution study of the relationships between *Atrina zelandica* and macrofauna along a physical gradient. *Marine ecological progress series*, 239, pp. 115-128

Hilden O. (1965) Habitat selection in birds. *Annales zoologici fennici*, 2, pp. 53-75

Hildrew A.G. and Giller P.S. (1994) Patchiness, species interactions and disturbance in the stream benthos. In P.S. Giller, A.G. Hildrew and D.G. Raffaelli (Eds) *Aquatic ecology: scale, pattern and process*, Oxford: Blackwell, pp. 21-62

Hirzel A.H., Hausser J., Chessel D. and Perrin N. (2002) Ecological niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology*, 83, pp. 2027-2036

Hocutt C.H. and Stauffer J.R. (1975) Influence of gradient on the distribution of fishes in Cononwingo Creek, Maryland and Pennsylvania. *Chesapeake science*, 16, pp. 143-147

Hogger, J. B. (1984) *A study of aspects of the biology and distribution of freshwater crayfish in the Thames catchment.* PhD thesis. Council for National Academic Admissions, London

Hogger J. B. (1988) Ecology, population biology and behaviour. In: D.M. Holdich and R.S. Lowery (Eds) *Freshwater crayfish: biology, management and exploitation*, London: Croom Helm (Chapman and Hall), pp. 114-135

Holdich D.M. (1988) The dangers of introducing alien animals with particular reference to crayfish. In: de Tiefenau G.P. (Ed) *Freshwater crayfish*, 7, pp. 15-30

Holdich D.M. (1991) The native crayfish and threats to its existence. *British wildlife*, 2, pp.141-151

Holdich D.M. (2003) *Ecology of the white clawed crayfish*. Conserving Natura 2000, Rivers Ecology Series No 1, English Nature:Peterborough

Holdich D. M. and Lowery R.S. (1988) *Freshwater crayfish: biology, management and exploitation*. London: Croom and Helm (Chapman and Hall)

Holdich D.M. and Pockl M. (2005) Roundtable session 2 - Does legislation work in protecting vulnerable species? *Bulletin Français de la pêche et de la pisciculture*, 376-377, pp. 809-827

Holdich D.M. and Reeve I.D. (1991) Distribution of freshwater crayfish in the British Isle, with particular reference to crayfish plague, alien introductions and water quality. *Aquatic conservation: marine and freshwater ecosystems*, 1, pp. 139-158

Holdich D.M., Reeve I.D. and Rogers W.D. (1995) Introduction and spread of alien crayfish in British waters- implications for native crayfish populations. *Freshwater crayfish,* 8, pp. 99-112

Holdich D.M. and Sibley P.J. (2009) ICS and NICS in Britain in the 2000s. In: J. Brickland J., D.M. Holdich and E.M. Imhoff (Eds). *Crayfish conservation in the British Isles*. Proceedings of a conference held on 25th March, 2009 in Leeds, U.K.

Holdich D.M. Harlioglu M.M. and Firkins I. (1997) Salinity adaptations of crayfish in British waters with particular reference to *Austropotamobius pallipes*, *Astacus leptodactylus* and *Pacifastacus leniusculus*. *Estuarine, coastal and shelf science*, 44 , 147-154

Holdich D.M., Sibley P. and Peay S. (2004) The white-clawed crayfish- a decade on. *British wildlife* 15, pp. 153-164

Holdich D.M., Peay S., Foster J., Hiley P.D. and Brickland J.H. (2006) Studies on the white clawed crayfish (*Austropotamobius pallipes*) associated with muddy habitats. *Bulletin Français de la pêche et de la pisciculture*, 380, pp. 1055-1078

Holdich D.M., Reynolds J.D., Souty-Grosset C. and Sibley P.J. (2009) A review of the ever increasing threat to European crayfish from non-indigenous crayfish species. *Knowledge and management of aquatic ecosystems.* 394-395, pp. 1-46

Holm S. (1979) A simple sequentially rejective multiple test procedure. *Scandinavian journal of statistics*, 6, pp. 65-70

Holmlund C.M. and Hammer M. (1999) Ecosystem services generated by fish populations. *Ecological economics*, 29, pp. 253-268

Horton R.E. (1945) Erosional development of streams and their drainage basins: hydro-physical approach to quantitative morphology. *Geological society of America bulletin*, 56, pp. 275-370

Hutchinson G.E. (1978) *An introduction to population ecology*. New Haven: Yale University press

Ibbeken H. and Schleyer R. (1986) A method for grain-size analysis of coarse-grained, unconsolidated bedding surfaces. *Earth surface processes and Landforms*, 11, pp. 59-77

International Union for Conservation of Nature (2010) Numbers of threatened species by major groups of organisms (1996-2010) [Online] Available at: www.iucnredlist.org/documents/summarystatistics/2010_4RL_Stats_Table_1.pdf [Accessed 15/12/10]

Intergovermental panel on climate change (IPCC) Pachauri R.K. and Reisinger A. (Eds.) (2007) *Contribution of working groups I, II and III to the fourth assessment report of the IPCC.* Geneva, Switzerland

Jaggs E. (2009) *White clawed crayfish (Austropotamobius pallipes) species action plan, Northumberland biodiversity action plan.* [Online] Available at: www.northumberlandbiodiversity.org.uk/documents/Action_Plans/White_Clawed_Crayfish.pdf [Accessed 18/10/09]

Jay, D. and Holdich D.M. (1976). The pH tolerance of the *Austropotamobius pallipes* (Lereboullet). *Freshwater crayfish*, 3, pp. 363-370

Jay D. and Holdich D.M. (1981) The distribution of the crayfish *Austropotamobius pallipes* in British waters. *Freshwater biology*, 11, pp. 121-129

Jeffers J.N.R. (1998) The statistical basis of sampling strategies for rivers: example using River Habitat Survey. *Aquatic conservation: marine and freshwater ecosystems*, 8, pp. 447-454

Jelinski D.E. and Wu J. (1996) The modifiable areal unit problem and implications for landscape ecology. *Landscape ecology*, 11, pp. 129-140

Jiménez-Valverde A., Lobo J.M. and Hortal J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions*, 14, pp. 885-890

Johnson D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, pp. 65-71

Johnson M.D. (2007) Measuring habitat quality: a review. *The Condor*, 109, pp. 489-504

Joint Nature Conservation Committee (JNCC) (2010) *Distribution of SACs/SCIs/SACs containing species 1092 Austropotamobius pallipes* [Online] Available at: jncc.gov.uk/ProtectedSites/SACselection/feature_map.asp?FeatureIntCode=S1092 [Accessed 14/01/10]

Joint Nature Conservation Committee (2010b) *The collective EU process and criteria for site selection* [Online] Available at: www.jncc.gov.uk/page-1469 [Accessed 14/11/10]

Jones J. (2001) Habitat selection studies in avian ecology. *The auk*, 118, pp. 557-562

Kolasa J. (1989) Ecological systems in hierarchical perspective: breaks in community structure and other consequences. *Ecology*, 70, pp. 36-47

Kondolf G.M. (1997) Application of the pebble count notes on purpose, method and variants. *Journal of the American water resources association*, 33, pp. 79-87

Kotliar N.B. and Weins J.A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, 59, pp. 253-260

Krebs C.J. (1999) *Ecological methodology* (Second edition). London: Harper and Row

Laurent P.J. (1988) *Austropotamobius pallipes* and. *A. torrentium,* with observations on their interactions with other species in Europe. In D. M. Holdich and R. S. Lowery (Eds) *Freshwater crayfish: biology, management and exploitation*. London: Croom and Helm (Chapman and Hall), pp. 341–364

Le Vay L., Ut V.N. and Jones D. (2001) Seasonal abundance and recruitment in an estuarine population of mud crabs, *Scylla paramamosain*, in the Mekong Delta, Vietnam. *Hydrobiologia*, 449, pp. 231-239

Lechowicz M.J. (1982) The sampling characteristics of electivity indices. *Oecologia*, 52, pp. 22-30

Leftwich K.N. and Angermeier P.L. (1997) Factors influencing behaviour and transferability of habitat models for a benthic stream fish. *Transactions of the American fisheries society*, 126, pp. 725-734

Legleiter C. and Kyriakidis P. (2006) Forward and inverse transformations between Cartesian and channel-fitted coordinate systems for meandering rivers. *Mathematical Geology*, 38, pp. 927-958

Leopold L.B. (1953) Downstream changes of velocity in rivers. *American journal of* science, 251, pp. 606-624

Levin S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, 73, pp. 1943-1967

Lewis A. and Morris F. (2008) Report on a major stranding of crayfish at Meldon, River Wansbeck, U.K. *Crayfish news: IAA newsletter*, 30, pp. 7-8

Lodge D.M. and Hill A.M. (1994) Factors governing species composition, population size, and productivity of cool-water crayfishes. *Nordic journal of freshwater research*, 69, pp. 111-136

Lodge D.M., Taylor C.A., Holdich D.M. and Skurdal J. (2000) Non-indigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. *Fisheries*, 25, pp. 7-20

Lowery R.S (1988) Growth, moulting and reproduction. In D.M. Holdich and R.S. Lowery (Eds) *Freshwater crayfish: biology, management and exploitation*. Croom Helm: London, pp. 83-113

Lyons R. and Kelly-Quinn M. (2003) An investigation into disappearance of *Austropotamobius pallipes* (Lereboullet) population in the headwaters of the Nore River, Ireland and the correlation to water quality. *Bulletin Français de la pêche et de la pisciculture*, 370-371, pp. 139-150

MacDonald J.H. (2009) *Kruskal-Wallis test and Mann-Whitney U test.* Handbook of biological statistics [Online] Available at: udel.edu [Accessed 14/01/11]

Manly B.F.J. (1971) A model for certain types of selection experiments. *Biometrics*, 30, pp. 281-294

Marcus W.A. (2002) Mapping of stream microhabitats with high spatial resolution hyperspectral imagery. *Journal of geographical systems*, 4, pp. 113-126

Martinez J.A. and Zuberogoitia I. (2004) Habitat preferences for long-eared owls *Asio otus* and little owls *Athene noctua* in semi-arid environments at three spatial scales. *Bird study*, 51, pp. 163-169

Mason J.C. (1974) Crayfish production in a small woodland stream. *Freshwater crayfish*, 2, pp. 449-479

Menard S. (2002) *Applied logistic regression analysis*. California: Sage Publications

Millennium Ecosystem Assessment (2005) *Ecosystem and human well-being: biodiversity synthesis.* World resources institute. Washington, D.C.: Island press

Minshall G.W., Brock J.T. and Lapoint T.W. (1982) Characterization and dynamics of benthic organic matter and invertebrate functional feeding group relationships in the upper Salmon River, Idaho (USA). *Internationale revue der gesamten hydrobiologie*, 67, pp. 793-820

Momot W.T., Gowing H. and Jones P.D. (1978) The dynamics of crayfish and their role in ecosystems. *American midland naturalist*, 99, pp. 10-35

Moriaty C. (1972) A study of Austropotamobius pallipes in Ireland. *Freshwater crayfish*, 1, 57-67

Moyle P.B. and R.A. Leidy (1992) Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. In: P.L. Fiedler and S.K. Jain (Eds) *Conservation biology: the theory and practice of nature conservation, preservation and management.* New York: Chapman and Hall, pp. 127–169

Naiman R.J., Meliilo J.M., Lock M.A., Ford T.E. and Reice S.R. (1987) Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. *Ecology*, 68, pp. 1139-115

National Rivers Authority (1992) *River corridor surveys: methods and procedures. Conservation Technical Handbook Number 1. National River Authority: Bristol*

Naura M. and Robinson M. (1998) Principles of using River Habitat Survey to predict the distribution of aquatic species: an example applied to the native white clawed crayfish *Austropotamobius pallipes*. *Aquatic conservation - marine and freshwater ecosystems*, 8, pp. 515-527

Nearhoof F.L. (1995) A protocol for collecting surface water samples in marshes of the Florida Everglades. *Water quality technical series*, 3, no. 25

Newson, M.D., Clark M.J., Sear D.A. and Brookes A. (1998a) The geomorphological basis for classifying rivers. *Aquatic conservation: marine and freshwater ecosystems*, 8, pp. 415–430

Newson M.D., Harper D.M., Padmore C.L., Kemp J.L. and Vogel B. (1998b) A cost-effective approach for linking habitats, flow types and species requirements. *Aquatic Conservation*: *marine and freshwater ecosystems*, 8, pp. 431–446

Nilsson C. and Berggren K. (2000) Alterations of riparian ecosystems caused by river regulation. *Bioscience,* 50, pp. 783-792

Nyström P. and Strand J.A. (1996) Grazing by a native and an exotic crayfish on aquatic macrophytes. *Freshwater Biology*, 36, pp. 673-682

Nyström P. (2002) Ecology. In: D.M. Holdich (*Ed.*) *Biology of freshwater crayfish.* 192-235. Oxfrod:Blackwell science

O'Neill R.V., Johnson A.R. and King A.W. (1989) A hierarchical framework for the analysis of scale. *Landscape ecology*, 3, pp. 193-205

Office for national statistics (2001) *Castle Morpeth parish headcounts* . [Online] Available at: www.neighbourhood.statistics.gov.uk/dissemination/viewFullDataset.do;jsessionid=ac1f930c30d5d5e3e2b753fd4ae5bebbc3e3a445af4d?instanceSelection=03070&productId=779&$ph=60_61&datasetInstanceId=3070&startColumn=1&numberOfColumns=4&containerAreaId=790479&nsjs=true&nsck=true&nssvg=false&nswid=1280 [Accessed 19/10/10]

Oidtmann B. (2000) Disease in freshwater crayfish. In: D. Rogers and J. Brickland (Eds), *Crayfish conference*. Leeds, 26th/27th April 2000. Environment Agency, pp. 9-18

Openshaw S. (1983) *Concepts and techniques in modern geography number 38 - the modifiable areal unit problem*. Norwich: Geobooks

Orians G. H. and Wittenberger J.F. (1991) Spatial and temporal scales in habitat selection. *American naturalist*, 37, pp.829-849

Osborne L. L. and Wiley M.J. (1992) Influence of tributary spatial position on the structure of warm water fish communities. *Canadian journal of fisheries and aquatic science*, 49, pp. 671-681

Padmore C.L. (1998) The role of physical biotopes in determining the conservation status and flow requirements of British rivers. *Aquatic ecosystems health and management*, 1, pp. 25-35

Palmer M. (1994) *Action plan for the conservation of the native freshwater crayfish Austropotamobius pallipes in the United Kingdom.* Joint Nature Conservation Committee, Peterborough

Parsons M., Thomas M. and Norris R. (2002) Australian River Assessment System: review of physical river assessment methods - a biological perspective. *Cooperative research centre for freshwater ecology monitoring river health initiative technical report number 21,* Environment Australia

Payette A.L. and McGaw I.J. (2003) Thermoregulatory behaviour of the crayfish *Procambarus clarki* in a burrow environment. *Comparative biochemistry and physiology- Part A: molecular and integrative physiology*, 136, pp. 539-556

Pearce J. and Ferrier S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological modelling*, 133, pp. 225-245

Pearson R.G. and Dawson T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology &* Biogeography, 12, pp. 361–371

Peay S. (2000) *Guidance on works affecting white-clawed crayfish*. English Nature:Peterborough

Peay S. (2002) Habitat for white-clawed crayfish and how to restore it. In: D. Holdich, Sibley P. (Eds) *Management and conservation of crayfish*. Environment Agency, Nottingham

Peay S. (2002b) Monitoring protocol for white-clawed crayfish: field testing in River Eden tributaries summer 2002. *Life in U.K. rivers,* English nature:Peterborough

Peay S. (2003) *Guidance on habitat for white clawed crayfish*. R&D Technical Report W1-067/TR, Environment Agency: Bristol

Peay S., Proud A. and Ward D. (2006) White-clawed crayfish in muddy habitats: monitoring the population in the River Ivel, Bedfordshire, U.K. *Bulletin Français de la pêche et de la pisciculture,* 380-381, pp. 1079-1094

Perry J.N., Liebhold A.M., Rosenberg M.S., Duncan J., Miriti M., Jakomulska A. and Citron-Pousty S. (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography*, 25, pp. 578-600

Petts G.E., Gurnell A.M., Gerrard A.J., Hannah D.M., Hansford B., Morrissey I., Edwards P.J., Kollmann J., Ward J.V., Tockner K. and Smith B.P.G. (2000) Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. *Aquatic conservation - marine and freshwater ecosystems*, 10, pp. 249-266

Pidgeon A.M., Radeloff V.C. and Matthews N.A. (2006) Contrasting measures of fitness to classify habitat quality for the blacthroated sparrow (*Amphisipiza bilineata*). *Biological conservation*, 132, pp. 199-210

Poff N.L. (1997) Landscape filters and species traits: toward mechanistic understanding and prediction in stream ecology. *Journal of the North American benthological society*, 16, pp. 391-409

Poizat G. and Pont D. (1996) Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. *Freshwater biology*, 36, pp. 611-622

Pratten D.J. (1980) Growth in the crayfish *Austropotamobius pallipes* (Crustacea: Astacidae). *Freshwater Biology*, 10, pp. 401-412

Rabeni C.F., Collier K.J., Parkyn S.M. and Hicks B.J. (1997) Evaluating techniques for sampling stream crayfish (*Paranephrops planifrons*). *New Zealand journal of marine and freshwater research*, 31*,* pp. 693-700

Randin C.F., Dimbo T., Dullinger S., Zimmerman N.E., Zappa M. and Guisan A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, 33, 1689-1703

Raven P.J, Holmes N.T.H., Naura M. and Dawson F.H. (2000) Using river habitat survey for environmental assessment and catchment planning in the U.K. *Hydrobiologia*, 422/423, pp. 359-367

Raven P.J., Fox O.P., Everand M., Holmes N.T.H. and Dawson F.H. (1997) River habitat survey: a new system for classifying rivers according to their habitat quality. In P.J. Boon and D.L. Howell (Eds) *Freshwater quality- defining the indefinable?* Edinburgh: The stationary office pp. 215-234

Ream H.M. (2010) *Microhabitat use and recolonisation in white-clawed crayfish: application to conservation.* M.Sc. thesis, Durham University

Reese G.C., Wilson K.R., Hoeting J.A. and Flather C.H. (2005) Factors affecting species distribution predictions. *Ecological applications*, 15, pp. 554-564

Renz M. and Breithaupt T. (2000) Habitat use of the crayfish *Austropotamobius torrentium* in small brooks and in Lake Constance, southern Germany. *Bulletin Français de la pêche et de la pisciculture*, 356, pp.139-154

Reynolds J.D. (1979) Ecology of *Austropotamobius pallipes* in Ireland. *Freshwater Crayfish*, 4, pp. 215-219

Reynolds J.D. (1997) The present status of freshwater crayfish in Ireland. *Bulletin Français de la pêche et de la pisciculture*, 347, pp. 693-700

Reynolds J. D. (1998) Conservation management of the white-clawed crayfish *Austropotamobius pallipes*. *Irish Wildlife Manuals*, Dublin: Dúchas, the heritage service

Reynolds J.D. (2002) Growth and reproduction. In D. Holdich (*Ed.*) *Biology of freshwater crayfish.* Oxford: Blackwell science

Reynolds J.D. and O'Keefe C. (2005) Dietary patterns in stream- and lake-dwelling populations of *Austropotamobius pallipes*. *Bulletin Français de la pêche et de la pisciculture*, 376-377, pp. 715-730

Reynolds J.D., Celada J.C., Carral J.M. and Matthews M.A. (1992) Reproduction of astacid crayfish in captivity - current developments and implications for culture, with special reference to Ireland and Spain. *Invertebrate reproduction and development*, 22, pp. 253-266

Reynolds J.D., Demers A. and Marnell F. (2002) Managing an abundant crayfish resource for conservation: *Austropotamobius pallipes* in Ireland. IAA European Meeting, *Bulletin Français de la pêche et de la pisciculture*, 367, pp. 823-832

Rice S. (1998) Which tributaries disrupt downstream fining? *Geomorphology*, 22, pp. 39-56

Rice S. and Church M. (1996) Sampling surficial fluvial gravels; the precision of size distribution percentile sediments. *Journal of sedimentary research*, 66, pp. 654-665

Rice S.P., Greenwood M.T. and Royce C.B. (2001) Tributaries, sediment sources, and the longitudinal organisation of macro-invertebrate fauna along river systems. *Canadian journal of fisheries and aquatic science*, 58, pp. 824-840

Richards K. S. (1976) The morphology of riffle-pool sequences. *Earth surface processes*, 1, pp. 71-88

Richards C., Johnson L.B. and Host G.E. (1996) Landscape-scale influences on stream habitats and biota. *Canadian journal of fisheries and aquatic sciences*, 53, pp. 295-311

Richardson J. S. and Mackay R.J. (1991) Lake outlets and the distribution of filter feeders: an assessment of hypotheses. *Oikos*, 62, pp. 370-380

Robinson C.A., Thom T.J. and Lucas M.C. (2000) Ranging behaviour of a large freshwater invertebrate, the white clawed crayfish *Austropotamobius pallipes*. *Freshwater Biology*, 44, pp. 509-521

Robson B. J. and Chester E.T. (1999) Spatial patterns of invertebrate species richness in a river: the relationship between riffles and microhabitats. *Australian journal of ecology*, 24, pp. 599-607

Rodríguez J.P, Brotons L., Bustamante J. and Seoane J. (2007) The application of predictive modelling of species distribution to biodiversity conservation. *Diversity and distributions*, 13 243-251

Rogers D. (2005) *White clawed crayfish survey, Northumbria area.* Unpublished report to Environment Agency

Rogers D. and Holdich D.M. (1995a) Conservation and management of British crayfish populations. *Freshwater crayfish*, 10, pp. 92-97

Rogers D. and Watson E. (2007) Increasing the chances of successful reintroduction of white clawed crayfish (*Austropotamobius pallipes*) in the Peak District national park, U.K. *International journal of biodiversity science, ecosystem services & management*, 3, pp. 209-216

Rogerson P.A. (2006) *Statistical methods for geography: a student's guide* (second edition). London: Sage

Royal Society of Wildlife Trusts (2010) About the Wildlife Trusts [Online] Available at: www.wildlifetrusts.org/index.php?section=about [Accessed 04/01/10]

Rushton S.P., Ormerod S.J. and Kerby G. (2004) New paradigms for modelling species distributions? *Journal of Applied Ecology*, 41, pp. 193–200

Sáez-Royuela M., Carral J.M., Celada J.D. and Pérez J.R. (2001) Effects of shelter type and food supply frequency on survival and growth of stage-2 juvenile white clawed crayfish (*Austropotamobius pallipes* Lereboullet) under laboratory conditions. *Aquaculture international*, 9, pp. 489-497

Sala O.E., Chapin F.S., Armesto J.J., Berlow R., Bloomfield J., Dirzo R., Hurber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M. and Wall D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, pp. 1770-1774

Schlosser I.J. (1991) Stream fish ecology: a landscape perscpective. *Bioscience*, 41, pp. 704-712

Schulz R., Stucki T. and Souty-Grosset C. (2002) Management: reintroductions and restocking. *Bulletin Français* de la *pêche et de la pisciculture*, 367, pp. 917-922

Schulz R. and Schulz H.K. (2004) Threats to indigenous crayfish populations- studies on a landscape level. *Bulletin Français* de la *pêche et de la pisciculture*, 372-373, pp. 447-456

Schumm S.A. and Lichty R.W. (1965) Time, space and causality in geomorphology. *American journal of science*, 263, pp. 110-119

Secretariat of the Convention on Biological Diversity (2010) *Global Biodiversity Outlook 3*. [Online] Montréal: UNEP. Available at: gbo3.cbd.int [Accessed 29/11/10]

Sedell J.R., Richey J.E. and Swanson F.J. (1989) The river continuum concept: a basis for the expected ecosystem behaviour of very larger rivers? In: D.P. Dodge (Ed.) *Proceedings of the international large rivers symposium*. *Canadian special publication of fisheries and aquatic sciences*, 106, pp. 49-55

Sheldon A.L. (1968) Species diversity and longitudinal succession in stream fishes. *Ecology*, 49, 194-198

Shelford V.E. (1913) *Animal communities in temperate America*. Chicago: University of Chicago press

Shreve R. (1966) Statistical law of stream numbers. *Journal of geology*, 74, pp. 17-37

Sibley P. J. (2003) Conservation management and legislation- the UK experience. In: J. Reynolds and C. Souty-Grosset (Eds) *The endangered native crayfish Austropotamobius pallipes, bioindicator and heritage species.* First thematic meeting of CRAYNET, Kilkenny, Ireland. *Bulletin Français de la pêche et de la pisciculture*, 370-371, pp. 209-217

Sibley P.J., Brickland J.H. and Bywater J.A. (2002) Monitoring the distribution of crayfish in England and Wales. *Bulletin Français de la pêche et de la pisciculture*, 367, pp. 833-844. IAA European Meeting, Poitiers France

Simberloff D. (1988) The contribution of population and community biology to conservation science. *Annual review of ecology and systematic*, 19, pp. 473-511

Slater F.M. and House E.V. (2001) *The current status of the white-clawed crayfish Austropotamobius pallipes in the Afon Edw and the impact of recent land use change on populations*. Countryside council for Wales, Report no. 454, Bangor

Smith E.P. (1982) Niche breadth, resource availability, and inference. *Ecology*, 63, pp.1675-1681

Smith V. and Söderhäll K. (1986) Crayfish pathology: an overview. *Freshwater Crayfish*, 6, pp. 199–211

Smith G.R.T., Learner M.A., Slater F.M. and Foster J. (1996) Habitat features important for the conservation of the native crayfish *Austropotamobius pallipes* in Britain. *Biological conservation*, 75, pp. 239-246

Smith J. D. and McLean S. R. (1984) A model for flow in meandering streams. *Water resources research*, 20, pp. 1301-1315

Smith R. L. and Smith T.M. (2001) *Ecology and field biology.* New York: Benjamin Cummings Soderall

Southwood T. R. E. and Henderson P.A. (2000) *Ecological methods* (Third edition). Cambridge: Blackwell science

Souty-Grosset C., Holdich D.M., Noel P.Y., Reynolds J.D. and Haffner P. (2006) Atlas of crayfish in Europe. *Collection patrimonies naturels, 64*, Paris: Museum national d'historie naturelle

Stancliffe-Vaughan A (2009). Non-native crayfish – a community research and trapping initiative on the River Lark, Suffolk. *Crayfish News: IAA Newsletter*, 31, pp. 5-7

Statzner, B. & Higler, B. (1985) Questions and comments on the River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 42, pp. 1038-1044

Statzner B., Fièvet R., Champagne J-Y., Morel R. and Heurouin E. (2000) Crayfish as geomorphic agents and ecosystem engineers: biological behaviour affects sand and gravel erosion in experimental streams. *Limnology and oceanography*, 45, pp. 1030-1040

Stenroth P. and Nyström P. (2003) Exotic crayfish in a brown water stream: effects on juvenile trout, invertebrates and algae. *Freshwater biology*, 48, pp. 466-475

Strauss B. and Biedermann R. (2007) Evaluating temporal and spatial generality: how valid are species–habitat relationship models? *Ecological modelling,* 204: 104-114

Surber E.W. (1936) Rainbow trout and bottom fauna production in one mile of stream. *Transactions of the American fisheries society,* 66, pp. 193-202

Synder N.F.R., Derrickson S.R., Beissinger S.R., Wiley J.W., Smith T.B., Toone W.D. and Miller B. (1996) Limitations of captive breeding in endangered species recovery. *Conservation biology*, 10, pp. 338-348

Talley T.S. (2007) Which spatial heterogeneity framework? Consequences for conclusions about patchy population distributions. *Ecology*, 88, pp. 1476-1489

Thomas W.J. and Ingle R.W. (1987) Dimorphism and the life cycle of *Austropotamobius pallipes* (Lereboullet) (Crustacea Astacidae) in the British Isles. *The Essex Naturalist,*32, pp. 349-360

Thorp J.H., Thoms M.C. and Delong M.D.(2006) The Riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River research and applications*, 22, pp. 123-147

Thrush S.F., Schneider D.C., Legendre P., Whitlatch R.B., Dayton P.K., Hewitt J.E., Hines A.H., Cummings V.J., Lawrie S.M., Grant J., Pridmore R.D., Turner S.J. and McArdle B.H. (1997a) Scaling-up from experiments to complex ecological systems: where to next? *Journal of experimental marine biology and ecology*, 216, pp. 243-254

Thrush S.F., Hewitt J.E., Cummings V.J., Green M.O., Funnell G.A. and Wilkinson M.R. (2000) The generality of field experiments: interactions between local and broad-scale processes. *Ecology*, 81, pp. 399-415

Torgersen C.E. and Close D.A. (2004) Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales. *Freshwater biology*, 49, pp. 614-630

Town and Country planning Act 1990 (c. 8) London: HMSO

Townsend C.R., Dolédec S., Norris R., Peacock K. and Arbuckle C. (2003) The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. *Freshwater biology*, 48, pp. 768–785

Trexler J. C. and Travis J. (1993) Non-traditional regression analysis. *Ecology*, 74, pp. 1629-1637

Trouilhe M.C., Ricard F., Parinet B., Grandjean F. and Souty-Grosset C. (2003) Management of the white clawed crayfish (*Austropotamobius pallipes*) in western France: abiotic and biotic factors study. *Bulletin Français de la pêche et de la pisciculture*, 370-371, pp. 97-114

Trouilhe M.C., Souty-Grosset C., Grandjean F. and Parinet B. (2007) Physical and chemical water requirements of the white clawed crayfish (*Austropotamobius pallipes*) in western France. *Aquatic conservation - marine and freshwater ecosystems*, 17, pp. 520-538

U.K. Biodiversity action plan (2007) *Priority species and habitats.* [Online] Available at: www.ukbap.org.uk/newprioritylist.aspx [Accessed 18/11/09]

U.K. Biodiversity Action Plan (1995) *Species action plan: Freshwater white clawed crayfish* (*Austropotamobius pallipes*). [Online] Department of the environment, London: HMSO*.* Available at: www.ukbap.org.uk/UKPlans.aspx?ID=124 [Accessed 08/10/09]

Van-Horne B. (1983) Density as a misleading indicator of habitat quality. *Journal of wildlife management*, 47, pp. 893-901

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. and Cushing C.E. (1980) The river continuum concept. *Canadian journal of fisheries and aquatic sciences*, 37, pp. 130-137

Vanreusel W., Maes D. and Van Dyck H. (2007) Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conservation biology*, 21, pp. 201-212

Vaughan I.P. & Ormerod S.J. (2005) The continuing challenges of testing species distribution models. *Journal of Applied Ecology*, 42, pp. 720–730

Vescovi L., Berteaux D., Bird D. and de Blois S. (2009) *Freshwater biodiversity versus anthropogenic climate change*. World water assessment programme side publications series. France, UNESCO [Online]. Available at: unesdoc.unesco.org/images/0018/001850/185075e.pdf

Ward J. V. (1989) The four-dimensional nature of lotic ecosystems. *Journal of the North American benthological society*, 8, pp. 2-8

Ward J.V. (1992) *Aquatic insect ecology, Vol. 1. Biology and habitat.* New York: John Wiley and Sons

Water resources Act 1991 (c. 57) London: HMSO

Wiens J. A. (1989) Spatial scaling in ecology. *Functional ecology*, 3, pp. 385-397

Wiens J.A. (1999) The science and practice of landscape ecology. In J. M. Klopatch and R. H. Gardner (Eds) *Landscape ecological analysis*, New York: Springer-Verlag, pp.371-383

Wiens J.A. (1985) Habitat selection in variable environments: shrubsteppe birds. In M.L. Cody (Ed). *Habitat selection in birds*. Orlando: Academic press Inc., pp. 227-251

Wiens J.A., Stenseth C.N., Van Horne B. and Ims R.A. (1993) Ecological mechanisms and landscape ecology. *Oikos*, 66, pp. 369-380

Wentworth C.K. (1922) A scale of grade and class terms for clastic sediments. *The journal of geology*, 30, pp. 377-392

Westman K. (1985) Effects of habitat modification on freshwater crayfish. In: J. S. Alabaster (Ed) *Habitat modifications and freshwater fisheries*, London: Butterworths, pp. 245-255

Wheatley M. and Johnson C. (2009) Factors limiting our understanding of ecological scale. *Ecological complexity*, 6, pp. 150-159

Whitehouse A. (2010) Selecting Ark Sites for White-clawed crayfish [Online] Available at: www.buglife.org.uk/conservation/currentprojects/Species+Action/Conserving+our+Crayfish/Crayfish+Ark+Site+Selection+Criteria [Accessed 02/12/10]

Whiteley N.M. and Taylor E.W. (1993) The effects of seasonal variations in temperature on extracellular and acid-base status in a wild population of the crayfish *Austropotamobius pallipes*. *Journal of experimental biology*, 181, 295-311

Whitman, S. M., Moran E.H. and Ourso R.T. (2003), Photographic techniques for characterizing streambed particle sizes. *Transactions of the American fisheries society*, 132, pp. 605– 610

Wildlife and Countryside Act 1981 (c.69) London: HMSO

Wolman M. G. (1954) A Method of sampling coarse river-bed material. *American geophysical union* 35, pp. 951-956

Wu J. and Loucks O.L. (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *The quarterly review of biology*, 70, pp. 439-466

Wu J. and Qi Y. (2000) Dealing with scale in landscape analysis: an overview. *Geographic information science*, 6, pp. 1–5